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MISSOURI

BOTANICAL GARDEN.

SIXTEENTH ANNUAL REPORT.

245751

ST. LOUIS, MO.:

PUBLISHED BY THE BOARD OF TRUSTEES.

1905.



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BOTANICAL GARDEN.



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*\*Ex-officio.*

<sup>1</sup> Elected President of The Academy of Science of St. Louis, January 16, 1905, to succeed Mr. Edwin Harrison, who had held that office for one year.

<sup>2</sup> Elected President of the Board of Public Schools of St. Louis, October 11, 1904, to succeed Professor C. M. Woodward, who had held that office for one year.



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PREFACE.

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Under direction of the Board of Trustees, the sixteenth annual report of the Missouri Botanical Garden is presented to the public.

The fifteenth volume was issued on April 30th, 1904, which is to be regarded as the date of publication of the scientific papers it contains except that by Professor Coulter, separates of which were distributed on March 24th, 1904.

These reports are sent to scientific institutions and journals in exchange for publications or specimens desirable for the Garden, and, when possible, reprints of the botanical articles they contain are presented to botanists occupied with a study of the subjects they refer to. Any of the Garden publications not out of print may be purchased at approximately the cost of publication from Mess. R. Friedländer & Sohn, Berlin, Germany; W. Wesley & Son, London, England; or the undersigned.

WILLIAM TRELEASE.

St. Louis, Mo., April 24, 1905.

(3)



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A SHADY RESTING PLACE.



## REPORTS FOR THE YEAR 1904.

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### REPORT OF THE OFFICERS OF THE BOARD.

SUBMITTED TO THE TRUSTEES JANUARY 11, 1905.

*To the Board of Trustees of the Missouri Botanical Garden:*

We submit for your consideration the financial results for the year ending December 31st, 1904.

We are gratified to announce an increase in the income from rentals over the previous year of \$10,385.61 and that the advance (with the exception of \$900.00, from one building) was not the direct result of the World's Fair but of a general and steady appreciation of business property, which condition will hold good for some years, and we estimate a further increase of \$3,000.00 for the coming year, as all the properties of the Board are occupied and no vacancies are anticipated.

We have disposed of only one piece of residence property, a lot of 50 feet on Flora boulevard, but we look for a demand in the early spring.

Our state, school, city and sprinkling taxes for the year 1904 amounted to \$35,463.17 which, compared with the receipts from rentals, \$120,221.60, looks at a glance unreasonable and out of proportion.

Mr. Shaw devised to the Board about 280 acres of land, excluding the Garden, located west of Grand avenue, leased either to market gardeners or vacant at the time of his death, and in about the same condition to-day, much of which we hope to dispose of as residence property when the streets and sewers are completed.



This property is scattered in parcels of from one-half to one hundred acres in size, and will in course of time become more valuable, but it is being eaten up by general taxes at the rate of \$12,546.61 per year, in excess of income, to say nothing about the loss of interest on the investment, as will be seen by the following statement: —

Tract.	Acres.	Income.	Taxes.
No. 1	72	\$1,080 00	\$9,321 82
" 2	20	704 00	1,491 92
" 3	25		3,910 91
" 4	00½	280 00	166 98
" 5	3	818 72	318 72
" 6	11	588 00	536 67
" 7	13		163 37
" 8	36	501 36	316 36
" 9	100	225 00	516 94
	<hr/>	<hr/>	<hr/>
	280½	\$4,197 08	\$16,743 69
Less Income . . . . .			4,197 08
			<hr/>
			\$12,546 61

We desire to call your attention to the large expenditure for streets, sidewalks and sewers, \$47,417.33, which was distributed as follows: —

Rock Spring Joint District Sewer (Thurman Avenue) . . .	\$11,604 88
Rock Spring Lateral Sewer (Tyler Place) . . . . .	3,572 97
Tower Grove Joint District Sewer . . . . .	31,300 89
Sundry Reconstructions and Repairs . . . . .	938 59

These sewers were much needed and have been paid for by a special tax levied by the city, and others are either built or under construction which must be paid for during the year 1905, and, in addition, large street improvements are contemplated by the city during the coming year, some of them, not actually necessary, yet, when completed, will place much of our cheaper residence property in condition



to market, the payment for which, however, will become a serious problem for the Board during the next ten years.

The improvements now completed or contemplated by the city, and which must be paid for during the year 1905, are as follows: —

Shaw Avenue Sewer (now due) . . . . .	\$ 6,720 99
Manchester Avenue Joint District Sewer (completed) . .	45,000 00
Improvement of McRee Avenue (400 feet) . . . . .	2,500 00
Improvement of Grand Avenue (476 feet) . . . . .	2,750 00
Improvement of Vandeventer Avenue (471 feet) . . . . .	2,500 00
Improvement of Shaw Avenue (2,812 feet) . . . . .	12,500 00
Total . . . . .	<u>\$71,970 99</u>

As the Board of Trustees have no power to borrow money, these improvements, if paid for in full, will have to be met by the balance of our savings unexpended and any savings we may make on the year's income, and by sale of residence property.

During the year we invested the balance of the fund received from the sale of the property at the corner of Main and Vine streets, in a new building at No. 218-20-22 Chestnut street at a cost of \$27,974.09 which we have leased for a long term at a good rental.

Necessary repairs have been made to the properties of the Board and all buildings are in reasonably good condition.

No permanent improvements have been made at the Garden outside of extensive planting in the N. American Synopsis, but the usual and necessary repairs to plant houses and buildings have been made.

The annual bequests made in Mr. Shaw's will have been carried out at an expenditure of \$2,983.19.

A large number of additions have been made to the Library and Herbarium by purchase and gift during the past year, and the following amounts have been credited to Stock Account: —



Library . . . . .	\$5,547 77
Herbarium . . . . .	3,615 75

After spending upon the Garden, for its support, \$47,652.21, paying all other charges of every nature, and charging Real Estate Account with the cost of new sewers, \$46,478.47, we have carried forward as a surplus of receipts over expenditures, \$24,023.22.

For further information concerning operations at the Garden, you are referred to the Director's annual report.

## RECEIPTS.

Rentals . . . . .	\$120,221 60	
Interest and dividends . . . . .	2,716 62	
Garden pasturage above expenses . . . . .	438 34	
Garden hand-book sales . . . . .	1,208 83	
Publication sales . . . . .	10 35	
Total income collections . . . . .	\$124,595 74	
Insurance, damage to green-houses by hail . . . . .	152 18	
Sales under decree of Court . . . . .	7,318 00	
Bonds, stocks and certificates sales . . . . .	45,937 50	\$178,003 42
Cash on hand January 1st, 1904 . . . . .		6,749 44
Total receipts . . . . .		<u>\$184,752 86</u>

## DISBURSEMENTS.

Garden Account,		
Labor pay-roll . . . . .	\$19,715 71	
Student pay-roll . . . . .	1,423 80	
Office assistance . . . . .	1,244 50	
Fuel . . . . .	1,896 84	
Water . . . . .	180 00	
Repairs and supplies . . . . .	2,627 06	
Plants and seeds . . . . .	2,190 11	\$29,278 02
Herbarium Account,		
Salaries . . . . .	1,148 09	
Fuel . . . . .	101 54	
Current expenditures . . . . .	1,813 09	3,062 72
Library Account,		
Salaries . . . . .	1,672 79	
Fuel . . . . .	101 59	
Current expenditures . . . . .	3,424 61	5,198 99
<i>Carried forward</i> . . . . .		<u>\$37,539 73</u>



REPORT OF THE OFFICERS OF THE BOARD. 11

<i>Brought forward</i> . . . . .		\$37,539 73
<b>Office Account,</b>		
Salaries . . . . .	\$4,580 80	
Fuel . . . . .	101 60	
Current expenditures . . . . .	568 65	5,251 05
<b>Research Account,</b>		
Salaries . . . . .	484 96	
Drawing plates . . . . .	87 64	
Current expenditures . . . . .	258 60	831 20
<b>Scholarship Account,</b>		
Instruction . . . . .	721 90	
Care of Lodge . . . . .	240 00	
Fuel . . . . .	72 09	
Current expenditures . . . . .	135 08	1,169 07
Total maintenance expenditure . . . . .		\$44,791 05
<b>Garden Improvement Account,</b>		
Growing houses . . . . .	436 70	
Chemical laboratory . . . . .	604 43	
Restoring plants and plant house damaged by fire . . . . .	1,532 26	
Garden storm repairs . . . . .	287 77	2,861 16
Total amount expended on Garden . . . . .		\$47,652 21
<b>Publication Account,</b>		
Fifteenth annual volume . . . . .	1,460 88	
Garden hand-book, second edition . . . . .	957 05	
“ “ third “ . . . . .	555 00	
Exhibit at Louisiana Purchase Exposition . . . . .	100 00	3,072 93
<b>Property Expenses,</b>		
State, school, city and sprinkling tax . . . . .	35,463 17	
Streets, sidewalks and sewers . . . . .	47,417 33	
Insurance . . . . .	5,799 67	
Repairs . . . . .	3,596 96	
Improvements . . . . .	2,387 85	
New building . . . . .	398 90	95,063 88
<b>Office Expenses,</b>		
Salaries . . . . .	4,200 00	
Office rent . . . . .	900 00	
Printing, advertising, telephone, etc.. . . . .	864 57	5,964 57
<b>Bequests,</b>		
Annual Flower Sermon . . . . .	200 00	
Annual Flower Show . . . . .	235 00	
Trustees' Annual Banquet . . . . .	1,627 80	
Gardeners' Annual Banquet . . . . .	331 86	
Washington University, School of Botany . . . . .	588 53	2,983 19
<i>Carried forward</i> . . . . .		\$154,736 78



## MISSOURI BOTANICAL GARDEN.

	<i>Brought forward</i> . . . . .		\$154,736 78
Sundries,			
	Real estate purchased . . . . .	\$27,974 08	
	Commissions . . . . .	123 75	
	Legal expenses . . . . .	279 97	28,377 80
	Total disbursements . . . . .		\$183,114 58
	Cash on hand December 31st, 1904 . . . . .		1,638 28
			<u>\$184,752 86</u>

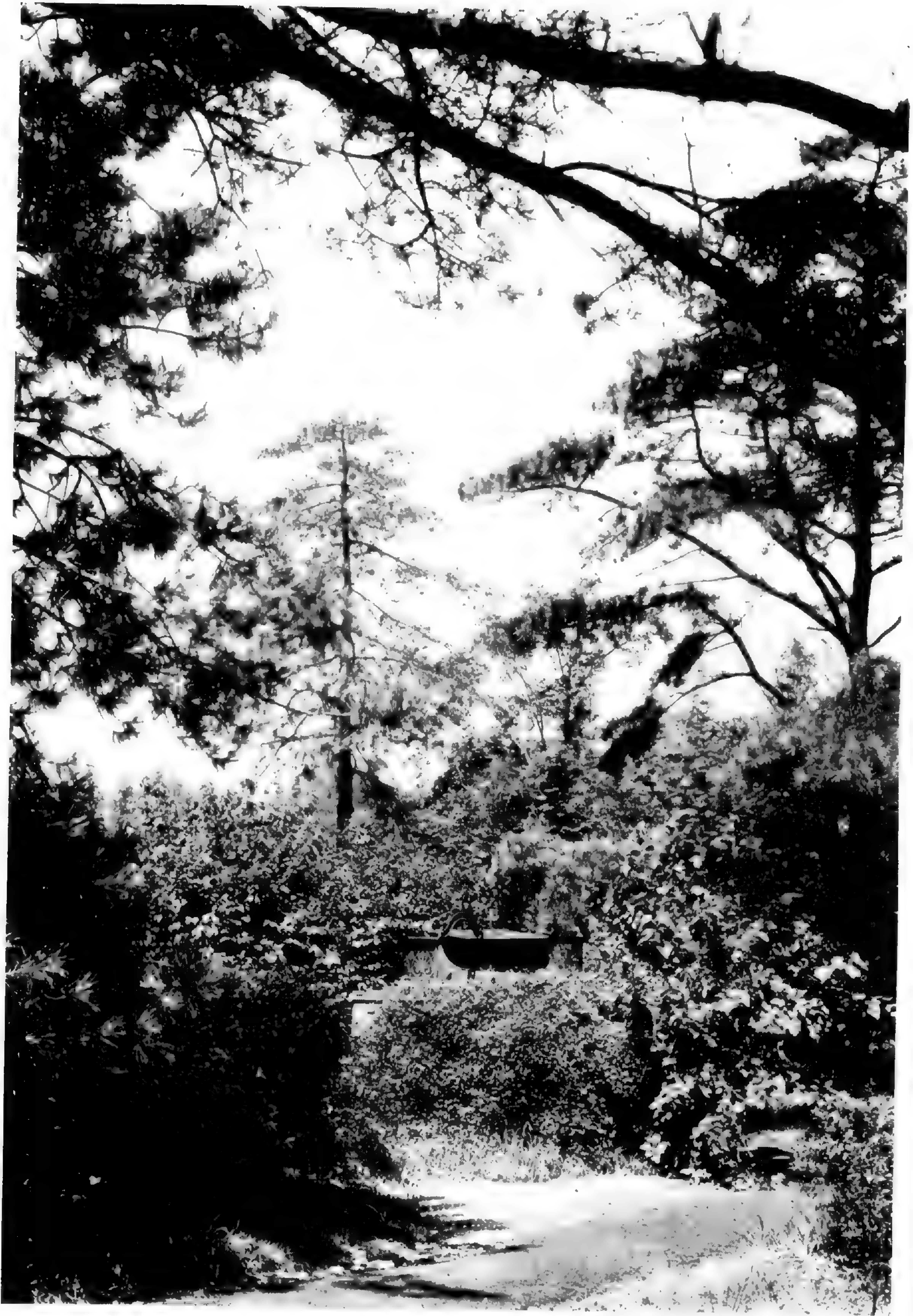
Respectfully submitted,

R. J. LACKLAND, President.

Attest:

A. D. CUNNINGHAM, Secretary





SCREEN PLANTING IN THE ARBORETUM.



## SIXTEENTH ANNUAL REPORT OF THE DIRECTOR.

SUBMITTED TO THE TRUSTEES JAN. 11, 1905.

*To the Board of Trustees of the Missouri Botanical Garden:*

The following report for the year 1904, on the Missouri Botanical Garden and the School of Botany there-with connected, is respectfully submitted in compliance with the rules of the Board.

### ORNAMENTAL FEATURES.

No marked changes have been made in either the quantity or variety of the plants used for general decorative effects, but increased care in the selection of plants for this purpose has resulted in a notable improvement in the quality of the bedding. For the first time in the history of the Garden the entire parterre was this year used for bulbs before being planted with the customary summer foliage plants, and those who saw it during the flowering period of the tulips witnessed an unusually beautiful display of these showy flowers, harmoniously and instructively arranged. The number and variety of dahlia, gladiolus and chrysanthemum plants grown has also been greater than ever before, and the dahlia and chrysanthemum collections, in particular, attracted much favorable attention.

The total number of accessions for the year amounted to 326, comprising 62,080 plants or packets of seeds, and though the number of separate entries is considerably smaller than that for 1903, discriminating selection by the Superintendent, Mr. H. C. Irish, and his assistants, has enabled me to record a notable increase in the variety of plants cultivated. Of the total, 1,747 plants or seed packets, valued at \$452.00, were collected, and 26,587, valued at \$1,861.09, were propagated, by Garden employees,



the two comprising 32 of the 326 entries for the year; 24,748, representing 204 entries and valued at \$4,387.80, were presented or received in exchange for material or publications from the Garden; and 8,998, representing 90 entries, were purchased at a cost of \$2,190.11.

Among the unusually large gifts were 6,970 cacti, orchids, etc., appraised at \$2,564.20, presented by the Mexican National Exposition Commission, which added 85 species or varieties not before represented at the Garden; 4,810 fiber-yielding plants and young forest trees, appraised at \$511.50, presented by the United States Department of Agriculture; 161 tropical plants, appraised at \$196.50 and of which 35 species were new to the collections, presented by the Cuban Commission; 38 plants, appraised at \$39.25, of which 3 were new to the Garden, presented by the Chinese Commission; and 17 plants, appraised at \$20.00 and adding 10 new species to the collections, presented by the Brazilian Commission. To these donors, as well as the Philippine Commission, the Japanese Commission, the Californian Commission, and other foreign and states Commissions and private exhibitors from whom smaller but valuable gifts were received, the Garden is under great indebtedness. Opportunity has also been found at the Exposition to purchase a considerable number of choice plants sent to St. Louis for exhibition,— among them a well-grown Japanese Wistaria, some 50 of the best Japanese tree paeonies, and a pair of enormous and very old plants of *Cycas revoluta*, said to have been in cultivation in this country for about 300 years.

The records show that from all sources 3,050 species and varieties, not represented at its beginning, were added to the Garden collections during the year, while 200 were dropped from cultivation or lost, leaving a net gain for the year of 2,850 and bringing the total up to 14,207, in contrast with the 11,357 noted for 1903.\*

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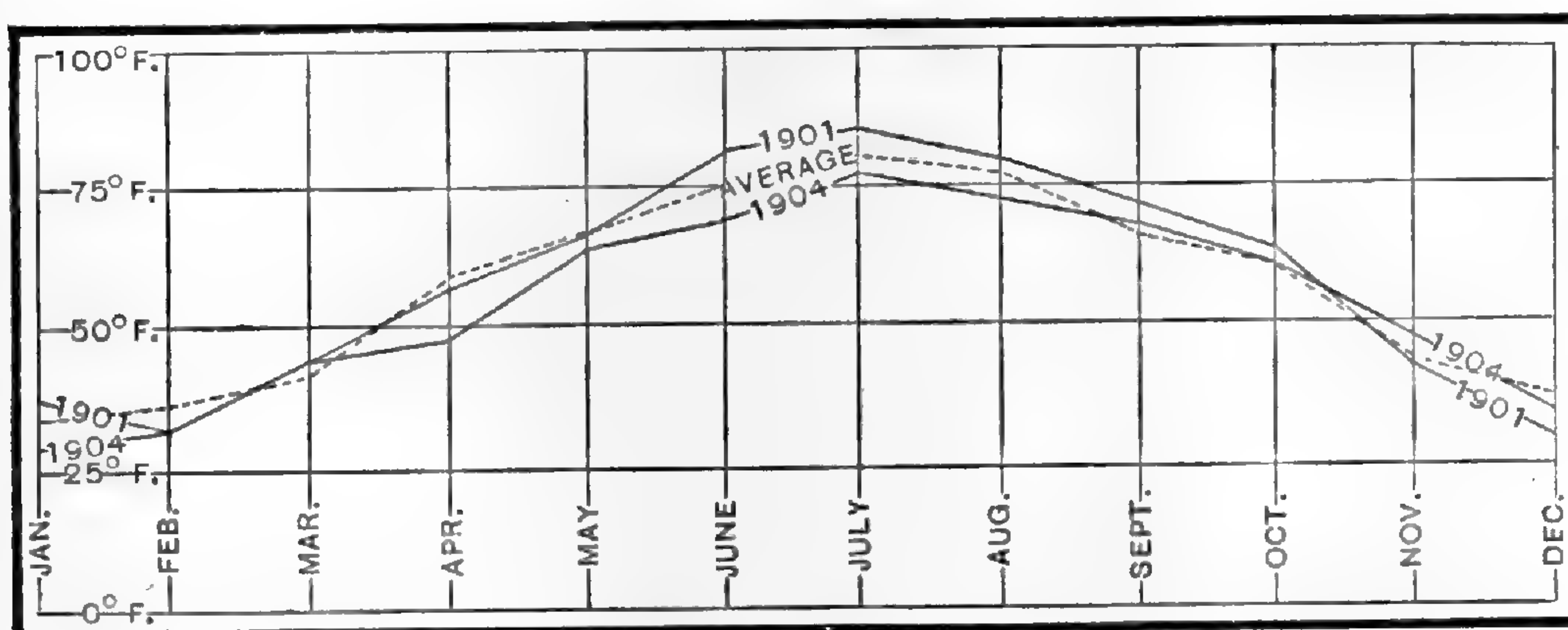
\* Rept. Mo. Bot. Gard. 15: 17.



The distribution of exchange material has consisted in 450 packets of seeds, valued at \$22.50, and 2,269 plants, valued at \$214.60; and 727 surplus plants were presented to the schools of the city.

The past season has been one of the coolest and most uniform in temperature ever recorded for St. Louis, as may be seen from the accompanying diagram (A), which is compiled from the monthly sheets issued by the local Weather Bureau. The average daily temperature for the entire year has been 1.8° F. below the normal. Rainfall

DIAGRAM A.

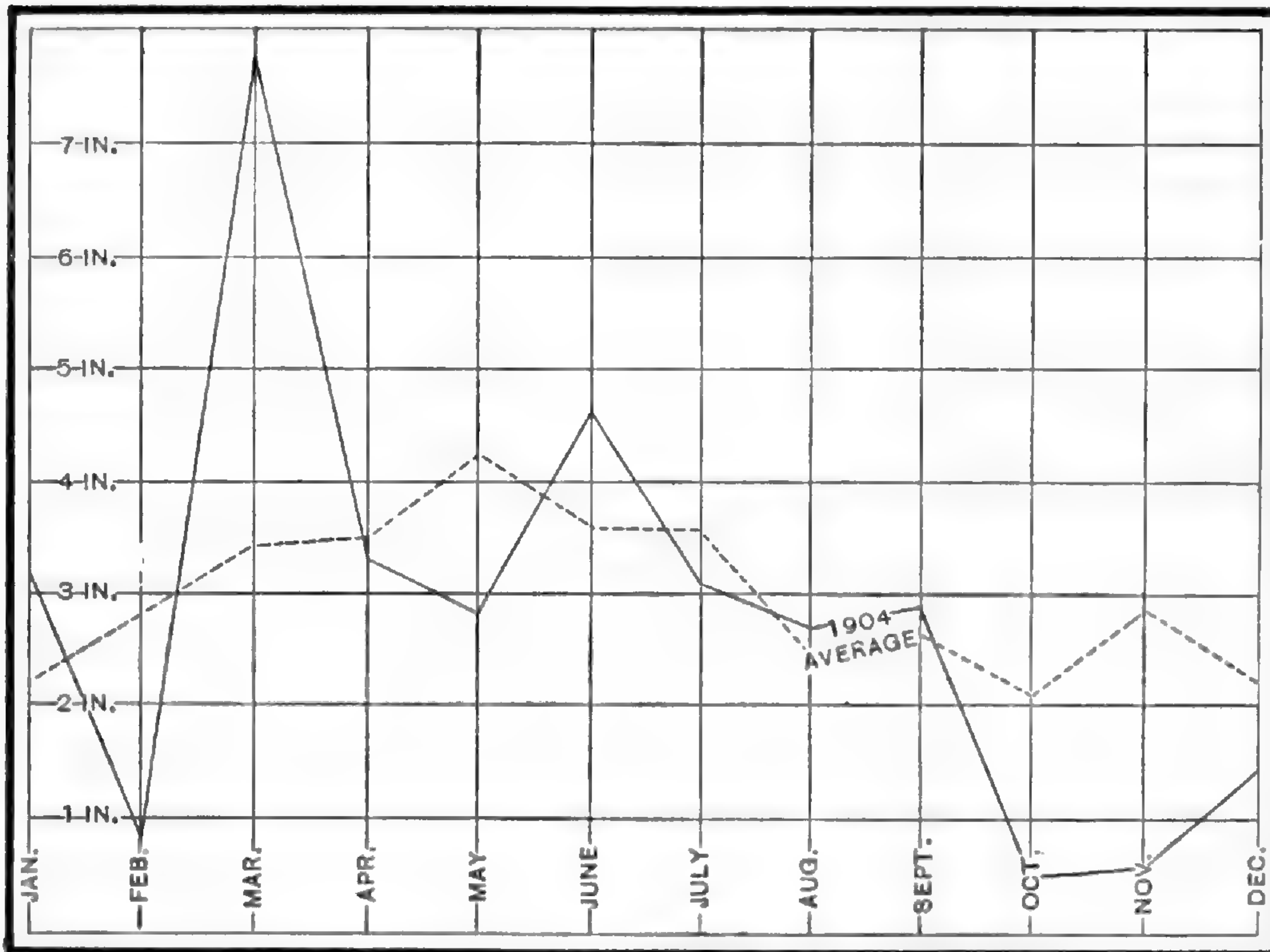


MEAN TEMPERATURES.

was abnormally high in March, but fell much below the average in February, May and the last three months of the year, and the precipitation has been 3.3 inches less than the yearly average. Its distribution is shown in the accompanying diagram (B), compiled from the same source. On the whole, the season has been favorable for gardening, though some of the tropical plants have made less than their customary growth and serious havoc was wrought by two severe hailstorms, while the autumnal drought has necessitated unusual care of trees and shrubs planted in the fall.



DIAGRAM B.



PRECIPITATION.

VISITORS.

The total number of persons who visited the Garden in 1904 is 316,747. Of these, 25,446 were recorded for the first Sunday afternoon in June, and 33,690 for the first Sunday afternoon in September, the remaining 257,611 being week-day visitors.

As was to be expected, this number greatly exceeds that for any preceding year (the highest earlier total record — for 1902 — being 112,314), owing to the large number of strangers drawn to St. Louis by the Louisiana Purchase Exposition. The week-day number represents a little more than 2 per cent. of the entire paid admissions to the Exposition as reported by the daily press (12,804,616), from which it may be inferred, perhaps, that about one in ten



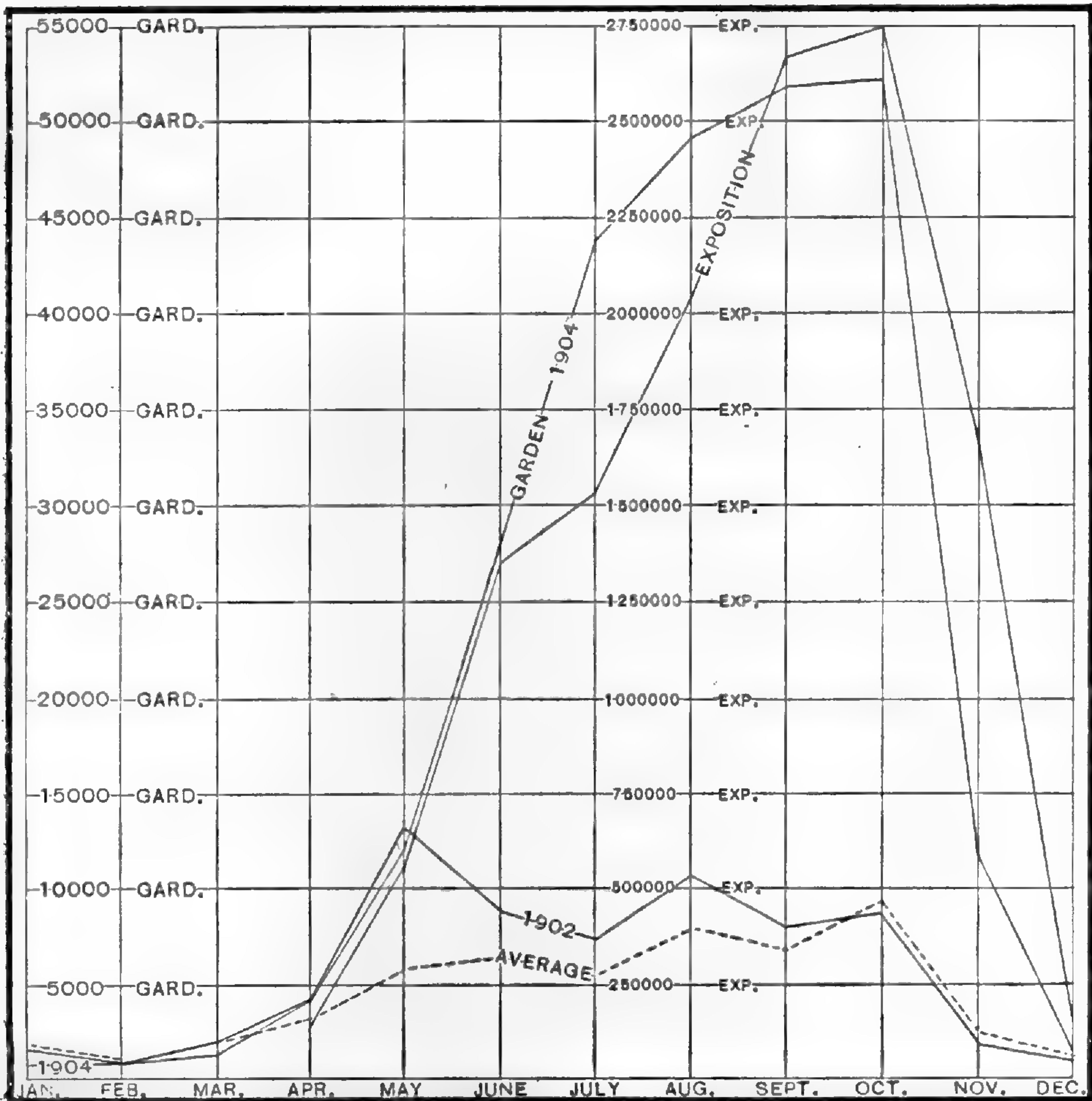


THE PARTERRE.



of the persons who came to the Exposition also visited the Garden, since it is probable that a person who visited the Garden once spent about five days at the Exposition. The appended diagram (C), showing the Garden week-day vis-

DIAGRAM C.



VISITORS ON WEEK-DAYS.

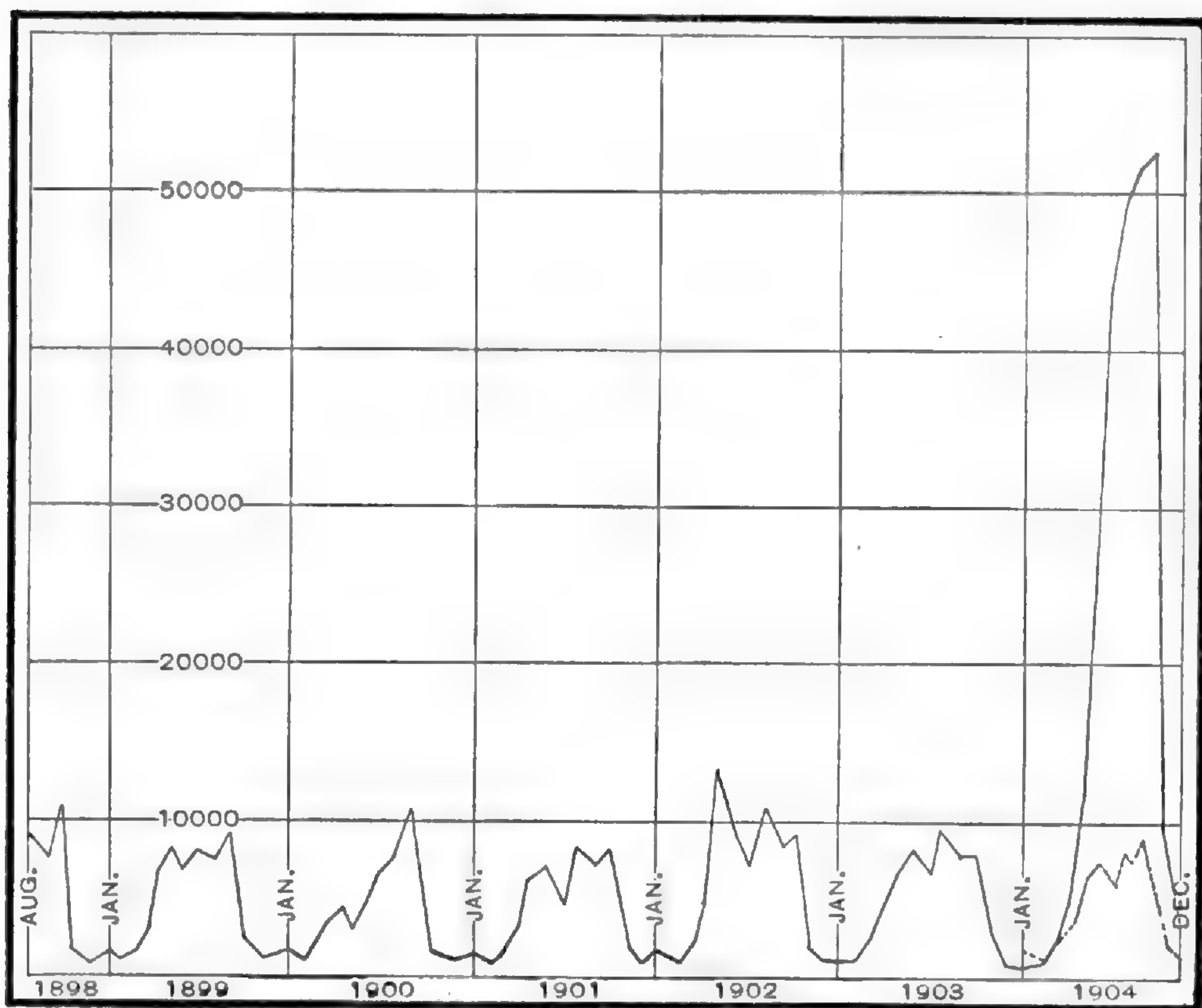
itors for 1904 and for the aberrant year 1902,\* and the average for the period covered by records with the exception of these two years, graphically indicates their distribution by months. For comparison, the Exposition paid admis-

\* Rept. Mo. Bot. Gard. 14:17.



sions (reduced to a scale of 2 per cent.) are platted on the same diagram. It is of interest to note that the latter curve shows a decided check in July, corresponding to the usual Garden curve, although the latter this year is very regular until the autumnal drop. The seasonal fluctuation and the great increase in visitors for the past year are also rendered evident to the eye by another diagram (D), rep-

DIAGRAM D.



VISITORS ON WEEK-DAYS.

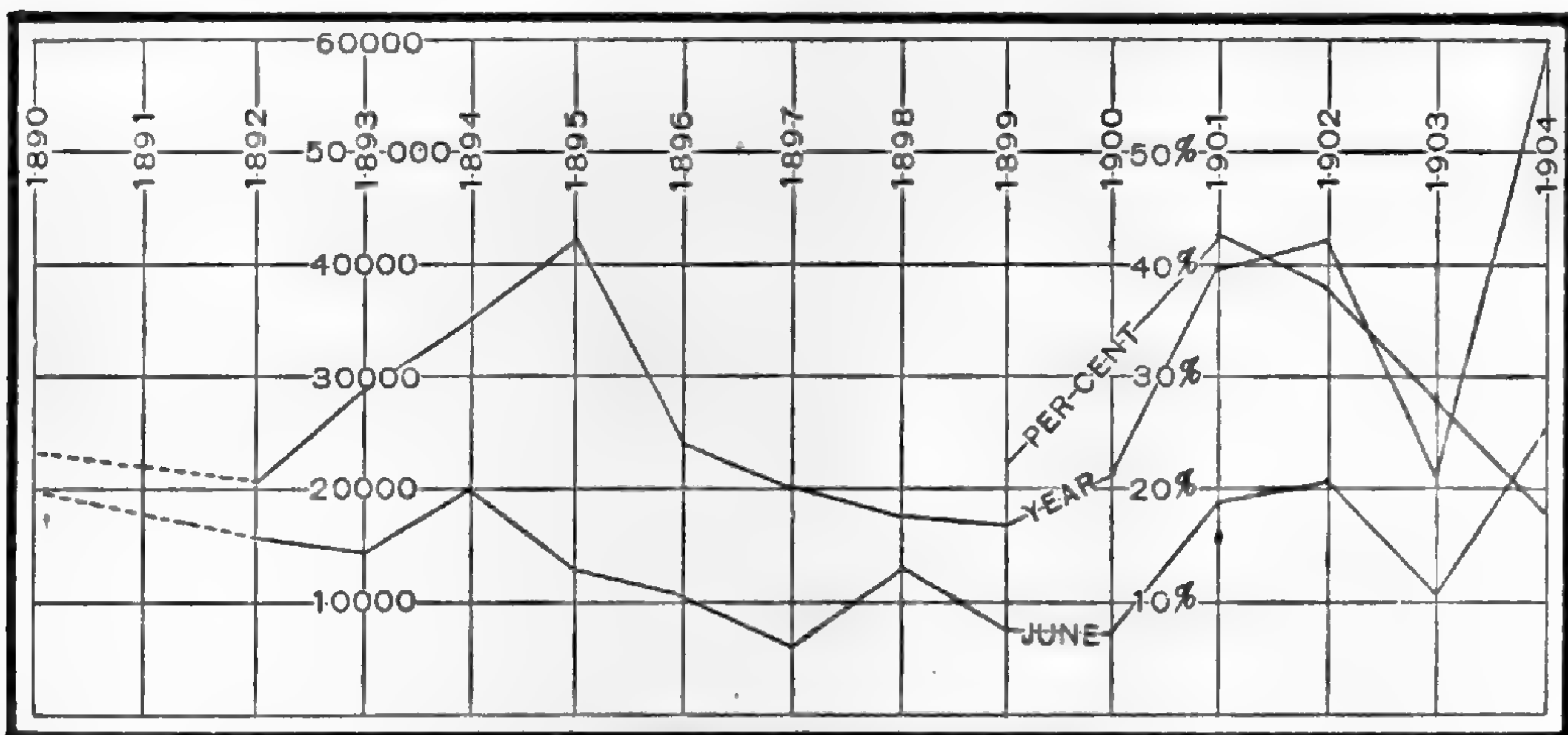
resenting continuously the entire period covered by records. A further diagram (E) shows the number of Sunday visitors and their percentage of the yearly totals, — the latter, as was to be expected, being smaller in 1904 than ever before.

Notwithstanding the exceptionally large number of persons who frequented the Garden last year, no unusual



restrictions were put on their actions, and they were not confronted by a single barrier or request to "Keep off the Grass." As a rule they manifested a desire to refrain from acts likely to result in injury to property or inconvenience to other visitors, and thefts of flowers and minor acts of vandalism have hardly exceeded those of ordinary years in proportion to the larger number of visitors. The experience of the season, however, has shown that if this number were to continue it would be necessary to withdraw from use some of the turf walks and to protect or remove

DIAGRAM E.



SUNDAY VISITORS.

the grass borders surrounding flower beds, some of the lily ponds, etc., where considerable unintentional injury was caused before the end of the season.

#### THE HERBARIUM.

Through the energetic efforts of my assistant, Mr. A. G. Johnson, and his helpers, most of the unincorporated herbarium material has been mounted with the exception of some of the Bernhardt cryptogams, the Chapman fascicles, and a few collections received near the end of the year. The incorporated additions amount to 24,133 specimens,



of which 3,206, valued (unmounted) at \$160.30, were presented or received in exchange for duplicate material or for publications; 3,283, valued at \$164.15, were collected by employees of the Garden; and 17,644 were purchased, — the expenditure for specimens and material amounting to \$1,813.09. Among the noteworthy collections incorporated was the herbarium of the late Sadie F. Price, composed of 2,912 sheets, of which 965 are sketches, largely in color; and sets of Rabenhorst's Algen Europas (1,623) and Algen Sachsens (1,087).

Duplicate unmounted material to the extent of 1,604 specimens, valued at \$80.20, has been distributed to correspondents, and 28 mounted duplicates, valued at \$4.20, have been withdrawn from the general herbarium for the same purpose.

The herbarium, so far as now mounted, consists of:—

The Engelmann Herbarium (all groups) about . . . 97,859 specimens.

The General Herbarium: —

Higher plants.

The J. J. Bernhardt Herbarium	61,338		
The J. H. Redfield Herbarium	16,447		
The Sturtevant and Smith Herbarium . . . . .	7,446		
The Gustav Jermy Herbarium .	4,172		
The Chapman Herbarium* . .	3,536		
The Sadie F. Price Herbarium .	2,912		
Other specimens . . . . .	254,901	350,752	“

Thallophytes.

The J. J. Bernhardt Herbarium*	610		
The Gustav Jermy Herbarium .	1,659		
The Wm. Trelease Herbarium .	11,000		
Other specimens . . . . .	27,430	40,699	“

Making a total of . . . . . 489,310 “

Valued at . . . . . \$73,396 50†

Shelved in the library, in bound fascicles, but included in the preceding count and valuation of the herbarium, are the following exsiccatae: —

\* So far as yet incorporated.

† This valuation, at the rate of \$15.00 per hundred mounted sheets.



Arthur and Holway, Uredineae	4 fascicles containing	60 specimens.	
Ayres, Mycologia Britannica . . .	1	" "	50 "
Berkeley, British Fungi . . .	3	" "	290 "
Cavara, Fungi Longobardiae.	5	" "	250 "
Cocks, Algarum Fasciculi . . .	2	" "	20 "
Collins, Holden and Setchell, Phycotheca . . . . .	27	" "	1,275 "
Cooke, Fungi Britannici . . .	7	" "	700 "
Craig, New Zealand Ferns . . .	1	" "	26 "
Ellis, North American Fungi . .	36	" "	3,600 "
Gray, North American Gra- mineae . . . . .	2	" "	200 "
Grout, Hand-lens Mosses . . .	4	" "	100 "
Herpell, Hutpilze . . . . .	1	" "	135 "
Krieger, Fungi Saxonici . . .	35	" "	1,750 "
Lange, Herbarium f. d. Landö- kon. Botanik . . . (9 in)	5	" "	170 "
Libert, Plantae Arduennae . . .	4	" "	400 "
Linhart, Fungi Ungarici . . .	5	" "	589 "
Rabenhorst, Algen Sachsens and Algen Europas . (259 in)	128	" "	2,710 "
— Bryotheca Europaea . . .	27	" "	1,350 "
— Cryptogamen-Sammlung . . .	1	" "	74 "
— Herbarium Mycologicum . . .	8	" "	800 "
Ravenel, Fungi Americani . . .	4	" "	800 "
— Fungi Caroliniani . . . . .	5	" "	499 "
— " " (author's copy) . . . . .	5	" "	499 "
Seymour and Earle, Economic Fungi . . . . . (10 in)	7	" "	500 "
Shear, New York Fungi . . . . .	3	" "	400 "
Smith, Central American Fungi .	3	" "	150 "
Spegazzini, Hongos Sud-Amer- ikas . . . . .	1	" "	50 "
Sydow, Mycotheca Germanica . .	6	" "	252 "
de Thuemen, Mycotheca Uni- versalis . . . . .	23	" "	2,300 "
Tilden, American Algae . . . . .	6	" "	600 "
Wagner, Cryptogamen-Herba- rium . . . . .	1	" "	195 "
— Gras-Herbarium . . . . .	2	" "	265 "
— Herbarium z. ersten Cursus . .	3	" "	118 "
— Phanerogamen Herbarium . . .	1	" "	200 "
Westendorp and Wallis, Herbie- Cryptogamique . . . . .	12	" "	700 "
Together . . . . .	388	" "	22,077 "



In addition to the herbarium and exsiccatae, the following material should be noted as of the same general character:—

Wood specimens of various sizes . . . . .	800		valued at \$ 55 00
Wood veneers.			
Spurr's cabinet of veneers from the			
Jesup collection . . . . .	541 veneers,		
Hough, American Woods, 10 fascicles	750	"	
Michel, Feine Holzschnitte, 2	285	"	
Nördlinger Querschnitte, 11	1,100	"	
Sykyta, Das Holz . . . . .	1	"	25 "
Tokyo Imperial Museum,			
Useful Woods . . . . .	1	"	255 "
Together . . . . .	25	"	2,956 " valued at \$175 00
Microscope slides.			
Penhallow, N. A. Coniferae . . . . .	268 slides,		
Other slides . . . . .	958	"	
Together . . . . .	1226	"	valued at \$285 00
Total valuation . . . . .			\$515 00

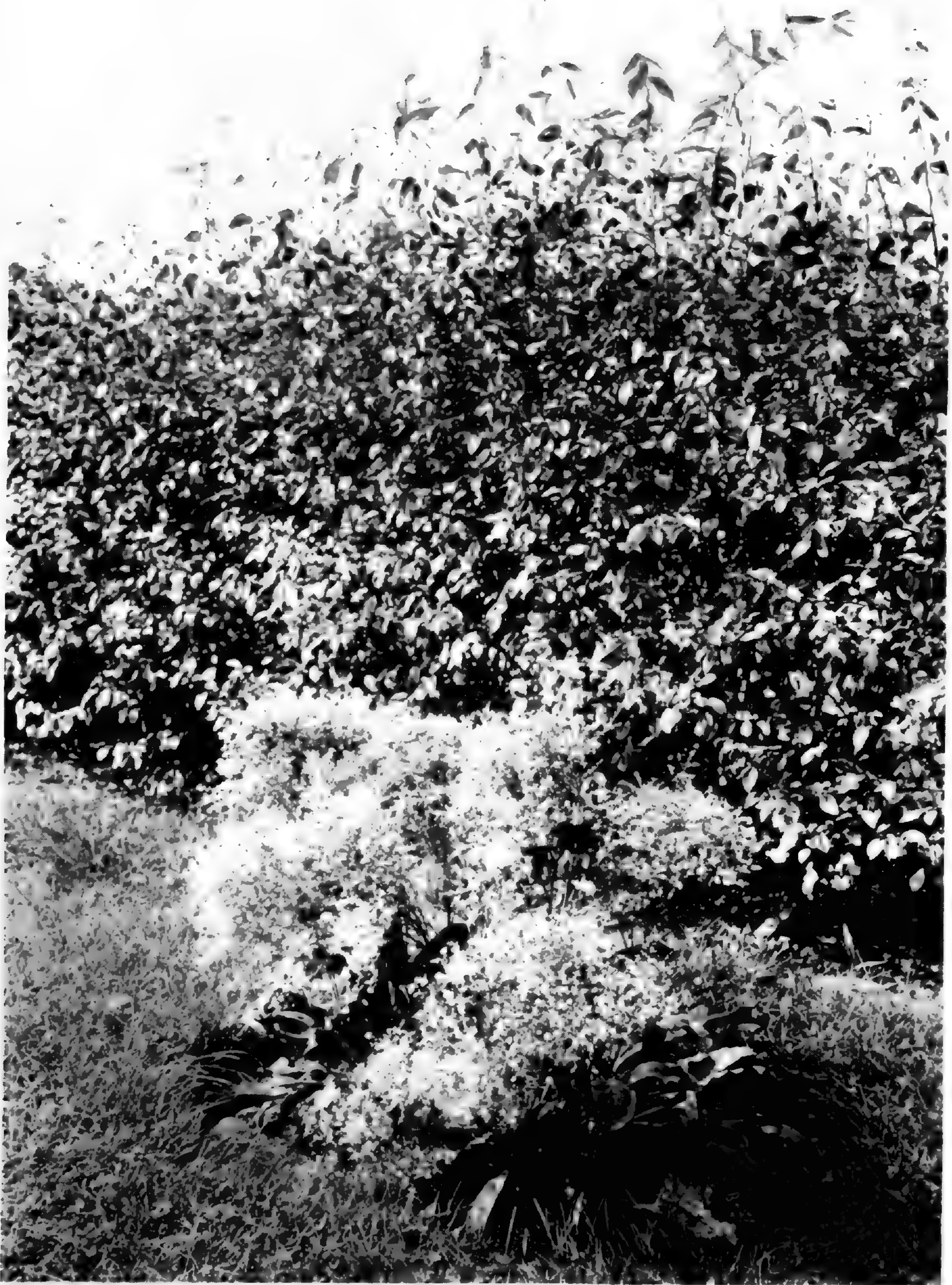
While its valuation remains the same as a year ago, the composition of this miscellany has been considerably changed through the withdrawal of the wood-wedges mentioned in an earlier report\* as forming part of the Engelmann collection, — ownership of which has been asserted by the Academy of Science; and the addition of two fascicles of Hough's American Woods, and of 174 microscope slides illustrating in part the studies of floral ecology which Dr. Harris is prosecuting.

#### THE LIBRARY.

No special appropriation having been made for the library in 1904, few large sets have this year been purchased, but difficulty has not been found in providing for the purchase of procurable works needed for current research or of desirable new publications, and limitation of the use of what

\* Rept. Mo. Bot. Gard. 5: 15.





STATICE LATIFOLIA.



remained from the special appropriation of the preceding year has resulted in an unusual advance in suitably binding the large accumulation of unbound works, through the effort of Dr. J. A. Harris, the Librarian.

The additions for the year comprise 589 books, valued at \$1,118.50, and 2,219 pamphlets, valued at \$414.40, presented or received by way of exchange; and 708 books and 103 pamphlets bought, — the expenditure for purchases and binding for the year amounting to \$3,189.45.

The card index has been increased by the incorporation of 71,542 cards, of which 35,162 were written by employees; 18,364 were purchased or paid for as piece-work; and 18,016 were presented. Of the latter, some 17,480 are a series of references constituting the framework of a Flora Gastronomica (some 2,700), a Dictionary of Agriculture and Horticulture (some 12,300), and a large number of minor subject groupings, prepared by the late Dr. E. Lewis Sturtevant, which with eleven valuable Index Rerum manuscript volumes were presented by Dr. Sturtevant's daughters shortly after they had visited the Garden in the spring, and which materially add to the research facilities given during Dr. Sturtevant's lifetime.\*

The distinct serial publications now received at the library number 1,250, of which 100 represent subscriptions; and 1,150, issued by 875 institutions or publishers, are received in exchange for the Reports of the Garden. This total is 65 larger than the number reported at the end of 1903.

As now constituted, the library contains: —

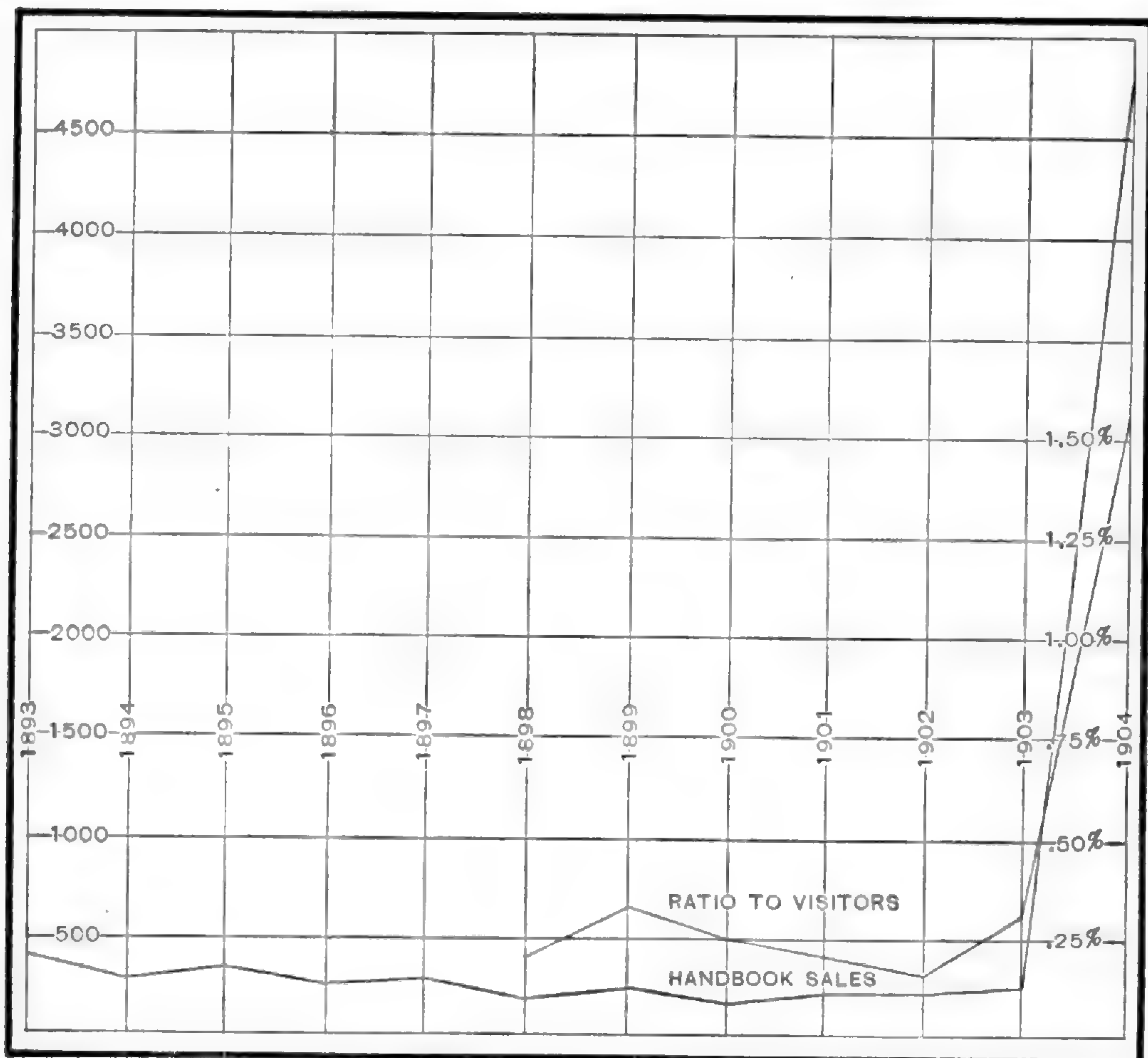
Pamphlets . . . . .	25,110		
Books . . . . .	20,705		
	<u>45,815</u>	valued at . . . . .	\$75,153 20
Manuscript volumes . . . . .	<u>77</u>	“ “ . . . . .	<u>910 00</u>
Total . . . . .	45,892	“ “ . . . . .	\$76,063 20
Index cards . . . . .	382,760	“ “ . . . . .	<u>3,827 60</u>
Total valuation of library . . . . .			\$79,890 80

\* Rept. Mo. Bot. Gard. 4: 15. 5: 16. 7: 123. 8: 21. 10: 19, 20. 14: 233.



The little souvenir Handbook of the Garden, of which 5,000 copies were published in 1893, had become so antiquated that, though a large number of copies remained unsold, the Board decided early in 1904 to issue a revised edition of 5,000 copies. Of these 280, — 100 of them specially bound, — were reserved for presentation purposes,

DIAGRAM F.



SALES OF HANDBOOK.

and the remaining 4,720 copies have been sold since the first of June, when they were placed on sale. Of the older Handbooks, 75 copies had been sold in 1904 prior to receiving the new books, and 13 were subsequently sold at a reduced price. To meet the needs of the next few years, a



third edition, of 2,550 copies, again revised, has been printed.

The appended diagram (F) shows graphically the sales of Handbooks from the issuance of the first one in 1893; and though the number of sales in 1904 was undoubtedly influenced by the appearance of a new and more attractive edition, this diagram once more emphasizes the unusual number of persons who have this year visited the Garden for the first time. On it is also shown by another curve the ratio of Handbook sales to the total number of visitors since 1898, when the latter were first counted, this averaging .246 of 1 per cent. prior to this year, reaching its minimum (.16 of 1 per cent) in 1902, when the number of local sight-seers was unusually great, and in 1904 amounting to 1.51 per cent. of the entire number of visitors.

#### RESEARCH AND USE OF FACILITIES.

Owing to the presence at the Exposition of a large number of persons interested in botany and floriculture, the Garden collections have been used for study to an exceptional extent this year, and every possible courtesy has been extended to visiting botanists, several of whom in return have given valuable assistance in naming plants with which they were familiar and by suggestions as to the care of difficult groups. It has been particularly gratifying to observe through the year an unusually large number of persons going through the Garden with care, note-book in hand.

The chemical laboratory reported a year ago as being equipped for the use of Mr. J. B. Nagelvoort, a distinguished student of the chemistry of plants, as a result of his death in March last has been turned to other purposes appropriate to the research plans of the founder of the Garden, — partly in connection with the timber studies being carried on under Dr. von Schrenk for the United



States Department of Agriculture and partly in a study of the gas contents of water plants under the direction of Dr. Harris.

As was stated in my last report, in every feasible way the library, herbarium and living collections of the Garden are made useful to investigators, whether connected with the institution or not. When they can be used here, every possible facility for such use is given visiting botanists. If this is not possible, they are sent to trustworthy persons or institutions when their safe return is guaranteed; and, except for specimens or books of special value which could not be replaced in case of loss, or those in constant use, the Garden has always stood ready to place its library and other collections for a reasonable time at the disposal of botanical departments of colleges or of capable investigators not having official connection with the centers of learning.

#### THE HENRY SHAW SCHOOL OF BOTANY.

With the opening of the current college year, the instructional force of the School of Botany was increased by the appointment to an instructorship of Mr. A. C. Life. The increase in both beginning and advanced classes noted in my last report continues. At the 1904 commencement of Washington University the degree of Doctor of Philosophy was conferred on Professor S. M. Coulter, whose major work was in botany and whose thesis was published in the last Garden Report.\* There are now enrolled in the University three candidates for the Master's degree, and two for the Doctor's degree, with botany as a major study.

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\* Rept. Mo. Bot. Gard. 15 : 38-71. *pl.* 1-24.





CEROPEGIA WOODII.



## GARDEN PUPILS.

No changes have been made in the provision for instruction in theoretical and practical gardening; though the small body of garden pupils has undergone a great change.

In March last, C. W. Fullgraf and J. H. Tull, who had completed the prescribed work and passed the requisite examinations, were granted the customary certificate of proficiency. The two scholarships so vacated were filled, on the result of competitive examinations, by the appointment of William A. Federer, of St. Louis, and Hubert M. Jones, of Chicago. In April, Walter Gillies resigned the scholarship which he had held for a year on the nomination of the St. Louis Florists' Club, and on the same nomination it was assigned in May to Paul Roper. In October, Hubert M. Jones, a bright and studious young man to whom one of the scholarships had been awarded in the spring, died at his home in Chicago, after an illness of several months; and Walter H. Hummel, who had held a scholarship since April, 1903, resigned it, to undertake college preparatory work. An announcement that these vacant scholarships will be awarded in March next, on the result of competitive examinations, was issued in December, and distributed in the customary manner.

## THE GARDEN STAFF.

The only changes to be reported in the office force are the appointment of Dr. J. A. Harris as Librarian, and of Miss Nellie L. Harris as Cataloguer, in June, to succeed Miss Ida Norton, who had severed her connection with the Garden. A number of temporary assistants have been employed through most of the year in both library and herbarium.

I am pleased to be able to report that in several depart-



ments the gardening force has been strengthened by the enrollment of men of both knowledge and experience, through whose efforts I hope for the enlargement and gradual utilization for research of some of the more important collections of living plants.

#### SPECIAL TESTAMENTARY PROVISIONS.

Four special events provided for in the will of Mr. Shaw have taken place in 1904, as follows: —

The annual flower sermon was preached in Christ Church Cathedral, St. Louis, on the morning of May 15th, by Rt. Rev. Charles S. Olmsted, D.D., Bishop of Colorado.

The fifteenth banquet to the Trustees of the Garden and their guests was given at the Buckingham Club, on the evening of September 22d. Covers were laid for 185 gentlemen, among whom were many of the distinguished participants in the International Congress of Arts and Science, then meeting in St. Louis. Mr. Chaplin presided, and after the dinner speeches appropriate to the occasion were made by the Right Honorable James Bryce of London, President D. R. Francis of the Louisiana Purchase Exposition, Professor Wilhelm Ostwald of Leipzig, Mr. A. R. von Stibral, Commissioner-General for Austria; Dr. Paul Mayer of Paris, and Signor Attilio Brunialti of Rome.

By authority of the Board, the fifteenth banquet to the gardeners of the institution and invited florists, etc., was given as a collation served in the Linnean House on the afternoon of August 19th, when 465 members of the Society of American Florists were received as the guests of the Garden.

In connection with the Exposition, a "World's Fair Flower Show Association" was formed in the autumn, under the auspices of which a flower show was held on the Exposition grounds from November 7th to 12th, inclusive. By authority of the Trustees of the Garden, there were



offered at this flower show twelve "Shaw Medals," of a value of \$25.00 each,\* and cash prizes to the amount of \$160.00. The latter were awarded by the judges and paid for worthy exhibits of flowering orchids; and three of the offered medals were awarded by the judges, and issued as follows: — to Vaughan's Seed Store, for the Baby Rambler Rose; to John Scott, for *Nephrolepis Scottii*; and to F. R. Pierson, for *Nephrolepis Piersoni elegantissima*.

At this flower show, which was characterized by the floricultural press as one of the largest and best exhibits of the kind ever held in the United States, the Garden for the first time in its history made competitive entry, exhibiting a mass of some fifty varieties of chrysanthemums and two large specimen plants of *Rhapis flabelliformis* — for the former of which the first prize was awarded, while the latter, entered in a class for which no special premiums were offered, was accorded a "highly commended" award by the judges.

#### THE EXPOSITION.

Some time before the opening of the Louisiana Purchase Exposition, the authorities of Mill Hill School, near London, — at which Henry Shaw was entered as a pupil on March 25, 1815, as I learn from Professor J. D. Butler, — sent over a number of photographs illustrating the school and its surroundings and faculty, with the request that these be combined with the exhibit of the Garden founded by Mr. Shaw.

By direction of the Garden Trustees this was done, the Garden exhibit itself consisting in a portrait of its founder, a series of photographs illustrating planting and methods of gardening instruction, water-color sketches by Mrs. Vieh of several striking plants in the living collections,

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\* Rept. Mo. Bot. Gard. 5:18.



a full series of the Garden publications, showing its development and scientific activity during the fifteen years of its existence under the care of the Trustees, and a collection of edible and poisonous mushrooms which occur about St. Louis, contributed by Dr. N. M. Glatfelter. For the exhibit of its publications (group 83), the Garden was awarded a grand prize; and a similar award was made for its exhibit of results of original research and practical work (group 105 of the Exposition classification). By agreement between the Flower Show Association and the Exposition officials, exhibits entered in the flower show were also judged for Exposition awards, and I am informed that the Garden received a gold medal for its chrysanthemum group and specimen palms, referred to above. Through the season, from time to time, vegetables and fruits were placed in the hands of the Missouri State Commission for incorporation in their general exhibit at the Exposition, and the Commission inform me that one of these, a house-grown cucumber exhibit, was separately entered and awarded a silver medal. With these unexpected recognitions of the scientific and horticultural success of the Garden, the Board of Trustees has just cause to be gratified.

Very respectfully,

WILLIAM TRELEASE,

Director.





HYDRANGEA QUERCIFOLIA.



## SCIENTIFIC PAPERS.

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### THE IDENTIFICATION OF WALTER'S GRASSES.

BY A. S. HITCHCOCK.

One of the earliest works treating of the flora of the eastern United States, using the binomial system of nomenclature, was the *Flora Caroliniana* by Thomas Walter, "Agricola." It was published in London in 1788 at the expense of J. Fraser. Many plants were described here for the first time, and from a historical and nomenclatorial standpoint this comparatively rare work is extremely important. The following extract from the preface to this flora is interesting: —

"Notam dubietatis ad nomen genericum ponere, et differentias typis italicis indicare, saepe contentus fuit.

"Libertatem appellativè assignandi paucis tantùm concedendam sentit, quamobrem iis qui in hâc scientiâ meritò duces sunt, jus reliquit dicendi quaenam sint nomina plantis nunc primùm descriptis.

"Stirpes plus mille hoc opere comprehendi mirum fortasse videatur, quum cognitum fuerit vix non omnes collectas fuisse ex area non ampliore quàm quae linea bis duplicata quinquaginta millium passuum circumscribi potest. Etiam multae adhuc latent, ut quotidie docet experientia. Gramina et plantae classi Cryptogamiae appertinentes, plerumq. intacta remanent. Praeterea plures omittuntur arbores, frutices et herbae, quorum fructificatio auctori nondum satis patuit." The preface is subscribed: "Carolinae Meridialis, ad Ripas Fluvii Santee, 30 Dec. 1787."

Walter's herbarium is now deposited in the Natural History Section of the British Museum, South Kensington, London, England. The herbarium seems to have been in the possession of the Fraser family for many years after its formation, and was presented in 1849 to the Linnaean



Society, from whom it was purchased by the British Museum at a sale of the Society's Surplus Collections.\*

The herbarium suffered before it came into the possession of the Museum and many of Walter's types are missing, especially among the grasses. The plants are mounted in a large book, usually several specimens on a page, the labels being fastened to each plant. The specimens are for the most part very fragmentary, often consisting of a leaf or an inflorescence. When the herbarium was obtained by the Museum, most of the plants were mounted, but a few were loose and have been subsequently mounted at the end, following the others. All the grasses appear in this second part (pp. 112 *et seq.*). There are 18 specimens of the grasses. In the following notes I have attempted to identify the species of grasses published by Walter in his Flora, considering the specimens in his herbarium, the descriptions, which are often meager, and tradition as shown by the disposition made of his species by Michaux, Pursh, and Elliott, who worked over the same territory and must have been familiar with Walter's work.

Walter seems to have followed in his identifications the second edition of Linnaeus' Species Plantarum or the twelfth edition of the Systema, which is about the same. The use of italics for certain specific names is not quite clear. Those thus printed appear to be new species, but many of those printed in Roman are also new names. Many of Walter's names as applied to grasses are yet doubtfully identified or entirely unidentified and probably must remain so.

#### MONANDRIA. DIGYNIA.

[P. 59] 2. CINNA. Cal. gluma 2-valvis, 1-flora. Cor. gluma  
2-valvis. Sem. 1.

\* See note in Journ. Bot. 37:485. 1899.



*glomerata* 1. spicis bifidis glomeratis terminalibus; bracteis clavatis plumosis.

Specimen in herbarium consists of top of culm with panicle, labeled "*Cinna glomerata* 815." This is *Andropogon macrourus* Michx. Michaux quotes *Cinna glomerata* Walt. as synonym, as does also Elliott.

*lateralis* 2. spicis bifidis lateralibus solitariis. Bracteis clavatis plumosis.

The specimen in the herbarium consists of about six inches snipped from the tops of two culms and labeled "Cinna." Since this agrees with the description, it is probably the basis of his *C. lateralis*. It is one of the forms of *Andropogon virginicus* L. Michaux and Elliott quote *Cinna lateralis* Walt. as synonym under *Andropogon dissitiflorum* Michx.

#### DIANDRIA. DIGYNIA.

17. ANTHOXANTHUM. Cal. gluma 2-valvis, 1-flora. Cor. [P. 65]  
gluma 2-valvis, acuminata. Semen 1.

*giganteum* 1. floribus aristatis, plumosis, panicula conferta, magna, calycibus unifloris. Culmo 8-pedali.

The specimen in the herbarium consists of a large panicle, about fourteen inches long, labeled "*Anthoxanthum*." As this agrees with the description and is the only species of this genus that he describes, it may be taken as the type. It is *Erianthus saccharoides* Michx. and is cited by Michaux under this name. Persoon and Pursh cite this under *Saccharum giganteum* Pers.

#### TRIANDRIA. DIGYNIA.

29. PANICUM. Cal. 3-valvis, valvula tertia minima. [P. 71]



\* Spicata.

- [P. 72] alopecuro- spica tereti, involucris setaceis basi ciliatis  
deum 1. fasciculatis unifloris flosculo quadruplo  
longioribus.

No specimen. Elliott cites this under *P. glaucum* L., and Pursh cites it under *P. verticillatum* Willd. It is probably a *Setaria* and would naturally be one of the common species in the Carolinas. He describes only two species that can be referred to *Setaria*, the other being *P. italicum*. *S. glauca* and *S. imberbis* are both common. The description states that the bristles are four times longer than the flower, which applies better to *Setaria imberbis* R. & S. (*P. imberbe* Poir.). *P. alopecurodeum* L. is an Old World plant, but Linnaeus' description is used by Walter.\*

- italicum 2. spica composita, spiculis glomeratis setis  
immixtis, pedunculis hirsutis.

No specimen. Probably correctly named as cited by Elliott, *Panicum italicum* L., the description of which Walter copies.

- hirtellum 3. spica composita: spiculis adpressis alternis,  
calycibus geminis: valvulis omnibus aris-  
tatis: arista extima longissima. Culmis  
4-pedalibus erectis nec repentibus.

There are three specimens in the herbarium: (1) A panicle and upper leaf, the flowers long-awned, labeled

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\* The descriptions were compared with those in the second edition of Linnaeus' *Species Plantarum*, with which they agree more closely than with those of the first edition. I have not observed that the descriptions agree any more closely with those in the twelfth edition of the *Systema Naturae*.



“*Panicum hirtellum*.” This is the long-awned form of *P. crus-galli* L. (2) A panicle only of a densely flowered long-awned form labeled “*Panicum hirtellum* 603.” This is *P. hispidum* of Muhlenberg, who cites *P. hirtellum* Walt. (3) A piece of leaf and portion of panicle labeled “*Panicum hirtellum* 817.” This is *Panicum virgatum* L.

Elliott cites *P. hirtellum* Walt. under *P. crus-galli* L. Pursh cites this under his *P. Walteri* together with *P. muricatum* Michx. (which is *P. crus-galli* L.) and says “v. s. in Hb. Lambert, nec non Walter.” It is impossible to tell from the description whether Walter refers to the tall erect form of *P. crus-galli* common in the South or to *P. hispidum* Muhl. which has hispid sheaths. Walter probably included both in one species, and I think his *P. hirtellum* should stand as a synonym of *P. crus-galli* L. *P. hirtellum* L. is an *Oplismenus*.

*anomalum* 4. spica composita, spiculis secundis horizontalibus alternis oppositis ternisque; calycibus laevibus confertis in triplici ordine; corollis trivalvibus; culmo decumbente; fol. longis, laevibus.

No specimen. I have not found this cited as a synonym by any of the earlier authors, and it is impossible to identify the species. From the statement “spica composita,” one would suppose that the panicle was similar to that of his *P. italicum* and *P. hirtellum*.

*dimidiatum* spicis 4–7 dimidiato-secundis, rachi lineari  
5. membranacea (ut paspalorum), extrorsum  
floribus aggregatis.

No specimen. Muhlenberg and Elliott state that this is *P. Walteri* Ell. (*P. hemitomum* Schultes; *P. Curtisii*



Chapm.). From the description it might be this or *P. colonum*. Neither species has a decidedly membranaceous rachis "as in *Paspalum*."

\* \* Paniculata.

capillare 6. panicula capillari erecta patente, caule piloso.

No specimen. Cited by Elliott under *P. strigosum* Muhl. Apparently *P. capillare* L.

miliaceum? panicula patente, culmo ramoso geniculato  
7. decumbente, staminibus flavis, pistillis  
purpureis.

No specimen. Cited by Elliott under *P. geniculatum* Muhl. to which is also referred *P. dichotomiflorum* Michx. This is evidently *P. proliferum* L. Walter does not use Linnaeus' description of *P. miliaceum*.

[P. 73] latifolium 8. panicula racemis lateralibus simplicibus, foliis  
ovato-lanceolatis collo pilosis.

The specimen in the herbarium consists of a fragmentary panicle and two leaves which are smooth except for the ciliate margin at the base. There is a slight ciliate ring at the nodes. Labeled "*Panicum* 469." The specimen and the description appear to refer to *P. latifolium* L., as the leaves are ovate-lanceolate and the nodes are barbed. Walter uses Linnaeus' description.

brevifolium paniculatum, foliorum vaginis longitudinali-  
9. ter ciliatis. Praecedenti nimis affinis?

There is a specimen in the herbarium labeled "*Panicum* 448," which is probably this species. It consists of a panicle and two upper leaves. The spikelets are



about as in the preceding, slightly hairy. Leaves about the same shape, sparsely hirsute. Sheaths quite hirsute on the margin. Elliott refers this doubtfully to *P. nervosum* Muhl. (*P. commutatum* Schultes), which it may be, as this is common in that region. *P. brevifolium* L. is from India, but Linnaeus' description is copied by Walter.

*nudum* 10. culmo geniculato sesquipedali erecto, floribus solitariis remotis verticillatis, pedunculis longissimis; foliis caulinis nullis.

No specimen. Muhlenberg suggests that this may be his *P. divergens* (*P. cognatum* Schultes; *P. autumnale* Bosc), while Pursh refers it doubtfully to *P. melicarium* Michx. It may be *P. cognatum* Schultes, as the culm is about a foot and a half high with the flowers (spikelets) on long peduncles, and the leaves are mostly near the base of the culm. I do not know just what is *P. melicarium* Michx. From the description it might be *P. hians* Ell. Walter's plant can scarcely be this, as suggested by Pursh, for the description of *P. melicarium* states that there is a rudimentary flower at the base of the perfect flower, and "ramulis raris, subappressis."

*coloratum* 11. fol. amaris, longissimis, fauce villosis; culmo folioso, 3-pedali, panícula patentissima laxiuscula ramis filiformibus. Antheris croceis; pistillis saturate violaceis.

No specimen. Referred by Pursh to *P. virgatum* L. and by Michaux doubtfully to the same species. The statement as to the bitter leaves applies to *P. amarum* Ell., but the remainder of the description applies also to *P. virgatum*. Elliott states that Walter has confused the two species which the former now separates. *P.*



*coloratum* Walt. should then stand as a synonym of *P. virgatum* L. rather than of *P. amarum* Ell. Both species are common in Walter's region. Not *P. coloratum* L., which is a north African plant.

*speciosum* 12. panicula longa erecta geniculata, ramis 4, 6, s. 8 verticillatis simplicibus brevibus, e singulis nodis radiatis; flor. solitariis subsessilibus, fuscis, longitudine eorum remotis.

No specimen. It is possible that this may be *Sporobolus junceus* Kunth.

30. CORNUCOPIAE? Involuer. 0. Calyx subteres bivalvis: valvulis oblongis acutis aequalibus. Cor. 1-valvis, figura magnitudine et situ valvulae glumae calycis simillima.

*hyemalis* 1. culmo erecto, panicula diffusa verticillata, foliis angustis subteretibus.

No specimen. Undoubtedly *Agrostis hyemalis* as referred by Michaux under *Trichodium laxiflorum*.

[P. 74] *perennans* 2. culmis subdecumbentibus; foliis latioribus; panicula longa diffusa, ramis trichotomis verticillatis. Gramen undique laeve, saccharinum, aestatem sustinens, in hyeme vicens, radicibus geniculisque se cito propagans. Donum inaestimabile, Conditore ad hanc diem reservatum, hoc aevum, me instrumento, locupletatum!

No specimen. Michaux refers this to his *Trichodium decumbens* (*A. perennans* Tuckerm.). As I have stated elsewhere, this is the form of *Agrostis perennans* sepa-



rated by Professor Scribner as *A. intermedia*. In 1789, the year following the publication of Walter's work, Fraser, who was familiar with Walter's plants, wrote an article in the "Gentleman's Magazine," entitled "Fraser's Carolina Grass," in which he gives a good description accompanied by a plate, and cites *Cornucopiae perennans* Walt. as a synonym. A specimen of this is in the herbarium of M. de Candolle at Geneva.

*altissima* 3. culmo erecto, duro; panicula coarctata; flor. magnis.

No specimen. Pursh refers this to his *Trichodium elatum* along with *Agrostis dispar* Michx. The latter is *Agrostis alba* L., and I think it much more likely that this is also the basis of Walter's *C. altissima*. It is true that his generic description calls for a "1-valved corolla," but the palet in *Agrostis alba* is not easily seen and might well have been overlooked. *Trichodium elatum* is a comparatively rare plant, especially in Walter's region, and if seen he is not likely to have separated it from his *C. perennans*, judging from his work in general.

31. ALOPECURUS. Cal. 2-valvis. Cor. 1-valvis, apice simplici.

*pratensis* 1. culmo spicato erecto, glumis villosis.

There is a specimen in the herbarium labeled "Alopecurus 470," which consists of a spike and portion of culm but no leaves and only a few spikelets remaining at the base of the spike. The awn is about twice the length of the spikelet. It appears to be *A. geniculatus*. Whether this represents his *A. pratensis* or *A. carolinianus* it is impossible to say. Elliott refers *A. pratensis* Walt. doubtfully to *A. geniculatus*. The brief description which is copied from Linnaeus applies well enough.



*carolinianus* culmo radicante, panicula subspicata, glumis  
2. laevibus, corollis aristatis.

No specimen. Pursh refers this doubtfully to his *A. subaristatus*. He quotes Michaux's description (who describes the plant under the name *A. aristulatus*), and adds "v. s. in Herb. Walter." He seems to have seen only Walter's specimen and yet gives a new name to Michaux's plant and refers Walter's plant here doubtfully. Michaux's plant (from the swamps of Canada) is said to have an erect culm and awn scarcely exerted (our native *A. aristulatus* Michx.), while Walter's description calls for a rooting culm and aristate corolla. Moreover Walter says of this, "panicula subspicata," as distinguished from "culmo spicato erecto" in *A. pratensis*. This species must remain doubtful.

32. ARISTIDA. Cal. 2-valvis. Cor. 1-valvis, aristis 3 terminalibus.

*adscensionis* panicula ramosa, spicis sparsis.

1.

No specimen. Referred to *A. stricta* Michx. by Elliott and to *A. oligantha* Michx. by Pursh. The description applies better to the latter species than to any other species growing in the Southeast. The panicle is few-flowered and loosely branched. Not *A. adscensionis* L. from Ascension Island, but Walter copies Linnaeus' description.

33. PHALARIS. Cal. 2-valvis, carinatus, longitudine aequalis, corollam includens.

*caroliniana* 1. panicula spicata ovata, petalis aristatis, calycibus striatus.

No specimen. The name is used by Muhlenberg.



Seems to refer to the common *Phalaris* of that region, *P. intermedia* Bosc, but in this the flowering glume is not awned as stated by Walter.

34. PASPALUM. Cal. 2-valvis, aequalis, suborbiculatus. Corolla ejusdem figurae. Stigmata penicilliformia.

No specimens of *Paspalum* are in the herbarium.

dissectum 1. spicis secundis axillaribus et terminalibus, [P. 75]  
rachi membranacea, floribus alternis;  
foliis et caule pilosis.

Elliott suggests that this may be *P. debile* Michx., while Pursh refers it to *P. setaceum* Michx. Walter's statement that the spikes are axillary and terminal would place this in the *setaceum* group, the different species of which were probably not distinguished. The leaves and stems are described as pilose, which applies better to *P. debile* Michx., or some one of the more recent pubescent segregates from *P. setaceum*, than to the true *P. setaceum*, which is sparingly pilose. I have not examined the specimens in Michaux's herbarium critically, but his *P. setaceum* is sparingly pilose and *P. debile* quite woolly as to leaves and sheaths. Walter does not use Linnaeus' description of *P. dissectum*.

membrana- culmo ramoso longissime procumbente; spica  
ceum 2. composita spiculis 6 s. 7 alternis laevibus  
secundis, floribus duorum ordinum; recep-  
taculo membranaceo lato flores subvolventi.

Now recognized under the above name. Elliott suggested that this might be his *Ceresia fluitans* (*Paspalum fluitans* Kunth), which has numerous spikes



instead of 6 or 7 as described by Walter. Pursh says it is *Paspalum laeve* Michx., which does not have the extensively creeping culm called for by the description. Schultes bases his *P. Walterianum* upon *P. membranaceum* Walt.

*praecox* 3. spica composita spiculis alternis, basi villosis, 5. s. pluribus *trium* ordinum florum; glumis calycinis aequalibus, rachi membranacea *angusta*; antheris luteis, stigmatibus purpureis. *Flos medius sessilis*.

The name is used by Elliott, Michaux and others and is now generally accepted by American botanists. Pursh states that Walter's plant is *Cynodon dactylon* and that he had seen it ("v. s. in herb. Walt."), but *Cynodon* does not have the spikes alternate nor are they villous at the base as in what is generally understood to be *P. praecox*.

*paniculatum* spicis paniculatis, *verticillato - aggregatis*.  
4. *Panicula longa; spicae angustae, longae; flores alterni, acutiusculi, duplici ordine digesti*.

Renamed by Muhlenberg *P. mucronatum* because of Walter's mistaken identification with *P. paniculatum* L. of tropical America. Pursh refers Walter's plant doubtfully to *P. plicatulum* Michx., which does not have the verticillate spikes. Walter uses Linnaeus' description but adds all after "aggregatis."

*distichum* 5. spicis duabus, altera subsessili.

The two spikes identify this as the *P. distichum* L.



*virgatum* 6. spica composita spiculis 10 s. 11 secundis, alternis, basi villosis, ordine quadruplici, pedunculis bifloris, culmo suberecto; calycibus aequalibus, fol. longis purpurascenscentibus intus ad faucem subvillosis.

This is identified by the several spikes, villous at base, the spikelets in four rows and the purplish leaves, and is probably *P. Boscianum* Flügge (*P. purpurascens* Ell.). Elliott gives *P. virgatum* Walt. not L. as synonym of his *P. purpurascens*. Pursh refers Walter's plant doubtfully to *P. Floridanum* Michx., which it can scarcely be, as the spikelets of the latter are not in four rows. Linnaeus' description is "P. spiculis paniculatis alternis basi villosis."

35. SYNTHERISMA. *Crop-grass* vulgo.

[P. 76]

Cal. 1-florus, 2-valvis: valvulis planis, acutis interiore minore recta, exteriori lateribus corollam subamplexante. Cor. 2-valvis: valvulis magnitudine et figura valvulae majori calycis simillimis.

Stam. filamenta tria capillaria. Antherae oblongae.

Pist. germen subrotundum. Styli duo capillares, longitudine floris. Stigmata plumosa.

Per. nullum.

Semen unicum, calyce corollaque persistentibus vestitum.

*praecox* 1. culmo decumbente, laevi, subtereti, geniculis in aquosis radicanti; foliis collo et fauce villosis; spica composita spiculis oppositis erectis linearibus secundis; dentibus bifloris; flore altero sessili.



No specimen in herbarium. There is not much doubt but this refers to *Panicum sanguinale* L. (*Digitaria sanguinalis*), as stated by Elliott and Michaux.

*serotina* 2. culmo decumbente laevi subtereti; foliis collo et fauce villosis; spica composita spiculis secundis erectis linearibus; dentibus *trifloris* alternis; floribus omnibus pedicellatis:

No specimen in herbarium. Taken up by Michaux under *Digitaria*. Walter's description does not distinguish clearly between this and the preceding, the two points brought out not being satisfactory, — flowers in threes, and all pedicellate, instead of twos, and one of them sessile. However, these two species are the only creeping *Digitarias* found commonly in the Carolinas.

[P. 77] *villosa* 3. culmo erecto, foliis ad medium usque villosissimis, panicula terminali composita spicis secundis alternis, dentibus bifloris, floribus subhirsutis.

The specimen in the herbarium consists of several leaves and a panicle. The leaves are narrow and villous. The glumes, especially the narrow lower one, are somewhat villous. This is what has been confused with *P. filiforme* L. but is distinguished by the villous leaves and the elongated spikes of more pubescent spikelets. Michaux and Pursh refer this to *Digitaria pilosa* Michx.

36. DACTYLIS. Cal. 2-valvis, compressus; altera valvula majore carinata.

*cynosuroides* 1. spicis sparsis secundis *scabris*, calycibus unifloris.

The specimen in the herbarium is *Spartina polysta-*



*chya* Willd. Walter inserts "calycibus unifloris" in place of "numerosis" in Linnaeus' description.

*maritima* 2. spicis approximatis secundis *glabris*, calycibus unifloris.

Probably *Spartina stricta* Roth (*S. glabra* Muhl.) as indicated by Muhlenberg.

37. AGROSTIS. Cal. 2-valvis, uniflorus, corolla paulo minor. Stigmata longitudinaliter hispida.

*indica* 1. panicula contracta mutica, racemis lateralibus alternis erectis.

*virginica* 2. panicula contracta conferta mutica, foliis involuto-subulatis rigidis extantibus, *paniculis saepe fuligineis*.

These two species are doubtless correctly identified with the Linnaean species as indicated by Elliott. In both cases the descriptions are somewhat changed from those of Linnaeus. These species are now included in *Sporobolus*.

38. STIPA. Cal. 2-valvis, uniflorus. Cor. valvula exteriore arista terminali, basi articulata.

No specimen of *Stipa* in the herbarium.

*avenacea*?  
1. aristis nudis longis, calycibus semen aequantibus, pedunculis longis sparsis unifloris, seminibus basi pungentibus.

This is referred by Michaux to his *S. barbata*, by Pursh to *S. bicolor* Vahl, and by Elliott to *S. avenacea* L., which latter identification is probably correct. Linnaeus' description is somewhat altered.



- [P. 78] *villosa* 2. aristis basi villosis, calycibus villosis, floribus paniculatis, pedunculis longis.

Elliott suggests that this is *Andropogon nutans* L. The description applies to this species very well, although the awn is scarcely villous at the base nor are the empty glumes conspicuously villous. The sterile pedicels are, however, villous.

- diffusa* 3. aristis nudis, panícula diffusa, floribus parvis.

Elliott refers this doubtfully to his *Agrostis sericea* (*Muhlenbergia capillaris* Trin.). It probably is this species, which is common in that region.

- spicata?* 4. aristis nudis, receptaculo elongato in spicam dentibus bifloris plumosis, floribus alternis muticis, alternis aristatis; calycibus alternis concavis, alternis convexis.

This may be *Andropogon tener* Kunth, though the spike is not plumose. It would appear to be an *Andropogon* from the spikelets in pairs, one awned and one awnless.

39. AIRA. Cal. 2-valvis, 2-florus. Flosculi absque interjecto rudimento.  
*purpurea* 1. culmo erecto; foliis subulato-setaceis; panícula sparsa, floribus purpureis; corollae glumis, alia plana bifida nervo aristata, alia integra plumosa extus concava.

No specimen in herbarium. The name is used by Pursh and Elliott. It is *Triplasis purpurea* Chapm.



aegilopsoi- spicis secundis; corollarum glumae valvula  
des 2. altera ovata, acuminata, altera columnari,  
obtusa.

The description applies very well to *Chloris*. There is a specimen of *Chloris petraea* in Walter's herbarium, consisting of the upper part of a culm, one leaf and four spikes. This is labeled "Aegilops an Aira?" The last word is scarcely decipherable, but I take it to be as above.

40. MELICA. Cal. 2-valvis, 2-florus. Rudimentum floris inter flosculos.

No specimen in herbarium.

altissima 1. petalis imberbibus, panicula ramosissima, floribus subacutis.

mutica 2. petalis imberbibus, panicula laxa pauciflora, floribus magnis muticis obtusis.

There is but one species of *Melica* growing in the Carolinas. Whether Walter describes two forms of this, or whether one of them may be a plant of some other genus, I am unable to determine. Pursh, Elliott and Michaux refer *M. mutica* Walt. to *M. glabra* Michx. Michaux also refers *M. altissima* Walt. to this species, while Pursh refers it to his *diffusa*, which is probably the same species. It is possible that *Festuca nutans* is the plant which Walter has described under *M. altissima* (a European species). To Linnaeus' description of *M. altissima* Walter adds "floribus subacutis." Elliott states that he has a variety from Columbia "with the leaves pubescent, the flower evidently smaller, the valves more acute, less membranous at the summit, and handsomely spotted with purple. It



is probably the *M. altissima* Walt. but it has scarcely character enough for a distinct species."

- [P. 79] 41. *CENCHRUS*. Involucrum echinatum biflorum.  
*carolinianus* spica glomerata, glumis globosis muricato-  
 1. spinosis laevibus.

There is no specimen of this in the herbarium, but there is no reason to suppose that it is not *C. tribuloides* L. except that the latter is described as having hirsute glumes.

42. *UNIOLA*. Cal. multivalvis, valvis ventricos-subulatis,  
 spicula ovata, compressa, carinata.  
 paniculata 1. paniculata, spiculis ovatis.

The specimen in the herbarium consists of a panicle and two leaves. It is *U. paniculata* L., the description of which Walter copies.

- spicata 2. panicula coarctata spiculis 3 ad 5-floris, fol.  
 involutis rigidis.

No specimen in herbarium. There seems to be no doubt that this is *Distichlis spicata* Greene. Linnaeus' description of *U. spicata* has been altered by Walter

43. *BRIZA*. Cal. 2-valvis, multiflorus. Spicula disticha.  
 Valvulis cordatis obtusis: interiore minuta.

No specimen in herbarium.

- caroliniana* panicula decomposita, paniculis partialibus  
 1. ramosis, spiculis cordato-lanceolatis, flos-  
 culis quindecim. *Rami breves. Spiculae vix tremulae.*



Probably *Eragrostis major* Host (*Briza Eragrostis* L.) as identified by Pursh.

virens? 2. spiculis ovatis, calyce flosculis (7) aequali,  
pedunculis sublongis.

Pursh takes up this name from the description, not having seen the plant. It may be a *Panicularia*, e. g. *P. obtusa* Kuntze, which, however, is scarcely common so far south. It might be *Uniola latifolia* Michx., but the pedicels ("pedunculis"?) of this species are quite long instead of "sublongis." Walter has added to Linnaeus' description the words "pedunculis sublongis."

44. POA. Cal. 2-valvis, multiflorus. Spicula subovata;  
valvulis margine scariosis acutiusculis.

No specimen in herbarium.

annua 1. panicula brevi diffusa angulis rectis, spiculis  
obtusis, culmo obliquo compresso.

Probably *P. annua* L. Walter has merely inserted the word "brevi" in Linnaeus' description.

*simplex* 2. panicula diffusa, culmo erecto *angulato*,  
spiculis remotis trifloris, caly- [P. 80]  
cibus inferioribus unifloris, foliis collo to-  
mentosus.

Agrees well with the description of *Poa hirsuta* Michx. (*Eragrostis hirsuta* Michx., not *Eragrostis simplex* Scribn.) as referred by Elliott.

flava 3. panicula diffusa, spiculis ovato-oblongis niti-  
dis, floribus subobtusis.

The description agrees very well with that of Grono-



vius for the plant named by Linnaeus *Poa flava* (*Triodia cuprea* Jacq.), but the latter seems to be included by Walter with *P. pratensis*. I am unable to suggest just what Walter's species is. Walter has used Linnaeus' description, adding "floribus subobtusis."

glomerata 4. panicula coarctata longa, spiculis sub 8-floris glomeratis, culmo erecto.

This is referred by Elliott to his *Poa conferta* and transferred to *Eragrostis* by Dewey as *E. glomerata* (Walt.) Dewey. The description agrees well except "spiculis glomeratis." The spikelets are certainly not glomerate, a character which seems to have attracted Walter's attention, judging from the specific name. The panicle is often contracted and more or less interrupted at base, which may have suggested *glomerata*.

*Eragrostis*? 5. panicula subverticillata, pedicellis flexuosis, spiculis decemfloris lanceolatis serratis, confertis, foliis longis angustis collo villosis, culmo suberecto.

This is probably *Eragrostis pilosa* Beauv., since the plant which Elliott describes under the name of *Poa Eragrostis* is *E. pilosa* (*E. Purshii* Schrad.), as shown by Elliott's herbarium.

amabilis? 6. panicula diffusa virgata, ramis nutantibus ramulo uno alterove, spiculis lanceolatis remotis quindecimfloris.

Probably *Eragrostis nitida* (Ell.) Chapm., although Elliott and Muhlenberg refer it to *Poa refracta* Muhl. and Pursh to his *P. spectabilis*. The 15-flowered spikelets refer better to *nitida* than to *spectabilis* (*pectinacea*).



*P. amabilis* L. is an Indian species. The Linnaean description was not used by Walter.

capillaris 7. panicula laxa patentissima, culmo ramosissimo, pedicellis praelongis, spiculis ovatis 3 s. 4-floris, culmo sesquipedali.

Agrees well with *Eragrostis capillaris* Nees. The Linnaean description of *P. capillaris* was not used by Walter.

compressa 8. panicula secunda coarctata, culmo obliquo compresso, flosculis saepius ternis.

Probably *Poa compressa* L., to which description Walter has added, "flosculis saepius ternis."

pratensis 9. panicula longa diffusa, spiculis quinquefloris glabris ovatis, culmo erecto tereti 4-pedali.

Agrees well with *Triodia cuprea* Jacq. (*Poa quinquefolia* Pursh; *P. seslerioides* Michx.), to which it is referred by Elliott. Walter has used Linnaeus' description but has inserted "longa" and added "4-pedali," thus making considerable change.

crinata 10. panicula spicata, spiculis quadrifloris, pedunculo longioribus.

This is stated by Elliott to be *Poa rigida* L. (*Scleropoa rigida* Griseb.), which is introduced in South Carolina, "common around Beaufort."

45. FESTUCA. Cal. 2-valvis. Spicula oblonga teretiuscula. [P. 81]  
Glumis acuminatis.

No specimen in the herbarium.



- quadriflora* 1. panicula subcoarctata, spiculis quadrifloris,  
floribus seta longa terminatis.

Probably *Festuca sciurea* Nutt. Michaux and Elliott erroneously refer this to *F. myuros* L., for which both of them mistook *F. sciurea* Nutt.

- octoflora* 2. panicula erecta, spiculis octofloris acuminatis.

Michaux refers this doubtfully to *F. bromoides* L. The name has been taken up to replace the later *F. tenella* Willd.

- multiflora* 3. repens, paniculis erectis ovatis, spiculis 8 ad 40-floris, acutis, foliis angustis, acutis, fauce subplumosis.

Probably *Leptochloa fascicularis* (*Festuca polystachya* Michx., *F. procumbens* Muhl.) as indicated by Elliott, who remarks that the descriptions do not agree exactly.

46. BROMUS. Cal. 2-valvis. Spicula oblonga teres disticha, arista infra apicem.  
*ciliatus* 1. panicula nutante foliis utrinque vaginisque subpilosus, glumis corollinis valde pilosis, calycinis nudis.

No specimen in the herbarium. The description agrees with the plant now known by this name. To Linnaeus' description Walter has added all after "glumis" in place of "ciliatis."

47. AVENA. Cal. 2-valvis, multiflorus, arista dorsali contorta.  
*caroliniana* 1. panicula attenuata.



No specimen in the herbarium. Probably *Trisetum Pennsylvanicum* B.S.P. (*Avena Pennsylvanica* L.). Pursh refers it to *Avena palustris* Michx., which is the same as *A. Pennsylvanica* L. Walter has cut out of Linnaeus' description of *A. Pennsylvanica* all after *attenuata*.

48. ARUNDO. Cal. 2-valvis, brevis, inaequalis. Cor. 2-valvis: valvis basi ventricosus, apice acutis (*flosculis nec lana cinctis*).  
*gigantea* 1. calycibus 5 ad 10-floris, panicula laxa; fol. fauce setosis; stipulis internodiis *dimidio brevioribus*, marcescentibus.

There is a specimen in the herbarium consisting of a shoot with two mature leaves, the sheaths bearded at the throat. It is *Arundinaria gigantea* Nutt.

- tecta* 2. *culmis tectis* stipulis internodios superantibus, foliis fauce setosis.

No specimen in the herbarium. Is *Arundinaria tecta* Muhl.

49. HORDEUM. Cal. 2-valvis, lateralis, uniflorus, ternus. [P. 82]  
 nodosum? flosculis lateralibus masculis *setis brevibus*,  
 1. involucellis setaceis laevibus. Setis longitudine florum.

The specimen in the herbarium is *Elymus Virginicus* L., the long-awned form with somewhat hairy flowering glume. Linnaeus' description of *H. nodosum* has been altered.

50. CYNOSURUS. Cal. 2-valvis, floribus variis. Receptaculum proprium unilaterale.



- indicus 1. spicis digitatis ternis seu quaternis, spiculis quadrifloris alternis, culmo stricto declinato, fol. longis intus subpilosis.

The specimen in the herbarium is *Eleusine indica*. Linnaeus' description has been much altered.

- uniflorus* 2. spicis digitatis quaternis patulis secundis subbrevibus, calycibus acutis alternis *unifloris* sessilibus, culmo geniculato repente laevi internodiis brevibus, *foliis alternis* brevibus subpilosis acutis, ramis suberectis pedunculo sublongo terminatis.

I think this is *Cynodon dactylon* Pers. There is no specimen in the herbarium.

51. ELYMUS. Cal. lateralis multiflorus bivalvis aggregatus.  
*carolinianus* spica erecta laevi, spiculis trifloris, flore  
 1. intermedio pedicellato sterili, involucris spiculas aequantibus, aristis longitudine florum.

No specimen in the herbarium. Elliott refers this to *Elymus Virginicus* L.

#### MONOECIA. TRIANDRIA.

- [P. 225] 358. COIX. Masc. in spicis remotis. Cal. gluma 2-flora mutica. Cor. gluma mutica.  
 Fem. Cal. gluma biflora. Cor. gluma mutica.  
 Stylus 2-partitus. Sem. calyce ossificato tectum.  
*Lacryma* 1. seminibus ovatis.

No specimen in herbarium, but this is doubtless *C. Lacryma* L., the description of which Walter uses.



## POLYGAMIA. MONOECIA.

403. ISCHAEMUM. Hermaphrod. Cal. gluma communis [P. 249]  
 2-flora. Cor. 2-valvis. Stam. 3. Styli 2.  
 Sem. 1.  
 Mas. Cal. et Cor. ut in priore. Stam. 3.

No specimen in herbarium.

- secundatum* 1. spicis *subsecundis*, floribus receptaculo nidu-  
 lantibus.

*Stenotaphrum secundatum* Kuntze, to which it is referred by Elliott and Pursh (*Rottboellia dimidiata*).

- scariosum* 2. spicis filiformibus, floribus acuminatis exstantibus laevibus.

Probably *Rottboellia rugosa* Nutt.

- glabrum* 3. spicis teretibus glabris nitidis, floribus subreconditis, sem. magnis.

*Tripsacum dactyloides* L. as indicated by Pursh.

404. AEGILOPS ? Hermaphrod. Cal. gluma subtriflora, cartilaginea, arista dorsali horizontali, valvis inaequalibus. Cor. gluma arista sub apice erecta simplici. Stam. 3. Styli 2.  
 Sem. 1.  
 Mas. Cal. gluma eadem. Cor. ut in priore. Stam. varia.

- aromaticum* 1. spica secunda, culmis erectis, glumis quadrifloris.

The specimen in the herbarium is *Campulosus aromaticus*.



*icus* Scribn. (*Ctenium Americanum* Spreng.) as indicated by Elliott and Pursh under other names.

*saccharinum* spica secunda, culmis decumbentibus, glumis  
2. trifloris.

The specimen in the herbarium is *Dactyloctenium Aegyptium* Willd.



## A SYSTEMATIC REVISION OF THE GENUS *CEREUS* MILL.

BY ALWIN BERGER.

Most species of *Cereus*, etc., have been named and described by their authors from small specimens in cultivation. Neither flower nor fruit of many of them has until now been known. Whilst this state of things lasted, a real botanical treatment of the genus proved to be an impossibility. Every author who had to deal with the genus felt obliged, for the sake of bringing some order into the arrangement, to make it entirely dependent upon external characters of the habitus of the plants. Schumann, the most recent monographer of Cactaceae, did likewise, grouping the species according to the size, form and color of their stems into thirty "Reihen," to which he added in his "Nachträge" two more.

Engelmann was the first who made the flower and fruit the chief character to depend upon, when he founded his genus *Echinocereus*.\* This he afterwards reunited† with *Cereus* together with *Lepidocereus*, *Eucereus* and *Pilocereus*, as subgenera. *Pilocereus* was established as a genus by Lemaire, and *Cephalocereus* by Pfeiffer. In their original form these two genera were identical. In 1860 Lemaire published *Aporocactus*, and in 1861 *Cleistocactus*. Philippi, the famous explorer of the Chilian flora, founded at the same time his genus *Eulychnia*. In 1897 Console's *Myrtillocactus*, founded upon *Cereus geometrizzans*, was published. But these genera found little favor with other botanists.

Since then many *Cerei* cultivated in European gardens

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\* Engelmann in Wislitz. Tour North. Mexico. 91. (1848).

† Engelmann in Cactaceae of Pl. Fendlerianae (1849), Mem. Amer. Acad. 4: 50; Coll. Works. 114.



have flowered, and their descriptions were collected by Schumann and incorporated in his *Monographia* or successively published in the *Monatsschrift für Kakteenkunde* by various cultivators of cacti.

A thorough study of the plants in question and their various peculiarities has shown me that there exist *a number of well defined and most natural subgenera*.

The subgenera here proposed are such as can be established with our present knowledge. Some may be imperfect, like all first attempts. With the extending exploration of Central and South America, and with our ever-increasing knowledge, corrections will of course be made.

My attention was first drawn to this by observing several *Cerei* at La Mortola in Sir Thomas Hanbury's famous gardens, and afterwards while arranging their flowers in my herbarium. To my first obvious observations facts were constantly being added until the whole scheme was worked out. There exists a far greater variety in the characters of flowers and fruits than I at first supposed.

It is a well-known fact that many connecting forms exist in Cactaceae, even between the greater genera. On account of this Dr. Kuntze\* reunites most of them under one single genus, *Cactus*. There can be no doubt that connecting forms will also be found between the subgenera, but this cannot affect the fact of their existence. Of course these subgenera may be considered distinct genera by those who accept the new genera of Crassulaceae recently published by Britton and Rose.† Most of these subgenera have distinct geographical areas.

I am fully convinced that Engelmann was perfectly right to include *Pilocereus* as a subgenus under *Cereus*. As it now stands, it is an artificial genus, which required a

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\* Kuntze & Post, *Lexicon Generum Phanerogamarum*. (1904).

† N. L. Britton and J. N. Rose, *New or noteworthy North American Crassulaceae*. *Bull. New York Bot. Gard.* 3 : 1-45. (1903).



critical revision. Everybody will perceive this who reads carefully the descriptions of the flowers of the plants at present united under *Pilocereus* by Schumann and Weber. These flowers differ from each other in important details. There remains nothing to maintain the genus in its old form, except the hairy areoles of the stems, a character which is not even the same in all. The greater number of these plants are rare in gardens, and many have never flowered, so that our knowledge of them is very insufficient and does not permit any further critical study.

Equally with *Pilocereus*, *Cephalocereus* of Pfeiffer and Schumann has also to be reunited with *Cereus*, as it is well connected by two other subgenera with the rest of the genus.

Before speaking of each subgenus, I give an analytical synopsis, which will help the reader to understand the matter at once.

#### SYNOPSIS OF THE SUBGENERA OF *CEREUS*.

I. Flowers rising from a distinct cephalium.

I. *CEPHALOCEREUS* Pfeiff.

II. Flowers not from a cephalium, several from one and the same areole.

A. Areoles of the flowering part differing from the rest, more closely set, with numerous long setulose bristles; flowers reddish or yellowish, stamens included; fruit scaly.

II. *LOPHOCEREUS* A. Berg.

B. Areoles of the flowering part not different, with spines, but without setulose bristles; flowers white, stamens exerted; fruit smooth.

III. *MYRTILLOCACTUS* Console.

III. Flowers single from the areoles.

A. Flowers actinomorphic.

1. Flowers short, more or less campanulate or tubular. (See also Nos. XV and XVI, with short flowers!)

a. Flowers tubular.

\* Ovary and tube with wool and hairs or bristles.

† Ovary densely woolly; petals short, spatulate; fruit very woolly and prickly.

IV. *PACHYCEREUS* A. Berg.



†† Flowers hairy; style exserted; fruit hairy; plants covered with long hairs.

V. OREOCEREUS A. Berg.

\*\* Ovary and tube naked or the ovary with some very short wool or a few stiff hairs.

† Flowers larger, greenish white; plants very tall.

VI. LEPIDOCEREUS Engelm.

†† Flowers small, reddish or brown; plants not gigantic.

VII. STENOCEREUS A. Berg.

b. Flowers campanulate.

\* Ovary and tube scaly, often hairy and setuliferous, style short, deeply divided into numerous stigmata; fruit woolly, setuliferous or prickly.

VIII. EULYCHNIA Phil.

\*\* Ovary and tube with very few scales, naked; style often much exserted, with short stigmata; fruit smooth.

IX. PILOCEREUS A. Berg.

2. Flowers larger, more or less funnel-shaped; stamens generally very numerous, inserted along the tube in two groups, the uppermost adnate at the base of the petals, radiating, the lower ones free and declining.

a. Flowers with a very few minute scales, soon falling off neatly above the ovary; fruit naked, crowned by the remaining recurved style.

X. PIPTANTHOCEREUS A. Berg.

b. Flowers with larger scales or hairs and bristles, perianth after flowering drying and finally deciduous or remaining; fruit never naked.

\* Scales of ovary and tube foliaceous, increasing in size with the growing fruit, in their axils neither wool, hairs nor spines; stems triangular, sarmentose, rooting.

XI. HYLOCEREUS A. Berg.

\*\* Scales of ovary and tube not foliaceous, always with wool, hairs or bristles.

† Tube of perianth with hairs or wool, but not armed with bristles.

‡ Ovary and tube without bristles, but more or less densely covered with long curled hairs; fruit not colored, unarmed, hairy.

XII. TRICHOCEREUS A. Berg.

‡‡ Ovary often with a few spines and with copious white wool, also the tube woolly in the axils of the scales; fruit red, often prickly, pulvilli more or less raised.

XIII. ERIOCEREUS A. Berg.



- C. (Cephalocereus) columna-Trajani* Karw. l. c. 198. — Mexico.  
*C. (Cephalocereus) macrocephalus* (Web.) A. Berg. l. c. 197. — Mexico.  
*C. (Cephalocereus) melocactus* (Vell.) A. Berg. l. c. 199. — Brazil.  
*C. (Cephalocereus) senilis* DC. l. c. 201. — Mexico.

## II. LOPHOCEREUS A. Berg.

Areoles of the flowering part of the branches differing from the rest, more closely set, with short white wool and long stiff setulose bristles. Flowers small (4 cm.), several from one and the same areole; ovary roundish with a few naked scales; tube funnel-shaped, with several deltoid-lanceolate scales; perianth leaves not very numerous, exterior lanceolate, acute, interior ones oblong, obtuse, spreading, reddish or yellowish; filaments inserted below the middle of the tube, not very numerous, not exceeding the petals; style longer than the stamens, with 5-6 short stigmata. Berry ca. 1 cm. in diameter, red, with a few broadly deltoid scales; seeds comparatively large, slightly keeled, with shining black smooth testa. — *Plate 8, f. 4-8.*

*Cereus Schottii* Engelm. is the type of this subgenus. When the plant is old and about to flower, the areoles grow closer together and produce a profusion of long setulose bristles, which give the plant a very curious aspect. This species has been considered to be a *Pilocereus*, but the bristles are much unlike the hairs of this genus; besides, the flowers are very different, and in *Pilocereus* they are always single.

Schumann\* was inclined to unite this plant with *Myrtillocactus*, but I think it better to create a proper subgenus, on account of the great difference in the general appearance of the plant, the larger reddish flowers with enclosed stamens, and the scaly fruit.

According to Mr. Brandegee, however, there occurs a variety of *C. Schottii* Engelm. near Todos Santos, in Baja California, which has not such setulose bristles, but only the small spines of the juvenile state. When better known, this plant will perhaps form a transition from this subgenus to *Myrtillocactus*.

\* Nachtr. 64.



†† Tube and ovary with hairs or wool, but always with a greater or less number of often setulose bristles; fruit aculeate.

‡ Flowers large, with a long and slender tube.

XIV. *EUCEREUS* Engelm.

†† Flowers short.

Stems slender, much elongated.

XV. *LEPTOCEREUS* A. Berg.

Stems short, stigmata invariably green.

XVI. *ECHINOCEREUS* Engelm.

B. Flowers zygomorphous.

1. Perianth narrowly tubular, curved in form of an  $\curvearrowright$ , with small and numerous appressed scales; ovary and tube woolly; petals small. : : : XVII. *CLEISTOCACTUS* Lem.

2. Perianth tubular, slightly bent upwards above the ovary in form of an  $\surd$ , with patent sepaloid and petaloid, rather broad perianth leaves; ovary with stiff hairs.

XVIII. *APOROCACTUS* Lem.

I. *CEPHALOCEREUS* Pfeiffer in Otto & Dietr. *Allgemeine Gartenztg.* 6: 142. (1838). — K. Sch. in Engler & Prantl, *Nat. Pflanzenfam.* III. 6a: 181.

This subgenus is characterized by the formation of a cephalium, — that is to say, the floriferous region of the plant is differentiated from the rest. The ribs are divided into little isolated mamillae surrounded by long hairs and spines. The flowers, which are small, rise singly from the top of the mamillae.

The reader will be best informed about this subgenus if he looks at plate 3, and pages 92–93 of K. Goebel's excellent *Pflanzenbiologische Schilderungen*, I Theil. (Marburg, 1889.)

Our knowledge of these plants is lamentably poor, and material for further investigation is greatly needed.

The following five species, all tall arborescent plants from Mexico and Brazil, are enumerated by Schumann: —

*Cereus (Cephalocereus) chrysomallus* Hemsley. — K. Schumann, *Monographia*. 200.\* — Mexico.

\* As I do not wish to give full references to literature, I have thought it advisable to mention only K. Schumann's *Monographia Cactacearum*, 1899, where all references can easily be found.



Very likely also *Pilocereus scoparius* Pos., which is said to be closely related to *C. Schottii*, belongs here.

I have a very fine dried specimen of *C. Schottii*, which I received from Mr. F. De Laet, of Contich. It has 8 ribs, the areoles very closely set, and grayish tortuose bristles, which are flexible, not very pungent and spirally twisted just as the seta of many mosses are.

*Cereus (Lophocereus) Schottii* Engelm. l. c. 171. — North Mexico, Baja California, Arizona.

*C. (Lophocereus?) scoparius* (Poselg.) A. Berg. l. c. 179. — Mexico.

*C. (Lophocereus?) Urbanianus* (K. Sch.) A. Berg. l. c. 193. — Guadeloupe Island.

### III. MYRTILLOCACTUS Console in Bollet. Reg. Ort. Bot. Palermo. 1: 10. (1897).

Flowers very small (2 cm.), several (5-9) from one and the same somewhat enlarged and woolly areola; ovary naked; tube short funnel-shaped with a few minute scales; perianth leaves few, sepaloïd brownish, petaloïd white, linear-spatulate; filaments inserted near the base of the petals, exserted. Berry small, smooth, reddish brown.

*Cereus (Myrtillocactus) geometrizans* Mart. K. Sch. Monogr. 104. — Mexico, Baja California.

This plant is very common in cultivation, but generally in small specimens. It forms a small richly branched tree. A large plant flowers and fruits annually in the Botanic Garden at Palermo, upon which Console founded his genus. Also a small cutting flowered and fruited once at La Mortola.

The flowers, in size and color, resemble orange blossoms. The fruit is sold in Mexico. It is called Garambullos and is eaten raw with sugar or preserved.

### IV. PACHYCEREUS A. Berg.

Ovary ovate to globose, densely covered with small imbricated scales and woolly hairs and bristles; petaloïd perianth leaves short, spatulate, little expanded; stamens numerous, inserted along the tube; style not exserted. Fruit globose, densely covered with wool and numerous long, thin bristles. *Plate 1.*



Gigantic species. Some of these were wrongly included under *Pilocereus*. Similar to *Lepidocereus*, but easily distinguished by flower and fruit.

*Cereus (Pachycereus) Pringlei* Wats. l.c. 71. — Sonora, California, etc.

*C. (Pachycereus) pecten aboriginum* Engelm. l. c. 75. — Mexico, Sonora, Baja California.

*C. (Pachycereus) Thurberi* Engelm. l. c. 73. — Sonora, North Mexico.

*C. (Pachycereus) fulviceps* (Web.) A. Berg. l. c. 176. — Mexico.

*C. (Pachycereus) Orcuttii* Kath. Brand. l. c. Nachtr. 24. — Baja California.

*C. Thurberi* Engelm. (Cact. Bound. 44) has been considered by Engelmann as a *Lepidocereus*, but no doubt it is more closely related to *C. Pringlei* than to *C. giganteus*. The fruit is prickly, although the bristles soon fall off.

The flowers of *C. Pringlei* are covered with a fine and dense velvety yellowish tomentum. They are very unlike all other cactus flowers. The fruit of *C. Pringlei* is covered with a great number of neat balls of wool, which are somewhat deciduous. In *C. pecten aboriginum* the spines are more persistent, and for this reason the natives use them as hair brushes.

The drawing of the flower of *C. Pringlei* was prepared from a specimen kindly sent me by Herrn Geheimrat Prof. Dr. A. Engler, Director of the Royal Botanic Garden and Museum, Berlin.

## V. OREOCEREUS A. Berg.

Ovary roundish, like the tube covered with fleshy acute imbricated scales, with long woolly hairs from their axils; sepaloid perianth leaves narrow, acute, petaloid ones narrowly spatulate, slightly expanded; stamens very numerous, inserted along the tube and at the bottom of it, as long as or longer than the petals; style much exerted, with about 8 short stigmata. Fruit globose, scaly and hairy (dried remains of the perianth persistent?). — *Plate 2*.

*Cereus (Oreocereus) Celsianus* (Lem.) A. Berg. l. c. 180. — Andes of Bolivia.

*Oreocereus* forms part of the old genus *Pilocereus*.



*Cereus Celsianus* A. Berg. (= *Pilocereus Celsianus* Lem.) is a very stately plant, stout and vigorous, covered with long white hairs. There exist many varieties of it, chiefly differing in the spines and the more or less dense covering of hairs. It is quite hardy on the Riviera. There is a fine plant at La Mortola, from which the flower represented in plate 2 has been drawn.

It is very likely that the old *Cereus lanatus* P. DC. (*Cactus lanatus* HBK.) is also an *Oreocereus*. It has never flowered in Europe, and from the original description this is not quite evident. It is much grown in gardens as *Pilocereus Dautwitzii* Fr. A. Haage, and is a very fine plant, densely involved in long white hairs.

VI. *LEPIDOCEREUS* Engelm. Syn. of the Cact. of the Terr. of the U. S. etc. Proc. Am. Acad. 3. (1856); Coll. Works. 140.

Flowers rather large, white; ovary oblong, with deltoid imbricated scales bearing in their axils very little short wool, and sometimes a few deciduous bristles; tube funnel-shaped with similar but gradually increasing scales, the inferior only woolly; sepaloïd perianth leaves obovate, obtuse, green, petaloïd ones white, recurved spatulate and very obtuse or notched; filaments very numerous, shorter; style with 12-18 stigmata. Fruit obovoid or pear-shaped, with small and remote deltoid scales, in their axils scarcely woolly, dried remains of the flower deciduous; pulp red; seeds small, very numerous, shining, black.

*Cereus (Lepidocereus) giganteus* Engelm. l. c. 76. — Arizona, Sonora, etc.

Engelmann states that *Cereus chilensis* Colla also belongs to his subgenus *Lepidocereus*, but according to the description of this species given by Schumann it is a *Trichocereus*.

The subgenus as established by Engelmann comprises also *C. Thurberi*, which I include under *Pachycereus*. There is no other *Cereus* known to me of which the flowers and fruits resemble those of *C. giganteus*.



The figure given in the Botanical Magazine, pl. 7222, differs somewhat from that of Engelmann, the latter having apparently been prepared from a dried specimen.

This gigantic plant has often been figured and described and has in later years frequently been introduced. It has flowered only once in Europe, in the Royal Botanic Gardens at Kew, in July, 1891. In its native land the fruits are much valued as food and the Indians preserve them like dried figs.

## VII. STENOCEREUS A. Berg.

Flowers small (4-8 cm.), tubular, reddish or usually brownish; ovary globose with deltoid scales, naked or with a few setulose hairs and little wool; tube with elongate naked appressed scales; sepaloid and petaloid perianth leaves small, ovate-lanceolate; filaments little shorter, numerous, inserted in the middle of the tube, forming there a distinct ring; styles not exerted, with about 6-8 short stigmata. Fruit globose, (3-4 cm.), brownish, with reddish pulp. — *Plate 3.*

Chiefly Mexican species of columnar or frutescent growth. Type: *Cereus stellatus* Pfeiff.

*Cereus (Stenocereus) Chiotilla* Web. l. c. 83. — Mexico.

*C. (Stenocereus) Dumortieri* Salm. l. c. 92. — Mexico.

*C. (Stenocereus?) marginatus* DC. l. c. 90. — Mexico.

*C. (Stenocereus) sonorensis* Runge. l. c. Nachtr. 27 (sub *C. stellatus* Pfeiff.!) — Sonora.

*C. (Stenocereus) stellatus* Pfeiff. l. c. 79. — Central Mexico.

The flowers of this subgenus are small and of a dull tint. The inner petals only are somewhat brighter. In some species (*C. stellatus*, *sonorensis*, *Chiotilla*) the flowers come from the highest areoles of the stems; in *C. Dumortieri* and *C. marginatus* they are lateral. In the latter they are said to come sometimes in pairs from one areole.

*C. stellatus* Pfeiff. flowers every year at La Mortola. *Cereus sonorensis* Runge is a distinct species, although Schumann united it with the first. *C. Alamosensis* Coult. is the juvenile form of the latter according to Mr. Weingart, of Nauendorf.



The flowers of *C. stellatus* Pfeiff. open fully only for a very short time. I have seen them open on a dark morning for about two hours, but otherwise failed to observe them expanded, and for a long time I believed them to be cleistogamous. Soon after flowering they fell off, producing no fruit. The lower part of the tube secretes much nectar, so much that it finally reaches the stamens or even fills the whole flower.

*Cereus Aragoni* Web., from western Costa Rica, seems also to belong to this subgenus according to the description of the flower given by Weber.\* This plant is now cultivated in some gardens in Europe, and I am informed by Mr. Weingart, of Nauendorf, that it seems closely allied to *C. pruinatus* Otto and *C. eburneus* Salm. If this is true, these two species also may probably belong here. *C. resupinatus* Salm has also been united by Schumann with *C. eburneus*, but this is certainly a mistake. Mr. Weingart, of Nauendorf, possesses this plant, which agrees exactly with the figure (no. 93) in Förster-Rümpfer.

It is not clear from the description whether *Pilocereus Tetetzo* Web. (K. Sch. l. c. 175) is also a *Stenocereus*.

#### VIII. EULYCHNIA Phil. Flor. Atac. 23. pl. 11a. (1861).

Flowers campanulate with a short and broad tube; ovary globose or turbiniform, like the tube with numerous deltoid or acute scales, often densely covered with wool, setulose hairs or bristles; sepaloid and petaloid perianth leaves small, reddish or white; filaments numerous, little shorter; styles deeply divided into numerous stigmata. Fruit globose, more or less woolly, setuliferous or prickly. — *Plate 4, f. 1.*

Frutescent or columnar species from the Andes of South America.

Philippi has given no clear definition of his genus. He founded it upon the very setuliferous flower of *C. breviflorus* K. Sch. and afterwards added to it two other species

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\* Les Cactées de Costa Rica. Bull. Mus. d'Hist. Nat. Paris. No. VI. 455. (1902).



(*C. acidus* K. Sch. and *C. castaneus* K. Sch.) which have not such setulose hairs. But if we take as principal characters the short flower with small sepals and petals and the deeply divided style, the genus of Philippi can be kept up for a certain number of Andean species.

But I am quite aware that in this form the subgenus *Eulychnia* is more artificial than natural. For instance, *C. macrostibas* A. Berg. differs greatly from the rest, especially by its enlarged and prolonged flowering areoles, which seem to form real "Kurztriebe." But the material at hand is so scanty that I must refrain from any further statement. I shall be very grateful if some botanist of South America will supply me with further information concerning any of these plants.

*Cereus macrostibas* A. Berg. was originally described by Schumann as a *Pilocereus*, and as such it is another heterogeneous form of this conglomerate genus. The flowers are stated to be of the form of those of *C. Celsianus* A. Berg., but they differ in every possible way.

*Cereus aureus* K. Sch. was originally described by Pfeiffer as an *Echinocactus*. Indeed the short and campanulate flowers of *Eulychnia* are almost those of *Echinocactus*, and there remain only very faint distinctions between this subgenus of *Cereus* and *Echinocactus*. Generally in *Eulychnia* the petals are reddish or white, but in *C. aureus* they are golden yellow, hence it is probable that this may be better replaced in *Echinocactus*.

*Cereus breviflorus* K. Sch. has recently been collected by Dr. Otto Kuntze. His splendidly prepared specimens are now in the Royal Herbarium at Berlin, whence they were kindly lent me. The drawing was prepared from them. I am indebted to Mr. Stolp, of Santiago, Chile, for a photograph of the same plant.

The following species may be considered as belonging to *Eulychnia*: —



- Cereus (Eulychnia) acidus* K. Sch. l. c. Nachtr. 22. — Chile.  
*C. (Eulychnia?) aureus* K. Sch. l. c. 124. — Peru.  
*C. (Eulychnia) breviflorus* K. Sch. l. c. 58. Nachtr. 23. — Chile.  
*C. (Eulychnia) castaneus* K. Sch. l. c. Nachtr. 22. — Chile.  
*C. (Eulychnia) Dusenii* Web. Monatsschrift f. K. 1904: 68. — Patagonia.  
*C. (Eulychnia) erythrocephalus* (K. Sch.) A. Berg. l. c. 195. — Argentina.  
*C. (Eulychnia) hypogaeus* Web. l. c. 289. Nachtr. 38. — Chile.  
*C. (Eulychnia) iquiquensis* K. Sch. Monatsschrift f. K. 1904: 99. — Chile.  
*C. (Eulychnia?) macrostibas* (K. Sch.) A. Berg. Monatsschrift f. K. 1903: 168. — Peru.  
*C. (Eulychnia) melanotrichus* K. Sch. l. c. 71. — Bolivia.  
*C. (Eulychnia) patagonicus* Web. l. c. Nachtr. 61. — Patagonia.

## IX. PILOCEREUS A. Berg.

Flowers short and campanulate, of a dull color and disagreeable smell; ovary and tube nearly naked or with a very few scales; sepaloid and petaloid perianth leaves short, little expanded; stamens numerous, inserted along the tube, as long as the perianth; style very often much exerted, rarely not exceeding the perianth, with 5-10 or more short stigmata. Fruit globular, naked, crowned by the dried remains of the flower. — *Plate 4, f. 2-5.*

The name *Pilocereus* was originally employed for *Cephalocereus*. These were separated by Schumann, whilst *Pilocereus* was made the recipient of any strange-looking *Cereus*, especially of those with hairy areoles. By degrees *Pilocereus* has become a very heterogeneous and senseless genus.

I maintain the name, as it is so much in vogue among cactus growers, for those species having the characters above given. In this way the subgenus becomes a very natural one.

Most of these species have hairy areoles, and sometimes hairs of a beautiful silky white. Frequently the flowers are surrounded by a great brush-like profusion of such hairs. In some species the flowers are produced from one side of the stem only, and so the appearance of a cephalium is presented.



They are all columnar, curious-looking plants and general favorites of cactus growers, but fine specimens are nevertheless extremely rare.

According to their descriptions, the following species form this subgenus: —

*Cereus (Pilocereus) chrysacanthus* (Web.) A. Berg. l. c. 178. — Mexico.

*C. (Pilocereus) exerens* Link. l. c. 184. — Brazil.

*C. (Pilocereus) Hermentianus* Monv. l. c. 186. Nachtr. 66. — Haiti.

*C. (Pilocereus?) Hoppenstedtii* (Web.) A. Berg. l. c. 177. — Mexico.

*C. (Pilocereus) Houletii* (Lem.) A. Berg. l. c. 182. — Mexico.

*C. (Pilocereus) lanuginosus* Mill. l. c. 183. — West Indies.

*C. (Pilocereus) Royeni* Haw. l. c. 181. — West Indies.

*C. (Pilocereus) strictus* P. DC. l. c. 188. — West Indies, South America.

*C. (Pilocereus) Ulei* (K. Sch.) A. Berg. l. c. Nachtr. 66. — Haiti.

*Cereus Hoppenstedtii* A. Berg. was formerly included by Schumann in *Cephalocereus*. I have never seen its flowers. The plant resembles *Cereus senilis* DC. much more closely than any *Pilocereus*.

## X. PIPTANTHOCEREUS A. Berg.

Flowers naked, with a very few minute scales on the somewhat elongated ovary and scarcely any wool or hairs in their axils; tube elongated, funnel-shaped with a few remote obtuse scales, often slightly furrowed; sepaloid perianth leaves obtuse, the following acute; petaloid perianth leaves broader, acute, mostly white; stamens numerous in two groups; style as long or longer, with numerous stigmata; flowers large and showy, nocturnal, soon falling off a little above the ovary; style persistent. Fruit oblong or globose, naked, reddish, at the top deeply umbilicate, the remaining style bent downwards; pulp white; seeds numerous, with opaque, black, finely punctate testa. — *Plate 5, 6, 7, f. 1-4.*

Arborescent or frutescent species, natives of Atlantic tropical America from Argentina to the West Indies.

This is a very natural and easily recognizable subgenus. The perianths fall off, soon after flowering, a little above the ovary, as neatly as if they had been cut off. The style remains. The fruit is naked.



In drying, the flowers of *Piptanthocereus* invariably turn black, whilst others, for instance *Eucereus*, *Aporocactus*, etc., keep their beautiful colors for a long time in the herbarium. .

The following species belong here: —

- Cereus* (*Piptanthocereus*) *azureus* Parm. l. c. 118. — Southern Brazil.  
*C.* (*Piptanthocereus*) *Cavendishii* Monv. l. c. Nachtr. 40. — South America.  
*C.* (*Piptanthocereus*) *chalybaeus* Otto. l. c. 120. — Argentina.  
*C.* (*Piptanthocereus*) *coerulescens* Salm. l. c. 121. — Argentina.  
*C.* (*Piptanthocereus*) *Forbesii* Otto. l. c. 111. — Argentina.  
*C.* (*Piptanthocereus*) *euchlorus* Web. l. c. 84. — Brazil.  
*C.* (*Piptanthocereus*) *Hankeanus* Web. l. c. 88. — Argentina.  
*C.* (*Piptanthocereus*) *Hildmannianus* K. Sch. l. c. 110. — Brazil.  
*C.* (*Piptanthocereus*) *Jamacaru* DC. l. c. 112. — Brazil.  
*C.* (*Piptanthocereus*) *lamprospermus* K. Sch. l. c. Nachtr. 33. — Paraguay.  
*C.* (*Piptanthocereus*) *lepidotus* Salm. l. c. 109. — Cuba.  
*C.* (*Piptanthocereus*) *pachyrhizus* K. Sch. l. c. Nachtr. 33. — Paraguay.  
*C.* (*Piptanthocereus*) *paraguayensis* K. Sch. l. c. Nachtr. 34. — Paraguay.  
*C.* (*Piptanthocereus*) *Paxtonianus* Monv. l. c. 134. Nachtr. 40. — South America.  
*C.* (*Piptanthocereus*) *peruvianus* Mill. l. c. 113. — Brazil, W. Indies, Mexico.  
*C.* (*Piptanthocereus*) *phatnospermus* K. Sch. l. c. Nachtr. 43. — Paraguay.  
*C.* (*Piptanthocereus*) *Pitahaya* DC. l. c. 116. — Brazil, Uruguay.  
*C.* (*Piptanthocereus*) *Spegazzinii* Web. l. c. Nachtr. 42. — Paraguay.  
*C.* (*Piptanthocereus*) *stenogonus* K. Sch. l. c. Nachtr. 31. — Paraguay.  
*C.* (*Piptanthocereus*) *tetragonus* Haw. l. c. 86. — Brazil.  
*C.* (*Piptanthocereus*) *xanthocarpus* K. Sch. l. c. Nachtr. 32. — Paraguay.

The flower and large fruit of plate 6 are from the tall *Cereus* represented by the photograph of plate 5. This plant is one of the most remarkable specimens of this family on the Riviera. It stands in the garden of the Casino at Monte Carlo. Flowers and fruits were sent to me by the Director of this garden, Mr. Van den Daelen. The same plant has been figured in the *Monatsschrift für Kakteenkunde*, 1900, p. 7, under the name of *Cereus peruvianus*. At Monte Carlo it is named *Cereus validus* Haw.



The species of *Piptanthocereus* are however not enough known, and I cannot give exact names either of this plant or of the other which produced the smaller fruit shown in plate 7.

Mr. Weingart, of Nauendorf, has undertaken the task of studying the different species of *Cereus*, and, according to him, many of the species of older botanists, which were reduced to synonyms, will prove to be true species.

### XI. HYLOCEREUS A. Berg.

Flowers funnel-shaped, very large and showy, white or red; ovary and tube with more or less large, often foliaceous scales, without wool, hairs or spines; sepaloid and petaloid perianth leaves numerous; stamens numerous, in two groups; style with numerous stigmata. Fruit roundish, covered with large, often foliaceous scales; pulp white or red; seeds large.

- Cereus (Hylocereus) extensus* Salm. l. c. 161. — Trinidad.  
*C. (Hylocereus) Lemairei* Hook. l. c. 160. — Antigua Island.  
*C. (Hylocereus) Napoleonis* Grah. l. c. 159. — Antilles.  
*C. (Hylocereus) Ocamponis* Salm. l. c. 159. — Mexico.  
*C. (Hylocereus) stenopterus* Web. l. c. Nachtr. 57. — Costa Rica.  
*C. (Hylocereus) triangularis* Haw. l. c. 157. — Mexico.  
*C. (Hylocereus) trigonus* Haw. l. c. 158. — Puerto Rico.  
*C. (Hylocereus) trigonus* var. *costaricensis* Web. l. c. Nachtr. 56. —  
 Costa Rica.

A very natural subgenus comprising the *Triangulares* of Schumann with the exception of *Cereus setaceus* Salm. They are all climbers and produce roots along their triangular stems. The nocturnal flowers are among the largest and the most beautiful of the whole genus. The fruit is large, red, and furnished with foliaceous scales, which increase in size during the growth of the fruit

*Cereus triangularis* Haw. is much grown on the Riviera and flowers every year, but as yet I have not seen any fruit from these plants.

*Cereus trigonus* var. *costaricensis* Web. is much grown for its fruit in Costa Rica. There is a fine drawing of it at La Mortola.



XII. *TRICHOCEREUS* A. Berg.

Ovary and tube with more or less densely imbricated acute scales, from the axils of which rise long and curled or woolly hairs in great profusion, but no bristles; sepaloïd and petaloïd perianth leaves numerous; stamens numerous, in two groups; style as long or longer with numerous stigmata. Fruit uncolored, roundish, scaly and hairy, with the dried remains of the flowers more or less persistent.

Flowers showy, nocturnal, white, yellowish or red, trumpet-shaped.—  
*Plate 8, f. 1-3.*

Chiefly Andean species: —

- Cereus (Trichocereus) andalgalensis* Web. l. c. 168. — Argentina.  
*C. (Trichocereus) Bridgesii* Salm. l. c. 107. — Bolivia.  
*C. (Trichocereus) candicans* Gill. l. c. 69. — Argentina.  
*C. (Trichocereus) chilensis* Colla. l. c. 61. — Chile.  
*C. (Trichocereus) fascicularis* Meyen. l. c. 57. — Peru.  
*C. (Trichocereus) Huascha* Web. l. c. 70. — Argentina.  
*C. (Trichocereus) lamprochlorus* Lam. l. c. 60. — Argentina.  
*C. (Trichocereus) macrogonus* Salm. l. c. 115. — Andes?  
*C. (Trichocereus) nigripilis* Phil. l. c. Nachtr. 20. — Chile.  
*C. (Trichocereus) Pasacana* Web. l. c. 77. — Argentina.  
*C. (Trichocereus) pterogonus* Lem. l. c. 152. — New Granada.  
*C. (Trichocereus) Spachianus* Lem. l. c. 67. — Argentina.  
*C. (Trichocereus) strigosus* Salm. l. c. 68. — Argentina.  
*C. (Trichocereus) thelegonus* Web. l. c. 78. — Argentina.

The description of the flower of *Cereus macrogonus* Salm in K. Schumann's Monographia is not correct; see *Monatsschrift für Kakteenkunde*, 1904, p. 190.

*Cereus andalgalensis* Web. is the same as *Cereus Huascha* Web. var. *rubriflora* Web., as I have been informed by Weber himself.

The genus *Echinopsis* comes so near to this subgenus that there seems to be no obstacle, except for its seeds, to reuniting it with *Cereus*, as done by Pfeiffer and Otto, and by Bentham and Hooker (*Gen. Plant.* 1: 849). *Cereus candicans* Gill. and *C. lamprochlorus* Lem., on the other hand, have been considered by Weber as *Echinopses*. *Echinopsis obrepanda* K. Sch., *E. cinnabarina* Lab. and *E. Pentlandii* Salm, have been included by other authors under *Echinocactus*.



## XIII. ERIOCEREUS A. Berg.

Ovary roundish with deltoid acute scales; tube with similar but larger and more remote scales, in their axils with more or less copious white wool, on the ovary sometimes with a few spines; sepaloid perianth leaves acute, greenish brown; petaloid ones white; stamens numerous, in two groups. Fruit roundish, with the dried remains of the flower more or less persistent, red, with the pulvilli more or less raised, scales often a little increased, with wool and often spines in their axils; pulp white, seeds numerous, black, opaque, compressed, strongly papillous along the crest. — *Plate 7, f. 5-6; plate 9, f. 1; plate 10.*

This subgenus comprises most of the *Tortuosi* of K. Schumann. It approaches *Eucereus*, from which, however, it is distinguished by the larger scales of the ovary and by the white wool of the pulvilli and tube. The tube is never armed with bristles except in *Cereus Martinii* Lab. Stems of the species mostly procumbent. Flowers showy, white, nocturnal, very uniform. *Cereus tortuosus* Forb. may be considered the type of this subgenus.

*Cereus (Eriocereus) Bonplandii* Parm. l. c. 135. — Paraguay.

*C. (Eriocereus) Jusberti* Rebut. l. c. 137. — ?

*C. (Eriocereus) Martinii* Lab. l. c. 141. — Argentina.

*C. (Eriocereus) pomanensis* Web. l. c. 136. — Argentina.

*C. (Eriocereus) repandus* Haw. l. c. 94. — Antilles?

*C. (Eriocereus) tephraanthus* Lab. l. c. 80. — Bolivia.

*C. (Eriocereus) tortuosus* Forb. l. c. 139. — Argentina.

*Cereus Jusberti* Rebut is, according to repeated assurances of Abbé Beguin, a hybrid between an *Echinopsis* and a *Cereus*, raised by him.

All these plants are quite hardly at La Mortola and flower annually. *Cereus tortuosus* Forb. produces its beautiful flowers in great quantity every summer and ripens many fruits, from which this species has been widely distributed. *Cereus pomanensis* Web. comes very near to it, but has an unarmed fruit. The form of the seeds of *Eriocereus* is very characteristic.



XIV. EUCEREUS Engelm. Syn. of the Cact. of the Terr. of the U. S. etc., Proc. Am. Acad. 3. (1856); Coll. Works. 139; Cact. Bound. 40.

Ovary and tube with numerous small deltoid acute scales, those of the tube larger and remote; from the axils of all of them rise hairs, wool and setulose, more or less stiff bristles; tube funnel-shaped, rather slender; perianth leaves numerous. Fruit more or less roundish and reddish, covered with spines often in deciduous clusters.—*Plate 11; plate 12, f. 1.*

The numerous species falling under *Eucereus* easily group themselves in a few natural subsections, which are given below:—

Subsection I. NYCTOCEREUS A. Berg.

Stems more or less upright, cylindrical, ribbed. Flowers nocturnal.

The following species seem to belong here:—

*Cereus (Nyctocereus) baxosus* Web. l. c. 84. — Mexico.

*C. (Nyctocereus?) candelabrum* Web. l. c. 106. — Mexico. (Description too poor.)

*C. (Nyctocereus) Cumengei* Web. l. c. 85. — Baja California.

*C. (Nyctocereus) Eruca* Brandg. l. c. 125. — Baja California.

*C. (Nyctocereus) gummosus* Engelm. l. c. 124. — Baja California.

*C. (Nyctocereus) Hirschtianus* K. Sch. l. c. 130. — Nicaragua.

*C. (Nyctocereus?) multangularis* Haw. l. c. 66. — Peru?

*C. (Nyctocereus) nesioticus* K. Sch. l. c. Nachtr. 37. — Galapagos Islands.

*C. (Nyctocereus) Neumanni* K. Sch. l. c. Nachtr. 37. — Nicaragua.

*C. (Nyctocereus) queretaroensis* Web. l. c. 83. — Mexico.

*C. (Nyctocereus) serpentinus* P. DC. l. c. 129. — Mexico.

*Cereus serpentinus* P. DC. possesses the largest seeds of *Cereus* known to me. There are only a few in each fruit, bedded in the crystalline red pulp. Several varieties of this species occur in gardens. There are two very pronounced forms at La Mortola. One has weaker and more serpentine stems, with smaller spines and smaller flowers. This never produces any fruit. The other form has stronger, upright stems with longer spines. Its flowers



are remarkably larger and produce a great quantity of fruits. The former variety seems to have undeveloped stigmata, and it may prove to be the male plant. Similar cases of heterogamy are known in *Opuntia* and *Mamillaria*, but nothing of the kind has ever been shown in *Cereus*. This male form at La Mortola corresponds well with the figure in the Botanical Magazine, pl. 3566. Strictly terminal flowers, as shown in this plate, are also occasionally produced by our plant.

*Cereus Martianus* Zucc. is generally considered as an ally of *Cereus flagelliformis* Mill. Its flowers, however, are those of *Eucereus*; the tube bears bristles. Its position in *Eucereus* still remains doubtful. — *Plate 12, f. 1.*

#### Subsection II. SELENICEREUS A. Berg.

Stems slender, elongated, sarmentose, rooting. Flowers nocturnal, always very large; ovary mostly (not always) with long hairs and bristles.

- Cereus (Selenicereus) Böckmannii* Otto. l. c. 147. — Cuba.  
*C. (Selenicereus) calcaratus* Web. l. c. Nachtr. 54. — Costa Rica.  
*C. (Selenicereus) coniflorus* Weingart. in Monatschr. f. K. 1904: 118. — Haiti ?  
*C. (Selenicereus) Donkelaeri* Salm. l. c. 150. — Brazil.  
*C. (Selenicereus) grandiflorus* Mill. l. c. 144. — Haiti.  
*C. (Selenicereus) hamatus* Scheidw. l. c. 155. — Mexico.  
*C. (Selenicereus) hondurensis* K. Sch. Weingart in Monatschr. f. K. 1904: 147. — Honduras.  
*C. (Selenicereus) inermis* Otto. l. c. 156. — Venezuela.  
*C. (Selenicereus) Kunthianus* Otto. l. c. 150. — Honduras.  
*C. (Selenicereus) MacDonaldae* Hook. l. c. 149. — Honduras?  
*C. (Selenicereus) miravallensis* Web. l. c. Nachtr. 49. — Costa Rica.  
*C. (Selenicereus) nycticalus* Link. l. c. 146. — Haiti, Mexico.  
*C. (Selenicereus) spinulosus* P. DC. l. c. 148. — Mexico.  
*C. (Selenicereus) setaceus* Salm. l. c. 162. — Brazil.

This subsection comprises the Principales and Rostrati of K. Schumann. In some of the flowers bristles are wanting, and for this reason they would come in close contact with *Trichocereus*, but their long slender tube removes all doubt as to their true relationship. *Cereus setaceus* Salm



has a somewhat isolated position. The flower is far less hairy, and the stems, when adult, are triangular. For this reason it is generally placed under the Triangulares, but the prickly fruit and the setuliferous tube of the flowers remove it far from those species.

Most of the species of *Selenicereus* are garden plants, much grown for the sake of their beautiful nocturnal flowers, which sometimes have a delicious scent, as for instance those of *C. grandiflorus* Mill., the well-known "Queen of the Night." *Cereus MacDonaldae* Hook. has about the largest flowers.

### Subsection III. PENIOCEREUS A. Berg.

Rootstock tuberous, stems slender. Flowers with a long narrow tube, nocturnal, white or red.

*Cereus (Peniocereus) Greggii* Engelm. l. c. 96. — Texas, North Mexico.  
*C. (Peniocereus) striatus* Brandg. l. c. 134. (= *C. Diguettii* Web. l. c. 30 ?). — Baja California.

Of these two (or three?) species, *C. Greggii* Engelm. is the best known plant. It flowered last summer at La Mortola (see *Monatsschrift für Kakteenkunde*, 1904, p. 134). The stems are covered with short velvety hairs. The tube of the flower is broader than in Engelmann's excellent plates (*Cact. Bound.* pl. 63, 65).

### Subsection IV. ACANTHOCEREUS Engelm. in Additions to the Cactus Flora etc.; Coll. Works. 225.

Stems elongated, 3-4-angled. Flowers white, nocturnal; tube with a few scales and stiff bristles.

*Cereus (Acanthocereus) Baxaniensis* Karw. l. c. 98. (= *C. princeps* Hort. = *C. acutangulus* Otto = *C. variabilis* Engelm.). — Central America.

*Cereus Baxaniensis* Karw. is a very variable plant, a fact which accounts for the numerous synonyms under which it has been described by different authors. Young



plants further differ greatly from fully grown specimens. *Cereus Dussii* K. Schumann l. c. 89 is the same plant.

#### Subsection V. HELIOCEREUS A. Berg.

Stems more or less upright, 3-4-angled. Flowers red or white, diurnal.

- Cereus (Heliocereus) amecaensis* Heese. l. c. 154. — Mexico.  
*C. (Heliocereus) coccineus* Salm. l. c. Nachtr. 53. — Mexico.  
*C. (Heliocereus) Schrankii* Zucc. l. c. Nachtr. 52. — Mexico.  
*C. (Heliocereus) speciosus* K. Sch. l. c. 153. — Mexico.

These few species are very closely related.

The *Heliocerei* are much grown for the sake of their most brilliant flowers, especially *C. speciosus*. This latter species has given origin to many of the much admired hybrids with *Phyllocactus*.

#### Subsection VI. PHYLLOCEREUS A. Berg.

Epiphytic, climbing, stems flat resembling those of *Phyllocactus*. Flowers large with hairs and bristles similar to those of Subsection II. *Selenicereus*.

- Cereus (Phyllocereus) Wittii* K. Sch. l. c. Nachtr. 50. — Brazil.

This is a most interesting *Cereus*. The numerous and densely set areoles along the borders are armed with small bristles. It forms a beautiful connecting link with *Phyllocactus*, though it doubtless belongs to *Cereus*.

If anyone wishes to reunite *Phyllocactus* with *Cereus*, it ought to be placed here as a subgenus next to *Eucereus-Phyllocereus*.

Weber has described a *Phyllocactus lepidocarpus* from Costa Rica, which has the ovary and the fruit densely covered with scales. This would be a transition from *Phyllocactus* to *Phyllocereus*.



XV. *LEPTOCEREUS* A. Berg.

Flowers short, turbinate-campanulate, fleshy; ovary and tube with short scales with wool and clusters of bristles upon the pulvilli; perianth leaves rather short, little expanded; stamens numerous from the middle of the thickened tube; style as long as the perianth, with 5-6 short styles.

Tropical *Cerei* with short flowers and climbing, elongated stems form this subgenus. *Cereus assurgens* Griseb. may be considered the type.

*Cereus (Leptocereus) assurgens* Griseb. l. c. 140. — Cuba.

*C. (Leptocereus) Gonzalezii* Web. l. c. Nachtr. 58. — Costa Rica.

*C. (Leptocereus) Tonduzii* Web. l. c. Nachtr. 59. — Costa Rica.

A *Cereus Weingartianus* Hartmann has lately been published, but Weingart himself recognized it to be the old *C. assurgens* Griseb. (See *Monatsschrift für Kakteenkunde*, 1904: 155, and 1905: 8).

XVI. *ECHINOCEREUS* Engelm. in Wisliz. Tour North. Mexico. 91. (1848).

Flowers diurnal, short, rarely tubular; ovary and tube with woolly and prickly pulvilli; sepaloid and petaloid perianth leaves numerous and showy, mostly patent; stamens numerous, inserted along the tube. Style longer, ending in short green stigmata. Fruit round, reddish or green, aculeate; seeds small, obovate or subglobose, compressed, punctate.

A very natural subgenus and easily recognized.

Subsection I. *GRACILES* Engelm.

*Cereus (Echinocereus) tuberosus* Poselg. l. c. 249. — Texas etc.

Subsection II. *SUBINERMES* K. Sch.

*Cereus (Echinocereus) Knippelianus* (Liebn.) A. Berg. l. c. 251. — Mexico.

*C. (Echinocereus) pulchellus* Pfeiff. l. c. 252. — Mexico.

*C. (Echinocereus) subinermis* Hemsl. l. c. 250. — Mexico.



## Subsection III. PROSTRATI K. Sch.

1. *Melanochlori* K. Sch.

- Cereus (Echinocereus) Salm-Dyckianus* Web. l. c. 255. — Mexico.  
*C. (Echinocereus) Scheeri* Salm. l. c. 253. — Mexico.

2. *Nigricantes* K. Sch.

- Cereus (Echinocereus) Berlandieri* Engelm. l. c. 256. — Texas, Mexico.  
*C. (Echinocereus) Blankii* Poselg. l. c. 257. — Mexico.  
*C. (Echinocereus) papillosus* (A. Lke.) A. Berg. l. c. 258. — Texas.  
*C. (Echinocereus) Poselgerianus* (A. Lke.) A. Berg. l. c. 257. — Mexico.

3. *Pentalophi* Salm.

- Cereus (Echinocereus) leptacanthus* Salm. l. c. 260. — Mexico.  
*C. (Echinocereus) procumbens* Engelm. l. c. 259. — Mexico.

4. *Oleosi* K. Sch.

- Cereus (Echinocereus) glycimorphus* (Först.) A. Berg. l. c. 261. — Mexico.

5. *Leucacanthi* K. Sch.

- Cereus (Echinocereus) cinerascens* P. DC. l. c. 262. — Mexico.  
*C. (Echinocereus) Ehrenbergii* Pfeiff. l. c. 262. — Mexico.  
*C. (Echinocereus) enneacanthus* Engelm. l. c. 264. — Texas, Mexico.  
*C. (Echinocereus) Leonensis* (Maths.) A. Berg. l. c. 263. — Mexico.

## Subsection IV. ERECTI K. Sch.

1. *Pectinati* K. Sch.

- Cereus (Echinocereus) ctenoides* Engelm. l. c. 269. — Texas, Mexico.  
*C. (Echinocereus) chloranthus* Engelm. l. c. 266. — Texas, New Mexico.  
*C. (Echinocereus) dasyacanthus* Engelm. l. c. 268. — Texas.  
*C. (Echinocereus) longisetus* Engelm. l. c. 265. — Mexico.  
*C. (Echinocereus) pectinatus* Engelm. l. c. 270. — Mexico, S. W. U. S.  
*C. (Echinocereus) Roetteri* Engelm. l. c. 272. — Texas, Arizona, Mexico.  
*C. (Echinocereus) viridiflorus* Engelm. l. c. 267. — U. S.



2. *Decalophi* Salm.

- Cereus* (*Echinocereus*) *acifer* Otto. l. c. 286. — Mexico.  
*C.* (*Echinocereus*) *conglomeratus* (Först.) A. Berg. l. c. 278. — Mexico.  
*C.* (*Echinocereus*) *dubius* Engelm. l. c. 276. — Texas, Mexico.  
*C.* (*Echinocereus*) *Engelmannii* Parry. l. c. 275. — Southwest U. S.  
*C.* (*Echinocereus*) *Fendleri* Engelm. l. c. 274. — New Mexico, Sonora, Arizona, etc.  
*C.* (*Echinocereus*) *Leeanus* Hook. l. c. 287. — Mexico.  
*C.* (*Echinocereus*) *maritimus* Jones. l. c. 273. — California.  
*C.* (*Echinocereus*) *Merkeri* (Hildm.) A. Berg. l. c. 277. — Mexico.  
*C.* (*Echinocereus*) *mojavensis* Engelm. & Bgl. l. c. 279. — New Mexico, Arizona, California.  
*C.* (*Echinocereus*) *paucispinus* Engelm. l. c. 280. — Texas, New Mexico, etc.  
*C.* (*Echinocereus*) *phoeniceus* Engelm. l. c. 282. — Colorado, New Mexico, Arizona, Sonora, etc.  
*C.* (*Echinocereus*) *polyacanthus* Engelm. l. c. 285. — Mexico, Texas, California, etc.  
*C.* (*Echinocereus*) *Roemeri* Engelm. l. c. 284. — Texas, New Mexico, Utah.  
*C.* (*Echinocereus*) *stramineus* Engelm. l. c. 273. — Mexico, Texas, Arizona, etc.

There is no reason to keep *Echinocereus* as a distinct genus, unless one accepts as genera the other subgenera as well. Engelmann, Kew Index, Coulter and Weber report it as a subgenus only.

The position of *Cereus Emoryi* Engelm. (*Echinocereus Emoryi* Rümpl.) remains still doubtful. I have not yet seen a flower of it.

XVII. *CLEISTOCACTUS* Lem. in *Illustr. Hort.* 8. (1861). Misc. 35. (as genus).

Flowers short and narrowly tubular, curved in the shape of an  $\smile$ , and the limb somewhat zygomorphic; ovary subglobose, like the tube with numerous small appressed scales, bearing woolly hairs in their axils; sepaloid and petaloid perianth leaves small, lanceolate, hardly expanded; filaments inserted below the middle of the tube, somewhat exserted and grouped together near the upper lip; style little longer. Fruit



globular, small, red, with remote small scales and little wool, crowned with the dried remains of the flower; pulp white; seeds small, glossy black, slightly punctate. — *Plate 9, f. 2-5; 12, f. 2.*

Lemaire founded his genus upon

*Cereus (Cleistocactus) Baumannii* Lem. l. c. 133. — Uruguay, Paraguay.

Perhaps also *C. hyalacanthus* K. Sch., from Argentina, *C. laniceps* K. Sch. and *C. parviflorus* K. Sch., both from Bolivia, may belong here.

*C. Baumannii* var. *smaragdiflora* Web. is said to have regular flowers. I have not yet seen it, and perhaps it does not even belong to *C. Baumannii* Lem., but may be a different species.

*Cleistocactus* is a very natural subgenus, as can be seen from the flower and fruit represented in the plates. It is surprising that it has met with so many objections.

XVIII. APOROCACTUS Lem. in *Illustr. Hort.* 7. (1860). *Misc.* 67. (as genus).

Flower small, bright red; ovary globose, densely covered with deltoid scales and long, somewhat firm white hairs; tube slender, slightly bent upwards above the ovary, with sepaloïd linear-lanceolate acute and patent perianth leaves, the inferior with a few hairs and smaller, the upper increasing in size; petals broader, acute, zygomorphically bent upwards and downwards, nearly forming 2 lips; filaments inserted near the base of the tube, exserted; style longer, with 5-7 red stigmata. Fruit globose, small, reddish, squamose and setose; pulp greenish yellow; seeds not very numerous, reddish brown, obovate.

This also is a very natural subgenus. It comprises the *Flagriformes* of K. Schumann with the exception of *C. Martianus* Zucc., which in spite of its slender stems and small red flowers is a true *Eucereus*.

*Cereus (Aporocactus) flagelliformis* Mill. l. c. 142. — Mexico.

*C. (Aporocactus) flagriformis* Zucc. l. c. Nachtr. 46 — Mexico.

*C. (Aporocactus) leptophis* DC. l. c. Nachtr. 47. — Mexico.



*Cereus Kerberi* K. Sch. from Mexico is stated to have flowers of the form of *Cereus flagelliformis* Mill. Certainly it does not belong to *Aporocactus*, and perhaps it is a *Eucereus* of the subsection *Heliocereus*, to judge from the quadrangular stems.

These small and graceful plants with their slender, dependent stems are very showy when well grown and in full flower.

There remain a great number of species of *Cereus* and "*Pilocereus*" of which the systematic position is still quite uncertain, as little or nothing is known about their flowers and fruit. I refrain from giving a list of them, as it would needlessly lengthen this paper.

Species to be excluded: —

*Cereus obtusangulus* K. Sch. in Flor. Brasil. 198; Monogr. Cact. 127.—  
*Epiphyllum obtusangulum* G. A. Lindberg, ex K. Sch. l. c.

This very strange little plant, still rare in cultivation, cannot be considered either a *Cereus* or an *Epiphyllum*. But no doubt it is much more nearly allied to the latter than to the former genus. Schumann brought it into *Cereus* on account of its round and ribbed stems, but there exists no *Cereus* of a similar articulated growth; only with *Rhipsalis* and *Epiphyllum* can it be compared. The plant resembles somewhat a minute *Platyopuntia*. The joints are slightly flattened and have numerous little prominent areoles distributed spirally all over the surface. In this it differs greatly from *Epiphyllum*, with which it agrees in all the characters of the flowers, the angular nearly alate ovary and especially in the inner stamens being united at the base into a small incurved membrane. Also, the fruit resembles more that of an *Epiphyllum* than of a *Cereus*. The flowers rise from the top of the joints as in *Epiphyllum*. The plant is best considered as generically dif-



ferent from both, but must be placed with *Ephiphyllum* and *Rhipsalis* among the Inarmatae of K. Schumann. I propose for it the name

***Epiphyllanthus obtusangulus*** (G. A. Lindbg.) A. Berg. — Brazil.

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Imperfect as this paper may be, I shall be glad if it draws the attention of other botanists to these plants. They are full of interest in many a point and there remains much to be done. The facts as here stated all need careful verification. I wish them to be considered as an attempt only, for the material from which these statements have been derived has not been at all sufficient. Botanists who have the opportunity will find ample field for observation. The cacti of the United States and Mexico are pretty well known, but those of Central and South America and of the islands quite insufficiently. Furthermore, in the study of these plants, there are observations still to be made upon their pollination, on the opening of the fruits and dissemination, on the development from the seed to the full-grown plant, and on the geographical distribution and economic value of the different species, etc.

Cacti, as well as other succulent plants, can never be understood unless they can be studied from a large collection in a subtropical garden, where they are grown in quantities in the open and where every possibility is offered for their natural development. But at present there exists no such opportunity.

My grateful acknowledgments and thanks are extended to Sir Thomas Hanbury, who has always taken great interest in my studies of succulents and has given me every possible help. I further have to thank Herrn Geheimrat Engler for valuable herbarium specimens lent me from the Royal Botanical Museum in Berlin; the Herbar Boissier; and, last but not least, Dr. William Trelease for so kindly providing for the publication of this paper.



## EXPLANATION OF PLATES.

Plate 5 is from a photograph by the author, and plate 12 from photographs by Mr. E. Dams, of Berlin. The other illustrations are from the author's drawings.

Plate 1. — PACHYCEREUS: *Cereus Pringlei* Wats. — 1, Flower, natural size. 2, Flower, longitudinal section (from specimens collected by Pringle, in the Royal Herbarium at Berlin). 3, Fruit (after K. Schumann). 4, Seeds, natural size and enlarged.

Plate 2. — OREOCEREUS: *Cereus Celsianus* A. Berg. — 1, Flower. 2, Flower, longitudinal section; both natural size. From La Mortola, Ventimiglia, Italy.

Plate 3. — STENOCEREUS: *Cereus stellatus* Pfeiff. — 1, Flower. 2, Flower, longitudinal section; both natural size. 3, Scale from the ovary, enlarged. 4, Petal, natural size. From La Mortola. — *Cereus sonorensis*, Runge. — 5, Flower (after K. Schumann).

Plate 4. — EULYCHNIA: *Cereus breviflorus* K. Sch. — 1, Flower, longitudinal section, natural size (from Dr. Kuntze's specimen in the Royal Herbarium at Berlin). PILOCEREUS: *Cereus strictus* P. DC. — 2, Flower (after plate 3125, Botanical Magazine, as *C. Royenii*). — *Cereus Houletii* A. Berg. — 3, Flower, longitudinal section (after K. Schumann). 4, Fruit, reduced (after Rümpler). — *Cereus lanuginosus* Mill. — 5, Seeds, natural size and enlarged.

Plate 5. — PIPTANTHOCEREUS: *Cereus spec.?* (*C. validus* Haw.?). Plant in the garden at Monte Carlo.

Plate 6. — PIPTANTHOCEREUS: *Cereus spec.?* (*C. validus* Haw.?). — 1, Flower, closed,  $\times 3/5$ . 2, Fruit, with spines from the stem attached,  $\times 3/5$ . 3, The same, longitudinal section. 4, Seeds,  $\times 3/5$ , and enlarged. From Monte Carlo.

Plate 7. — PIPTANTHOCEREUS: *Cereus Pitahaya* DC. — 1, Sterile fruit, with spines from the stem attached, natural size (from L. Winter's gardens, at Bordighera). — *Cereus spec.?* (*C. Jamacaru* DC.?). — 2, Fruit, natural size. 3, The same, longitudinal section. 4, Seeds, natural size and enlarged. ERIOCEREUS: *C. pomakensis* Web. — 5, Fruit, natural size. 6, Seeds, natural size, and enlarged. All from La Mortola.

Plate 8. — TRICHOCEREUS: *Cereus strigosus* Salm. — 1, Flower, natural size. — *Cereus Spachianus* Lem. — 2, Fruit, natural size. 3, Seeds, natural size, and enlarged. From La Mortola. LOPHOCEREUS: *Cereus Schottii* Engelm. — 4, Flower, natural size. 5, Ovary and base of tube, showing insertion of stamens, natural size. 6, Fruit, natural size (4, 5, 6 from specimens collected by Pringle, in the Royal Herbarium at Berlin). 7, 8, Seeds, natural size and enlarged.

Plate 9. — ERIOCEREUS: *Cereus tortuosus*. — 1, Flower, natural size. From La Mortola. CLEISTOCACTUS: *Cereus Baumannii* Lem. — 2, Fruit,



natural size. 3, Fruit, longitudinal section, natural size. 4, Seeds, natural size, and enlarged. 5, Part of testa, enlarged. From L. Winter's gardens, Bordighera.

Plate 10. — ERIOCEREUS: *C. Martinii* Lab. — 1, Fruit, natural size. 2, Seeds, natural size and enlarged. — *C. Bonplandii* Parm. — 3, Fruit, natural size. 4, Seeds, natural size and enlarged. From La Mortola.

Plate 11. — EUCEREUS: *Cereus serpentinus* P. DC. — 1, Flower, 2, Fruit, 3, Seed (from La Mortola). — *Cereus hamatus* Scheidw. — 4, Fruit (after K. Schumann). 5, Seeds. All  $\times 5/9$ , except the enlarged seed of f. 5.

Plate 12. — EUCEREUS: 1, *Cereus Martianus* Zucc. CLEISTOCACTUS: 2, *Cereus Baumannii* Lem.

LA MORTOLA, VENTIMIGLIA, ITALY.





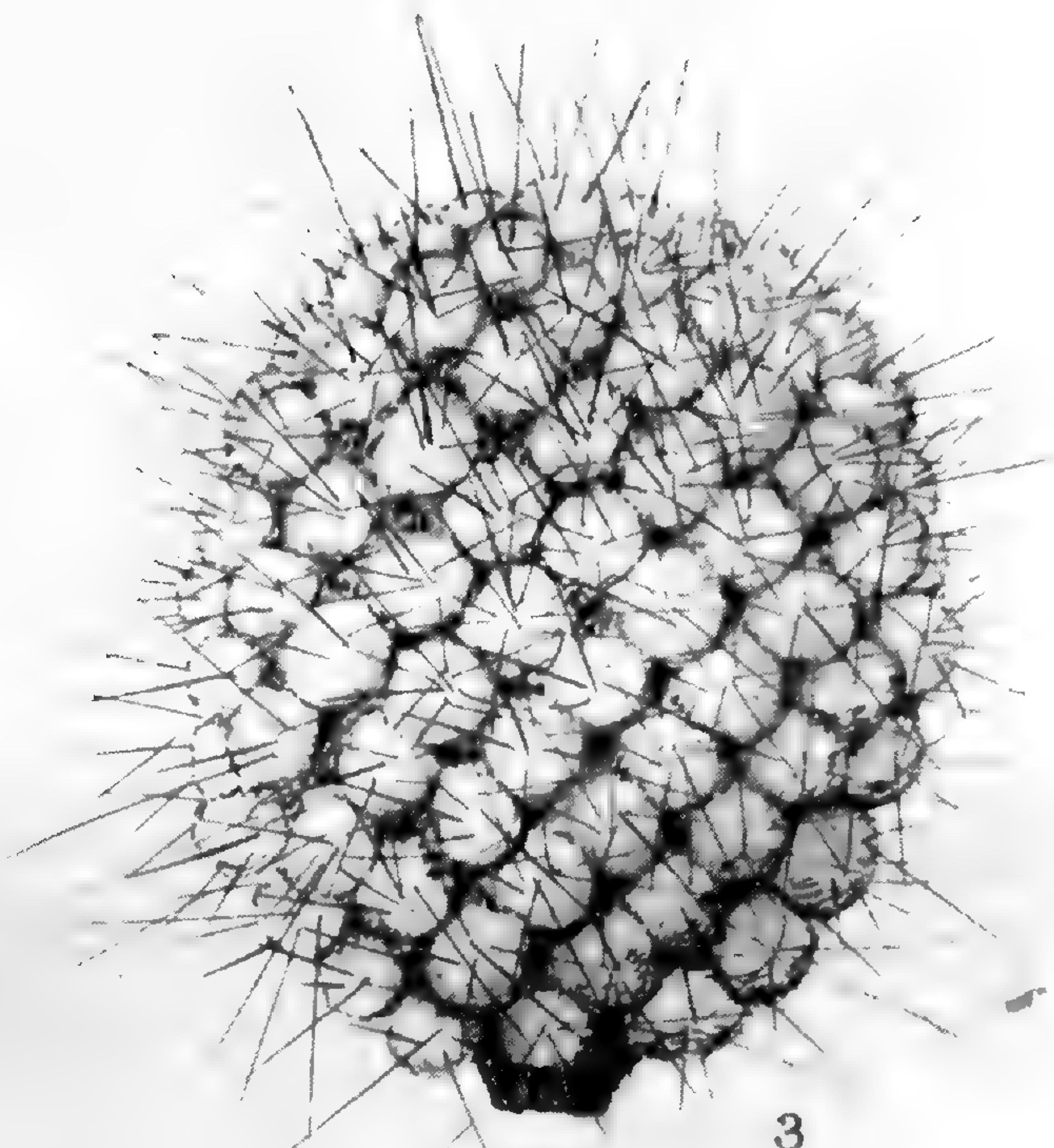
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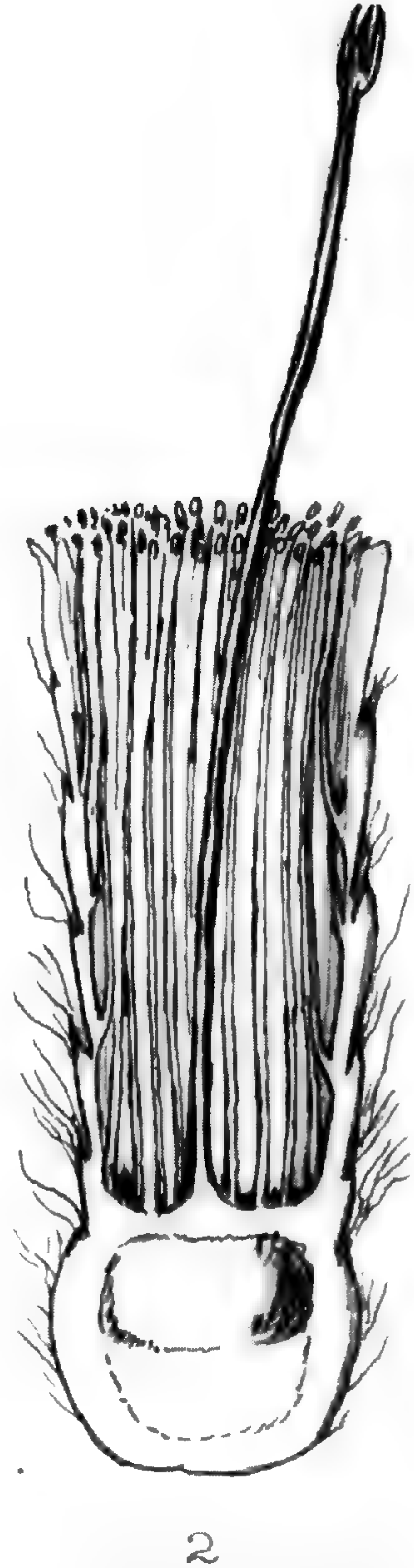
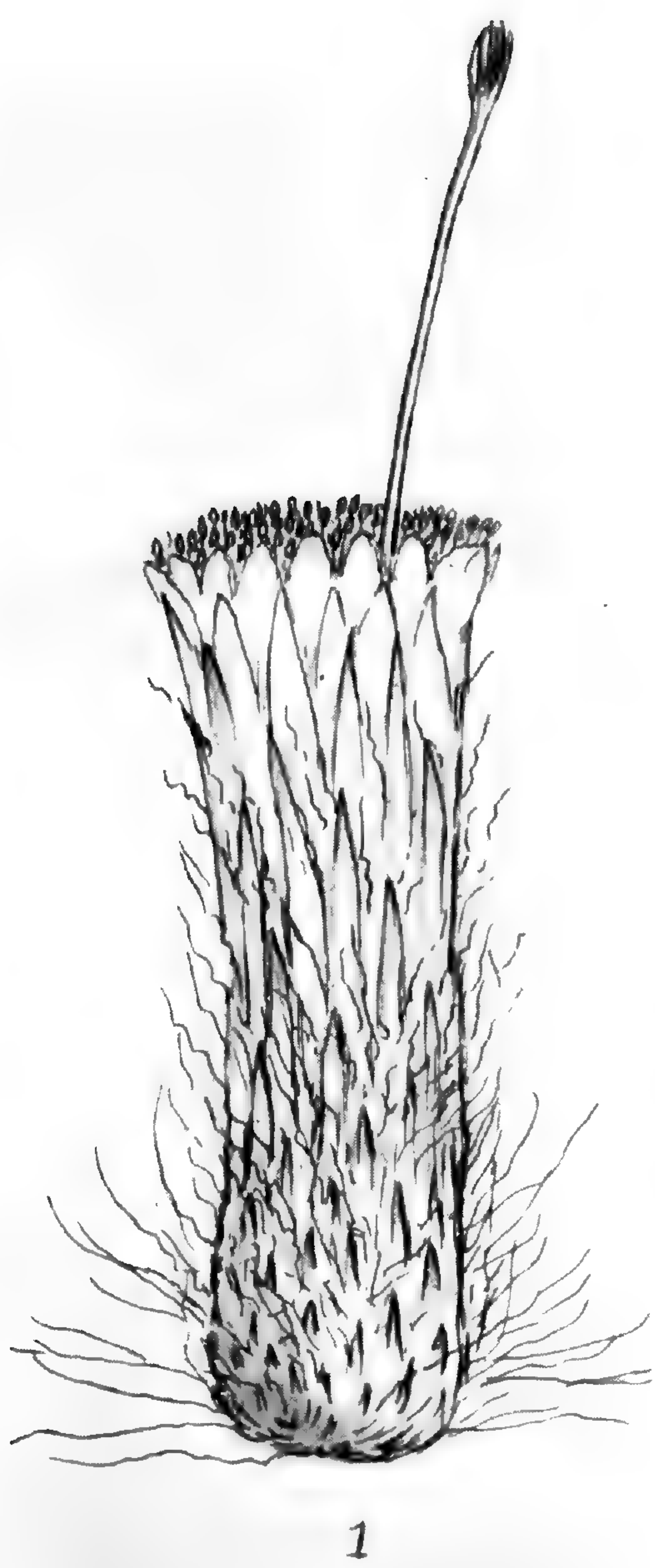


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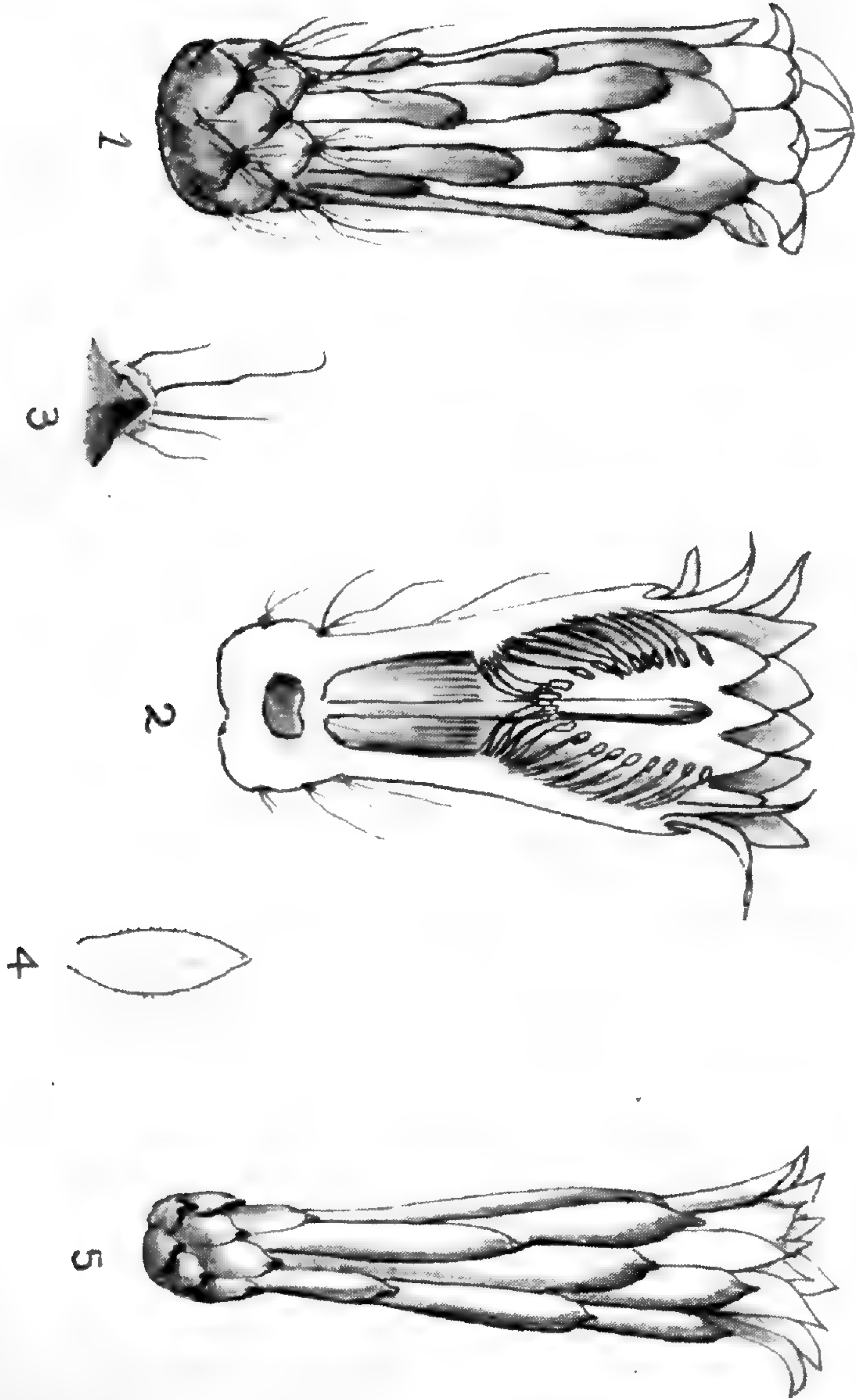
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CEREUS. — V. OREOCEREUS.





CEREUS. — VII. STENOCEREUS.





CEREUS.—VIII. EULYCHNIA: IX. PILOCEREUS.





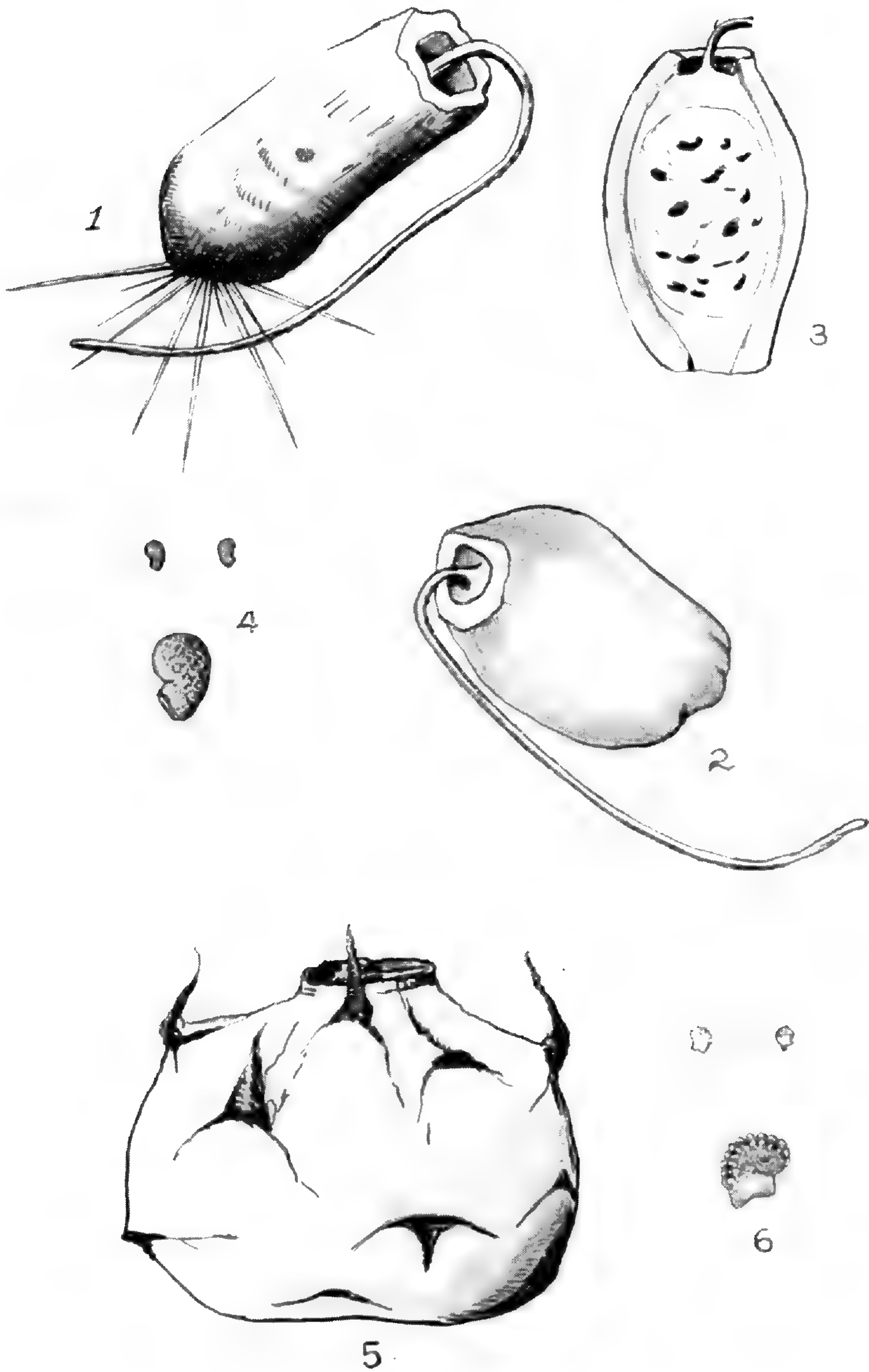
CEREUS. — X. PIPTANTHOCEREUS.





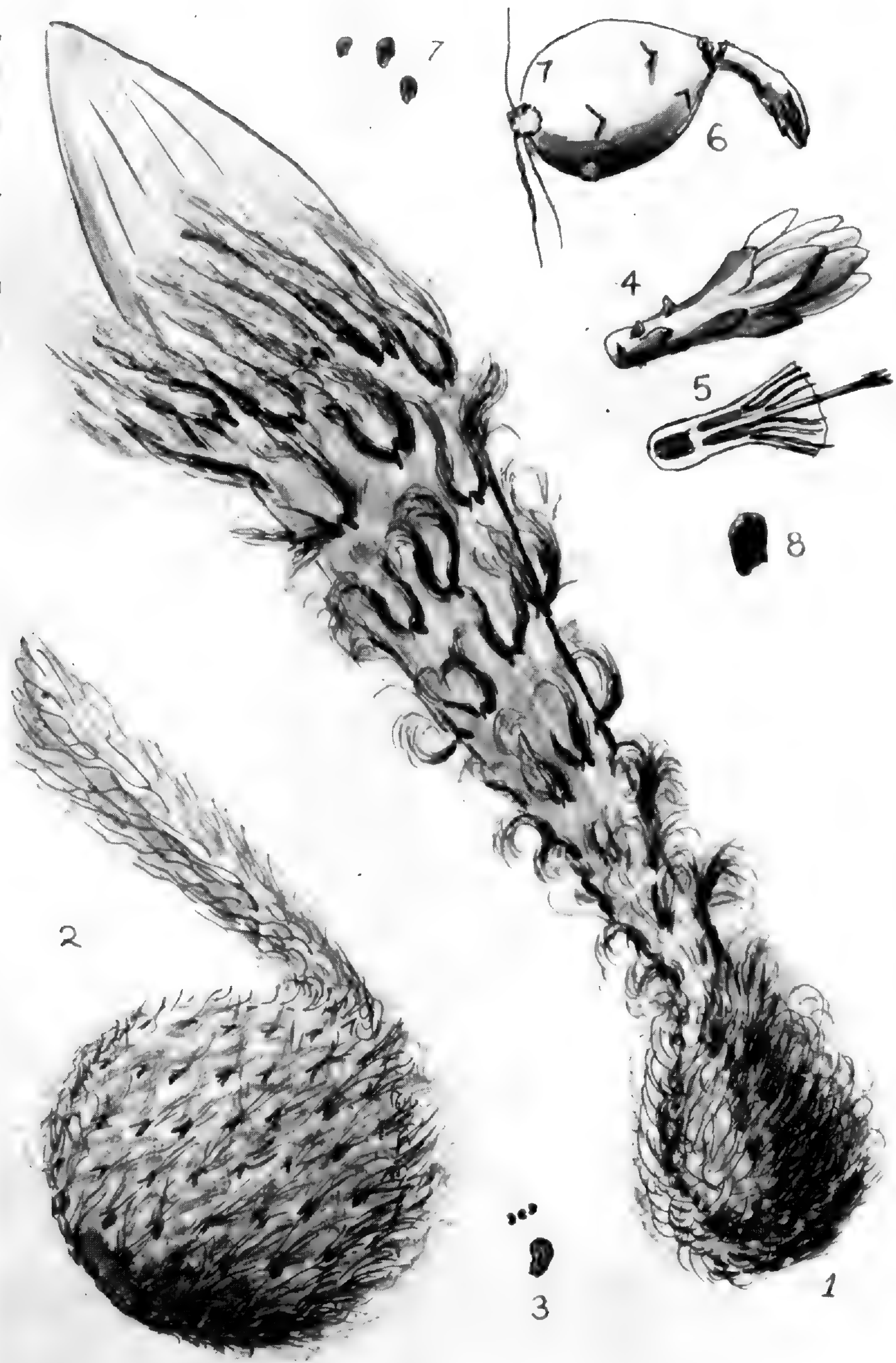
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CEREUS.—X. PIPTANTHOCEREUS: XIII. ERIOCEREUS.





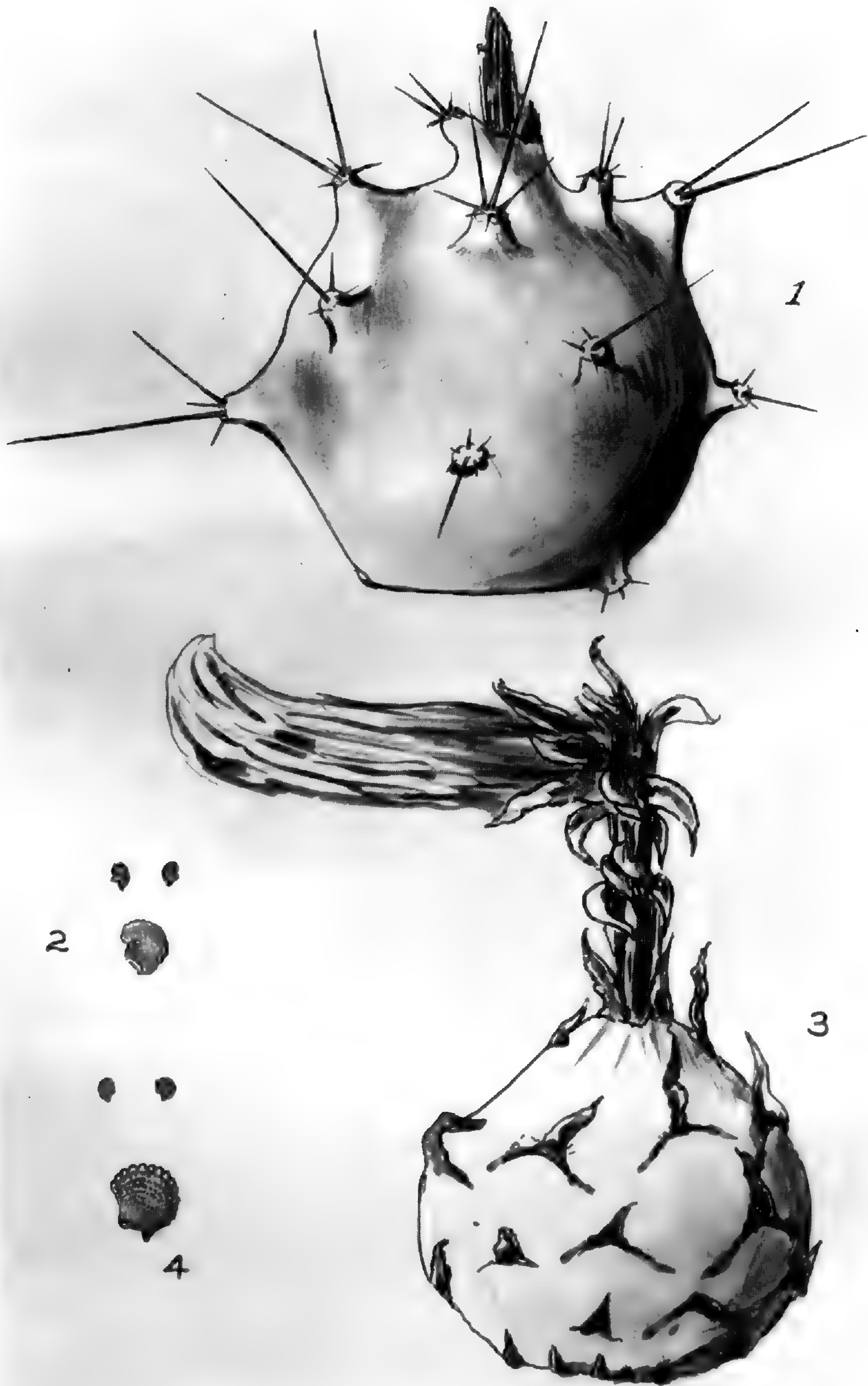
CEREUS. — XII. TRICHOCEREUS: II. LOPHOCEREUS.





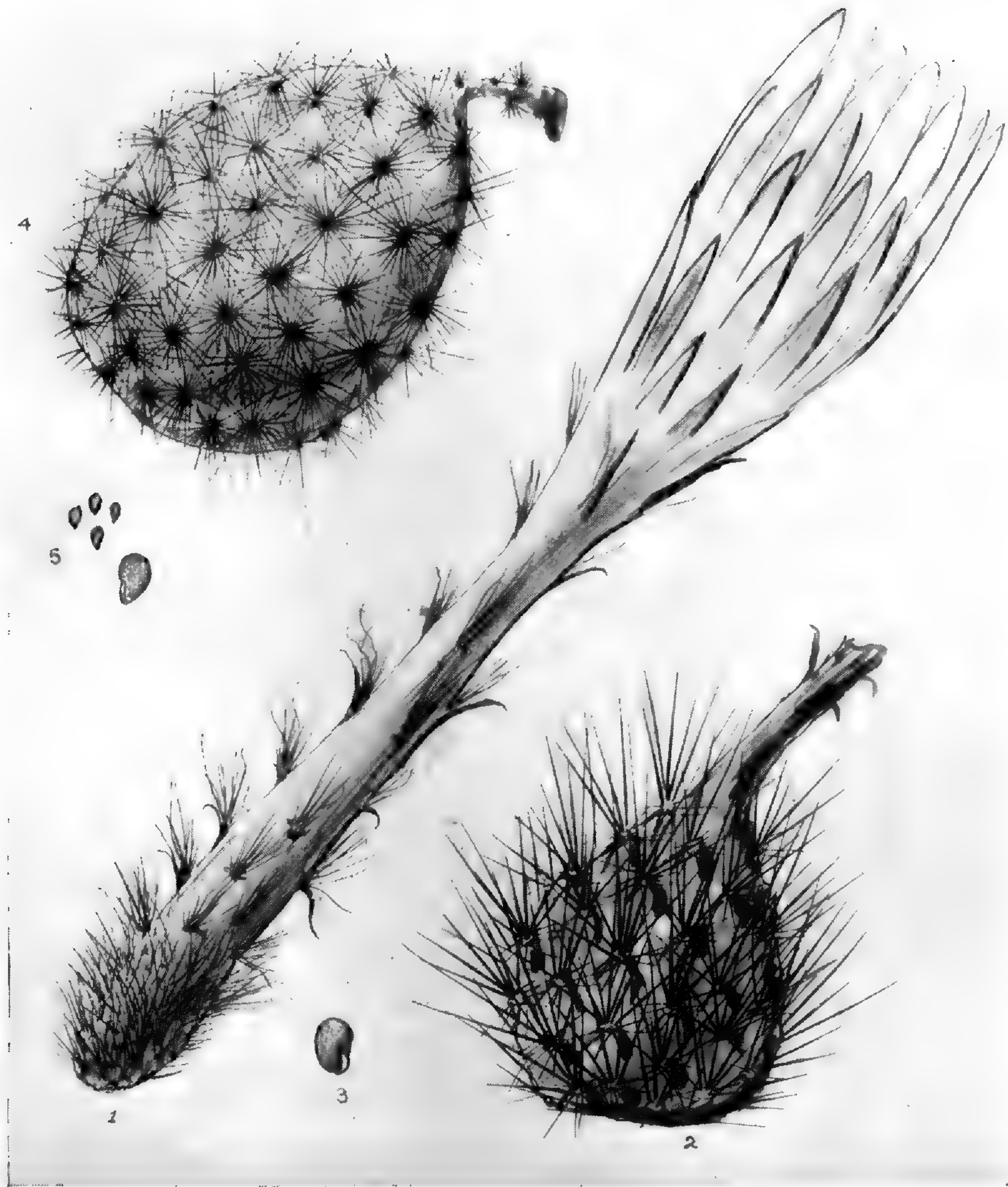
CEREUS. — XIII. ERIOCEREUS: XVII. CLEISTOCACTUS.





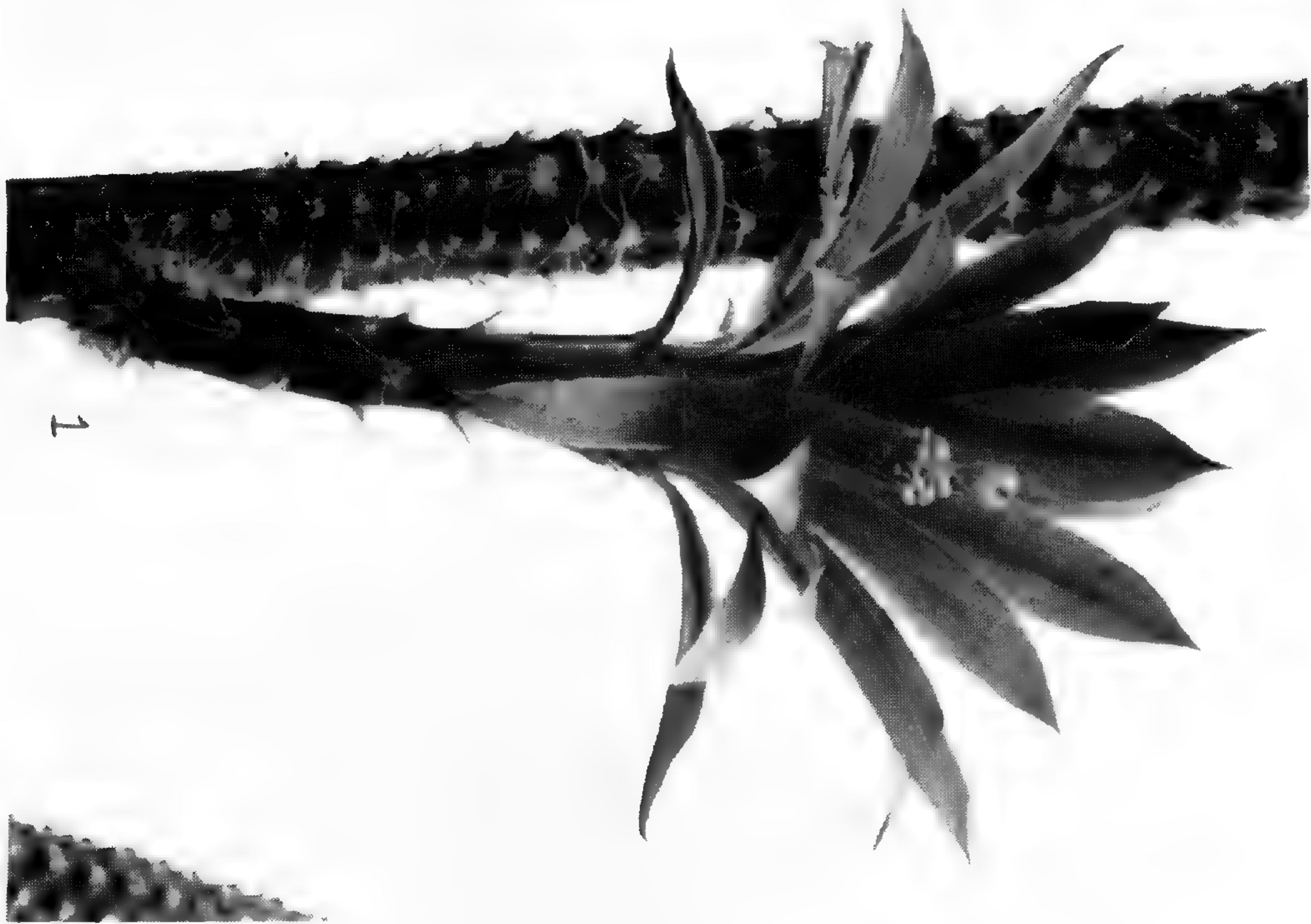
CEREUS. — XIII. ERIOCEREUS.





CEREUS. — XIV. EUCEREUS.





CEREUS. — XIV. EUCEREUS: XVII. CLEISTOCACTUS.



## THE NORTH AMERICAN SPECIES OF FUIRENA.

BY B. F. BUSH.

There has not been a clear presentation of the species of this genus since Mr. Coville published his "Revision of the United States species of *Fuirena*" in 1890,\* in which he recognized three species and two varieties, one of which he later on raised to specific rank. However, Mr. Coville's conception of the species was but little better than that of Torrey, Gray, Chapman and various other writers, and it is the purpose of the present paper to present the species in a much better light than has heretofore been done. It has been my good fortune to have been able to examine a much greater amount of herbarium material than was available heretofore, through the kindness of Mr. C. D. Beadle of the Biltmore Herbarium, of Professor Wm. Trelease of the Missouri Botanical Garden, and of Mr. Richard Rathbun of the United States National Museum,† who have enabled me to complete this paper by placing in my hands for study all the specimens in their care.

The distinctive characters of the species of *Fuirena* are to be found in the flowers alone, although certain other characters are of specific value in the first two mentioned. The size of the plants, hairiness of the stems and leaves, and size of the inflorescence, vary so much in all the rest of the species, as to be unworthy of much consideration in separating the species. Given a certain amount of variation, however, the perianth scales, bristles and achenes ex-

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\* Bull. Torr. Bot. Club. 17:6. (1890).

† For the sake of convenience I have used the letters B, M and N to signify specimens from the Biltmore Herbarium, the herbarium of the Missouri Botanical Garden, and that of the United States National Museum, respectively.



hibit quite constant characters that may be relied on for specific distinctions.

The species herein treated have been variously regarded by authors as varieties or forms of *Fuirena squarrosa*, but in my opinion it is better to regard them as species, as they are clearly distinct from one another by characters that seem to be very constant.

Torrey, in 1824, rightly understood *F. scirpoidea*, *F. squarrosa* and *F. hispida*, but curiously enough interchanged the identity of the two latter. Gray, in various editions of the Manual, completely ignored Michaux's *F. squarrosa*, rightly recognized Elliott's *F. hispida*, and relegated *F. squarrosa* to Torrey's var. *pumila*. Chapman, in 1860, rightly understood Elliott's *F. hispida*, which thirty-five years afterward he asserted was a good species, but he applied Michaux's name *F. squarrosa* to the species which thirty years later was described by Coville as *F. squarrosa breviseta*, although he had collected and distributed the real *F. squarrosa* which he did not recognize. Mr. Coville in his revision gives Louisiana as the western limit of *Fuirena squarrosa*, as does also Britton in the Illustrated Flora and in the Manual of the Northern States and Canada, and the same range is assigned to this species by Dr. Small in his Flora of the Southern United States; but I have not seen any specimens from west of Florida, all those examined from west of that State belonging either to *F. breviseta* or *F. hispida*.

Dr. Britton, in the works above-mentioned, gives Nebraska as part of the range of *F. squarrosa*, as does Dr. Small in his Flora, but I think this rests on an error of determination, for I do not think that *F. squarrosa*, which is a strictly maritime species, could be found in Nebraska where only plants of sandy plains or saline soil are found. It is very probable that specimens of *F. simplex*, a species of sandy plains, have been mistaken for *F. squarrosa*.



## ANALYSIS OF THE SPECIES OF FUIRENA.

Leaves, at least the lower ones, reduced to bladeless sheaths.

Sheaths all bladeless.

1. *F. SCIRPOIDEA*.

Upper sheaths with short leaf-blades.

2. *F. LONGA*.

Leaves with well-developed blades.

Awn, when present, borne on the apex of the sepal, which tapers into it.

Bristles longer than the perianth-scales and achene.

Spikelets large, 12 to 20 mm. long.

3. *F. CYLINDRICA*.

Spikelets small, 5 to 12 mm. long.

4. *F. SQUARROSA*.

Bristles reaching the middle of the achene, or shorter.

Bristles smooth, not exceeding the stipe of the achene.

5. *F. BREVISETA*.

Bristles smooth, or downwardly barbed, reaching the middle of the achene.

Smooth; stems, leaves and sheaths densely white-villous; leaves strongly ciliate.

6. *F. CILIATA*.

Barbed; stems, leaves and sheaths somewhat hispid; leaves but little ciliate.

7. *F. HISPIDA*.

Awn arising from the back of the sepal, just below its apex.

8. *F. SIMPLEX*.

1. *FUIRENA SCIRPOIDEA* Michx.

*Fuirena scirpoidea* Michx. Fl. Bor. Am. 1:38. (1803).

Rootstocks slender, elongated; stems 2 to 6 dm. tall, widely tufted, very slender, resembling an *Eleocharis* in appearance; leaves all reduced to bladeless sheaths; bracts of the involucre 2 to 6 mm. long, appressed to the spikelets, acute or cuspidate; spikelets sessile, solitary, or 2 to 3 together in the clusters, oblong-ovate, 6 to 12 mm. long, dark brown at maturity; scales oblong or obovate, finely pubescent, mucronate or aristate, the points appressed; sepals 3; blades obovate-orbicular, obtuse or apiculate at the apices, with a long tapering base about as long as the stalks, scabrous on the upper part of the margins; perianth-bristles retrorsely hispid, as long as the stalks of the sepals; achenes triquetrous, constricted at each end, with concave sides, black at maturity, fully 1 mm. long, tipped by the antrorsely hispid style which is one-half as long as



the achene. — Low sandy ground, near the coast, Georgia and Florida, west to Mississippi. Spring to autumn.

*Specimens examined.* — GEORGIA: Camp Cornelia, *Harper* 1490, August 9, 1902 (M N). FLORIDA: Apalachicola, *Chapman*, September, 1896 (B M N); no locality given, *Chapman*, without date of collection, many collections (B M N); Miami, *Garber*, June, 1877 (M); Indian River, *Palmer*, 591, 1874 (M); Tampa, *Ferguson*, August, 1898 (M); Palma Sola, *Tracy* 6980, May 14, 1900 (B M N); Polk County, *Ohlinger* 564, May 15, 1894 (M); Suwanee County, *Hitchcock*, June–July, 1898 (M); Jacksonville, *Curtiss* 4863, June 16, 1894 (B N), 4097, June 17, 1893 (N), June, 1877 (N); Eustis, *Nash* 12, March 12–31, 1894 (M N), 2081, June 16–30, 1895 (B N), *Hitchcock*, June and July, 1894 (M); Lake Monroe, *Garber*, March, 1876 (M); St. John's County, *J. D. Smith*, March 4, 1882 (N); St. Augustine, *Canby*, April, 1869 (M N); East Florida, *Leavenworth*, without date of collection (M); no locality given, *Chapman*, without date of collection, in part, the single slender plant (M); no locality given, *Hart Wright*, without date of collection (M). ALABAMA: Mobile, *Mohr*, July, year not given (N), August, 1893 (M); Perdido, collector not given, June 26, year not given (M). MISSISSIPPI: Biloxi, *Tracy* 1526, July 12, 1891 (N), 1526, July 12, 1891, in part, the slender plants with single spikelets (N), 1633, July 15, 1891 (N), 1649, July 10, 1891 (N); Ocean Springs, *Tracy* 1649, July 10, 1891 (N.), *Skehan*, September 14, 1895 (M); Horn Island, *Tracy* 4813, June 1, 1891 (M N); Bay St. Louis, *Langlois* 138, September, 1883 (N).

## 2. *FUIRENA LONGA* Chapm.

*Fuirena longa* Chapm. Fl. S. U. S. 3 ed. 541. (1897).

Rootstocks slender, elongated; stems 8 to 12 dm. tall, erect, robust, resembling *Dulichium* in appearance; leaves



towards the base of the stem reduced to acuminate sheaths, on the upper part of the stem with narrow, acuminate blades 2 to 5 cm. long; bracts of the involucre linear, 8 to 25 mm. long, acuminate-cuspidate; spikelets sessile, oblong-ovoid, 2 to 6 together in the clusters, 10 to 15 mm. long, light brown at maturity; scales obovate or oblong, several-ribbed, roughish-pubescent, with awns about as long as the bodies; sepals 3; blades deltoid-ovate, obtuse or apiculate at the apices, truncate at base, minutely scabrous nearly all around, longer-stalked than in the last species; perianth-bristles one-half as long as the stalks of the sepals, reaching to the middle of the achene, or shorter, retrorsely-hispid; achenes oblong, acutely triquetrous, with concave sides, yellow-brown at maturity, tipped by the long antorsely hispid style, which is as long as the achene. — Low pine barrens, Florida to Mississippi. Summer and autumn.

*Specimens examined.* — FLORIDA: Apalachicola, *Chapman*, without date of collection, type (M), *Chapman*, September, 1890 (B); no locality given, *Chapman*, without date of collection (B); no locality given, *Chapman*, without date of collection, in part, the stouter plants (M). MISSISSIPPI: Biloxi, *Tracy* 1526, September 1, 1894, in part, the stouter plants with several spikelets in the clusters (N).

### 3. FUIRENA CYLINDRICA Bush, sp. nova.

Rootstocks short, thick; stems tall, slender, not very leafy, 3 to 4 dm. tall; leaf-blades short, flat, thin, smooth above, closely pubescent beneath, 2 to 4 cm. long, 2 to 3 mm. wide; sheaths very short, smooth; spikelets sessile, 2 to 5 together in the capitate clusters, oblong or mostly cylindrical, 11 to 20 mm. long, 3 to 5 mm. in diameter; scales obovate, deep reddish-brown, more or less hispid-pubescent, 3-nerved, each tipped with a stout erect hispid awn



nearly as long as the body; sepals 3; blades spatulate or fiddle-shaped, tapering at the base, nearly sessile, obtuse and rounded at the apex, the lower half semi-translucent, the upper half thick and granular-incrusted, awnless, or with a short, slightly downwardly-barbed awn from the apex; perianth-bristles longer than the achene and sepals, nearly or quite smooth; achenes oblong, triquetous, tapering at the base, light yellow at maturity, tipped by the antrorsely-hispid style, which is as long as the achene. — Sandy soil, southern Texas. Summer and autumn.

*Specimens examined.* — The only specimen seen is that of the type, collected in the Valley of the Rio Grande, below Dona Ana, Donna Ana County, New Mexico, by *Mexican Boundary Survey* 1523, 1848, in part, the other two plants on this sheet being, one, an *Eleocharis*, the other *F. simplex* (N).

It has been referred to *F. simplex macrostachya* (Britton) Coville, but differs conspicuously in the cylindrical spikelets, slender stems, small leaves, and especially in the shape of the sepals and position of the awn.

#### 4. *FUIRENA SQUARROSA* Michx.

*Fuirena squarrosa* Michx. Fl. Bor. Am. 1: 37. (1803).

*Fuirena squarrosa pumila* Torr. Fl. U. S. 1: 68. (1824).

Rootstocks scarcely any, rarely tuber-bearing, more commonly with fibrous roots, the plants being annual; stems tufted, glabrous, sometimes slightly ciliate on the margins; sheaths pubescent, the lower sometimes densely so; spikelets sessile, solitary, or 2 to 8 together in the capitate clusters, ovoid or ovoid-oblong, 6 to 12 mm. long, 3 to 5 mm. in diameter; scales ovate or oblong, brown, pubescent, mostly obtuse and rounded at the apex, 3-nerved, each tipped with a short, spreading or recurved awn nearly as long as the body; sepals 3: blades oblong, long-stalked, semi-translucent, usually narrowed at both ends, acuminate



into a rough, downwardly barbed or rarely smooth, awn; perianth-bristles mostly much longer than the sepals and achene, retrorsely rough-barbed; achenes triquetrous, fully .8 mm. long, tipped by the hispid style, which is as long as the achene, yellow-brown at maturity.—Sandy shores, eastern and southern Massachusetts, Rhode Island and southern New York to the coasts of Virginia, North Carolina, and Florida, being therefore a maritime species: also in the interior about the Great Lakes. Summer and autumn.

*Specimens examined.* — MASSACHUSETTS: Plymouth, Oakes, 1842 (M N); Springfield, Maria L. Owen, 1890 (N). RHODE ISLAND: Providence, Olney, without date of collection (N); no locality given, Thurber, 1846 (M). NEW JERSEY: Cape May, Parker 8598, August 20, 1869 (M); no locality given, Eaton, 1860 (M); *Bernhardi Herbarium* (M). NEW YORK: Wading River, Long Island, E. S. Miller, September 26, 1875 (M); Long Island, Hart Wright, without date of collection (M). VIRGINIA: Virginia Beach, Heller 1232, August 22, 1893 (M N), Kearney 2039, August 4, 1898 (N), 2067, October 1, 1898 (N). INDIANA: Dune Park, Agnes Chase 902, August 4, 1898 (M N). NORTH CAROLINA: Wilmington, Coville 141, June 27, 1890, approaching *F. hispida* in the thicker reddish sepals (N); no locality given, Curtis, without date of collection, approaching *F. hispida* in the thicker reddish sepals (M). SOUTH CAROLINA: No locality given, Ravenel, 1872 (M), Elliott, without date of collection (M). FLORIDA: Lake City, Rolfs 916, October 13, 1893, approaching *F. hispida* in the thicker reddish sepals (M), Hitchcock, June-July, 1898, approaching *F. hispida* in the thicker reddish sepals (M); Eustis, Hitchcock, June and July, 1894, in part, the smaller plant, approaching *F. hispida* in the thicker reddish sepals (M), Nash 910, June 1-15, 1894 (M N); Aspalaga, Chapman, October, 1897, in part, the smaller



plant (M), no locality given, Curtiss, 1875, a very large form with abnormally opposite leaves, approaching *F. hispida* in the hispid sheaths and leaves.

5. *FUIRENA BREVISETA* Coville.

*Fuirena breviseta* Coville, Bull. Torr. Bot. Club. 28 : 466. (1901).

*Fuirena squarrosa breviseta* Coville, Bull. Torr. Bot. Club. 17 : 6. (1890).

*Fuirena squarrosa* Chapman, Fl. S. U. S. 514, (1860); not *Fuirena squarrosa* Michx. l. c. (1803).

Rootstocks stout, elongated; stems tall, robust, leafy, 3 to 8 dm. tall; leaf-blades flat, thickish, densely pilose beneath, minutely pubescent above or sometimes smooth, nervose, acuminate at apex; sheaths on the upper part of the stem smooth, on the lower part often densely finely pilose; spikelets sessile, 2 to 8 together in the capitate clusters, ovoid or ovoid-oblong, 6 to 12 mm. long, 4 to 6 mm. in diameter; scales obovate or oblong, brown, more or less hispid-pubescent, 3-nerved, each tipped with a stout spreading or recurved awn nearly as long as the body; sepals 3; blades oval, obovate or suborbicular, acutish at the base, rounded or truncate at the apex, and with a minute apiculation; perianth-bristles short, not longer than the stipe of the achene, smooth; achenes oblong, triquetrous, light yellow at maturity, tipped with the antrorsely hispid style, which is as long as the achene. — Sandy soil along the coast, from eastern North Carolina to Florida, west along the Gulf coast to southern Texas. Summer and autumn.

*Specimens examined.* — NORTH CAROLINA: No locality given, *Kearney* 1963, August 1, 1898 (N), *McCarthy*, July, 1885 (N); Washington, *Biltmore Herbarium*, July 17, 1897 (B). SOUTH CAROLINA: No locality given, *Gibbes*, without date of collection (N). GEORGIA: *Leslie*, *Harper* 403, August 17, 1900 (M N); *Empress*, *Harper* 1628, September 13, 1902 (M N); no locality given, *Beyrich*, 1833 (M). FLORIDA: *Miami*, *Garber*, July, 1877, type



(M N); Eustis, *Nash* 1038, June 16-30, 1894 (B M N), *Hitchcock*, June and July, 1894, in part, the larger plant (M); Jacksonville, *Curtiss* 4098, July 13, 1893 (N), 5064, September 17, 1894 (M N), 5582, October 30, 1895 (B M N); Rosewood, *Garber*, June, 1876 (N); Duval County, *Curtiss* 3068, July, year not given (N); Jefferson County, *Hitchcock*, June and July, 1898 (M); Myers, *Hitchcock* 412, July and August, 1900 (M N); no locality given, *Chapman*, 1897 (M), *Chapman*, without date of collection (M), *Simpson*, 1889 (N). ALABAMA: Mobile, *Mohr*, 1897 (B). MISSISSIPPI: Tchouteco Bouffe River, *Tracy* 4814, October 9, 1898 (M); Biloxi, *Tracy* 6321, June 22, 1899 (B N); Ocean Springs, *Tracy* 54, July 19, 1899 (N), *Skehan*, 1895 (M), *Seymour* 14, August 21, and September 11, 1891 (M). LOUISIANA: Lake Charles, *Mackenzie* 437, August 25 to September 10, 1898 (M); Hammond, *Biltmore Herbarium*, September 17, 1900 (B). TEXAS: Hockley, *Thurrow*, without date of collection (N); Eastern Texas, *Nealley*, 1888 (N); Orange, *Letterman* 547, August 11, 1886 (M).

## 6. FUIRENA HISPIDA Elliott.

*Fuirena hispida* Elliott, Sk. 1: 579. (1821).

*Fuirena squarrosa hispida* (Ell.) Chapman, Fl. S. U. S. 514. (1860).

Rootstocks slender, usually tuber-bearing; stems smooth or rarely a little pubescent, few-leaved, 3 to 8 dm. tall; leaf-blades linear, 5 to 12 dm. long, short-pubescent above, long-pubescent beneath, sheaths densely hispid with long spreading hairs; spikelets sessile, 3 to 8 together in the capitate clusters, ovoid or ovoid-oblong, 6 to 12 mm. long, 4 to 6 mm. in diameter; scales obovate or oblong, brown, more or less hispid-pubescent, 3-nerved, nearly as long as the body; sepals 3; blades deltoid-ovate, acuminate at apex, truncate or cordate at base, thick, reddish, opaque or nearly so, tapering into a



thick unbarbed point or tip; perianth-bristles reaching to the middle of the achene or rarely to its tip, retrorsely barbed; achenes fully 1 mm. long, triquetrous, light yellow at maturity, tipped by the antrorsely hispid style, which is one-half as long as the achene. — Sandy fields and woods, New Jersey to Florida, west to Texas, north to Kentucky and Indian Territory. Summer and autumn.

*Specimens examined.*—NEW JERSEY: Forked River, *Britton*, August, 1889 (N); no locality given, *Knieskern*, without date of collection (M N), *Dr. B.*, without date of collection (N). DISTRICT OF COLUMBIA: Washington, *Ward*, 1879 (N), *Coville*, September 29, 1889 (N). MARYLAND: Salisbury, *Holmes* 185, August 1, 1890 (N); Beltsville, *Olds*, September, 1898 (N). NORTH CAROLINA: Salisbury, *Heller* 188, August 21, 1890 (M). SOUTH CAROLINA: Aiken, *Ravenel*, September, 1869 (N); Blue Ridge, *Redfield* 8600, September 3, 1876 (M); Graniteville, *Eggert*, August 6, 1898 (M). GEORGIA: Clarke County, *Harper* 89, June 29, 1900 (M N); Tifton, *Harper* 665, September 19, 1900 (N); Oconee and Gwinnett Counties, *Small*, July 14, 1893 (M N); Cordele, *Tracy* 1511, July 20, 1890 (N); Washington, *Chapman*, without date of collection (B). FLORIDA: Aspalaga, *Chapman*, October, 1897 (B M); *Chapman*, October, 1897, in part, the larger plant (N); Pablo Beach, *Combs* 47, July 21, 1898 (N); Indian River, *Palmer*, 1874 (M); Lake City, *Rolfs* 885, September 6, 1893 (M); no locality given, *Buckley*, without date of collection (M N). ALABAMA: Auburn, *Earle & Baker*, August 11, 1897 (B M), September 8, 1897 (M); Spring Hill, *Bush* 74, August 22, 1897 (M); Montgomery, *McCarthy*, August, 1888 (M); Greensboro, *Biltmore Herbarium*, August 4, 1899 (B); no locality given, *McCarthy*, August, 1888 (N), *Bigelow*, without date of collection (M). MISSISSIPPI: Waynesboro, *Pollard* 1230, August 8 and 9, 1896 (M N). TEXAS: Rusk County, *Vinzent* 28, July, August, year not



given (M); Hempstead, *Hall* 693, June 1, 1872 (M), 693, June 1, 1872, in part, the three larger plants (MN); Millcreek, *Lindheimer* 107, August, 1843 (M); Tyler, *Reverchon* 2302, September 20, 1900 (M); Eastern Texas, *Nealley*, 1884, 1888 (N); Southwestern Texas, *Lindheimer* 187, 1843 (M). INDIAN TERRITORY: Atoka, *Sheldon* 63, June 23, 1891 (N).

7. FUIRENA CILIATA Bush, sp. nova.

Rootstocks stout, elongated, tuber-bearing; stems stout, leafy, 4.5 to 6 dm. tall, densely and softly pilose with long white hairs; leaf-blades numerous, 3 to 8 on the stems, broad and long, 5 to 15 cm. long, 4 to 6 mm. wide, densely pilose on both sides, and ciliate on the margins with long white hairs; sheaths densely pilose with long spreading white hairs; spikelets sessile, 3 to 8 together in the capitate clusters, ovoid or ovoid-oblong, 6 to 12 mm. long, 4 to 6 mm. in diameter; scales obovate or oblong, 3-nerved, densely hispid and ciliate with long white hairs, tipped with a long slender ciliate awn, much longer than the body; sepals 3; blades deltoid-ovate, truncate at base, tapering into a blunt tip, thick, reddish, opaque; perianth-bristles reaching to the middle of the achene, smooth, unbarbed; achenes oblong, sharply triquetrous, with concave sides, rather more than 1 mm. long, tipped with the style, which is about one-half as long as the achene, white at maturity. — Swamps, eastern Texas. Summer and autumn.

*Specimens examined.* — The only specimens seen are those of the type, collected at Swan, Smith County, Texas, by *J. Reverchon* 2911, June 10, 1902 (M), and those collected at Palestine, Texas, by *H. Eggert*, June 10, 1899 (M).

8. FUIRENA SIMPLEX Vahl.

*Fuirena simplex* Vahl, Enum. 2: 384. (1806).

*Fuirena squarrosa aristulata* Torr. Ann. Lyc. Nat. Hist. N.Y. 3: 291. (1836).

Rootstocks slender, usually fibrous, not tuber-bearing;



stems commonly robust, 1 to 8 dm. tall, smooth, leafy; leaf-blades flat, linear, 3 to 25 cm. long, 3 to 10 mm. wide, smooth above, sometimes sparsely pubescent beneath, sometimes slightly ciliate on the margins, acuminate at the apex; sheaths smooth on the upper part of the stem, sometimes pubescent on the lower part; spikelets sessile, 2 to 8 together in the capitate clusters, ovoid or ovoid-oblong, 6 to 12 mm. long, 5 to 8 mm. in diameter; scales obovate or oblong, brown, pubescent, 3-nerved, each tipped with a short, slender, spreading awn; sepals 3; blades ovate-oblong, obtuse or retuse at the apex, the retrorsely-barbed awn arising from just below the apex, sometimes wanting; perianth-bristles retrorsely-hispid, equaling or exceeding the short-stalked achene; achenes triquetrous, fully 1 mm. long, bright white at maturity. — Sandy plains and saline soil, Nebraska (?), Missouri and Kansas, to western Arkansas, Texas, New Mexico and Mexico. Summer and autumn.

*Specimens examined.* — MISSOURI: Courtney, *Bush* 223, October 24, 1897 (M); Irondale, *Glatfelter*, August 21, 1895 (M); Annapolis, *Russell*, September 25, 1899 (M); Piedmont, *Russell*, date of collection not given (M). ARKANSAS: Fulton County, *Blankinship*, August, 1888 (N). INDIAN TERRITORY: Sapulpa, *Bush* 1400, September 29, 1895 (M); Sand banks of the Canadian River, *Bigelow*, 1853-54 (N). KANSAS: Comanche County, *Hitchcock* 861, 1896 (M N). TEXAS: Dallas, *Reverchon* 2301, August 10, 1900 (M), 3602, 1880 (M), 1000, 1880 (M), *Letterman*, 1881 (N); Squaw Creek, Gillespie County, *Jermy* 538, 1389 (N); Moore County, *Carleton* 426, August, 1891 (N); San Antonio, *Bush* 1224, October 2, 1900 (M N), *Eggert*, September 8, 1900 (M); Kerrville, *Heller* 1937, June 26-30, 1894 (B M N); Columbia, *Bush* 1312, October 5, 1900 (M); Orange, *Letterman* 547, August 11, 1886 (M); New Braunfels, *Lindheimer* 184,



May, 1846 (M N), 185, 186, May, 1846 (M); Hempstead, *Hall* 693, June 1, 1872, in part, the two smaller plants (M N); Southwestern Texas, *Palmer* 1335, September, 1879, to October, 1880 (M); Western Texas, *Wright* 718, May-October, 1849 (N); Devil's River, *Eggert*, September 10, 1900 (M); Valley of Rio Grande, below Dona Ana, Donna Ana County, New Mexico, *Mexican Boundary Survey* 1523, 1848, in part, the stouter broken stem (M N). NEW MEXICO: On Arkansas River, *Fendler* 125, without date of collection (M). MEXICO: States of Coahuila and Nuevo Leon, *Palmer* 1336, February to October, 1880 (N); Hacienda de Angostura, *Pringle* 3690, July 26, 1891 (M).



## TWO NEW TEXAS TRADESCANTIAS.

BY B. F. BUSH.

In a recent number of the Transactions of The Academy of Science of St. Louis\*, I gave an account of the Texas species of *Tradescantia*, in which it appeared necessary to describe ten new species besides enumerating eight others already described. It would seem that these eighteen species were all that could be expected from the State of Texas, and from the amount of material examined I had thought the field pretty well gleaned.

But since presenting my paper last December, I have received from Mr. C. D. Beadle, of the Biltmore Herbarium, three species of *Tradescantia* for identification, collected in Texas by Mr. T. G. Harbison, one of which is *T. australis*, but the other two I can not refer to any of the species given in my paper. In order that our knowledge of the Texas species of *Tradescantia* may be as complete as possible, I append the following descriptions of these two species:—

### TRADESCANTIA HARBISONI Bush, sp. nova.

Stems short, slender, weak, 1 to 2 dm. long, much branched at the base, decumbent or ascending, densely white-woolly throughout with long spreading white hairs, dark yellowish-green; leaf-blades linear-lanceolate, flat, thin, long-hairy on both sides, 1 to 2 dm. long, 6 to 10 mm. wide, one on each stem; sheaths almost none, very loose and thin, beautifully nerved and rose-colored, hairy like the leaves; bracts of the involucre 2, unequal, broader than the leaves, 8 to 15 mm. wide, broadest below the middle, the longer one 1 to 1.5 dm. long, thin, flat, hairy like the leaves, tapering to a blunt point, beautifully nerved and rose-colored at the thin papery bases; cymes

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\* Trans. Acad. Sci. St. Louis. 14: 7. (Dec. 30, 1904).



about 10- to 25-flowered; pedicels 3 to 5 cm. long, villous with long white hairs; sepals ovate, obtuse, 8 to 10 mm. long, densely pubescent with white hairs; corolla very large, deep purple, the large obovate petals very thin and beautifully veined. — Sandy soil, Texas. Spring.

This species is nearest *T. Texana* Bush, but is abundantly distinct. Named for Mr. T. G. Harbison, collector of this and the following.

*Specimens examined.*—TEXAS: The only specimens seen are those of the type, collected at Bryan, Brazos County, by *T. G. Harbison* 200, April 11, 1903.

*TRADESCANTIA DIFFORME* Bush, sp. nova.

Stems at first simple, later much branched from the root, erect, stout at base, 2 to 3 dm. tall, few branched above, smooth and glaucous; branches erect, slender; leaf-blades long-linear, acuminate, 1 to 2 dm. long, 6 to 10 mm. wide, straight, flat or a little conduplicate, very smooth; sheaths somewhat imbricated at base of stem, very smooth and glaucous; bracts of the involucre 2, those of the primary stems very short, unequal, 3 to 5 dm. long, conspicuously saccate at the bases, very smooth and glaucous, those of the later stems and branches much longer, unequal, saccate at the bases and glabrous; cymes about 10- to 15-flowered; pedicels 1 to 3 cm. long, sparsely glandular-pubescent; sepals lanceolate, acuminate, 8 to 10 mm. long, sparsely glandular-pubescent and tipped at the apices with a tuft of long white hairs; corolla large, of a beautiful rose-color, the large obovate petals very thin and beautifully veined. — Sandy soil, Texas. Spring.

This is probably most nearly related to *T. gigantea* Rose, but lacks the characteristic velvety pubescence of that species.

*Specimens examined.*—TEXAS: The only specimens seen are those of the type, collected in Brazos County, by *T. G. Harbison* 14, 791, April, 1903.



NEW PLANTS FROM MISSOURI.

BY K. K. MACKENZIE AND B. F. BUSH.

SAGITTARIA BREVIROSTRA Mack. & Bush, sp. nova.

A glabrous monoecious perennial growing in swamps. Leaf-blades with petioles about 3 dm. long, deep green and shining, strongly sagittate, resembling narrow-leaved forms of *S. latifolia* Willd.; basal lobes 2 to 3 dm. long, long acuminate, pointing downwards, the middle lobe 2 to 2.5 dm. long, also acuminate, pointing upwards; scape tall, stout and robust, 4- to 6-angled, the larger often 25 mm. thick, noticeably taller and stouter than that of *S. latifolia*, with which it is associated, often 8 dm. tall, and exceeding the leaves; bracts separate or very slightly united at base, lanceolate, tapering to a long acumination, especially the lower ones, the acumination of which is sometimes 3 to 4 cm. long, exceeding the pedicels in length, reflexed in age; whorls of the inflorescence numerous, usually branching below, the lower ones bearing pistillate, the upper ones staminate, flowers; pedicels straight, the fertile ones usually 2 cm. or less long, those bearing the staminate flowers a little longer; flowers barely 25 mm. across, with spreading white petals; sepals about 10 mm. long, ovate, obtuse; filaments glabrous; mature fruiting heads depressed-globose, 2 to 3 cm. in diameter; achenes about 2.5 mm. long, obovate-cuneate to nearly square, winged on one margin only and ridged on the side, the wing extending above the body of the achene; beak erect, lateral, minute, .5 mm. or less long.—In shallow sloughs along the Missouri River bottoms, western Missouri. Summer and autumn.

Readily distinguished from all forms of *S. latifolia* by the minute erect beak of the achene, *S. latifolia* having a



horizontal or oblique much longer beak. From *S. arifolia* Nutt., the entirely different leaves and extremely long pointed bracts usually differentiate it, and from *S. cuneata* Sheldon, it is distinguished not only by the last named character, but by the fact that *S. cuneata* is an aquatic provided with phyllodia, which our plant does not possess. In addition to the above characters, the achene of our plant is winged on one margin only, and the beak is at the edge of the top of the achene on the unmargined side, while *S. arifolia* has achenes strongly margined on both sides, and the beak in the center of the top of the achene. *S. longiloba* Engelm. differs in its much longer basal leaf lobes, its smaller bracts, and different-shaped achenes. While, as above stated, *S. arifolia* usually differs from our plant very strongly in size and aspect, specimens collected by Mr. Cratty in Northern Iowa approach it in these particulars, but as far as we have seen, the achene characters given above are very constant.

*Specimens examined.*—The only specimens seen are those of the type, collected at Courtney, Jackson County, by *B. F. Bush* 2175, August 14, 1904, and October 10, 1903.

HEUCHERA PUBERULA Mack. & Bush, sp. nova.

Foliage merely puberulent. Rootstocks slender, short; stems delicate and slender, 2 to 3 dm. tall, or less, pubescent merely, leafless, but bearing a few slender, minute, entire bractlets; leaf-blades reniform-cordate, from 4 to 12 cm. wide, and from 2.5 to 7.5 cm. long, puberulent on both sides and short-pubescent on the veins beneath, thin, green above, usually strongly reddened beneath, the basal sinus rather shallow, more deeply lobed and the teeth sharper than in *Heuchera parviflora* Bartl.; petioles 2 dm. or less long, puberulent merely; panicle 3 to 20 cm. long, rather one-sided, the axis and main branches glabrate or puberulent, the pedicels and especially the hypanthiums short-pubescent; hypanthium campanulate, fully 2 mm. long



during anthesis, the obtusish sepals about one-third the length of the tube, enlarging later; petals white, linear-spatulate, twice the length of the sepals; stamens long-exserted. — Rocky cliffs, southern Missouri. Summer and autumn.

Related to *Heuchera parviflora* Bartl., to which it has been constantly referred, but distinguished by the italicized portions of the above description. In *H. parviflora* the petioles are villous to pubescent, and the lobing of the leaves is very shallow.

*Specimens examined.* — MISSOURI: Monteer, Shannon County, *Bush* 1119, October 23, 1901, type, 195, July 27, 1899; Shannon County, *Bush*, September 12, 1888; October 21, 1893; Carter County, *Trelease* 289, September 10, 1897.

CONVOLVULUS FRATERNIFLORUS Mack. & Bush, sp. nova.

*Convolvulus sepium fraterniflorus* Mack. & Bush, Man. Fl. Jackson County, Mo. 153. (1902).

Sparingly short-pubescent or glabrate. Stems trailing or twining, much branched, the branches much interwoven and twisted, 1 to 2 m. long, glabrate or short-pubescent; leaf-blades hastate, rarely nearly sagittate, *short-pubescent on both surfaces*, especially on the upper surface, acute, deeply cordate at base, the basal lobes spreading, and either entire or in vigorous plants obliquely truncate and toothed, 3.5 to 9 cm. long, and from 2.5 to 9 cm. wide at base; petioles 2 to 5 cm. long; peduncles one or *more often two in the axil of each leaf*, strongly quadrangular, *the angles noticeably winged*, shorter or occasionally longer than the petioles; bracts of the calyx *large, strongly cordate*, acute or obtusish, pubescent without, 2 to 4 cm. long, *entirely overlapping and concealing the sepals at flowering time*; calyx much shorter than the bracts, glabrous; sepals obtusish, ovate or oblong-ovate, 10 to 15 mm. long; corolla



pure white, about 5 cm. long; mature capsules not seen.— Dry banks and prairies, western Missouri. Summer and autumn.

This plant is easily distinguished by the italicized portion of the description above, the large bracts being especially noteworthy.

*Specimens examined.*—MISSOURI: West Belton, Cass County, *Mackenzie* 100, August 4, 1902; Oak Grove, Jackson County, *Mackenzie* 75, July 30, 1902; Lee's Summit, *Mackenzie*, July 6, 1900; Martin City, *Mackenzie, Bush*, July 9, 1899, type.

*DASYSTOMA CALYCOSA* Mack. & Bush, sp. nova.

Perennial, perfectly glabrous. Stems 5 to 15 dm. tall, glaucous, diffusely much branched; lower leaves about 1 dm. long, the blades strongly veined, ovate-lanceolate or ovate-oblong in outline, the lower portion typically very deeply pinnatifid, often leaving the middle portion but 2 mm. wide, the 2 to 6 segments from oblong-linear to triangular, entire or with 1 to 3 teeth, the terminal portion of the blade lanceolate or ovate-lanceolate, irregularly cleft and jagged, the margins of the blade ciliolate, the upper surface scabrous-pubescent; petioles ciliate; inflorescence branching, the very slender elongated branches widely spreading; bracts narrowly linear-lanceolate, acuminate, entire, the blades 2 to 4 cm. long, tapering to petioles some 5 mm. long; pedicels stout, usually strongly curved, 3 to 8 mm. long; body of the calyx 6 to 8 mm. long, nerved strongly; sepals linear-awl-shaped, 7 to 10 mm. long when developed and exceeding the body of the calyx, one or more often abortive; corolla 3 to 4 cm. long, rather narrowly funnel-form for the genus; capsules broadly oval-ovate, pointed, 10 to 15 mm. long.— Rocky wooded hills in the Ozark region. Missouri and Arkansas. Summer and autumn.

This species may be readily distinguished from the



eastern *Dasystoma Virginica* (L.) Britton, which we have not seen from west of the Mississippi, by its much more divided leaf-blades which are scabrous-pubescent above, its very narrow corolla tube and especially by its long calyx teeth, the eastern plant having short triangular or short oblong calyx teeth, which are shorter than the body of the calyx.

*Specimens examined.* — MISSOURI: Monteer, Shannon County, *Bush* 219, July 31, 1899, type, 722, August 21, 1901; Bay Mills, Ripley County, *Mackenzie* 412, July 24, 1897; Hunter, *Trelease*, July 31, 1895; Pilot Knob, *Russell*, September, 1897; *Glatfelter*, August 20, 1895; Einstein Mine, Madison County, *Trelease* 529, August 18, 1897; Flat River, St. François County, *Trelease* 530, October 13, 1897; Iron County, *Trelease* 532, August 18, 1897. ARKANSAS: Little Mamelie, *Engelmann*, September, 1835; Little Rock, *Hasse*, September 20, 1885.

XANTHIUM INFLEXUM Mack. & Bush, sp. nova.

*Xanthium speciosum* M. & B., Man. Fl. Jackson County, Mo. 187. (1902), not of Kearney.

Glabrate, or the upper part from sparingly to strongly roughened with small white papillae. Stems 1 to 1.5 m. tall, upright, much branched; leaf-blades cordate or ovate-cordate, strongly irregularly crenate-dentate, 3-lobed, the middle lobe much the largest, in outline resembling the leaf of *Malva sylvestris* L., strongly acuminate, from nearly glabrous to roughened below, slightly roughened above; petioles 5 to 15 cm. long, rather slender, strongly roughened with small white papillae; burs densely clustered, 2.5 cm. or less long, glandular-pubescent or glandular short-pubescent all over the body and the lower part of the prickles and beaks, never hispid, the body oblong-elliptical, 2 cm. or less long, and less than half that in width, somewhat tapering at the base; prickles longer than the diameter of the body of the bur, numerous, rather



slender, strongly hooked, glandular-pubescent or glandular short-pubescent below, glabrate above, those near the top of the bur sometimes considerably longer and sometimes considerably shorter than those near the base; body of the bur never concealed by the prickles; beaks stout, about 10 mm. long, at maturity abruptly bent at the middle, inflexed and at length greatly overlapping, hooked at the apex. — Sandy bottoms along the Missouri River in western Missouri. Autumn.

In the sandy bottoms near Courtney, Missouri, *Xanthium glabratum* (DC.) Britton, *X. commune* Britton, and *X. Pennsylvanicum* Wallr., abound, the last two species probably freely intergrading. The species above proposed as new is less common than the others, but is the most distinct of all. The leaves are more acuminate and toothed than is common with the other species, while the bur with its long and irregular prickles and inflexed overlapping beaks forming a circle, presents a markedly peculiar aspect.

*Specimens examined.* — MISSOURI: Courtney, *Bush* 869, September 13, 1900, 1916, October 5, 1903, type, 1804, 1806, October 21, 1902.

SENECIO SEMICORDATUS Mack. & Bush, sp. nova.

*Senecio aureus* Mack. & Bush, Man. Fl. Jackson County, Missouri. 207, (1902), not of L.

Perennial, 5 dm. or less tall, growing in small clumps, usually soon very glabrous all over, with the exception of some pubescence along the margins of the lower portions of the radical leaves, rarely a slight pubescence remaining elsewhere; blades of radical leaves *ovate-oblong*, very obtuse or rounded at the apex, *shallowly cordate*, *semicordate* or *truncate at base but never deeply cordate*, veiny, glabrous, crenate-dentate, typically 5 to 7.5 cm. long, 3.5 to 4 cm. wide, the petioles 9 to 15 cm. long; stem-leaves oblong-lanceolate, more or less clasping, the lower about



7.5 cm. long, the upper shorter, irregularly cleft or lacinate; heads few to many, in a simple or compound corymb, the long-acuminate bracts 6 to 7 mm. long; heads 8 to 12 mm. high, 10 to 14 mm. broad (without the rays); rays conspicuous, 8 to 12, toothed at the apex, 5 to 6 mm. long; achenes glabrous. — Low prairies, Illinois, Iowa and Missouri to Kansas and Texas. Spring.

*Senecio aureus* L., with its cordate-ovate to reniform basal leaves which are very deeply cordate at base, is very readily distinguished from this species.

Much more closely related to *S. pseud aureus* Rydb., of the Rocky Mountain region, but consistently has much less sharply serrate and more oblong lower leaves, much less pinnatifid upper leaves, and usually smaller heads and shorter rays.

*Specimens examined.* — MISSOURI: Levasy, Jackson County, *Bush* 1678, May 18, 1902, type; Independence, *Mackenzie*, May 4, 1896; Adam's Station, Jackson County, *Mackenzie*, May 23, 1897; Sheffield, *Mackenzie*, June 4, 1899. ILLINOIS: West Chicago, *Umbach*, May 25, 1897. IOWA: Johnson County, *Fitzpatrick*, May, 1896. KANSAS: Bourbon County, *Hitchcock*, May 5, 1897. TEXAS: Austin, *Bray*, March 10, 1898; San Marcos, *Stanfield*, 1898.



A DISEASE OF BLACK OAKS CAUSED BY POLYPORUS  
OBTUSUS BERK.

BY PERLEY SPAULDING.

Of the numerous fungi which attack living deciduous trees by gaining entrance through wounds or dead branches, *Polyporus obtusus* is not very generally known. The disease caused by this fungus is quite destructive locally to several species of oak trees which are of minor importance as timber trees. Because so little seems to be known of this fungus, and also because of the ever increasing importance of the inferior timber trees, it has seemed advisable to find out as much as possible concerning this disease, which has been discovered in certain localities in central Missouri and northern Arkansas. The disease which is caused by the fungus *Polyporus obtusus* in living trees of *Quercus marilandica* and *Q. velutina* has been found only in the above mentioned places, but it is more than probable that it is present in many others where it has not been noted. Because of the insects which eat the sporophores very rapidly, usually totally destroying them and rarely leaving a single one intact for any length of time, the damage caused by the fungus is very hard to estimate and it is impossible to determine the percentage of diseased trees. The thick, dark-colored, deeply furrowed bark covers injuries very effectually so that it is impossible to detect affected trees unless the sporophores are still upon them.

*Polyporus obtusus* seems to occur only in North America. In the United States it has been collected and reported from widely scattered localities as follows: Alabama by Mohr and Underwood & Earle; Arkansas by Hedgcock and Spaulding; Iowa by Holway, McBride, and von Schrenk;



Maryland by Ricker; Missouri by von Schrenk and Spaulding; New Jersey by Ellis; Tennessee by von Schrenk.

As stated above, this fungus seems to be limited to North America, as no references have yet been found citing its occurrence elsewhere. Berkeley, who published the first description of it, mentions a "Mr. Drummond" who collected the type specimens, probably while with Franklin on his second journey to the polar sea. Very probably the collection was made in Canada, but where, cannot be ascertained.



DISTRIBUTION OF BLACK OAKS AND FUNGUS.

This fungus seems to be limited as to its hosts as well as in distribution, for it is reported only from different species of the oaks. Berkeley, who named it, gave no host; Ellis in his North American Fungi number 309 records it from "dead standing trunks of *Quercus coccinea*;" McBride found it on "bur oak" trees killed by fire; Underwood and Earle found it once on *Quercus rubra*; Mohr reports it from *Quercus texana*; von Schrenk has found it on the black oaks; and the writer has found it on trees of



*Quercus marilandica* and *Quercus velutina*. In all cases where the scientific name is given so that there can be no mistake as to the identity of the host, the fungus is seen to occur only on members of the "black oak" group. The range of the different host species has been ascertained and covers the region east and south of the curved black line in figure, including the eastern portion of the United States. The localities from which the fungus is known are indicated by stippling. In this way one may see what is the probable distribution of the fungus and in what localities it is likely to be found in the future.

As far as there is any mention made, the inference is that *Polyporus obtusus* is a saprophyte only, and there is not the slightest hint of its occurring as a wound parasite. Living trees of *Quercus marilandica* and *Quercus velutina* have been found by the writer in two quite widely separated localities with this fungus occurring as a wound parasite. It not only grows on the trees but it sooner or later causes the death of the affected trees.

On investigation it was found that the sporophores were growing out of the entrances of burrows made by some wood-boring insect. The insect itself has not been seen but the burrow corresponded exactly with the descriptions of the work of an oak-boring insect known as *Prionoxystus robiniae* Peck. This insect is mentioned by Packard\* as occurring from Maine to Texas and California in the wood of the oaks. It works on living trees and burrows in heart and sap wood alike. The moth is two and possibly three years in reaching maturity. Red oak is attacked in Maine. Packard found it in pin oak at Houston, Texas, and it is said to attack willow in some sections. It is known from California and probably occurs wherever black, red, and white oak and locust trees grow in this country. Fitch†

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\* Packard, Report U. S. Entomological Commission. 5: 53-58. (1890).

† Fitch, Report on the noxious, beneficial and other insects of the State of New York. 5: 4. (1859).



says "It perforates a hole the size of a half inch auger, or large enough to admit the little finger. \* \* \* This hole running inward to the heart of the tree, and admitting the water thereto from every shower that passes, causes a decay in the wood to commence and the tree never regains its previous soundness." The moth seems to lay her eggs on either healthy or injured trees with no decided preference for either one. The burrows found with the fungus growing in them were partly in apparently perfectly sound trees and partly in trees having some injury partially healed over.

The spores of the fungus were evidently blown into the entrances of the burrows and the fungus then started to grow and followed the burrow until the heart of the tree was reached. The heart wood itself becomes affected and the rot extends throughout the wood of the tree trunk until the top is broken over by the wind or the weight of the tree.

As stated above the disease has been found occurring locally in Missouri and northern Arkansas in trees of *Quercus marilandica* and *Q. velutina*. In the places where found, the timber had formerly been cut off and a new growth of mixed oaks had taken the place of the cut forest. This new growth was very thick and reached the height of about twenty-five feet, and six inches in diameter. The sporophores appeared within about six or seven feet of the ground below the lower branches of the trees. In the localities where the disease was found nearly all of the trees of the two species mentioned above were affected, while the trees of white oak which were scattered among the others were never seen to have the fungus upon them. This is just what one would naturally expect under the circumstances, as the insect seems to have a preference for the two affected species and not to attack the white oak at all.

The rot extends up and down in the heart wood until



the tree is so weakened that it breaks over or dies outright. All gradations in the severity of the disease were found between those where the rot extended only a very short distance from the burrow itself (plate 18, figure 1) and those with the tree nearly or quite dead, and having practically all of the wood rotted (plate 19, figure 1). As the disease progresses in the heart wood the sap wood becomes affected, in that it constantly becomes thinner and thinner until the death of the tree, which latter event is usually caused by the sap wood becoming so thin that it cannot any longer hold the weight of the upper parts of the tree, or the sap wood becomes so affected that it can no longer carry on its proper functions in supplying water to the upper portions of the diseased tree. As above mentioned, the rot in the early stages extended only a few inches each way from the original infection, but in the late stages the whole tree trunk may become affected for its whole length. From what could be gathered by observation, it seemed that the fungus works remarkably fast in causing the death of the attacked trees.

The heart wood of the black oaks is naturally rather dark in color but when affected by *Polyporus obtusus* it turns a light yellowish tint and in the last stages becomes almost white. The diseased wood retains its fibrous appearance but breaks much easier than does the healthy wood. It does not have the shrinkage cracks which are so characteristic of some of the wood rots. Neither does the affected tissue crumble between the fingers nor break very easily into small flakes. Wherever there is room enough for such formations to occur, strings and sheets of mycelium are formed, which are nearly or quite white in color. In trees which are not yet badly affected the color turns darker as we go from the rotted portion toward the bark of the tree until we reach the unaffected sap wood. In quite badly diseased trees there is a more or less distinct



darker line at the edge of the heart wood, while the sap wood itself is darkened where it is apparently taking on the characteristics of heart wood prematurely. A tree which has a sporophore upon it is always more or less seriously affected and the rot extends from a few inches to as many feet longitudinally in the tree.

In the earlier stages of the disease the cell walls do not seem to have any single component extracted to any very serious extent. In the last stages of the disease, however, there are quite extensive streaks and patches of cells in the spring wood which have been so affected that their walls give the cellulose reaction. These areas are always located in the early wood of the annual rings, but the late wood still retains its normal yellow color. On testing the wood it was found that the white portions turned blue with chlor-iodide of zinc, and the cells are very readily seen to have the middle lamellae dissolved so that the cells separate from each other. The wood fibres are seen lying loosely beside each other and stained blue with chlor-iodide of zinc. The starch, which is commonly so plentiful in the medullary rays, is wholly absent in the whitened tissues. In the earlier stages of the rot scattering medullary ray cells are found containing considerable quantities of starch. These starch grains took the blue color and seemed to be rather smaller than normal. In medullary ray cells of medium stages of the disease a quite definite layer is seen lining the cell and not taking the stains for lignin and also not taking the stain for cellulose. Tests made upon the white tissues of the early wood of the annual rings seemed to show that the lignin was wholly extracted. Maule's potassium permanganate test gave a bright red only in the unaffected tissues. This was true also with phloroglucin and other lignin tests, while chlor-iodide of zinc gave the blue reaction in the white and worst affected tissues. As mentioned above, the middle lamellae were dissolved wherever the lignin was extracted from the walls.



Comparatively few instances have yet been recorded where the larger fleshy fungi attack trees by means of insect burrows. Probably the best known case is that of *Polyporus volvatus*\* Peck, which has been found by von Schrenk to occur exclusively in the burrows of certain insects. *Polyporus pinicola* † is also said to enter trees by the same means. *Schizophyllum alneum* and *Lentinus lecomtei* have been found by the writer growing in insect burrows in standing trees. *Polyporus rimosus* is mentioned by von Schrenk ‡ as follows: "Infection takes place through the older branches and through the tunnels made by the locust borer." There are undoubtedly many of the Polyporaceae which occasionally enter trees in the same manner.

The writer desires to avail himself of this opportunity to express his thanks to the Director of the Missouri Botanical Garden for the use of the facilities of the Garden in this and other work done by him at the Mississippi Valley Laboratory of the United States Department of Agriculture, located at the Garden.

#### EXPLANATION OF PLATES.

Plate 13.—1, Upper surface of a sporophore of *Polyporus obtusus* Berk. 2, Lower surface of a sporophore of *Polyporus obtusus* Berk. The large irregularly shaped pores are well shown.

Plate 14.—1, *Polyporus obtusus* Berk. growing out from the entrance of a burrow of *Prionoxystus robiniae* in a tree of *Quercus marilandica*. This tree was but slightly injured by the fungus. 2, Sporophore of *Polyporus obtusus* Berk. in burrow of oak borer on a tree of *Quercus velutina*. This and the preceding figure show the general shape of the fungus sporophore very well.

Plate 15.—1, *Polyporus obtusus* on a tree of *Quercus marilandica*. The tree is but slightly affected in the neighborhood of the insect burrow.

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\* von Schrenk, Bull. Div. Phys. & Path., U. S. Dep. Agric. 25:13-14. (1900).

† Spaulding, Report Mo. Bot. Garden. 15: 75-76. (1904).— von Schrenk, Bull. Div. Veg. Phys. & Path., U. S. Dept. Agric. 25: 14. (1900).

‡ von Schrenk, Report Mo. Bot. Garden. 12: 24. (1901).



2, A tree of *Quercus marilandica*, killed by *Polyporus obtusus* Berk. The trunk is rotted throughout heart and sap wood.

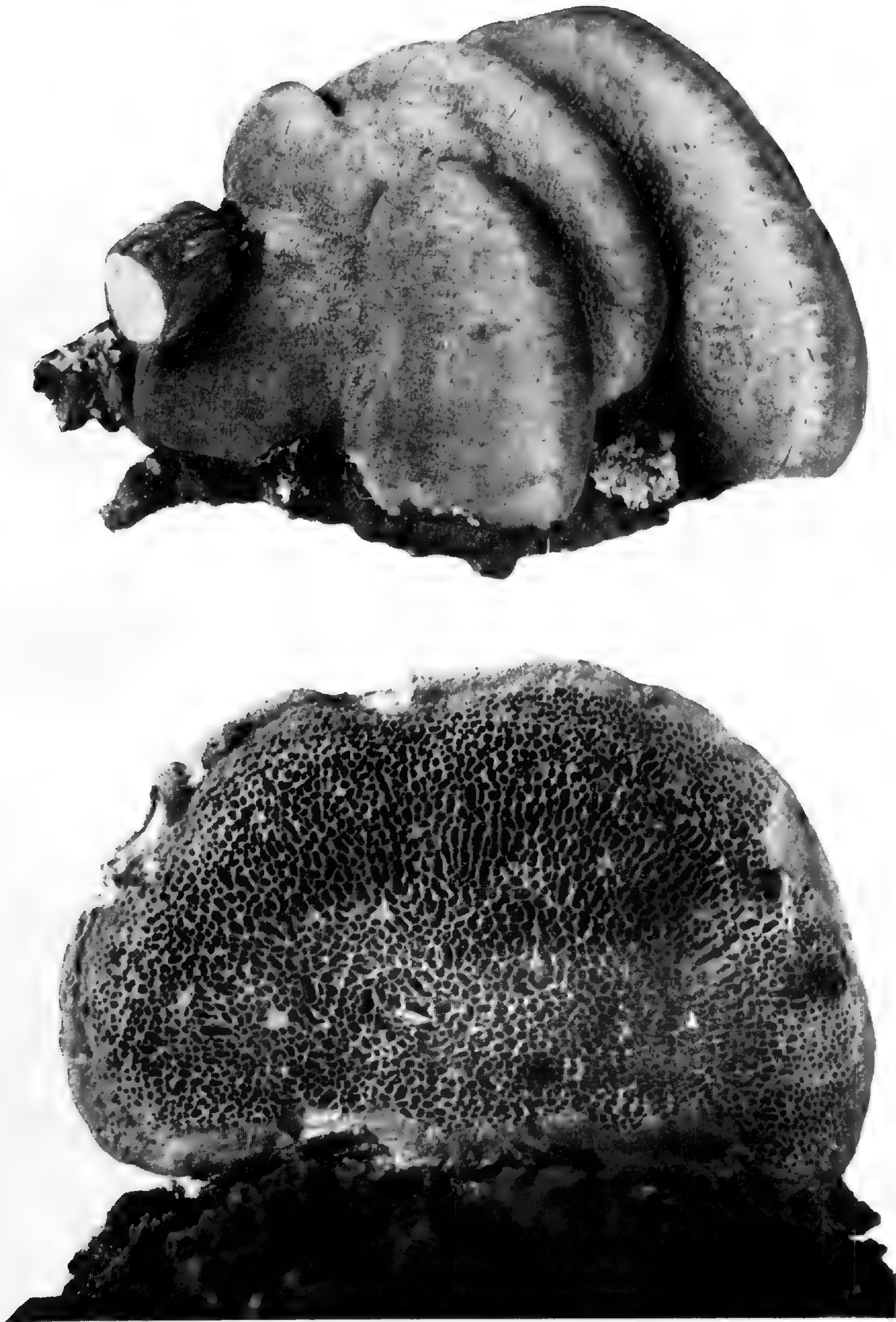
Plate 16. — 1, Cross section of a tree of *Quercus marilandica* rotted by *Polyporus obtusus* Berk. Only a small part of the heart wood is here affected. 2, Cross section of a tree of *Quercus velutina* showing the rotted heart wood with an insect burrow partially filled with the mycelium of *Polyporus obtusus* Berk.

Plate 17. — Stem of *Quercus velutina* split to show the insect burrow, which is on the left side, running upward from the opening in the bark midway the length of the block toward the center of the tree. To the right and above the upper end of the burrow is seen the lighter colored rotted heart wood. The burrow is filled with a mass of mycelium of the fungus, *Polyporus obtusus* Berk.

Plate 18. — Section of a tree of *Quercus marilandica* with an insect burrow on the right. There is but a small area of white rotted wood adjacent to the burrow.

Plate 19. — Section of a tree of *Quercus marilandica* which was killed by the fungus. The insect burrow shows very plainly. The entire stem was rotted except on the extreme left next to the bark, where a thin darker layer of the sap wood is seen.





POLYPORUS OBTUSUS.





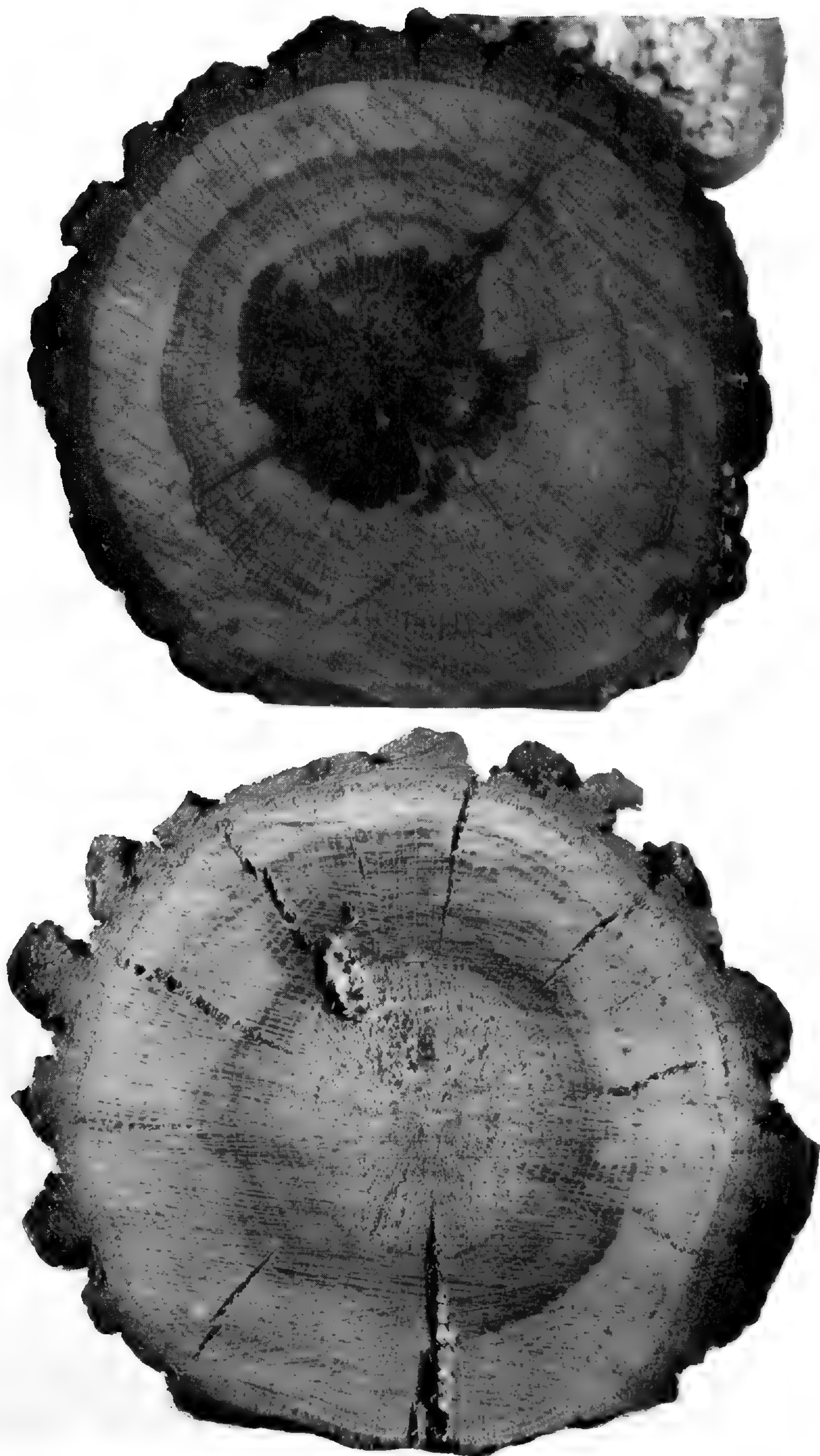
POLYPORUS OBTUSUS.





POLYPORUS OBTUSUS.





ROTTED OAK WOOD.





PRIONOXYSTUS BURROW IN OAK.





PRIONOXYSTUS BURROW IN OAK.





PRIONOXYSTUS BURROW IN OAK.



## GLASSY FIR.

BY HERMANN VON SCHRENK.

During the past winter some specimens of wood of the balsam fir (*Abies balsamea*) were received at the Missouri Botanical Garden, which showed peculiar smooth spots at various points on cross sections. Two views of pieces of wood of this character are shown on plate 20. It will be noted that the sections there shown present a rough appearance, usually found when pieces of wood are cut with a cross-cut saw. There are certain irregular areas, however, which are perfectly smooth and shiny, as if they had been planed. Some of these areas extend out from the heart to the sap wood, while some of them form irregular circumscribed spots, one of which shows prominently on the lower figure of the plate. In all of the specimens sent in, the sap wood had the same appearance as the irregular smooth spots. A careful examination made with a hand lens showed no signs of decay in these smooth areas, nor could they be distinguished in any way from balsam fir wood, after it has been planed with a sharp plane.

The specimens were sent from the forests in southwestern Maine, in the region of the Androscoggin River. A good deal of balsam fir is cut in that region for pulp wood. Some of the balsam fir logs were rejected because of the "glassy" or "icy" appearance. It was claimed by some that the glassy appearance indicated a defect in the wood. From information obtained it is apparent that this glassy appearance shows itself in the balsam fir quite regularly during the winter months. It occurs both in old and young trees and apparently, as far as outward appearances go, in perfectly sound wood.

A microscopical examination was made of the glassy areas, and the sections so made were compared with sim-



ilar ones obtained from the roughened areas. To all intents and purposes, the sections from the two different regions were perfectly alike. There was no sign of fungus attack in the glassy regions, the cell walls were perfectly normal in thickness and color, and, in fact, the wood from the glassy regions could not be distinguished from that in the rough areas. In seeking for an explanation of the peculiar appearance of the wood, it was found that most of the glassy areas surrounded the healed-over portions of old branches, or they were at any rate near such regions. Where these areas were isolated they were generally near some check. In all cases, the sap wood had the glassy appearance.

All of the specimens examined were cut during the months of February and March, in other words at a time when the temperature in the Maine forests is 32° Fahrenheit, or generally very much lower. The following explanation was finally adopted as explaining the peculiar glassy appearance. It is very probable that during the months of February and March, the water present in the trees was frozen, and that all cells that had water in them were then filled with solid ice. When the trees were cut down by means of a saw, the teeth of the saw tore the fibres of the spring wood, giving the appearance of roughened areas, usually seen when a soft wood like the balsam fir is cut with a saw. Wherever these wood cells were filled with ice, however, the latter acted as a reinforcing material, and when the saw cut through the fibre, enclosed on all sides by the solid ice, the fibres were not torn as is usually the case. The result was that when the sawing operation was complete, those areas which were filled with solid ice presented a smooth appearance. The ice, in other words, acted very much in the way any imbedding material like collodion, paraffin, etc., acts in sustaining weak cell-walls during the operation of cutting sections with a knife.

In order to test this theory, sections were made with a



sharp saw through several of the blocks of wood, cutting both through the glassy area and the roughened area. These sections were so made that the point at which the cut was made was not more than one-quarter of an inch below the glassy surface. In all cases the surface was rough over its entire extent, irrespective of whether it was an isolated glassy spot, or the rough wood.

In order still further to see whether the smooth appearance of the wood was due to freezing, several pieces of loblolly pine (*Pinus taeda*) were boiled for several hours in water so as to thoroughly water-soak them. The pieces were chosen from specially wide-ringed trees. After the soaking, the pieces were laid out of doors, and were allowed to freeze thoroughly. The thermometer during the particular night when they were exposed was below zero. The following morning the pieces were sawed half way through while in the frozen condition, the section being made about an inch from the outer surface. An ordinary cross-cut saw was used for the purpose. The pieces were then brought into the laboratory, where they were allowed to thaw out completely. After some 10 hours the section which had been partially sawed off in the frozen condition was completely cut off. In other words, one-half of the section was sawed while in the frozen condition, and the other half after the wood had thawed out. On plate 21 a photograph of one of the sections is reproduced. The part on the upper side of the figure was the portion sawed while the wood was frozen; the lower half, after the wood had thawed out. It will be noted that there is a marked line of demarcation between the two parts, the frozen part being smooth, the other half showing the rough surface usually found when a pithy wood of this character is cut with a cross-cut saw.

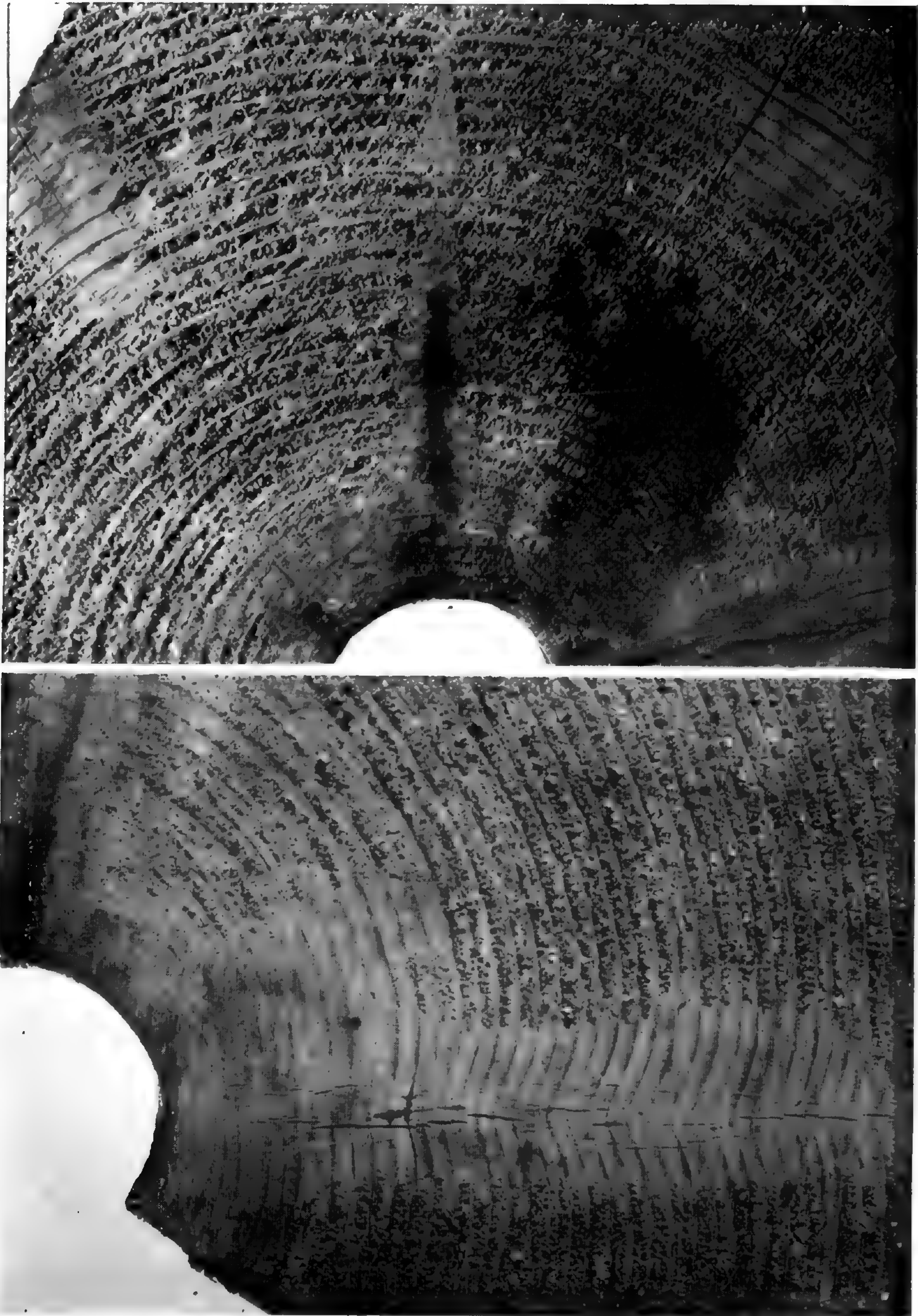
Similar tests were made with red fir and white spruce, and in all cases the peculiar glassy appearance was obtained in the frozen portion of the wood.



The result of these experiments seems to prove conclusively that the smooth appearance of certain of the areas is probably due to the reinforcing action of the ice which filled the wood cells. The peculiar distribution of the glassy spots along the lines of former branches, or at least close to them, becomes readily intelligible when one remembers that the lowering of temperature is more likely to take place along such channels as are in communication with the outer portions of the tree trunk. Many of the branches are frequently in direct communication with the outside air. In cooling, the first part of the tree in which the water would probably freeze is the part immediately under the bark, that is the sap wood. This, as has been stated, has a uniform glassy appearance in all the specimens. The lowering of temperature would then gradually proceed inward. It would take place most rapidly along radial channels such as the older branches. The presence of liquid water in any of the cells is another factor to be considered. As a rule, the heart wood of a tree like the balsam fir usually has very little liquid water in the cells, most of it being held by the cell walls. It is very well conceivable that there should be more water, first of all, in the sap wood and again in the healed-over branches. Isolated spots like the one shown in the upper right-hand corner of the upper figure of plate 20 may be explained by the fact that certain portions of the wood, for reasons not yet clear, frequently have a higher water content than the wood mass at large. Where such quantities of water occur, it would be possible to get smooth spots of the character referred to.

From a practical lumbering standpoint, the glassy fir should be regarded as in no way defective. Further studies concerning this appearance are in progress and will probably throw more light on the conducting capacity for heat of various portions of a tree trunk.





GLASSY FIR.



ON THE OCCURRENCE OF PERONOSPORA PARASITICA ON  
CAULIFLOWER.

BY HERMANN VON SCHRENK.

During the winter months of 1903 the cauliflower plants in a greenhouse of the Missouri Botanical Garden were universally attacked by the crucifer mildew (*Peronospora parasitica*, De Bary). The fungus made its appearance very suddenly, and within a week had spread over practically all of the plants in the affected greenhouse, attacking both the old and the young leaves. So virulent was the attack that it looked for a time as if the whole crop would be destroyed. So far as one could determine, this was the first appearance of this mildew on the cauliflower, at least for a long period of years, in the greenhouses of the Missouri Botanical Garden, and probably in the western States.

The crucifer mildew is one of the most widespread of all the mildews, having been observed on a large number of cruciferous plants. It is extremely common on many of the wild Cruciferae, appearing generally early in the spring. *Cardamine hirsuta* and *C. laciniata* are particularly subject to it, and, of cultivated plants, radishes and cabbages are frequently attacked by this fungus. Halsted\* was one of the first to call attention to its occurrence on cultivated plants, particularly on radishes and cabbage. He reports finding it on *Alyssum maritimum* † and notes its occurrence on species of *Lepidium*, *Raphanus* and *Brassica*.

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\* Halsted, B. D., Twelfth Annual Report, New Jersey Agricultural Experiment Station, page 248. (1892).

† Halsted, B. D., 13th Annual Report, N. J. Agr. Experiment Station, page 277. (1893).



Humphrey\* reports it growing on purple topped white turnips together with *Cystopus candidus* (Pers.) Lev. McCarthy † describes briefly the appearance of a destructive stem rot or blight, which may be caused by *Peronospora parasitica* or *Albugo candida* (Pers.) O. Kze. (*Cystopus candidus*, Pers., Lev.) which are generally found together. "This disease attacks turnips, mustard, kale, collards, and various weeds belonging to the collard tribe, especially shepherd's purse or pepper grass."

The only case which appears to have been reported of the occurrence of this fungus on cauliflower, in a destructive manner, is cited by Marchal, ‡ who states that *Peronospora* caused much loss in France to market gardeners, growing cauliflower that winter.

In the case of the plants of the Missouri Botanical Garden, the fungus made its appearance on the under side of the younger leaves (plate 23), distributed in irregular patches over the entire surface of the leaves. The areas immediately affected by the fungus turned white, giving the cauliflower a speckled appearance, as shown in plate 22.

The fungus grew rapidly through the tissues and after several days the entire leaf was usually affected. In the later stages the leaves dried considerably and became much torn and shriveled, as shown on plate 24.

Combative measures against this fungus have usually been attended with considerable success. McCarthy (loc. cit.) recommended removing all Cruciferae, as far as possible, from the fields, and treating the compost and stumps with lime. The plants themselves, he advises treating in the seed bed with iron sulphate, potassium sulphide, or

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\* Humphrey, J. E., 7th Report, State Agr. Exp. Sta., Amherst, Mass., page 222.

† McCarthy, Gerald, Bull. N. C. Exper. Station, No. 84, pg. 15. (1892).

‡ Marchal, E., Report on fungus diseases studied at the Agricultural Inst. of Gembloux during 1900. (Bull. Agronomique. Brussels. 17: 4-18. 1901.)



sulphur powder, and repeating this treatment several times after transplanting to the field. Marchal, on the advice of Cornu, recommended spreading sawdust saturated with copper sulphate around the plants as a mulch. He states that where this was used, the disease was practically stopped.

In the case of plants affected by the *Peronospora* at the Garden, a number of sprays were used including copper sulphate, copper ammonium carbonate, and potassium sulphide. In order to make these solutions stick to the leaves small quantities of glue were added, and it was found that this formed a very effective way of holding the solutions on the leaves of the cauliflower. Good results were obtained with all of these sprays, with the exception of copper ammonium carbonate, which, while it killed the fungus, induced the formation of an enormous number of oedemata, on the lower surface of the leaves in particular. This will form the subject of another paper. The fungus disappeared during the spring months. The following winter the beds of this greenhouse were carefully treated with lime, and since that time there has been no further attack of the cauliflower in these houses.

It is of interest to note the very local and sporadic appearance of the *Peronospora parasitica* in this instance. Although careful search was made for it in other greenhouses of this vicinity, this was practically the only case where it occurred. Inquiries made in other parts of the United States, at the time, failed to show its occurrence on cauliflower at other points. This is rather striking because the fungus itself is a common one on the native wild plants in most parts of the United States, and it might be expected that it would show itself on cultivated cruciferous plants more frequently than it does. The possible explanation may lie in the fact that there are certain physiological strains on different species of cruciferous plants, similar



to those recorded for *Erysiphe graminis* by Salmon.\* Magnus † mentions this fungus especially as being one which is largely dependent upon the state of development of the host, citing the case where it attacks the host plant through the medium of *Albugo* galls. It is very probable that in the instance herein described, the cauliflower plants were in a condition particularly susceptible to the attack of the *Peronospora*, a condition which has not reappeared since that time.

#### EXPLANATION OF PLATES.

Plate 22. — Upper surface of leaf of cauliflower, showing the characteristic spots due to the growth of *Peronospora parasitica*, natural size.

Plate 23. — Lower surface of leaf, showing the tufts of the fungus, natural size.

Plate 24. — Lower surface of leaf in a more advanced stage of the disease, natural size.

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\* Salmon, Ernest S., Cultural experiments with biologic forms of the Erysiphaceae. (Phil. Trans. 197: 107. 1904).

† Magnus, P., Das Auftreten der *Peronospora parasitica*, beeinflusst von der Beschaffenheit und dem Entwicklungszustande der Wirtspflanze. (Berichte d. d. bot. Ges. 12. Generalversammlungsheft. pg. 39. 1894).





FROZEN LOBLOLLY PINE.





CAULIFLOWER ATTACKED BY PERONOSPORA.





PERONOSPORA ON CAULIFLOWER.





PERONOSPORA ON CAULIFLOWER.



## INTUMESCENCES FORMED AS A RESULT OF CHEMICAL STIMULATION.

BY HERMANN VON SCHRENK.

### GENERAL DESCRIPTION.

During the winter of 1903, the cauliflowers at the Missouri Botanical Garden were attacked by the crucifer mildew, *Peronospora parasitica*. The plants were sprayed with various copper sprays, to which a small amount of fish glue had been added in order to cause the spray to adhere more firmly to the surface of the leaves. Several days after the spraying, a large number of peculiar wart-like structures began to form on the lower surface of the sprayed leaves. A brief description of these structures was presented in a paper read before the Washington meeting of the Association for the Advancement of Science, and a brief note concerning them was published at that time<sup>24</sup>. It was found that these wart-like formations were in reality large swellings produced in the leaves, which resembled intumescences, a large number of which have been described from time to time on various plants. Owing to pressure of other work, further study of these intumescences had to be dropped at that time, and not until recently, with the reappearance of similar intumescences formed as a result of spraying cauliflowers, was their study taken up again. As stated before, these peculiar warts appeared on the leaves which had been sprayed to stop the mildew. A careful examination was made of all the unsprayed plants in this particular greenhouse, but in no case were such warts found on unsprayed plants.

On plate 25 the photograph of a cauliflower leaf is reproduced, taken from a plant sprayed with copper

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<sup>24</sup> Exponential figures refer to the bibliography at end of the paper.



ammonium carbonate, five days after the spraying. It will be noted that the entire lower surface of the leaf is covered with isolated raised warts, which are irregularly scattered over the entire surface of the leaf. These warts are shown somewhat enlarged on plate 26. They form more or less circular, raised knobs of a yellowish color, growing lighter as they grow older, and, after ten days or two weeks, becoming almost white. The individual warts are well defined, rising immediately from the surface of the leaf in a sharply defined circle. Many of the warts grew to a very large size, projecting out from the surface of the leaf, in some cases for one-eighth of an inch.

In the early stages the warts appear as small swellings of the epidermis; the latter, however, was soon broken, or, more correctly, was lifted up on the surface of the growing wart. After six or seven days, a distinct star-like appearance developed under the larger warts. There appeared to be a more or less central body from which lines extended out in a radial direction, giving the appearance of a star-shaped wreath around a central solid body. Reference to plate 26 will show many of the bodies in this condition. At this period the warts were almost uniformly white in color. From the period of this star-like structure, the growth evidently ceased and after several weeks the warts gradually dried up, so that after three weeks or thereabouts they had practically shriveled up. Although both surfaces of the leaves were sprayed, the warts appeared almost entirely on the lower surface of the leaves.

A microscopic examination of the healthy cauliflower leaves shows a well-defined spongy parenchyma layer on the lower surface of the leaves, and a palisade parenchyma, composed of several rows of more or less rectangular cells (plate 27, fig. 1). Sections made through the early stages of the swellings (plate 27, fig. 2) show some of the spongy parenchyma cells enlarged to many times their



size, lifting up the epidermis. In the stage shown in fig. 2, the epidermal cells had shriveled and were practically indistinguishable. Successive stages show an increasing development of giant cells, and a condition after six or seven days as shown in plate 28. Protruding from the surface of the leaf were large masses of enormously elongated very thin-walled cells in a condition of vigorous development. The epidermis had been entirely broken away, and growth was taking place directly out from the center of the mass of tissue and in a lateral direction. The outermost cells, in the stage shown on plate 28, were gradually drying. The giant cells themselves were very thin-walled, closely packed together and practically empty, that is, they were filled with air. In the lower ones, that is those well within the leaf body, very much reduced chlorophyll grains could be found. The whole structure had the appearance of the bodies originally described by Sorauer<sup>26</sup>, and called by him intumescences. There were no signs of either fungi or bacteria in the early stages of the wart formation. A study of the drawing shown on plate 28 explains the peculiar outward appearance of the warts, the central body being the cells growing perpendicularly to the surface of the leaves, and the apparent rays constituted by the long hairlike cells pushing out from either side of the central cells. The whitish appearance is explained by the fact that the cells were full of air.

The giant cells originated at first in the outer spongy parenchyma layer, but as the growth progressed, the palisade cells likewise started to enlarge so that in the later stages the entire mesophyll contributed to the formation of the oedematous cells.

Since the formation of the first warts, just described, others have been produced artificially. They agree in most respects with those first formed, with one possible exception. It was found that the size and shape of the warts could be modified at will, depending upon the man-



ner in which the sprays were placed upon the leaf. Where the spray was strictly in the form of small drops, the distinct warts, as shown on plates 25 and 26, were always formed. Where the individual drops ran together making more or less large blotches of the spray, either the entire leaf became oedematous, or there were areas from one-fourth to one-half inch square swelled out, forming enormous masses of giant cells, as shown in plate 31. It will be noted that not only is the leaf lamina affected, but the tissue immediately surrounding and composing the veins of the leaf has likewise been affected. In this case, long lines of oedematous tissue formed on both sides of a vein, breaking out much as in the case of the more circumscribed areas described above.

The formation of the intumescences or oedemas has been known for a long time, both on the leafy and woody parts of a large number of plants. Sorauer<sup>28</sup> designated by the name "Intumescentia" all those structures which appear as small wart-like eruptions on the surface of leaves, generally yellowish in color and which show a more or less unusual stretching of cells. On leaves the swellings generally originate in the mesophyll cells and consist of hypertrophied cells, having a very thin lining of protoplasm, very thin cell walls, and much reduced chlorophyll grains, if any. In the majority of cases a simple stretching of certain cells takes place, but in other cases an actual division and multiplication of cells. This is not confined to the mesophyll, but may also take place with the epidermal cells, as described by Sorauer<sup>33</sup>, in the case of intumescences formed on pinks. It will not be necessary to describe in detail the various structural modifications which have been described from time to time for various forms of intumescences on all kinds of plants. The reader is referred to the writings of Sorauer<sup>28-35</sup>; Küster<sup>11,12</sup>; Prillieux<sup>20</sup>; Dale<sup>3</sup>; Trotter<sup>37</sup>; and Atkinson<sup>1</sup>.



## CAUSE FOR FORMATION.

As to the factors which determine the formation of the intumescences there have been various explanations made from time to time. First among these is the explanation which Sorauer made, when he described these structures, and which he has seen no reason to change in later years. He states<sup>28, 28</sup>, "Intumescences are formed when the plants, which for some reason have a reduced assimilatory activity, are brought into conditions which bring about an abnormal turgescence in the cells." "I have therefore regarded the intumescences as a symptom of a disturbance which is caused by an excess of water during a period of low assimilation." Then, again, quoting Sorauer<sup>34</sup>: "So far as can be concluded from my knowledge of the vegetative conditions operative at the time of the formation of these intumescences, all cases point to the conclusion that the affected plants suffered a stimulus because of a heightened temperature, combined with an excess water supply in the tissues, at a time when their assimilatory activity was depressed because of weak illumination, and that as a result of this stimulus, a reaction took place in the form of a stretching of the cell walls at the expense of the cell contents." \* \* \* "Since I have succeeded at other times in producing intumescences experimentally in two cases (*Ficus elastica* and *Impatiens fulva*), one must now without question regard these formations as a symptom of an abnormal elevation of temperature and excessive water supply."

Prillieux<sup>20</sup>, Noack<sup>16</sup>, Atkinson<sup>1</sup>, Trotter<sup>37</sup>, and others in general hold with Sorauer that high temperatures combined with a humid atmosphere and abundant water supply are largely responsible for the formation of intumescences.

In addition to the abnormal elevation of temperature



and excessive water supply, the light factor has been considered as having varying influence on the formation of intumescences. Sorauer<sup>34</sup> refers to the fact that weak illumination favors the formation of intumescences because of its lowering the assimilatory activity of the plants. Atkinson<sup>1</sup> holds a similar view, explaining the higher turgescence of the leaves because of the reduced transpiration in poorly lighted greenhouses. He furthermore refers to the fact "that the lack of light not only favors the accumulation of water, \* \* \* but it prevents the plants from building up strong tissue." He even goes so far as to state that "possibly artificial light might be used to advantage" (pg. 108). Trotter<sup>37</sup> likewise says that semi-darkness favors the development of the intumescences. Küster<sup>11</sup>, in producing artificial intumescences on poplar leaves, found that intumescences were formed on the leaves which were exposed to intense light, particularly on the sides lying on the water, but that in general intumescences were formed both in the dark and in the light. Too strong light according to him, however, stops the formation, possibly on account of the reduced transpiration. He concludes by saying: "that the formation of intumescences is due to a specific action of light, I am inclined to doubt; it seems more likely that in the bright light, even in the closed dishes, the upper (actual, and not morphologically upper) surface transpired actively, and that therefore no intumescences were formed on that side."

As against the claims that darkness favors the formation of intumescences a number of recent investigations seems to indicate that light is extremely necessary to their formation. Dale<sup>3</sup> finds that white light, or in particular the yellow or red rays, are absolutely essential to the development of the intumescences. In the dark, or in green or blue light, no intumescences were formed on *Hibiscus*. Viala and Pacottet<sup>38</sup>, in a description of the intumes-



cences formed on grape leaves, in greenhouses, make the very definite statement, "We have established the fact by means of direct experiments that the intumescences are caused by an excess of light in a humid atmosphere." \* \* \* "The light is the predominating factor." \* \* \* "It is only during periods of the most brilliant illumination and directly under the glass of the houses, that the intumescences form in quantity. One does not observe them in the same greenhouse on leaves which are in a diffuse light, or in the shade." They explain this apparent action of the light by stating that the oedematous leaves protect themselves like succulent plants by the formation of a false palisade tissue "against chlorovaporization and an excessive transpiration," which latter is accentuated by the direct action of the sunlight, both because of light and heat radiation. They recommend preventing the formation of intumescences by shading the glass of the houses.

Observations made in the greenhouse of the Missouri Botanical Garden during the present season on grape vines which were covered with these intumescences, fully bear out the observations made by Viala and Pacottet. The intumescences were found only on the leaves immediately under the glass, while all the leaves in the shade were free from them.

The above quotations seem to leave the question as to what the influence of light on the formation of these intumescences is, in a rather indefinite condition, and it is evident that a good deal of careful experimenting will have to be done to determine the exact nature of the light stimulus, should there be such a one.

Practically all of the explanations made for the production of intumescences have, as has been shown, been caused by conditions of excessive humidity and temperature, possibly with the aid of light. The formation of intumescences because of chemical stimulation has been referred to but twice so far as known. Sorauer<sup>31</sup> in describing the



effects of spraying potatoes with Bordeaux mixture and sulfo-stearite (?) of copper, notes the formation of some burnt spots on the leaves at points where the copper solution stuck to the leaves. Not infrequently the entire upper surface of the leaves turned slightly brown. Under these spots the palisade parenchyma cells had stretched to an abnormal extent and had formed wart-like bodies on the surface of the leaves. In extreme cases this stretching of the cells was so large that the epidermis was torn, exposing the underlying giant cells. These generally had very little chlorophyll and were frequently divided by cross walls. It should be noted, however, that Sorauer found these oedemas not only on the plants which were sprayed with the copper, but also on the unsprayed plants. In all cases the epidermal cells overlying the enlarged mesophyll were apparently dead and brown and corky. Sorauer calls attention to the fact that it has been shown for other plants that such intumescences arise when the assimilatory activity of the leaves has been reduced, combined with a large water absorption and high temperature, and he states that the formation of these intumescences in the leaves of the potato is to be regarded as a sign of lessened assimilatory activity. He states, furthermore, that this is a fairly regular appearance during later stages of development on the leaves, referring in these cases to plants which have not been sprayed. Referring to the leaves sprayed with copper salts he says, "Where this appearance (intumescences) occurs on leaves which are still at the height of their development it must be due to the effect of the copper, and the intumescences must be regarded as resulting from a condition of high turgescence existing in the leaf cells, which would not equalize itself throughout the leaf lamina because of the death of certain epidermal areas." He regards the frequent and numerous appearance of these oedemas as a proof that the copper salts inhibit to a certain extent the normal development of the leaf.



The fact that Sorauer found these oedemas in both sprayed and unsprayed leaves would lead one to suggest that the formation of the oedema in the potato leaves was not always directly connected with the spraying with copper salts.

Küster<sup>11, 12</sup>, discussing the formation of intumescences, expressed the belief that intumescences might be formed as a result of the introduction of nutrient or poisonous substances. He refers to the relationship existing between intumescences and the galls produced on poplar leaves by *Harmandia tremulae* and *H. globuli*. He found that the leaves affected with the galls had a tendency to form excessively vigorous intumescences around the base of the galls when placed on the surface of a culture medium. Küster is not certain whether this excessive development of intumescences is due to the action of the gall forming poison, or whether it is connected with the unusual concentration of nutritive substances which form as a result of the gall formation.

The production of giant cells such as form in intumescences has been noted in several instances in connection with insect galls. Woods<sup>39</sup> in describing changes brought about in the leaves of carnations, as a result of punctures by aphids, says that "the cells of diseased spots were found to be much larger than normal, and thin walled and oedematous." In the early stages of the disease, the chloroplasts were undeveloped or smaller than in the healthy cells, and were colorless or yellow. Other instances of the formation of giant cells in insect galls have been reported from time to time<sup>9, 13</sup>.

Summing up our present knowledge of the cause for the formation of giant cells, especially in intumescences, it may be said that these are generally formed because of the presence of excessive moisture and heat in enclosed houses, aided possibly by the action of light, and that they have



been reported once as being due to the probable action of copper sulphate.

In the case of the intumescences formed on cauliflower in the Missouri Botanical Garden, the factors of moisture, heat and light played absolutely no part whatever. As stated above, in no case were any intumescences formed except as the immediate result of spraying with various fungicides. The first intumescences which formed on the cauliflower leaves, showed on those leaves which had been sprayed with a standard solution of copper ammonium carbonate, to which a certain amount of fish glue had been added. No intumescences appeared on the leaves sprayed with Bordeaux mixture or potassium sulphide, the other sprays used at the time. It would appear from this that the intumescences must have been caused either by the copper ammonium carbonate or by the glue, or by some substance formed as a result of the combination of copper ammonium carbonate and the glue. In order to test which one of the substances brought about the formation of the intumescences a number of thrifty cauliflower plants were selected which were sprayed as follows: —

Plant No. 1. Four leaves sprayed with fish glue in its concentrated form.

Plant No. 2. Two leaves sprayed with fish glue diluted 50% with water.

Plant No. 3. Four leaves sprayed with Bordeaux mixture, 6 lbs.  $\text{CuSO}_4$ , 4 lbs. lime and 50 gallons water.

Plant No. 4. Four leaves sprayed with Bordeaux mixture to which about  $\frac{1}{3}$  glue was added.

Plant No. 5. Four leaves sprayed with ammonium copper carbonate.

Plant No. 6. Four leaves sprayed with ammonium copper carbonate to which about  $\frac{1}{3}$  glue was added.

The plants were sprayed about twelve o'clock and in the bright sun. The spots of Bordeaux mixture and ammonium copper carbonate dried in about two hours. Five days after the spraying the following condition was noted: —

Plant No. 1. With glue. The tissue under the glue spots had shrunken and died, both on the upper and lower surface of the leaves. There was no sign of oedematous tissue under or near any of the spots.



Plant No. 2. 50 per cent. of glue. The same condition as noted for the first plant was true here.

Plant No. 3. The plant sprayed with Bordeaux mixture showed no change whatever under the sprayed spots.

Plant No. 4. The plants sprayed with Bordeaux mixture and glue showed no change whatever.

Plant No. 5. Leaves sprayed with ammonium copper carbonate showed a discoloration of the leaves, not only under the immediate spot where the drops of solution struck the leaves, but extending considerably beyond these spots. On the lower side of two of the sprayed leaves, small warts were forming in considerable numbers, some of which had already broken through the epidermis.

Plant No. 6. The same condition as noted for plant No. 5 was true in this case. That is, on most of the leaves which were sprayed warts were forming on the lower surface.

It appeared from this experiment that the intumescences were not formed by the glue, or by the Bordeaux or by the combination of glue and Bordeaux mixture. It furthermore appeared that the glue was not a necessary element to their formation, when mixed with ammonium copper carbonate, for the ammonium copper carbonate produced the intumescences without the glue addition. The plants were examined again after 11 days and no change whatever had taken place, except in the case of plants sprayed with ammonium copper carbonate and its glue addition. By that time the plants which had been sprayed with ammonium copper carbonate alone showed a great number of swellings, particularly on the lower surface of the leaves. Where the spray struck the leaves in large blotches, the eruptions took place chiefly around the edges of the sprayed spot. In the case of the plants to which the glue had been added, the eruptions were practically confined to the small spots, for with the glue addition the spray came out very fine. The eruptions in this case were generally not more than two to three millimetres in width.

Several experiments were then made with ammonium copper carbonate alone and it was found in practically every instance that within five or six days large numbers of intumescences could be produced as a result of the



spray. The conclusion may therefore safely be drawn that the spray with the standard solution of copper ammonium carbonate is capable of producing typical intumescences on plants, such as are usually formed as a result of excessive moisture absorption at a time when the plant is in a condition of weakened vitality. The demonstration was a very striking one because in no case did any of the plants, except the sprayed ones, produce a single intumescence. Both old and young leaves were sprayed and it was found that the young leaves had as a rule produced a larger number of intumescences and bigger ones. The lower surface of the leaves produced larger numbers than did the upper surface. From the result of Dale's experiments<sup>3</sup>, in which it was shown that the intumescences sometimes form under a stoma, it was thought possible that the more frequent occurrence of the intumescences on the lower surface of the leaves of the cauliflower might have some connection with the unequal distribution of the stomata on the upper and lower surface of the leaves. It was found, however, although the number of stomata on the lower side of the leaf is about twice that on the upper side, that the location of the intumescences bore no relation to the position of the stomata.

Having shown that the intumescences were formed as a direct result of the application of ammonium copper carbonate, the next point to be determined was whether the active agent in the formation of the intumescences was the ammonia or the copper. The copper carbonate solution used in the test was made according to the standard method, as follows: 5 oz. copper carbonate, dissolved in a mixture of 3 pints ammonia to 50 gallons of water. The solution was found to contain 1.57% ammonia. Some of the solution used in the first experiment was neutralized with hydrochloric acid and this neutral solution was used in spraying a number of plants. In every instance the tissue underlying the spots formed where the solution dried, died



within three days. The influence of the solution was evidently a very caustic one because the injurious effect was made evident within twenty-four hours after the spraying. The leaf tissue was killed throughout its entire thickness, as shown on the upper side of the leaves, where the surface appeared shrunken and discolored. Grape leaves sprayed at the same time with this solution likewise had a browned appearance after twenty-four hours, and in a very few days all of the tissue struck by the spray was killed.

A third series of experiments consisted in spraying a number of thrifty cauliflower plants with various solutions of copper salts, without any ammonia addition, and another set of plants with ammonia solution and ammonium carbonate solution. The plants sprayed were as follows:—

Series No. 1. Sprayed with ammonium copper carbonate, using the same solution as in the previous experiments.

Series No. 2. Sprayed with copper nitrate solution (15 gr. copper nitrate  $[\text{Cu}(\text{NO}_3)_2 + 3\text{H}_2\text{O}]$  per litre).

Series No. 3. Sprayed with copper acetate solution (12 gr. per litre).

Series No. 4. Sprayed with copper chloride solution (10 gr. per litre, the copper being equivalent of the amount in Bordeaux mixture).

Series No. 5. Sprayed with copper sulphate ( $\text{CuSO}_4 + \text{H}_2\text{O}$ , 15 gr. per litre).

The ammonia used was an aqueous solution containing 41.88% total ammonia as hydrate. Based upon this determination various strengths of solution were made.

Series No. 6. Were sprayed with 10% ammonia (that is, 4.188% actual ammonia).

Series No. 7. Sprayed with 2% ammonia (that is, .837% actual ammonia).

Series No. 8. Was sprayed with an aqueous solution of ammonium carbonate  $(\text{NH}_4)_2\text{CO}_3$ , 5% solution.

After four days these plants showed the following conditions:—

Series No. 1. Ammonium copper carbonate. Younger sprayed leaves show distinct eruptions on the lower surface, which were strictly confined to the places where the spray struck the surface of the leaf. The eruptions were in every way characteristic intumescences. Where the spray struck the leaf in any quantity the eruptions were in large masses.



Series No. 2. Copper nitrate. Where the copper nitrate struck the leaves the tissue underneath was killed entirely (plate 28, fig. 1). Where infinitesimally small drops struck the surface of the leaf, eruptions the size of a pin began to form.

Series No. 3. Copper acetate. The copper acetate solution practically killed the leaf surface wherever it struck in any quantity. Where very small drops struck the surface, exceedingly minute eruptions began to form.

Series No. 4. The copper chloride solution killed the leaf surface wherever the solution struck the leaf (plate 30, fig. 2). Where the spray stuck to the leaves in small drops eruptions started. This was particularly true of the very young leaves.

Series No. 5. Copper sulphate. Plants sprayed with copper sulphate had practically the same appearance as those sprayed with copper chloride and copper nitrate. The sprayed areas were practically killed where the spraying solution had adhered, except where very small quantities of spray stuck to the leaf. It was very striking that not only were the areas immediately touched by the spray killed, but all adjacent areas, as if there had been a decided diffusion of the salt through the leaves (plate 30, fig 1).

Series No. 6. 10% ammonia. Leaves sprayed with 10% ammonia were killed outright in the region touched by the spray (plate 29, fig. 2). Very definite circumscribed spots as shown in the figure were formed. Absolutely no sign of any eruptions.

Series No. 7. 2% ammonia. After four days there was practically no sign of any change in the leaves sprayed with 2% ammonia. Several days later, however, most decided eruptions formed on these leaves and developed in the characteristic manner.

Series No. 8. Ammonium carbonate. The younger leaves showed decided eruptions in blotches wherever the spray struck the leaf. These were beginning to stretch through the epidermis much as the small warts did with the ammonium copper carbonate.

The sprayed plants were examined daily for a period of two weeks and the general conclusions drawn were as follows: —

Plants sprayed with the copper salts without the addition of ammonia were generally killed where the spray struck the leaf areas in any quantity. Where very minute quantities of the spray touched the leaves, eruptions formed. The plants sprayed with ammonia were killed when the stronger solution was used, but the weak solution produced characteristic eruptions. The ammonium copper carbonate produced decided eruptions wherever used.



The results of these experiments seem to indicate that the formation of the intumescences on the cauliflower leaves might have been due to either the copper or the ammonia in the ammonium copper carbonate solution. The ammonium carbonate solution was selected for the experiments because ammonium carbonate gives off ammonia very slowly when exposed to the air. The experiment just described was repeated several times, using the ammonia in various concentrations, and ammonium carbonate, and in nearly every instance eruptions of a characteristic form were produced. In applying the spray to the leaves, a glass atomizer was used in which the copper solutions had likewise been placed for the first tests. Although several days had elapsed since using the copper solutions in the atomizer and although it was thoroughly cleaned and washed, it was thought barely possible that some copper might have been retained by the walls of the glass vessel, as described by Nägeli<sup>15</sup>. On that account the tests were repeated, using ammonia and ammonium carbonate, and this time the sprays were applied to the leaves by means of brushes, so that all chances for the possible contamination with copper were avoided. In this last series of experiments all of the plants sprayed with ammonium copper carbonate, two of the plants sprayed with ammonium carbonate and two of the plants sprayed with 2% ammonia developed intumescences. Two of the plants sprayed with 2% ammonia showed only discolored spots. Of the plants sprayed with ammonium carbonate, one only showed discolored spots. While several of the sprayed spots undoubtedly formed intumescences as a result of spraying with ammonium carbonate or ammonia, owing to the negative results of several plants it will not be possible without further tests to definitely ascribe the formation of these intumescences to the ammonia.

At the same time that the cauliflower leaves were



sprayed, experiments were made with various other plants, including beets, grapes, radishes, violets and a species of *Mesembryanthemum*. On none of these leaves were any intumescences formed, such as appeared on the cauliflower leaves.

One of the most striking results of the spraying with the copper salts was the different effect of the solution when sprayed onto the leaves in large quantities and in very minute drops. When in quantity, the copper solution almost invariably killed the entire underlying tissue completely, whereas in very fine drops the spray evidently stimulated the leaf tissue, forming intumescences. This result was similar to the one obtained by Dandeno<sup>4</sup>, who found that "dilute solutions applied in drops stimulated the leaf tissue in a ring, whereas if the solutions are concentrated, the entire area covered by the drop is affected."

Summarizing the results obtained from spraying, it may be stated: First, that spraying uninjured cauliflower leaves with dilute solutions of copper ammonium carbonate, or with other copper salts, results in the formation of marked intumescences which are particularly prominent on the lower side of the leaves. Second, spraying leaves with dilute solutions of copper chloride, copper nitrate, copper sulphate, and copper acetate, kills the leaf tissue where the spray strikes the same in any quantity. Where very minute drops of the spray struck the leaf surface, small intumescences formed much as they do with copper ammonium carbonate. Third, these intumescences are formed as a direct result of the spraying, and they have no connection whatever with conditions which have usually prevailed in the formation of intumescences, such as excessive water supply and high temperature. In other words the intumescences form as a result of a direct chemical stimulation. Fourth, cauliflower leaves are particularly susceptible to such stimulation. Leaves of the grape, violet, radish, beet and *Mesembryanthemum* did not react.



The effects of spraying with various solutions on leaves, have been made the subject of numerous investigations, particularly with reference to the action of various fungicides on growing leaves. The apparent stimulating effects which various copper solutions in particular have upon crops, have become generally recognized. Rumm<sup>22</sup> ascribed the more vigorous appearance of leaves sprayed with Bordeaux mixture, to a stimulation exerted by the copper salt. He, however, left out of consideration the possible influence of the lime. Frank and Krüger<sup>27</sup>, finding that the development of potatoes was hastened by spraying with Bordeaux mixture, as evidenced by healthier leaves, more chlorophyll, etc., came to the conclusion that the copper was the active agent in stimulating the plants. They found no proof that the copper entered into the cells and regarded the stimulating activity of the Bordeaux mixture as due to chemotactic stimulation, exerted by the copper, much as did Rumm<sup>22</sup>. Galloway and Woods<sup>8</sup>, experimenting on the influence of Bordeaux mixture on potatoes, came to the conclusion that while the spraying with Bordeaux without question stimulated the growth of certain plants, the beneficial effect may be in part due to the presence of the mixture in the soil as well as on the leaves. Sebelieu<sup>26</sup>, Woods and Bartlett<sup>40</sup> and Pierce<sup>19</sup>, among many others, testify to the beneficial effects of spraying with Bordeaux mixture; in each case ascribing the beneficial effects to the action of the spray upon the leaves. The general consensus of opinion at this day seems to be that either the copper hydrate or lime, or both acting together, in some way stimulates the leaves of various plants to a healthier activity.

On the other hand, it has been found now and then that copper sulphate sprays exerted a more or less harmful influence upon the development of sprayed leaves. Duggar<sup>5, 6</sup> reports the production of shot-hole injuries on leaves when sprayed with Bordeaux mixture. He also obtained similar



results with formalin, picric acid and corrosive sublimate. Dandeno in a recent paper<sup>4</sup> describes at considerable length a number of experiments which he performed to test the effects of water and solutions of various salts on foliage leaves. He finds "that pure water *may be* absorbed." Nutrient solutions (?) he finds are absorbed when sprayed upon the growing leaf, as evidenced by the increased dry weight. The part of his paper which has a particular bearing upon the present subject deals with the effect of "a solution applied to the leaf surface." He experimented with a m/4 strength solution of  $MgCl_2$ ,  $ZnSO_4$ ,  $Na_2CO_3$ ,  $KBr$ ,  $NaHCO_3$ ,  $K_3PO_4$ ,  $Na\bar{A}$ ,  $KClO_3$ ,  $KI$ , and with a m/56 solution of  $CuSO_4$ , and nutrient solution. The plants used were *Ampelopsis*. He likewise experimented with  $CaH_2(CO_3)_2$  and  $Ca(OH)_2$  on leaves of *Begonia*, *Primula obconica*, *P. stellata*, *Pelargonium* and *Heliotropium*. As a result of his tests he finds that some of the solutions produced yellow and some brown spots on the surface of the leaves, that many of the salts are absorbed through both surfaces of the leaves, as indicated by the absence of any distinct spot when the water evaporates. The solutions were absorbed more easily by the lower side than by the upper side.

Only in one case did he notice any structural changes in the leaves. In spraying tobacco leaves with caustic soda, 1% and 2½% strength, peculiar spots were formed. The tissues in these spots were dead in the center and surrounded by a ring of expanded spongy parenchyma cells which contained larger and more numerous chlorophyll grains than the normal tissue of the leaves. He suggests that the increase in the number and size of the chloroplasts might be due to a stimulus exerted by the caustic solution and refers to the results of Griffon, Ewart and Mayer and others, who found that potassium nitrate and potassium carbonate affected the chloroplasts in some way, resulting in increased dimensions and, in general, in a deeper green



color of the leaves. Dandeno concluded from his research that "the alkali kills the tissue in direct contact with the irritant; it stimulates the abnormal development of the tissue immediately around the spot."

Aside from the stimulating activity noted above, there have been frequent references to the stimulating effect of various salts on both higher and lower plants. Small additions of zinc or magnesium have frequently been found to increase the crop of spores in fungi<sup>17, 21</sup>. The results of all of these investigations show that various dilute solutions, generally of inorganic salts, may have a beneficial effect upon growing cells up to a certain concentration. This beneficial effect is evidenced in more vigorous assimilatory activity and increased production of chloroplasts, and in some cases in an increased cell production. After reaching a certain concentration, the action of the salt has usually been that of an irritant poison, which usually resulted in the temporary disabling and generally in the death of the cells affected. The only cases where the action of a probable poison resulted in growth at all comparable to the intumescences above described, is in connection with various insect galls. It is probably true that the formation of insect galls is due to some chemical influences exerted either by the parent insect, the egg or the larvae, and as a result of these influences, oedematous cells are sometimes produced, as described by Küstermacher<sup>13</sup>, Küster<sup>10</sup>, and Woods<sup>39</sup>.

In none of the effects noticed as a result of the action of chemicals on leaves, with the possible exception of insect galls, has any change in the tissues, such as the oedemas described, been noted. Where copper salts were absorbed there was either a stimulus in the way of increasing production of cell contents, or increased assimilation, or where stronger solutions were used, the cells were destroyed entirely. In the case of the cauliflower intumescences, there is a very evident stimulation resulting from the appli-



cation of various salts, which shows itself in the development of giant cells, or in a state of excessive turgescence. The salts of copper and ammonia must be regarded as exerting a poisonous effect, that is they produce a functional derangement in the organism which sooner or later results in death of the affected parts. The action of poison in accelerating growth has been frequently noted, as for instance in the case of chloroform or ether which may start into growth, or accelerate growth of, resting organs. "Poisons," says Pfeffer<sup>18</sup>, "like all other chemical influences, cause not only a retardation but also accelerate either temporarily or permanently, the sum total of the activities or special functions."

In the case of the leaves of the cauliflower sprayed with copper and ammonium salts, a very definite reaction took place which showed itself soon after the application of the sprays in the very much increased turgidity of the spongy parenchyma underlying the sprayed spots. This increased turgidity may have been due to one of two causes. A reaction may have taken place between the stimulating salt and certain elements of the protoplast, resulting in the formation of compounds within the protoplast having enormously high osmotic coefficients. In order to have a poisonous effect, as indicated by Pfeffer, most poisons must be not only actively in contact with the protoplasts, but they must actually enter into contact with the same. "The action of the poisonous heavy metals is probably due to their union with bodies which form parts of developing proteid substances" (Pfeffer<sup>23</sup>). It is easily conceivable that the copper salts might have penetrated into the leaf tissue, resulting in the formation of a compound as suggested. The second explanation is that possibly the various salts exerted some stimulating influence on the protoplasts, of a character not understood, which resulted in a reaction causing the production of a large amount of organic acids, which would explain the increased turgidity of the



cells. As indicated by tests made with 2% gum guaiac solution, the oedematous cells were universally very much richer in oxidizing enzymes than were the healthy cells. What possible effect the production of such oxidizing enzymes will have, will for the present have to remain undetermined. Sorauer<sup>31</sup> explains that the intumescences formed as a result of spraying with Bordeaux mixture on potatoes, were due to a tendency on the part of the plant to equalize the water present within the cells as a result of the death of the overlying epidermal cells; but this can hardly hold in the case of the cauliflower intumescences because these formed within the leaf tissue before there were any signs of death on the part of the epidermal cells.

Whatever the actual relationship between the sprayed salts and the protoplast may be, one is obviously dealing with a condition of chemical stimulation of living cells hitherto unrecorded. Detailed tests on a large scale are at present in progress, and it is expected that these experiments may throw further light on this peculiar formation.

#### SUMMARY.

The results of the present investigation may be briefly stated as follows; —

1. Cauliflower plants sprayed with copper ammonium carbonate produced large numbers of intumescences as a direct result of the spraying.

2. Similar intumescences were produced by means of weak solutions of copper chloride, copper acetate, copper nitrate and copper sulphate when sprayed in very fine drops on the surface of the leaves.

3. The intumescences were formed in larger numbers on the lower surface of the leaves than on the upper surface of the leaves.

4. Intumescences were formed independent of soil or atmospheric conditions, so that the heat and water supply had nothing to do with their formation.

5. Intumescences must be regarded as a result of the stimulating activity of chemical poisons, sprayed upon the leaf in weak solutions.

6. The stimulating activity exerted is probably due to the formation of compounds within the cells of high osmotic tensions, these com-



pounds being either compounds formed by the copper salts with parts of the protoplast, or compounds formed as a result of a stimulus exerted, as evidenced by the presence of large amounts of oxidizing enzymes as a result of an indirect stimulus exerted by the salts sprayed upon the leaf surface.

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33. SORAUER, P. In Deutschland beobachtete Krankheitsfälle. — Intumescenz an Blättern [der Nelken]. (Zeit. f. Pflanzenkrank. **8**: 291. 1898).
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40. WOODS, C. D., and BARTLETT, J. M. Experiments with potatoes. (Bull. Maine Agr. Exp. Station, No. 57, page 145. 1899).

#### DESCRIPTION OF PLATES.

Plate 25. — Photograph showing the under surface of cauliflower leaf sprayed with copper ammonium carbonate. Appearance five days after spraying.

Plate 26. — Photograph showing a small portion of cauliflower leaf sprayed with copper ammonium carbonate, five days after spraying. Approximately natural size.

Plate 27. — Sections of cauliflower leaf. 1, Section through a healthy leaf, showing the shape of the cells. The cell contents have been omitted for the sake of clearness. 2, Section of leaf through a growing intumescence, showing the enlarged spongy parenchyma cells.

Plate 28. — Section through a fully formed intumescence on cauliflower leaf, five days after spraying with copper ammonium carbonate.

Plate 29. — 1, Cauliflower leaf sprayed with copper nitrate, showing the dead areas, wherever the spray struck the leaf. 2, Cauliflower leaf sprayed with 10 per cent. ammonia, showing the killed areas of the leaf.

Plate 30. — 1, Cauliflower leaf sprayed with copper sulphate, showing the dead area wherever spray struck the leaf. 2, Cauliflower leaf sprayed with copper chloride, showing dead area where the spray struck the leaf.

Plate 31. — Cauliflower leaf sprayed with copper ammonium carbonate, showing how the leaf was killed where the spray struck in large quantities, with intumescences where small drops struck.





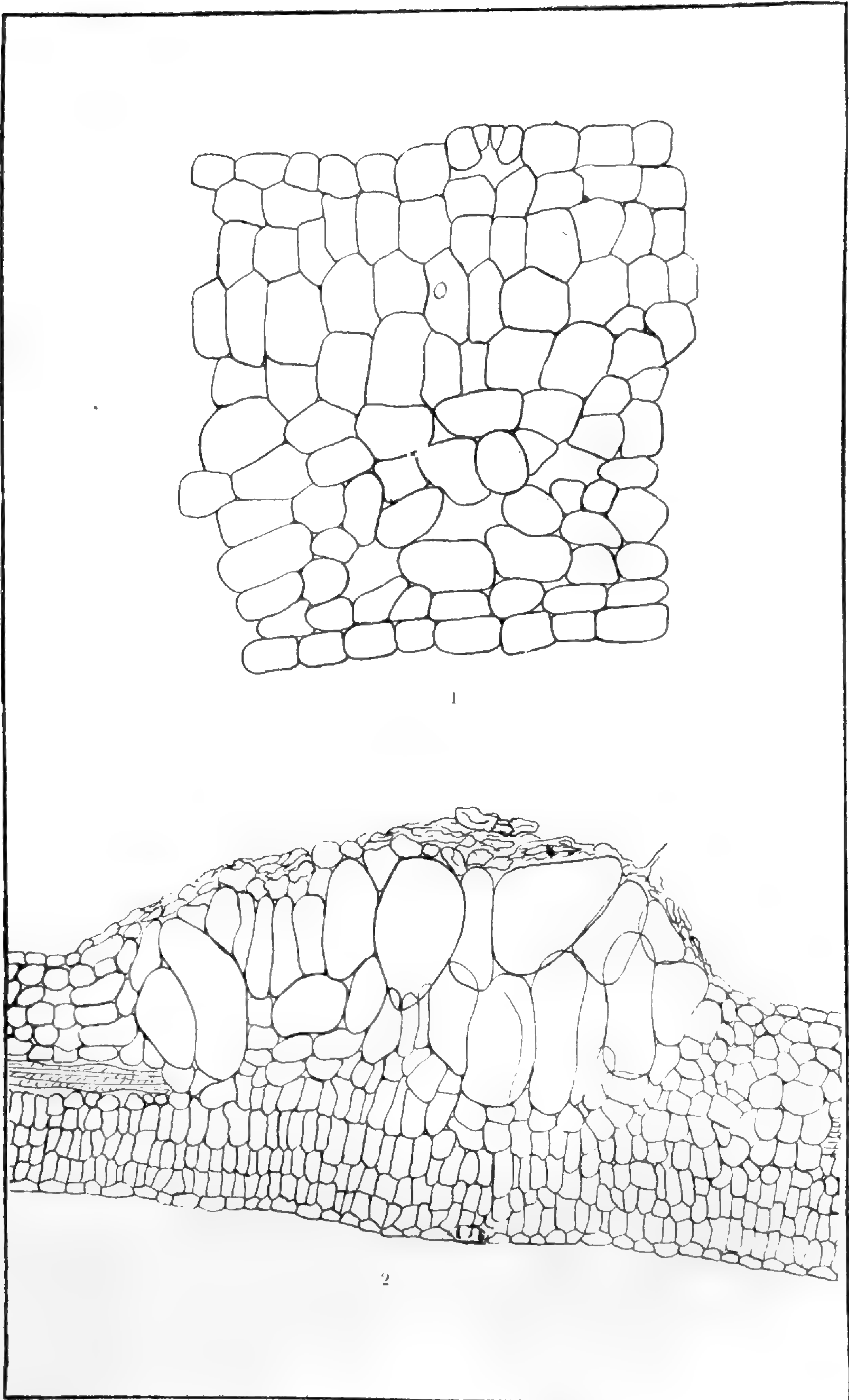
INTUMESCENCES OF CAULIFLOWER.





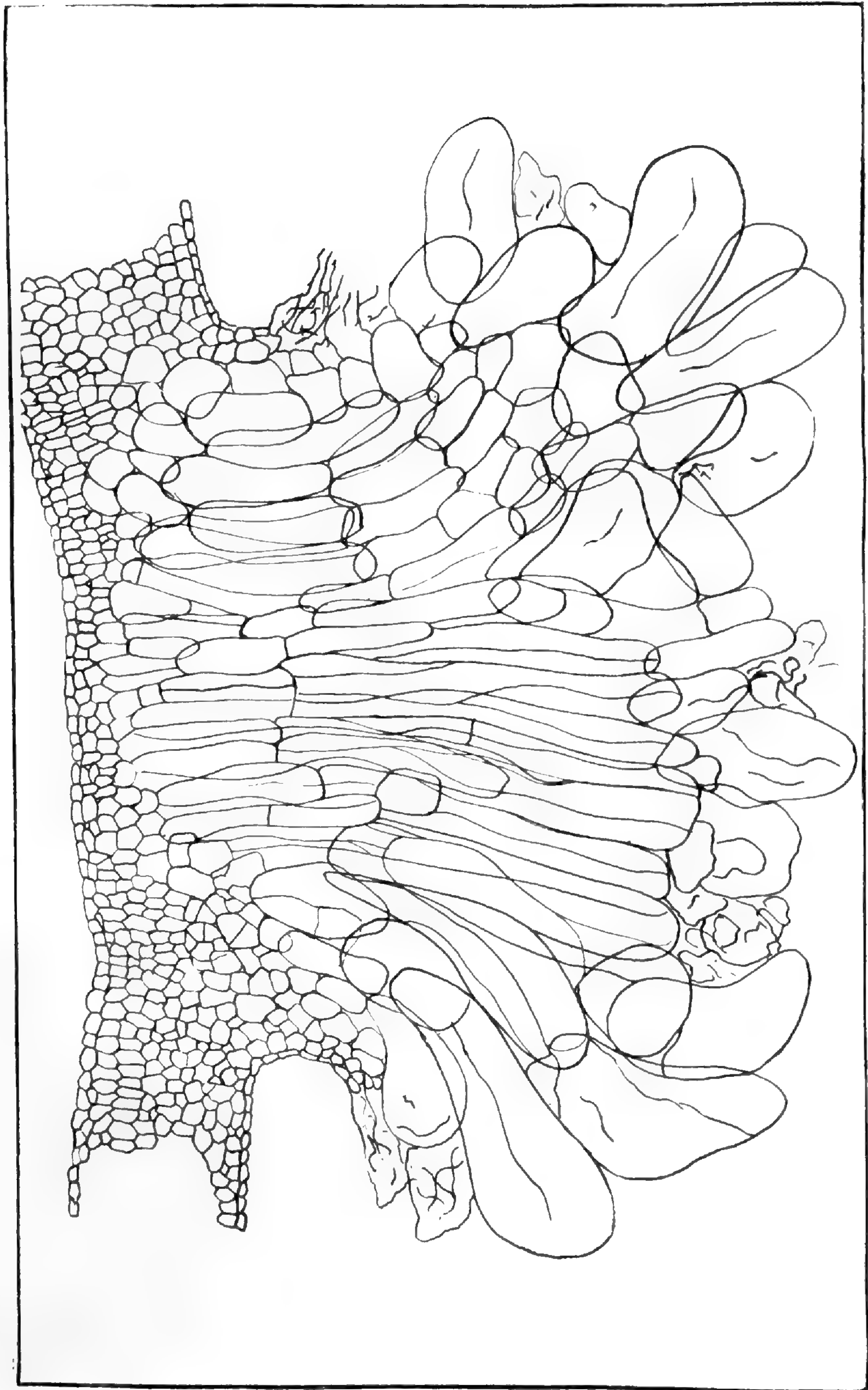
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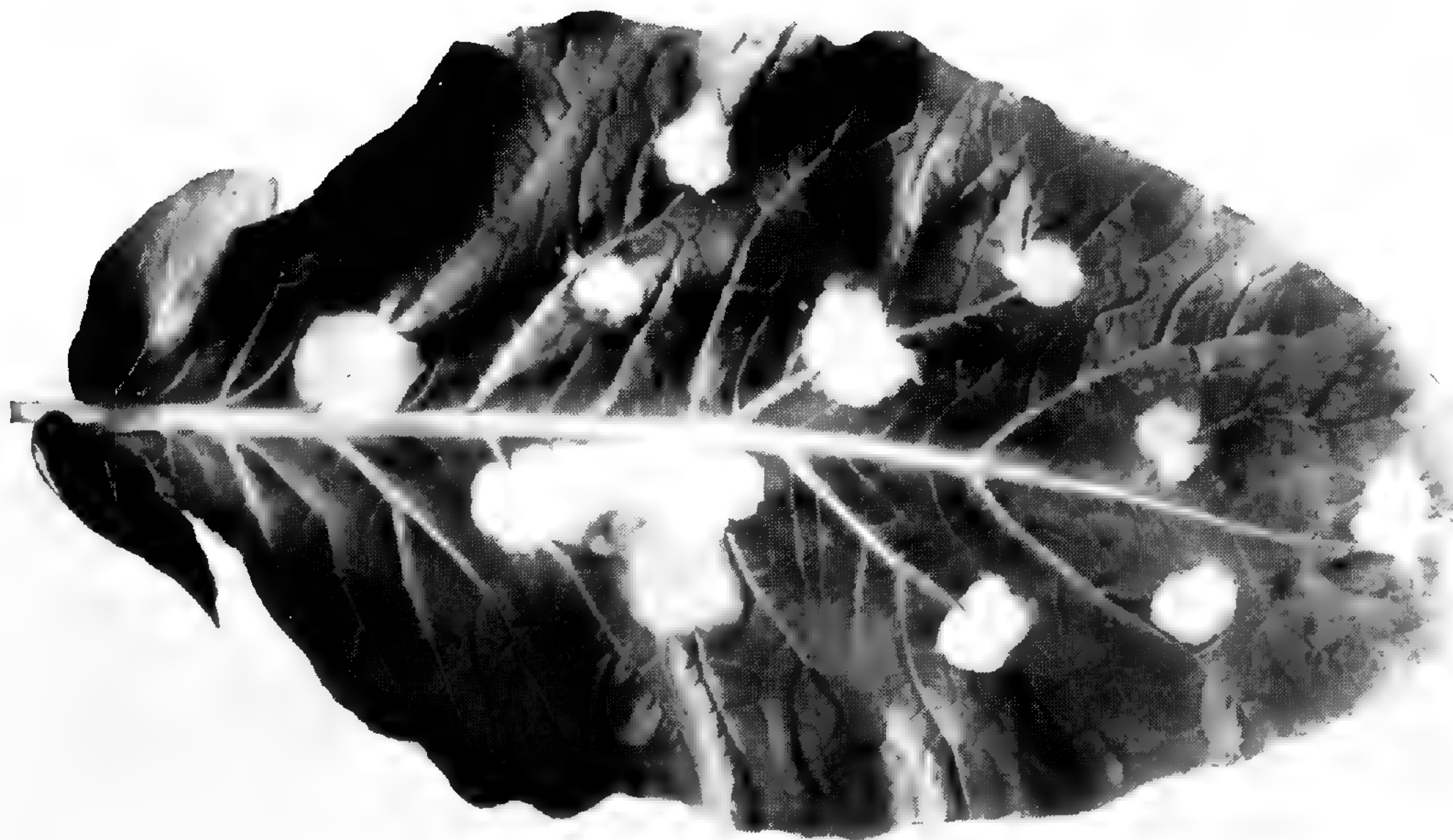
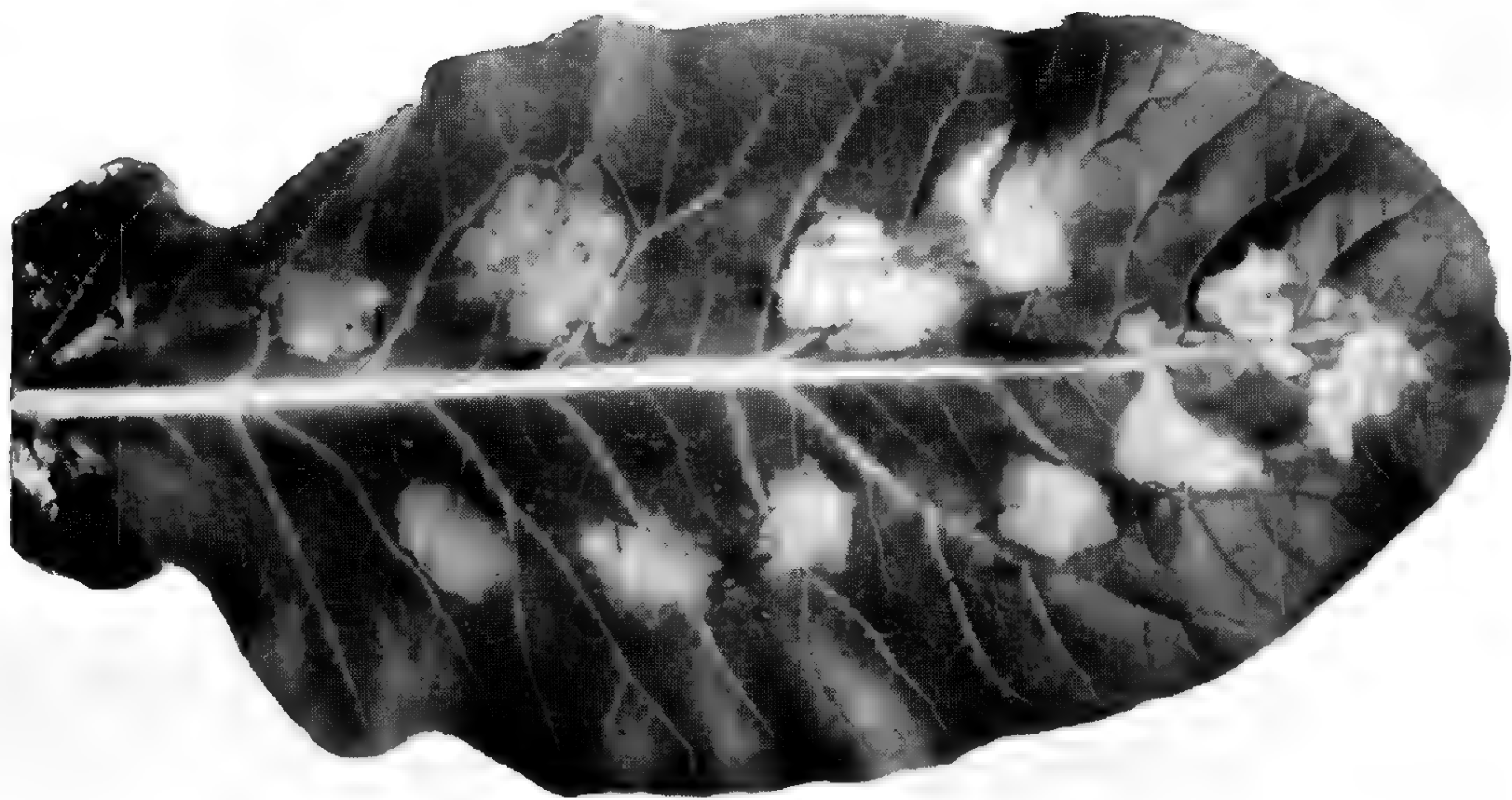
LEAF STRUCTURE OF CAULIFLOWER.





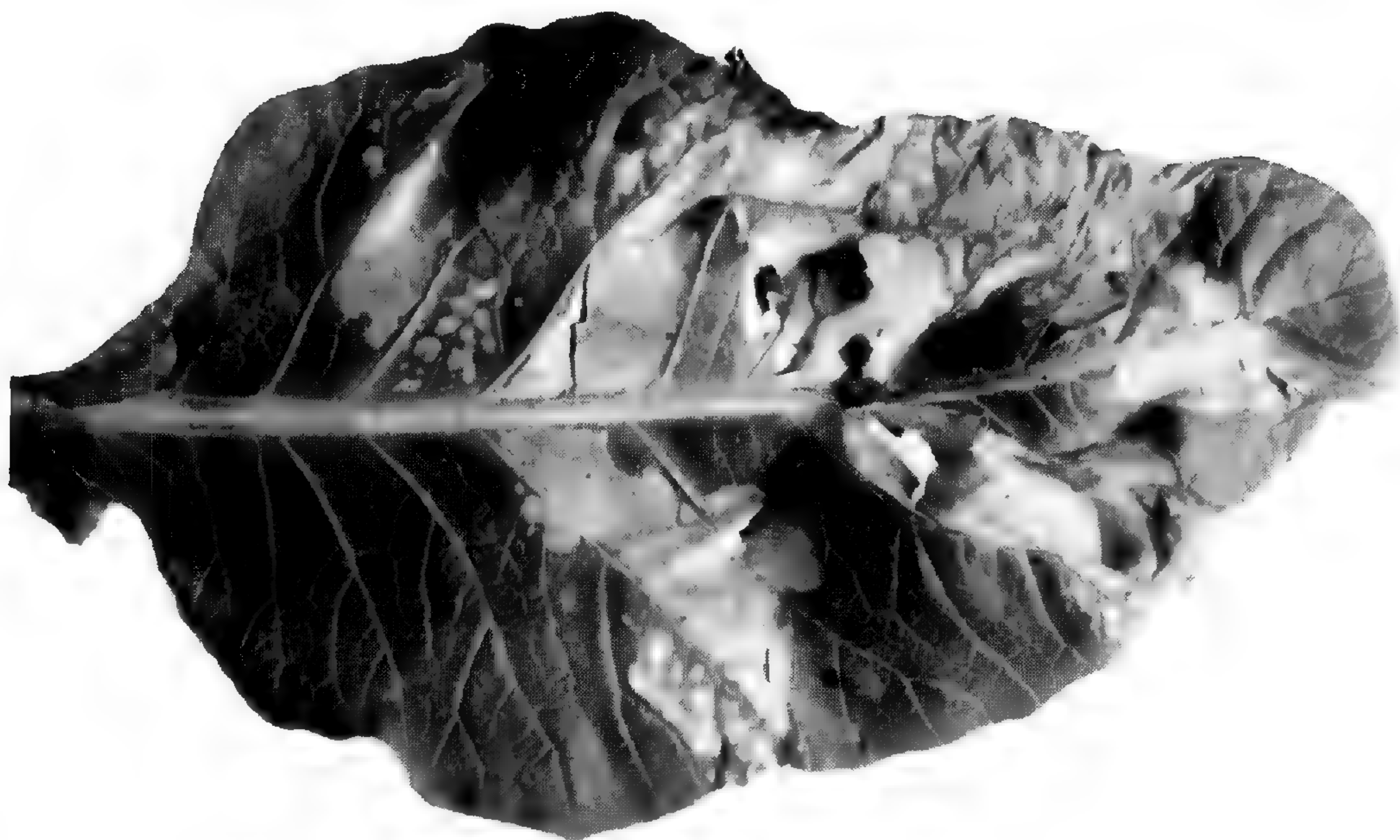
INTUMESCENCE OF CAULIFLOWER.





SPRAYED CAULIFLOWER.





SPRAYED CAULIFLOWER.





SPRAYED CAULIFLOWER.



A DISEASE OF CAULIFLOWER AND CABBAGE CAUSED BY  
SCLEROTINIA.

BY GEORGE GRANT HEDGCOCK.

The cabbage, cauliflower, and related plants are more often diseased by the black rot due to *Pseudomonas campestris* (Pammel) Smith than by all other causes combined. During the past two years plants of both cauliflower and cabbage have been observed at the Missouri Botanical Garden and elsewhere in the vicinity, decaying with a dark rot, often accompanied by numerous tiny black specks. This at first was thought to be a form of the bacterial rot. When specific cases on the cauliflower were brought to our immediate attention, the differences between this disease and the bacterial one were noted. Cultures carefully taken from the interior of decaying cauliflower stems, quite uniformly produced colonies of a fungus with a white, fluffy mycelium. These were transferred and the fungus studied throughout all its stages and identified as *Sclerotinia Libertiana* Fckl. It has been grown under careful bacteriological methods, and inoculations have been made, the results of which verify its nature as a parasite, and also confirm the investigations of Ralph E. Smith on *Botrytis* and *Sclerotinia*.\*

The rot of cauliflower produced by *Sclerotinia Libertiana* is more watery than that caused by *Pseudomonas campestris*, and the diseased tissues are not so dark in color. Sclerotia are not always present, and when found are usually sparse in number. The fungus penetrates through the cell walls of the host in every direction, causing a collapse of the cell walls, and wherever the epidermis becomes ruptured a rapid escape of the protoplasm of the

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\* Bot. Gaz. 29: 369-406. (Jun. 30, 1900).



decomposed tissues takes place. The collapse is apparently hastened by a dissolution of the cellulose walls by an enzyme secreted by the fungus. The younger, growing portions of the plant are favorite places for attack. The petioles of the leaves are often rotted away at the base, the leaves droop, and the fungus grows down through each leaf, rotting it, often forming sclerotia on the thinner portions. Sometimes older cauliflower plants are attacked at the base and rotted off, before the head becomes diseased.

Pure cultures of the fungus were obtained from the cauliflower in February, 1904, and grown in potato, rice and agar tubes. These all formed prominent sclerotia in a few weeks, only a few being produced in each tube. At the same time cultures of *Botrytis cinerea* Pers. were obtained from a number of sources, and grown for comparison. These bore numerous smaller sclerotia. Sclerotia from old, dry cultures of both species were placed in pots of soil, previously sterilized in an autoclave at 15 pounds pressure for three hours. They were barely covered with the soil and placed in a moist room, and kept in moist soil for about three months. In seven weeks the *Sclerotinia* sclerotia threw out from each a number of brown or gray stalks, and in a week or two more, apothecia developed upon the stalks. These at first were trumpet shaped with a convex cup, but flattened out and became concave when mature. In color they were a light brown.

The apothecia contained eight-spored asci. The ascospores were slightly granular, but without guttules. In poured agar plates they germinated readily and developed rapidly into dense white fluffy colonies. The mycelium was destitute of conidia at every stage. In less than two weeks sclerotia were formed on colonies transferred to potato or rice tubes. Inoculations with both the ascospores from the apothecia and the mycelium from pure cultures produced the typical rot of the cauliflower, control plants



wounded but not inoculated remaining free from the disease. The fungus was again isolated from the inoculated plants and grown in pure cultures with the same results as in the former instance.

*Sclerotinia sclerotia*, after remaining dry for over a year, threw out filaments, developed an extensive mycelium, and formed new sclerotia in less than two weeks from the date they were placed in fresh potato tubes. This indicates the great vitality of the fungus while in this stage.

Fewer cultures of *Botrytis* were used than of *Sclerotinia* in the parallel experiments, but later over 200 cultures of *Botrytis* have been grown and a large number of *Botrytis* sclerotia placed in pots of sterile soil. No apothecia have developed from this latter experiment, which is still in progress at the time of writing.

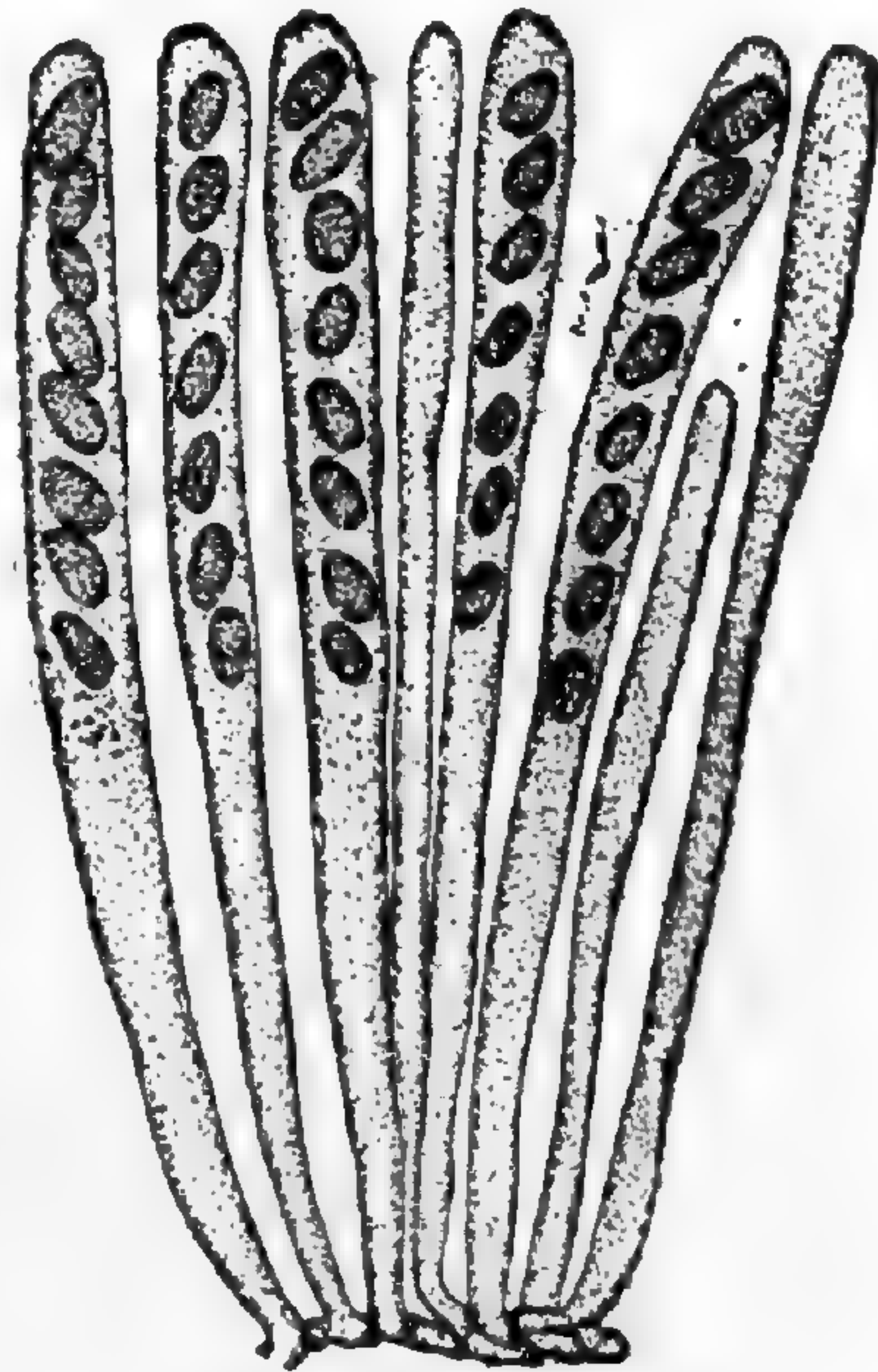
MISSISSIPPI VALLEY LABORATORY.

#### EXPLANATION OF PLATES.

Plate 32. — *Sclerotinia Libertiana*. 1, Upper view of a group of apothecia, most of which are mature. 2, Sclerotia with apothecia developing.

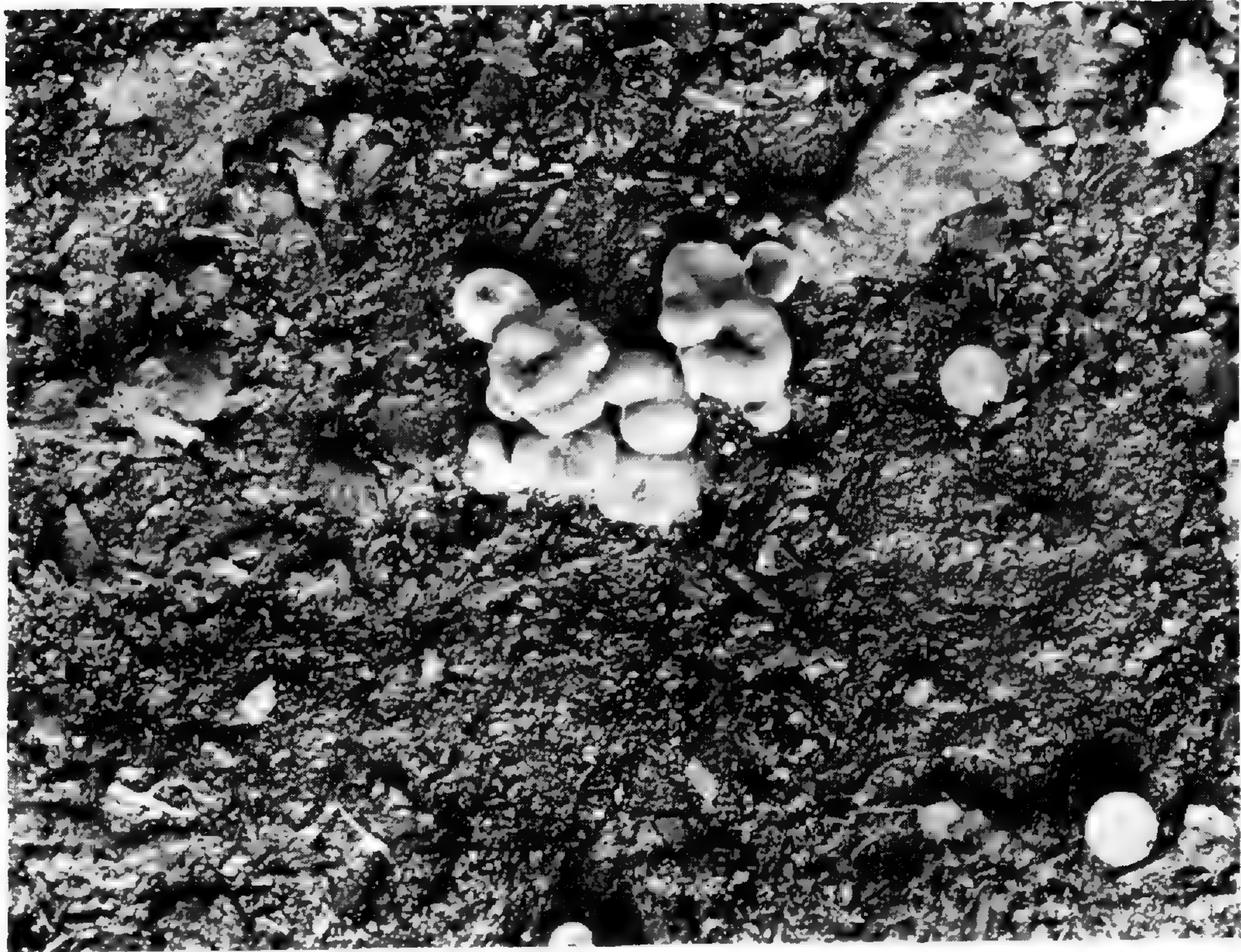
Plate 33. — *Sclerotinia Libertiana*. 1, 2, Sclerotia before, during, and after the development of apothecia.

Plate 34. — *Sclerotinia Libertiana*. Pure cultures on agar slant tubes. The dark bodies are sclerotia.



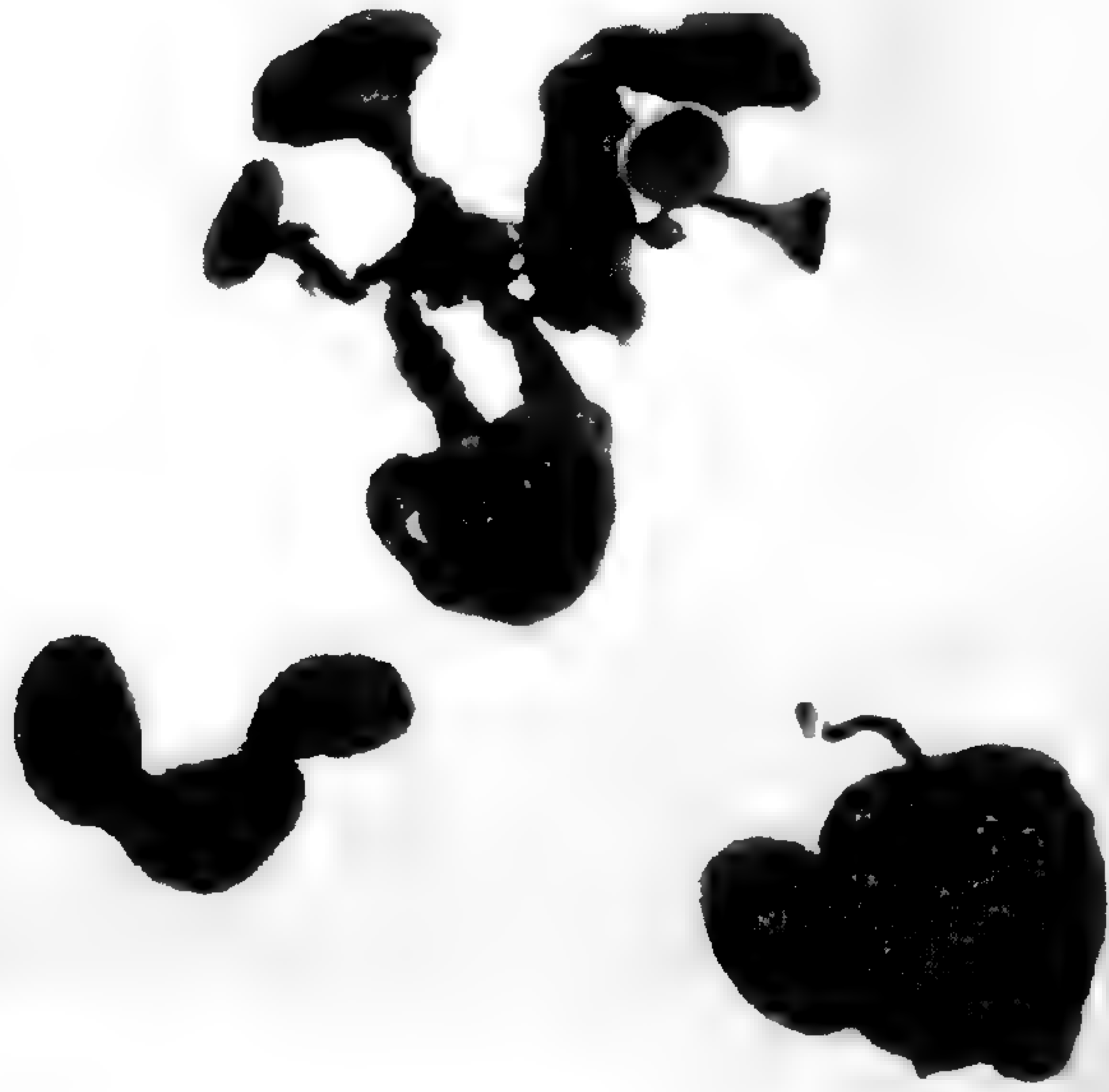
SCLEROTINIA ASCI.





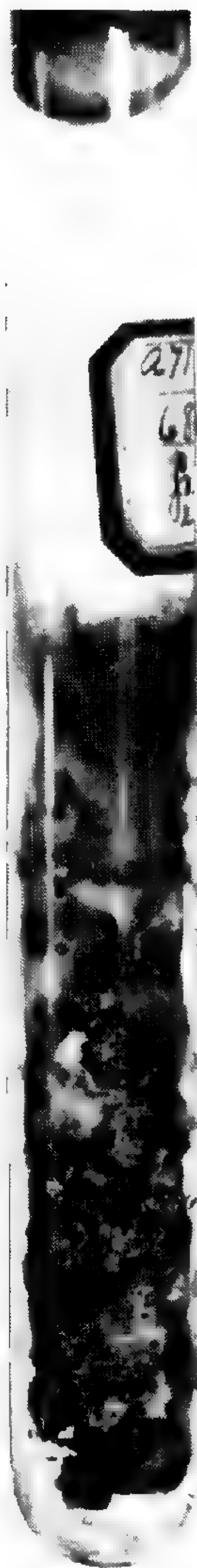
SCLEROTINIA OF CAULIFLOWER.





SCLEROTINIA OF CAULIFLOWER.





SCLEROTINIA OF CAULIFLOWER.



A DISEASE OF CULTIVATED AGAVES DUE TO COLLETO-  
TRICHUM.

BY GEORGE GRANT HEDGCOCK.

A number of small agave plants of the species *Agave Utahensis*, secured from its natural home, were potted during the spring of 1904, and during the earlier part of the summer. These were placed along with a large number of agaves of various species in the soil on a western exposure of one of the greenhouses of the Missouri Botanical Garden. In a short time many plants were found dying from a disease which first attacked the older leaves. A microscopical examination of a number of the diseased leaves revealed the constant presence of a fungus, apparently of the genus *Gloeosporium*; but later more careful search showed that in all the older acervuli of the fungus the characteristic setae of *Colletotrichum* were present, thus placing it under this genus.

Inoculations with conidia taken from plants placed in a moist chamber were made by wounding the leaves of healthy plants with a sterile scalpel and inserting masses of the spores in the wounds. Control plants were similarly wounded, but not infected. The inoculated plants in about two weeks became diseased in the same manner as those from which the spores were taken, and in a short time after produced characteristic acervuli of *Colletotrichum*.

Cultures were made from conidia taken from masses exuding from acervuli on the leaves of plants under bell jars, using the most careful methods with agar plates and tubes. Colonies were secured which grew to a diameter of one to two inches. A dark mycelium, with numerous knotted masses of abortive pycnidia, was obtained in a number of



cultures on various vegetable and agar media, but no mature conidia were developed. It therefore was not possible to inoculate with conidia from pure cultures. A few inoculations were made with the mycelium. Of these only one or two were successful, indicating a low vitality of the fungus when under culture.

The disease often has a striking appearance. The conidia of the fungus apparently germinate on the surface of the host and gain entrance through either the stomata or wounds. The tissues are penetrated by the mycelium in all directions, forming either a circular or elliptical spot, which at first is darker in color than the adjacent tissues, changing as the tissues die to either a brown or gray color. The adjacent tissues of the host under moist conditions turn brown and rot rapidly, the mycelium penetrating to all parts of the leaf. Under less humid conditions, however, the adjacent tissues slowly darken in color, often assuming a purple tinge. It was found in such cases that there is a death of the tissues far beyond the region penetrated by the mycelium, indicating the presence of an enzym secreted by the fungus. Bacteria are never associated with the latter type of the disease, but are often present with the former.

The acervuli are usually formed in concentric rings. This character was so constant, that, taken along with other characters, it was thought at first that we have here a new species of *Colletotrichum*. The examination of both fresh and herbarium material at the Garden, at Washington, D. C., and elsewhere has revealed the fact that such characters are variable and that the fungus is probably identical with *Colletotrichum Agaves* Cav., described as occurring on the cultivated agaves at Pavia. The following is the description of our fungus: —

Spots circular or elliptical, often becoming confluent, olive, changing to gray or brown; acervuli spherical to oblong, usually breaking through the epidermis of the host in concentric rings and ejecting orange colored



masses of conidia; setae acute to blunt, light brown, 3- to 5-septate, 110 to  $170 \mu \times 5$  to  $6 \mu$ ; conidia oblong to cylindrical, hyaline, with one to two guttules, 16 to  $31 \mu \times 5$  to  $6 \mu$ ; conidiophores erect, hyaline, usually simple, 6 to  $7 \mu$  in diameter, but very variable in length in different acervuli. No ascigerous stage was found.

Habitat: On the leaves of *Agave Americana*, *A. atrovirens*, *A. horrida*, *A. marmorata*, *A. potatorum*, *A. Utahensis*, and *A. spp.*, — often causing the death of younger plants.

The plants of the species *A. Utahensis* were the first to be diseased, and it is thought that the fungus was introduced into the greenhouse with this species. After a short time the disease spread to other species, none of which suffered so much as the original host.

A search for the fungus on agaves in the Southwestern United States has thus far failed to locate the disease, either on wild or cultivated plants. In the herbarium of the Missouri Botanical Garden, however, there are specimens named *Gloeosporium macropus* Sacc., which developed during a fortnight's detention in the collecting box of mature leaves of an undescribed large-leaved *Agave* of the *Americanae* group collected at La Barca, Mexico, by Dr. Trelease in the summer of 1901. Some of the zonate acervuli of these specimens show the characteristic setae of *Colletotrichum*, while their other characters agree with those of *C. Agaves*.

Mr. C. H. Thompson of the Garden has been quite successful in checking the spread of the disease, which is favored by moist conditions. He places all of the diseased plants in a separate locality, and removes the lower leaves as fast as they become slightly diseased. In case of older plants, the spread of the fungus is checked. Young plants often die in spite of the removal of the leaves, the fungus apparently penetrating the whole plant. Bordeaux mixture of the ordinary formulae is beneficial in preventing the spread of the fungus to adjacent plants.



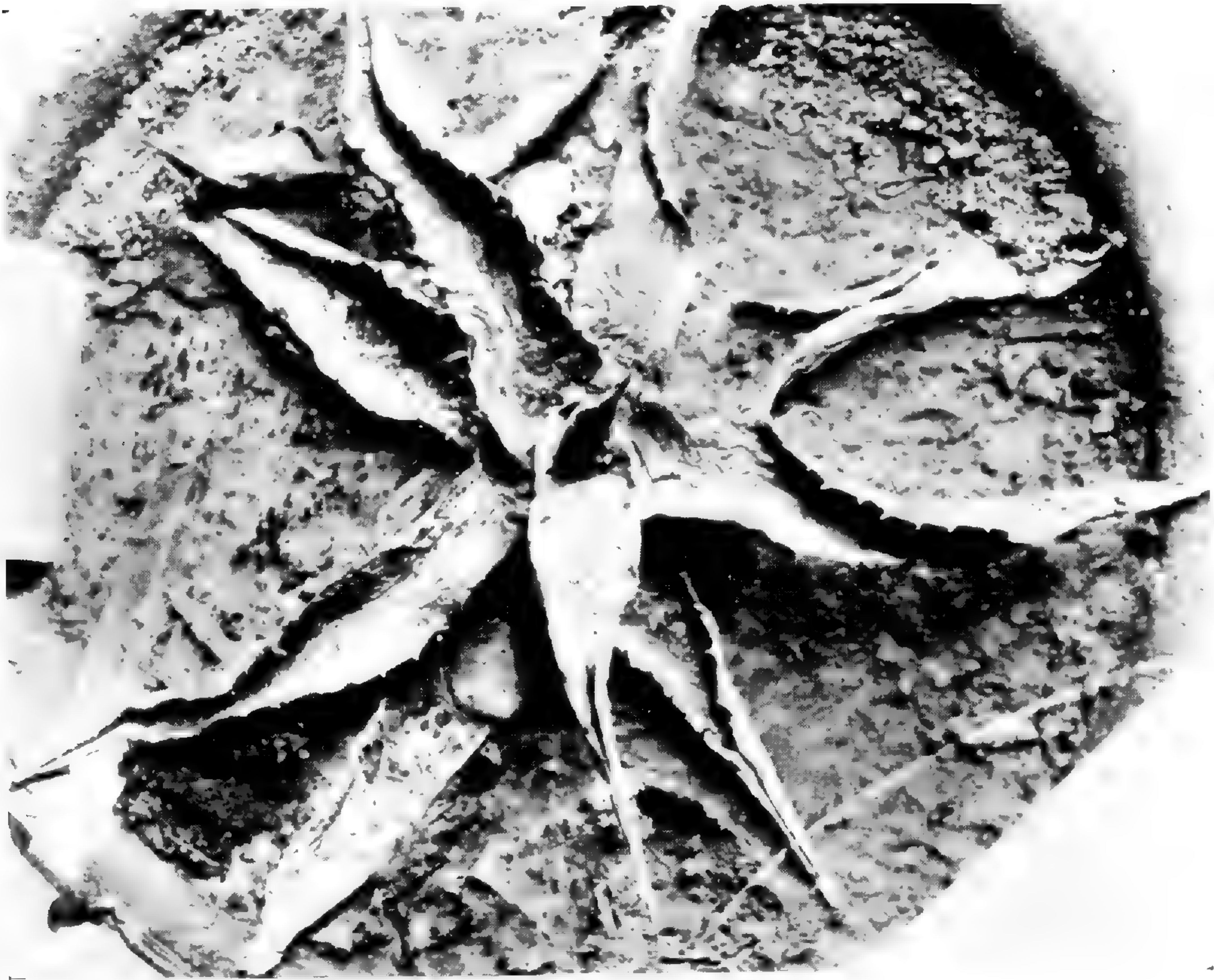
## EXPLANATION OF PLATES.

Plate 35. — 1, A young plant of *Agave Utahensis* killed by *Colletotrichum Agaves*. 2, A plant partially killed, showing the fungus with typical concentric lines of acervuli.

Plate 36. — 1, 2, Typical diseased areas with acervuli of *Colletotrichum Agaves*.

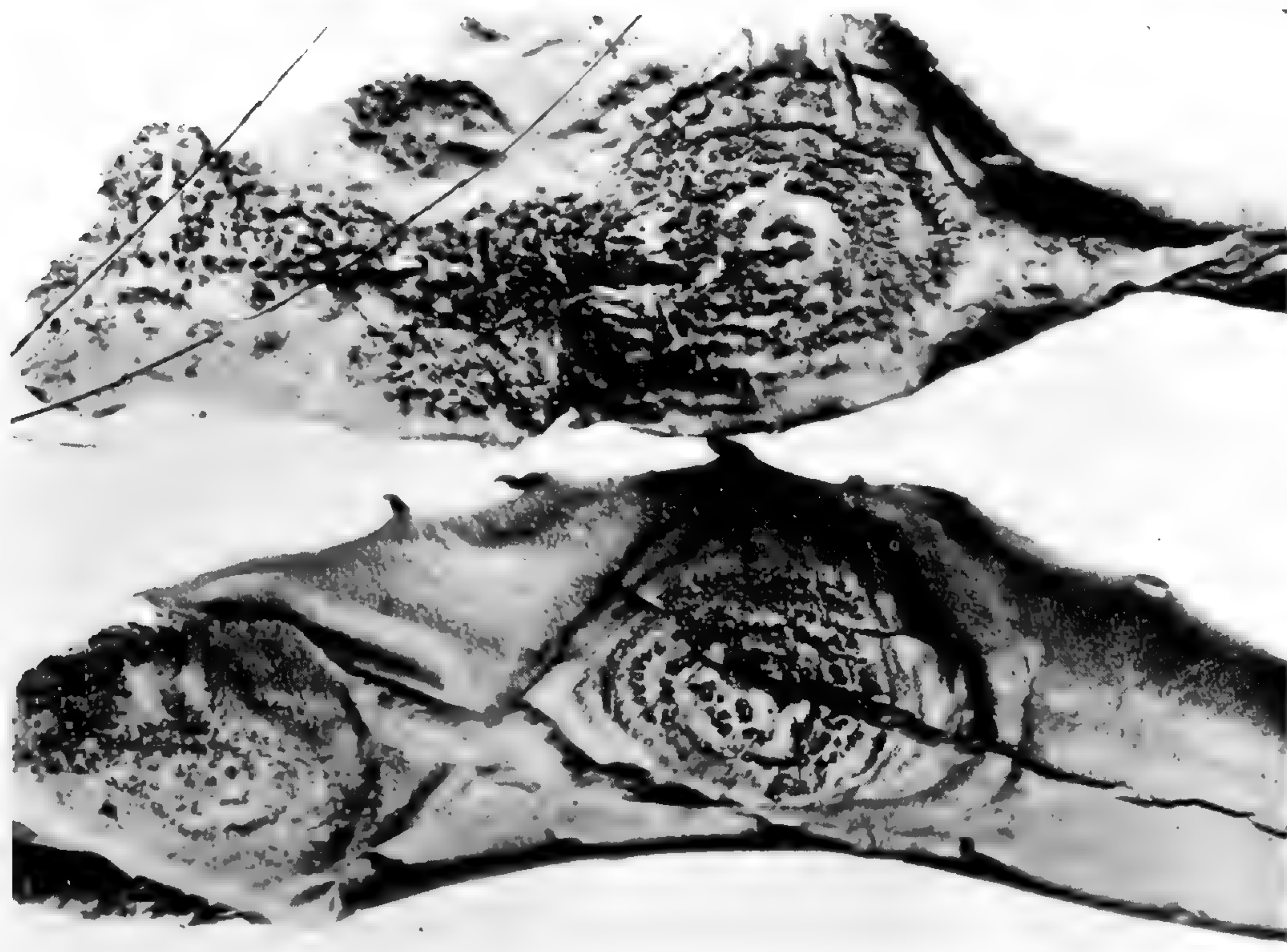
Plate 37. — 1, Acervulus of *Colletotrichum Agaves* bursting through the epidermis of the host. 2, Conidia showing guttules. 3, Setae and conidiophores bearing immature conidia. 4, Conidiophores with immature conidia.





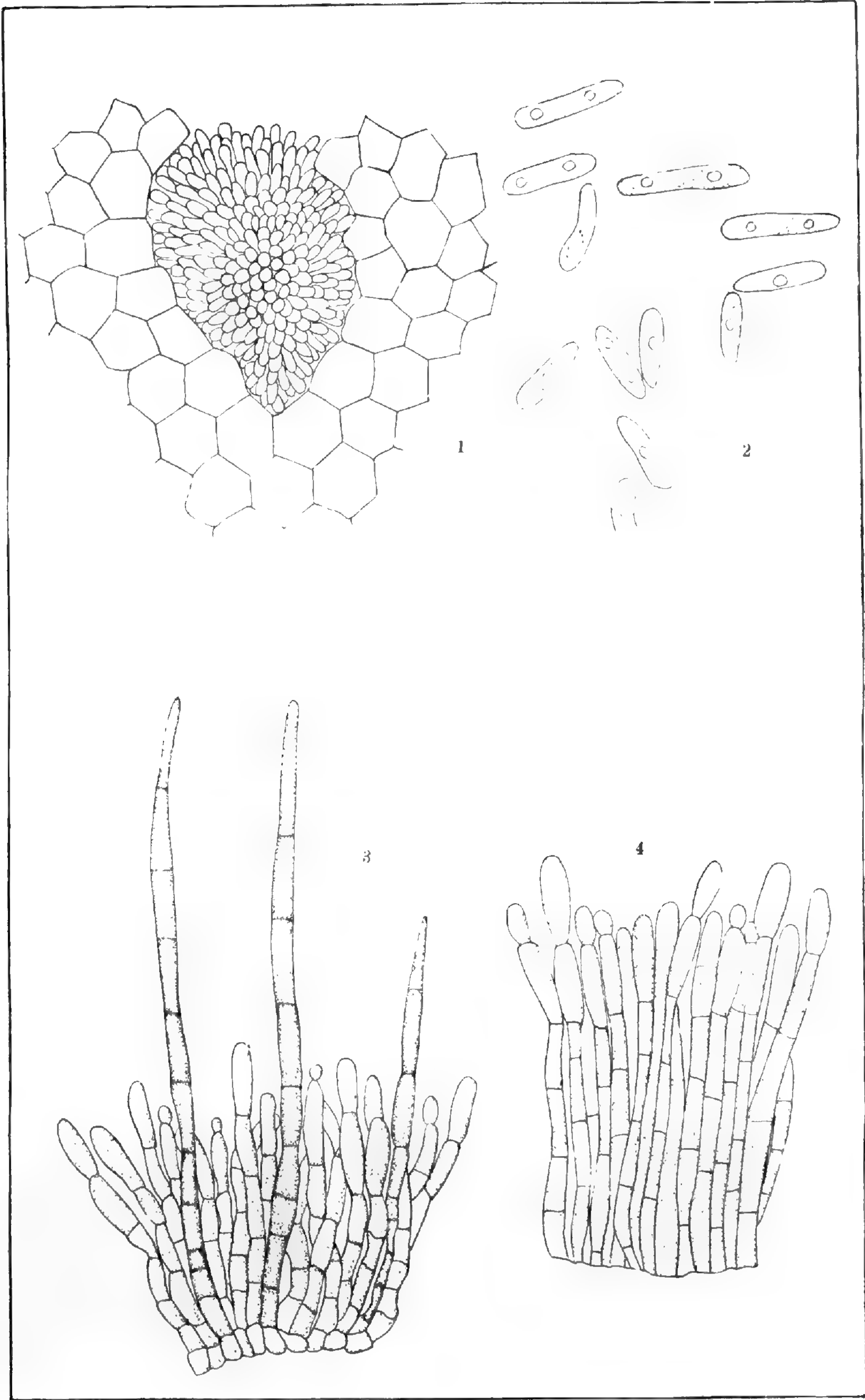
COLLETOTRICHUM AGAVES.





COLLETOTRICHUM AGAVES.





COLLETOTRICHUM AGAVES.



## VEGETATIVE STRUCTURE OF MESOGLOIA.

BY A. C. LIFE.

As very little work has been done upon the vegetative structure of *Mesogloia divaricata*, it seemed an inviting field for investigation, and accordingly work was begun upon it at Wood's Hole, Mass., at the Biological Station, in the summer of 1904.

This work has been continued in the Shaw School of Botany of Washington University.

Previous work has been done mainly by Reinke and Henckel. Reinke\*, in 1881, worked out some points of the structure of what he called *Chordaria divaricata*, which Farlow† states is the *Mesogloia* of the New England coast. Engler and Prantl‡ describe the genus *Mesogloia*, but are not definite in the description of its structure.

Henckel§ in 1903 published an account of both *Chordaria flagelliformis* and *C. divaricata* in connection with *Cystoclonium*. His conclusions are different from those of Reinke, concerning the method of growth.

The *Mesogloia divaricata* which was studied in this work was collected at Wood's Hole, Mass., during the early part of August, 1904. It was obtained from water one to two feet in depth at low tide, where it grew attached to rocks and the silty bottom.

The material was fixed in a weak chromo-acetic acid solution in sea water. It was allowed to remain in the

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\* J. Reinke, Atlas deutscher Meeresalgen. 2: 57. pl. 39. (1889).

† Marine algae of New England. (Report U. S. Fish Commission. 1879: 84.)

‡ Die Natürlichen Pflanzen-Familien. Teil I. Abteilung 2. p. 229.

§ Sur l'anatomie et la biologie des algues marines. (Scripta Botanica Hort. Universit. Imp. Petropol. 20: 81.) 1903.



fixing fluid about 15 minutes and then washed in sea water. The grades of alcohol used in dehydrating were mixed with sea water. Sections were made by imbedding in paraffin and cutting with the microtome.

The first preparations were stained with Flemming's safranin-gentian-violet-orange stain. This stain did not prove very satisfactory, as it overstained the cell walls. Later in the work Haidenhain's iron-alum haematoxylin method was used with good results.

In the study of the apex both longitudinal and cross sections were made and mounts were also prepared by crushing in glycerin under the cover-glass. The growing point of *Mesogloia divaricata* so commonly turns to one or the other side of the line of the axis of the stem, as to making it a little difficult to get sections parallel to the axis in this region.

The apex of the stem consists of a central axial row of cells terminating in an apical cell, surrounded by a sheath of cortical cells except at its very tip (plate 38, f. 1). From these cortical cells arise hairs and paraphyses, the "Assimilationsfäden" of Reinke. Further from the tip there may be two or more layers of cells in the cortical sheath (figures 3, 4). In still older parts of the stem there is a central cylinder consisting of the central row of cells with two or more layers of thick-walled cells surrounding it. As mentioned by Henckel,\* these are cells that have been cortical cells in the younger stem. Bounding the central cylinder near the apex is a zone of thin-walled cortical cells from which the paraphyses and hairs arise (figures 4, 5).

The contents of the central cells soon begin to break down. The nucleus first degenerates, then the protoplasm becomes grouped here and there in small masses. Soon the cross-walls break down and the contents of the central

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\* *Loc. cit.*



tube thus formed become granular, and do not stain readily, being probably mucilaginous in nature.

Frequently the interior of the central cylinder has a growth of hyphae and short club-shaped branches resembling paraphyses, from its inner surface.

The branches in the material that I studied had their origin in the cortical cells immediately surrounding the central row of cells. The branching, as shown by the accompanying figures (2, 7), in each case is from the cells adjoining the central row of cells but not from those cells.

Reinke's\* account of the method of growth of *Chordaria*, including *C. divaricata*, according to Henckel, has not been verified by any observer since. He claims that the growth is intercalary and extends over the tip of the stem at the basal segments of the paraphyses which stud the tip. However, in point of structure, his figures and account are verified by my sections except that the apex of the central filament does not end in a globular cell as he shows in his figures†. Henckel states that the growth proceeds from a single terminal cell which cuts off lateral cells parallel to the axis of the stem. He shows a similarity of growth to that of *Dictyosiphon* as described by Murbeck. From my own observations, I infer that the growth in length depends upon the lengthening of the central row of cells, which proceeds in a twofold manner. One is real growth of the apex of the central row of cells from an apical cell. The other is increase in length of the central cells by stretching. This stretching is at least partially, if not wholly, caused by the growth of the cortical cells which proceeds both upward and downward from its point of origin from the lateral cells cut off from the central row of cells. Growth in thickness originates by the cutting off of the cortical cells from cells

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\* Algenflora der westlichen Ostsee, deutschen Antheils. (Bericht der Kom. zur Untersuch. der Deutschen Meere in Kiel. 17-19<sup>1</sup>: 67. (1889).

† *Loc. cit.*



of the central row (figure 1). The further growth of cortical cells to several layers in thickness has not been sufficiently studied to make clear the method of growth. In treating of *Desmarestia*, Jönsson\* states that the divisions of the cortical cells are radial and that the outer cells only divide. As the structure of *Mesogloia* is quite similar to that of *Desmarestia* as described by Jönsson, it seems plausible that the same division may occur here.

The above investigation was suggested by Dr. Bradley M. Davis of the University of Chicago, to whom I am indebted for several valuable suggestions.

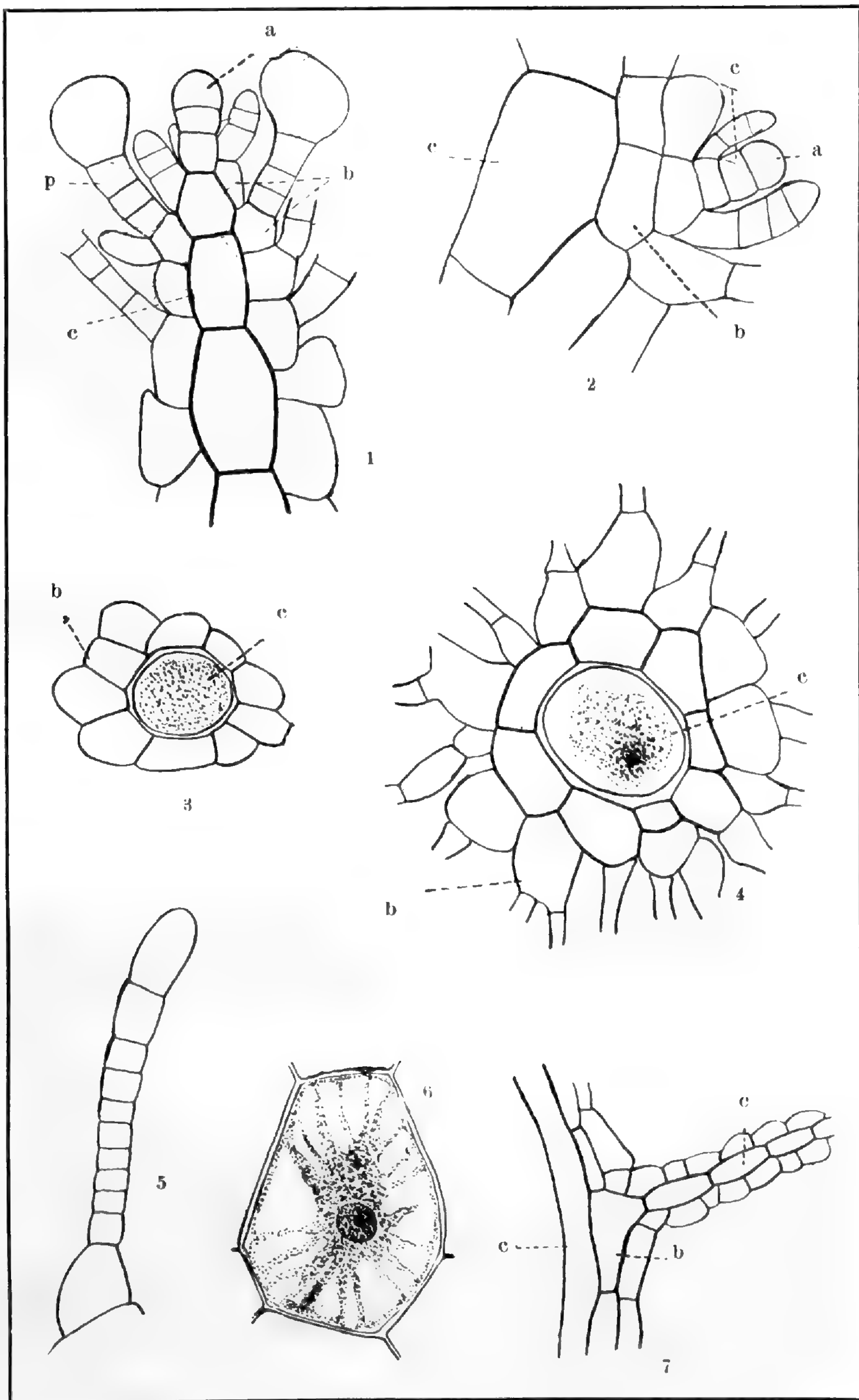
#### EXPLANATION OF PLATE.

Plate 38. — 1, Median longitudinal section of the apex of the stem of *Mesogloia divaricata*: *a*, apical cell; *b*, cortical cell; *c*, central filament; *d*, paraphysis,  $\times 600$ . 2, Longitudinal section of stem near apex, through primordia of a branch: lettering the same as in figure 1,  $\times 600$ . 3, Cross section of stem just back of apex, showing cortical cells,  $\times 600$ . 4, Cross section of stem further from apex, showing thickening of the walls of the cortical cells to form the central cylinder,  $\times 600$ . 5, Hair, nearly mature,  $\times 600$ . 6, Cell from the central row, near the apex,  $\times 720$ . 7, Origin of branch from cell adjoining central row of cells: a later stage than that shown in figure 2,  $\times 360$ .

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\* Kentniss des Baues und der Entwicklung des Thallus bei den Desmarestiaeen. (Lunds Universitets Aarskrift. 37. Afd. 2. No. 6.)





MESOGLOIA DIVARICATA.



## ILLUSTRATIONS OF A "STRANGLING" FIG TREE.

BY WILLIAM TRELEASE.

Visitors to the tropical Atlantic American coast region frequently speak of the curious sight of a large deciduous tree growing with its trunk variously wound and netted about that of some other tree, commonly a palm, which they have been told is ultimately choked or smothered to death. English speaking people sometimes call the attacking tree "the strangler." The Mexican country people have for it the name higo, or its augmentative higon, into which the Latin ficus, changed in our language into fig, has been softened in the Castilian; though when mentioned in print it is more commonly and properly called higuero or higuieron, the name of the tree, — the preceding words pertaining rather to its fruit.

The species illustrated in the accompanying plates 39 to 45 is very abundant in the vicinity of Rascon, on the Tampico branch of the Mexican Central railway, at the edge of the picturesque Huasteca district. When mature, it is a large wide-spreading tree with thick irregular trunk, shortly petioled coriaceous elliptical or ovate rather round-based mostly bluntly acuminate glabrous leaves paler beneath, and short-stalked coarsely pale-warty somewhat turbinate solitary fruits with a rather large sunken apical pit in which lies the 3-bracted foramen (plate 45).

It might be assumed to be this species that Pringle (no. 3554) distributed from the Tamosopo cañon, a few miles up the mountain from Rascon, which, with specimens collected elsewhere in the Huasteca by other botanists, is ranged by Watson\* with or beside his *Ficus fasci-*

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\* Watson, Proc. Amer. Acad. 26: 152.



*culata* of the Sonoran coast with the suggestion that all may perhaps be referrible as forms under the Central American *F. sapida* Miquel; but a few leaves which I owe to Mr. Pringle, and his note that they are from a small tree found on limestone ledges, make this assumption improbable.

From descriptions and the illustration of *F. sapida* given by Seemann,\* showing decidedly narrow acute-based leaves, I should hesitate to connect the Rascon fig closely with the typical form of that species, though the limits of foliage variability in these figs of the section *Urostigma* have not been sufficiently noted by accurate field observers to warrant one in drawing too rigid conclusions from single herbarium sheets or figures. Its affinities are evidently with the group of species centering about *F. populnea*, of which the west-coast *F. fasciculata* and *F. padifolia* and the east-coast *F. ligustrina* are representatives. For the present I should place it under the last-named species, which, under the name *Urostigma Schiedeianum*, has been noted by Miquel† from somewhat further down the eastern coast of Mexico.

Because of their customary final effect on the trees with which they are intimately associated, these strangling figs are often spoken of as parasites, a designation which has crept into good and even recent books.‡ The expressions epiphytic and epiphytal employed respectively by Schimper§ and Sargent¶ are more accurate, since the trees usually if not always lack a haustorial or even graft-like connection with the host, though their own roots intergraft; and the

\* Seemann, Bot. Herald. pl. 35.

† Miquel, Hooker's Journ. of Bot. 6: 539.

‡ Nuttall, Sylva. 2: 4. — S[argent], Garden & Forest. 1: 128; Silva. 7: 95. — Small, Flora S. E. U. S. 362. — All referring to *F. aurea*.

§ Schimper, Epiphytische Vegetation Amerikas. 60. (Bot. Mittheil. aus den Tropen. 2).

¶ Sargent, Silva of N. A. 7: 97.



term hemi-epiphyte, later applied to these figs and plants of similar habit by Schimper\* still more truly indicates their relation to the host, as they "germinate and pass through their earliest development on trees but subsequently become connected with the ground by their roots" thus passing from the epiphytic to the ordinary mode of nutrition.

In the genus under consideration Schimper† finds the largest representatives of his hemi-epiphytes, among the banyans and other figs of the tropics of both hemispheres. Striking pictures of some of these plants have been published by various writers.‡ Perhaps the most interesting individual case is that of the famous banyan (*F. Indica*) of the Calcutta botanical garden, which in its mature form has served as the subject of many photographs and engravings. According to Hooker,§ in 1782 its site was occupied by a wild date-palm out of the crown of which the banyan sprouted; but the palm has long since disappeared, while the fig of late years is said to have lost a number of its horizontal branches so that in places it is broken into a ver-

\* Schimper, Pflanzen-Geographie. 340, 343; English translation. 319, 320.

† Schimper, Pflanzen-Geographie. 344; English translation. 321.—One of the younger plants of this type is shown in *f. 158*; a seedling, in *f. 160*; and a good illustration of one of the species overgrowing a Venezuelan *Copernicia*, in *f. 200*.

‡ Schimper, Epiphytische Vegetation Amerikas. *pl. 1* (an unnamed Sikkim-Himalayan species). — Kerner, Pflanzen-Leben. **1**; English translation. **1**:159, 704. *f. 168-9* (*F. Benjamina* "incrusting" some myrtaceous tree on one of the Nicobar islands, *f. 169*; and an unnamed species in the earlier stages of its root development, *f. 168*). The plants are called "tree-constrictors"). — Wettstein, Vegetationsbilder aus Südbrasilien. *pl. 31*. — A quotation from Tennent's Ceylon, in *The Garden*. **25**:446, gives an interesting general account of the phenomenon in that island. — *Gardeners' Chronicle*. III. **18**:327. *f. 61* (a species doubtfully referred to *F. Isiala*, on the mango).

§ Hooker, Himalayan Journals. **2**:254. — See also Bailey's *Cyclop. Amer. Hort.* **2**:582.



itable grove of distinct trees though for its greater extent it is still one many-columned tree.

Curious freaks of the roots of various species of the genus, aside from this biological peculiarity, are noted by Hooker,\* Kerner,† and others; and the production of columnar roots beneath the branches of banyans and some other figs is too well known to require more than passing mention.‡

In the Huasteca region, large areas are occupied by almost pure forests of the east-coast tree palmetto (*Sabal Mexicana* of most writers; *Inodes* sp. of Cooke). When not injured by fire, — for the pastures in which they stand are frequently burned over at the end of the dry season, — these palms have the upper part, at least, of the stem covered by long-persistent petiole bases from which the old leaves have broken away. These form a very good nidus for the bird-disseminated seeds of the fig, which, germinating, give rise to plants that live for a few years as true epiphytes, forming bushy growths below or among the apical leaves of the palm (plates 39, 43).§ Later, begins the characteristic formation of descending and encircling, often anastomosed, roots (plates 39, 40, 43). It is these which, becoming at length largely or entirely confluent (plate 41), constitute the pseudo-trunk of the fig, — hollow at the center through which the original palmetto host passes, often persisting until a very advanced age and size of the strangler have been attained (plates 42, 43), its

\* Hooker, *Himalayan Journals*. 2: 271. *frontispiece*.

† Kerner, *Pflanzen-Leben*; English translation. 1: 710. *f. 171*. 2: 758. *f. 428*.

‡ See, for a few striking illustrations: Kerner, *l. c.*, English translation. 1: 757. — Schimper, *l. c.*, English translation. 322. *f. 162* (*F. Bengalensis*). — *Gardeners' Chronicle*. III. 4: 214. *pl.* — S[argent], *Garden & Forest*. 1: 128. *f.* (*F. aurea*).

§ *F. Bonplandiana* has been distributed by Pringle (no. 3997) from Micos, somewhat further up the mountain, with a note showing that it develops in the same way.



final disappearance leaving the fig tree of the adult form shown in plate 44. Meantime the latter, itself, has become the host of numerous orchid, bromeliad and fern epiphytes, and may even bear secondary plants of its own species, some of which themselves may effect a connection with the ground (plate 42). Morphologically, therefore, the main pseudo-trunks of these hemi-epiphytic figs, like the columnar props which some of them form under their branches, are roots and not stems, — a fact which must be taken into account in studying their anatomical structure.

## EXPLANATION OF PLATES.

The illustrations are from photographs by the author, all made about Rascon, in the State of San Luis Potosi, Mexico.

Plate 39. — Palmetto with upper part of stem covered with petiole-bases in the axils of which are established a large epiphytic bromeliad, and a rather small fig the roots of which have already closely invested the middle part of the trunk.

Plate 40. — At the left, a palmetto the petiole bases of which support numerous small epiphytes. In the center, a palmetto with two well established figs.

Plate 41. — Part of the trunk of the central tree of plate 40, showing the characteristic roots of the fig and the influence of such obstacles as petiole bases of the palmetto on the direction of their growth.

Plate 42. — An old but openly branched fig tree with the axile palmetto still vigorous. The fig itself bears clusters of ferns, *Tillandsia*, etc.. A small independent trunk is shown at the right.

Plate 43. — At the left, a palmetto bearing a well started young fig. At the right, an old fig tree the dense branches of which closely surround the leaf cluster of the central palm.

Plate 44. — A very large mature fig tree from the center of which the original palmetto host has entirely disappeared.

Plate 45. — Fruiting spray of the strangling fig of Rascon (*F. ligustrina?*), natural size.





MEXICAN "STRANGLING" FIG.





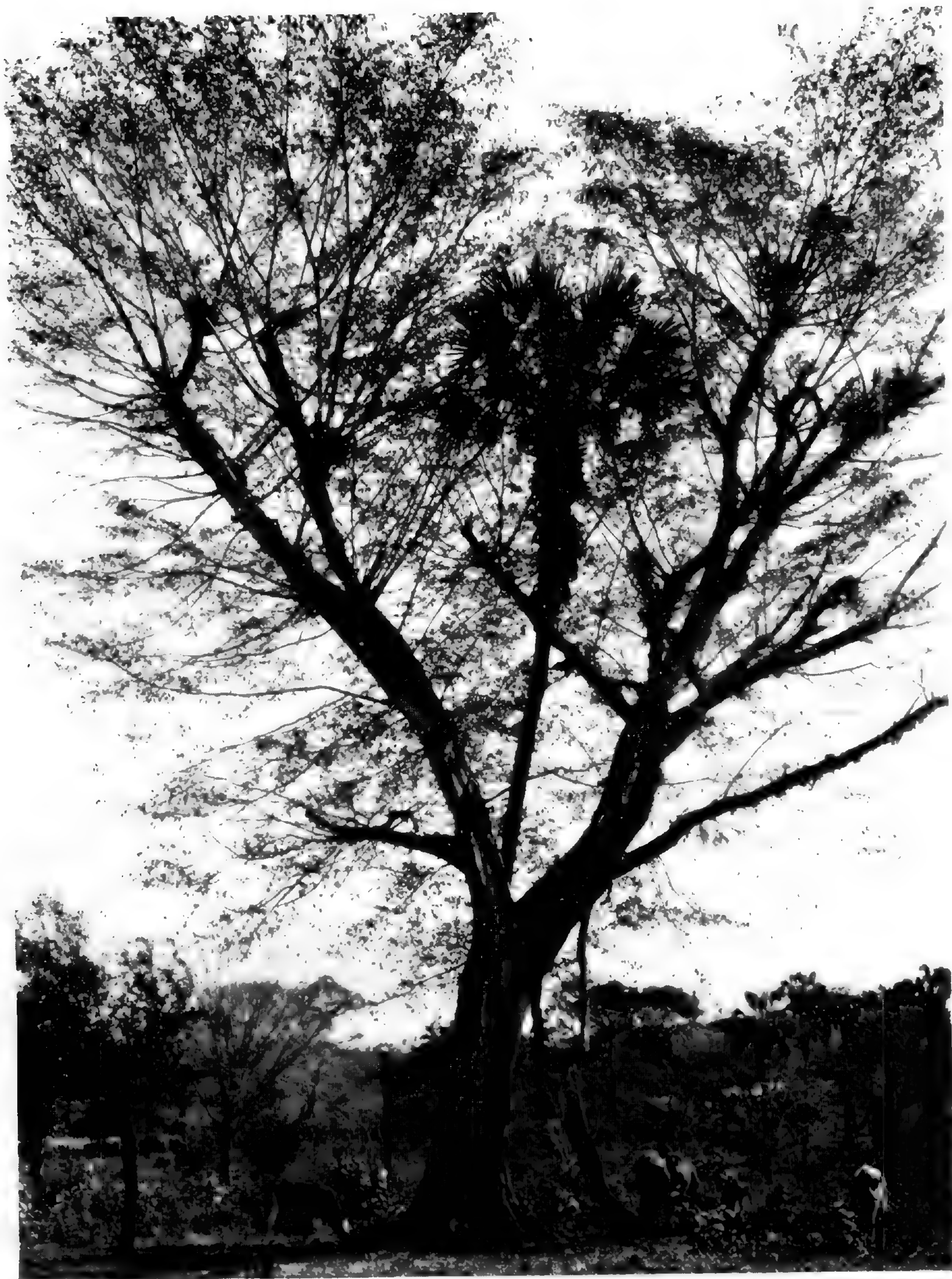
MEXICAN "STRANGLING" FIG.





MEXICAN "STRANGLING" FIG.





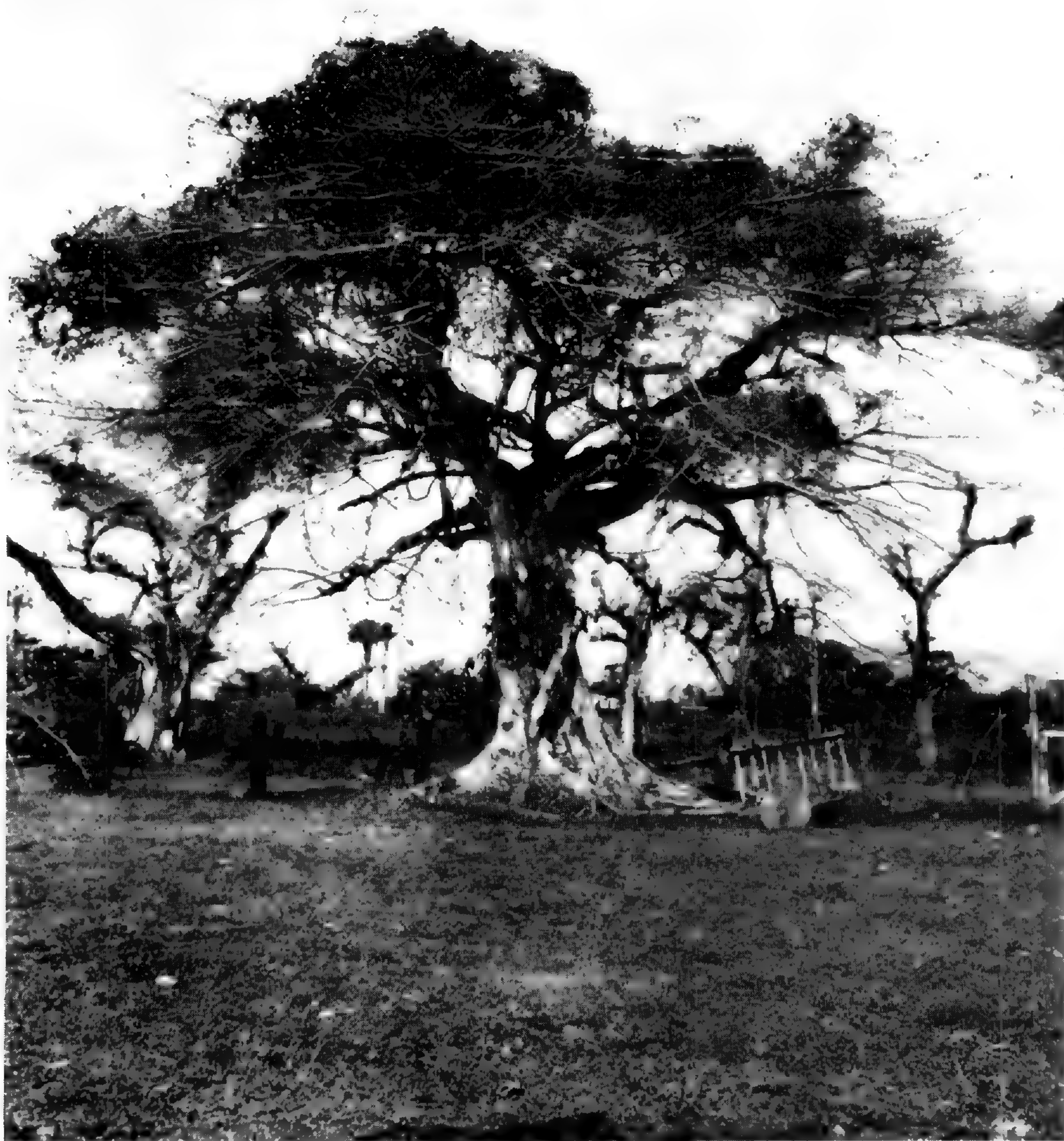
MEXICAN "STRANGLING" FIG.





MEXICAN "STRANGLING" FIG.





MEXICAN "STRANGLING" FIG.





FICUS LIGUSTRINA?



## THE DEHISCENCE OF ANTHERS BY APICAL PORES.

BY J. ARTHUR HARRIS.

### INTRODUCTION.

#### HISTORY OF THE PRESENT INVESTIGATION.

During the summer of 1901, I became much interested in the pollination of *Solanum* and *Cassia* and, assisted by a student, published a paper giving the results of our investigations. At the time of the preparation of that paper, I was fully aware of a number of points meriting further field study and especially comparison with similar forms in other genera, and, upon taking up my work at the Missouri Botanical Garden, was glad to avail myself of the facilities offered by the herbarium and library for a comparison of the floral structures of other species of these large genera and for the accumulation of notes on some analogous types of flowers in other families.

While working on *Solanum* and *Cassia*, I was impressed by the close resemblance of the floral constitution of these systematically widely separated genera and by the similarity of their ecological relations. My interest was deepened when I observed that the same close agreement in the structure and frequently in the ecology of apically dehiscent forms is to be found in other families. Later, there came the question whether the great differentiation of *Solanum*, *Cassia* and the Melastomataceae in South America and the occurrence there of several smaller genera with apically dehiscent anthers might be significant. Obviously the question could be answered only by a comparative and statistical study of all genera and species showing dehiscence by apical pores, and the collection of data for



this purpose was immediately begun by examining Engler and Prantl's *Die Natürlichen Pflanzenfamilien*, Bentham and Hooker's *Genera Plantarum* and several of the more important floras, for the purpose of preparing a descriptive list of all forms in which the anthers have been described as opening by apical pores. This was intended to serve as a foundation for structural comparisons, and so far as might be possible, for a comparative treatment of the floral ecology of these forms.

The data secured and the conclusions which they seemed to indicate proved highly interesting and were presented in April, 1903, to the Faculty of Washington University as a thesis for the degree of Doctor of Philosophy. Since that time I have been able to secure a large amount of valuable material for study and have devoted much of my time which has been available for research to this problem. My manuscript has grown so large that it is inadvisable to publish it in full at present, especially since I have in hand further studies which I hope will add materially to its value but which cannot be completed for some months. It seems best to present an abstract outlining the problem and giving the essential points in the conclusions which seem justified by the comparisons so far carried out, with a much condensed statement of the data upon which they are based. The detailed treatment of the subject is being increased by structural, comparative, and ecological studies, and I hope to publish it in full, possibly with discussions of other floral types, at some future time.

I wish to avail myself of this opportunity to express my obligation to several gentlemen who have had the kindness to send material from their herbaria to the Missouri Botanical Garden for my use. These are: Dr. F. Kurtz, Universidad Nacional, Cordoba, Argentina; Dr. R. A. Philippi, Museo Nacional, Santiago de Chile; Dr. W. R. Guilfoyle, Botanic and Domain Gardens, Melbourne, Australia; Dr. J. M. Wood, Durban, Natal; Dr.



J. C. Willis, Royal Botanic Gardens, Ceylon; Dr. M. Treub, Jardin Botanique, Buitenzorg; Dr. J. H. Maiden, Government Botanist, Sydney, N. S. W.; Dr. I. Urban, Königlicher botanischer Garten und Museum, Berlin; Dr. T. Durand, Jardin Botanique de l'État, Bruxelles; and Dr. N. L. Britton, New York Botanical Garden.

This material, which was asked for only after the most of the data for this paper had been gathered and classified, has been consulted in the preparation of these pages but is being used mainly for a histological investigation of these types of anthers, and so my future memoir will owe even more to their generosity than the present one, which is very largely a library contribution. Perhaps nowhere else could this paper have been prepared so easily as at the library of the Missouri Botanical Garden, with its large collections of living and preserved plants also accessible for consultation, and I wish to express my gratitude to the Director, Dr. William Trelease, not only for access to these facilities, but for the most generous conditions under which I have used them while connected with the Garden and with Washington University. For several months Mr. Dean H. Rose has assisted me in this and in other research work, and while the most of his time has been given to phases of the subject which will be treated later, I wish to express in advance my hearty appreciation of the earnest and efficient service he has given me. My sister, Miss Nellie L. Harris, has been of great help to me in the preparation of the statistical portions of the paper.

#### EARLIER INVESTIGATIONS.

That in a comparatively limited number of Phanerogams, the pollen is shed through terminal pores instead of longitudinal slits is a fact of general knowledge which has been utilized in the characterization of families, genera, and species.



The method of the shedding of the pollen in the Angiosperms is a subject very briefly treated in the general works on morphology and physiology. Goebel in his *Organographie* calls attention to the obscure nature of many points in this phenomenon, and Coulter and Chamberlain in their recent work on the morphology of Angiosperms speak of the need of a thorough investigation of the subject, especially from the developmental point of view. Most general works treat this point with the same or greater brevity and need not be mentioned separately.

Histologically, anthers have been investigated and their minute anatomy interpreted more or less satisfactorily by several writers, among whom may be mentioned Mohl, Purkinje, Schrodt, Leclerc du Sablon, Chatin, and Steinbrinck.

So far as I am aware, no special treatment of the apically dehiscent anther has been attempted from a morphological, histological or ecological point of view.

#### PURPOSE OF INVESTIGATION AND SCOPE OF PRESENT PAPER.

My purpose in undertaking the present investigation was threefold: 1. The compilation of a systematically arranged descriptive list of genera or species showing dehiscence by pores, for use in future biological work. 2. The demonstration of any similarity of structure in apically dehiscent forms of different systematic affinities or the existence of possible correlative modifications in the parts of the flowers showing this method of dehiscence, if such exist. 3. The establishment or the refutation of the hypothesis that the flora of certain of the main divisions of the earth's surface is richer in apically dehiscent forms than that of others.

These three purposes were quite satisfactorily accomplished in the spring of 1903. During the time which has elapsed since the writing of my first manuscript I have added practically no new genera or species to my list. I



have, however, been able to supplement my descriptive data very materially by a comparison of the rich materials generously supplied by the directors and curators of botanical gardens and herbaria in various parts of the world. I have also been able to carry out several detailed and time-consuming comparisons between the apically and the longitudinally dehiscent members of the several families in which dehiscence by apical pores has been described. This I did to determine whether the type of floral structure which is repeated with such uniformity by the apically dehiscent members of several little related families, is of frequent occurrence in these families, or whether the form of the anthers and the general habit characteristic of these apically dehiscent genera or species are aberrant in the systematic groups to which they have been assigned by taxonomists.

I have been able to satisfy myself more fully concerning the distribution of forms by tabulating according to arbitrarily limited floristic regions the distribution of all the genera of Phanerogams. The distributional phase of the problem is still far from satisfactory and must necessarily long remain so. These tabulations, however, confirm my early impression of the greater richness of the flora of some regions in species with apically dehiscent anthers.

Floral structures are to be fully interpreted only through a knowledge of their ecological relations, past and present. I have been able to compile a considerable series of such data bearing upon the forms under consideration and while these, with the few observations which I have been able to make, represent only a beginning, they seem to justify some very suggestive hypotheses for further investigation.

Convinced that the great systematic differentiation attained by the Apidae in South America might have a significant bearing upon the problem, I have tabulated the distribution of this family, and by way of comparison, that of all families of the Hymenoptera.



It is a pleasure to say that the work which has been done since the spring of 1904 has not materially modified the conclusions then reached, but has added more convincing evidence from many sides.

In this place I shall not give a systematically arranged list of the forms I have considered. This, with the necessary bibliographic citations and descriptive text and illustrations, would require far more space than is available. I shall rather divide the former into groups or types and describe these briefly, mentioning, when desirable, the names of the genera assigned to the particular types, with their geographical distribution, and comparing their structure briefly with the forms to which they are systematically related. It is to be understood that these groups or types are not sharply defined categories, but transgressive assemblages. The justification for the division of the material into these groups or types is found in the fact that the majority of the species do fall clearly into one or the other of the groups, while those which represent transitions or are quite aberrant in structure are much rarer. These groups are to be regarded as tentative, and, while for the most part natural, they are established primarily for the convenience of the present discussion. Their great justification is to be found in the convenience of treatment and interpretation which does result from their use.

Four of these types I shall consider very briefly, merely describing in general terms their differential characters. The fifth, sixth and seventh will be treated in greater detail, and in addition to the description and comparison of the morphological features, I shall discuss their ecological relations and geographical distribution.

In this place I shall not review the work of others on the microscopic structure of the apically dehiscent anther or present the results of my own studies in this phase of the problem. I wish here to confine my attention to a discussion of the general morphological features and the ecologi-



cal relations of three groups, leaving the detailed treatment of these and the other types until a later time.

It seems hardly necessary to define here the terms dehiscence by apical pores, or apically dehiscent anthers. The terms have been used in the same sense as that in which they are regularly used by systematists. It may be proper to remark, that a precise definition offers considerable difficulty. Some genera have anthers opening by a single pore, sometimes at the tip of a rostrate prolongation of the anther, which is never increased down the sides by longitudinal slits; but, except for the Melastomataceae, in an equal or greater number of forms the pores are soon continued more or less down the sides in longitudinal slits. Between dehiscence by the most perfected terminal pore or pores and the primitive longitudinal dehiscence there is a complete series of gradations. In this paper I have followed quite closely the usage of the best systematists in the description of my material. If an anther shows well defined openings at the tip and there is reason for believing that the pollen is shed largely through these pores, it is generally designated in descriptive works and floras as apically dehiscent, or described: "anthers dehiscing by apical pores soon continued down the sides in longitudinal slits." Only living material would permit of an absolute determination. A large proportion of the anthers are thinner along the lateral furrows where dehiscence usually occurs in forms in which the anthers do open by lateral slits, and in herbarium material they are liable to be broken along this line even when such might not occur normally in the living plant. Sections cut from anthers which have not broken along this line are very apt to break apart at this point. It is far from easy or even quite impossible to determine whether the lateral slit is a natural occurrence or whether it is due to manipulation. These points will be considered for the forms examined in my final paper,



but for the present I have used the term in the rather general sense in which it is employed in descriptive botany.

In this paper I have omitted all reference to the literature. It is proper to state that I have examined all the most important systematic works treating of the forms here discussed as well as the special literature of floral ecology. These citations I hope to include with ample descriptions and illustrations of all of the forms considered, in the final paper.\* I have also sought to avoid all references to theoretical considerations and to confine myself as strictly as possible to the facts and the problem of grouping them in as logical and significant a manner as possible.

#### THE TYPES OF APICALLY DEHISCENT ANTHERS.

The classes recognized are the following: —

1. ARACEOUS TYPE.
2. GRAMINEOUS TYPE.
3. POLYGALACEOUS TYPE.
4. ERICACEOUS TYPE.
5. DILLENACEOUS TYPE.
6. SOLANUM-CASSIA TYPE.
7. MELASTOMACEOUS TYPE.

The first four are to be merely touched upon in the present paper. The last three, on the other hand, are to be considered in some detail; they are characterized by many similarities of structure and doubtless of ecological relationship as well, and while, as it seems to me, they are separated, on the whole, by sharp mean differences, there is often difficulty in drawing the limits of the groups. Since they are to be understood only when examined com-

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\* Most of the titles to which reference has been made by the author's name only in this essay, may be found in the bibliographies in the English edition of Müller's *Fertilisation of Flowers*, the continuation of this list from 1883 to 1889 published by MacLeod in the *Botanisch Jaarboek*. 2: 195-254, 1890, or the more complete bibliography of Knuth's *Handbuch der Blütenbiologie*.



paratively, their essential points of difference may be stated.

The Ericaceous type as limited in this paper contains some forms which are closely related to those of the three following, but they will be left out of consideration here.

The Dilleniaceous, Solanum-Cassia and Melastomataceous types have in common a widely patent corolla, or at least a widely expanded corolla limb, and elongate, usually linear, basifixed anthers. The Dilleniaceous type differs from the other two in the possession of a larger number of stamens, with anthers inserted on generally long filaments, and often separate styles. The Solanum-Cassia type differs from the Dilleniaceous in the number of stamens, their much reduced filaments, and their frequent approximation around the style. The Melastomataceous type is characterized by anthers of the same general form as those of the Solanum-Cassia type, but it is sharply separated by the elongate and highly differentiated filament.

#### I. ARACEOUS TYPE.

Flowers usually densely crowded on a spadix; perianth generally much reduced; filaments usually shortened; anthers free or very often connate in a synandrium, bilocular or multilocellate, each locule dehiscing by a more or less irregular apical rent, or in a few cases, through a produced tubular process; pollen free or conglomerate in a vermiform column.

To this type belong many of the genera of the Araceae and Balanophoraceae. Other genera of these families shed their pollen through longitudinal slits in the usual way. The Loranthaceae and Lacistemaceae furnish interesting forms for comparison.

The geographical distribution and the floral ecology of this type will not be discussed here. It is clearly distinct from others to be treated later and to which I wish to direct especial attention.



## II. GRAMINEOUS TYPE.

In the characteristic anthers of the grasses the locules usually open by longitudinal slits extending from above downward, but more rarely (in some *Andropogoneae*) by a hole at the apex, often finally continued down the side in slits. This type likewise is clearly distinct from all others, and I shall not consider it further in this place.

## III. POLYGALACEOUS TYPE.

Flowers strongly zygomorphic, with highly differentiated perianth; androecium included in a ventral carina, usually monadelphous; anthers short, generally cupuliform, basifixed, dehiscing by a large, upper, terminal opening embracing both locules (*Polygalaceae*) or by two terminal pores (*Fissicalyx*).

This group contains the *Polygalaceae* and the single genus of the *Papilionatae* in which the anthers open by apical pores. In structure and geographical distribution, this is an interesting type, but cannot be treated in detail.

## IV. ERICACEOUS TYPE.

Under this type I have grouped with its special representatives a number of structurally very dissimilar forms. This has been done largely because of the systematic relationship of the material; it has been deemed best to treat all the *Ericaceae* together and in this paper I have placed with them a few other genera systematically related or similar in their floral structure. This type will not improbably be broken up later, but at the present time I do not care to treat in detail the various forms which I have here assigned to this type, and since they are, for the most part, quite distinct from those to which I intend devoting the body of this paper, they may be passed over with merely a general description.

Flowers hermaphrodite, regular or rarely zygomorphic;



corolla gamopetalous, globose, urceolate, tubular, infundibuliform, campanulate or almost rotate, generally 4–5-lobed, very rarely divided to the base; stamens usually twice as many as the lobes of the corolla, equal or alternately unequal, free or nearly free from the corolla, exerted or more generally included; filaments usually long, various in form; anthers basifixed or dorsifixed at the base or below the middle, rarely at the apex, dehiscing by large apical pores or more or less extensive slits, sometimes produced in one or two often very long terminal tubes opening at the top with small pores or more or less extensive slits, sometimes provided dorsally with aristae or setaceous appendages.

All Ericaceae are here included in this type. *Galanthus* and *Leucojum* of the Amaryllidaceae, with their pendulous flowers and perianth closely approximated around the androecium, may also be tentatively assigned to this type. *Pentaphragax*, the type of a family from China, may best be treated here, as may also *Clethra* of the Clethraceae, *Costaea* of the Cyrillaceae, and *Chimaphila* and *Pirola* of the Pirolaceae.

The floral ecology of this group is not discussed here. Our knowledge is chiefly of the Ericaceae and the two genera from the Amaryllidaceae. Many of the data bearing upon these will be found recorded in the Handbuch of Knuth.

#### V. DILLENACEOUS TYPE.

Both whorls of perianth usually developed, but one or both sometimes reduced, usually campanulate or rotate in disposition; *stamens indefinite in number*; filaments long or short, free or variously united; *anthers mostly elongate, basifixed*; flowers usually actinomorphic throughout, but androecium sometimes zygomorphic, gynoecium of distinct or variously united carpels; flowers generally highly colored and conspicuous.



The sharp distinction of several of the members of this type from those of the following classes is quite impossible, but it seems helpful to make the division.

This class exhibits, with the possible exception of the Ericaceous type, the widest range of form and structure of any recognized. To it I have assigned four species of *Hibbertia*, *Acrotrema* *Schumacheria*, *Dillenia* and *Saurauia* of the Dilleniaceae, *Elaeocarpus*, *Sloanea*, *Vallea*, *Aristotelia* and *Dubouzetia* of the Elaeocarpaceae, *Ochna*, *Lophira* and *Cespedesia* of the Ochnaceae, *Tremanthera* of the Theaceae, *Bixa* of the Bixaceae, and *Plagiopteron* of the Flacourtiaceae.

#### Dilleniaceae.

The flowers of the Dilleniaceae are hermaphrodite, polygamous or dioecious, with usually five persistent sepals and as many deciduous petals which are patent during anthesis. The stamens are indefinite, usually numerous, and various in form, the gynoecium is usually composed of several more or less united carpels with free and for the most part widely divergent pistils with simple stigmas.

In *Hibbertia* (about 100 species, mostly confined to Australia) the dehiscence is said to be by pores in one section represented by 4 species, but I am not sufficiently acquainted with the forms. *Acrotrema* (about 12 species of India, Farther India and Ceylon) has many — 15–50 — stamens, free or more or less united into 3 or 4 bundles, and linear or sometimes ovate anthers generally opening by two apical pores. *Schumacheria* (with 3 species in Ceylon) is distinguished by zygomorphy. The linear or broadly linear anthers open, according to Gilg, at the top with two little holes which gradually increase more or less down the sides in longitudinal slits. *Dillenia* (of about 23 species distributed over tropical Asia, the Indo-Malay region, New Guinea, the Philippines, and Australia) has usually very long anthers which generally open at the top by two pores which may sometimes become confluent into



one or may be increased down the sides in longitudinal slits. The flowers are often very large and conspicuous; *Saurauia* (with about 98 species of tropical Asia and America, rare in Brazil and Guiana) has the anthers turned outward in the bud, but reversed and erect at the time of flowering, each of the two short, sometimes somewhat divergent locules opening by large pores or, more rarely, by longitudinal slits.

An indefinite number of stamens is characteristic of the Dilleniaceae, but in many forms a marked tendency to numerical reduction is observable, as is well seen in *Hibbertia*, but from the data available I am unable to draw any definite conclusions as to the relation between the number of elements in the androecium and the method of dehiscence. The forms of filament and anther are quite various. Apical dehiscence is confined almost exclusively to the elongate, basifixed anther. With the exception of one genus, the apically dehiscent forms all occur in the Dillenioideae with basifixed anthers and, in the exception, *Saurauia*, the versatile anthers are attached near one end and assume a more or less erect position at the time of flowering.

#### Elaeocarpaceae.

An important difference between the Elaeocarpaceae and the preceding family is found in the gynoecium. In the Elaeocarpaceae, the pistil is simple and filiform with only a possible indication of the compound nature of the ovary in the slightly lobed stigma of some forms.

*Elaeocarpus* (over 100 species of tropical Africa, Asia, Australia, the Pacific Islands, New Caledonia and New Zealand), *Sloanea* (50 species in the tropics of both hemispheres), *Vallea* (3 species in the mountains of New Granada and Peru) and *Aristotelia* (7 species, 3 in Australia, 3 in New Zealand, 1 in Chile) have campanulate or more or less patent, often highly colored and fringed perianth segments; stamens indefinite in number; anthers linear, basi-



fixed, obtuse or provided with a terminal appendage, dehiscing by 1 or 2 apical pores, sometimes continued down the side in slits.

In *Crinodendron* (2 species in Chile) and *Antholoma* (2 species in New Caledonia) the corolla is urceolate and the anthers open by longitudinal slits, which may open more widely above or originate in a poriform opening, or may be confined to the upper portion of the anther. *Dubouzetia* (represented by 1 or perhaps more species in New Caledonia) has in some ways a very similar floral structure, but the dehiscence is by a single bilabiate terminal pore.

The Elaeocarpaceae is a highly interesting group and I am far from satisfied with the treatment which can be given it in this paper.

#### Ochnaceae.

All genera of the Ochnaceae are to be considered in a paper on apically dehiscent anthers. The flowers show a considerable diversity of form and are to be referred to different types.

*Ochna* (about 25–30 species distributed over tropical Asia and Africa, only a few species — 3, *vide* *Flora Capensis* — in the Cape region) has numerous stamens with long, filiform filaments and oblong or linear, basifixed anthers dehiscing by apical pores or longitudinal slits. It belongs clearly to the Dilleniaceous type. *Lophira* (1 species in central and west Africa) with the linear anthers dehiscing by short, terminal, almost poriform slits, belongs here, as does also *Cespedesia* (3–4 species in Peru, New Granada and Panama) with 40–60 elongate, linear, curved anthers on short filaments, all turned toward the same side of the flower during anthesis.

*Elvasia* and *Godoya* may be mentioned here as forms in which the stamens are more numerous than is common in the *Solanum-Cassia* type, but for other structural reasons, these, as well as the other members of this family, will be considered with the members of that group.



## Theaceae.

With *Tremanthera* (1 species in New Guinea), the single apically dehiscent genus of the Theaceae, I am not sufficiently acquainted, but the indefinite number of stamens with long-ovate anthers would indicate that it should be placed in this class.

## Bixaceae.

In the Bixaceae, *Bixa* (1 species of tropical America, now widely distributed in the tropics) is a unique form characterized by its numerous, horse-shoe shaped anthers on long filaments. It may most conveniently be placed in this type. The other two apically dehiscent genera will be treated under the Melastomataceous type.

## VI. SOLANUM-CASSIA TYPE.

Perianth usually quite large, mostly actinomorphic, segments campanulate or *more generally patent or reflexed* in disposition; androecium of few members, usually 5 or 10, very rarely as many as 15, staminodia sometimes present as reduced members of these numbers in zygomorphic forms or more rarely from a multi-staminate androecium; filaments *much reduced in length*; anthers basifixed, oblong to sagittate or linear, often more or less connivent around the filiform style with its small, generally simple stigma, or at least erect, very rarely distant; flowers generally conspicuous and highly colored.

This is the type upon which my interest has been for the most part centered. It shows a great uniformity of character and in this lie its especial interest and importance as a source of data towards the solution of the problem of the influence of insects upon the form of flowers and the geographical distribution of different floral types. In view of this fact, the treatment of this class is more detailed than that of the others.

As I have insisted above, the distinction between dehiscence by pores and by longitudinal slits, and between the



Solanum-Cassia type and any other is not an absolute one. The number of apically dehiscent genera or species might be easily increased or decreased by including forms in which the lateral slits first open more widely at the tip, or including all those in which the pores are finally supplemented by lateral slits at length continued more or less down the side. The number of genera as I have limited it is, I feel confident, approximately right so far as may be determined from systematic literature and the examination of herbarium material.

To the Solanum-Cassia type I have assigned 59 genera. Of these, 19 are Monocotyledons and 40 Dicotyledons. The Monocotyledons are: *Mayaca* (Mayacaceae), *Schoenoccephalum*, *Stegolepis*, *Rapatea*, *Saxo-Fridericia*, *Cephalostemon*, *Spathanthus* (Rapateaceae), *Cartonema*, *Dichorisantra* (Commelinaceae), *Monochoria* (Pontederiaceae), *Walleria*, *Agrostocrinum*, *Dianella*, *Calectasia*, *Luzuriaga* (Liliaceae), *Conanthera*, *Cyanella*, *Zephyra*, *Tecophilaea* (Amaryllidaceae). The Dicotyledons are: *Cheiranthra* (Pittosporaceae), *Cassia*, *Koompassia*, *Distemonanthus*, *Labichea*, *Dicorynia*, *Baudouinia*, *Duparquetia*, *Krameria*, *Martusia* (Leguminosae), *Platytheca*, *Tetra-theca*, *Tremandra* (Tremandraceae), *Thomasia*, *Guichenotia*, *Lysiosepalum*, *Lasiopetalum* (Sterculiaceae), *Oura-tea*, *Brackenridgea*, *Godoya*, *Elvasia*, *Blastemanthus*, *Wallacea*, *Schuurmansia*, *Poecilandra*, *Luxembergia*, *Euthemis*, *Leitgebia* (Ochnaceae), *Stemonoporus*, *Monoporandra* (Dipterocarpaceae), *Kiggelaria* (Flacourtiaceae), *Begonia*, sections *Solanthera* and *Parvibegonia* (Begoniaceae), *Ardisia*, sections *Icacorea*, *Stylogyne*, and *Monoporus* (Myrsinaceae), *Gardneria* (Loganiaceae), *Exacum*, *Cotylanthera* (Gentianaceae), *Solanum*, *Cyphomandra* (Solanaceae), *Argostemma*, and *Strumpfia* (Rubiaceae).

#### Mayacaceae.

In the Mayacaceae, with the single genus *Mayaca*, we



have a very good representative of this type, although the anthers offer some peculiarities of structure. (Ten species; all but one, which is found in Lower Guinea, are American; 1 very similar to and possibly identical with a South American form occurs in eastern North America, 1 occurs in Cuba, and the others in Brazil, Peru and Guiana. Brazil has six species.)

#### Rapateaceae.

The Rapateaceae is a family of six genera and about 19 species in tropical South America. Its position in this group is somewhat questionable on account of the moderately long perianth tube formed by the lower portion of the segments. The limb, however, is patent, the anthers basifixed and linear and shedding their pollen through terminal pores or a single terminal pore, sometimes provided with a terminal, spoon-like prolongation of the tip of the anther.

#### Commelinaceae.

The Commelinaceae is represented by two genera besides the highly interesting *Cochliostema* to be described later. *Cartonema* (5 or 6 species confined to tropical Australia) shows a considerable range of form in the structure of the anther. In some species, dehiscence is by longitudinal slits; dehiscence by pores seems to be in a less perfected state than in the tropical American *Dichorisandra* (about 27 species, almost exclusively Brazilian). This genus is a highly interesting and very characteristic representative of the *Solanum-Cassia* type.

Except for minor differences, a considerable degree of uniformity prevails in the floral structure of the Commelinaceae. The petals are patent, except in about 3 genera in which they are unguiculate and united into a usually narrow tube, and 1 in which the perianth is tubular below, but even here the limb is generally patent. The basifixed anthers show a wide range of form, while the



filaments may be naked or provided with hairs. Thus, excepting the character of dehiscence, with perhaps a slight elongation of the anthers, the flowers of the two forms treated here do not differ widely from the other genera of the family. In floral structure, the most highly organized member is *Cochliostema*, to be discussed later.

#### Pontederiaceae.

*Monochoria* (3 species, 1 in tropical East Asia, 1 in tropical and subtropical Asia and East Africa, and 1 in Australia), of the Pontederiaceae, has the corolla and the form of the anthers of this type. The filaments are not so reduced in length as is generally the case, and the terminal pores are soon continued down the sides in longitudinal slits.

A comparison of the disposition and form of the stamens in their relation to the length and form of the perianth tube in the other genera of this family is interesting. In *Heteranthera* the perianth tube may be very long and narrow, but the limb is widely patent. In the other genera, the perianth is more widely expanded from the base but still shows a tube of considerable length. Only in *Monochoria* is the tube wanting and the elements of the perianth, which are almost free to the base, widely patent. Concerning the form of the stamens it may be said that in *Eichornia*, *Pontederia* and *Reussia*, the markedly zygomorphic androecium is characterized by filaments of considerable length with basifixed or nearly basifixed and short, thick anthers which may be included or widely exerted. In *Heteranthera* the anthers are sometimes more elongate, approaching linear in form. The filaments, inserted at the top of the corolla tube, may be of the same length as the anthers or much longer. In *Monochoria*, the filiform filaments are of about the same length as the anthers, which seem to be the most elongate in the family, and, perhaps, with walls of firmer texture.



## Liliaceae.

Of the Liliaceae, five genera may be mentioned: *Walleria* (three species, or perhaps only three varieties of the same species, in tropical Africa, with 1 extending into South Africa, and another from Madagascar) is one of the finest illustrations of this type which I have seen. *Agrostocrinum* (1 Australian species) is another good representative with somewhat zygomorphic flowers. *Dianella* (11 species, 1 widely distributed in the Mascarine Islands, tropical Asia, Australia, New Caledonia and the Sandwich Islands, 8 more in Australia, 1 in New Zealand, Norfolk and Fiji and Society Islands and 1 in the Isle of Pines and New Caledonia), with variously thickened filaments and anthers in which the pores are sometimes continued downward in introrse longitudinal slits, also belongs here. The flowers of *Calectasis* (1 West Australian species) are among the most beautiful of those assigned to this type. *Luzuriaga* is a highly interesting genus of South Pacific or antarctic distribution. Four species are described. In three species (of which 1 is confined to New Zealand, 1 occurs in Patagonia, Tierra del Fuego, Falkland Islands and New Zealand, and 1 is found only in Chile and Peru) the flowers have a very close similarity to other members of the Solanum-Cassia type, but dehiscence seems to be by longitudinal slits, although it has been described as by pores and it may be so at first, as in *Monochoria* and various other forms. The fourth species (reported only from South Chile) has a different floral structure. The anthers are borne on longer filaments and at the time of flowering are reflexed and open, at least at first, by two basal pores. The reflexed stamens are quite closely approximated around the ovary so that the general habit of the flower agrees very closely with that of many other forms in this class.

*Odontostomum* is an aberrant form from California which will be considered later.



## Amaryllidaceae.

Pax in his treatment of the Amaryllidaceae in *Die Natürlichen Pflanzenfamilien*, characterizes two tribes, Galanthinae and Conanthereae, as dehiscing by apical pores. The genera of the Galanthinae have been mentioned under the Ericaceous type.

*Conanthera* (3 or 4 species in Chile) has the anthers connivent in a cone and dehiscing by pores at the tip or by introrse slits extending almost to the base. They are provided at the tip with a simple or bifid acumen and are either exerted or included in the campanulate perianth tube. *Cyanella* (4 or 5 species in the Cape region) is a beautiful example of this type with some species showing zygomorphic flowers, in some respects very similar to those of *Cassia*. *Zephyra* (1 species in Chile) and *Tecophilaea* (2 species in Chile) are aberrant, zygomorphic forms which cannot be described in detail here.

A point of interest in the relation of the apically dehiscent genera of the Liliaceae and Amaryllidaceae to the other members of the families is that in the arrangement of Engler and Prantl the apically dehiscent genera of the former are found associated with sometimes several of the longitudinally dehiscent forms in as many of the ultimate groups as there are genera, belonging to three of the subfamilies of that system, while in the Amaryllidaceae, the four genera assigned to the Solanum-Cassia type all belong to the same ultimate group.

A comparison of these groups in the two families is interesting. In the Amaryllidaceae the four apically dehiscent genera belong to a single group and are structurally very similar, differing largely in the characteristics of the variously zygomorphic androecium. In the Liliaceae, however, the differences to be noted within the same group are much greater, as may be most strikingly illustrated by the comparison of *Walleria* with *Gloriosa*



*Sandersonia*, and *Tricyrtis*, while other members of the group also show considerable differences in structure, and none of them at all closely approach the form of the apically dehiscent genus. In the twenty genera of the Anthericinae, the group to which *Agrostocrinum* belongs, however, the floral habit is quite uniform. In all, the corolla is rotate; in several, the filaments are long and the anthers short, but in others the filaments are much reduced in length and the anthers oblong to linear and sometimes tending to be more connivent around the style.

Space will not permit a detailed discussion of the floral structure of the two families. The two illustrations just given from the Liliaceae are perhaps representative. I think it may be said for these families that in the Amaryllidaceae the prevalent habit of the perianth is, roughly speaking, infundibuliform while in the Liliaceae it is patent or campanulate. In the Amaryllidaceae the four apically dehiscent genera stand almost alone as representatives of this floral habit while in the Liliaceae there are many genera with patent or broadly campanulate perianth. In the most of these genera the filaments are filiform, more or less elongate, and bear short, usually versatile anthers, but in several the filament is reduced in length while the anther is of the more elongate form commonly seen in the apically dehiscent genera. The forms which in their general structure bear a close resemblance to the apically dehiscent *Solanum-Cassia* type are almost wanting in the Amaryllidaceae. It must not be understood that they are identical with the apically dehiscent genera except for the difference in the method of the opening of the anthers. I do not go so far as to state that they represent incipient stages of members of this class, for in the interpretation of such facts as these, the greatest caution must be exercised. It must be pointed out, however, that in the general habit of the flower there is not the sharp line of distinction be-



tween apically and longitudinally dehiscent forms in the Liliaceae that there is in some other families.

We may now pass to the Dicotyledons.

#### Pittosporaceae.

We find in *Sollya* (2 Australian species) of the Pittosporaceae a form similar in structure to the section *Lycopersicum* of *Solanum*, but not showing dehiscence by pores, and *Cheiranthera* (4 Australian species) which is an excellent, slightly zygomorphic representative of this type.

In the Pittosporaceae the five petals, frequently more or less unguiculate, are erect and connivent or coherent in a tube at the base and spreading above. In only a few species besides those of the genera *Sollya* and *Cheiranthera* are the petals more or less patent from near the base. Another most important difference between these two genera and the others of the family is the relative size and proportion of the parts of the stamen. The anthers are longer than the filaments in *Sollya* and *Cheiranthera*, while in the other genera they are shorter than the filaments, and, in relation to other parts of the flower, smaller than in the genera considered here. These two genera are aberrant forms in the family.

#### Leguminosae.

In the Leguminosae the apically dehiscent genera are, with one exception, confined to the Caesalpinioideae, and in this sub-family, with one exception, to the Cassieae.

*Cassia*, serving as one of the types of this group, is too well known to require description. (About 412 species of tropical and subtropical distribution are known, extending in America from Patagonia into the United States and reaching their highest differentiation in the tropics of the New World — 290 species. Australia has about 33 species, tropical Africa 27, the Indian, Malayan and Oceanic Island region about 34, and the Cape region 5 or 6).

In *Koompassia* (represented by 2 or 3 species, gigantic



trees, confined to Malacca and the Malay Archipelago) the stamens of the species differ considerably in form, those of one species being much broader than those of the other, and possibly in dehiscence.

*Distemonanthus* (1 species found in Upper Guinea) is a strongly zygomorphic form with only two fertile stamens, clearly belonging here.

*Labichea* (5 Australian species) is very closely related to *Cassia* and with almost identical floral structure except that the stamens are reduced to two.

*Storckiella* has the perianth quite widely patent and the linear anthers of this type, but the elongate filaments make it necessary to place it in the Melastomataceous type.

*Dicorynia* (4 species in Guiana and North Brazil), with its two short, thick anthers, one of which is sometimes eight-locellate at the tip, is a unique form, but one which seems best treated here.

*Baudouinia* (2 species in Madagascar) has linear-sagittate, basifixed, apically acuminate and penicillate anthers, both locules of which open at first by an introrse subapical fissure which soon extends in two introrse longitudinal slits to the base.

In *Duparquetia* (a single species, a richly flowering shrub, in west tropical Africa) the flowers are, with the possible exception of *Krameria*, the most strongly zygomorphic in this type. The four anthers dehisce by short, terminal slits which are not continued down the side for more than a third of the whole length of the anther.

*Martinsia* (2 species in Brazil and British Guiana) is one of the largest-flowered and most typical, slightly zygomorphic, representatives of this type.

*Krameria* (23 species, distributed from warmer North America to Chile), of somewhat uncertain systematic affinities, is now placed next to the Cassieae in the Leguminosae. Structurally it is the most aberrant form assigned



to this type, but it may be treated here, provisionally, at least.

In the Leguminosae, the apically dehiscent forms of this type are confined, with the single exception of *Krameria*, to the Cassieae of the Caesalpinioideae. The genera of the Cassieae are distinguished from all others of this subfamily except *Krameria* by their usually basifixed, apically dehiscent anthers, those of all other genera being dorsifixed and versatile and with longitudinal dehiscence. In examining the genera of the Cassieae itself I find that the apically dehiscent forms have, as compared with the others, a more elongate anther and a shorter filament. The patent corolla is general in the Caesalpinioideae but the form of the anthers in the apically dehiscent genera will, I think, be found quite different from that of the other genera.

#### Tremandraceae.

The Tremandraceae (represented by 3 genera of about 23 species endemic in West and South Australia) constitute the only dicotyledonous family in which all the species are apically dehiscent. The four parallel cells in the same plane in the anthers of *Platytheca*, and the terminal tube opening by a single pore in this genus and *Tetratheca* merit especial mention. The genera of this family, while offering some minor points of difference from the others, must be regarded as among the most highly specialized of this type.

#### Sterculiaceae.

In the Sterculiaceae, *Hermannia* shows dehiscence by longitudinal slits, but the habit of the androecium is so similar to that of *Solanum*, *Borago* and some other forms that it may be mentioned for comparison.

In *Thomasia* (21 species, all but 1 confined to Australia) much the same condition prevails except that here the ovate or oblong anthers, connivent in a cone around the ovary, dehisce by short, sometimes almost poriform, introrse



slits, finally extending more or less down the sides. The pistil sometimes considerably exceeds the tips of the stamens.

*Guichenotia* (5 species endemic in West Australia) has anthers opening by introrse terminal pores or slits which may be continued down the side.

*Lysiosepalum* (2 species are found in West Australia) has the anthers subulate to linear and dehiscing by apical poriform slits which may be finally continued down the sides.

*Lasiopetalum* (25 Australian species, mostly confined to West Australia) is probably the best representative of the *Solanum-Cassia* type to be found in the Sterculiaceae. Even here the pores of the anthers are continued down the sides and the style is sometimes much exserted and covered with stellate hairs.

It is unnecessary to discuss in detail here the polymorphic and often complicated floral organization in the Sterculiaceae. The forms showing dehiscence by pores or short slits are found only in the *Lasiopetaleae*, which differs very essentially from the other tribes in its floral structure. All members of this group agree in the possession of a patent perianth. The petaloid nature of the sepals and the reduction of the petals to scale-like structures, the peculiar style in some species and the floral habit of other genera of the family to which these forms have been assigned give them a peculiar interest, but our knowledge of them is entirely too meager to permit of any suggestions as to the significance of the forms.

#### Ochnaceae.

In the Ochnaceae, we have a family particularly difficult of treatment on account of the numerical reduction in the androecium. Transitions are present between the *Dilleniaceae* and the *Solanum-Cassia* type, while some of the



forms are strongly suggestive of the Melastomataceous type.

*Ouratea* (76 species in tropical America and 26 in the Old World) is one of the finest examples of the Solanum-Cassia type, sometimes with more or less rugose anthers. *Brackenridgea* (5 species, 2 in the Fiji Islands, 1 in Penang, 1 in Queensland, 1 in Zanzibar) is an excellent representative of the floral habit of this type, but the anthers open by longitudinal slits or at first by apical pores which are later increased more or less towards the base in longitudinal slits. *Godoya* (3 species in Peru and New Granada) has 10 to 20 stamens but their form is such that they seem to be more properly treated here than in the Dilleniaceous type. *Elvasia* (4 species in Brazil and Guiana) with stamens 8 or indefinite, up to 20, with oblong or nearly oval anthers basifixed on more or less elongate, filiform filaments, suggests in some of its species the Melastomataceous type, but in others the filaments are reduced in length and the anthers more elongate, so it may be treated here.

*Blastemanthus* (2 species from the upper Amazon, of which 1 also occurs in Guiana) has the 10 declinate stamens with very long anthers on short filaments surrounded by numerous staminodia. As far as form is concerned, *Wallacea* (1 species in the upper Amazon region) is an excellent representative of this type. The fertile stamens are 5 in number and turned to one side at the time of flowering. Staminodia are present, and the terminal pores, or single terminal pore, of the anthers are said to be later continued down the sides in lateral slits. In *Schuurmansia* (3-4 species in the Indian Archipelago) the floral structure seems to be very similar to the preceding. *Poecilandra* (1 species in northern Brazil and British Guiana) may be placed without question in this type. *Luxembergia* (7 species, all in Brazil) is a peculiar genus in which the indefinite, usually few, anthers are aggregate or connate in a column on one side of the ovary. *Euthemis* (3-4



species in the Indo-Malay Archipelago) is a good example of this type.

The numerical reduction in the androecium of the Ochraceae may be mentioned in this connection. The family is characterized by elongate, basifixed anthers, generally dehiscing by apical pores, with some species of several of the genera showing, at least finally, longitudinal slits. I have been unable to convince myself of any unquestionable relation existing between the stage of reduction in the number of stamens and the perfection of dehiscence by pores in this family except in the following special cases. While too much weight must not be attached to the limited evidence, the condition of stamens and staminodia in certain genera may be described.

In *Neckia* (3 species in the Indo-Malay Archipelago) the staminodia of the inner whorl, about 10 in number, are clavate and cohere with the filaments of the longitudinally dehiscent anthers at the base. In *Leitgebia* (1 species in the savannahs of Brazil) a similar condition occurs with only 1 whorl of 5 spatulate staminodia and anthers dehiscing at first by apical pores. In *Sauvagesia* (11 species, confined, with the exception of 1 of universal tropical distribution, to tropical Brazil) two whorls are present, the outer of filiform staminodia, the inner of 5 petaloid structures, closely approximated in a cylinder around the longitudinally dehiscent anthers. In *Lavradia* (6 species endemic in Brazil) is to be seen a still more modified condition. The outer whorl of staminodia is entirely wanting while the members of the petaloid whorl are connate in a coniform or almost urceolate corona surrounding the shortened anthers which seem to show no trace of apical pores, but open longitudinally from the first. These aberrant forms may be profitably compared with *Antholoma* of the Elaeocarpaceae. While the evidence is far from comprehensive, it



strongly suggests the significance of the exerted condition of the anthers in apical dehiscence.

#### Dipterocarpaceae.

In the Dipterocarpaceae, species of *Shorea*, *Anisoptera* and *Vatica* have anthers opening more or less terminally, but the only genera to be considered in this paper are *Stemonoporus* (12-13 species endemic in Ceylon), and *Monoporandra* (2 species endemic in Ceylon), both of which in the general habit of the flower fall clearly into the Solanum-Cassia type.

#### Flacourtiaceae.

Of the Flacourtiaceae, *Kiggelaria* (3 South African species) may be assigned to this type.

#### Begoniaceae.

In the Begoniaceae, *Begonia* is the principal genus, being represented by about 400 species throughout the warmer regions of the whole world. In all the species, the stamens are numerous, anthers basifixed, rarely almost spherical, usually ovate or oblong to linear, connective produced in various forms beyond the locules or not, filaments long or short as compared with the anthers, free or monadelphous. The dehiscence is by lateral slits. In two Brazilian species, forming the section *Solanthera*, the filaments are free, anthers linear, obtuse, much longer than the filaments and opening at the apex through two pores. In the section *Parvibegonia*, of 8 Indian species, dehiscence is said to be lateral, by short, subapical slits in six species, and by "pores" in the other two. My knowledge of the Indian species is very incomplete, but the Brazilian forms may certainly be placed in this type.

#### Myrsinaceae.

In the Myrsinaceae, *Cybianthus*, with small broad anthers dehiscing by elongate or short and subapical, some-



times almost poriform slits, is an interesting form but hardly merits consideration as one in which dehiscence is by apical pores.

*Ardisia* is a large genus of over 200 species much in need of revision. The stamens are 5 in number, with short sagittate or lanceolate anthers usually opening by longitudinal slits. In the section *Icacorea*, however, according to Pax, the anthers open by apical pores. This section seems to comprise about 7 South American species. The anthers of the second section, *Stylogyne*, with 1 Brazilian and 1 Malayan species, are described as opening by terminal pores. In the single representative of the third section, *A. paludosa* of Madagascar, the anthers open by a single terminal pore. In the two other sections of the genus containing the remainder of the species, distributed throughout the tropics of both hemispheres, dehiscence is by lateral slits. My knowledge of this genus is very imperfect, but I think it probable that an examination of suitable material would show that in the most of the above species described as apically dehiscent the pores are not permanent, but merely the beginnings of longitudinal slits.

#### Loganiaceae.

In the 32 genera assigned to the Loganiaceae only 5 or 6 have any species with a rotate corolla, the tendency being towards tubular, salver-form or campanulate. *Gardneria* is the only genus characterized by a rotate corolla with oblong to linear exserted anthers. Three species are found in Japan and India. In *G. nutans* (of Japan) the slits are said not to extend to the base as in the others, but to be confined to the tip of the anther.

#### Gentianaceae.

In the Gentianaceae, two genera belong clearly to this type: *Exacum* (29 species, distributed over tropical and sub-tropical Asia, the Malay Archipelago, Madagascar and



tropical Africa, with 4 species in tropical America), and *Cotylanthera* (3 species, saprophytic herbs, from Java, Mariana Islands and the Himalayas). *Chironia* and *Deianira* are interesting for comparison, though they can hardly be included in the list.

In the Gentianaceae the corolla is infundibuliform, hypocrateriform, campanulate or sometimes rotate. In both *Exacum* and *Cotylanthera* the corolla has a short, subglobose tube with patent limb and stamens inserted in the throat. A detailed comparison of the floral habit of these genera with the other members of the family is precluded by lack of space. Several genera approach the rotate corolla characteristic of the *Solanum*-*Cassia* type either by way of a broadly campanulate corolla or by a hypocrateriform corolla with a usually shortened cylindrical tube and prominent patent limb. In some of these forms the stamens are included while in others they are exerted, but with short, versatile anthers on longer filaments. In some cases the anthers are linear but versatile, while in others they are linear and basifixed. A few forms approach very closely in their floral habit the two apically dehiscent genera.

#### Solanaceae.

In the Solanaceae, two forms are to be considered, *Solanum* and *Cyphomandra*. *Solanum* (of about 970 nominal species 630 occur in Tropical America, 70 in extratropical South America, 27 in tropical Africa, 10 in the East African islands, 34 in the Indian, Malay and Oceanic Island region, 26 in South Africa and 52 in Australia) is too well known to require description: attention may be directed to the few zygomorphic forms constituting the section *Nycterium*, and to the considerable number of species showing incipient stages of this characteristic, and to the condition prevailing in the small section *Lycopersicum*. In many of the species the pores are later continued down the sides of the anthers, sometimes to the base, in



longitudinal slits. *Solanum* furnishes one of the classic illustrations of the apically dehiscent anther, and the large number of species in which the pores are continued down the sides in longitudinal slits stands as a justification for including in the apically dehiscent category several genera in which the pores are later supplemented by lateral slits. Between the two forms of dehiscence, no sharp line exists although in the individual cases it is usually not difficult to decide very satisfactorily to which category a form should be referred.

In *Cyphomandra* (about 35 tropical American species, especially numerous in Brazil, and 2 extratropical South American species), the species of which were formerly treated under *Solanum*, the structure of the anther differs somewhat from that of *Solanum*. In some of the species at least, the walls are very thin and elastic, so that the pollen is puffed out by a bellows-like action. This genus is, in my present judgment, to be regarded as a specialized representative of the *Solanum*-*Cassia* type.

In the Solanaceae the gamopetalous corolla is tubular, infundibuliform, hypocrateriform, campanulate or rotate. I shall not give here a detailed discussion of the structure or distribution of the genera or species which approach *Solanum* in floral habit, but from quite careful comparison I may state with some confidence that *Solanum* represents the form in which the anthers have attained the greatest length and the filaments are the most reduced.

#### Rubiaceae.

In *Argostemma* (30–40 species in tropical East Asia, 1 in West Africa), of the Rubiaceae, we have an interesting genus, some species of which belong clearly to this type. Only a few of the 30–40 species show dehiscence by pores, and I have not data which enable me to state which or how many these species are.

*Neurocalyx* (about 6 species especially in Ceylon, but



also extending to the island of Borneo and oriental Asia) is an interesting form for comparison, in which the anthers are connate in a cylindrical tube and open internally. The monotypic *Strumpfia*, of the rocky coast of the Antilles, is another form which may be profitably compared. The five anthers form a conical synandrium around the pistil. The locules open in a more or less irregular manner at the tip, the outer wall of the synandrium extending considerably above the inner one. To attempt a statement of the condition of the corolla, androecium, and gynoecium in the genera of this family, even were data for such a statement available, demands an unprofitable amount of space and time. A quite careful examination of the genera, however, has shown that in the most of those with a rotate or almost rotate corolla, the androecium is characterized by elongate filaments and short anthers. In some cases the anthers may be elongate or linear, but in these cases they are usually dorsifixed, sometimes near the base, and distant instead of connivent around the style. With the exception of *Argostemma*, *Neurocalyx* and *Strumpfia*, I have found no genera which I could confidently refer to the floral habit exemplified by *Solanum* or *Cassia*. All of these forms may be profitably compared with the section *Lycopersicum* of *Solanum* or with *Sollya* of the Pittosporaceae.

#### VII. MELASTOMATACEOUS TYPE.

This type is practically coextensive with the Melastomataceae, which furnishes almost all of its members. Possibly some of the genera from this family should be included under the *Solanum-Cassia* type on purely structural grounds, but considering the nature of the characteristics separating the two groups, it has been thought best to retain all such forms here.

The essential distinguishing characteristic of this type is, in my opinion, the elongated filaments. There is the same conspicuous, patent perianth as in the *Solanum-Cassia* type



with little indication of a special receptacle for nectar. The number of stamens is usually small. The anthers are basifixed and have generally the same elongate, linear or subulate, form as in the preceding type. The pores are often minute, both locules usually opening through a single pore, and are very rarely continued down the sides. Often the anther has thin, flexible walls which make possible a bellows-like action in the ejection of the pollen.

In the Melastomataceae, considering the size of the family, the floral structure is quite uniform. Flowers usually 4- or 5-merous; petals usually large and highly colored, never absent though sometimes reduced, rarely connivent into a tubular or campanulate corolla; stamens usually twice as many as petals, rarely as many, or in some cases indefinite, all similar or alternately reduced or imperfect; filaments long or short, thick or slender, straight or arcuate, glabrous or glandular; anthers basifixed, almost spherical or cuneiform to linear or subulate, the oblong to linear or subulate being the prevalent type, straight or variously curved, dehiscing by a single terminal pore, rarely by two terminal pores and very rarely by lateral slits or by four terminal pores. The connective shows many modifications and is often produced below the locules and variously appendaged. Style filiform, straight or curved; stigma usually minute, rarely capitate.

It seems unnecessary to enumerate or describe the genera. The more essential structural points and the geographical distribution of the forms may be obtained from the work of Bentham and Hooker or Engler and Prantl, the splendid elaboration of the South American forms in *Flora Brasiliensis* or the detailed monograph of the family by Cogniaux. An examination of the individual genera reveals the fact that there prevails in this family a marked structural uniformity which instead of being obscured by numerous minor differences, is only made more conspicuous by them. The family includes



161 genera of tropical and subtropical distribution, 98 occurring in South America, 31 in the Indian region, 19 in the tropical African region and the others of various distribution.

Outside of this family I have assigned only three genera to this type: *Storckiella* of the Leguminosae, and *Maximiliana* and *Amoreuxia* of the Bixaceae. Possibly some others, as, for instance, *Cheiranthera* of the Pittosporaceae and *Exacum* of the Gentianaceae should also have been placed here instead of in the Solanum-Cassia type.

*Storckiella* (2 species in Oceanica) is the only member of the apically dehiscent Cassieae not clearly belonging in the Solanum-Cassia type. It is the only form with long filaments and it seems best for this reason to separate it from the genera to which it is systematically related.

In the Bixaceae, *Bixa* has been treated under the Dilleniaceous type. *Maximiliana* (13 species, 6 in tropical America, 3 in Africa, 1 in tropical Africa and southern Asia, 3 in North Australia and Queensland) with large actinomorphic flowers, and *Amoreuxia* (3 species in Central America) with zygomorphic flowers, have long filaments and rather elongate anthers which open by well-formed terminal pores. These forms should possibly have been placed in the Dilleniaceous type too, but the form of the stamens is very suggestive of the Melastomataceous type so they have been placed here.

#### ABERRANT FORMS.

As mentioned above, a few genera in which the anthers have been described as opening by pores do not fall readily into any of the above types. The fact that the most of the forms described as apically dehiscent belong clearly to one of these categories has led me to designate these simply as aberrant forms. Here as elsewhere classification should not be too much influenced by the number of individuals or named groups of individuals which may be assigned to any



particular subdivision, but in our almost total ignorance of their ecology and in some cases of their structure it seems best to treat these forms in this way.

These so-called aberrant forms are the following:—

*Odontostomum* (1 species in California) of the Liliaceae has a hypocrateriform corolla with patent or reflexed lobes with erect, basifixed, ovoid anthers which are only about one-half or one-third as long as the filaments.

In the Euphorbiaceae, *Poranthera* (5 Australian species, of which one also occurs in Tasmania and New Zealand, and a sixth endemic in New Zealand) has small flowers with five stamens having 4-locellate anthers opening in four terminal pores which are quite distinct or sometimes confluent into two.

In the Ebenaceae, the anthers of the three species of the section *Leucoxylum* (2 in Madagascar and 1 in the Indian monsoon region) of *Diospyros* (about 120 species of wide distribution, especially numerous in the Indian region) are described as opening by lateral pores at the tip instead of by longitudinal slits as in the other species. The corolla in *Diospyros* is urceolate, campanulate, tubular, or salverform; stamens 4 to indefinite, usually 16; anthers oblong, linear or lanceolate. In the three species which have been described as apically dehiscent the flowers are small, the corolla seems to be openly campanulate and the stamens 10–16 in number. It may be that these species might be properly assigned to the *Solanum-Cassia* type. Sargent describes the sixteen anthers of *D. Texana* included in the urceolate corolla as dehiscing only near the apex and his figure represents the openings as almost poriform.

The condition prevailing in the Acanthaceae is one of particular interest. Here we have 7 genera which are said to have, in some species at least, anthers opening by apical pores. Of these, *Staurogyne* need not be considered, since dehiscence in this genus can hardly be justly described as by apical pores. *Ophiorrhiziphyllon* (1 species in Marta-



ban) is insufficiently known to me. The anthers of *Afromendoncia* (3 species in tropical Africa) are peculiar among those opening by apical pores. In *Hiernia* (1 species in Angola), *Mendoncia* (about 20 species in tropical America), *Monachochlamys* (1 species in Madagascar) and *Pseudocalyx* (1 species in Madagascar and Nossi Be Island) the anthers are of the simple oblong to linear type with the more or less shortened filament so characteristic of the apically dehiscent anthers of most of the preceding families. Except in one or two of these six forms, however, dehiscence is not by the clearly-defined, round pores found in so many of the genera described above, but by more or less elongate apical slits.

It is not necessary in this place to enter into a detailed discussion of the structure of the stamens in the usually strongly zygomorphic flowers of the Acanthaceae, but attention may be called to the fact that the form of stamens found in the four genera just mentioned is not at all common, in fact is almost unique, in this large family. In almost all the forms discussed above, the linear anthers on short filaments are exerted from a widely open corolla. In the Acanthaceae the corolla is rarely open enough to be designated as campanulate from the base and it is never rotate. In *Hiernia* the limb is patent and the somewhat declinate linear anthers exerted so that except for the considerable length of the tube the habit of the flower is much the same as if the anthers were inserted by short filaments on a rotate corolla. The presence of the long perianth tube alone prevents the placing of this interesting genus in the Solanum-Cassia type. In *Ophiorrhiziphyllon* the two fertile stamens with long filaments and short anthers are described as much exerted from the zygomorphic corolla. *Afromendoncia* has the tube somewhat expanded above and the characteristic anthers project only slightly. In *Monachochlamys* the corolla is tubular to campanulate, with the stamens clearly included, while in the two other



genera, *Mendoncia* and *Pseudocalyx*, the same condition prevails with a less widely open corolla tube and more elongate anthers. Data are too limited to justify speculation, but the association of a tubular corolla with apically dehiscent anthers of the form so generally found when the corolla is patent, is interesting. The inclusion of a linear anther in a cylindrical corolla tube is nothing out of the ordinary, but the cases detailed above are the only ones in which the dehiscence is by pores. The condition described in certain aberrant Elaeocarpaceae and Ochnaceae will be recalled in this connection.

In contrast with the preceding family, the Rubiaceae has many genera and species in which the corolla is more or less widely open and several in which it may be characterized as patent. Attention has already been called to some of these in the section devoted to the Solanum-Cassia type. Here we are concerned with only two genera.

The anthers of *Tresenthera* (2 species, 1 in Venezuela, the other in the West Indies), somewhat exserted from the campanulate corolla, are rather unique in their form and mode of dehiscence, opening as they do by a triangular valve below the tip. In *Rustia* (5 species ranging from Central America to beyond the province of Rio de Janeiro in Brazil) the linear basifixed anthers are of the form so generally found in apically dehiscent genera. In some species the anthers are included in the tubular portion of the corolla while in others they are exserted their entire length from the throat while the rather large lobes of the limb are patent. The occurrence of linear anthers in this genus is not so worthy of comment as in *Mendoncia*, *Pseudocalyx*, and *Hiernia* of the Acanthaceae, where the anthers are generally very short, for in the Rubiaceae the anthers are frequently linear in form and included in the corolla tube.

Too much significance must not be attached to the condition found in these genera, but it is suggestive when



compared with that of typical forms in the same family and with the typical and aberrant forms in apically dehiscent groups.

SYSTEMATIC RELATIONSHIP AND MORPHOLOGICAL CHARACTERISTICS OF APICALLY DEHISCENT FORMS.

Dehiscence by pores may be characteristic of families, genera or species. In the Rapateaceae, Tremandraceae, and, with the exception of comparatively few genera and species, in the much larger Melastomataceae, dehiscence by pores is of regular occurrence. It may be found, however, in only a few of the genera, as in *Solanum* of the Solanaceae, *Cassia* of the Caesalpinioideae, *Cheiranthra* of the Pittosporaceae and other examples which might be advanced. Probably the best illustration is the monotypic *Fissicalyx*, the single apically dehiscent genus among over 300 belonging to the Papilionatae. Only certain species of a genus, again, may have anthers with pores instead of longitudinal slits. The two Brazilian, and possibly two Indian species, of the 400 assigned to *Begonia* may be recalled in this connection, as may also three species forming the section *Leucoxylum* of *Diospyros*. The apically dehiscent habit has unquestionably been assumed independently by many unrelated genera and doubtless at various times. The regular occurrence of this method of dehiscence in several large groups indicates that in these cases the habit of dehiscence is much older, perhaps as old as the group itself. There is much to suggest that the apically dehiscent forms of the *Solanum*-*Cassia* and *Melastomataceous* types have originated from actinomorphic forms with more or less patent perianth. Evidences of exceptions to this generalization are, however, to be seen in several cases and in view of our almost complete ignorance of primitive floral types we can hardly venture to hazard any statements as to the phylogeny of these forms.

While evidence is too meager to permit of any conclu-



sions as to the type of flower from which an apically dehiscent form of any of the classes here recognized may have been derived, it seems that there is little relation between the systematic affinities of a group and the possibility of its containing apically dehiscent genera or species.

STRUCTURAL SIMILARITY OF MEMBERS OF THE SEVERAL  
TYPES.

Structurally, the apically dehiscent forms may be assembled into more or less natural and sharply limited categories. The Araceous type is a natural and sharply limited one, distinguished by a uniformity of gross structure that renders unnecessary any summary of morphological characteristics. The crowding of the anthers or their fusion into a synandrium renders apical dehiscence the most simple and the necessary mode, but the recognition of this fact does not furnish an explanation of the changes which have taken place in the development of the structure now prevailing or indicate the forces which have been active in producing them. Considerable is known of the pollination of these forms but upon the basis of the data which I have so far collected I am not yet prepared to discuss the significance of insects as a factor in the development of this floral type, or, to state the matter differently, to say in how far apical dehiscence in this type and the other structural characteristics correlated with (or determining) it are to be regarded as adaptations for fertilization by certain groups of animals. This much is certain, that the members of the Araceous type are distinct in every way from the others considered.

This last statement also applies to the Gramineous type which may also be dismissed from our further consideration.

The Polygalaceous type shows a great uniformity of structure. The locules of the short, broad anthers open



by a large terminal gap which may hardly be appropriately designated as a pore. These forms are evidently bee flowers in which the essential organs are inclosed in a ventral carina and this inclusion doubtless has a large significance in the form and size of the opening of the anther.

The Ericaceous type is one of the most important, but demands for its adequate treatment much more space than can be given to it in this place and many more data than have so far been secured. The most conspicuous characteristic of this type is the pendulous habit of the flower, with tubular, urceolate or globose corolla. In this paper, several forms which differ in the essential features from the most prevalent characteristics of the type as I have limited it have been classed with this group largely on account of their systematic affinities. The class as a whole, however, may, I think, be regarded as a very natural one.

The opening of the anther in this type varies greatly in form and size. The presence and form of the aristae on the anthers in many genera also furnish interesting characteristics and are of importance in the pollination of the flowers.

The Ericaceae are known to be largely dependent for their fertilization upon Apidae, but the epitomizing of the observations on the ecology or the geographical distribution of this large class lies outside the scope of the present paper.

The Dilleniaceous, Solanum-Cassia and Melastomataceous types must be considered together. These types are not so sharply separated as the preceding but in some degree transgressive. It is this general group of floral forms to which the present paper is devoted. The others are considered only in such detail as will show their relations, or rather the lack of any relation, to these types.

It has been impracticable to give structural details in the



preceding pages and many interesting points must be left quite untouched. Some of the major characteristics, however, seem to be significant. To these three types belong 227 genera represented by about 4,923 species. Among these the conspicuous portion of the perianth, calyx or corolla, is almost without exception campanulate or more generally widely patent and sometimes reflexed. The stamens regularly show an elongate form and are basifixed on long or short filaments. The pistil is usually simple with filiform style and small, punctiform stigma, but to this there are rare exceptions.

The Dilleniaceous type is distinguished from the others by numerous stamens and sometimes separate pistils. The number of genera assigned to this type is few. In it, dehiscence by pores seems to be the least specialized of these three types. The anthers are for the most part elongate but rare exceptions to this general rule are to be found; the pores are not infrequently continued down the sides in longitudinal slits.

In the Solanum-Cassia and the Melastomataceous types there is, as compared with the preceding, a reduction of the number of the stamens and the pistil is always simple, usually with a punctiform but sometimes slightly lobed stigma.

The minor differences exhibited by the individual genera and species of the Solanum-Cassia type are somewhat confusing but the conviction of the existence of an essential similarity in the organization of the flowers of the forms assigned to this type becomes stronger as the material is studied. Here, as everywhere else, nature seems in large measure regardless of fixed categories, and yet the structural agreement of many of these genera or species from widely separated families and of discontinuous geographical distribution — an agreement which is often so close that one would almost assert that the flowers of the several unrelated genera indigenous in the most widely separated por-



tions of the globe had been cast in the same mould or formed by the same skilled artisan — is so exact and the general structural habit of the aberrant forms is with all of the minor differences so uniform in essentials that it seems necessary to attribute it to some single factor or co-operative group of factors of environment.

Before we attempt to determine this factor, however, it will be well to assure ourselves as fully as possible of the real existence of such a structural uniformity.

Of the structural characteristics, our knowledge is fairly satisfactory, although many points can be determined only by the examinations of living material. The large series of icones, many of them executed from living material, in the library to which I have had access while carrying on this work has enabled me to make extensive comparisons otherwise impossible. It may, I think, be demonstrated beyond confutation, that the apically dehiscent forms other than the genera which have been assigned to groups designated as the Araceous, Gramineous, Polygalaceous and Ericaceous types (and all of which are, with the exception of the last, perfectly natural and sharply defined categories) may also be grouped in classes few in number and uniform in their essentials of structure.

The close structural agreement among themselves of the apically dehiscent forms assigned to any class is relatively easy of demonstration or refutation although specific variability in many genera, the presence of minor structural characteristics which tend to obscure the more essential features, and the inadequacy of our knowledge of many forms, renders this no light task.

The demonstration of a general structural similarity in all the parts of flowers, which have been brought together for comparison on the basis of a single characteristic — in the present case the mode of dehiscence of the anther — indicates that there exists a correlation between this character and the other structures of the same flower.



The nature of this correlation we cannot consider here. For the present, we are concerned only with ascertaining if an interdependence really exists. An examination of the apically dehiscent genera and species alone yields very convincing evidence in favor of this hypothesis, but theories based upon one class of data are open to criticism and especially so when the mass of material is so small as it necessarily is in the few apically dehiscent genera assigned to the Dilleniaceous or the Solanum-Cassia type.

ABERRANT NATURE OF APICALLY DEHISCENT FORMS IN  
THEIR SYSTEMATIC GROUPS.

A satisfactory kind of supplementary evidence will be furnished by a comparison of the apically dehiscent genera from the several families with the other members of the same systematic group. If in addition to an approximate conformity to the characteristics of their own type in an artificial class limited primarily by a single character, the several genera are found to be aberrant in the groups of the phylogenetic system in respect to the assemblage of their floral characteristics, we shall be justified in concluding that there is some direct and demonstrable relation between the selected character and the others pertaining to the flowers under consideration.

A thorough comparison such as that here suggested involves numerous almost insurmountable difficulties. Taxonomists are by no means agreed as to the limitations of systematic groups or as to their monophyletic or polyphyletic origin, and under these circumstances what shall serve as our basis of comparison? Not only are the limits of groups variously and oftentimes ill defined but the data available on the floral structure of species or genera are sometimes very meager. The labor involved in searching through many volumes of descriptions and figures to secure the data for such comparisons is very great and even then



the many details cannot be satisfactorily known. Few herbaria are rich enough in material to permit of an examination of a majority of the forms which should be considered and even were this the case the time and material required would in most cases be out of all proportion to the results obtained.

In making these comparisons all characters must be taken into consideration. The *Solanum-Cassia* type is not distinguished by linear, basifixed, or apically dehiscent anthers alone, or by a patent corolla, but by the association of all these characters — the patent corolla and the linear, basifixed anthers approximated around the simple style and opening by terminal pores. Excepting the essential character of dehiscence, any one of these may usually be found and often represented by a large number of genera in the family or group from which the apically dehiscent genera under consideration are taken but the combination of all the characters except that of the apical opening of the anthers in one flower is, in the systematic groups which I have examined, much more rare.

The general results of a quite detailed examination of a number of the families, are presented below: —

#### Dilleniaceous Type.

We find in the Dilleniaceae that while the numerous structural differences are very confusing it seems quite clear that apical dehiscence is confined almost exclusively to those forms with long, basifixed anthers. The presence of several free, spreading pistils in this family is unique among flowers with apically dehiscent anthers.

In the Elaeocarpaceae dehiscence may be by pores or longitudinal slits in the same genus, all genera but one having at least some species with apical pores. This single exception is *Antholoma* which has the essential floral structure of other elaeocarpaceous genera except for the gamopetalous, urceolate corolla instead of the usual polypetalous,



generally more or less campanulate, perianth of other representatives of the family. The stamens in this family are usually linear and basifixed on filaments of varying but usually considerable length and, in this respect, conform to the ideal type of this class.

Elongate, basifixed, usually apically dehiscent anthers are characteristic of the Ochnaceae. Other points will be taken up under the Solanum-Cassia type to which the most of the representatives of this family have been assigned.

Of the Theaceae my knowledge is insufficient to permit of comparisons.

*Bixa* of the Bixaceae is an anomalous form.

#### Solanum-Cassia Type.

Turning now to the Solanum-Cassia type we find material which yields more satisfactory results.

The Mayacaceae is monotypic and its relationship is not so evident as to justify comparisons of its floral structure with that of other families.

All of the genera of the Rapateaceae are apically dehiscent. The family is considered most closely related to the Xyridaceae and Eriocaulaceae.

A patent perianth is characteristic of the Commelinaceae and, except for a slight elongation of the anthers, the apically dehiscent genera do not differ essentially from some others to be found in the family. At the same time the various structure of the anthers and the filaments of many of the genera distinguish them at once from the apically dehiscent forms.

In the Pontederiaceae, *Monochoria*, the anthers of which open only at first by apical pores which are soon continued down the sides in slits, has the corolla tube most reduced and the limb more widely patent than any forms except some species of *Heteranthera* with a long tube. The filaments and anthers are of about equal length, but the



anthers have probably the greatest relative length in the family.

The floral structure of the Liliaceae and Amaryllidaceae is hardly to be summarized in general terms. We may, however, repeat that in the Amaryllidaceae the prevalent habit of the perianth may perhaps best be described as infundibuliform, while in the Liliaceae it is more frequently patent or campanulate. In the Amaryllidaceae the four apically dehiscent genera stand almost alone as representatives of the Solanum-Cassia floral habit while in the Liliaceae there are many genera with patent or broadly campanulate perianth and in some of these the filaments are reduced in length, and the anther is of the more elongate form commonly seen in the apically dehiscent genera.

*Sollya* and *Cheiranthra* are quite aberrant forms in the family Pittosporaceae in which they belong, both as regards form of perianth and structure of stamens.

In the Leguminosae the apically dehiscent genera belong to a group in which the perianth is generally patent, but they differ in the relative length of the filament and anther and in the insertion of the anther upon the filament.

The Tremandraceae contains only apically dehiscent genera and species.

The sterculiaceae genera which have been mentioned as having anthers opening at least at first with pores are marked by a great similarity of structure, a greater similarity than that between the apically dehiscent genera and the other genera of the Lasiopetaleae, to which all of the apically dehiscent genera belong, in which the anthers open from the first by longitudinal slits. The Lasiopetaleae itself differs very essentially in its floral structure from other tribes of the Sterculiaceae so that there can be no question as to the unique structure of these forms in this family.

The Ochnaceae has the elongate, basifixed anthers of the Solanum-Cassia type and most of the genera have anthers



which open at least at first by terminal pores. Since the floral habit of this family conforms to that of our Dilleniaceous and Solanum-Cassia types, the only opportunity for comparisons is between the genera which may be assigned to these two types and certain aberrant forms to be mentioned below. We may postulate that the Solanum-Cassia type has in some cases been derived from the Dilleniaceous type by a numerical reduction of the androecium accompanied in most instances by a shortening of the filaments. On the whole, dehiscence by pores seems to be more perfected in the Solanum-Cassia type. A family containing representatives of both types should furnish data of value for a study of this question but, as pointed out above, the evidence available in the present case is too meager. A strong reduction in the androecium has clearly taken place so that the family is broken up into more than one floral type, but whether this reduction occurred entirely subsequent to the development of the apically dehiscent habit or whether it largely preceded it is a question which cannot be easily decided. The anthers of some species of this family which have been assigned to the Solanum-Cassia type show no more specialized apical dehiscence than some which have been assigned to the Dilleniaceous type. On the other hand it is to be noticed that certain genera are very suggestive of the Melastomataceous type—a group of forms the evolution of which has apparently progressed along a very different line from that of the Solanum-Cassia type—and this may explain the equal perfection of apical dehiscence in forms with numerous stamens with long filaments and in those with few stamens with short filaments.

In certain anomalous genera the staminodia are so modified as to form a more or less perfected tubular or urceolate corona. In these genera, the anthers open by longitudinal slits and since the same condition prevails in other genera with an urceolate perianth in families in which the perianth is usually patent and the dehiscence apical, it seems legiti-



mate to conclude that the exerted condition is a factor of importance in the development or permanence of the apically dehiscent anther. Comparative evidence would suggest that these forms with cylindrical or urceolate perianth are not primitive, but of recent origin. The anthers seem to open at first by a terminal gap and it may be that longitudinal dehiscence has been reassumed by these forms as a result of the changes in the form of the perianth.

Only a thorough knowledge of the living plants in their own environment supplemented by histological studies will decide some of these questions.

*Stemonoporus* and *Monoporandra* differ in the structure of the androecium from all other Dipterocarpaceae.

In *Begonia* the perianth is patent in all forms. The two apically dehiscent species of the section *Solanthera* have more elongate anthers than many species of the genus, but the distinction here is not a very sharp one.

The structure of *Gardneria* seems to be unique among the Loganiaceae.

In the Gentianaceae a few forms approach very closely the structure of the apically dehiscent genera and many agree in some characteristics, but on the whole it seems to me that *Exacum* and *Cotylanthera* depart markedly from the type of the family.

A long corolla tube is characteristic of most Solanaceae. Several genera have a more or less widely open corolla. Among these, *Solanum* is the genus in which the anthers have attained the greatest length and the filaments are most reduced.

Comparisons in the Rubiaceae are rendered very difficult by the size of the family, the inadequacy of our knowledge of the floral structure and especially by the large number of genera which show some of the characteristics of the flowers of the *Solanum-Cassia* type; but when all characters are considered, *Argostemma*, *Neurocalyx* and *Strumpfia* seem to be unique in this vast family.



## Melastomataceous Type.

In the Melastomataceous type, the Melastomataceae need not engage our attention here. We have already noticed the similarity of floral structure in the Melastomataceae. The floral structure is quite unique and a comparison with groups to which it is more or less closely related is not possible in this place.

The essential structural difference between the Solanum-Cassia type and the Melastomataceous type seems to be the length of the filaments. The long filaments make possible the highly organized anthers found in the latter. The structure of the flowers need not be redescribed here. The essential similarities may be gathered from any series of descriptions or plates of the genera of this family, while the minor details are too numerous and perplexing for consideration.

The species from other families which have been assigned to this type are very few. *Storckiella* is the only genus of the Cassieae with elongate filaments. *Maximiliana* and *Amoreuxia* of the Bixaceae have the form of anther which is so frequently seen in this type and long, filiform filaments. The stamens are more numerous than is usually seen in the Melastomataceae. The Bixaceae comprises four genera belonging to three tribes. The first contains the unique *Bixa*, the second *Maximiliana* and *Amoreuxia* and the third *Sphaerosepalum*, exhibiting numerous stamens with long, filiform filaments and nearly globose, dorsifixed, versatile anthers dehiscing by longitudinal slits. The structure of the two genera which I have assigned to this type is, then, quite unique in this family.

As I have insisted above, the limitation between the Solanum-Cassia and the Melastomataceous type is not a sharp one and it may be that such forms as *Cheiranthera* of the Pittosporaceae and *Exacum* of the Gentianaceae would have been best treated under this type. Here, a



knowledge of the living plants such as may be gathered by those who know them in the field is most desirable.

#### RECAPITULATION.

The evidence assembled in the preceding paragraphs seems to point clearly to certain easily stated conclusions. Not only do the apically dehiscent forms show a high degree of similarity *inter se* but the several forms are very frequently aberrant in respect to the totality of their characters in the systematic groups to which they belong. In other words, apical dehiscence of the three types here considered occurs only in flowers of a certain structural habit. The objection which might be raised that I have included in these three groups only such forms as *are* similar in the totality of their characters is disarmed by the fact that these three classes are sharply distinguished from the first four types recognized and that anomalous forms are very few. The fidelity to type of the apically dehiscent genera and in many cases their aberrant floral habit when compared with other members of the same systematic group speak strongly in favor of a correlation between the floral parts and the form and mode of dehiscence of the anther. The exact significance to be assigned to the broad term correlation must be defined in each case if ambiguity is to be avoided. Interdependence of parts may be real or apparent, due to internal or external forces. In this paper, I have sought to avoid all theoretical considerations and I shall not discuss the nature of the correlation observed in these forms. I have used the term in the broadest sense, indicating any reciprocal relationship of parts; the ground for the assumption of such a relationship is found in the constancy with which the characteristics in question are found associated in the apically dehiscent forms.



## FLORAL ECOLOGY OF APICALLY DEHISCENT FORMS.

It was the similarity of adaptation which first aroused interest in the morphological peculiarities described above. We may now examine the data available upon these floral structures regarded as adaptations.

The ecology of the Araceous, Gramineous and Polygalaceous types is quite foreign to our present considerations. That of the Ericaceous type has many points of interest but material is not yet satisfactorily arranged for a summarized statement and the individual data are too numerous for consideration here.

## ECOLOGY OF DILLENACEOUS TYPE.

In the Dilleniaceae, Ducke saw *Melipona bipunctata* abundant on an unidentified *Tetracera* at Para in Brazil and also a small species of *Halictus* visiting the flowers of *Davilla rugosa* in great numbers. On *Saurauia* the interesting habit of producing inflorescences from the lower regions of the main stem has been described in some detail. Knuth observed in Java numerous small insects upon the flowers of *S. cauliflora*: "Vor allem war Thrips sehr häufig in den Blüten, Musciden flogen unster von Blüte zu Blüte und hielten sich in jeder einzelnen mehrere Sekunden auf, mit grossen Ballen weissen Pollens wieder hervorkommend, und auch kleine Bienen (*Podalirius?*) flogen ab und zu." As a visitor of *S. nudiflora* he saw *Podalirius* clinging to the flowers from below and diligently collecting pollen. It is unfortunate that the evidence is so meager that one is only able to surmise that these are pollen flowers, perhaps very similar to *Rosa*.

Observations on the Elaeocarpaceae are of the characteristic meagerness. According to Thomson, *Elaeocarpus Hookerianus* of New Zealand has perfect, white, protandrous flowers in which a glandular ring at the base of the stamens secretes nectar freely; it appears to be entomophil-



ous. Dahl saw the honeyless (?) flowers of *E. Pankinsoni* visited by two birds — *Charmosyna* and *Myzomela* [for what purpose?]. In *Aristotelia Maqui* there are said to be bright yellow male flowers with two whorls of stamens and smaller physiologically female flowers with one whorl. In Chile Johow found the flowers industriously visited by the honey bee.

In New Zealand according to Thomson *A. racemosa* shows transition stages from hermaphrodite to purely staminate or pistillate flowers. These are red and destitute of odor or nectar; the light, pulverulent pollen suggests anemophily. *A. fruticosa* of the same region has polygamous flowers which lack odor and nectar, but here anemophily is doubtful.

The unique form of the anthers and perianth in the Elaeocarpaceae renders a fuller knowledge of their floral ecology highly desirable.

On the large, red flowers of *Bixa*, of the Bixaceae, Ducke observed at Para the females of several species of bees belonging to *Centris*, *Euglossa*, *Bombus*, *Xylocopa*, *Melipona*, especially large species, and *Halictus*.

#### ECOLOGY OF SOLANUM-CASSIA TYPE.

Fortunately our knowledge of the floral ecology of the members of the Solanum-Cassia type is much fuller and so it will not be so necessary to cite the special observations as it has for the Dilleniaceous type.

Delpino divides the twelfth class (Apparecchi prensili) of his biological classification of floral forms into two types, "Tipo Boragineo" and "Tipo Verbascino." The first of these is of very particular interest in this place since the Solanum-Cassia type as limited in this paper is, so far as observations and conclusions from analogy go, very nearly synonymous with it.

The Borago floral type is, according to Delpino, characterized by pendulous or quasi-pendulous flowers. The long



anthers, inserted on short, thick filaments, are connivent in a cone, through the center of which passes the style. Dehiscence is at the apex by pores which may be continued longitudinally. The pollen is dry and smooth, and necessarily falls upon the ventral surface of the visiting insect at the moment when it grasps the staminal pyramid. In order that the insect may cling to the staminal column the expansion of the flower is generally considerable. Nectar is absent or present only in small quantities. In the former case the bee collects only pollen. This type is exclusively melittophilous, "e sorprendentemente si ripete co' suoi essenziali caratteri in molte famiglie di piante, cioè' nelle *Boraginee*, *Primulacee*, *Solanacee*, *Scrofulariacee*, *Amarillidee*, *Asparaginee*, *Pittosporee*, *Loasacee*."

In this type he places, with comments upon many forms, *Borago officinalis*, *Cyclamen europaeum*, *C. coum*, *C. persicum* and other species, *Dodecatheon Meadia*, *D. integrifolium*, *Solanum Dulcamara*, *S. nigrum*, *S. tuberosum*, *S. Lycopersicum*, *S. insanum* and many other species of the genus, *Verbascum Myconi*, *Galanthus nivalis*, *Leucjum vernum*, *Conanthera bifolia*, *Cajophora lateritia* and many species of *Loasa*, *Sollya linearis*, *Dianella coerulea* and other species of this genus.

Delpino's division of floral forms into fixed categories has been censured, and one of the most severe criticisms by Müller refers to this type. Without intending an evaluation of the classification as a whole I must say that it seems to me that Delpino's generalizations for this type have been very satisfactorily substantiated by the observations which have been accumulated since his essay appeared. In their relations to insects the forms which are here placed in the *Solanum-Cassia* type are in close agreement with Delpino's *Borago* type. For the purposes of this paper the classification is extended so as to include the zygomorphic forms so common in *Cassia* and occurring in



some other genera, forms which should perhaps be placed in the Melastomataceous type as Delpino has done. It must be recognized, however, that between these types there is no sharp distinction and that the groupings adopted are merely for the purpose of more convenient comparisons. In treating the floral ecology of the Solanum-Cassia type it seems best to discuss in some detail the two type genera and compare with them other members of their respective families, taking up afterwards the other forms in their systematic sequence.

We may first consider briefly the actinomorphic Solanums.

*S. Dulcamara* has been most thoroughly studied. It belongs clearly to Delpino's Borago type. The Syrphidae and Lepidoptera observed as visitors by Müller must be regarded as accidental or insignificant. According to most reports, *S. Dulcamara* is little visited, but Hoffer found the visitors in one locality very abundant and active, no less than seven species of *Bombus* and one of *Osmia*, as well as *Rhingia*, *Volucella* and *Argynnis* being observed. *S. nigrum* and *S. Carolinense* have been observed to be sparingly visited by *Bombus*. On *S. elaeagnifolium* at Las Vegas, N. M., Cockerell took eighteen species of Apidae belonging to fifteen different genera. At Para, Ducke observed as visitors of *S. grandiflorum* (said in systematic works to have a violet corolla  $2\frac{1}{2}$ -3 inches in diameter) one species each of *Oxaea*, *Xylocopa*, *Bombus* and *Halictus* and six of *Centris*. At the same place he observed one species of *Halictus*, seven species of *Euglossa* and a large species of *Melipona* visiting the flowers of *S. toxicarum*. On an unidentified species with blue flowers he records only species of *Melipona*, especially *M. fasciata*, *Bombus cayennensis* and *Halictus*.

Darwin reports observations by F. Müller on *S. pollinacanthum* at Sta. Catharina, Brazil. He found it visited ex-



clusively by pollen collecting bees, *Melipona*, *Euglossa*, *Augochlora*, *Megacilissa*, *Ephila* and others.

I have observed that *S. sisymbriifolium* has a very pronounced perfume, suggesting more abundant insect visits than in many other species in which no fragrance is to be detected. In the summer of 1903, I found large bees with the greatest frequency collecting pollen. In his paper on Brazilian solitary bees Schrottky gives *S. Balbisi* (= *S. sisymbriifolium*) as one of the principal flowers visited by *Xylocopa*.

Though few, these observations indicate clearly the true method of pollination in the actinomorphic species of this large genus. A few species are zygomorphic. Upon two of these, direct observations have been made. Both have been shown to be exclusively adapted to pollination by the larger bees, *Apis* and *Bombus* having been observed as well as some of the smaller Apidae. The numerous interesting points incident to their zygomorphy and their accompanying lateral asymmetry cannot be detailed here.

Between the zygomorphic Solanums and Cassias a most remarkable ecological similarity prevails and it was this which first called attention to the problem in hand.

The floral ecology of the genus *Cassia* has attracted considerable attention, the first suggestive observations being those of Delpino and Leggett in 1871 to 1881. The paper by Todd on *Solanum rostratum* and *Cassia chamaecrista* called particular attention to both of these genera and has been the incentive to most of the later work. The more important papers are those by Todd, Müller, Burck, Harris and Kuchs and the recent treatment in the third volume of Knuth's Handbuch.

Since the appearance of Todd's paper and the more general one by Müller the attention of writers has been chiefly devoted to the "division of labor" in the stamens and the curious phenomenon of right- and left-handedness, or enantiostyly as it has been called.



These morphological features of *Cassia* may not be discussed here although they have figured conspicuously in all the ecological discussions pertaining to these genera. Their true significance has probably not yet been correctly interpreted.

On *C. chamaecrista* in Iowa Todd saw a small humble bee. In Illinois Robertson observed four species of *Bombus* collecting pollen. "Landing upon the anthers, they seize them between their mandibles and stroke them downwards with a sort of milking motion." In a later paper he states that the flowers are visited by the pollen collecting female of the oligotropic *Podalirius walshii*. In eastern Kansas, Harris and Kuchs observed one species each of *Apis*, *Agapostemon*, *Melissodes* and *Bombus*. Near St. Louis I have observed *Bombus*.

According to the observations made by Meehan, Robertson and myself, *C. Marylandica* is visited by *Bombus*. Pollen is collected only from the smaller upper stamens, the three lower ones serving the insect only as a supporting platform if at all. Flowers protected against insect visits do not produce fruits. The pollen from the large lower or the three smaller upper stamens, may effect fertilization, but whether there is a difference in the efficiency of that from the two kinds of stamens is not known.

In an unidentified species from Brazil related to *C. laevigata* Fritz Müller observed *Bombus violaceus* and species of *Centris* collecting pollen from the short, central anthers while the two long, lower anthers and similarly shaped pistil are so much curved as to strike with the anther tips and the stigma the dorsal surface of the abdomen of the visiting insect. The large, lower stamens are of the same color as the smaller, central ones and were observed to be visited extensively by small insects which despoiled them of their contents without effecting pollination: *Trigona elegantula*, *T. lilliput* and a large



species of *Augochlora*. *Trigona ruficrus* often bites the anther quite in pieces.

Burck considers that the floral mechanism of *Cassia* favors autogamy, basing his conclusions on the fact that in several species studied by himself the tip of the pistil returns to the median plane of the flower by a new curvature of the style so that it will not come in contact with the region of the insect's body previously supplied with pollen from the pores of the larger stamens, and that in others the stigma comes almost in contact with the tips of the stamens.

Burck's paper contains some interesting observations, but it seems that his conclusions can hardly be accepted without further investigation. For a more detailed comparison of his statements and conclusions, reference must be made to his own paper.

According to him, *C. glauca* differs from the other species in having coriaceous instead of indurated anther walls. The large bees — *Xylocopa* and *Bombus* — which visited this, and other species observed by him, alight in the middle of the flower and "devour the grains of pollen" of the five short stamens or they may destroy in part or entirely both the anther walls and the pollen. Only the two large stamens remain intact and undespoiled of their pollen. Knuth's observations on *C. Horsfeldii*, considered by some a synonym of *C. glauca*, confirm Burck's observations on this point. The bee flies directly towards the small stamens, grazing but rarely the large anthers; when these are touched, it is with the ventral surface of the body. He never saw the stigma in contact with the body of the visiting insect but thinks that this might occur, especially at the moment when the insect leaves the flower. But even then, the chances are that the dorsal surface of the insect's body, rather than the ventral surface to which the pollen adheres, will touch the stigma.

The significance of the elongation of these lower anthers



is, he thinks, their protection from the insect visitors. According to the observations of O. Schmiedenknecht this species in the garden at Buitenzorg is visited principally by species of *Ceratina*. *C. bacilluris* has indurated anthers, so that, according to Burck, the insect can secure pollen only by inserting its proboscis into the terminal pores. Knuth speaks of the anthers being so completely milked out that only a few grains remained. In the Buitenzorg garden, 4 species of *Xylocopa* and unidentified Syrphidae were observed as visitors.

*C. alata* has been described by Burck, Lindman, Ducke, and Knuth. Lindman saw large and small bees visiting this form in large numbers. He states that in this species, as also in *C. aculeata*, the large anthers sometimes contained no pollen even in the bud. Ducke saw at Para and Macapá, 4 species of *Centris*, 3 of *Xylocopa* and 4 of *Euglossa*. At Buitenzorg, *Ceratina* was the principal visitor observed.

Some of the species studied by Knuth at Buitenzorg have already been mentioned. We may summarize his observations on the other species by saying that he usually found only *Xylocopa* as a visitor. In rare cases he observed *Podalirius zonatus* and *Megachile opposita*. *Centris* and *Euglossa* do not occur there. O. Schmiedenknecht also observed several species of *Ceratina* on *Cassia* flowers at Buitenzorg. Knuth thinks that cross fertilization is favored since the projecting stigma will be touched first by a visiting insect. In all cases supplementary self-pollination may occur when the flowers are visited by bees, but spontaneous autogamy he considers possible only in the species with small flowers which close after a time, bringing the stigma into immediate contact with the anthers. In St. Louis, I have taken *Bombus* and smaller bees collecting pollen from *C. sophera*.

According to Müller, *C. multijuja* at Blumenau, South Brazil, is visited by *Xylocopa artifex* and another large,



apparently undescribed species, and by *Centris lineolatus*.

Trelease saw *C. obtusifolia* visited by *Bombus* in central Alabama.

Schrottky observed *Centris discolor* regularly collecting pollen on *C. splendida* at S. Paulo, Brazil. Here he also saw species of *Centris* collecting the pollen of *C. bicapsularis*.

At Para, Ducke observed on *C. Hoffmansegii* and other species with very large flowers, *Xylocopa*, *Centris*, and *Euglossa*.

In Chile, Johow saw *C. closiana* visited by *Bombus chilensis*.

In Chile, Darwin saw a *Mimus* with its head yellow with pollen, from, as he thought, a *Cassia*. Delpino records *Cassia* (?) as visited by *Nectarinia platura*. Fries once observed *C. bicapsularis* visited for insects by *Chlorostilbon auriventris*. He found the species regularly visited and pollinated by *Bombus carbonarius*.

Our knowledge of forms other than *Solanum* and *Cassia*, is, so far as direct observations are concerned, very fragmentary. Brown studied the flowers of *Labichea lanceolata*, and, finding the same right- and left-handed arrangement as in *S. rostratum*, concluded that the method of pollination is the same. It can hardly be doubted that the other forms of the Cassieae are, at least for the most part, dependent upon the larger pollen-collecting bees for their fertilization.

On the ecology of the Mayacaceae and Rapateaceae no observations have been published.

Of the floral ecology of the Commelinaceae under consideration we are quite ignorant. I have been able to examine living material of one species of *Dichorisandra* and to convince myself that there is no secretion of nectar. The ecology of the flowers of some genera of the family is quite well known, and comparative evidence makes it very



probable that most of the Commelinaceae are without nectar and are visited by pollen-collecting bees.

Before leaving this subject, I will refer briefly to the anomalous *Cochleostema*. It is the most magnificent member of the Commelinaceae, with flowers two or two and one half inches in diameter, sepals and petals highly colored and patent, androecium of six elements in two whorls, fertile stamens 3, 1 from outer and 2 from inner whorl, forming a pedicelled staminal column with the anthers all spirally twisted and dehiscing longitudinally; one horizontal at the base of a corniform hood formed by involute, petaloid outgrowths from the other two which inclose all three stamens.

The habit of this most complex flower is almost exactly identical with that of some of the zygomorphic, apically dehiscent forms, as for instance, *S. rostratum*, the form of the perianth and the position of the pistil being the same and the staminal hood simulating almost exactly the arcuate anther. Loew and Appel in Knuth's Handbuch devote considerable space to a discussion of this remarkable plant and I shall add the further suggestion that the fragrant, nectarless flowers may be adapted to the larger Apidae which seek the hairs of the staminodia or other juicy portions of the flower and effect pollination in the same way as in apically dehiscent forms.

When I first saw a habit figure of *Cochliostema* I thought it an apically dehiscent form with one large anther similar to *S. rostratum*. If the suggestion just offered prove the right one, we have a most remarkable case of parallel adaptation.

Nothing is known of the pollination of *Monochoria*. *Pontederia* is visited for nectar and sometimes for pollen by large bees. *Heteranthera* has been described as a pollen flower. The secretion of nectar is not abundant if it occurs at all in *Eichornia*, at least when grown in the north. On *E. azurea*, Müller observed only bees belonging to the



genera *Melipona* and *Anthophora*. I am inclined to believe that in *Monochoria* we have a highly developed pollen flower, connected by various stages with other members of the family showing a deep nectar bearing tube.

In the Liliaceae, all forms of which, with the exception of the aberrant *Odontostomum*, belong to the Solanum-Cassia type, zygomorphy is not so pronounced as in several other families, the Amaryllidaceae for instance, apparently only *Agrostocrinum* having a zygomorphic habit. The flowers are all of a good size and usually highly colored, the anthers quite often in sharp contrast with the perianth. Thomson states that *Luzuriaga parviflora* has white, fragrant pollen flowers! Delpino considers *Dianella coerulea* and other species as pollinated in the same way as *Borago* or *Solanum*.

In the Amaryllidaceae, direct observations are wanting, but the zygomorphic condition of *Zephyra* and *Tecophilea* and especially of *Cyanella* indicate ecological relations similar to those of the zygomorphic Solanums or Cassias.

Nothing is known of the ecology of the two representatives of the Pittosporaceae considered, but their structure is so similar to species which are well studied biologically that there can be little doubt as to their insect visitors. The little that is known of other genera indicates a wide difference in the insect relations of the typical and the aberrant members of the family.

The Tremandraceae are doubtless entirely dependent upon pollen-collecting bees for cross fertilization. This cannot be said with the same confidence of the Sterculiaceae considered above, but from the structure of some of the forms it seems not improbable that they are visited and pollinated in the same manner as *Solanum* or *Borago*.

Gilg considers that in the absence of direct observation it is to be assumed without question that the flowers of the Ochnaceae are insect pollinated. The magnificent flowers, the zygomorphic disposition of the anthers in some species,



especially the peculiar condition of the anthers connate in masses in *Luxemburgia*, and the pleasant odor observed for others (the odor of violets in *Schuurmansia Henningsii*) all speak strongly in favor of this conclusion. Visitors are recorded for but one species. Ducke observed *Xylocopa barbata* visiting the flowers of an unidentified *Ouratea*.

Of the method of pollination of the Dipterocarpaceae we know nothing, and can only surmise from the structure of the flowers. The same is true of the Flacourtiaceae under consideration.

Nectar has never been demonstrated in the showy but usually odorless flowers of *Begonia*. Warburg noticed numerous small insects visiting the flowers in their native habitat. On an undetermined Javan species Knuth observed *Apis*, *Bombus* and *Podalirius* (presumably collecting pollen.)

Of the Myrsinaceae and Loganiaceae in question we know nothing.

Mr. J. C. Willis, Director of the Royal Botanic Gardens, Peradeniya, kindly sends me the following note on *Exacum* of the Gentianaceae: "The only Melastomaceae I have actually seen pollinated yet are our common big pink Osbeckias, which are visited by the big carpenter bee, *Xylocopa*, sp., apparently for pollen. The bee pollinates our big blue *Exacum macranthum*, which looks just like a Melastomaceae. It squats down on the flowers and bunches up the stamens with its legs, and must get lots of pollen jerked out of the apical pores onto its body. In fact I have usually found flowers visited by it to have the stigmas well pollinated, and have hardly ever seen any other insect visit them at all. There is little or no honey, so far as I have noticed, in these flowers or in those of Melastomaceae."

*Solanum* has been discussed above. I have been able to examine one species of *Cyphomandra* in a living condition. There appears to be no free nectar. The walls of



the anthers are thin and elastic so that the pollen is ejected by a bellows-like action as in some Melastomataceae.

Of the Rubiaceae we know nothing.

#### ECOLOGY OF MELASTOMATACEOUS TYPE.

As one glances over the icones of the numerous genera he is impressed with the high degree of organization and the splendid colors, often heightened by the marked contrast between the androecium and the perianth, of the flowers of the Melastomataceae. The natural conclusion is that these represent forms dependent in high degree upon insect visitors. It is very disappointing that our knowledge of the floral ecology of these forms is so meager.

Ule remarks: "In vielen Fällen scheint es bei den schönblühenden Melastomaceen nur darauf anzukommen, dass die Staubgefässe in Bewegung gesetzt werden, und deshalb stehen sie auch noch auf einer niederen Stufe der Anpassung an Insektenbesuch. Der Mangel an Insekten, welche die Blüten der Melastomaceen aufsuchen, verursachte wahrscheinlich das intensive Farbenkleid mit dem viele die Gegenden zu Zeiten schmücken, wie es keine andere Pflanzenfamilie in Brasilien thut. Ich erinnere hier an andere auffallende und grosse Pollenblumen, wie z. B. *Papaver*, *Tulipa*, *Rosa*, etc." Ducke says of the family at Para: "Es ist auffallend, dass diese hier so artenreiche Familie nur sehr wenig von Apiden besucht wird; höchstens findet man ab und zu *Halictus* an diesen Blüten. Nur eine baumartige Melastomacee sah ich hier öfters von Hummeln (*Bombus cayenensis*) umschwärmt."

Leggett first described the bellows-like action of the stamens of *Rhexia Virginica* and observed *Bombus* visiting the flowers. Unfortunately he does not state whether nectar is present. According to Bailey the pollen of *Heterocentron roseum* is ejected in the same way. According to Müller and Forbes certain species of *Melastoma* and *Heeria* agree in the essentials of their floral mechanism.



The flowers need not be described here in greater detail than to state that the larger lower anthers are of the same color — violet or red — as the vertical patent corolla, against which the shorter, bright yellow, central stamens form a striking contrast. Müller observed only a small fly (Syrphidae) collecting pollen from the yellow anthers and *Trigona ruficrus* visiting first the small anthers and then often the larger ones, offering a more generous pollen store, as well, working on them with their mandibles and often devouring them entirely. Forbes speaks of the pollination of such forms as follows: “I have witnessed in many instances the visitation by various species of large Hymenoptera, such as *Xylocopa* and *Bombus*, of species especially of the genus *Melastoma*, possessing stamens in all points corresponding to that occurring in the *Heeria* described in the letter referred to, and what takes place seems to be as follows. The large bees evidently make for the yellow platform offered by the short stamens, perhaps because they do not perceive the pistil and long stamens owing to their projection against the broad petaled corolla of the same color in the background, and invariably receive the pistil between their legs, their feet settling on the fork of the connective, the instant effect of which is to collect the whole of the long stamens into a bunch, and to depress their anthers downwards and away from the body of the visiting bee, while the pistil remains in constant contact with its ventral side. At the moment of the bee's departure the hooks on the bee's feet by pulling on the connective fork, raise the anthers of the long stamens, so as to bring the tips of the collected bunch into contact with its sides and abdomen. Dr. Müller's statement ‘by moving the connective fork of the larger ones’ is somewhat ambiguous; for it is movement only in one direction that is of avail in *raising* the anthers of the larger stamens, pressure at the connective hook of course tends to depress the anthers and keep them apart from the



bee's abdomen while a very slight backward pull at once raises the anther."

Forbes and Burck were able to detect differences in the pollen of the two types of stamens. "The pollen from the short stamens was large and three-cornered, while that of the longer ones was very much smaller and of a more oval shape; and while both forms were found on the pistil, only the pollen from the long stamens seemed to be fertile. We could not detect any of the short-stamened pollen with tubes opened." In a later paper Forbes records *Bombus senex* as a visitor. In his paper on division of labor in the stamens of pollen flowers, Müller records further observations by his brother in which incipient stages of the color dimorphism were observed in a melastomataceous genus, probably *Pleroma*. The significance of color dimorphism has already been alluded to under the *Solanum-Cassia* type.

Ule studied some species of *Tibouchina* for comparison with *Purpurella*. The visitors of these flowers with splendid colors he found relatively few while they were much more active on the inconspicuous flowers of *Croton*, *Spermacoce*, *Sida*, etc., growing near by. Butterflies, flies and birds do not visit these forms which secrete no free nectar but offer only pollen difficult of collection which various pollen-collecting Hymenoptera are able to gather. The pollen is not so dry as in *Purpurella* but a little sticky. A few times he saw humble-bees visiting the flowers, and once he was able to examine in detail the action of one on a shrub of *T. Moricandiana*, "die immer schnell den Kopf noch dem Mittelpunkt der Blüten steckte und bald einen Strauch abgeernt hatte. Warscheinlich fängt sie so den ausspritzenden Blütenstaub in den Haaren auf und kann dann leicht Fremdbefruchtung erzeugen. Häufiger sind kleine und winzige Bienen, welche die dünne, gefaltete Antherenhaut durchnagen und so den Pollen einsammeln, wie ich mich öfter überzeugt und sogar die



Bienen mit ihrem pollenbeladenen Höschen eingefangen habe. Bei dieser Arbeit verweilen diese Bienen allerdings längere Zeit in jeder Blüthe." Another group of insects attack the stamens and sometimes devour them entirely, and he often found large wasps on the flowers of *T. gloriosa*, while in this class are also to be placed Coleoptera, as species of *Cytonia* and *Buprestis* which are especially to be sought in the handsome flowers of the Melastomataceae. The attractiveness of the stamens for insects and the secretion of nectar by these organs in *Purpurella* led to a microscopic examination of these parts of *T. gloriosa* with the demonstration of an abundance of sugar which, however, is never excreted in visible form. In many species of *Tibouchina* a pronounced change in color in different ages of the flower is demonstrable, and of this several examples are given.

A note from Mr. Willis on the pollination of the Melastomataceae and *Exacum* has been quoted above under the Solanum-Cassia type.

From the detailed discussion by Lagerheim, *Brachyotum ledifolium* seems to be adapted to pollination by birds. The depth of the nectar and the size of the opening in connection with the consistency of the perianth and the position of the flower tend to exclude insect pollinators with the exception of the Sphingidae, and these are hardly to be considered on account of the lack of perfume in the flowers and the insufficiency of a soft proboscis for the ejection of the pollen from the anthers. As visitors he observed *Rhamphomicron herrani* and *Metallura tyrianthina*. These inserted their beaks into the small opening of the flower for the purpose of obtaining insects or nectar secreted by the filaments and forced a puff of pollen from the bellows-like anthers by pressing them with the tip of the beak. By pressing the elastic anther wall with a rounded match the pollen may be ejected for a distance of three centimeters, after which the wall assumes its original



position and the pollen collects in the small portion of the anther until by repeated compressions it shall all have been ejected. The stigma projects beyond the anthers and so is first touched by the visiting bird. Presumably other species of the genus are also ornithophilous, but *B. Benthamianum* would seem from the floral structure to be dependent upon bees for pollination.

Very interesting observations were made by Burck upon *Memecylon edule* var. *ramiflorum*. He describes the prominent, active, yellow nectary on the dark violet connective spur. He finds the flowers well protected from a large destructive ant by smaller ones which secure nectar secreted from the outside of the calyx tube, but not from the staminal glands. As pollinators he found small, active flies such as are concerned in the pollination of *Aristolochia*. These flies do not seem to fear the ants and he suggests that after the flower had developed in adaptation to bee visitors, these found the more recently arriving ants uncongenial, and upon their desertion of the plant another adaptation to insects of a very different type became necessary and then the recent staminal nectaries arose.

As pointed out in the descriptive portion of this paper, the disposition of the petals in the Melastomataceae is very rarely campanulate. One such form, *Brachyotum*, has been described above. In *Purpurella cleistopetala* from the Serra do Itatiaia of Brazil, as described by Ule, the flowers never open. The discussion of structural points need not be repeated here. He at first suspected that *Bombus* was the insect concerned in pollination, but repeated observations revealed only a small ant covered with pollen. A larger species of ant destroys the flowers. Other forms found in the mountains, as *P. hospita*, have pendulous campanulate flowers.

According to Darwin *Centradenia floribunda*, *Rhexia glandulosa*, *Monochaetum ensiferum*, *Heterocentron Mexicanum* and species of *Pleroma* are self sterile or but rarely



produce fruit when left to themselves, but produce seed abundantly when artificially self-fertilized.

Little is known of forms outside the type family. Ducke observed *Centris* and *Xylocopa* visiting the magnificent golden yellow flowers of *Cochlospermum* (= *Maximiliana*) *insigne* but nothing is recorded concerning the objects of the visits.

#### RECAPITULATION.

Summarizing this section, we may say that our knowledge of the ecology of these forms is far from satisfactory. Our acquaintance with the ecological relations of the Dillenaceous type justify no conclusions, but for the Solanum-Cassia and the Melastomataceous types nearly all the direct observations which we have and the entire mass of comparative data indicate adaptation to the Apidae and among these, for the most part, to those which are active in the collection of pollen. The absence of nectar practically limits the range of visitors to pollen-feeding flies and pollen-collecting Apidae. The evidence for adaptation to the latter is very great. As to the origin or method of evolution of these types of adaptation, our evidence will not justify any conclusions, but of the reality of their existence, we may have a high degree of confidence.

We must now leave this phase of the subject which I hope to take up briefly again after considering the data of two other sides of the problem.

#### THE GEOGRAPHICAL DISTRIBUTION OF APICALLY DEHISCENT FORMS.

In the introduction to this paper, it was suggested that the flora of certain regions is richer in apically dehiscent forms than is that of others. The examination of this hypothesis was one of the principal objects of the investigations described.

The Solanum-Cassia type seems to be the one best adapted for a first study of this question.



Of the Monocotyledons one family, the Rapateaceae of 6 genera, is endemic in tropical South America. *Mayaca* has 8 of its 10 species there. Of the two apically dehiscent Commelinaceae, the genus in which dehiscence by pores is most perfect is endemic in tropical South America, as is also the highly interesting *Cochliostema*. In the Liliaceae and Amaryllidaceae, 4 of the 8 apically dehiscent genera are endemic in extratropical South America.

Thus, 11 of the 19 genera of the Monocotyledons are endemic in South America and another has 8 of its 10 species there.

Turning now to the Dicotyledons, we find that of the 40 genera, 11 are endemic in South America and 7 others occur there.

In the Monocotyledons, then, 57.8 per cent of the genera are endemic in South America, another has 8 of its 10 species there, while the two others may possibly have been derived from the same region; 63.1 per cent of the apically dehiscent monocotyledonous genera occur in South America. Among the Dicotyledons, we have 27.5 per cent endemic in South America and 7 more genera have some of their species, and in five cases the most of their species, in South America. Together, 18 of the 40 apically dehiscent genera of Dicotyledons are represented in South America, or 45 per cent.

Taking both Monocotyledons and Dicotyledons, we have 30 of the 59 genera assigned to this type represented in South America, or 50.8 per cent.

These genera contain from one to over nine hundred species; in some, all of the species are apically dehiscent, while in others, as in *Begonia* of about 400, and *Ardisia* of about 200 species, only a few species are apically dehiscent. To this question of the geographical distribution of species, we shall recur later. Here we may merely note that *Solanum* has about 700 of its 970 species in



South America, while *Cassia* has about 300 out of 412 in the same region.

In comparison with the above forms the distribution of the Melastomataceae is of great interest.

The family belongs to the tropical zone but is also represented in the subtropical, occurring between 30° N. and 40° S. Latitude. The family reaches its highest differentiation in tropical America where 6 (I, IV, V, VII, X, XI) of the tribes are exclusively found, 1 more (III) occurs in South America and extratropical North America, and another (XV) is found in tropical America, the Antilles, islands of the Pacific Ocean and tropical Africa. The other 7 are confined to the Old World. The tropical American tribes include 95 genera and three more are added by the two tribes of more general distribution while the single genus (*Rhexia*) in North America brings the number of American genera up to 99, with about 2,000 species all but 7 of which occur south of the United States (in this included the species of the Antilles) as compared with 62 genera with about 700 species from the remainder of the range. It is of interest to note that in the Memecyleae (Tribe XV), the only South American tribe occurring elsewhere, the dehiscence in the South American genus (*Olisbea* is by some regarded as merely a section of *Mouriria*) is by short slits which in many cases much resemble pores while in the other genera it is described as by longitudinal slits. Of this tribe there are 44 American and 101 Old World species. It will be noticed that in the tribes showing dehiscence by longitudinal slits (XII, XIV, XV) 2 genera with 44 species are American while 10 genera with 156 species are found elsewhere.

These figures are certainly suggestive, and seemed more so when it was found that the Apidae, the insects of the greatest importance in the fertilization of these forms, are strongly represented in South America, India and Austra-



lia. I resolved to carry out, so far as the nature of the data might permit, a statistical investigation of the problem.

At the present time, the importance of statistical methods is being emphasized by many writers. In floral ecology, attempts have long been made, and very successfully, too, in many cases, to estimate exactly the relative importance of each class of visitors in the evolution of a given flora. The problem at present in hand differs essentially from those which have preceded it in that it is an attempt to separate certain floral types and estimate their relative numerical importance in any flora.

The difficulties encountered are very great and the result obtained with the present material is not wholly complete. The following is the method employed and the results it has yielded.

The first requisite was the determination of the distribution of the apically dehiscent forms.

For the sake of convenience, the earth was divided into fourteen regions. It hardly need be remarked that in the present state of our knowledge any division into great and sharply defined phytogeographic regions is purely artificial and intended to serve merely as a convenience for further study. Fourteen divisions were recognized, since, after careful consideration, it seemed best to adopt so far as possible the floristic regions of Drude.

It was deemed best to have the regions represent, so far as possible, systematic rather than ecological units. It should be remembered that my own data had no influence in the selection of the divisions to be used. The principal need which led to the employment of a series of regions was the desirability of making a statistical comparison of the percentages of apically dehiscent genera belonging to the various types in the several floras. To facilitate tabulation, I have modified the regions as outlined by Drude by making their limits conform to geographical, or, in some cases, even political boundaries. Without this precaution,



it would hardly have been possible to gain any numerical idea of the relative frequency of the various forms as compared with the other members of the floras. These modifications have seemed perfectly justifiable in view of the purpose which the regions are to serve.

The divisions have been limited as follows: —

#### I. TROPICAL REGIONS.

1. TROPICAL AFRICAN REGION. Arabia and the continent of Africa south of the Tropic of Cancer to Cape Colony, South Bechuanaland, South African Republic, Basuto Land, and Cape Colony; also Sokotra Island.
2. EAST AFRICAN ISLAND REGION. a, Madagascar; b, Mascarin Islands and Rodrigues; c, Seychelles Islands.
3. INDIAN REGION. Western and eastern peninsulas of India and all islands lying between 17° N. lat. and the Tropic of Capricorn.
4. TROPICAL AMERICAN REGION. a, Brazil, Uruguay, Ecuador; b, Guiana, Venezuela, Colombia, Central America; c, Antilles and Bahamas; d, Mexico and Southern California.

#### II. AUSTRAL REGIONS.

5. SOUTH AFRICAN REGION. Continental South Africa south of the tropical region, and the island of St. Helena.
6. AUSTRALIAN REGION. Australia and Tasmania.
7. AUSTRAL AMERICAN REGION. Argentina, Chile, Patagonia and Tierra del Fuego.
8. NEW ZEALAND REGION. The island.
9. ANTARCTIC REGION. Land masses lying south of the above austral regions.

#### III. BOREAL REGIONS.

10. MEDITERRANEAN-ORIENTAL REGION. The Atlantic Islands (Canaries to Azores), Africa and Arabia north of the tropical region (Tropic of Cancer), Spain, Italy, Turkey in Europe and Asia, Transcaucasia, Persia, Baluchistan, Afghanistan, and the lands included by the outer limits of these.
11. CENTRAL ASIAN REGION. Turkestan, Mongolia and Tibet.
12. EAST ASIAN REGION. China, Manchuria, Korea, and Japan except Sakhalin Island.
13. CENTRAL NORTH AMERICAN REGION. Roughly commensurate with the United States.
14. NORTHERN REGION. Land masses of Europe, Asia and America above the limits of the four boreal subtropical regions described above.



It is evidently of great importance to ascertain just what per cent of the total number of plants known is to be found in each of these regions. The per cent of apically dehiscent forms occurring there can then be compared with this and it may be readily seen whether it is relatively greater or less than in other regions. A difference in the number of genera with a given floral habit in two floras which are being compared has little significance if the relative number of genera in the two floras varies in the same ratio. There must be some basis for comparison; the general conditions of life permit of a greater differentiation in some regions than in others of the same area and the extent of this differentiation must be known to serve as a basis for comparisons of the development of particular elements.

Being unable to find any suitable statement of the relative richness of the floras of different areas it became necessary to tabulate them especially for the present purpose. A comparison by species would probably be the most satisfactory, but it soon became evident that this presented too many difficulties. I therefore decided to tabulate the genera only and to take the data for this purpose from *Die Natürlichen Pflanzenfamilien*.

In the preparation of these tabulations the 8,541 genera of flowering plants were first set down in order followed by the numbers of the regions in which they occur. These were then summarized by families, the number of genera endemic and occurring in each region being indicated.

I present in Table A a summary of the distribution of all of the flowering plants arranged according to regions. In the first column is given the number of the several regions, in the second the number of endemic genera and the per cent which this is of the total number of genera of flowering plants, in the third column the number of genera occurring but not endemic, and in the fourth column the



total number of genera occurring and the per cent which this is of the whole number of plants.

TABLE A.

## ALL GENERA OF FLOWERING PLANTS.

Region.	Endemic.	Others.	Total.
1	542 = 6.34%	1116	1658 = 19.41%
2	259 = 3.03%	579	838 = 9.81%
3	1126 = 13.18%	1344	2470 = 28.91%
4	1968 = 23.04%	1160	3128 = 36.62%
5	394 = 4.61%	468	862 = 10.09%
6	444 = 5.19%	712	1156 = 13.53%
7	175 = 2.04%	506	681 = 7.97%
8	23 = .27%	187	210 = 2.45%
9	4 = .04%	21	25 = .29%
10	455 = 5.32%	819	1274 = 14.91%
11	68 = .79%	549	617 = 7.22%
12	171 = 2.00%	846	1017 = 11.90%
13	335 = 3.92%	871	1206 = 14.12%
14	73 = .85%	654	727 = 8.51%

The second table, B, gives the number and the per cent of the 59 genera of the Solanum-Cassia type endemic and occurring in the several regions.

TABLE B.

## GENERA OF SOLANUM-CASSIA TYPE. DISTRIBUTION.

Region.	Endemic.	Others.	Total.
1	2 = 3.38%	8	10 = 16.94%
2	1 = 1.69%	7	8 = 13.55%
3	7 = 11.86%	9	16 = 27.11%
4	17 = 28.81%	9	26 = 44.06%
5	2 = 3.38%	3	5 = 8.47%
6	12 = 20.33%	6	18 = 30.50%
7	4 = 6.77%	4	8 = 13.55%
8	.....	2	2 = 3.38%
9	.....	..	..
10	.....	2	2 = 3.38%
11	.....	2	2 = 3.38%
12	1 = 1.69%	4	5 = 8.47%
13	.....	4	4 = 6.77%
14	.....	1	1 = 1.69%



A comparison of the per cents of this table with those of the one representing the distribution of all of the flowering plants is facilitated by subtracting the per cent of all genera in a region from the per cent of apically dehiscent forms and so indicating the relative abundance of the latter in plus and minus quantities, as in Table C.

TABLE C.

GENERA OF SOLANUM-CASSIA TYPE. RELATIVE ABUNDANCE.

Region.	Endemic.	Total.
1	— 2.96	— 2.47
2	— 1.34	+ 3.74
3	— 1.32	— 1.80
4	+ 5.77	+ 7.44
5	— 1.23	— 1.62
6	+ 15.14	+ 16.97
7	+ 4.73	+ 5.58
8	— .27	+ .93
9	— .04	— .29
10	— 5.32	— 11.53
11	— .79	— 3.84
12	— .31	— 3.43
13	— 3.92	— 7.35
14	— .85	— 6.82

This reveals some suggestive points. In all regions except 4, 6 and 7, the per cent of apically dehiscent genera endemic is below that of all forms endemic in the same region. In all regions except 2, 4, 6, 7 and 8, the per cent of all apically dehiscent genera found is lower than that of other forms occurring in the same regions. In regions 4, 6 and 7, the average relative abundance of endemic apically dehiscent forms is 8.54 more than the average for the whole number of endemic forms while in the other eleven regions it is 1.66 less. For the apically dehiscent genera occurring in regions 4, 6 and 7 the average is 9.99 above while for the other eleven regions it is 3.22 below that of all genera occurring.

The great specific differentiation of *Solanum*, *Cassia* and



of many melastomataceous genera in tropical America first called my attention to the problem of the geographical distribution of these floral types.

It would appear that in general the most satisfactory statistical comparison of the floras of two or more regions is to be made not on the basis of genera but of species.

While this proposition would seem to hold for general comparisons of floras, we have in the present problem a special case in which the morphological differentiation of certain organs of the species entering into the composition of the floras rather than the taxonomic differentiation of the floras as a whole is to be considered. The comparison in this case should be based upon morphological rather than taxonomic units, but it becomes at once clear that it is quite impossible to separate the two conceptions.

I think that on the whole the special data which we seek are furnished by the characteristics of genera rather than by the peculiarities of species. In the limitations of the former, the floral organization has been assigned a more important place than in the separation of the latter where the vegetative features are usually more minutely studied and described. But even if all species of a genus have an identical floral structure it must not be forgotten that specific differentiation may permit of adaptation to more varied environmental conditions and so increase the relative importance of the genus as a constituent of the flora where the area under consideration is so large as to present a multiplicity of conditions.

In a comparison which embraces ecological considerations, as the present one does, there is one strong objection to taking the number of genera as data. In ecological comparisons, dominance is obviously of much significance. In floral ecology where the anthophilous fauna is the environment, one species may have characteristics which enable it to secure more visits than a dozen others. It is obviously incorrect to present merely a numerical statement of the



relative number of genera or even species represented in a region as indicative of the ecological conditions prevailing there. Only direct field observations of the fauna and flora will yield the exact data requisite for a satisfactory solution of the problem of the mutual interdependence of the distribution of floral structures and the organic environment to which they are adapted. Even these field studies cannot lay before us the past history of the species or structures in question and our knowledge must always lack the exactness of some other phases of biological investigation. These limitations notwithstanding, we should attempt to bring our knowledge to the greatest exactness possible. The broad outlines of a problem are often obscured for the naturalist in the field by the details of his observations and must be formulated by the worker in the herbarium and library.

I have been unwilling to forego an attempt at a comparison of the several regions by species. The difficulties in the way of such an undertaking are known only to those who have made a similar attempt. In the very beginning of the present study, it became evident that a comparison of the regions by per cents of the apically dehiscent species in the flora was quite out of the question, and even a comparison by genera, rough and unsatisfactory as it is, has required many months more than was originally anticipated.

The accompanying table, D, is a summary of the number of species of the Solanum-Cassia type occurring in each region and the per cent of the total number of apically dehiscent species of this type known, 1,827.



TABLE D.

SPECIES OF THE SOLANUM-CASSIA TYPE.

Region.	Species.	Region.	Species.
1	107 = 5.85%	8	2 = .10%
2	42 = 2.29%	9	.....
3	163 = 8.92%	10	40 = 2.18%
4	1142 = 62.50%	11	4 = .21%
5	37 = 2.02%	12	13 = .71%
6	186 = 10.18%	13	29 = 1.58%
7	100 = 5.47%	14	5 = .27%

This table shows that tropical America has 62.5 per cent of all the apically dehiscent species of the *Solanum-Cassia* type, the Indian region 8.9 per cent, the Australian region 10.1 per cent, the extratropical American region 5.47 per cent, while the other ten regions average but 1.52 per cent.

*Solanum* and *Cassia* comprise 1,382 of the 1,827 species of the foregoing tables. Anticipating the suggestion that the great differentiation of *Solanum* and *Cassia* in tropical America may account for the very high percentage of apically dehiscent species found there, I have given in Table E the distribution in numbers and per cents of all the apically dehiscent species except those of these two genera and, for comparison, have figured the per cents of these genera occurring in each region.



TABLE E.

SPECIES OF SOLANUM AND CASSIA COMPARED WITH OTHERS OF SAME TYPE.

Region.	Solanum.	Cassia.	Others.
1	5.98%	6.55%	22 = 4.94%
2	1.34%	2.43%	19 = 4.26%
3	7.22%	8.49%	59 = 13.25%
4	64.85%	70.39%	223 = 50.11%
5	2.68%	.73%	8 = 1.79%
6	5.36%	8.01%	101 = 22.69%
7	7.53%	4.13%	12 = 2.69%
8	.10%	.....	1 = .22%
9	.....	.....	... ..
10	2.66%	3.39%	... ..
11	.....	.31%	1 = .22%
12	.82%	.49%	3 = .67%
13	1.44%	2.67%	4 = .89%
14	.52%	.....	... ..

The similarity of these per cents is very striking, and, as it seems to me, significant.

For comparison with this I had selected at random from the indices of the several phanerogamous volumes of *Die Natürlichen Pflanzenfamilien*, 330 genera, the distribution of the species of these tabulated and the average number of species per genus in each region obtained. These averages are based upon too small a series to be of great value for comparison, but an estimate of the number of species for each region made on the basis of the number of genera occurring and the average number of species per genus, as shown by the sample selected, indicates that there is not the wide difference in the floras in general that is shown by the special forms under consideration.

The evidence from the Solanum-Cassia type seems clear and unmistakable. We may now apply this method of comparison to the two other floral types considered in this paper.

To the Dilleniaceous type have been assigned 16 genera



represented by 376 species, found in ten of the fourteen regions as indicated in Table F.

TABLE F.

## DILLENACEOUS TYPE.

Region.	Genera.	Species.
1	4 = 25.00%	14 = 3.72%
2	2 = 12.50%	15 = 3.99%
3	10 = 62.50%	220 = 58.50%
4	6 = 37.50%	75 = 19.95%
5	1 = 6.25%	3 = .77%
6	6 = 37.50%	22 = 5.85%
7	1 = 6.25%	7 = 1.86%
8	2 = 12.50%	6 = 1.60%
11	3 = 18.75%	8 = 2.13%
12	3 = 18.75%	6 = 1.60%

It is unnecessary to compare the figures for this type with those for all plants. It will be seen that there is considerable similarity to the results obtained for the Solanum-Cassia type, but several points of difference may be in part due to the small number of genera and species assigned to this type.

The distribution of the Melastomataceae has already been considered in general terms. The distribution of the 152 genera assigned to the Melastomataceous type is shown in Table G.

TABLE G.

## GENERA OF MELASTOMATACEOUS TYPE.

Region.	Endemic.	Others.	Total.
1	13 = 8.55%	6	19 = 12.50%
2	8 = 5.26%	2	10 = 6.57%
3	22 = 14.47%	9	31 = 20.39%
4	96 = 63.15%	1	97 = 63.81%
5	3 = 1.97%	1	4 = 2.63%
6	.....	4	4 = 2.63%
12	.....	6	6 = 3.94%
13	1 = .65%	0	1 = .65%



These figures require no comment. The distribution of the species of the Melastomataceae, I have not figured. Cogniaux in his monograph of the family recognizes about 2,000 species from tropical America and 700 from Asia, Africa, Oceanica and Australia. The per cent of species in the fourth region is higher for this type than for any other, being roughly 73, while the remaining 27 per cent are found almost exclusively in the first, second and third regions.

Summarizing the distribution of the 227 apically dehiscent genera of all three types, we obtain the figures given in Table H.

TABLE H.  
SUMMATION OF GENERA, ALL TYPES.

Region.	Endemic.	Others.	Total.
1	16 = 7.04%	17	33 = 14.53%
2	9 = 3.96%	11	20 = 8.81%
3	34 = 14.97%	23	47 = 20.70%
4	116 = 51.10%	13	129 = 56.82%
5	5 = 2.20%	5	10 = 4.40%
6	13 = 5.72%	15	28 = 12.33%
7	4 = 1.76%	5	9 = 3.96%
8	.....	4	4 = 1.76%
9	.....	..	.....
10	.....	2	2 = .88%
11	.....	5	5 = 2.20%
12	1 = .44%	13	14 = 6.16%
13	1 = .44%	4	5 = 2.20%
14	.....	1	1 = .44%

THE GEOGRAPHICAL DISTRIBUTION OF THE APIDAE.

I was early impressed by the great number of Apidae, especially the larger species, occurring in South America. A preliminary tabulation of the tenth volume of Dalla Torre's Catalogus Hymenopterorum confirmed the impression derived from a casual examination of various special monographs, and the Apidae were then tabulated from this work according to the same regions as those used



for the plants. It hardly need be remarked that the regions recognized for the Apidae are identical with those used for the plants simply to facilitate comparison and not from any evidence derived from the classification or morphology of the former.

I present here in condensed form, in Tables I and J, a summary of the tabulations of the Apidae alone, and, by way of comparison, of all the genera of Hymenoptera (including Apidae) treated in Dalla Torre's voluminous work. These are arranged by regions in the same manner as the tabulations of the plants considered above.

To the Apidae belong 137 genera and to all Hymenoptera, including the Apidae, 2,407 genera.

TABLE I.  
GENERA OF APIDAE.

Region.	Endemic.	Others.	Total.
1	.....	25	25 = 18.24%
2	3 = 2.19%	11	14 = 10.21%
3	.....	23	23 = 16.78%
4	27 = 19.77%	37	64 = 46.71%
5	.....	17	17 = 12.40%
6	12 = 8.76%	22	34 = 24.81%
7	15 = 10.95%	24	39 = 28.46%
8	.....	4	4 = 2.91%
9	.....	.....	.....
10	4 = 2.91%	47	51 = 37.22%
11	.....	38	38 = 27.73%
12	.....	26	26 = 18.97%
13	4 = 2.91%	36	40 = 29.19%
14	4 = 2.91%	46	50 = 36.49%



TABLE J.

ALL GENERA OF HYMENOPTERA.

Region.	Endemic.	Others.	Total.
1	44 = 1.82%	173	217 = 9.01%
2	7 = .29%	85	92 = 3.82%
3	120 = 4.98%	268	388 = 16.12%
4	283 = 11.75%	462	745 = 30.95%
5	10 = .41%	122	132 = 4.51%
6	50 = 2.07%	186	236 = 9.80%
7	40 = 1.66%	130	170 = 7.06%
8	6 = .24%	45	51 = 2.10%
9	...	...	...
10	125 = 5.19%	383	508 = 21.10%
11	14 = .58%	92	116 = 4.40%
12	29 = 1.20%	130	159 = 6.60%
13	210 = 8.72%	631	841 = 34.94%
14	699 = 29.04%	729	1428 = 59.30%

Expressing the distribution of the Apidae as compared with that of the Hymenoptera in plus and minus quantities, we have the accompanying table, K.

TABLE K.

GENERA OF APIDAE. RELATIVE ABUNDANCE.

Region.	Endemic.	Total.
1	- 1.82	+ 9.23
2	+ 1.90	+ 6.39
3	- 4.98	+ .66
4	+ 8.02	+ 15.76
5	- .41	+ 7.89
6	+ 6.69	+ 15.01
7	+ 9.29	+ 21.40
8	- .24	+ .81
9	...	...
10	- 2.28	+ 16.12
11	- .58	+ 23.33
12	- 1.20	+ 12.87
13	- 5.81	- 5.75
14	- 26.03	- 22.81



Regions 3, 4, 6 and 7 average + 4.75 for endemic genera, while the remaining nine regions from which Hymenoptera have been recorded average — 4.06. Turning to the total number of forms occurring in the several regions we find that 3, 4, 6 and 7 average + 13.17, while the other nine regions average + 5.28.

Conclusions concerning the distribution of the Hymenoptera must be only tentative since the vast order has been very little investigated, even in its most highly specialized family, the Apidae. The distribution by species need not be discussed in this place.

The points of agreement of these several tables are too apparent to need further comment. To facilitate comparison, the distribution of plants and insects has been summarized in the form of percentage curves. A glance at the accompanying diagrams, L and M, will make clear the relative proportion of the different elements in the flora and fauna and show the striking similarity between the distribution of the apically dehiscent genera and the Apidae. In this series of curves, the fourteen ordinates represent the fourteen regions, and the percentage of plants or insects endemic or occurring in a given region is indicated on these by the curves. A is the curve for the apically dehiscent forms, B for all genera; a for the Apidae, and b for all Hymenoptera. The high percentage of Apidae and other Hymenoptera in regions 10 to 14 is doubtless to be accounted for by the greater thoroughness with which these regions have been studied.

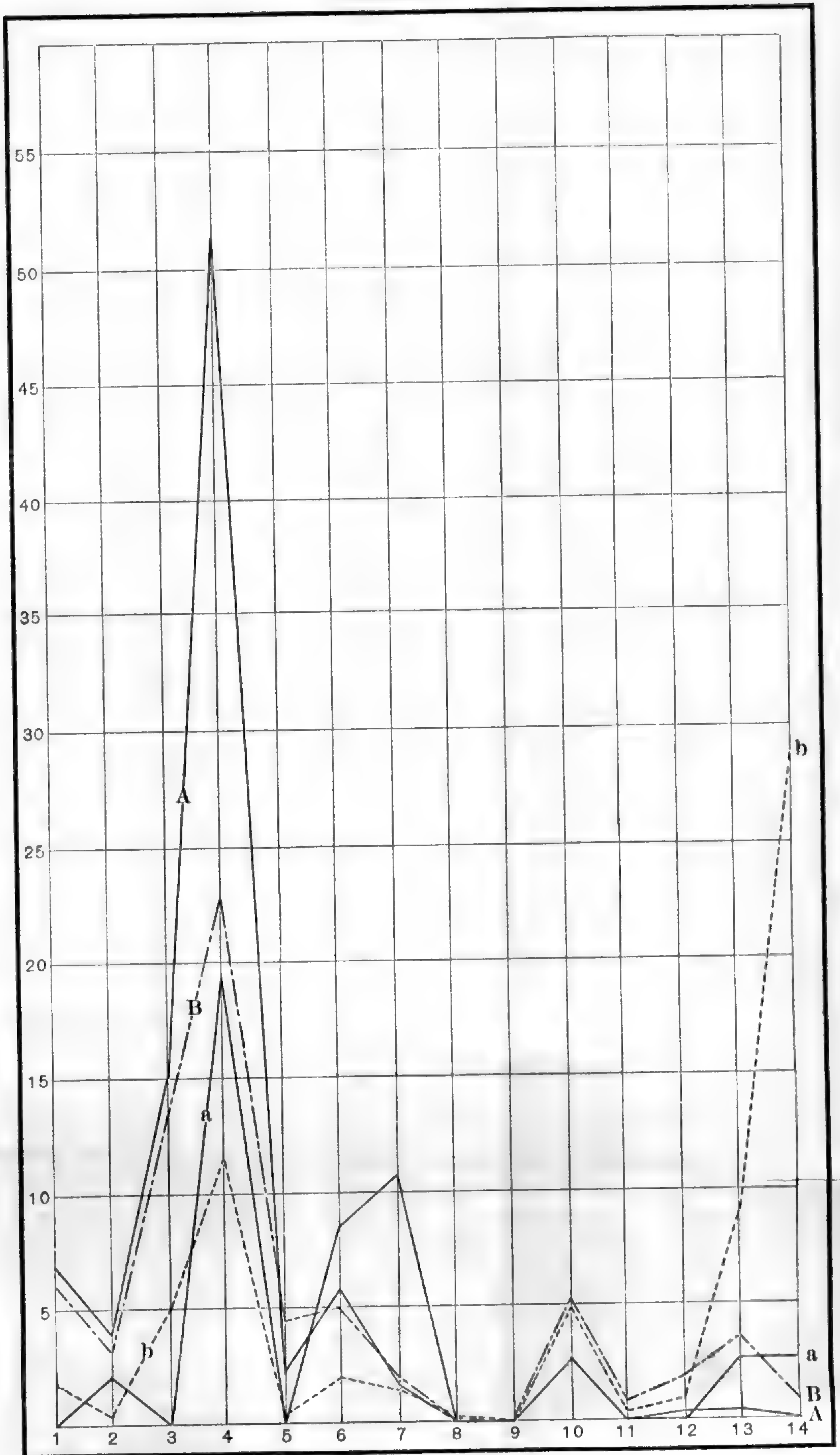
#### COMPARISON OF DISTRIBUTION OF FAUNA AND FLORA.

We seem to have in the data which have just been presented strong indications of a direct relation between the geographical distribution of the Apidae and that of the floral types which we have studied.

It is somewhat surprising that so little has been done towards the investigation of the distribution of floral



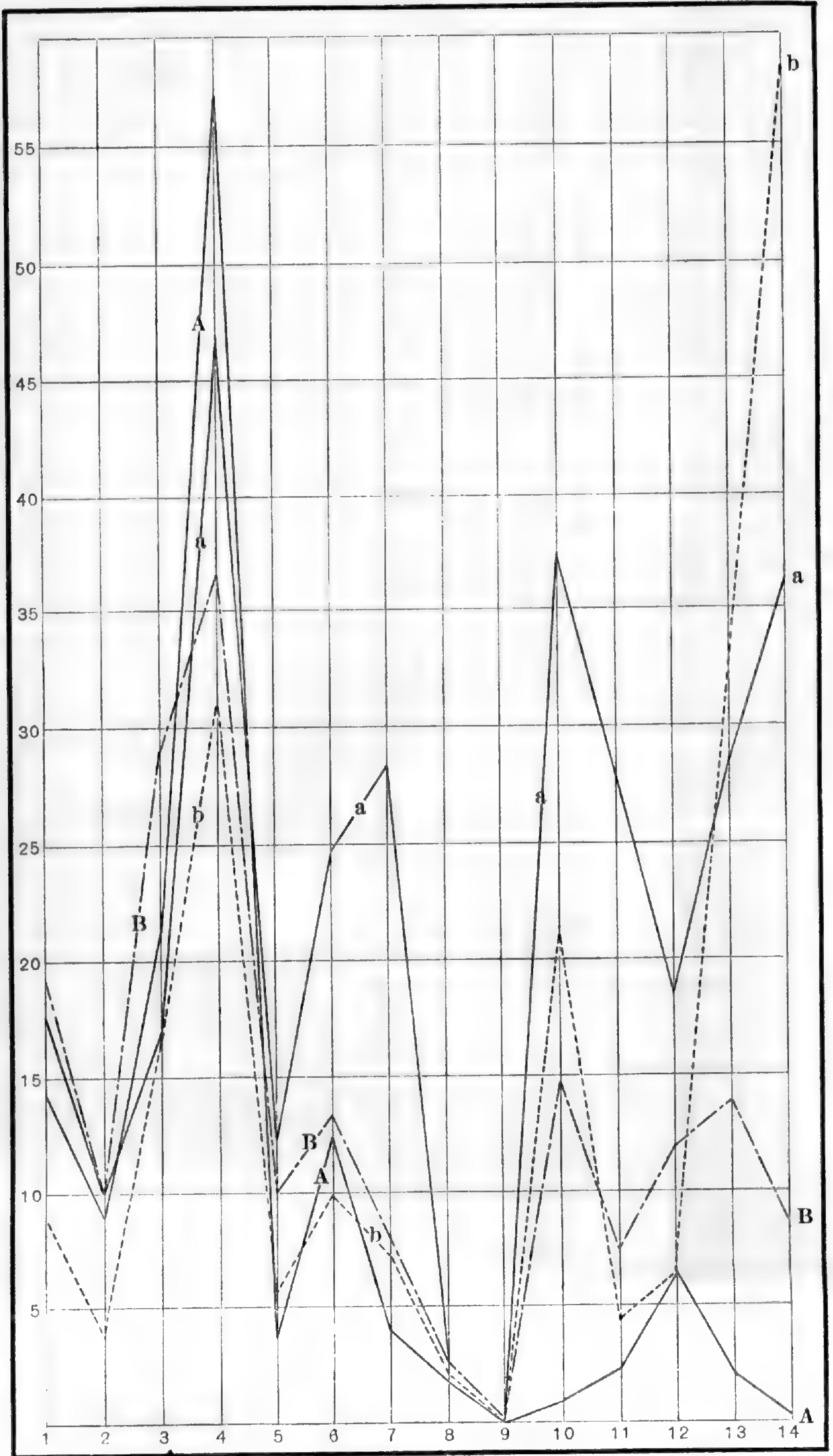
DIAGRAM L.



DISTRIBUTION OF ENDEMIC GENERA.



DIAGRAM M.



DISTRIBUTION OF ALL GENERA.



structures. The relation of flowers to insects is one of the oldest phases of ecology, and while Sprengel's beautiful observations of over a century ago were neglected until the theories and researches of Darwin and his contemporaries showed their importance, it was not long after the revival of interest in this fascinating branch of natural history that students began to see that if flowers show a reduced degree of fertility with their own pollen and are so closely adapted to some special visitor or group of visitors that others are unable to pollinate them, their geographical range will depend largely upon the distribution of the animals which are able to effect their pollination. That this phase of morphology and geography should have been neglected seems all the more remarkable in view of the significance assigned to floral structures in classification.

In the sixth chapter of his *Plant Geography*, Schimper considers animals as factors in plant distribution. Certain floral types, he considers, are undoubtedly limited in their geographical distribution by the range of the animals which pollinate them. The problem of adaptation for the protection of the plant from animal enemies has been much less satisfactorily investigated except in the case of myrmecophilism.

One of the best classes of data for the investigation of this problem is that furnished by ornithophilous flowers, since birds which are of importance as pollinators are of restricted range, and the adaptations, when they are real and not merely apparent, are evidently dependent in their range upon that of the organisms to which they are adapted. Comparatively few plants are ornithophilous, but the evidence offered is of such a character as to give us confidence in attacking the more difficult problem offered by entomophilous forms. Entomophily is the more general condition and in its geographical range is practically coextensive with the limits of the Phanerogams. Only three orders of insects seem to have influenced essentially the



structure of flowers, the Diptera, Lepidoptera and Hymenoptera. These groups are of general distribution, and species with flowers adapted to representatives of each of them may be found in almost every flora. The problem here is much more involved. Conclusions must, in this case, rest upon the demonstration of the interdependence of fauna and flora and statistical comparisons of the floras and faunas of different regions.

It is well known that the three orders of insects mentioned are represented in very different proportions in different regions, and the investigations of several workers have shown that there are corresponding differences in the constitution of the flora.

It is Hermann Müller to whom our knowledge of the influence of the insect fauna upon the constitution of the flora is largely due, for it was his contribution of the statistical methods of work which has made possible much which has been done since his time. So long as observations were confined to individual species showing adaptations to a single insect visitor or groups of visitors, conclusions were necessarily much limited and unsatisfactory. The development of methods which would permit of a statistical comparison of the adaptations of different flowers as a whole to insect visitors is clearly a step of fundamental importance, and, if the methods be trustworthy, permits of advances and conclusions of an accuracy otherwise quite unattainable, though the number of factors is so great and conditions are so complex that comparisons must remain only approximate.

In several papers, Müller developed various phases of the statistical methods, but it was in his book on Alpine flowers that he especially applied and illustrated these methods, and a review of the theoretical portion of this classic work will explain and illustrate the statistical method as developed by the German naturalist. Thomson, Loew, Warming, Lindman, Bonnier, MacLeod, Willis and Burkill, Knuth,



Robertson and others have made valuable contributions to this branch of statistical investigation.

The scope of this paper does not include a general review of the several attempts which have been made to demonstrate a relationship between the geographical distribution of flowers and the insect environment. MacLeod in the introduction to his careful investigation of the insect relations of the flowers of the Pyrenees has given such a review of the more important papers. Schimper and Drude have doubtless performed a great service for this phase of biological investigation by recognizing animals as representing one of the factors in physiological plant geography.

In this paper I have sought to approach the problem from a point of view different from that usually taken. Previous researches have been almost exclusively examinations of the range of individual species or genera which are clearly adapted exclusively to a single pollinating agent, with the range of the organism to which they are adapted, or statistical comparisons by the methods of Müller and MacLeod of floras of different regions, lowland and alpine, insular and continental, temperate and tropical and boreal.

I have tried to select all floral forms of a given type and after assuring myself of the reality of their morphological semblance and, so far as our limited knowledge of the plants in their living state would permit, of the similarity of their ecological relationships, I have considered their geographical distribution throughout the main divisions of the globe.

This method as applied to the problem of the morphology and biology of the apically dehiscent anther has yielded results which are, I think, of some importance in the larger problem of the evolution of floral structures.

Any problem in geographical distribution is necessarily dependent upon the validity of taxonomic or morphological



data, and writers who may speak with the greatest authority have repeatedly insisted that biogeographical researches are of the greatest value only when prosecuted by those who are deeply versed in the morphology and taxonomy of the forms treated. When the problem is one of physiological plant geography, and we have for consideration the additional factor of the environmental conditions and adaptations thereto, the problem becomes more complex. Upon the morphological and ecological data of the problem I have hardly touched in the present paper. I have sought, however, to carry out my comparisons with the greatest care, and I feel confident that the publication of the whole mass of evidence with all the exceptions to the more general laws and transgressions of the categories recognized would convince others of the validity of the propositions offered in this paper.

A point which will doubtless occur to all who examine into this phase of biology is that in the present work I have compared the morphology and geographical distribution of a single type of adaptation to a given factor,—believing that the *Solanum-Cassia* and *Melastomataceous* types may be considered as adapted to the peculiar habits of the *Apidae*,—with the form and distribution of all floral types, whether representing adaptations or not. For a final solution of the problem this method is obviously inadequate. It seems at first that the comparison should be confined to the entomophilous forms and that these should be segregated into their various types of adaptation for comparison; but the relation of all floral structures is one of such complexity that it seems that even this limitation of the field may be too narrowly drawn. Concurrence in both fauna and flora is here doubtless a factor of great importance, and far-reaching structural and field investigations must be made before the real relations will be finally made clear. In justification of the course which has been fol-



lowed in this study — if indeed any attempt at arrangement and interpretation of one class of data preliminary to the elaboration of all the material needs justification — it may be pointed out that these apically dehiscent types represent only two or three of the several types of flowers adapted to Apidae. Hypothetically all these types are well represented in regions which are rich in Apidae, and the relative values obtained for any type or types, as the *Solanum-Cassia* or *Melastomataceous*, would be too small rather than too large as an indication of the total influence of this factor of the environment, since the several types of adaptation to this factor, for instance the *Solanum-Cassia* and the *Verbascum* type among pollen flowers adapted to Apidae, will be in direct competition with each other as well as with all other types of adaptation.

Space has not permitted of the discussion of points of theory, such as the nature of the correlation between the different floral parts, the amount and nature of the influence of the fauna upon the evolution of these floral types, or the significance of these conclusions for current conceptions of floral evolution, nor would such be desirable in the absence of a more detailed presentation of the data upon which the conclusions actually drawn are based. In my final paper, I hope to point out the nature of some of these problems and to offer some suggestions as to the interpretation of the evidence already accumulated.

#### SUMMARY.

The three objects of the present investigation seem to be satisfactorily accomplished, and there only remains the working out of the large number of minor and detailed structural, ecological and geographical problems. A descriptive bibliographic list of apically dehiscent forms is nearly completed and the available material for a monographic treatment of their floral ecology brought together.



The work on the gross structure is being supplemented by a histological investigation of the anthers of the forms in question, and some hundreds of microscopical slides have been prepared and examined. Because of the great variety and in many cases complexity of structure this promises to be one of the most important phases of the work.

It has been shown that apically dehiscent forms for the most part fall into well defined categories exhibiting a striking uniformity of structure in genera or species from widely separated families. Structural parallelism in a series of floral forms assembled from phylogenetically widely separated groups necessarily implies the anomalous structure of many of the forms in the groups to which they systematically belong, among the forms to which they are genetically related. Of the real process by which this parallelism has been evolved I do not yet care to say anything. Many of the conclusions drawn from ecological studies are of little value because of the inadequacy of the data considered. Comparative researches attain their fullest value only when based on the largest series of material. At the present time, it seems to me, one of the most important things is to determine in how far floral organizations do really fall into well defined groups and in how far the structural characteristics of such groups may be regarded as adaptations. The first of these problems may be an herbarium and library investigation while the solution of the second is to be approached only by field studies.

Of the third and last problem little need be said. The tables presented show clearly that the apically dehiscent genera and species are not only much more abundant numerically in tropical America, Australia and the Indian region, but also that they form there a larger proportional constituent of the flora than they do in other regions. This distribution seems to depend in large measure upon the relative abundance of the Apidae in the several divisions.



So far as a biological science can be an exact science, plant geography and ecology must become exact sciences. One of the most promising methods of investigation, it seems to me, is to divide plant structure into classes limited as sharply and as naturally as possible, and to study the ecology and geographical distribution of these. When this is not done, the confusion of details is apt to obscure the results of the greatest value.

