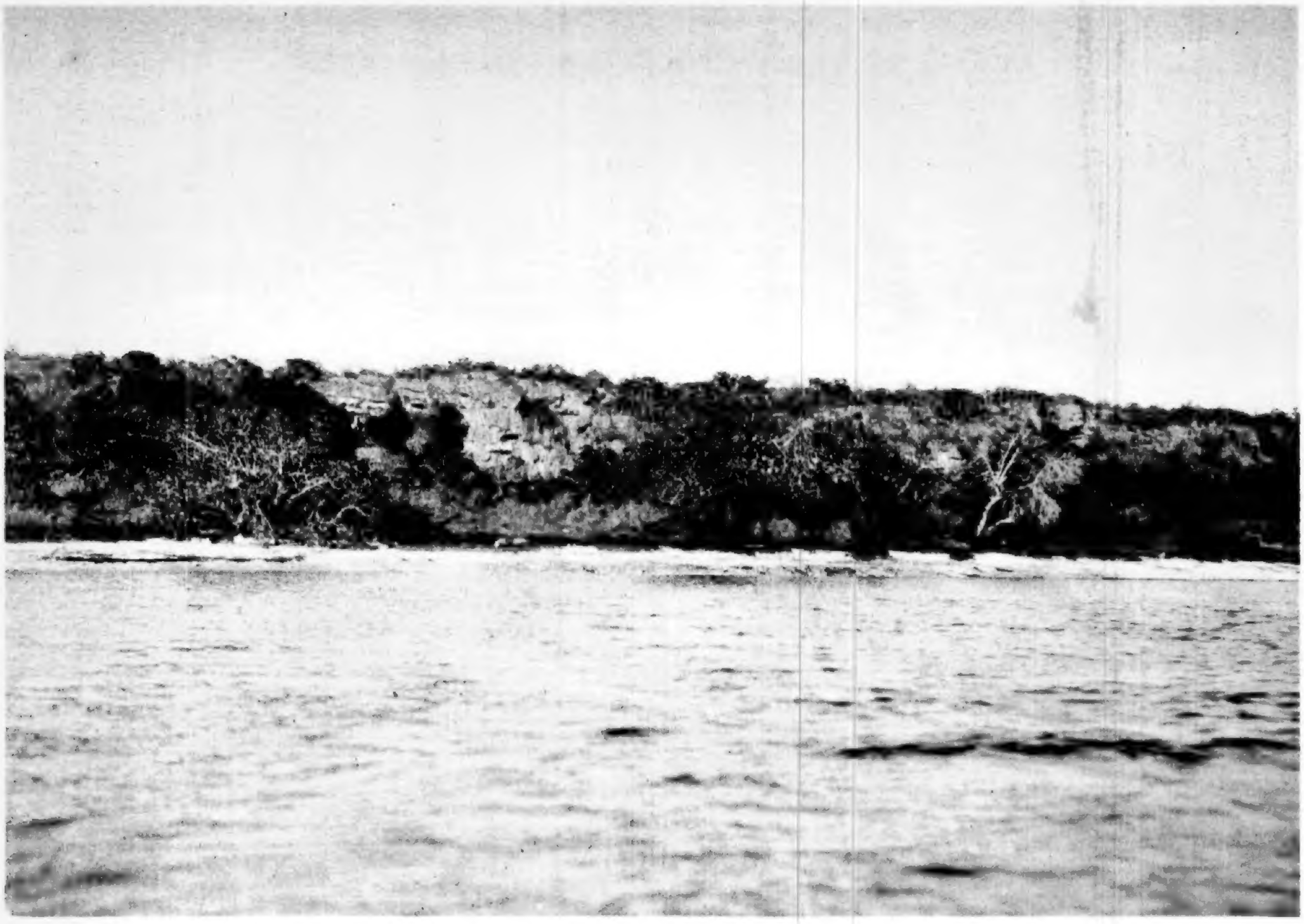

Fig. 1

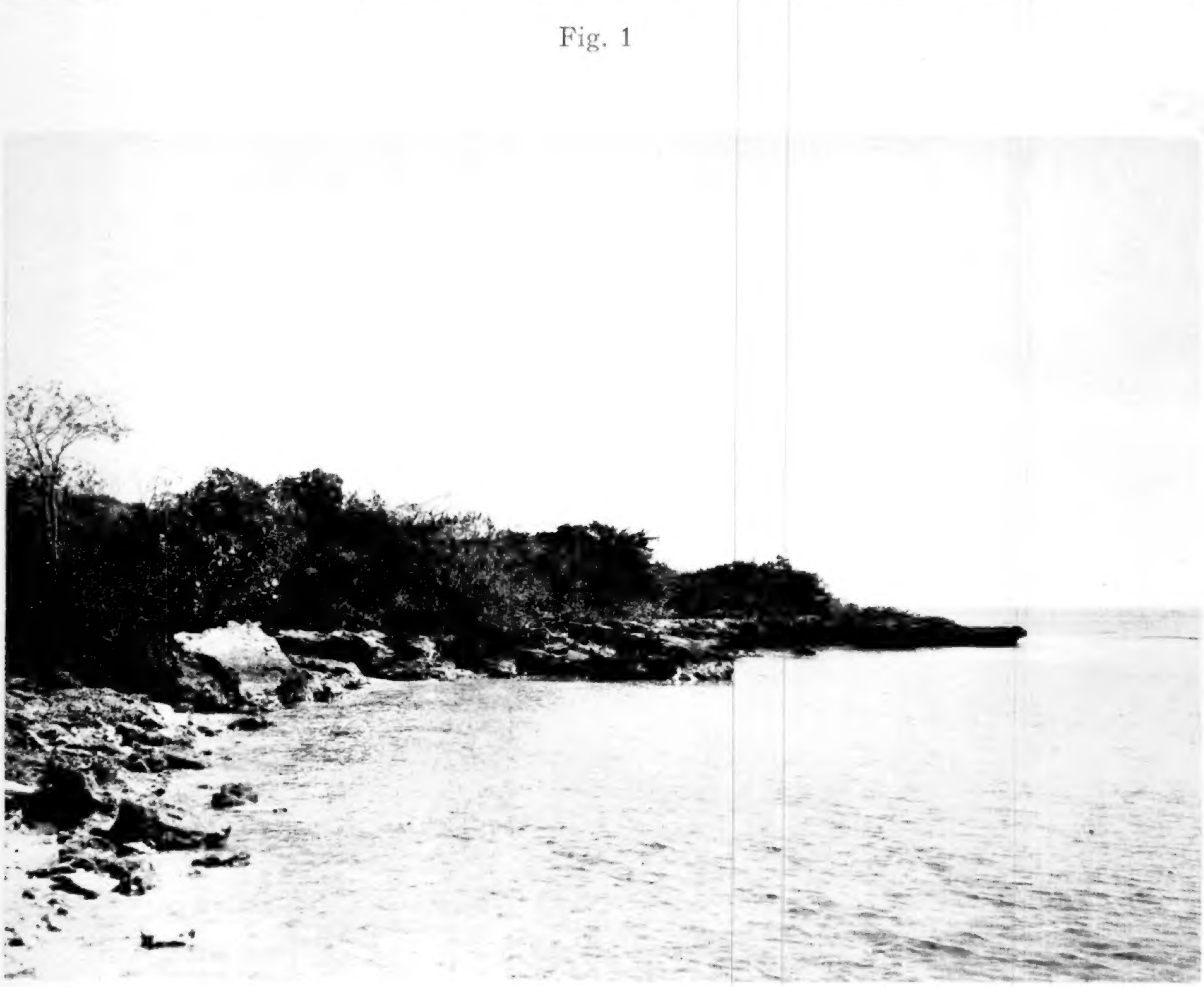

Fig. 2

BRITTON—VEGETATION OF MONA ISLAND

COCKAYNE, BOSTON

ANNALS

OF THE

MISSOURI BOTANICAL GARDEN

Annals

of the

Missouri Botanical Garden

Volume II
1915

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THE TWENTY-FIFTH ANNIVERSARY CELEBRATION

The twenty-fifth anniversary of the organization of the Board of Trustees of the Missouri Botanical Garden was celebrated at the Garden on October 15 and 16, 1914. A list of the American and foreign scientists in attendance, the complete program of the anniversary exercises, the banquet proceedings, and the papers presented at the scientific meetings will be found respectively on pages 1–3, 4–5, 6–27, and 29–401.

DELEGATES AND VISITING SCIENTISTS

MR. S. ALEXANDER
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DR. FRANK M. ANDREWS
Indiana University, Bloomington, Indiana

DR. O. APPEL
Kaiserlichen Biologischen Anstalt, Berlin, Germany

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Texas Agricultural Experiment Station, College Station, Texas

DR. N. L. BRITTON
New York Botanical Garden, New York City

DR. MICHAEL LEVINE
Commercial High School, New York City

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University of Missouri, Columbia, Missouri

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Carnegie Institution, Tucson, Arizona

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Indianapolis, Indiana

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Field Museum of Natural History, Chicago, Illinois

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Indiana University, Bloomington, Indiana

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University of Wyoming, Laramie, Wyoming

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University of Illinois, Urbana, Illinois

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University of Colorado, Boulder, Colorado

DR. ELDA R. WALKER
University of Nebraska, Lincoln, Nebraska

DR. HENRY B. WARD
University of Illinois, Urbana, Illinois

DR. JOHANNA WESTERDIJK
Phytopathological Laboratory, Amsterdam, Holland

DR. KARL M. WIEGAND
Cornell University, Ithaca, New York

DR. E. MEAD WILCOX
University of Nebraska, Lincoln, Nebraska

DR. N. WILLE
University of Christiania, Christiania, Norway

DR. WILLIAM L. WOODBURN
Northwestern University, Evanston, Illinois

DR. R. B. WYLIE
State University, Iowa City, Iowa

PROGRAM

Thursday, October 15

10:30 A.M. AUTOMOBILE RIDE THROUGH THE CITY FOR DELEGATES AND VISITING SCIENTISTS

1:00 P.M. LUNCH AT THE GARDEN

2:00 P.M. FIRST SCIENTIFIC PROGRAM (Graduate Lecture Room)

ADDRESS OF WELCOME - - - - Director George T. Moore

THE VEGETATION OF MONA ISLAND
DIRECTOR-IN-CHIEF N. L. BRITTON
New York Botanical Garden, Bronx Park, New York

THE FLORA OF NORWAY AND ITS IMMIGRATION
PROFESSOR N. WILLE
University of Christiania, Christiania, Norway

THE PHYLOGENETIC TAXONOMY OF THE FLOWERING PLANTS
PROFESSOR CHARLES E. BESSEY
University of Nebraska, Lincoln, Nebraska

THE BOTANICAL GARDEN OF OAXACA
DIRECTOR CASSIANO CONZATTI
Botanical Garden of the State of Oaxaca, Mexico
(Read by Title)

THE SCIENTIFIC SIGNIFICANCE OF THE IMPERIAL BOTANIC GARDEN OF PETER THE GREAT, WITH SPECIAL REFERENCE TO THE FLORA OF ASIA
DR. WLADIMIR I. LIPSKY
Jardin Impérial Botanique de Pierre le Grand, St. Petersburg, Russia
(Read by Title)

COMPARATIVE CARPOLOGY OF CRUCIFERAE WITH VESICULAR FRUITS—SOME GENERAL BIOLOGICAL AND SYSTEMATIC CONCLUSIONS
DIRECTOR J. BRIQUET
Jardin Botanique de la Ville Genève, Geneva, Switzerland
(Read by Title)

THE ORIGIN OF MONOCOTYLEDONY
PROFESSOR JOHN M. COULTER
University of Chicago, Chicago, Illinois

THE HISTORY AND FUNCTIONS OF BOTANICAL GARDENS
ASSISTANT DIRECTOR ARTHUR W. HILL
Royal Botanic Gardens, Kew, England
(Read by Title)

8:30—11:30 P.M. RECEPTION. DIRECTOR'S RESIDENCE

PROGRAM (*Continued*)

Thursday, October 16

10: 30 A. M. SPECIAL PERSONALLY CONDUCTED TRIP THROUGH THE CONSERVATORIES AND GROUNDS OF THE GARDEN; INSPECTION OF LABORATORY, LIBRARY, AND HERBARIUM.

12: 30 P. M. LUNCH AT THE GARDEN

1: 30 P. M. SECOND SCIENTIFIC PROGRAM (Graduate Lecture Room)

RECENT INVESTIGATIONS ON THE PROTOPLASM OF PLANT CELLS AND ITS COLLOIDAL PROPERTIES

PROFESSOR FREDERICK CZAPEK
Physiologisches Institut der K. K. Deutschen Universität, Prag, Austria
(Read by Title)

EXPERIMENTAL MODIFICATION OF THE GERM-PLASM

DIRECTOR D. T. MACDOUGAL
Department of Botanical Research, Carnegie Institution of Washington, Tucson, Arizona

HORMONE IM PFLANZENREICH

DIRECTOR HANS FITTING
Botanische Anstalten der Universität Bonn, Bonn, Germany
(Read by Title)

THE RELATIONS OF SCIENTIFIC BOTANY TO PHYTOPATHOLOGY

GEHEIMER REGIERUNGSRAT DR. O. APPEL
Kaiserlichen Biologischen Anstalt für Land- und Forstwirtschaft, Berlin-Dahlem, Germany

THE LAW OF TEMPERATURE CONNECTED WITH THE DISTRIBUTION OF MARINE ALGAE

PROFESSOR WILLIAM A. SETCHELL
University of California, Berkeley, California

UEBER FORMBILDUNG UND RHYTHMIK DER PFLANZEN

DIRECTOR GEORG KLEBS
Botanisches Institut Universität Heidelberg, Heidelberg, Germany
(Read by Title)

PHYTOPATHOLOGY IN THE TROPICS

DIRECTOR JOHANNA WESTERDIJK
Phytopathological Laboratory, Amsterdam, Holland

PHYLOGENY AND RELATIONSHIPS IN THE ASCOMYCETES

PROFESSOR GEORGE F. ATKINSON
Cornell University, Ithaca, New York

THE ORGANIZATION OF A MUSHROOM

PROFESSOR A. H. REGINALD BULLER
University of Manitoba, Winnipeg, Canada
(Read by Title)

A CONSPECTUS OF BACTERIAL DISEASES IN PLANTS

DR. ERWIN F. SMITH
Bureau of Plant Industry, U. S. Department of Agriculture, Washington, D. C.

7: 30 P. M. TRUSTEES' BANQUET. LIEDERKRANZ CLUB.

BANQUET

MR. EDWARDS WHITAKER

Toastmaster

Ladies and Gentlemen: This being an epoch in the history of the Missouri Botanical Garden, it was thought that a short biography of its founder and benefactor would be interesting.

Henry Shaw was born in Sheffield, England, July 24, 1800. He received his primary education at Thorne, a village a few miles distant from his birthplace, and at this early age developed a fondness for flowers and plants. Completing his course at Thorne, he continued his education at Mill Hall, twenty miles distant from London, where he was a student for six years.

In 1817 he entered the service of his father, who was a manufacturer and dealer in metal wares, such as andirons, grates, etc.

In 1818 his father sailed from England with his family for America, landing in Canada. We are without reliable information as to the exact place in which he located. The same year, probably in the late fall, he sent his son to the city of New Orleans to familiarize himself with the planting and growing of cotton. The climate of New Orleans did not suit him and the business was not to his liking, and his stay in Louisiana was short. He decided to seek his fortunes elsewhere, and so took passage on the "Maid of Orleans," and landed at St. Louis, May 3, 1819.

With the assistance of his uncle, James Hoole of Sheffield, he started a cutlery and hardware business in a room on the second floor of a building in the business district, which served as warehouse, show-room, office, and dwelling, doing his own cooking and housework, as he was without, and never was blessed with, a better half.

His business was successful and uniformly profitable, and, at the age of 39, he had amassed a fortune, as he thought, large enough for any one and sufficient to gratify his taste for botany and the sciences.

He retired from business in 1840, and took a trip abroad, the first since leaving his native shore. This trip was evidently of short duration, as in 1842 he arranged his affairs and sailed a second time for the Old World, remaining three years, traveling extensively and making the acquaintance of botanists and scientists.

Holding the English idea that a gentleman of fortune and leisure should maintain a town house and country home, he commenced the erection of his country home on the Garden grounds in 1848, completing it in 1849, and in 1851 built his town house at the corner of Seventh and Locust Streets, the site now occupied by the Mercantile Club.

His last trip abroad was in 1851, and in 1858 he commissioned Dr. George Engleman of this city, a noted botanist then traveling in Europe, to procure material and information that he thought would be of service to a botanical garden; and at the suggestion of Sir William J. Hooker, then Director of Kew Gardens, began to prepare a laboratory and erected a museum building, and this was the commencement of Shaw's, now the Missouri Botanical, Garden.

While constructing the garden along the lines suggested by Sir William J. Hooker, he commenced the improvement of a tract of land immediately south of the Garden, now known as Tower Grove Park. In 1857 he had an act of the legislature passed authorizing the city to receive, under certain conditions, as a donation this tract for a park. Among them was that the park was to be managed and controlled by a board of park commissioners of his appointment; secondly, that appropriations were to be made sufficient to complete it in accordance with the plans already adopted; and the third condition, that an annual appropriation sufficient for its maintenance should be made; and in 1868 he deeded the property to the City.

Having in mind the conveying to Trustees of his estate to be administered by them for the benefit of the Garden, and a question having arisen whether such a trust was legal and could be administered in this state, he had an act of the legislature passed declaring his intentions, and authorizing him to

transfer his property to trustees and further declaring it lawful. Shortly afterwards, the Supreme Court of the state decided in the case of Chambers vs. The Mullanphy Relief Fund Bequest, that such trusts were legal and could be administered in this state, thereby removing the doubt entertained by some of the legal profession.

In 1866 Mr. Shaw secured the services of Mr. James Gurney from the Royal Botanical Garden in Regents Park, London, who was Head Gardener during Mr. Shaw's lifetime and for several years afterward, and is now Head Gardener Emeritus, and also Superintendent of Tower Grove Park.

There is no record of Mr. Shaw ever having had a public opening of the Garden, and a committee of trustees appointed to investigate and report on the date the Garden was established, decided that the Missouri Botanical Garden began its existence in 1889, upon the organization of the trust declared by Mr. Shaw's will.

Mr. Shaw executed his will January 26, 1885, devising his estate, with the exception of a few minor bequests, to a board of trustees of seventeen, the original members of which were designated in the will, and the board thus constituted, exclusive of certain *ex-officio* members, was to be self-perpetuating. The five trustees by virtue of the offices they hold were the Mayor of the City of St. Louis, the Chancellor of Washington University, the Episcopal Bishop of the Diocese, the President of the Board of Public Schools, and the President of the St. Louis Academy of Science. There were two honorary trustees appointed, Professor Asa Gray of Harvard University, and Professor Spencer F. Baird of the Smithsonian Institution.

Before the death of Mr. Shaw, on August 25, 1889, and the probating of his will, on September 17, both of the honorary trustees had passed away as well as two of the active members of the Board.

The remaining trustees met October 14, 1889, at Mr. Shaw's late residence, Seventh and Locust Streets, and effected an organization of the Board, electing Mr. Rufus J. Lackland President, Mr. Henry Hitchcock Vice-President, Mr. A. D.

Cunningham, Secretary and Treasurer, and appointing Professor William Trelease Director.

Immediately thereafter, by-laws were adopted and committees appointed so that the estate could be efficiently managed. There were four committees—the Garden Committee, the Auditing Committee, the Lands Committee, and the Ways and Means Committee—the President of the Board being *ex-officio* member of all committees. All actions of the committees require the approval of the Board before becoming operative.

There have been three Presidents, three Vice-Presidents, one Secretary and Treasurer, and two Directors of the Garden since the organization of the Board. Of the original trustees named in the will but one survives, Mr. William H. H. Pettus, whose feeble health prevents his being with us this evening. There are but two salaried officers connected with the estate, the Secretary and Treasurer, and the Director, the trustees serving without compensation.

And I wish here to correct an impression prevailing among many that this estate is exempt from taxation. That is erroneous. With the exception of the Garden grounds proper, the estate pays taxes the same as any citizen, and I may add that this item consumes about one-fourth of the gross income, the remainder being used for the maintenance of the Garden and other objects of the trust.

Mr. Shaw was a man of independent thought and action, and while devising his estate to trustees, he at the same time appointed the public administrator of the City of St. Louis the executor of his will.

Among provisions of the will was an annual appropriation for a flower sermon to be preached at such church and by such minister as the Bishop of the Diocese may select; an annual banquet for florists and gardeners in and about St. Louis, at which the Director of the Garden was to preside; a banquet for the trustees and the guests they may invite—literary and scientific men and friends and patrons of the natural sciences.

Another provision of the will was that his residence at Seventh and Locust Streets was to be taken down and rebuilt

upon the Garden grounds. It also provided that the Garden should be open to the public every day in the week, excluding holidays and Sundays with the exception of the first Sunday of June and September in each year, when the Garden should be open from 2:00 p. m. to sundown. This latter provision was literally carried out until the spring of 1912, when the Board thought the best interests of the Garden would be promoted by adding additional Sundays, and, having legal advice that there was no objection to their so doing, it was opened from April 1 to December 1, from 2:00 o'clock until sundown. This action proved to have been wise, as the attendance at the Garden increased threefold.

Such, briefly, ladies and gentlemen, were the objects and the accomplishments in the life of Henry Shaw, a man of whom any City, State or Nation might well be proud, and I request that this assemblage rise and drink with me, in silence, to the memory of Henry Shaw.

[This toast was then drunk by those assembled.]

The Toastmaster then presented as follows the apologies of the Hon. Henry W. Kiel, Mayor of the City of St. Louis, who had been expected to respond to a toast:

Mr. Shaw in his wisdom appointed as one of the Trustees the highest official of the City of St. Louis. He was with us a short time this evening and was compelled to leave, owing to a previous engagement that he thought it would be impossible to break, and I have promised him to make his apologies for not remaining.

In introducing the next speaker of the evening, Dr. Johanna Westerdijk, Director of the Phytopathological Laboratory, Amsterdam, Holland, the Toastmaster spoke as follows:

We are complimented by the presence this evening of a lady from a foreign shore, whose achievements have given her a high position in the botanical world. It is my privilege to introduce Dr. Johanna Westerdijk, of Amsterdam.

DR. JOHANNA WESTERDIJK

Mr. Chairman, Ladies and Gentlemen: This is a delightful day, but I am sorry that not our great Holland botanist is in

our midst. He would be so much more able to express his feelings for America and for the Missouri Botanical Garden, which I know he loves so well. But since he is not here, I think it is a great honor for me to express my feelings, and I know that these feelings are the feelings of all the Dutch botanists, who all love botanical gardens, from the day of Boerhaave up to recent times.

Mr. Chairman and Trustees, and Mr. Director Moore of the Botanical Garden, I thank you in the name of Holland for the delightful day, for the splendid reception I have had here; and if I may express myself in a bit of your American slang at a most solemn banquet, I thank you for the most jolly time I have had in this most delightful bunch of interesting American botanists.

Geheimer Regierungsrat Dr. O. Appel, of the Kaiserlichen Biologischen Anstalt, Berlin-Dahlem, Germany, was next called upon by the Toastmaster in the following words:

We have been favored by the presence of a number of foreigners, among them a neighbor of Dr. Westerdijk, and I trust that, being in the Liederkranz Club, he will feel sufficiently at home to give us his impressions of our country, through which he has travelled extensively. I take pleasure in introducing Dr. O. Appel, of Berlin.

DR. O. APPEL

Ladies and Gentlemen: If I should speak to you of my botanical or phytopathological work, I could use your language; but to express my feelings I must use my mother tongue, the German language!

Sie haben zu dem Tage, den Sie heute festlich begehen, auch eine Anzahl europäischer Fachgenossen eingeladen und die Beteiligung von einer groszen Anzahl erwartet. Die Gründe, die die meisten Ihrer europäischen Gäste am Erscheinen verhindert haben, sind Ihnen bekannt und werden wohl von Ihnen allen bedauert.

Dasz eine grosze Anzahl hervorragender Vertreter des Auslandes hier erwartet wurde, hat seine Berechtigung, denn in den Jahren seines Bestehens hat der Botanische Garten von

St. Louis sich würdig in die Reihe der gröszeren derartigen Institute eingegliedert, und trotz der groszen Entfernung hat schon mancher europäische Botaniker diese Stätte der Wissenschaft ausgesucht und die Kunde von seiner raschen Entwickelung in ferne Länder getragen.

Aber nicht nur durch den Beweisz sind die Bande zwischen unseren deutschen Botanikern und den am Shaw's Garden arbeitenden Fachgenossen geknüpft worden, auch durch mannigfachen Austausch von Material und Gedanken haben sich viele Beziehungen ergeben, die heute eigentlich ihren Ausdruck durch das Erscheinen einiger unserer bedeutendsten Fachgenossen, Klebs und Fitting, ihren Ausdruck haben finden sollen.

Da dies nun nicht sein konnte und äuszere Umstände mir als dem einzigen deutschen Botaniker die Teilnahme an Ihrer Feier vergönnt haben, so möchte ich nicht versäumen, Ihnen im Namen der deutschen Botaniker die besten Wünsche auszusprechen.

Fünfundzwanzig Jahre erscheinen als eine kurze Spanne Zeit und doch haben Sie ein Recht den Abschlusz dieser fünfundzwanzig Jahre zu feiern. Dieser erste Zeitabschnitt ist einer der wichtigsten, vielleicht überhaupt der wichtigste, denn in ihm sind die Grundlagen für die ganze Zukumft des Gartens geschaffen worden. Was in diesen Jahren geschaffen worden ist, das haben Sie alle gesehen. Noch erkennt man da und dort die kleinen und einfachen Verhältnisse, unter denen die Arbeit begonnen worden ist, aber daneben und sie überragend hat schon die neue Zeit dem Garten und seinen Gebäuden ihr Gepräge aufgedrückt. Uberall sieht man, mit welcher Planmäszigkeit und Groszzügigkeit die Entwickelung gefördert worden ist und wie sowohl der wissenschaftlichen Arbeit, wie der Nutzbarmachung für die grosze Allgemeinheit in jeder Weise Rechnung getragen wird.

Aber auch denen, die nicht in der Lage sind, die Schätze des Gartens, der Laboratorien direkt zu benutzen, haben Sie eine Quelle der Belehrung und Anregung gegeben durch die Herausgabe der beiden periodischen Schriften 'Annals of the Missouri Botanical Garden' und 'Missouri Botanical Garden

Bulletin,' von denen die erste für die Gesamtheit der botanischen Welt bestimmt ist, während die letztere sich an alle die in Ihrer eigenen Heimat wendet, die für die Botanik als *scientia amabilis* Sinn und Verständnis haben.

So gehört denn keine grosze Prophetengabe dazu, dem Shaw's Garden eine weitere gedeihliche Entwickelung vorherzusagen.

Dasz aber auch die deutschen Botaniker immer da, wo sie können, und wo ihre Mitwirkung erwünscht ist, gerne mit Ihnen Hand in Hand arbeiten werden, dafür bringt Ihnen die Art der deutschen Wissenschaft, die stets die Förderung jeglicher Forschung zum allgemeinen Besten im Auge gehabt hat und auch in der Zukunft als höchstes Ziel im Auge behalten wird, den Beweis.

Meine Wünsche aber erlauben Sie mir zusammenzufassen in den Ruf:

Hortus botanicus Shawensis vivat, crescat, floreat!

(A translation of Dr. Appel's address follows.)

For this day which you are celebrating, you had invited also a number of European colleagues and expected that of these a large proportion would participate in the exercises. The causes which have prevented most of your European guests from being present are known to all of you and doubtless are regretted by you all.

The expectation of a larger number of foreign representatives is justified, for during the years of its existence, the Botanical Garden of St. Louis has deservedly taken its place in the ranks of the larger institutions of its kind, and, despite the great distance, many a European botanist has already sought out this scientific center and carried the message of its rapid development to distant lands.

But the ties that exist between our German botanists and their colleagues working at Shaw's Garden have been established not alone by such visits, but also by the abundant exchange of material and ideas, in which relationships have developed which to-day were to have found expression through

the appearance and participation of two of our most noteworthy colleagues, Klebs and Fitting.

But since this could not be, and circumstances have graciously willed it that I should be the only German botanist to participate in your celebration, I wish to express to you on behalf of the German botanists our best wishes.

Twenty-five years appear as a short interval of time and yet you have a right to celebrate the completion of these twenty-five years. This first period is one of the most important, if not the most important, for in it have been established the foundations for the entire future of the Garden. You have all seen what has been created in these years. One still recognizes here and there the simple conditions under which the work was started, but these are eclipsed by the imprint which later years have left on the Garden and its buildings. One sees everywhere with what ability and foresight the development of the Garden has been promoted and every provision made for the scientific work and the increased usefulness of the Garden to the public.

But you have also provided a source of information and stimulation to those who are not in a position to directly make use of the resources of the Garden by the publication of the two periodicals, 'Annals of the Missouri Botanical Garden' and 'Missouri Botanical Garden Bulletin,' of which the former is intended for the entire botanical world, whereas the latter goes to those in your home who have an interest in, and an understanding for, botany as a *scientia amabilis*.

It does not, therefore, require a great gift of prophecy to predict for Shaw's Garden a further deserving development.

Wherever German botanists can help and wherever their coöperation is desired, they will always gladly work hand in hand with you, proof of which is furnished by the very character of German science, which has always sought to further each and every investigation for the greatest general good, an ideal which will not be lost sight of in the future.

My wishes you will permit me to express thus:

Hortus botanicus Shawensis vivat, crescat, floreat!

The Toastmaster next called upon Professor N. Wille, of the University of Christiania, Christiania, Norway, as follows:

We have also a friend and botanist from Norway, who, I understand, had a rather peculiar experience in this country. He told me that he had for forty-eight hours or more lost his better half by having the tickets and she starting without any Pullman accommodations. I know he can talk to us interestingly, and we will be glad to hear from Professor N. Wille, of Christiania.

PROFESSOR N. WILLE

The Members of the Board of Trustees, Fellow Scientists, Ladies and Gentlemen: I am deeply grateful to the members of the Board of Trustees of the Missouri Botanical Garden for the kind invitation to participate in this celebration. Had it not been for this I should perhaps never have known America. In the short time that I have been here I have learned much, and I only regret that it is not possible for me to remain in your country longer. When I see the splendid botanical equipment of the Missouri Botanical Garden, I can only lament that it has not been possible for me to prosecute my work under such unusually favorable circumstances. My best wishes for the continued scientific development of the Missouri Botanical Garden.

In introducing Captain Henry King, the Toastmaster spoke as follows:

We have now reached one of the very many interesting subjects of the evening, namely the press. Who is there among us who has not, at some time and some place, received flattering notices at its hand, while again, hard knocks, administered without warning and at the most unexpected moment. If I may be permitted to make a suggestion to the speaker who is to follow me, it is that he go easy with us scientists and delvers in the soil, and in the language of a son of Erin's Isle, "If you can't go easy, go as easy as you can." It is my privilege to introduce Captain Henry King, Editor of the 'St. Louis Globe-Democrat.'

CAPTAIN HENRY KING

It is the paramount duty of the newspaper editor to tell the truth. I do not mean literally and completely, but approxi-

mately and within the rule of reason and the zone of safety. Less is expected of other people, apparently, or the editor would not so often find it so hard to get the truth when he wants to print it. Take, for example, the tremendous and deplorable situation now presented in Europe. With all our anxiety and all our facilities, we can not be certain how much or how little of the wild and whirling daily reports from there —news from hell, so to speak—is dependable. We have not yet even found out definitely what it is all about, and why hundreds of thousands of industrious and inoffensive citizens have been taken from their homes and affairs, and sent forth with all kinds of murderous weapons to slay one another as fast as possible. The most that we can be sure of is that a war of unparalleled dimensions and appalling severity is raging, and that about the only really good thing in it is that white messenger of pity and succor, the Red Cross nurse. And yet I am assured by a leading St. Louisan just returned from the seat of war that the reports in the St. Louis papers are more rational, consistent and enlightening, after all, than those in the papers of any of the cities on the other side of the Atlantic. This man's word is good and his judgment accurate. You all know him. I refer to the Hon. Charles Nagel.

The lesson of Mr. Nagel's gratifying statement is a timely and an important one. It goes to show that in a case of world-wide interest and illimitable consequences, where the truth veritably lies at the bottom of a well, the St. Louis press gets nearer to it by care and candor, by unprejudiced analysis and fair-minded discrimination, than the press of Europe. This example is an extreme one, perhaps, but I feel safe in saying that it is characteristic and relatively prevalent in all cases. I am here, as you have been advised, to talk about the press, or at least to use it as a text. You do not expect me, I am sure, to stand here on this festive and botanical occasion and confess the sins of my esteemed contemporaries, or to acknowledge my own, for that matter. So, if you please, I am going to sidestep the sins, for the present, and declare from personal knowledge and daily comparison that St. Louis has ample reason to be proud of her newspapers. They are not perfect, to be sure,

which is only saying that human life is not perfect, for they are made out of life as life is lived in this goodly city and elsewhere from day to day. They tell you the current history of the community, of the country, of the universe, and they tell it as correctly as the limitations of human nature permit. They have defects of temperament, faults of accident and misinformation, I frankly admit. If they had not these delinquencies, mingled with their excellences, as has the life out of which they are made, they would soon become too good for this world and their home would be in heaven, and you would not have any use for them here on this rolling and imperfect planet. They make mistakes, yes—just as you do, and all men (and some women) do, just as the busy life out of which they are made is in great measure a matter of mistakes, which constitute what we call experience, and experience is only another name for news.

Bear with me, I beg you, if I seem to be too ardent in this topic of the St. Louis press. But I am putting aside, for this occasion, the proverbial modesty of my profession, with a view to telling you the naked truth as if I were under oath. And let me remind you, while I think of it, that the only monument in the world to "The Naked Truth" stands only a short distance from where we are assembled, and its purpose is to typify and commemorate the lives and services of three great St. Louis newspaper editors, Schurz, Preetorius and Daenzer. I am talking to you of the successors of those men, whom I know like a book— my neighbors, my friends, my fellow-workers—,the men who direct and adorn and give tone and influence to the St. Louis press. I know them to be tireless in their pursuit of facts, in their zeal for the public welfare, in their ambition to promote the growth and progress of this admirable city. It is sometimes said in criticism of them that they are governed mainly by commercial considerations, and one of the pestiferous sort of professional reformers has lately sent forth a book in which he goes so far as to charge that their policies are absolutely dictated by their big advertisers. Well, if it wasn't for the big advertisers, you would hardly be able to get the modern wonder and recognized necessity of a daily newspaper

for the absurd price of a penny a copy, the cheapest of all known commodities of general use; and I often think that the advertisements constitute the most interesting and serviceable part of the paper. That is not the only reason why we print so many of them, I am bound to admit, but it certainly tends to ameliorate the condition and to make the habit almost innocent. As for the advertiser as a dictator of editorial policy, we do not find him very insistent or obstreperous. In a lifetime of experience, I have never yet known an advertiser to solicit any selfish advantage or assert any right of arbitrary interference on account of his patronage; but it is a common thing to have them come forward in earnest and practical support of projects for the common good. We owe it largely to the advertisers, the business men, that we have the Veiled Prophet with us every year; that we had an incomparable World's Fair; that we produced the unequaled Pageant and Masque; and I don't believe they will permit the reproach of failure to overtake the Symphony Orchestra. And I'm going to include the Free Bridge in this assurance, though just now I do not see any practicable way to connect with it.

This brings me to the point of chief interest, to the Missouri Botanical Garden, with its immense display of floral splendor, its infinite sources of delight and instruction, of admonition and of consolation. I wish I could botanize about it in the thorough and skillful manner of our distinguished scientific visitors. But alas, I have to make the bashful admission that I probably know less about botany as a science than any other person on your program to-night—unless it may be your Toastmaster. The fact is, I have had less to do with flowers than with quadrupeds, such as the Donkey, the Bull Moose, and the Elephant—God bless him—begging the pardon of those of you who don't happen to like him as well as others of us do. But I am tolerably familiar with the part which flowers have played in the affairs of the world. I know how all literature is pervaded by their fragrance and their symbolism. I am not unmindful of their cherished associations in the lives of all classes, from the cradle to the grave. I know how, in many instances, when wisdom reaches its limit and language fails,

they have the gift of talking to us and for us, in a form of expression which we can grasp only with our feelings and emotions, and which our hearts rather than our heads must interpret and utilize.

But I must not deviate too far from the relation of the editor to floriculture, which is similar to that of the boy in Mr. Lincoln's story who, being asked if he liked gingerbread, replied, you remember, "I reckon I like gingerbread better than any boy in this town, and get less of it." So it is mainly with the editor and the bouquets. He is more apt, as a rule, to have stale vegetables thrown at him, figuratively speaking, and to be condemned to wait for his flowers until he reaches that point in his career where he no longer has use for anything else. But, happily, the editor is nothing if not a philosopher. The discipline of his profession teaches him patience and tolerance and sweet reasonableness. In the nature of things, he gives more attention to other people's affairs than to his own—so much so, indeed, that now and then he is accused of being over-zealous, not to say over-inquisitive, in that respect. If a bouquet comes his way it surprises and confuses him, since it contradicts his personal experience that if virtue be not its own reward, then it usually remains unrewarded. Nevertheless, he goes on boosting instead of knocking, because it is his mission to spread the gospel of good cheer and make more room in the sun for those who inhabit the earth. He welcomes particularly an occasion like this, where he can help to celebrate the choice taste, the fine civic spirit, the munificent public benefaction of a man like Henry Shaw. And his pleasure is doubled when to such an opportunity is added the chance to compliment the Missouri Botanical Garden upon having for President of its Board of Trustees a man with the many excellent qualities of Edwards Whitaker. Science is the basis of the great enterprise which Mr. Shaw founded, of course, but science needs trained business sense to invest its service with the highest practical usefulness. Mr. Whitaker has shown in a marked degree his realization of the possibilities of his position, and the steps by which the benefits of Shaw's Garden, as we familiarly call it, can be materially multiplied. I feel

authorized to say that in this important work he will have the hearty coöperation of the St. Louis press; and I am sure that he will in turn see to it that the editors get all the floral tributes that are due to them, at least when the time arrives for them to confront the ultimate River of Separation, and each of them shall need something of that sort to waft aloft in his behalf the beautiful message of Tennyson—

"For though from out our bourne of time and place,
The flood may bear me far,
I hope to see my Pilot face to face
When I have crossed the bar."

In the following words the Toastmaster called upon the next speaker of the evening, Dr. William G. Farlow:

We have with us this evening a guest who, I can truthfully say, is loved by every botanist in America, and I can also assert without fear of contradiction that he is recognized as their dean. I am proud to introduce Dr. William G. Farlow, of Harvard University.

DR. WILLIAM G. FARLOW

Mr. President and Ladies and Gentlemen: As I look upon this company and see how many there are here, all of whom are interested in the St. Louis Botanical Garden, I can't help asking myself the question: "Why are they interested in the Garden?" Some have one reason; some have another. Some like it for the flowers that are shown there; some like it for the scientific work done there. But whatever their reasons may be, I would like to take advantage of this occasion to say a few words about what seems to me to be the true object and aim of botanical gardens.

Let us go back to history. The first garden on record, I believe, was the Garden of Eden. That garden unfortunately was obliged to be closed to the general public only a short time after it was opened. But we learn some lessons even from the Garden of Eden. In the first place, do not mix zoölogy and botany. The Garden of Eden was not purely a botanical garden. You know what the snake did and will always do in botanical gardens. There is another curious thing about the

Garden of Eden. It is the only garden I ever heard of from which people were excluded because they had just begun to learn something, and it seems to be exceedingly cruel that they should have been turned out into a cold world merely because they knew something.

But it is a long step from the Garden of Eden, and history is a little more accurate in recent times than it was then. The traditional botanical garden, the one which has existed for centuries in Europe and to a less extent in this country, was a place where the seeds of a great many plants were sown; some came up and some did not, but they were all labelled. Now many plants are annual but labels are perennial and the unfortunate result in many of the older gardens was that there was a luxuriance of labels and a comparative poverty of plants corresponding to the labels.

The ideal garden is nature. We can never equal nature in anything like proximate perfection. Go up in the mountains or go out into the woods. You see nature where it has existed for ages, the result of centuries of work. What we see is not what has been planted a few years before. It is the result of the conflict of ages going on between natural forces, and what we see is the final result, such as can not be obtained by man. We find plants which grow where they naturally grow; we see moss where moss should grow; we see trees where trees should be. In a botanical garden of the present day, such as the Missouri Botanical Garden, we should imitate nature as far as is possible in a limited space and offer to the general public and the special students of botany an epitome of the vegetation of the world.

Those of our botanists who visited the Garden yesterday and to-day saw a superb display of cosmos. I don't know that St. Louis people fully appreciate what a fine exhibition of flowering plants we have seen here, but the cosmos are perfectly magnificent and you have reason to be proud of them. I hope your spring flowers are equally splendid, and there is no reason why in the summer you can't have groups of equally fine character. The old-fashioned botanical gardens had no beauty whatever. They were simply artificial and repulsive,

but at present a botanical garden must in the first place be beautiful. Although beauty is not the end of everything, we begin with beauty and end with science both practical and theoretical. Besides the flower beds and hothouses the casual visitor notices certain buildings of considerable size scattered here and there. What they are for is not perhaps known to many of those attracted by the floral display. Without these buildings and their contents and the experts in charge of them there could be no floral display of any real importance. Although they add little to the beauty of the Garden, in these buildings is done the work which gives to the Garden its scientific value and entitles it to recognition throughout the botanical world. The very valuable library and herbarium are, in a sense, the soul of the Garden, since from them is obtained a knowledge of the plants cultivated, and they are a necessity to those carrying on research in the laboratories.

At this late hour I cannot enter into details. It should be said, however, that for the library and herbarium, fire-proof buildings, always expensive, are necessary since if destroyed they could not be replaced by insurance. The laboratories for research are in a somewhat different position. The value of research in vegetable physiology and pathology and other subjects other than systematic botany, which is, of course, carried on in the herbarium, cannot be overestimated. Convenient and well-equipped laboratories are a necessity in a modern garden. They do not, however, require expensive fire-proof buildings. The outfit of the laboratories should be up to date, but new and improved instruments are invented from year to year and an occasional conflagration is not to be dreaded since the insurance on the older instruments can be used for purchasing better new ones. Furthermore, the trend of original research is constantly changing and, in trying to adapt themselves to the current demands of the scientific public, the nature of the work done in research laboratories and in consequence their equipment vary from time to time.

As I look at my audience, I am reminded of something I saw in the train coming to St. Louis the other day. I picked up what I believe was the last number of 'Life,' and glanced at

a cartoon, a crowd of persons seemingly very much pleased, and wishing to know why they were hilarious, I saw that the title was the "Millenium Celebration in Honor of the Abolishment of After Dinner Speeches." Your faces remind me somewhat of those of the crowd I saw in 'Life,' and I now close, fearing that you may be hoping that the millenium will arrive before we have another twenty-five year dinner, when I shall not be with you.

The Toastmaster next called upon the Hon. Charles Nagel, of St. Louis, in the following words:

Our city has had a number of her sons, and adopted sons, called to occupy positions of responsibility at the National Capital, one of whom, after four years' service in the Cabinet, has returned to the city of his adoption; and I am proud to introduce the Hon. Charles Nagel, ex-Secretary of Commerce and Labor.

HON. CHARLES NAGEL

Mr. Toastmaster, Ladies and Gentlemen: It appears to me that the last speaker was both wise and unkind in referring to the illustration from 'Life' at the close of his speech. I can assure him that my embarrassment was sufficient without that reference.

In endeavoring to account for my presence in a family of botanists, I have been compelled to go pretty far back in my life and to recall an incident when an aged grandmother, whom I never knew, sent me what Dr. Appel will pardon me for calling a "Botanisirbuechse," to encourage me in the collection of plants. It was only a trifle at the time, and yet I imagine I share the experience of most people in tracing my interest in nature to that early incident in my life. I would say that my love of nature is such that I would rather have my child love the virility and strength of an oak leaf than all the bouquets and flowers that can be gathered.

I believe that real love for the strength of nature is what we need, and not the pampering influences of the selected flower. I believe in the forests of New Hampshire that my friend, Dr. Farlow, loves; and I can see him now searching

for his specimens there, but never unmindful of the grandeur of all nature to which his specimen furnishes only a clue.

But studying of the plant means more than that. It means the reason of nature. I have sometimes thought that if we knew more of the reason for the decline of one plant and the triumph of another, we would have a better understanding of the meaning of the inevitable and unavoidable conflicts that are now tearing the world apart; and we Americans, if we knew more of the generating influence of the one and the survival of the other, would appreciate that it takes conflict and danger to make strong men and women.

I do not want to go too far, but while a park need not be a botanical garden, no park can succeed unless it has applied to it the science and the work of the school of botany. We can not have the city beautiful, with all our preaching, until we understand the true meaning of a school of botany and of our botanical gardens. If any one doubts it, let him look abroad. He who has seen the beautiful forests about Paris, the splendid forests about Berlin, the wonderful forests about the Hague, will say to himself, "Yes, this is nature, profound and beautiful"; but it is not an accident. It is the result of nature's force guided by experience and science.

That is what we need—politics, government, must take into counsel the man of wisdom and experience to produce those wonderful results which so far we cannot imitate. There is more than that. Abroad, not only the government utilizes the information which these men and women of science have to give, but every man and woman throughout the land consciously or unconsciously is influenced by the same teaching. Wherever you look and whatever you see demonstrates to you the result of that kind of work. It means not only the flowers and the plants, but it evidences the happiness of family life. Every field shows it; every home and every garden patch shows it. That is the lesson we have to take unto ourselves in this, our new country. That is what we have to do if, as a people, we are to succeed; and it is for this reason that we welcome the greetings of the distinguished guests who have joined us to-night.

True, all the countries are not represented; but we have the right to say to ourselves that science and civilization stand above all the conflicts of the day. Ultimately, the very nations who are now engaged in this conflict will again have to unite their hands to bear the standard of civilization jointly upon the Continent; and we have a right to say to-night that while only a few countries are represented, from the standpoint of science and civilization broadly speaking, the few representatives are here to speak to us for all the civilized nations of the world.

The last speaker of the evening, Dr. George T. Moore, was called upon by the Toastmaster as follows:

Mr. Shaw's will requires the Board to appoint a Director of the Garden, who is to reside upon the Garden grounds. He is virtually the executive of the board and the Garden Committee so far as Garden matters pertain, and he might be compared to the man behind the gun, as much of the success of the Garden depends upon him. The Director is known to so many of you, an introduction seems hardly necessary; but for form's sake I take pleasure in introducing Dr. George T. Moore, Director of the Missouri Botanical Garden.

DR. GEORGE T. MOORE

It was my pleasant task on yesterday to welcome those who honored us with their presence at the first formal exercises celebrating the passing of a quarter century in the life of the Missouri Botanical Garden. To-night has been delegated to me the duty of closing what at least for the Garden has been a most memorable festival, one which long will remain that delight which, joined with memory and hope, constitutes a perfect occasion.

An after-dinner speech is sometimes regarded as a sort of verbal culture medium for the propagation of words, and it is remarkable with what rapidity those who confine their efforts to media containing no solidifying substance can cloud an otherwise clear situation. With the example set me to-night, it behooves me to speak directly to the point and not spoil an evening which thus far has been faultless.

That the Missouri Botanical Garden was fortunate in its founder, I have tried to indicate early on this anniversary occasion, and it is not necessary, even if it were possible, for me to add anything to the appreciative words which have been spoken at this table.

I do feel, however, that perhaps not enough emphasis has been placed upon the fact that it is the organization of the Board of Trustees which furnishes the real reason for this anniversary, and that in honoring Mr. Shaw and in praising the courage and skill which he displayed, we are apt to forget the prolonged efforts of those men who have unselfishly given of their time and thought to make the dream of Henry Shaw come true.

You botanists present know that he who would keep up his scientific fire must also have the means of keeping up his material woodpile. Certainly no place in this country has a trust been so closely and so successfully administered as by that body of men who, from the very first, have labored without remuneration or recognition from those they served, the Board of Trustees of the Missouri Botanical Garden!

Every citizen of St. Louis, every visitor to the Garden, every botanist or individual who may have been assisted by the facilities of the Garden, library or collections, has reason to echo the words of George Washington, which, slightly altered, are just as applicable to the Board of Trustees of the Missouri Botanical Garden throughout its existence, as they were to Benjamin Franklin:

> "If to be venerated for wisdom, if to be admired for talents, if to be esteemed for service, if to be loved for devotion, can gratify the human mind, they must have had and have the pleasing consolation that they had not and will not have lived in vain."

In the long run, which is a sort of mathematical name for Providence, such services have their reward, but every twenty-five years, I think the Board of Trustees as a body—for the individuals wouldn't permit such a thing—should at least be entitled to a public statement of the facts.

We are grateful to all who, through their active participation or by their presence at the sacrifice of valuable time and by long journeyings, have contributed to the success of this

occasion. Especially do we owe thanks to those who by presenting such splendid papers have made the programs such as will be difficult to surpass in the future.

The celebration of an anniversary is a ground of congratulation or regret according as it marks the progress or decline of the event it commemorates. My only hope at this time is that on the next anniversary occasion of the Missouri Botanical Garden the advances made along the lines of the various activities in which the Garden is interested, may be far beyond those of the present, and that the celebration will exceed the twenty-fifth as many times as the Garden is years older.

The Toastmaster concluded the program of the evening with the following remarks:

The hour is growing late. A few words before parting. On behalf of the Board of Trustees of the Missouri Botanical Garden, I wish to thank one and all for their presence here this evening, especially those who have journeyed far to be with us, and to express the hope that we may enjoy this pleasure many years to come. Good night!

ADDRESS OF WELCOME

GEORGE T. MOORE
Director of the Missouri Botanical Garden

It becomes my pleasant duty at the beginning of the program celebrating the twenty-fifth anniversary of the organization of the Missouri Botanical Garden to formally do what I am sure has already been done over and over again by each member of the staff—welcome most heartily those guests who have done us the honor of coming to share with us the simple, yet I hope adequate, ceremonies which have been arranged for this occasion. At one time it was expected that this welcome would be extended by Mr. Houston, who, because of his triple offices, as a member of President Wilson's cabinet, a Trustee of the Missouri Botanical Garden, and Chancellor of Washington University, as well as the grace with which he would have addressed you, would most suitably have performed this duty. Pressure of public work has prevented the Secretary of Agriculture from being with us, however, and I can only hope that you will feel that the welcome extended to you now carries with it as much cordiality and good will as if it came from an officer of the Government, the Garden, and the University.

Nothing could be more fitting at this time than some account of the life and work of the founder of this Garden, who deserves, both because of his far-sighted planning and his magnificent gift, to rank as America's foremost patron of botany. Most of you are no doubt familiar with the simple but impressive biographical facts concerning Mr. Shaw. How he came to this country from England with his father in 1818, being eighteen years of age, and after brief stays in Canada and New Orleans, settled in St. Louis. With a small stock of hardware he began business in one room, which also served as his bedroom and kitchen. From such a small beginning—and this on borrowed capital—scarcely more than twenty years were required by this pioneer merchant to amass a

fortune, for at forty years of age Mr. Shaw retired from active business to devote the remaining forty-nine years of his life to travel, and later to the active and remarkably intimate creation and management of a garden—that garden of which, because of his intelligent planning and unprecedented forethought and liberality, we are to-day celebrating the silver anniversary.

The advice and counsel of such men as Dr. George Engelmann, Sir William Hooker and Professor Asa Gray was freely sought and as freely given. In this connection I should like to read a letter from Sir Joseph Hooker, written June 17, 1888:

"The Camp, Sunnydale, England.

"My Dear Mr. Shaw:—

"I have just received your most handsome present of Engelmann's Botanical Works, edited by our dear late friend, Dr. Gray, and I do thank you most heartily, no less for your kind gift than for the effective service to botany that this most valuable contribution to the science renders. It is indeed a noble tribute to a man whose labors as a most conscientious and painstaking botanist have never been surpassed, and I prize it for the sake of the man whom I knew so well and esteemed so highly. I shall never forget my visit to him and to you and the afternoon I spent in your garden and museum at St. Louis, in company with Dr. and Mrs. Gray.

"I have been most interested in all that Dr. Gray told me last year about the noble botanical institution that you have founded and in his hopes that it would be a center of diffusion of knowledge, the influence of which would be felt far and wide.

"I think that he was more proud of your consulting him in the matter of its organization than of any of the many services which he had rendered to American botany, and he certainly regarded his labor with you as the most pleasant episode of his later years and by far the most important.

"Believe me, my dear sir, most faithfully and gratefully yours,

Joseph D. Hooker."

The country home of Mr. Shaw was built on these grounds in 1849, and the breaking of the prairie for his garden is said to have begun in 1857. There is no record of any formal opening of the Garden to the public, however, the date 1858 on the entrance of the main gate probably being the year it was erected rather than the time it was first opened to visitors. The small "Museum and Library," as it is designated in the

stone over its entrance, was built in 1859, and this same year the installation of the Bernhardi Herbarium, previously purchased in Europe, marked Mr. Shaw's intention to make the Garden a center for scientific investigation and research. How successfully the founder of the Missouri Botanical Garden incorporated this idea in the document intended for the guidance of those who should administer this bequest, is evidenced by the remark of Judge Medill, one of the first members of the Board of Trustees, who, after the reading of the will, exclaimed: "That is a scientific institution and much should come of its services to botany!"

Mr. Shaw died August 25, 1889, and on September 10 the formal organization of the Board of Trustees, created by his will, took place. This is the anniversary we celebrate, for, as I have indicated, it is the only definite anniversary we have. Certainly as a "botanical institution, public in character," the Missouri Botanical Garden began its existence upon the organization of the trust declared by Mr. Shaw's will.

Two other notable bequests of Mr. Shaw require brief mention at this time, one indicating his desire for further scientific investigation in botany, the other the love for the beautiful in nature and his wish that all might have unlimited opportunity for acquiring and indulging this same passion. I refer, of course, to the endowment of the Henry Shaw School of Botany of Washington University, and the gift of Tower Grove Park to the city of St. Louis. The first is, owing to the broad-minded liberality of the Board of Trustees of the Garden and the untiring and unselfish efforts of its staff, taking a place among similar schools of the kind of which Mr. Shaw would not himself be ashamed. The latter, under the fatherly care of Mr. Gurney, its first and only Superintendent, whom we are proud to call the Head Gardener Emeritus of the Missouri Botanical Garden, is nobly fulfilling the purpose for which it was created.

It is proper, then, that this company of scholars should assemble here to do honor to the memory of Henry Shaw, to rejoice with us for the successful completion of twenty-five years of usefulness of the Missouri Botanical Garden.

Both personally and in my official capacity I welcome you not only to these ceremonies, but as coöperators in an era of even greater effort and achievement for the cause of the science which Mr. Shaw loved and honored and encouraged.

THE VEGETATION OF MONA ISLAND[1]

N. L. BRITTON
New York Botanical Garden

During the progress of the scientific survey of Porto Rico, organized by the New York Academy of Sciences with the aid of the American Museum of Natural History, the New York Botanical Garden and Columbia University, in coöperation with the Porto Rican Insular Government, exploration has been carried out not alone on the mainland of Porto Rico but on several small islands adjacent and politically a part of that colony. Two of these islands lie in the Mona Passage between Porto Rico and Santo Domingo, and being scientifically almost unknown, were made points of examination in February, 1914, when I visited them in company with Mr. John F. Cowell, Director of the Buffalo Botanic Garden, Dr. Frank E. Lutz, Assistant Curator of Invertebrate Zoölogy in the American Museum of Natural History, and Mr. W. E. Hess, Plant Propagator of the Porto Rico Agricultural Experiment Station at Mayaguez. The trip was made in a sloop chartered at Mayaguez.

Desecheo Island, lying about eighteen miles northwest of Mayaguez, was first visited, and explored during two days; this island is somewhat more than one square mile in area, bordered by rocky coasts, rising abruptly into several hills, and covered with low trees and shrubs. Its flora is essentially identical with that of the drier parts of Porto Rico and of Santo Domingo; the small tree *Morisonia americana* and the snowy cactus (*Mamillaria nivosa*) have, however, not yet been found on the Porto Rican mainland, although both occur on the Island of Culebra east of Porto Rico, and neither of them is known on Santo Domingo. The cactus *Opuntia haitiensis*, plentiful there, is otherwise known only in Hispaniola, and the shrub *Torrubia discolor* of Hispaniola and Cuba has not been found on Porto Rico. The collection made

[1] Issued May 17, 1915.

by us on Desecheo, together with one made by Professor F. L. Stevens and Mr. W. E. Hess in May, 1913, shows that the spermatophytes of Desecheo number about 90 species; further intensive exploration might reveal a few more. A single species of fern was seen, four species of mosses, and two species of hepatics. As there is no probability of this little island ever having been a part of the Porto Rico mainland, its plants must have reached it by natural agencies; there are probably as many fungi and lichens as of other land plants collectively, so the total land flora of Desecheo probably includes at least 200 species.

Mona Island, lying about thirty miles to the southwest of Desecheo, in the middle of the Mona Passage between Santo Domingo and Porto Rico, has an area of approximately twenty square miles. Prior to our visit, only one botanical collection had been made there, when it was visited by Professor F. L. Stevens in 1913, at which time he obtained specimens of about 150 species of flowering plants, and gave especial attention to the parasitic fungi. The considerable land area of this island made a complete knowledge of its flora desirable, from the standpoint of geographical distribution of West Indian plants, and we were able to devote five days to collecting. The greater portion of Mona is a limestone plateau elevated from 125 to 175 feet, the surface of this plateau being nearly level and devoid of hills; its soil is very sparse, consisting altogether of reddish loam in depressions of the limestone surface, and not of considerable extent at any point visited by us. The limestone is evidently very porous, and there are no streams or ponds, and only a single spring was seen; the limestone is honeycombed with caves and caverns, some of them of considerable size. The rainfall is evidently considerable, but there are no records of its amount. Despite the paucity of soil, the whole plateau is rather densely covered with shrubs and low trees of a considerable number of species, their roots, for the most part, penetrating into crevices of the limestone. Herbaceous vegetation is restricted to comparatively few species. Eight species of cacti inhabit this plateau, and in places are very abundant, the snowy cactus

(*Mamillaria nivosa*) being more plentiful here than on any other island visited by us; *Opuntia Taylori,* hitherto known from Hispaniola, Culebra and the Virgin Islands, was found as a single colony; this has not yet been detected on the Porto Rican mainland.

The limestone plateau of Mona is bordered nearly throughout by steep escarpments and is accessible at but few points, except along the southwestern side, where there is a low plain several miles long and averaging about half a mile wide, from which the plateau is reached at a number of points over a talus of large limestone blocks. At the foot of the escarpment and of the talus on this southwestern side, the moistest conditions of Mona occur, and several species of trees here reach large size, notably the manchioneel (*Hippomane Mancinella*) and two species of *Ficus*. Here also grow two species of ferns, several bryophytes, and a number of *Polyporaceae* infesting dead wood. The soil of the narrow plain is more abundant than that of the plateau, permitting agricultural operations on a small scale and supporting a low forest made up of a considerable number of kinds of trees, with more herbaceous vegetation than exists on the plateau. Among rare elements of this vegetation are two orchids, *Domingoa hymenodes,* hitherto known from Hispaniola and Cuba, and *Ibidium lucayanum,* of Porto Rico, Anagada and the Bahamas. The coastal sands, which extend almost uninterruptedly along the shore of the plain, are inhabited by characteristic West Indian sand-dune species.

Lichens are quite abundant on tree trunks and on rocks of the talus, including a considerable number of species. Professor Lincoln W. Riddle has examined the collection and has submitted the following report upon them:

"The exploration of Mona Island has yielded 42 numbers of lichens, 40 collected by Dr. N. L. Britton, Messrs. J. F. Cowell and W. E. Hess, and 2 collected incidentally by Dr. F. L. Stevens. These 42 numbers represent 26 species in condition for determination.

"The species growing on the limestone rocks constitute the most striking and interesting part of the collection. These include four species of *Omphalaria,* a species of *Collema,* and a species of the *Dermatocarpaceae,* which is, unfortunately, sterile and, therefore, not further determinable. The omphalarias are all little known species.

O. polyglossa Nyl., collected from limestone rocks in Cuba by Charles Wright, and not otherwise known, is apparently common on Mona Island, as it is represented by two numbers, each with several well-developed specimens. There occur also *O. lingulata* Tuck., previously known from Cuba and Bermuda; a sterile omphalaria related to *O. Wrightii* Tuck., but apparently not identical; and one other species of the genus, probably new. It has not yet been possible to identify the species of *Collema,* and that may also prove to be new. Curiously enough, none of these calciphile species has yet been detected among the material collected in Porto Rico.

"In marked contrast to the rock-lichens, the bark-inhabiting lichens are all common species, widely distributed in Tropical America. The genus *Trypethelium* is best represented, with the species *T. Eluteriae* (four numbers), *T. ochroleucum,* and its variety *pallescens,* and *T. mastoideum* (two numbers). There are also such characteristic species as *Graphis Afzelii, Melanotheca cruenta, Pyxine picta, Physcia alba* and *P. speciosa, Parmelia sulphurata* and *P. tinctorum,* and *Ramalina complanata* and *R. Montagnei.* Probably owing to the comparatively unfavorable conditions on Mona Island, the foliose and fruticose lichens are mostly small specimens, not well-developed."

The total flora of flowering plants, as indicated by the collection made by Professor Stevens and our own, includes about 230 species; some of them are found only in cultivated grounds on the coastal plain and have probably been introduced by man. The total flora of land cryptogams is probably as great or greater than that of flowering plants, so we may conclude that the land flora of Mona consists of as high as 500 species. So far as the investigation of the collections has proceeded, the only apparent endemic species are a *Chamaesyce,* which Dr. C. F. Millspaugh has described as new, a *Tabebuia,* the description of which is herewith included, and two very interesting riccias, here described by Dr. Marshall A. Howe. One or more of the lichens may be undescribed. Further exploration in Porto Rico and in Hispaniola may very well reveal their presence on these larger islands. It is interesting to have ascertained that the flora of this isolated limestone island is not more highly specialized. It is not necessary, in my opinion, to assume a former land connection between Mona and either Porto Rico or Santo Domingo, because all its native species may readily have reached it through natural agencies.

I append a list of the species collected as thus far determined, and have indicated in this list their known distribution, except that of the lichens and *Uredinales,* as regards Porto Rico, Curaçao, Hispaniola and the Bahamas, the nearest lands to Mona.

The names of new species, and new binomials, are printed in **heavy face** type.

List of Species inhabiting Mona Island

MONOCOTYLEDONS

VALOTA INSULARIS (L.) Chase
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

SYNTHERISMA DIGITATUM (Sw.) Hitchc.
Frequent in cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas.

PASPALUM CAESPITOSUM Fluegge
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

PASPALUM SIMPSONI Nash
Collected by Professor Stevens, not found by us: Porto Rico; Bahamas.

PANICUM UTOWANAEUM Scribn.
Frequent on the coastal plain and on the plateau: Porto Rico; Desecheo; [Cuba; Guadeloupe].

PANICUM BARBINODE Trin.
Sandy soil, Playa de Fajaro: native of South America. Naturalized in the West Indies.

PANICUM ADSPERSUM Trin.
Moist soil, coastal plain: Porto Rico; Bahamas.

PANICUM MAXIMUM Jacq.
Frequent on the coastal plain: Native of tropical Africa; naturalized in the West Indies.

LASIACIS DIVARICATA (L.) Hitchc.
Frequent in thickets, coastal plain and plateau: Porto Rico; Hispaniola; Bahamas.

CHAETOCHLOA SETOSA (Sw.) Scribn.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CHAETOCHLOA CAUDATA (Lam.) Scribn.
Occasional on the coastal plain: Desecheo; [Jamaica; Cuba; St. Thomas].

CHAETOCHLOA IMBERBIS (Poir.) Scribn.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CENCHROPSIS MYOSUROIDES (HBK) Nash
Frequent in cultivated ground on the coastal plain: Bahamas; Cuba.

CENCHRUS ECHINATUS L.
Common on the coastal plain and on sand dunes: Porto Rico; Hispaniola; Bahamas; Curacao.

CENCHRUS CAROLINIANUS Walt.
Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola; Bahamas; Curacao.

ARISTIDA BROMOIDES HBK.
Common on the coastal plain: Porto Rico; Bahamas; Curacao.

SPOROBOLUS VIRGINICUS (L.) Beauv.
Common on coastal sands and on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SPOROBOLUS ARGUTUS (Nees) Kunth
Frequent in moist soil on the coastal plain: Porto Rico; Hispaniola; Curacao.

CHLORIS PARAGUAIENSIS Steud.
Coastal plain, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

EUSTACHYS PETRAEA (Sw.) Desv.
Common on coastal sands and on the coastal plain: Porto Rico; Hispaniola; Bahamas.

ELEUSINE INDICA (L.) Gaertn.
Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

DACTYLOCTENIUM AEGYPTIUM (L.) Willd.
Cultivated ground, coastal plain: Porto Rico: Hispaniola; Bahamas; Curacao.

PAPPOPHORUM LAGUROIDEUM Schrad.
Wet soil, coastal plain, between Sardinera and Ubero: Desecheo [Cuba; St. Eustatius].

ERAGROSTIS CILIARIS (L.) Link
Common on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CYPERUS ELEGANS L.
Border of a marsh on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CYPERUS TENUIS Sw.
Occasional on the coastal plain: Porto Rico; Hispaniola.

CYPERUS LIGULARIS L.
Marsh, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

CYPERUS BRUNNEUS Sw.
Common on coastal sands: Porto Rico; Bahamas; Hispaniola; Curacao.

FIMBRISTYLIS SPATHACEA Roth.
Common on the coastal plain: Porto Rico; Bahamas; Hispaniola.

SCLERIA LITHOSPERMA (L.) Sw.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

? THRINAX PONCEANA O. F. Cook
Apparently this species, but determined from leaves only. Rare in thickets on the coastal plain, and not found either in flower or in fruit: Porto Rico.

TILLANDSIA UTRICULATA L.
Common on trees and on rocks: Porto Rico; Hispaniola; Bahamas; Curacao.

TILLANDSIA RECURVATA L.
Common on trees and shrubs: Porto Rico; Hispaniola; Bahamas; Curacao.

CALLISIA REPENS L.
Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Curacao.

COMMELINA VIRGINICA L. (*C. elegans* HBK.)
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

HYMENOCALLIS EXPANSA Herb.
Frequent in coastal sands. Determination from foliage only, therefore uncertain.

FURCRAEA TUBEROSA Ait. f.
Coastal plain between Sardinera and Ubero; probably introduced from Porto Rico. Determined from leaf specimens only: Porto Rico.

IBIDIUM LUCAYANUM Britton
Low woods, coastal plain near Sardinera: Porto Rico; Bahamas.

EPIDENDRUM PAPILIONACEUM Vahl
Common on shrubs and on the ground, coastal plain and plateau: Porto Rico; Hispaniola; recorded from the Bahamas.

DOMINGOA HYMENODES (Rchb. f.) Schltr.
On small trees between Sardinera and Ubero: Hispaniola [Cuba].

DICOTYLEDONS

PEPEROMIA HUMILIS (Vahl) A. Dietr.
Shaded limestone rocks near Sardinera. Plants with only the upper leaves opposite: Porto Rico; Hispaniola.

CELTIS TRINERVIA Lam.
Base of cliffs, Sardinera: Porto Rico; Hispaniola.

FICUS LAEVIGATA Vahl
Coastal plain and plateau; largest at the bases of cliffs: Porto Rico; Hispaniola.

FICUS STAHLII Warb.
Frequent along the bases of cliffs, eastern edge of the coastal plain. Trees up to 12 m. high. Determined from foliage only: Porto Rico.

CHLOROPHORA TINCTORIA (L.) Gaud.
Base of cliffs, Sardinera: Porto Rico; Hispaniola.

PILEA TRIANTHEMOIDES (Sw.) Lindl.
Frequent on the coastal plain: Porto Rico.

PILEA MICROPHYLLA (L.) Liebm.
Occasional on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

COCCOLOBIS UVIFERA (L.) Jacq.
Common on coastal sands and rocks: Porto Rico; Hispaniola; Bahamas; Curacao.

COCCOLOBIS OBTUSIFOLIA Jacq.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; ? Bahamas.

COCCOLOBIS LAURIFOLIA Jacq.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

COCCOLOBIS NIVEA Jacq.
Base of cliff, Sardinera: Porto Rico; Hispaniola.

AMARANTHUS TRISTIS L.
Waste and cultivated grounds on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

ACHYRANTHES INDICA (L.) Mill.
Frequent in cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

LITHOPHILA MUSCOIDES Sw.
Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola; Bahamas; Curacao.

CELOSIA NITIDA Vahl
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

MIRABILIS JALAPA L.
Waste grounds, uncommon: Porto Rico; Hispaniola; Bahamas.

BOERHAAVIA COCCINEA Mill.
Common on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

? PISONIA SUBCORDATA Sw.
Base of cliffs, Sardinera. Trees, 12 m. high or more, barren at the time of our visit and determination therefore uncertain: Porto Rico.

RIVINA HUMILIS L.
Common on the coastal plain on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

TRICHOSTIGMA OCTANDRUM (L.) H. Walt.
Frequent on the talus, vicinity of Sardinera, forming vines 20 m. long with trunks up to 1.5 dm. diameter: Porto Rico; Hispaniola.

PETIVERIA ALLIACEA L.
Occasional in thickets on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SESUVIUM PORTULACASTRUM L.
Common on coastal rocks and sands: Porto Rico; Hispaniola; Bahamas; Curacao.

TALINUM PANICULATUM (Jacq.) Gaertn.
Coastal plain, Sardinera: Porto Rico; Hispaniola.

PORTULACA PHAEOSPERMA Urban
Moist soil, coastal plain and plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

PORTULACA OLERACEA L.
Sandy soil, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas; Curacao.

NECTANDRA CORIACEA (Sw.) Griseb.
Base of limestone cliff, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

CASSYTHA AMERICANA Nees
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CLEOME GYNANDRA L.
Waste and cultivated grounds, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CAPPARIS CYNOPHALLOPHORA L. (*C. jamaicensis* Jacq.)
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CAPPARIS FLEXUOSA L. (*C. cynophallophora* Jacq.)
Common on the coastal plain: Porto Rico: Hispaniola; Bahamas.

LEPIDIUM VIRGINICUM L.
Common in waste and cultivated ground: Porto Rico; Hispaniola; Bahamas.

BRASSICA INTEGRIFOLIA (West) O. E. Schulz
Occasional in cultivated ground, coastal plain: Porto Rico; Bahamas.

CAKILE LANCEOLATA (Willd.) O. E. Schulz
Common on coastal sands: Porto Rico; Hispaniola; Bahamas.

PITHECOLOBIUM UNGIUS-CATI (L.) Benth.
Common in coastal thickets and occasional on the coastal plain. All specimens examined were spineless: Porto Rico; Hispaniola; Bahamas; Curacao.

CASSIA OCCIDENTALIS L.
Sandy soil, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas.

CHAMAECRISTA GRANULATA (Urban) Britton. (*Cassia portoricensis granulata* Urban.)
Common on the coastal plain and on sand dunes: Porto Rico.

CHAMAECRISTA DIFFUSA (DC.) Britton. (*Cassia diffusa* DC.)
Collected by Professor Stevens, not found by us: Porto Rico; Curacao.

? CAESALPINIA DOMINGENSIS Urban
On the plateau, Sardinera. Determined from description: Hispaniola.

GUILANDINA CRISTA (L.) Small
Occasional in coastal thickets: Porto Rico; Hispaniola; Bahamas.

GUILANDINA MELANOSPERMA (Urban) Britton. (*Caesalpinia melanosperma* Urban.)
Frequent on the coastal plain: St. Croix.

GUILANDINA DIVERGENS (Urban) Britton
Frequent on the coastal plain: Culebra [St. Thomas].

KRAMERIA IXINA L.
Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Curacao.

INDIGOFERA SUFFRUTICOSA Mill
Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CRACCA CINEREA (L.) Morong
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

STYLOSANTHES HAMATA (L.) Taub.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

MEIBOMIA SUPINA (Sw.) Britton
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

MEIBOMIA MOLLIS (Vahl) Kuntze
Occasional in cultivated ground on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

BRADBURYA VIRGINIANA (L.) Kuntze
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

GALACTIA STRIATA (Jacq.) Urban
Frequent on the coastal plain and on the plateau. A race with small leaflets and slender-peduncled racemes: Porto Rico; Hispaniola.

CANAVALIA LINEATA (Thunb.) DC.
Common on coastal sands: Porto Rico; Hispaniola; Bahamas.

? DOLICHOLUS MINIMUS (L.) Medic
Cultivated ground, Ubero. A race apparently of this species, with thick leaflets, strongly veined; not found either in flower or in fruit, the determination, therefore, uncertain.

DOLICHOLUS RETICULATUS (Sw.) Millsp.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

ERYTHROXYLON AREOLATUM L.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

GUAIACUM SANCTUM L.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

ZANTHOXYLUM PUNCTATUM Vahl
Coastal plain between Sardinera and Ubero: Porto Rico; Hispaniola.

AMYRIS ELEMIFERA L.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SURIANA MARITIMA L.
Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

ELAPHRIUM SIMARUBA (L.) Rose
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

STIGMAPHYLLON LINGULATUM (Poir.) Small
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola.

BYRSONIMA LUCIDA (Sw.) L. C. Rich
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

XYLOPHYLLA EPIPHYLLANTHUS (L.) Britton. (*Phyllanthus Epiphyllanthus* L.)
Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

PHYLLANTHUS NIRURI L.
Cultivated ground, coastal plain. Not collected: Porto Rico; Hispaniola; Bahamas; Curacao.

CROTON LUCIDUS L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

CROTON DISCOLOR Willd.
Common on the plateau: Porto Rico; Hispaniola.

CROTON BETULINUS Vahl
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola.

ARGITHAMNIA CANDICANS Sw.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

RICINUS COMMUNIS L.
Waste grounds, Ubero: Native of the Old World tropics.

HIPPOMANE MANCINELLA L.
Common on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CHAMAESYCE MONENSIS Millsp.
Limestone plateau, Ubero: Endemic.

CHAMAESYCE PORTORICENSIS (Urban) Millsp.
On limestone rocks, Ubero and Sardinera: Porto Rico.

CHAMAESYCE SERPENS (HBK.) Small
Moist soil, coastal plain and plateau: Porto Rico.

CHAMAESYCE HYPERICIFOLIA (L.) Millsp.
Common in cultivated ground on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CHAMAESYCE BUXIFOLIA (Lam.) Small
Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

AKLEMA PETIOLARIS (Sims) Millsp. (*Euphorbia petiolaris* Sims.)
Common on the coastal plain and on the plateau: Porto Rico.

POINSETTIA HETEROPHYLLA (L.) Kl. & Garcke
Sandy beach, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas.

PEDILANTHUS LATIFOLIUS Millsp. & Britton, sp. nov.

Shrubby, about 6 feet high, the young branches zig-zag, puberulent. Leaves ovate to ovate-orbicular, 4.5 inches long or less, very nearly sessile, dull-green, acute at the apex, roundish or subcordate at the base, very inconspicuously veined, glabrous, the midrib elevated but not keeled beneath. Inflorescence terminal, cymose, puberulent, bracteate; bracts lanceolate, acute, 3.5–4 x 2 lin., somewhat exceeding the peduncles; involucre about 10 x 4.5 lin., glabrous without and within, tube narrow anteriorly, main lobes lanceolate-oblong, rounded obtuse, ciliate at the apex, the accessory lobes equal or nearly so connivent with the main lobes to near the ciliate apices, fifth lobe elongate-ligulate, truncate ciliate, somewhat shorter than the accessory lobes and nearly closing the superior fissure of the tube; appendix large, strongly saccate, about one-third the length of the tube, split for half its length into two sarcous, ligulate slightly grooved and emarginate lobes; glands 4, of two sorts: the upper pair reniform at the summit of a broadly triangular stipe which is connivent with the surface of the appendix, anterior margins free and sharp; lower pair about one-half the size of the upper, discoid, peltate on a very short, free pedicel. Male pedicels numerous, glabrous; female pedicel glabrous; ovary glabrous; style 3-lobed at the apex, the stigmatic branches bifid. Fruit unknown.

Castle Point, Bermuda (*Brown & Britton, 820,* TYPE). Near Bath, Jamaica (*Britton, 3491*). Baracoa, Cuba (*Bemis*). Sanchez, Santo Domingo (*Rose, Fitch & Russell, 4397*). Mona Island (*Britton, Cowell & Hess, 1786*). Perhaps indigenous at the Santo Domingo locality cited; at all the others an evident escape from cultivation, or in gardens.

METOPIUM TOXIFERUM (L.) Krug & Urban
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

COMOCLADIA DODONAEA (L.) Urban
Frequent on the plateau: Porto Rico; Hispaniola.

RHACOMA CROSSOPETALUM L.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

GYMINDA LATIFOLIA (Sw.) Urban
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

SCHAEFFERIA FRUTESCENS Jacq.
Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CARDIOSPERMUM MICROCARPUM HBK.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

HYPELATE TRIFOLIATA Sw.
Coastal plain near Sardinera: Porto Rico; Hispaniola; Bahamas.

EXOTHEA PANICULATA (Juss.) Radlk.
Base of limestone cliffs, Sardinera: Porto Rico; Hispaniola; Bahamas.

DODONAEA EHRENBERGII Schl.
Common on the coastal plain and on the plateau: Hispaniola; Bahamas.

KRUGIODENDRON FERREUM (Vahl) Urban
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

REYNOSIA UNCINATA Urban
Frequent on the plateau: Porto Rico.

SARCOMPHALUS TAYLORI Britton
Occasional on the coastal plain: Bahamas.

COLUBRINA COLUBRINA (L.) Millsp.
Occasional along the base of the cliffs, coastal plain: Porto Rico; Hispaniola; Bahamas.

CISSUS TRIFOLIATA L.
Coastal thickets: Porto Rico; Hispaniola; Bahamas; Aruba.

CORCHORUS SILIQUOSUS L.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

CORCHORUS HIRSUTUS L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

ABUTILON UMBELLATUM (L.) Sweet
Frequent on the coastal plain: Porto Rico; Hispaniola; Curacao.

GAYOIDES CRISPUM (L.) Small
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

MALVASTRUM SPICATUM (L.) A. Gray
Cultivated ground, coastal plain: Porto Rico; Hispaniola; Curacao.

SIDA SPINOSA L.
Cultivated ground, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

SIDA GLABRA Mill. (*S. ulmifolia* Cav.)
Frequent on the coastal plain: Porto Rico; Hispaniola.

SIDA PROCUMBENS Sw.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

SIDA ACUMINATA DC.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

BASTARDIA VISCOSA (L.) HBK.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; recorded from Curacao.

MALACHRA CAPITATA L.
Occasional in cultivated ground, coastal plain: Porto Rico; Hispaniola.

PARITIUM TILIACEUM (L.) Juss.
Border of a swamp, Sardinera: Porto Rico; Hispaniola; Bahamas.

GOSSYPIUM BARBADENSE L.
Spontaneous after cultivation on the coastal plain. Apparently not native.

MELOCHIA TOMENTOSA L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

WALTHERIA AMERICANA L.
Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

AYENIA PUSILLA L.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas.

HELICTERES JAMAICENSIS Jacq.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

CLUSIA ROSEA Jacq.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

CANELLA WINTERANA (L.) Gaertn.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

TURNERA DIFFUSA Willd.
Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

PASSIFLORA SUBEROSA L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

PASSIFLORA FOETIDA L.
Sandy beach, Playa de Fajaro: Porto Rico; Hispaniola; Bahamas; Curacao.

CARICA PAPAYA L.
Common on the coastal plain about Sardinera, apparently established after cultivation. A race with small globose fruits. Original home unknown.

HARRISIA PORTORICENSIS Britton
Common on the talus and on the plateau: Porto Rico.

CEPHALOCEREUS ROYENI (L.) Britton & Rose
Common on the plateau: Porto Rico [St. Thomas to Antigua].

CACTUS INTORTUS Mill. (*Melocactus portoricensis* Suringar.)
Common on the plateau: Porto Rico [St. Thomas to Antigua].

CORYPHANTHA NIVOSA (Link) Britton. (*Mamillaria nivosa* Link.)
Very abundant on the plateau: Culebra [St. Thomas to Tortola; Antigua]; Bahamas.

OPUNTIA CATACANTHA Link & Otto
Common on the plateau; occasional on the coastal plain: Porto Rico [St. Thomas to Antigua].

OPUNTIA TAYLORI Britton
Top of cliff near Sardinera: Santo Domingo; Culebra [St. Thomas to Tortola].

OPUNTIA DILLENII (Ker.) Haw.
Common on the coastal plain and on the plateau. Not collected: Porto Rico; Hispaniola; Bahamas.

TERMINALIA CATAPPA L.
Occasional on coastal sands: Porto Rico; Hispaniola; [spontaneous after cultivation in the Bahamas].

CONOCARPUS ERECTA L.
Occasional in coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

BUCIDA BUCERAS L.
Coastal woods, Ubero: Porto Rico; Hispaniola; Bahamas.

LAGUNCULARIA RACEMOSA (L.) Gaertn.
Borders of marshes, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CALYPTRANTHES PALLENS (Poir.) Griseb.
Base of cliffs, Ubero: Porto Rico (?); Hispaniola; Bahamas.

EUGENIA BUXIFOLIA (Sw.) Willd.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

EUGENIA AXILLARIS (Sw.) Willd.
Frequent or occasional on the coastal plain, at the base of cliffs and on the plateau: Porto Rico; Hispaniola; Bahamas.

EUGENIA RHOMBEA (Berg.) Krug. & Urban
Coastal plain between Sardinera and Ubero: Porto Rico; Hispaniola; Bahamas.

ANAMOMIS FRAGRANS (Sw.) Griseb.
Occasional on the coastal plain: Porto Rico; Hispaniola. Recorded from the Bahamas.

JACQUINIA BARBASCO (Loefl.) Mez.
Common in coastal thickets and occasional on the coastal plain: Porto Rico; Hispaniola; Curacao.

? DIPHOLIS
Coastal plain, Sardinera. A tree about 12 m. high, in foliage only.

BUMELIA OBOVATA (Lam.) DC.
Frequent on the coastal plain. Not in flower or fruit at the time of our visit: Porto Rico; Hispaniola; Curacao.

PLUMIERA OBTUSA L.
Common on the coastal plain and on the plateau: Hispaniola; Bahamas.

RAUWOLFIA TETRAPHYLLA L. (*R. nitida* Jacq.)
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

ECHITES AGGLUTINATA Jacq.
Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola.

URECHITES LUTEA (L.) Britton
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

METASTELMA (undetermined)
Coastal rocks, Ubero.

METASTELMA (undetermined)
Occasional on the coastal plain and on the plateau.

EVOLVULUS GLABER Spreng.
Moist soil, coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

JACQUEMONTIA JAMAICENSIS (Jacq.) Hall. f.
Occasional on coastal sands: Porto Rico; Hispaniola; Bahamas.

JACQUEMONTIA PENTANTHA (Jacq.) D. Don
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

OPERCULINA AEGYPTIA (L.) House
Cultivated ground, coastal plain: Porto Rico; Hispaniola; Curacao.

? EXOGONIUM MICRODACTYLUM (Griseb.) House
Occasional on the plateau. Specimen insufficient for certain determination.

IPOMOEA PES-CAPRAE (L.) Roth.
Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

IPOMOEA TRILOBA L.
Frequent in cultivated ground on the coastal plain: Porto Rico; Bahamas.

CALONYCTION GRANDIFLORUM (Jacq.) Choisy. (*Ipomoea tuba* G. Don.)
Frequent in coastal thickets: Porto Rico; Hispaniola; Bahamas; Curacao.

VARRONIA GLOBOSA Jacq.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

BOURRERIA SUCCULENTA Jacq.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Curacao.

MALLOTONIA GNAPHALODES (L.) Britton.[1] (*Tournefortia gnaphalodes* R. Br.)
Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Curacao.

TOURNEFORTIA HIRSUTISSIMA L.
Base of limestone cliffs, Sardinera: Porto Rico; Hispaniola.

TOURNEFORTIA MICROPHYLLA Bert.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola.

HELIOTROPIUM CRISPIFLORUM Urban
Moist soil, coastal plain: Porto Rico. Closely resembles the Porto Rico plant but is lower and with shorter internodes; no flowering specimens were obtained.

HELIOTROPIUM PARVIFLORUM L.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

LANTANA SCABRIDA Ait.
Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola. Apparently specifically distinct from *L. Camara* L.

LANTANA INVOLUCRATA L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

VALERIANODES JAMAICENSIS (L.) Medic
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

VALERIANODES STRIGOSA (Vahl) Kuntze
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola.

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[1] **Mallotonia** (Griseb.) Britton, gen. nov.
Tournefortia Section *Mallotonia* Griseb. Fl. Brit. W. I. 483. 1861.
Type species: *Tournefortia gnaphalodes* (L.) R. Br.

SALVIA SEROTINA L. (*S. micrantha* Vahl)
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

HYPTIS PECTINATA (L.) Poit.
Cultivated ground on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

SOLANUM NIGRUM L. (*S. americanum* Mill.)
Cultivated ground, Sardinera: Porto Rico; Hispaniola; Bahamas; Curacao.

SOLANUM VERBASCIFOLIUM L.
Occasional at the bases of cliffs and on the coastal plain: Porto Rico; Hispaniola; Bahamas.

BRAMIA MONNIERIA (L.) Drake. (*Herpestis Monniera* HBK.)
Border of a pool, Sardinera: Porto Rico; Hispaniola; Bahamas.

CAPRARIA BIFLORA L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

SCOPARIA DULCIS L.
In moist soil on the coastal plain: Porto Rico; Hispaniola; Bahamas.

TABEBUIA HETEROPHYLLA (DC.) Britton. (*Raputia* (*?*) *heterophylla* DC.; *Tabebuia triphylla* DC., not *Bignonia triphylla* L.)
Frequent on the coastal plain and on the plateau. Leaves 1-foliolate to 5-foliolate: Porto Rico.

TABEBUIA LUCIDA Britton, sp. nov.
A tree up to 5 m. high. Leaves 3–5-foliolate; petioles slender, lepidote, 6 cm. long or less; petiolules of the larger, upper leaflets slender, lepidote, 8–20 mm. long; lower leaflets sessile or nearly so; leaflets thin-coriaceous, narrowly oblong or oblong-oblanceolate, 5–10 cm. long, 1–3 cm. wide, shining, reticulate-veined and lepidote on both sides, rather abruptly acute or obtusish at the apex, narrowed or obtuse at the base; flowers clustered; pedicels lepidote; calyx about 14 mm. long, 2-lipped; corolla pink, glabrous, about 5 cm. long, its cylindric tube 5–6 mm. long, its narrowly campanulate throat about 3 cm. long, its limb about 1.5 cm. long, the lobes nearly entire.
Limestone cliffs, Sardinera, Mona Island, Porto Rico (*Britton, Cowell and Hess, 1686*).

SESAMUM ORIENTALE L.
Cultivated ground, coastal plain. Native of the East Indies.

BLECHUM BROWNEI Juss.
Shaded rocks, Sardinera: Porto Rico; Hispaniola; Bahamas.

JUSTICIA PERIPLOCIFOLIA Jacq.
Occasional on the coastal plain, a narrow-leaved race: Porto Rico; Hispaniola.

JUSTICIA PECTORALIS Jacq.
Border of pool, Sardinera: Porto Rico; Hispaniola.

PLANTAGO MAJOR L.
Cultivated ground, coastal plain. Not collected. Native of the Old World.

EXOSTEMA CARIBAEUM (Jacq.) R. & S.
Frequent on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

RANDIA ACULEATA L.
Common on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

GUETTARDA ELLIPTICA Sw.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

STENOSTOMUM ACUTATUM DC.
Frequent on the coastal plain and on the plateau: Porto Rico; Curacao.

ERITHALIS FRUTICOSA L.
Common on sand dunes, on the coastal plain and occasional on the plateau: Porto Rico; Hispaniola; Bahamas; Curacao.

CHIOCOCCA ALBA (L.) Hitchc.
Occasional on the coastal plain and on the plateau: Porto Rico; Hispaniola; Bahamas.

STRUMPFIA MARITIMA Jacq.
Limestone plateau near Ubero, frequent: Porto Rico; Hispaniola; Bahamas; Curacao.

PSYCHOTRIA UNDATA Jacq.
Occasional on the coastal plain: Porto Rico; Hispaniola; Bahamas.

ERNODEA LITTORALIS Sw.
Common on coastal sands: Porto Rico; Hispaniola; Bahamas; Bonaire.

SPERMACOCE TENUIOR L.
Frequent on the coastal plain: Porto Rico; Hispaniola; Bahamas; Curacao.

CUCUMIS ANGURIA L.
Cultivated ground, Sardinera: Porto Rico; Hispaniola; Curacao.

EUPATORIUM ODORATUM L.
Common on the coastal plain: Porto Rico; Hispaniola; Bahamas.

EUPATORIUM ATRIPLICIFOLIUM Lam.
Coastal rocks, Sardinera: Porto Rico; recorded from Hispaniola and from the Bahamas.

LEPTILON PUSILLUM (Nutt.) Britton
Common in waste and cultivated grounds, coastal plain: Porto Rico; Hispaniola (?); Bahamas.

LEPTILON BONARIENSE (L.) Small
Cultivated ground, Sardinera: Porto Rico; Hispaniola.

PLUCHEA PURPURASCENS (Sw.) DC.
Borders of marshes, coastal plain: Porto Rico; Hispaniola; Bahamas.

BORRICHIA ARBORESCENS (L.) DC.
Occasional on coastal rocks: Porto Rico; Hispaniola; Bahamas.

WEDELIA PARVIFLORA L. C. Rich
Common on the coastal plain: Porto Rico.

ELEUTHERANTHERA RUDERALIS (Sw.) Sch. Bip.
Cultivated ground, coastal plain: Porto Rico; Hispaniola. Erroneously recorded from the Bahamas.

BIDENS CYNAPIIFOLIA HBK.
Collected by Professor Stevens, not found by us: Porto Rico; Hispaniola; Bahamas; Curacao.

PTERIDOPHYTA

(Determined by Miss Margaret Slosson)

ADIANTUM FRAGILE Sw.
Limestone cliff, Sardinera: Porto Rico; Hispaniola.

ACROSTICHUM AUREUM L.
Border of pool near Sardinera. Determined from barren leaf specimen: Porto Rico; Hispaniola; Bahamas; Curacao.

CYCLOPELTIS SEMICORDATA (Sw.) J. Smith
Shaded limestone rocks, Sardinera: Porto Rico; Hispaniola.

MUSCI

(Determined by Elizabeth G. Britton and R. S. Williams)

THUIDIUM INVOLVENS (Hedw.) Mitt.
On dead wood and shaded rocks: Porto Rico; Hispaniola.

TORTULA AGRARIA Sw.
On the ground near Sardinera: Porto Rico; Hispaniola; Bahamas.

HYOPHILA GUADELUPENSIS Broth.
Wet soil on the coastal plain between Sardinera and Ubero: Guadeloupe; Montserrat.

BRYUM MICRODECURRENS E. G. Britton
Wet soil on the coastal plain between Sardinera and Ubero: St. Thomas.

CALYMPERES RICHARDI C. Muell.
On tree trunks, base of cliff, Sardinera: Porto Rico; Hispaniola; Bahamas.

CALYMPERES (an apparently undescribed species)
On *Bourreria,* Ubero; Hispaniola.

HEPATICAE

JUNGERMANNIACEAE

(Determined by Professor A. W. Evans)

BRACHIOLEJEUNEA BAHAMENSIS Evans
On limestone, Ubero; on trunk of *Gymnanthes,* Sardinera: Bahamas.

MASTIGOLEJEUNEA AURICULATA (Wils. & Hook.) Schiffn.
On shaded limestone and on dead wood, Sardinera: Porto Rico; Bahamas.

LEJEUNEA (barren and undeterminable)
On shaded limestone, bark and dead wood.

FRULLANIA SQUARROSA (R. B. & U.) Dumort.
On trunks and logs on the coastal plain: Porto Rico; Bahamas.

FRULLANIA (barren and undeterminable)
On dead wood, Sardinera.

RICCIACEAE

(Contributed by Dr. Marshall Avery Howe)

RICCIA BRITTONII, sp. nov.
Thallus simple or once dichotomous, forming irregularly gregarious patches, oblong-ovate, linguiform, or obovate, 2–5 mm. x 1–2 mm., subacute or obtuse, conspicuously alveolate-reticulate and light green above, with a scarious-albescent border 80–175 μ wide, concolorous or very commonly brownish laterally and ventrally; median sulcus deep and acute except in older parts; ventral scales small, inconspicuous, hyaline, rarely exceeding the thin membranous ascending thallus-margins; transverse sections mostly 1.5–2.0 times as wide as high, the ventral outlines semi-orbicular in younger parts, becoming flattened in the older; cells of the primary dorsal epidermis cylindric dome-shaped or subhemispheric, soon collapsing, leaving shallow slightly indurated more or less persistent cup-like vestiges; monoecious; antheridial ostioles scarcely elevated; spores brown, becoming subopaque, soon exposed, 100–145 μ in maximum diameter, rather ob-

scurely or sometimes distinctly angled, often flattened, destitute of wing-margins, almost uniformly areolate over the whole surface, with age showing in profile obtuse or truncate papillae 3–5 μ long, areolae mostly 10–18 μ wide.

On wet, sunny soil, accompanied by *R. violacea*, between Sardinera and Ubero, Mona Island, February, 1914, *Britton, Cowell, & Hess, 1749a.*

Riccia Brittonii exhibits certain points of contact with *Riccia sorocarpa* Bisch. and *R. dictyospora* M. A. Howe.[1] It is close to *R. sorocarpa* in vegetative characters, though differing in the wider, more pronounced, scarious-albescent thallus-margins and slightly in the character of the epidermis, but it departs widely from this species in the spores, which are much larger (100–145 μ *vs.* 70–90 μ, max. diam.), are destitute of wing-margins, and commonly have the areolae of the inner faces almost as well and regularly developed as those of the outer face. From *Riccia dictyospora*, the species differs in the less elongate thallus (2–5 mm. *vs.* 4–10 mm.), the albescent instead of dark purple thallus-margins and scales, the more semicircular and less parabolic outlines of transverse sections of the thallus, and in the larger spores (100–145 μ *vs.* 95–116 μ, max. diam.), with larger areolae (10–18 μ *vs.* 8–12 μ.

RICCIA VIOLACEA, sp. nov.

Thallus simple or 1–3 times dichotomous, irregularly gregarious, 1.5–4.0 mm. long, the main segments oblong-obovate or linguiform, 0.65–1.15 mm. broad, rather obscurely and finely areolate and dark green above, dark violet or blackish at margins and on sides, this color encroaching on the surface here and there, especially in the older parts and at the sinuses; median sulcus shallow or obsolete except at apex; ventral scales very short or rudimentary, dark violet, rarely overlapping, commonly divided into a series of small irregular often tooth-like lamellae, each consisting of only a few cells; transverse sections plano-convex, somewhat flattened-semiorbicular, or occasionally biconvex, 1.5–2.0 times as wide as high; the margins obtuse or rounded, bearing especially toward the apex numerous or occasional violet or sometimes hyaline conic or subcylindric acute or obtuse papillae 30–110 μ long and 25–45 μ broad at base; cells of the primary dorsal epidermis subhemispheric or mammiform, soon collapsing and leaving inconspicuous vestigia; remaining parts unknown.

On wet, sunny soil, accompanied by *Riccia Brittonii*, between Sardinera and Ubero, Mona Island, February, 1914, *Britton, Cowell, & Hess, 1749b.*

In size, habit, and color, *R. violacea* is somewhat suggestive of *R. nigrella* DC., but the thallus has papillae or very short cilia at the margins, which are wanting in *R. nigrella*, the scales are much smaller, more rudimentary and more divided than in *R. nigrella*, and the cells of the primary epidermis are much less persistent. Its nearest affinity is doubtless with *R. atromarginata* Levier, which is known from Sicily, Sardinia, and Greece; from this it appears to differ (if one may judge from the descriptions alone) in the obtuse thallus-margins, the very short, rudimentary, divided, rarely overlapping scales, and the commonly violet papillae which are confined to the margins and sides while in *R. atromarginata* the hyaline incurved "pili" are said to cover also the anterior dorsal surface.

LICHENES

(Determined by Professor Lincoln W. Riddle)

ARTHOPYRENIA

On *Coccolobis obtusifolia*, Ubero.

PYRENULA

On bark, Sardinera.

MELANOTHECA CRUENTA (Mont.) Muell. Arg.

On *Gymnanthes*, Sardinera.

TRYPETHELIUM ELUTERIAE Spreng.

On *Pithecolobium*, Sardinera, and on *Coccolobis obtusifolia*, Ubero.

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[1]Bull. Torr. Bot. Club 28: 163. 1901.

TRYPETHELIUM MASTOIDEUM Ach.
On *Pithecolobium*, Sardinera.

TRYPETHELIUM OCHROLEUCUM Nyl.
On *Zanthoxylum*, between Sardinera and Ubero.

OPEGRAPHA
On *Ficus*, Sardinera; on *Calyptranthes*, Ubero.

GRAPHIS AFZELII Ach.
On *Zanthoxylum*, between Sardinera and Ubero; on *Pithecolobium*, Sardinera.

GRAPHIS
Collected by Professor Stevens.

CHIODECTON
On *Plumiera*, Sardinera.

LEPTOTREMA
On dead wood, Sardinera.

CLADONIA FIMBRIATA var. CONIOCRAEA (Floerke) Wainio
On dead log, Sardinera.

OMPHALARIA LINGULATA Tuck.
On limestone, Sardinera.

OMPHALARIA POLYGLOSSA Nyl.
On exposed limestone, Ubero.

OMPHALARIA
On limestone, Ubero.

COLLEMA
On limestone rocks, Sardinera.

LEPTOGIUM (sterile and indeterminable)
On *Torrubia*, Sardinera.

PARMELIA TINCTORUM Despv.
On a tree trunk.

PARMELIA SULPHURATA Nees and Flot.
On a dead log, Sardinera.

RAMALINA MONTAGNEI De Not.
On a twig, Sardinera. Collected also by Professor Stevens.

RAMALINA COMPLANATA (Sw.) Ach.
On a twig, Sardinera.

PYXINE PICTA (Sw.) Tuck.
On *Pithecolobium*, Sardinera; on *Zanthoxylum*, between Sardinera and Ubero.

PHYSCIA SPECIOSA (Wulf.) Nyl. (A small form)
On *Ficus*, Sardinera.

PHYSCIA ALBA Fee
On *Calyptranthes*, Ubero; also, not typical, on *Torrubia*, Sardinera.

The collection also contains a sterile plant near *Omphalaria Wrightii* Tuck., from wet, sunny soil between Sardinera and

Ubero, a sterile species of the *Dermatocarpaceae* growing on limestone at Ubero, and three other sterile and undeterminable specimens.

BASIDIOMYCETES
(Determined by Dr. W. A. Murrill)

LENTINUS CRINITUS (L.) Fries
On dead wood, Ubero: Porto Rico; Bahamas.

SCHIZOPHYLLUM ALNEUM (L.) Schroet.
Frequent on dead wood: Porto Rico; Bahamas.

DAEDALEA AMANITOIDES Beauv.
On dead wood, Ubero: Porto Rico; Bahamas.

INONOTUS CORROSUS Murr.
On dead wood, Sardinera: Porto Rico; Bahamas.

PYROPOLYPORUS DEPENDENS Murr.
On dead wood: Porto Rico; Bahamas.

POGONOMYCES HYDNOIDES (Sw.) Murr.
On dead wood: Porto Rico; Bahamas.

PYCNOPORUS SANGUINEUS (L.) Murr.
Frequent on dead wood at base of escarpment: Porto Rico; Bahamas.

CORIOLOPSIS RIGIDA (Berk. & Mont.) Murr.
On dead wood, Sardinera: Porto Rico; Bahamas.

CORIOLUS PINSITUS (Fries) Pat.
On dead wood: Porto Rico; Bahamas.

XYLARIA
On dead log, Ubero.

UREDINALES
(Determined by Professor J. C. Arthur)

COLEOSPORIUM PLUMIERAE Pat.
On *Plumiera obtusa.*

KUEHNEOLA GOSSYPII (Lagerh.) Arth.
On *Gossypium barbadense.*

PUCCINIA CENCHRI Dietr. & Holw.
On *Cenchrus.*

PUCCINIA CRASSIPES B. & C.
On *Ipomoea triloba* L.

PUCCINIA EUPHORBIAE P. Henn.
On *Aklenea petiolaris* (Sims) Millsp.

PUCCINIA INFLATA Arth.
On *Stigmaphyllon lingulatum* (Poir.) Small

PUCCINIA LATERITIA B. & C.
On *Ernodea littoralis* Sw.

PUCCINIA URBANIANA P. Henn.
On *Valerianodes strigosa* (Vahl) Kuntze

UREDO BIOCELLATA Arth.
On *Pluchea purpurascens* (Sw.) Kuntze

UREDO CAMELIAE Mayor.
On *Chaetochloa setosa.*

Many parasitic fungi collected by Professor Stevens have not yet been determined.

ALGA
(Determined by Professor N. Wille)

SCYTONEMA OCELLATUM Lyngb.
Flat limestone plateau, Ubero.

RECAPITULATION

Species indicated in the foregoing list	292
Deduct thallophytes (distribution little known)	47
	245
Deduct undetermined and doubtfully determined species	12
	233
Deduct certainly introduced species	8
	225
Deduct endemic species	4
	221
In common with Porto Rico	211
" " " Hispaniola	185
" " " Bahamas	155
" " " Curacao	87

SPECIES OTHER THAN ENDEMIC ONES AND THALLOPHYTES NOT KNOWN ON PORTO RICO (INCLUDING DESECHEO, CULEBRA AND VIEQUES)

Cenchropsis myosuriodes: Bahamas; Cuba.
Domingoa hymenodes: Hispaniola; Cuba.
Caesalpinia domingensis: Hispaniola.
Guilandina melanosperma: St. Croix.
Dodonaea Ehrenbergii: Bahamas; Hispaniola; Cuba.

Sarcomphalus Taylori: Bahamas.
Plumiera obtusa: Hispaniola; Bahamas; Cuba.
Brachiolejeunea bahamensis: Florida; Bahamas.
Hyophila guadelupensis: Guadeloupe; Montserrat.
Bryum subdecurrens: St. Thomas.

EXPLANATION OF PLATE

PLATE 1

Fig. 1. Escarpment, Mona Island, showing openings of caves.

Fig. 2. Part of Mona Island from the ocean, showing escarpments and plateau.

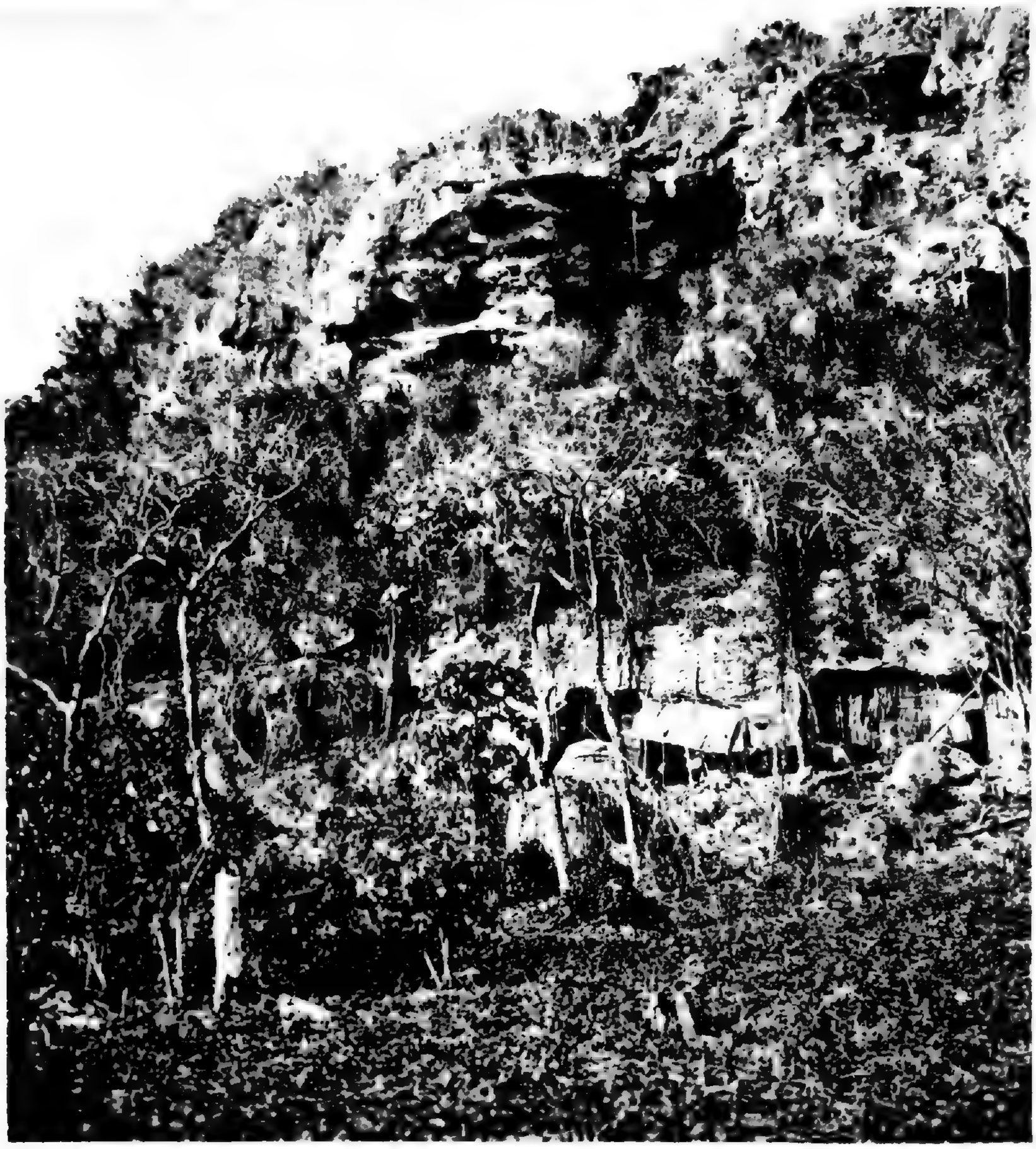

Fig. 1

Fig. 2

BRITTON—VEGETATION OF MONA ISLAND

COCKAYNE, BOSTON

EXPLANATION OF PLATE

PLATE 2

Fig. 1. Escarpment and tables, Mona Island.
Fig. 2. Coastal thicket, Mona Island.

THE FLORA OF NORWAY AND ITS IMMIGRATION

N. WILLE

Professor at the Christiania University

The phytogeographical investigations in a country may be carried on in the following three main directions:

Floristic phytogeography, or an investigation into the geographical distribution of the plant species. The result of this work should be charts of the distribution in the country of the various species. In a country with such varied conditions of life as Norway, this is a very comprehensive and very arduous task, requiring an infinitude of detailed investigations in all parts of the country.

Ecological phytogeography, which endeavors to find out how and why the different species of plants in various places and under various conditions of life come together in plant-communities. This branch of science, which was founded by Professor E. Warming, must be based upon phytoanatomy and phytophysiology, as the connection between the organization of the vegetable species and their external conditions of life must be investigated. Investigations such as these may yield interesting results in all countries, and are most easily carried on where the conditions of life are uniform over wide areas; but in a country like Norway, with its varied conditions, they present very great difficulties.

Historical phytogeography has for its aim the investigation of the changes that in the course of time have taken place in the vegetation of a country—to find out, for instance, when and whence important species have immigrated, how quickly they have spread, why others, that had formerly been more widely distributed, had a more restricted distribution in a later period, etc., etc.

With regard to this last branch of science, the Scandinavian countries, Denmark, Finland, Norway, and Sweden, present peculiarly favorable conditions; for there is no doubt that these countries were formerly buried under a continu-

ous covering of ice, which destroyed all vegetation except perhaps the most hardy. All other species of plants have immigrated subsequently from the neighboring countries, which were not covered with ice during the Glacial Epoch, and could therefore afford a dwelling-place for a more or less abundant flora.

In the following pages I shall endeavor to give an account of the results at which historical phytogeography may be said to have arrived as far as Norway is concerned.

SURVEY OF THE DISTRIBUTION OF THE NORWEGIAN FLORA

It will first be necessary, however, to give a general account of the most important points regarding the composition and distribution of the Norwegian flora throughout the country. I shall here consider only the vascular plants (about 1,500 species), however, as the distribution of the lower plants is not sufficiently known to enable us to draw definite conclusions.

The area of Norway is about 125,000 square miles, stretching from latitude 57° 58′ 43″ north to latitude 71° 10′ 20″ north. The conditions for plant life will thus be very different in the southern and northern parts of the country. But in addition to this, there is a great difference between the climate in the east and that in the west of southern Norway. In the valleys of the East Country, there is a very pronounced inland climate, with hot summers and a winter temperature that falls below —40°C., while on the west coast region there is a low summer temperature, but a mean January temperature of sometimes more than 2°C.

The most important condition affecting the distribution of plants in Norway is the temperature. In this connection we shall in the first place speak of the lowest winter temperature that the plants can survive. J. Holmboe ('13) has shown that the distribution of *Ilex aquifolium* in Norway coincides closely with the January isotherm for 0°C. Herbaceous plants which die down in the winter may of course be independent of the lowest winter temperature, as they are covered with snow; but they are not entirely independent of

the spring and autumn temperature. Plants are also in a great measure dependent on the height of the temperature in the period of vegetation, which, in Norway, comprises in the main the four months, June, July, August, and September.

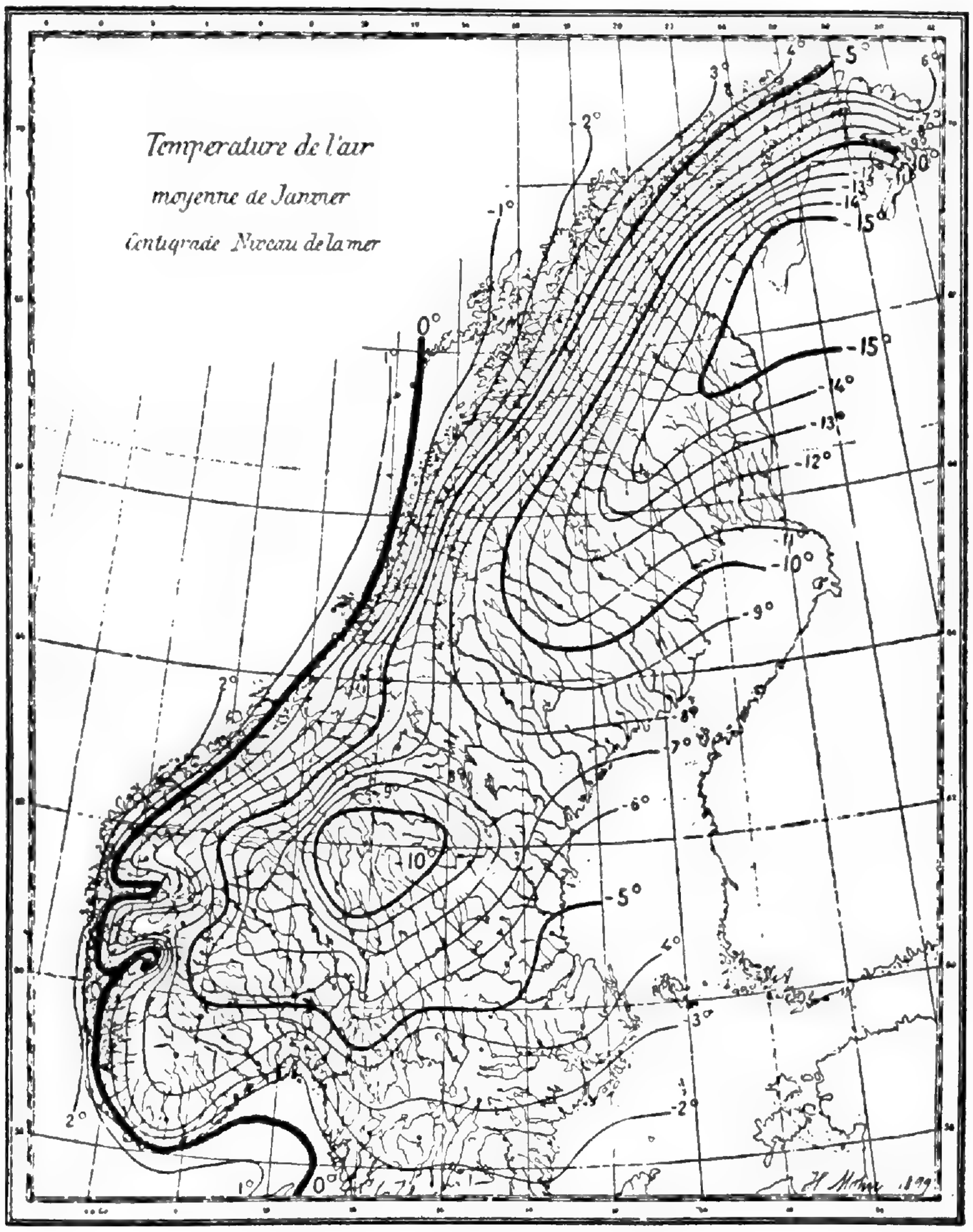

Fig. 1. Isotherms for January.

In this way, the conditions prevailing in Norway are very varied, the July isotherm for Christiania being 17°C., while for the west coast it is only from 12 to 14°C.

A. Helland ('12) has calculated that where the mean summer temperature in Norway is less than 13°C., the fruit

trees yield nothing worth mentioning; and where it is less than 11°C., the cultivation of grain is uncertain. The minimum limits of the necessary mean summer heat for the following wild Norwegian trees and shrubs appears to be as

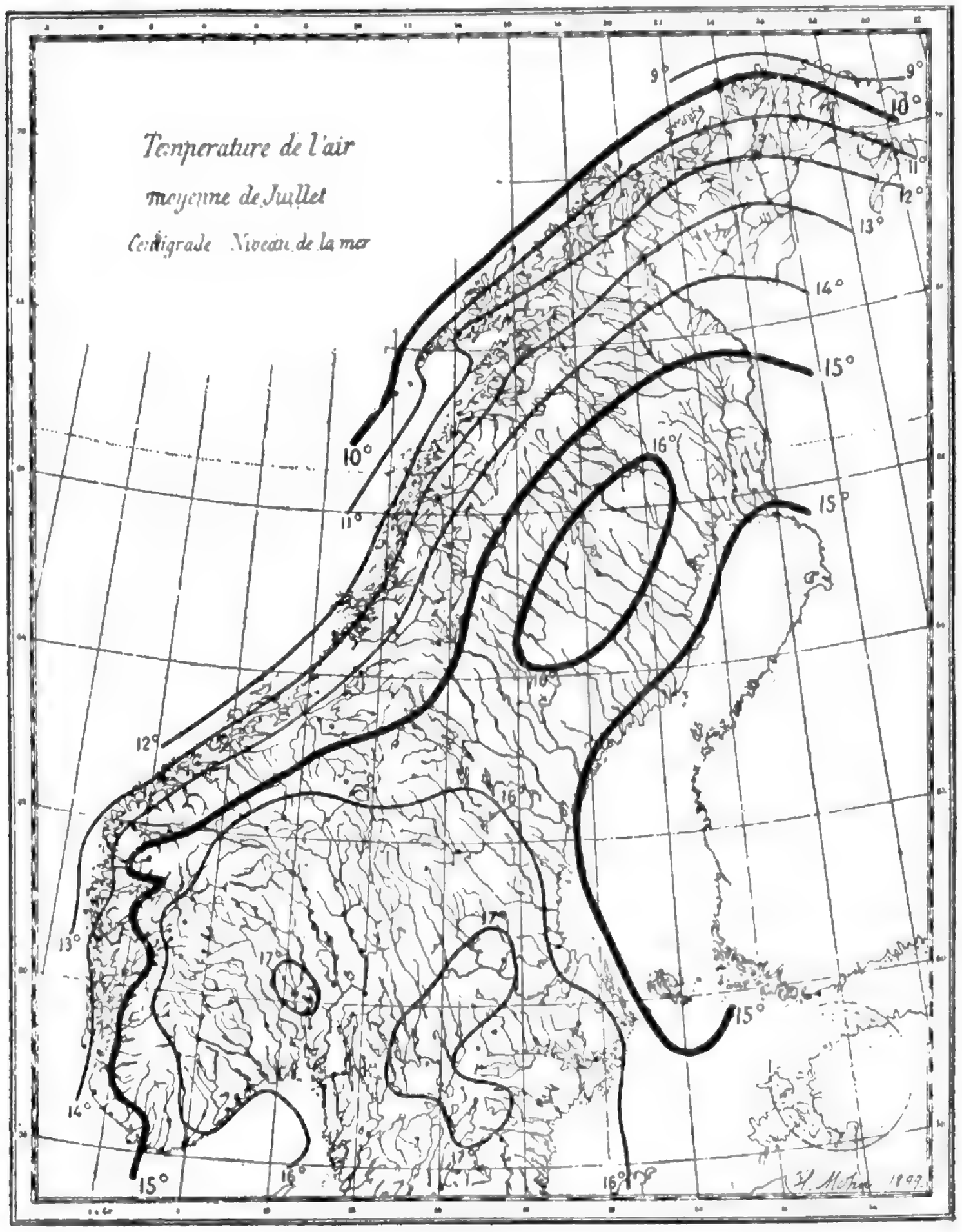

Fig. 2. Isotherms for July.

follows: for *Fagus sylvatica*, 13.4°C.; *Quercus pedunculata*, 12.6°C.; *Corylus Avellana*, *Acer platanoides*, and *Tilia cordata*, 12.5°C.; *Alnus glutinosa* and *Fraxinus excelsior*, 12.4°C.; *Sorbus Aria* and *Ulmus montana*, 11.2°C.; *Picea excelsa* and *Pinus sylvestris*, 8.4°C.; *Alnus incana*, *Prunus Padus*,

and *Sorbus Aucuparia*, 7.7°C.; *Populus tremula*, 7.6°C.; *Betula odorata*, 7.5°C.; *Juniperus communis* var. *nana*, 5.3° C.; and *Betula nana*, 4.3°C.

As the mean temperature of summer decreases with increasing height above sea-level very nearly 0.6°C. per 330 feet, the distribution of plants is greatly influenced by the circumstance that Norway is a mountainous country, its highest mountain, Galdhöpiggen, being 8,095 feet in height, and thus within the region of perpetual snow. But a peculiarity of the Norwegian mountains is that they form broad (as much as sixty-two miles broad), undulating mountain plateaus, which are intersected by deep or shallow valleys, where there are narrow lakes or small rivers. The edge of these mountain plateaus, in the south of Norway, lies at a height of from 2,950 to 3,280 feet above the sea, so that *Picea excelsa* and *Pinus sylvestris* disappear slightly below this height, the edge of the plateaus and the lowest valleys that intersect them being covered with *Betula odorata*. The great mass of the mountain plateaus, which rise above the birch-limit, is thus treeless.

It has been calculated that there are 26,333 square miles of forest land in Norway, of which 73 per cent consists of *Picea excelsa* and *Pinus sylvestris*, while the remaining 27 per cent is mainly *Betula odorata* with a little *Betula verrucosa*, *Quercus pedunculata*, and *Q. sessiliflora*, and a very little *Fagus sylvatica* in the south.

The vegetation limits are lower not only toward the north, as one would expect, but also toward the west, as they are lower near the sea than inland. This will be seen from the following height-limits in feet:

	Snow-line ft.	Birch-limit ft.	Pine-limit ft.
Gausta in Telemarken (south of Norway)	....	3450	3024-3113
Vos (west of Norway)	3936	3359	1994
Snehaetta, in the Dovre Mountains (central Norway)	5375	3464	2880
Rödö in Helgeland (just within the Arctic Circle)	3280	....	777
Alten in Finmark (70° N. Lat.)	3516	1476	777-1023

The distribution northward and height above sea-level of the various vegetable species, will be dependent mainly upon the temperature during the summer months.

The rainfall, which in various other countries plays so important a part as a factor in vegetation, is of less import-

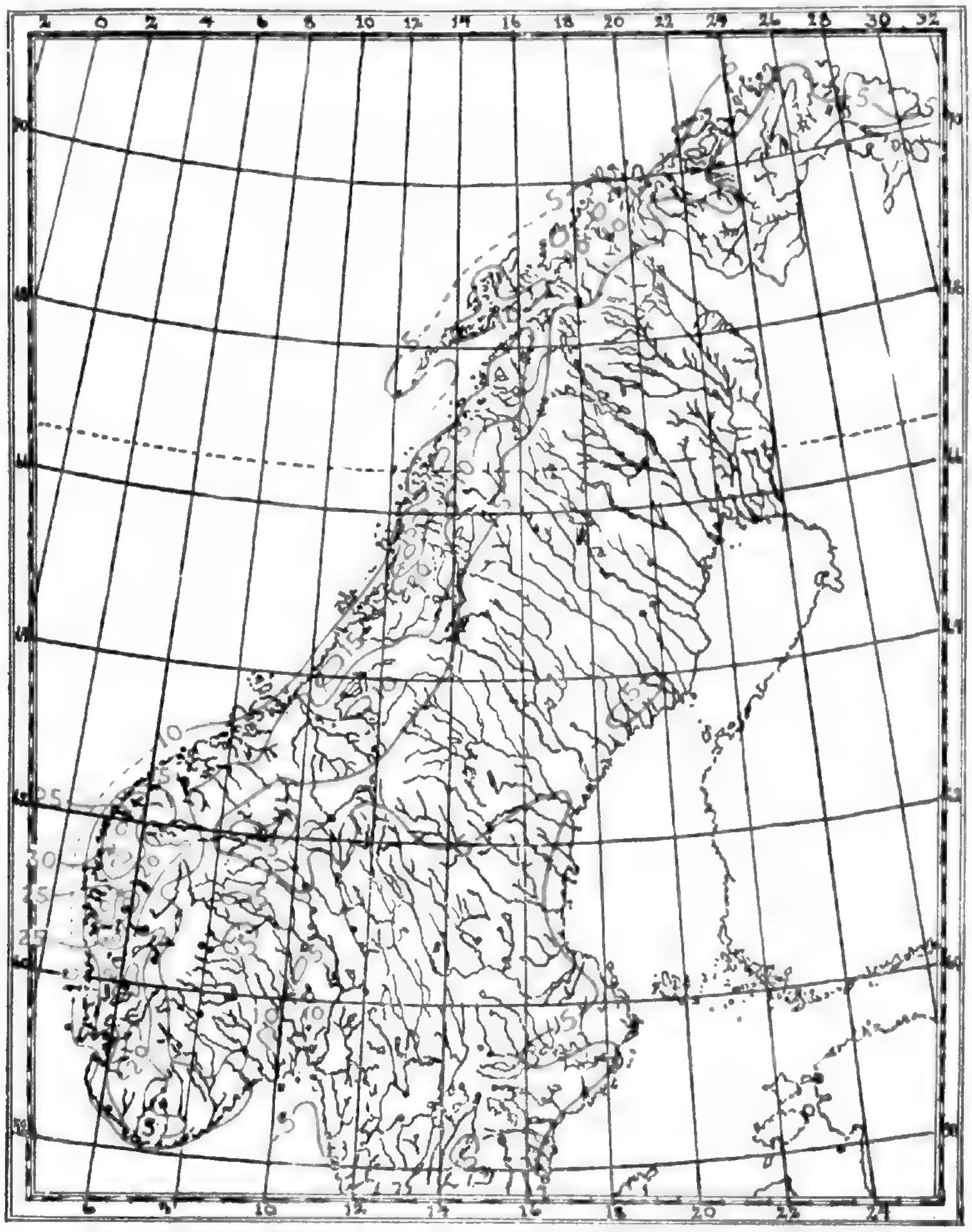

Fig. 3. The annual rainfall in Norway (in centimeters).—After M. Mohn.

ance in Norway, as even on the Dovre Mountains, where the rainfall is smallest (about 300 mm. per annum), there is sufficient rain to occasion, on account of the inconsiderable evaporation, swamps and peat-bogs, where even entirely hydrophilous communities thrive.

It was formerly supposed that the largest rainfall was on the outermost islands off the west coast of Norway, and that this was the cause of the Atlantic vegetation that is found there, with such characteristic plants as *Hymenophyllum peltatum, Erica cinerea, Scilla verna, Vicia Orobus,* etc. But more recent investigations have shown that the rainfall is greater a little way in from the coast, where the mountains begin. In Hovlandsdal, near the Sogne Fjord, a mean rainfall has been observed of 3,178 mm., and at Skaanevik, near the Folgefon, 2,945 mm., whereas the outermost islands off Bergen show a rainfall of only 1,300 mm., and off Florö of 1,900 mm. It is, therefore, clear that the occurrence of the above-mentioned Atlantic plants on the outermost islands is due not to a larger rainfall, but to a milder winter temperature.

There are, of course, species of plants that cannot thrive in the great humidity of the West Coast; but as there are also localities with comparatively dry soil, it may be rather the low summer temperature than the large rainfall that prevents them from thriving.

The importance of the soil for vegetable growth appears to depend, in Norway, mainly upon whether the soil is rich, or deficient, in lime. In addition to its chemical influence, a calcareous subsoil, especially when consisting of calcareous slate or limestone, is of consequence from the fact that it forms a warm soil. In Norway, therefore, most of the southern species are found only in the limestone country surrounding the Skien Fjord and the upper part of the Kristiania Fjord.

The terrestrial plants of Norway may be divided into five zones, according to the ability of the plants to ascend the mountains and extend northward in their growth, that is to say, according to their dependence on the mean temperature of the summer. These zones are here indicated by the upper limit of a characteristic species of plant.

I. THE QUERCUS PEDUNCULATA ZONE

In the east of Norway this tree is found as far as Lake Mjösen (60° 45′ N.), and in the west up to Nordmöre (62°

55′); but it is nowhere known to have reached a greater height above sea-level than 1,722 feet.

The oak can stand a winter temperature as low as —33.8° C., but requires a mean summer temperature of 12.6°C. It is now comparatively rare, and seems to be decreasing. It occurs in large quantities only on the Silurian and along the lower parts of the coast.

A number of deciduous trees that are susceptible to cold have about the same distribution as the oak, both in height and in northward extension. These are: *Acer platanoides, Alnus glutinosa, Betula verrucosa, Crataegus Oxyacantha, Fraxinus excelsior, Prunus avium, P. insititia, Pyrus Malus, Sorbus Aria, S. fennica, Taxus baccata,* and *Tilia cordata.* There are also a number of species of cryptogams. It may on the whole be said that the zone here designated the Oak Zone is that of Norway's most abundant flora.

Within the Oak Zone, large districts may in their turn be marked off that possess a characteristic flora, the occurrence of which is especially conditioned by circumstances of temperature and soil.

1. The Region of the Silurian Flora.—This is developed in an especially characteristic manner on the calcareous slate along the Langesund Fjord, the west side of the Kristiania Fjord, in Ringerike and Hadeland, and around Lake Mjösen. In some of these districts it is fairly cold in the winter, but very hot in the summer;[1] and as the soil is calcareous and warm, a xerophilous steppe-flora, with its characteristic *Labiatae, Boragineae,* and *Centaurea* species, and thistles, such as *Carlina vulgaris, Carduus acanthoides,* etc.—species which also occur in the steppe-regions of South Russia, can thrive well on southern slopes.

For the rest, the flora is rich in characteristic species, e.g., *Artemisia campestris, Brachypodium pinnatum, Carex praecox, Cephalanthera rubra, Cirsium acaule, Fragaria collina, Libanotis montana, Ononis campestris, Phleum phalaroides,*

[1] In Kristiania, the 30-years' average minimum atmospheric temperature for the month of January is —16.5°C., and the average maximum for the month of June +28.9°C.

Spiraea Filipendula, Thymus Chamaedrys, Trifolium montanum, Veronica spicata, etc.

Where the soil is deep and not too dry, the above-mentioned deciduous trees that are susceptible to cold form forests or copses, intermingled with *Corylus Avellana, Prunus spinosa,* species of *Rosa* and *Rubus,* and a luxuriant ground vegetation, among which are several orchids.

A few of these trees and the more hardy species of the Silurian flora, such as *Origanum vulgare* and others, may, like an advance-guard, overstep the boundaries of the Silurian regions, but then they generally occur in warm localities, in talus at the foot of cliffs, or in steep slopes that face southward, even high up the sides of the valleys, or in the upper parts of the West Country fjords.

But the number of species diminishes with increasing distance from the lowland Silurian regions, and there are only a few species that have advanced as far as north of the Dovre Mountains.

2. *The Region of Fagus sylvatica.*—This region is situated along the southeast coast of Norway, from the Swedish border to Grimstad, where it extends as far north as Holmestrand. There is a small beech-wood a little to the north of Bergen, but this is a solitary instance, and has nothing to do with the real distribution area of the beech.

The beech is purely a lowland plant, as there is only one place in which it goes to a height of 886 feet above the sea, its usual height being not more than 525 feet. When cultivated, it can grow almost as far north as *Quercus pedunculata,* but prefers a rather higher summer temperature (13.4°C.) and thrives best on comparatively warm gravel banks.

The beech is one of those plants which has recently appeared to spread to new regions; and there is no doubt that it has not yet nearly reached the limits of distribution to which it will little by little attain, especially along the low land of the south coast. This is due to the fact that it must have immigrated in fairly recent times.

The following plants may also be mentioned as occurring chiefly in the region of the beech: *Cladium Mariscus, Coron-*

illa Emerus, Epilobium obscurum, Laserpitium latifolium, Ligustrum vulgare, Luzula nemorosa, Melampyrum cristatum, Rubus corylifolius, R. Lindebergii, Selinum carvifolium, Sium latifolium, Viscum album, Vicia cassubica, V. lathyroides, etc. A few of these have a rather larger distribution than the beech has at present; others, which must have immigrated recently, are found only within quite a small area.

The region for the cultivation of wheat in Norway coincides in the main with that of the beech, but extends a little farther, namely westward as far as Mandal, and to a height of 1,246 feet above sea-level.

3. The Region of Ilex Aquifolium.—This region is situated a little to the west of that of the beech, and does not have a lower mean temperature for January than 1°C. It extends from Arendal to Christianssund (63° 7′ N. Lat.), but does not include the outermost islands on the west coast.

A large number of vegetable species occur in this region. As especially characteristic may be mentioned *Aeropsis praecox, Asplenium Adiantum nigrum, Cardamine hirsuta, Centaurea decipiens, C. nigra, C. pseudophrygia, Cerastium tetrandrum, Chrysosplenium oppositifolium, Circaea lutetiana, Conopodium denudatum, Corydalis claviculata, Cynosurus cristatus, Digitalis purpurea, Drosera intermedia, Gentiana Pneumonanthe, Geranium columbinum, Hedera Helix, Heracleum australe, Hydrocotyle vulgaris, Hypericum pulchrum, Hypochaeris radicata, Juncus squarrosus, Leontodon hispidus, Luzula sylvatica, Lysimachia nemorum, Meum athamanticum, Quercus sessiliflora, Pilularia globulifera, Polygala depressum, Primula acaulis, Rosa pimpinellifolia, Rumex obtusifolius, Sagina subulata, Scirpus setaceus, Sedum anglicum, Senecio Jacobaea, Stellaria Holostea, Teesdalia nudicaulis, Triticum acutum, T. junceum,* and *Weingartneria canescens.*

A few of these species, however, can bear a January isotherm that lies a little lower than 1°C. These species, among which are *Hedera Helix* and *Quercus sessiliflora,* occur, therefore, also in the beech region in the southeast of Norway, but have their chief distribution in the Ilex Region, and must therefore be assigned to that region.

4. The Region of the West-European Coast Flora.—This includes the outermost islands in the province of Bergen. The characteristic feature of the climatic conditions here, as we have already stated, is not the large rainfall, for this is in reality smaller than in certain parts of the Ilex Region; but it is the extremely mild winter temperature, and a comparatively low summer temperature.

For purposes of comparison we will here give the mean minima for February and the mean maxima for July, for Kristiania, which forms a center for the Silurian flora, Larvik, the center of the beech region, Mandal of the holly, and Utsire of the West-European coast flora.

	Mean minimum temperature for February	Mean maximum temperature for July
Kristiania	15.5° C.	28.8° C.
Larvik	14.5° C.	25.8° C.
Mandal	11.3° C.	24.8° C.
Utsire	5.7° C.	19.9° C.

On these outermost islands in the province of Bergen, the mean temperature for January is 2°C.

Among the plant species that are especially characteristic of this region may be mentioned *Asplenium marinum, Erica cinerea, Hymenophyllum peltatum, Scilla verna,* and *Vicia Orobus.* These species are found in England, and some of them southward along the shore of the Atlantic.

II. THE PINUS SYLVESTRIS ZONE

In the east of Norway *Pinus sylvestris* goes right down to the sea, and occurs in many places in the Oak Zone; but in speaking here of a special zone for *Pinus sylvestris,* we refer to the great continuous forests of *Pinus sylvestris* and *Picea excelsa,* which cover wide tracts of country from the upper limit of the Oak Zone to a height of 3,116 feet in the south of Norway, 1,640 in the central part, and 623 in the north. *Pinus sylvestris* avoids the sea, and is therefore absent from the outermost belt of islands; but inland it forms, either alone or together with *Picea excelsa,* a more or less continuous region of distribution below the above-stated height-limits up to latitude 70°N.

Picea excelsa, which immigrated much later than *Pinus sylvestris,* supplants the latter in favorable localities in the east of Norway; but in the west its field of distribution is very small, and extends only to latitude 69°N. Farther north, in the interior of Finmark, small spruce forests do indeed occur, but they are formed of *Picea obovata.*

The forests that are formed of *Pinus sylvestris* are light, but as they often grow upon dry, poor soil, they are poorly furnished with vegetable species. There may occur scattered specimens of *Betula odorata, Alnus incana, Juniperus communis, Sorbus Aucuparia,* and *Populus tremula,* and then a poor ground vegetation of mosses (e.g., *Polytrichum juniperinum*), and lichens (e.g., *Cladonia rangiferina, Cetraria islandica,* and *Peltigera*), among which grow some easily contented higher plants, especially *Aira flexuosa, Arctostaphylos officinalis, Calluna vulgaris, Empetrum nigrum, Festuca ovina, Luzula pilosa, Melampyrum sylvaticum, Pteris aquilina, Trientalis europaea, Vaccinium Myrtillus, V. uliginosum,* and *V. Vitis-Idaea.*

Where this forest, from some cause or other, has been destroyed, extensive heath-lands are often formed, consisting chiefly of *Calluna vulgaris,* among which occur *Empetrum nigrum* and species of *Vaccinium,* as also *Antennaria dioica, Aira flexuosa, Campanula rotundifolia, Festuca ovina, Nardus stricta,* and others.

Picea excelsa forms forests on more fertile soil; but as they are very dense and dark, other trees have difficulty in forcing an entrance, and even the ground vegetation is as a rule very poor, owing to the want of light. A thick carpet of mosses (especially *Hylocomium splendens*) covers the ground, and the only plants that thrive are fungi, *Polystichum spinulosum* and some other ferns, *Linnaea borealis, Milium effusum, Oxalis Acetosella, Pyrola uniflora,* and others.

Where the forests of *Picea* are less dense, or where *Pinus sylvestris* grows upon a more fertile soil, these conifers may be mingled with various deciduous trees, and in the lower districts even with less hardy deciduous trees, which otherwise belong to the Oak Zone. The ground vegetation in such

places is also much more abundant, and the ordinary lowland flora may be found fairly well represented.

Almost all cultivated land in Norway lies in the Oak and Pine Zones. Rye and oats ripen up to latitude 69°N., barley even up to 70°N.—in the south it can be grown up to a height of 2,066 feet above the sea. The potato is cultivated rather farther north and a little higher above sea-level than barley. Side by side with the growing of grain is that of forage plants, of which the most important species are *Trifolium pratense* and *Phleum pratense.*

III. THE BETULA ODORATA ZONE

Betula odorata also occurs in the lowlands, and extends farther toward the sea than *Pinus sylvestris,* but by its zone, as here defined, is meant the region above the height limit of *Pinus sylvestris* upon the mountains and north of its distribution. In the very south of Norway, *Betula odorata* goes up to about 3,600 feet above the sea, and northward as far as latitude 71° 10′ N. Thus beyond the Birch Zone there is only the northeastern part of Finmark and the highest mountain regions.

In the south of Norway the great proportion of the so-called "saeters" lies in the Birch Zone, as this tree generally occupies the margin of the mountain wastes, and fills the little valleys that intersect them with a short-stemmed forest of *Betula odorata* subsp. *alpigena.*

Side by side with this mountain form of birch, there may also grow *Alnus incana, Populus tremula, Prunus Padus* and *Sorbus Aucuparia.* The ground vegetation will be somewhat variable according to the degree of moisture in the soil.

On dry gravelly slopes, especially if they face the south, the following species of higher plants are generally found in addition to a few species of lichens, such as *Cetraria islandica, Stereocaulon,* etc.: *Arctostaphylos officinalis, Agrostis vulgaris, Aira flexuosa, Alchemilla alpina, A. vulgaris* var. *pubescens, Antennaria dioica, Anthoxanthum odoratum, Astragalus alpinus, Botrychium Lunaria, Betula nana, Calluna vulgaris,* some species of *Carex, Empetrum nigrum*

Euphrasia officinalis, Festuca ovina, Gnaphalium norvegicum, Juniperus communis, Lotus corniculatus, Luzula campestris, L. pilosa, Maianthemum bifolium, Melampyrum sylvaticum, Nardus stricta, Pedicularis Oederi, Peristylis viridis, Phleum alpinum, Poa alpina, Pyrola minor, Rhinanthus minor, Solidago Virgaurea, Trientalis europaea, Vaccinium Myrtillus, V. uliginosum, V. Vitis-Idaea, and *Vicia Cracca.*

Where the soil is deeper and damper, and along streams and in shady places, *Salix glauca, S. hastata, S. lanata, S. lapponum, S. Myrsinites* and their hybrids make their appearance. The vegetation here is more luxuriant, as in addition to most of the above-named, the following species are found: *Aconitum septentrionale, Agrostis rubra, Alchemilla vulgaris* var. *alpestris, Aira alpina, A. caespitosa, Bartschia alpina,* species of *Carex, Equisetum hiemale, Geranium sylvaticum, Gymnadenia conopea, Montia fontana, Mulgedium alpinum, Myosotis sylvatica, Orchis maculata, Polygonum viviparum, Pinguicula vulgaris, Polemonium caeruleum, Ranunculus platanifolius, Rumex Acetosa, Saussurea alpina, Selaginella spinulosa, Soyera paludosa, Spiraea Ulmaria, Viola biflora,* and others. Many of these species occur right down to sea-level, some also higher up in the next zone; but as they are always found in the Birch Zone and have their most abundant development there, it is best to refer them to that zone.

IV. THE ZONE OF DWARF WILLOWS

This zone occupies the northeast part of the Varanger peninsula in Finmark and the mountains above the birch limit, up to a height which, in the southernmost point, may be put at 4,133 feet above the sea. It is thus only the tops of the highest mountains which rise like islands above this zone. The mean summer temperature here will be from 8.5 to 4.3°C., according to the height and situation in higher latitudes. The composition of the vegetation varies greatly according to the moisture conditions of the soil, which in their turn to some extent depend on exposure to the sun, south slopes being dry, north slopes damp.

On the drier tracts there are low copses of *Betula nana* and *Juniperus nana,* with a ground vegetation of mosses and lichens and a poor selection of mountain plants, such as *Antennaria alpina, Arctostaphylos alpina, Azalea procumbens, Carex rigida, Hieracium alpinum, Juncus trifidus, Erigeron alpinus, E. uniflorus, Festuca ovina, Gnaphalium supinum, Luzula arcuata, Luzula nivalis, L. spicata, Lycopodium alpinum, L. Selago, Nardus stricta, Pedicularis lapponica, Polygonum viviparum, Rhodiola rosea, Salix herbacea, S. reticulata, Trientalis europaea, Vaccinium Myrtillus, V. uliginosum, V. Vitis-Idaea, Viscaria alpina,* and others.

Where the soil is very poor and the climate during the vegetation period very dry, as on the mountain moorlands in the east of Norway—'round the lake Faemundsoe, and between the valleys Oesterdal and Gudbrandsdal—there occur great lichen-covered heaths consisting of *Cladonia rangiferina, Cetraria nivalis, C. cucullata, Alectoria divergens,* and *A. nigricans,* which give a grayish white appearance to the mountains. Among the masses of lichens there are found only a few very easily satisfied mountain plants such as *Festuca ovina, Nardus stricta, Solidago Virgaurea,* etc.

Where, on the other hand, the soil abounds in lime, and the conditions otherwise are favorable, as in certain places on the Hardanger Plateau in the south, Lom and Dovre in the center, and several places in the north of Norway, rare mountain plants occur, such as *Alsine biflora, A. hirta, Dryas octopetala, Primula scotica, P. stricta, Oxytropis lapponica, Papaver radicatum, Rhododendron lapponicum, Salix polaris, Veronica saxatilis,* etc.

If the soil, on the contrary, is deep and damp, as in morasses and along streams, or where water trickles down the sides of mountains, there is quite a different and more abundant vegetation, consisting of mosses with thickets of *Salix glauca, S. lanata, S. lapponum,* and *S. Myrsinites,* often with an undergrowth of *Aira alpina, Andromeda hypnoides, Cardamine bellidifolia, Cerastium trigynum, Eriophorum capitatum, E. vaginatum, Juncus biglumis, J. castaneus, J. triglumis, Koenigia islandica, Oxyria digyna, Petasites frigida,*

Ranunculus glacialis, R. nivalis, R. pygmaeus, Saxifraga aizoides, S. caespitosa, S. rivularis, S. stellaris, Silene acaulis, Tofieldia borealis, Vahlodea purpurea, Veronica alpina, etc.

V. THE LICHEN ZONE

This embraces the often stony tracts above the preceding zone, i.e., the highest mountain tops and the ground from which they rise.

Rocks and stones are here covered with the blackish yellow *Lecidea geographica* and other lichens. Where there is a little soil, some hardy mosses grow, and under favorable conditions a very few species of higher plants.

I may mention, as an illustration, that in 1877, when visiting the mountain Haarteigen (5,546 feet) in Hardanger, i.e., in the south of Norway, I noted the following higher plants upon the comparatively flat top of the mountain: *Carex rigida, Luzula arcuata, L. spicata, Lycopodium Selago, Poa alpina, Polygonum viviparum, Ranunculus glacialis,* and *Rhodiola rosea.*

As already repeatedly stated, all plant species are not strictly confined to the zone under which they are mentioned as especially characteristic factors. It is very general for species somewhat to overstep the boundaries of their true zone, either upward or downward. Certain species are even found in all zones from the sea to the snow, since they have a remarkable ability of adapting themselves to all kinds of soil and to all kinds of climatic conditions. As instances of such species we may mention *Calluna vulgaris, Empetrum nigrum, Eriophorum vaginatum, Festuca ovina, Nardus stricta, Polygonum viviparum,* and the species of *Vaccinium.*

Another circumstance is that typical mountain plants are sometimes found in the lowlands right down to the sea, e.g., in Jaederen, *Alchemilla alpina, Arctostaphylos alpina, Bartschia alpina, Saxifraga aizoides,* and *Selaginella spinulosa. Betula nana* occurs in the southeast of Norway down to fifty feet above the sea, and *Dryas octopetala* occurs at Langesund and at Varaldsö in Hardanger at sea-level. These occurrences were formerly often explained as relics of a previ-

ous age with a colder climate, but I do not think we need have recourse to such an explanation. In all the steep-sided valleys, typical mountain plants spread downward along streams and rivers, and often appear far below their real habitat. Whether they will remain there depends only upon their ability to compete with lowland plants and to withstand the night frosts in the spring after the snow has melted.

I assume, therefore, that the occurrence of the above-mentioned mountain plants in the lowlands is due to a chance carrying of seed to places that were favorable to the welfare of the species, e.g., limestone at Langesund and Varaldsö for *Dryas octopetala,* a peat-bog for *Betula nana,* and so forth.

The Immigration of the Norwegian Flora

Geologists have long been agreed that Scandinavia and great parts of adjacent lands have once been covered with one entire ice-cap, as the interior of Greenland is at the present time. By degrees the view obtained that there have really been two such glacial epochs, separated by an intermediate warm period, in which the conditions probably more or less resembled those of the present day.

During the first, called the Great Glacial Epoch, the ice-cap extended as far as central Germany, over almost the whole of England, over the whole of Finland, and over a great part of northern Russia. It follows that under such conditions, all, or almost all, vegetation must have disappeared from the Scandinavian peninsula, from Norway and Sweden. I am inclined to believe that in places in Norway, the tops of high mountains rose above the ice-covering, and that a very few species of plants may have survived there; but this is a matter of no interest in the question upon which I shall now endeavor to throw light, namely, the immigration of the flora of Norway after the Last Glacial Period.

This was of considerably smaller extent. On the south the ice reached only as far as Mecklenburg, and the ice-boundary then ran obliquely northward up through Jutland in Denmark, of which, therefore, only a part was entirely covered with ice. There can be no doubt that the whole of

Sweden was covered by this ice-cap, but as regards Norway, the conditions are still a matter of dispute. Some geologists maintain that the ice went right out into the sea on all sides; others assume that in some parts there was an iceless coast-region, where only here and there great glaciers ran out into the sea.

The great majority of the species in the Norwegian flora must, however, have immigrated after the last Glacial Period; but with regard to their immigration and the conditions under which it took place, various theories have been advanced.

The first to take up this question, especially with regard to Sweden, was F. W. Areschoug ('66), who, in 1866, maintained that the present vegetation of Scandinavia was made up of at least three elements of different period and origin, namely:

(1) An arctic vegetation, which immigrated from the east during the latter part of the Glacial Period, and, from its origin, may be called the *North Siberian Flora;*

(2) A northeastern and eastern vegetation, which came into Europe from Siberia after the Glacial Period, but before the immigration of the beech. From its origin, it may be called the *Altai Flora;*

(3) A southeastern and southern vegetation, which came simultaneously with the beech, partly from the Caucasus and the countries 'round the Caspian and Black Seas, partly from the countries of the Mediterranean. This may be called the *Caucasian and Mediterranean Flora.*

Areschoug also pointed out that a number of arctic species in the north German and south Swedish lowlands must be regarded as relics of the vegetation of the high north, which, after the melting of the ice-cap, withdrew toward the north or up into the mountains.

This view received strong support in the discovery by A. G. Nathorst ('71) in 1870, in the fresh-water clays of the south of Sweden, of remains of typical arctic plants which do not grow there now, but only very much farther north, namely, *Betula nana, Dryas octopetala, Salix herbacea, S. polaris,* and *S. reticulata.*

In 1875, Axel Blytt ('76) first brought forward his well-known theory on the immigration of the flora of Norway during alternate wet and dry periods. According to Blytt's theory, the wild plants of Norway should be arranged in the following six groups: (1) the *arctic* (the mountain flora); (2) the *subarctic* (the vegetation of mountain and wooded slopes), which is more frequent in the arctic than in the more southern, lower regions; (3) the *boreal* (the vegetation of the rocky slopes covered with foliage trees), which has its widest distribution in the low land, but not the coast districts; (4) the *Atlantic* (Bergen coast vegetation), with distribution in the coast district, especially between Stavanger and Kristianssund; (5) the *sub-boreal,* which occurs in the southeast of the country, especially 'round the Kristiania Fjord; and (6) the *sub-Atlantic* (Kristianssand coast vegetation), which has its widest distribution in the coast district between Kragerö and Stavanger.

The arctic, boreal, and sub-boreal species of plants are warmth-loving, continental plants, while the subarctic, Atlantic, and sub-Atlantic keep chiefly to the coast districts and are insular in character. The former have immigrated during dry periods, the latter during damp periods, in the order in which they have been placed. Blytt assumed that within the period of history it is scarcely probable that any very great changes have taken place in climate or vegetation, and that the present is a dry period.

Blytt ('83) subsequently maintained that these changes of climate were due to cosmic causes, namely alterations in the eccentricity of the earth's orbit and alternate changes in the earth's position with regard to the sun, occupying periods of about 21,000 years. By the aid of this hypothesis he calculated the period from the conclusion of the Glacial Epoch down to the present time to be between 80,000 and 90,000 years. The damp and dry periods were thus of equal duration, namely 10,500 years.

As Blytt moreover started with the assumption that the plants could advance only step by step in their migrations, and could not be transferred direct from Denmark or England

to Norway, he supposed that the six different flora-elements had immigrated from the south through Sweden to the places in which they are now found, but during the subsequent change of climate had died out in the intermediate regions, in which they do not grow now.

Since then, Gunnar Andersson ('96, '06) has discussed this question with special reference to Sweden. He builds more particularly upon paleontological studies of the plants preserved in peat-bogs. He assumes that the climate, after the melting of the ice, continued to grow warmer until—since *Corylus Avellana,* according to fossil occurrences, had a far more northerly distribution area than at the present time—it showed a mean temperature in August that was about 2.5° C. higher than at the present time. The temperature has, therefore, fallen to that of the present day.

Gunnar Andersson designates the various periods after the Glacial Epoch according to the most characteristic plant, and assumes that the immigration has taken place in the following order:

(1) The *Dryas Flora* includes certain arctic species, e.g., *Dryas octopetala, Salix herbacea, S. polaris, S. reticulata, Oxyria digyna, Arctostaphylos alpina,* and others, which are supposed to have migrated into Sweden when the melting of the ice had begun, and followed this northward. The most northerly place, however, where these arctic plants are found in Sweden is in West Gothland, in about the latitude of Gothenburg. They have not been found, from this period, farther north.

(2) The *Betula odorata Flora* is more subalpine. With it came also *Salix aurita, S. caprea,* and *S. cinerea,* etc.

(3) The *Pinus sylvestris Flora* immigrated during a somewhat warmer period, which continued to grow warmer. In the lower, and thus older, part of the Pine Zone are found *Prunus Padus, Rubus idaeus, Rhamnus Frangula, Sorbus Aucuparia,* and *Viburnum Opulus*; in the upper, and therefore more recent, part, which has had a warmer climate, we find *Alnus glutinosa, Cornus sanguinea, Crataegus monogyna,*

Corylus Avellana, Tilia europaea, Ulmus montana, etc. Here we come to the transition to the next flora.

(4) *Quercus Flora,* which immigrated during the warmest period after the Glacial Epoch, when the mean summer temperature was about 2.5°C. higher than at the present day. In addition to *Quercus pedunculata* and *Q. sessiliflora,* there immigrated during this period *Acer platanoides, Fraxinus excelsior, Hedera Helix, Viscum album,* and a great number of warmth-loving plants, which have since kept to the warm slates and limestones.

As the last immigrants during the steady decrease of the summer temperature, Gunnar Andersson gives

(5) The *Fagus Flora* and (6) the *Picea excelsa Flora.*

What is new in this theory is that there is assumed to have been only one period with higher temperature since the Glacial Epoch. This, too, is supported by the results at which W. C. Brögger ('00) has arrived in his investigations of the Quaternary fossil mollusc fauna in the south of Norway.

Since then, the question of the immigration of the flora into Sweden has been treated in a series of papers by R. Sernander ('10), who rather inclines to A. Blytt's theory, and in Norway by J. Holmboe ('03), who subscribes to that of Gunnar Andersson.

The geological basis, however, upon which all investigations of the immigration of the flora into the Scandinavian peninsula must be built, has of late years undergone considerable alteration. A number of recent discoveries of fossil plants also give new points of support. There is still, however, uncertainty concerning many points, so that the opinions of geologists and phytogeographers by no means coincide.

In the first place, by counting the layers in stratified clay deposits in Sweden, Gerhard de Geer ('08) has succeeded in proving that not more than about 12,000 years have elapsed since the ice-cap of the last Glacial Period extended as far as Skaane in the south of Sweden. The ice had taken about 4,000 years to withdraw thus far from its southernmost boundary in Germany, and it afterwards took as much as about 3,000 years to withdraw to a range of terminal moraines

in central Sweden, and in the south of Norway to the morainic ridges that extend from Fredrikshald to Moss, Horten, Arendal, etc., and are designated by the Norwegian word "Ra."

According to G. de Geer, these great terminal moraines must have been formed about 9,000 years ago when the inland ice stood still along that line for a period of about 350 years. It is a matter of indifference to us that other geologists believe that this "Ra" period occurred somewhat earlier.

What is of great importance in the immigration of the flora, however, is that the extreme southeast of Norway and the center of Sweden, at the time of the "Ra" formation, lay much lower than at the present time, and sank still lower some time after the ice withdrew. It is supposed that the sea near Kristiania, during the "Ra" period, was about 660 feet higher than it now is, and a little later rose to 720 feet above its present height, which is the highest limit of the late glacial sea. But this limit differs in different parts of the country; it falls toward the coast, especially toward the west coast of Norway. At Larvik, for instance, it is about 426 feet; at Arendal, 246 feet; at Kristianssand, about 130 feet; at Mandal, 82 feet; and at Farsund, only 28 feet. Farther north it increases again, so that at Kristianssund it is about 246 feet, and at Trondhjem, 650 feet, or almost as great as at Kristiania.

THE DRYAS PERIOD

I have previously ('05) endeavored to show by *Dryas* and *Salix polaris,* which A. G. Nathorst has found in a fossil state in the south of Sweden, that the arctic flora cannot have made its way thence into Norway; for during the "Ra" formation the masses of ice went right out into the sea, and when the ice had withdrawn far enough to leave open land within the "Ra" line, the climate had already altered to such an extent that the arctic flora was extinct in the south of Sweden.

The earliest plants of which J. Holmboe ('03) has found remains in the southeast of Norway, prove also to be sub-

alpine; but farther west fossil arctic plants have been found in a number of places.

D. Danielsen ('09, '12) has found, between Kristianssand and Mandal, fossil leaves of *Salix polaris* from 46 to 59 feet, *Dryas octopetala* from 46 to 52 feet, and *Betula nana* from 46 to 52 feet above the sea. The uppermost marine boundary here is from 137 to 141 feet above sea-level, but the leaves are supposed to have been carried out by currents and deposited at a depth of perhaps 65 feet. Something similar may have taken place with most of those subsequently mentioned, as they are sometimes found covered with more or less loose material.

C. F. Kolderup ('08) has found, near Bergen, *Dryas octopetala, Salix polaris,* and *S. reticulata,* from 115 to 130 feet above the sea, while the marine boundary lies at a height of about 190 feet above sea-level.

J. Rekstad ('05, '06, '07, '08) has found *Salix polaris* 130 feet above the sea in Söndfjord, 187 feet above the sea in Nordfjord (marine boundary 250 feet above sea-level), and in Nordmöre sometimes 82 feet, sometimes from 344 to 377 feet, above sea-level; and *Salix herbacea* in Nordfjord 220 feet above the sea (marine boundary 360 feet above the sea), in Söndmöre 85 feet.

K. O. Björlykke ('00) has found *Salix reticulata* near Kristiania 540 feet above the sea, and near Trondhjem 340 feet above sea-level.

P. A. Oeyen ('04, '07) has found *Dryas octopetala* and *Salix reticulata* near Trondhjem at a height of 557 feet above sea-level, and *Salix polaris* in Asker, near Kristiania, 600 feet above the sea (the marine boundary at the latter locality is 692 feet above sea-level).

Remains have also been found of species that may have a subalpine occurrence, such as *Betula nana, Juniperus nana,* and *Salix phylicifolia;* but as they are less conclusive, they are not included here.

The point of especial interest is that these fossil plants on the west coast are found with remains of the high arctic mollusc *Yoldia arctica,* which is not now found on the shores

of Norway, but on the coast of Spitzbergen, and indicates a mean temperature of from —3 to —7°C. and thus quite an arctic climate. At Kristianssand these arctic plant-remains are found together with remains both of *Yoldia arctica* and *Mytilus edulis,* while *Salix polaris,* near Kristiania, is found with *Mytilus* and far below the highest marine boundary.

Two questions now present themselves, (1) did *Salix polaris* and other arctic vegetation continue to live during the Last Glacial Period upon a stretch of coast in the west and north of Norway that was not covered with ice, or (2) did *Salix polaris* and the other arctic plants immigrate from Jutland —where they lived during the Last Glacial Period—to the first land from which the ice disappeared at Kristianssand, and thence spread along the edge of the ice on both sides as the latter disappeared?

I have previously endeavored to uphold the first of these views as the more probable, having found ('05, p. 337) that the discoveries hitherto made of the remains of arctic plants favored the belief that 'during the Last Glacial Period there lived in Norway a high-arctic vegetation upon a strip of coast that was free from ice and must have extended about as far down as the Sogne Fjord. Subsequently, as time went on, several species of high-arctic plants that had immigrated from Russia and Siberia made their way for a greater or smaller distance southward in the north of Scandinavia.'

Various later discoveries of arctic plants all the way down to the south point of Norway go to prove that the iceless margin of coast may have extended thus far, at any rate partially. The isolated occurrence of *Saxifraga Aizoon,* growing upon the mountains in inner Ryfylke, east of Stavanger, is also difficult to understand unless it is assumed that it migrated thither from an iceless margin of coast, as this species, beyond being found in the Alps, is only known in Nordland in Norway, and in Iceland and Greenland.

But it seems probable that here a number of vegetable species from the interglacial period may have survived the Last Glacial Period. This must have been the case with

Artemisia norvegica, whose province of distribution in Norway is on the Dovre and adjoining mountains in the northwest (Troldheimen), some of which could scarcely have been covered with ice during the Last Glacial Period. It is even possible to name, with considerable accuracy, some of these plants, as they form the "Greenland element" in the arctic flora of Norway. I designate as such those plants which Norway has in common with Iceland, Greenland, or the north of North America, but that are not found in western Siberia. These are as follows:

Arnica alpina is found in the north of Norway from Salten to Alten, and also in the north of Sweden, on the Kola Peninsula and Novaja Semlja, but not again until the east of Siberia is reached. It is also found in Greenland and on the Alps.

Campanula uniflora is found in Norway from Lom to Reisen, in Swedish Lapland and Novaja Semlja, but elsewhere only in Greenland and arctic North America.

Carex nardina is found in Norway from Salten to Kvaenangen, and in Swedish Lapland, but elsewhere only in Iceland, Greenland, and arctic North America.

Carex scirpoidea is known in Norway in Salten, and elsewhere only in eastern Siberia and western Greenland.

Draba crassifolia is found in Norway, 'round Tromsö, but otherwise only in Greenland.

Pedicularis flammea is found in Norway from Salten to Lyngen, and in Swedish Lapland, but elsewhere only in Iceland and Greenland.

Platanthera obtusata is found in Norway in Reisen and Alten, but otherwise is known only from eastern Siberia and arctic North America.

A fact that possesses peculiar interest in the study of the occurrence of these and other similar species of plants in the Norwegian mountains, is the discovery in central Norway of interglacial remains of *Elephas primigenius* and *Ovibos moschata.* These great mammals became extinct at the beginning of the Last Glacial Period, but some of the plants that lived at the same time found a dwelling place upon the iceless

coast margin and there managed to survive that period, and then to some extent followed the retreating ice up to the mountains where they are now found.

Andr. M. Hansen ('04, '04[a]) even assumes that at least 300, perhaps as many as 500, kinds of vascular plants may have lived upon this supposed iceless strip of coast, which he assumes to have been fairly broad. These figures are perhaps rather high, but it is not possible to make more exact statements until paleobotanical investigations have been carried out in the peat-bogs in these regions.

Against the second possibility, namely, that the arctic plants may not have immigrated from Denmark to Kristianssand until after the ice had withdrawn, several facts may be cited.

These arctic plants, farther up the west coast of Norway (e.g., in Nordfjord), are found together with *Yoldia arctica,* and thus in a decidedly arctic climate, while those near Kristianssand, though, indeed, found with *Yoldia,* also occur with *Mytilus,* which indicates that the climate was somewhat milder and that the plants originated at a more recent period than those in Nordfjord. Thus the arctic plants, e.g., those in Nordfjord, cannot have immigrated thither from Kristianssand, but may be assumed to have been there during the Last Glacial Period.

On the other hand, *Salix polaris* near Kristiania, which appears to have originated at a somewhat later period, may have been able to immigrate thither along the margin of the ice from Kristianssand; but this cannot at present be stated with certainty, as no fossils have been found between the two points.

THE BETULA ODORATA PERIOD

As the ice-cap withdrew and the climate became milder, the land began to rise. In the center and south of Sweden, this took place so rapidly that a land connection was formed between Sweden and Denmark, and also between south and north Sweden, very much as it is at present. The Baltic thereby became a lake, its waters becoming gradually fresher and containing fresh-water animals, especially *Ancylus fluvia-*

tilis, which has given to this geological period the name of the Ancylus Period.

By this upheaval of the land, a broad migration road for

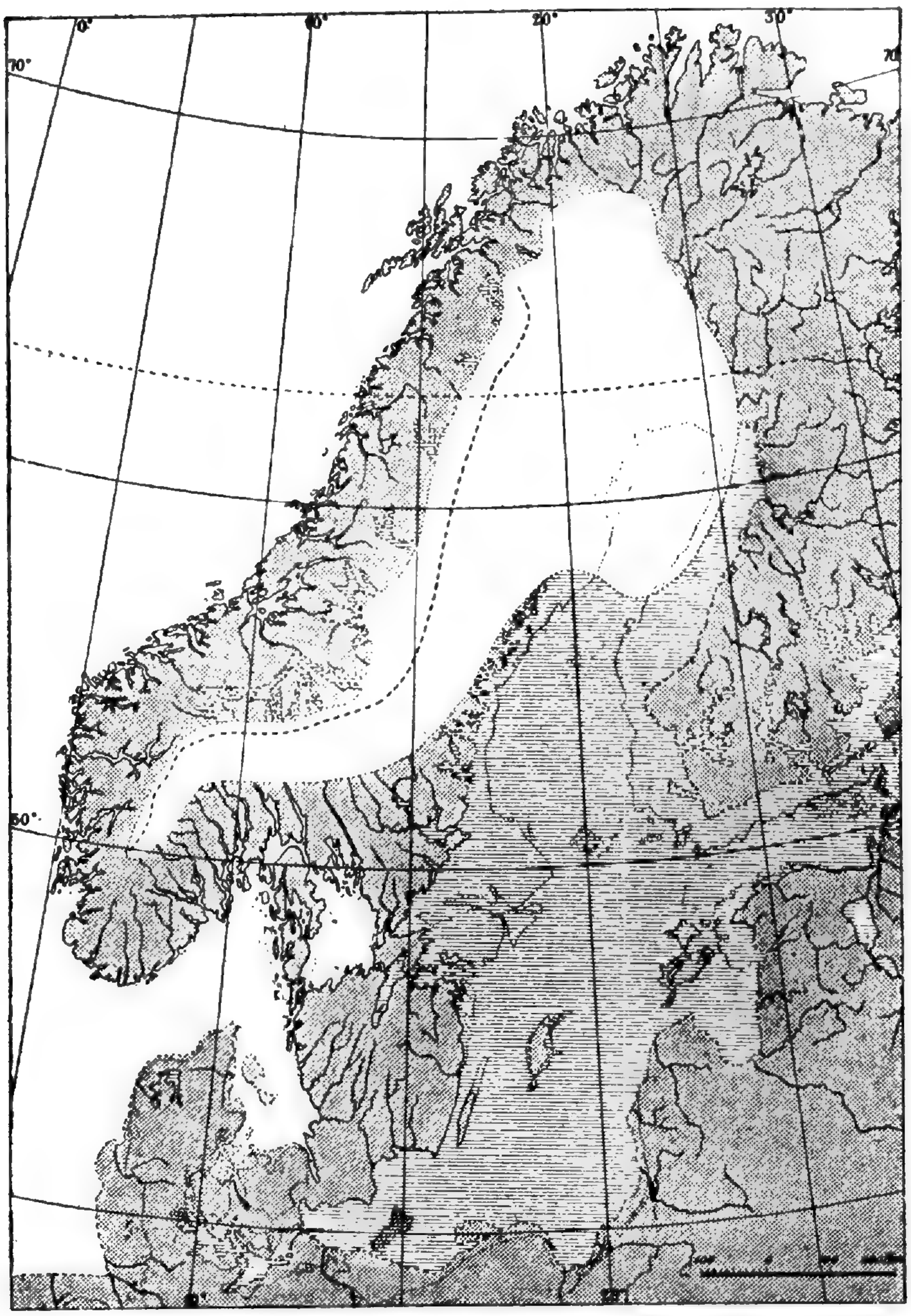

Fig. 4. Map of Scandinavia during the Ancylus Period: the white area represents the remainder of the great ice sheet; region indicated by parallel horizontal lines represents lake (water); region indicated by oblique cross-lines represents land.—Chiefly after De Geer.

plants was opened from the southeast and east to Norway. Seeds were probably carried over now and again before this upheaval of the land—as soon as land was vacated by the

ice in the southeast of Norway; but the direct land connection facilitated the spread of all species of plants.

Betula odorata was an early immigrant, and with it were a number of other plants of which fossil remains have been found, especially in peat-bogs in the southeast of Norway,[1] namely, *Betula nana, Carex ampullacea, C. filiformis, Cicuta virosa, Comarum palustre, Empetrum nigrum, Equisetum fluviatile, Hippuris vulgaris, Juniperus communis, Menyanthes trifoliata, Myriophyllum spicatum, Nymphaea alba, Potamogeton natans, Scirpus lacustris, Vaccinium Vitis-Idaea, Zannichellia polycarpa.*

But in addition to these, it may probably be assumed that the following species, which are found as subfossil remains from the subarctic or partially arctic period in Swedish peat-bogs,[2] may have migrated into Norway by this southeastern road as soon as some of the nearest land areas were free from ice. These are *Andromeda polifolia, Arctostaphylos alpina, A. Uva Ursi, Batrachium confervoides, Diapensia lapponica, Montia fontana, Myrtillus uliginosus, Oxyria digyna, Phragmites communis, Polygonum viviparum, Populus tremula, Potamogeton filiformis, P. praelongus, Salix aurita, S. caprea, S. cinerea, S. phyllicifolia, S. repens, Scheuchzeria palustris,* and *Stachys sylvatica.* During this period *Hippophaë rhamnoides* also immigrated to Sweden, but as it spread along the east coast of that country and thence through Jemtland to the north of Norway, this could not have taken place until much later, after the last of the central inland ice had melted.

THE PINUS SYLVESTRIS PERIOD

After *Betula odorata,* but during the so-called Ancylus Period in Sweden, *Pinus sylvestris* migrated to the southeast of Norway, while the climate was still comparatively cold; but, as we may gather from some of the plants that occur, especially in the latter part of the pine zone, the temperature became rather rapidly warmer.

J. Holmboe has found in the peat-bogs of Norway the following fossil plants in the pine zone: *Alisma Plantago, Alnus*

[1] By J. Holmboe ('03).

[2] By Gunnar Andersson ('96).

glutinosa, A. incana, Andromeda polifolia, Betula verrucosa, Carex Pseudocyperus, Cladium Mariscus, Corylus Avellana, Eriophorum vaginatum, Isoetes lacustris, Linnaea borealis, Lycopus europaeus, Naias marina, Nuphar luteum, Oxycoccus microcarpus, Rhamnus Frangula, Rubus Idaeus, Salix aurita, Scheuchzeria palustris, Solanum Dulcamara, Spiraea Ulmaria, and *Ulmus montana.*

In addition to these, Gunnar Andersson has found in Swedish peat-bogs from the pine period the following species: *Calla palustris, Caltha palustris, Carex riparia (?), C. vesicaria, Ceratophyllum demersum, Cornus sanguinea, Crataegus monogyna, Eriophorum angustifolium, Galium palustre, Iris Pseudacorus, Myriophyllum alterniflorum, Naias flexilis, Myrtillus nigra, Naumburgia thyrsiflora (?), Oxalis Acetosella, Pedicularis palustris, Potamogeton pectinatus, Prunus Padus, Ranunculus repens, Rubus saxatilis, Rumex Hydrolapathum, R. maritimus, Sorbus Aucuparia, Sparganium ramosum, Thalictrum flavum, Tilia cordata, Viburnum Opulus,* and *Viola palustris.*

But several of these latter species did not get as far as Norway until the succeeding warmer period, and we shall therefore find them again in the list of fossils that have been found in peat-bogs from the Oak Period. A few of them may also have immigrated by other routes, as a land connection with Sweden was established not only in the south but also in the east, the ice having withdrawn to the interior of the country, and at the close of the Ancylus Period probably melted away entirely. Various discoveries go to prove, for instance, that *Alnus glutinosa* migrated into Norway from the south, while *Alnus incana* came from the east.

There are in Norway two quite distinct forms of *Pinus sylvestris* L., which by some botanists are given as species, namely, var. *septentrionalis* Schotte, and var. *lapponica* (Fr.) Hn. The second of these, which is found in abundance in Finland and the far north of Sweden, also grows in Norway, especially in the north, and on the mountains farther south, where here and there it pushes down into the valleys. It may be assumed that this *P. sylvestris* var. *lapponica* did not im-

migrate from the northeast until much later—after the ice-cap had melted in the north of Norway and Sweden, and then made its way southward. The common *Pinus sylvestris,* on the contrary, as we have said, undoubtedly migrated into Norway from the southeast through Sweden, which is probably the way by which most of those species immigrated which are now found growing with it in the southeast of Norway.

THE QUERCUS PEDUNCULATA PERIOD

The climate gradually becomes warmer, the inland ice has quite disappeared, and simultaneously with its disappearance the land in a belt across central Sweden begins once more to sink (the Littorina Subsidence). When this subsidence culminated, the south of Sweden was a great island which, on the south, was separated—as it now is—from Denmark by Oeresund and by a broad arm of the sea, which ran from Skagerak through the district in which the lakes Venern and Vettern now lie right to the Baltic. This sea thus acquired an opening into the North Sea, and its waters gradually became salt.

This subsidence of the land, which took place when the land around Kristiania was about 230 feet lower than it now is, did not greatly affect Norway, for it amounted in the latter to only a few yards. But it may probably be assumed that so great an arm of the sea, with a current of Gulf Stream water that even brought Gulf Stream nuts (*Entada gigalobium*) with it to the shores of Bohuslaen—whence they are not carried at the present day—must have made the climate warmer and more insular than it now is. Before the subsidence, then, the climate must have been warm and dry, after the subsidence, warm and damp.

How much warmer the climate must have been is apparent from Gunnar Andersson's investigations—following the discovery of fossils—on the distribution of *Corylus Avellana* at that time, compared with its present distribution. It appears that the mean temperature of the summer months must have been about 2.5°C. higher than it now is. In the sea off the coast of Norway there lived at that time species of the more

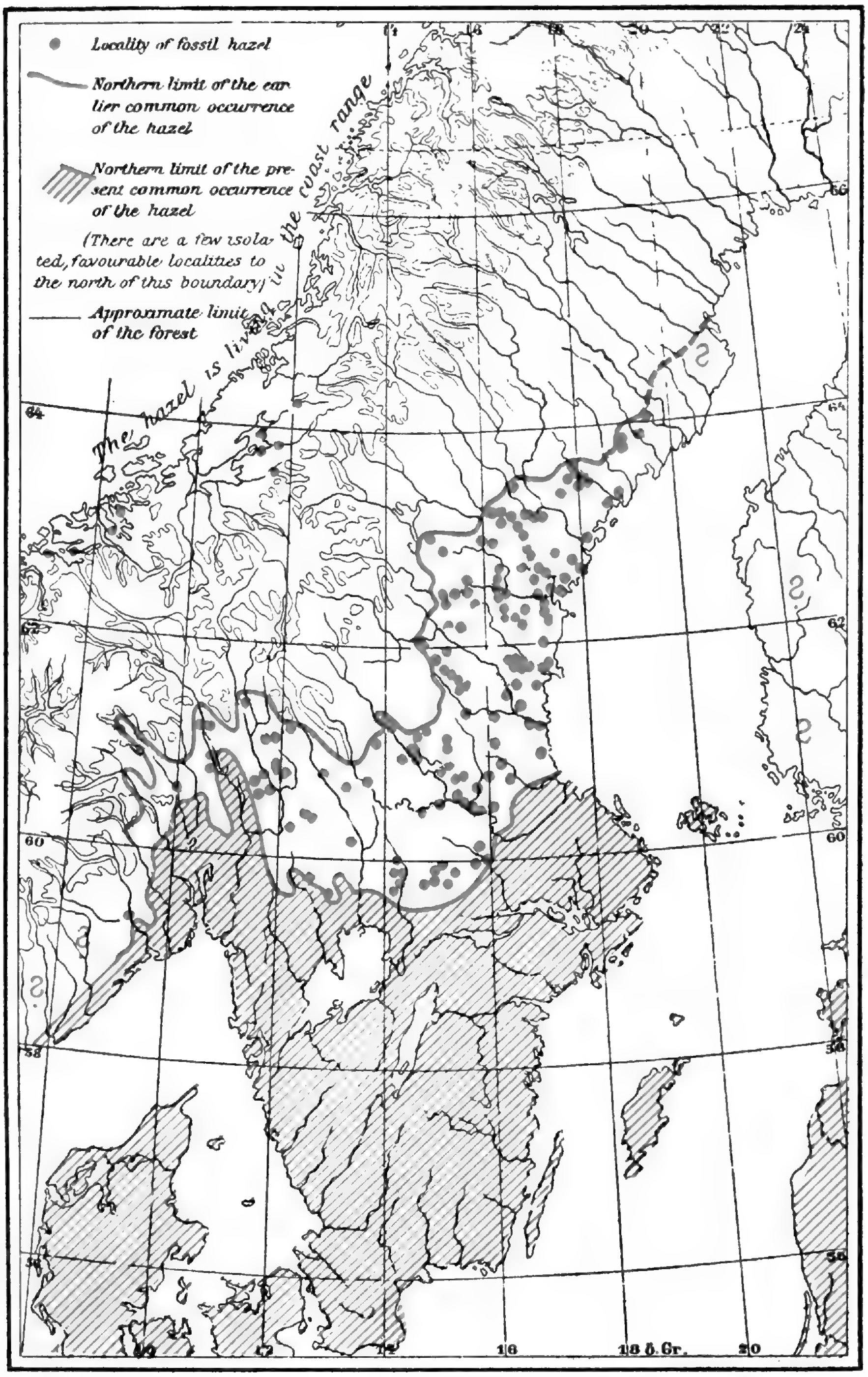

Fig. 5. Map of the present and the former distribution of *Corylus Avellana* in Sweden. The entire area from which *Corylus* has disappeared is about 32,420 square miles. (For key, see upper left-hand corner of figure.)—After Gunnar Andersson.

southern mollusc genus *Tapes,* which shows that the average annual temperature must have been between 8 and 9°C. (Brögger, '00).

Various opinions have been expressed as to whether the warmest period was before, at, or a little after, the maximum of the Littorina Subsidence in Sweden. This is of little importance here, but what is more important is that the earliest remains of stone implements in Norway date from this warmest period (the Tapes Period), which, therefore, in the opinion of archaeologists, must be assumed to have been about 7,000 years ago. This accords well with G. de Geer's calculations from the number of clay strata.

J. Holmboe has found the following species of plants, together with *Quercus pedunculata,* in Norwegian peat-bogs: *Acer platanoides, Aspidium Thelypteris, Bidens cernua, B. tripartita, Calla palustris, Carex stellulata, C. vesicaria, Ceratophyllum demersum, Crambe maritima, Fraxinus excelsior, Galeopsis Tetrahit, Iris Pseudacorus, Myrica Gale, Naias flexilis, Naumburgia thyrsiflora, Oxalis Acetosella, Peucedanum palustre, Potamogeton praelongus, Ranunculus repens, Rubus fruticosus, Ruppia rostellata, R. spiralis, Scirpus maritimus, Sorbus Aucuparia, Sparganium ramosum, Stachys sylvatica, Thalictrum flavum, Tilia cordata, Viola sp., Zostera marina.*

It will at once be seen that a good many of these species were enumerated as having been found in the south of Sweden during an earlier period, i.e., with *Pinus sylvestris.* This agrees very well with the assumed immigration route through Sweden, as it must have taken a considerable length of time for these plants to spread through Sweden into southern Norway. It must not, however, be forgotten that the occurrences of plants in the peat-bogs indicate only the minimum length of time of their existence in the place in question, as they may very well have lived there for a long time before being deposited in a peat-bog, to be found there through the investigations of a botanist.

In addition to the above, Gunnar Andersson has found the following fossil species in the Oak Period in Sweden, these

species being either unknown in Norway or found only in later deposits, some of them probably not having immigrated until later, together with *Picea excelsa.* They are *Angelica sylvestris, Cakile maritima, Cornus suecica (?), Helianthus peploides, Hedera Helix, Ledum palustre (?), Potamogeton crispus, Ranunculus Flammula, R. sceleratus, Sagittaria sagittifolia,* and *Viscum album.*

A. Blytt ('82) assumed that a great many warmth-loving species, constituting what he called the "boreal flora," must have immigrated at this time, especially several xerophilous plants, such as a number of *Labiatae, Boragineae,* etc. (some of which are now commonly found on the steppes of southern Russia), which still keep especially to warm slates and limestones in the Norwegian lowland in the east, the west, and the province of Trondhjem.

Andr. M. Hansen ('04) draws especial attention to the following among these species, constituting what he calls the "Origanum community," and which grow on open slopes with a very sunny exposure: *Agrimonia Eupatoria, Androsace septentrionalis, Arenaria serpyllifolia, Calamintha Acinos, Campanula Cervicaria, Carex muricata, Centaurea Scabiosa, Dianthus deltoides, Echinospermum lappula, Origanum vulgare, Plantago media, Polygala amara, Ranunculus Polyanthemos, Torilis Anthriscus, Trifolium medium, Turritis glabra, Verbascum nigrum,* and *V. Thapsus.* As they grow upon dry slopes, it is not very probable that remains of them will be preserved in peat-bogs or elsewhere. Paleontologically, therefore, their immigration cannot be determined, but something may be concluded as to their occurrence in the present day; for it appears that this warmth-loving plant community has its most connected province of distribution from the lowlands of the southeast of Norway, on the warm slates through Valdres and Gudbrandsdal, and are then met with once more on the low land of the western fjord valleys, and in the province of Trondhjem. To this last locality there is evidently also an immigration road through Jemteland from the east coast of Sweden. On the other hand, this plant community is wanting throughout so great a part of the

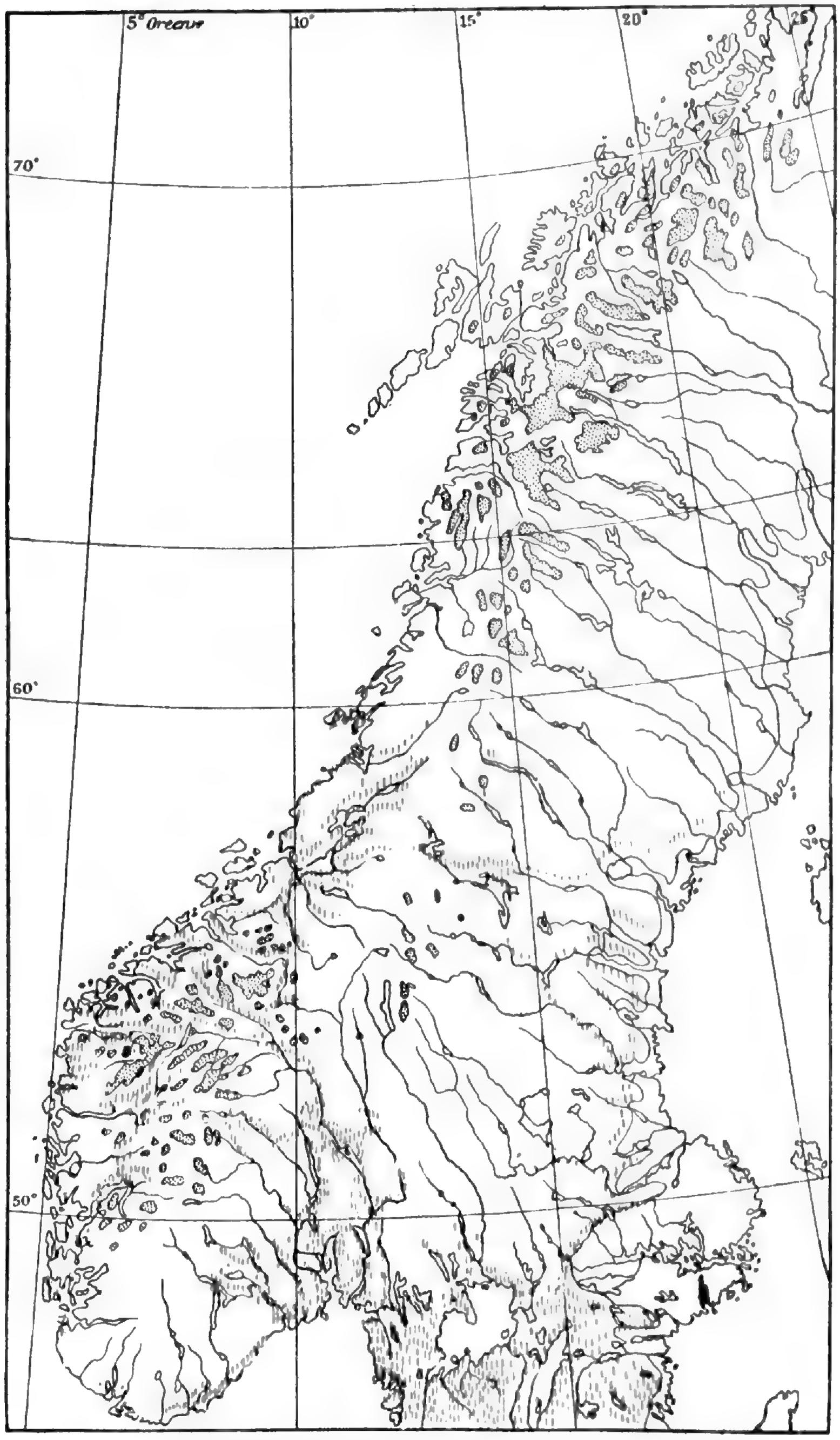

Fig. 6. Sketch-map showing the distribution and journeys of the *Origanum* community (vertical red lines) in Scandinavia. The extent of the montane region during the warmest post-glacial period is indicated by black-dotted areas.—After Andr. M. Hansen.

southwestern lowlands, that it can hardly be imagined that it migrated along the coast to the west and Trondhjem.

It must therefore be taken for granted that these plants migrated by way of the mountain passes, some of which now lie at such an altitude that even *Pinus sylvestris* cannot live in the highest localities. But I have already mentioned that the summer temperature during this period was about 2.5°C. higher than it now is. We see, moreover, that remains of pine forests are found on the mountains in Norway, e.g., on the Dovre Mountains in central Norway, and on the Hardanger plateau in the south of Norway, respectively 990 and 1,470 feet above the present highest limit of *Pinus sylvestris.* Under the then existing climatic conditions, the now treeless passes were clothed with forest, and warmth-loving plants were able to spread through them.

A. Blytt, and after him R. Sernander, distinguishes between a boreal and a sub-boreal flora, the members of which are supposed to have been lovers of warmth and dryness, but separated in their immigration by an Atlantic flora that loved humidity and warmth. With this I cannot agree. Several of the species that Blytt ('82) classes under "sub-boreal" are found in a fossilized state together with those he calls "boreal"; and around Kristiania many species of these so-called different floras grow together under exactly the same conditions in the same localities.

It seems likely, however, that the climate was more humid during the Littorina Subsidence, when the water of the Gulf Stream could make its way directly into the Baltic across central Sweden. A. Blytt ('82, p. 23) says: "Man darf deshalb mit einem hohen Grad von Wahrscheinlichkeit behaupten, dass die atlantische Flora in dieser Regenzeit eingewandert ist, und ihren Weg rund um den Christianiafjord gefunden hat (in derselben Weise, wie unter der folgenden Regenzeit die subatlantische)." I cannot agree in all respects with this. Those forms which Blytt calls "atlantische Arten" include a great number of species, of which some occur in what I have here called the "region of Ilex Aquifolium," others constitute what I have called the "west European

coast flora," while among other species belonging to Blytt's group *Rhynchospora alba, Alnus glutinosa, Myrica Gale, Arnica montana, Erica Tetralix, Ranunculus Flammula, Lychnis Flos-cuculi,* etc., may be mentioned, which grow on the low-lying land in many parts of southern Norway. As a rule, they prefer, it is true, damp places, but some species go right up to the Birch Zone on the mountains, so they may be presumed to have immigrated from the southeast through Sweden; but there is nothing to prove that this took place just at the maximum of the Littorina Subsidence. As instances, indeed, of the contrary, *Alnus glutinosa* from the Birch Period and *Myrica Gale* from the Oak Period are found in Norwegian peat-bogs and were, therefore, much earlier.

I believe that the west European coast flora on the west coast of Norway immigrated directly, by fits and starts, from England; but we will return to this later on.

THE PICEA EXCELSA PERIOD

According to archaeological calculations, the Scandinavian Stone Age lasted about 3,000 years, so that the Bronze Age in Scandinavia began about 4,000 years ago. During this period the climate was undoubtedly warmer than it now is, and it was not until the Bronze Age that any noticeable fall seems to have taken place.

At the beginning of the Stone Age the land around Kristiania lay 230 feet lower than at present, but during the Stone Age it was elevated about 184 feet, and during the Bronze Age it rose to about its present height above sea-level.

In the Bronze Age, or perhaps in the latter part of the Stone Age, *Picea excelsa* migrated into Norway from the east, from Finland through Sweden. In Finland it is still found as a fossil in the Oak Period, and in Sweden, especially in the north and east, it is so found, while spruce is not found fossilized in the south of Sweden or Denmark after the Glacial Epoch.

In the north of Norway (Finmark) there are occurrences of spruce that are entirely independent of the spruce's great province of distribution in the south of Norway. It appears

that these northern occurrences are of a distinct form (*Picea excelsa* [Lam.] Link f. *obovata* Ledeb.), which is classed by some botanists as a separate species, and has its distribution through the north of Finland and Russia. There can, of course, be no doubt that the spruces in these northernmost occurrences immigrated independently from Finland, and probably at a later period, as there is a tradition that they were imported thither by human beings (Lapps).

According to J. Holmboe, *Calluna vulgaris* came into Norway during the same recent period in which *Picea excelsa* made its appearance, but there is no doubt that the former immigrated from the west and then spread eastward, i.e., in the direction opposite to that in which *Picea excelsa* spread. Both these species have now a very wide distribution in Norway.

Strange to say, there has not been found in the deposits from the Pine Period in Norwegian peat-bogs a single plant that is not to be found in the earlier periods. In Sweden the only new species found is *Rubus Chamaemorus,* which, however, undoubtedly grew there long before, as it must on the whole be considered to be a subalpine species. This is sufficient to show that special conditions are necessary in order that parts of plants may be preserved in bogs, and that it will, therefore, always be only a small proportion of the plants growing around the bogs which will be so preserved.

It is strange, for instance, that *Taxus baccata* is not found in Norwegian peat-bogs. It is found as a fossil from the Oak Period in Sweden, and must have been far more common in Norway in the early Iron Age than it is at the present time, as H. Conwents found, on examining twenty-three vessels in the Archaeological Museum in Kristiania, that eighteen of them were of *Taxus* and only one of *Picea excelsa.*

According to R. Sernander ('10) the period of greatest warmth must have occurred in the Bronze Age, and he believes that it was then that *Corylus Avellana* was most widely distributed northward. The Bronze Age, however, judging from the molluscs that were then found off the south coast of Norway, seems to have had a cooler climate than that of the

Tapes Period, i.e., the Scandinavian Paleolithic Age. On the other hand, R. Sernander believes that at the beginning of the Iron Age—about 2,400 years before our own day—so great a decline in temperature ensued that the montane plants made their way into the lowlands in many places. He interprets the present occurrences of alpine plants in the lowlands as relics from that period. This can, however, be the case only to a certain extent, for there is no doubt that at the present day alpine plants spread down to the lowlands and continue to grow there, provided the conditions are favorable. R. Sernander gives to his assumed cold, damp period at the beginning of the Iron Age the name employed by A. Blytt, the "sub-Atlantic period"; but the two have, in reality, very little to do with one another. A. Blytt states that his sub-Atlantic period occurred when the south coast of Norway lay from 30 to 50 feet lower than its present level, which would answer to the beginning of the Bronze Age. He mentions, among other species that immigrated during the sub-Atlantic period, *Carex Pseudocyperus* and *Cladium Mariscus*, which had already immigrated in the Pine Period, and *Ceratophyllum demersum*, which had immigrated in the Oak Period, besides two or three species that were certainly imported later in foreign grain and grass seed.

I do not yet consider R. Sernander's cold, damp "sub-Atlantic period" at the beginning of the Iron Age to have been clearly proved, although there are a few facts that speak in its favor. But even if such a cold, damp period did supervene, its principal effect would have been to decimate the oak flora—in localities that were not especially warm—more rapidly than if the climate had gradually become colder from the Stone Age to the present time, as most people believe. Similarly, it may have promoted the occasional descent of montane plants to the lowlands, but it appears that this can also take place under the present climatic conditions, without the necessity of having recourse to relic occurrences from the "sub-Atlantic" or even from the "Dryas Period."

An instance of such an occurrence is that of *Dryas octopetala* at Langesund in southeastern Norway. This species

is found there right down to the level of the sea, and is very common on the limestone of the locality. Together with J. Holmboe ('03), I have endeavored to prove that over the whole of the area in which *Dryas* appears, the latter can scarcely have existed for more than 100 years. I cannot ascribe any convincing power to the objections that have been raised against this line of argument.

THE FAGUS SYLVATICA PERIOD

In Norway, as already mentioned, *Fagus sylvatica* grows upon the southeast coast, with Larvik as a center. There is, in addition, an isolated beech-wood in Seim, to the north of Bergen, 280 miles from the nearest occurrence of beech.

It was formerly believed by A. Blytt that this beech-wood in Seim was a relic of a connected distribution of beech along the coast; but no discovery of fossils favors this idea. On the contrary, these two occurrences of beech appear to be perfectly independent of one another.

J. Holmboe ('05, '09) has endeavored to find out when the beech appeared at Larvik and in Seim. He has come to the conclusion, judging from what has been found in the peat-bogs, that at Larvik the beech immigrated considerably later than *Picea excelsa*. It can thus actually be assumed to have immigrated in the Iron Age, or perhaps as late as the time of the Vikings. This late immigration is in harmony with the fact that in the southeast of Norway the beech is making very rapid advance at the present time. Holmboe says that the beech-wood in Seim, from a geological point of view, is very recent, but that in any case its age should scarcely be put lower than about 1,000 years.

It seems to me most probable that the beech was introduced into Norway by man in the time of the Vikings, when there was ample communication with those countries in which this so generally useful tree formed extensive forests. In Seim, near Bergen, where the beech grows, the Norwegian King Haakon the Good, who was educated in England at the court of King Athelstan, and reigned from 935 to 961, had one of his estates; and it is not unnatural to suppose that he may

have tried to introduce a tree that he knew so well from his childhood and youth in England.

It is certain that in the course of time man has assisted in introducing many species of plants, some consciously, as, for instance, plants for cultivation, others by chance and unconsciously.

In the famous Viking ship from Oseberg, which is believed with certainty to have originated in the first half of the ninth century, fruit, seeds, and other remains of plants have been found, and have been determined by J. Holmboe ('06). The following cultivated plants were among them: *Avena sativa, Corylus Avellana, Isatis tinctoria, Juglans regia, Lepidium sativum, Linum usitatissimum, Pirus Malus,* and *Triticum vulgare.* As *Isatis tinctoria* is found growing apparently wild, in certain places in Norway, there can scarcely be any doubt that it has found its way thither from localities where it had previously been cultivated as a dye-plant. This is probably also the case with *Serratula tinctoria* in Jaederen, near Stavanger. The weeds found in the Oseberg ship were as follows: *Capsella Bursa-pastoris, Chenopodium album, Galeopsis Tetrahit, Lamium* (*purpureum?*), *Polygonum Convolvulus, Stellaria media,* and *Urtica urens.* Several of these, it is true, had immigrated earlier, as has been said of *Galeopsis Tetrahit;* but it shows that as early as the time of the Vikings, there were opportunities of importing foreign weeds.

In monastery gardens various medicinal, household, and ornamental plants were cultivated, and one is inclined to believe that several of these which now have quite a wide distribution in Norway, e.g., *Aquilegia vulgaris, Berberis vulgaris, Sambucus nigra,* etc., originally spread with the monasteries as centers.

It is still easier to demonstrate a number of species of weeds that have been imported recently, and of which some appear to have a really astonishing power of spreading. J. Holmboe ('00) has traced the spread of the following weeds from the year when they were first observed in Norway: *Alyssum calycinum* (1857), *Anthemis tinctoria* (1772?, 1807), *Barbarea vulgaris* (1790), *Berteroa incana* (1826), *Bunias*

orientalis (1812), *Campanula patula* (1870), *Cerastium arvense* (1817), *Chrysanthemum segetum* (1704), *Cotula coronopifolia* (1875), *Conringia orientalis* (1859), *Erigeron canadensis* (1874), *Galinsoga parviflora* (1880), *Lepidium perfoliatum* (1875), *L. virginicum* (1889), *Matricaria discoidea* (1850), *Rudbeckia hirta* (1880), *Senecio viscosus* (1804-1808), *Thlaspi alpestre* (1874), and *Xanthium spinosum* (1872). Some of these plants are now among the most troublesome weeds in large and small areas in Norway.

There can, I suppose, be no doubt that man, directly and indirectly, in the 7,000 years in which he has lived in Norway and maintained a lively intercourse—especially during the last 2,000 years—with the rest of Europe, must have assisted in introducing a great number of plants in addition to the above named. Among the former may be mentioned *Agrostemma Githago, Anchusa arvensis, Anthemis arvensis, Avena fatua, Brassica campestris, B. nigra, Bromus secalinus, Carduus crispus, Centaurea cyanus, Chenopodium capitatum, C. hybridum, C. glaucum, C. polyspermum, C. rubrum, Circium arvense, Convolvulus arvensis, Euphorbia Helioscopia, E. Peplus, Fagopyrum tataricum, Fumaria officinalis, Galeopsis angustifolia, G. Ladanum, G. speciosa, Galium Aparine, G. Mollugo, Lolium temulentum, Matricaria Chamomilla, Raphanus Raphanistrum, Sinapis alba, S. arvensis, Sonchus asper, S. oleraceus, Spergula arvensis, Spergula vernalis, Thlaspi arvensis,* etc. In addition to these there are a great many species that are generally classed in the floras under the heading "run wild" or "perhaps originally run wild," and concerning which it may certainly be assumed that they have been introduced by man's mediation in some way or other.

It is no longer possible to maintain the old dogma which held that the entire plant community migrated step by step, like a regiment of soldiers, and took possession of the country under climatic conditions that were favorable to the various species, while the previous vegetation was decimated and only survived in especially favorable localities; for *vegetable*

species generally immigrate singly and independently of one another.

It is not only man that assists in carrying plants across large sea surfaces; the wind, ocean currents, and especially birds from time to time transport seeds and other parts of plants, which, under favorable conditions, continue to grow.

I will not here go further into this complex question in its entirety, but will refer to R. Sernander's ('01) detailed work on the conditions for spreading in a great number of Scandinavian plants. I must, however, mention a few examples of probable, or certain, chance distribution. At Vaage Lake, far up the valley Gudbrandsdal, 990 feet above sea-level and separated from the innermost fjords of the west coast by 56 miles of very high mountains, grows the typical sea-shore plant, *Elymus arenarius*. That this occurrence represents a relic is absolutely out of the question, for the sea cannot have reached the height of Vaage Lake since the Silurian Period. But I have seen gulls flying over the lake, and they may possibly have carried seeds with them, which have found a favorable soil in the long sandy shores.

In 1837, *Coleanthus subtilis* was found upon a flooded river bank a little north of Kristiania, and in 1842 a great number of specimens were collected in the same locality, probably all that existed there, for in spite of the most careful search for a number of years, the plant has never subsequently been found in that or in any other place in Norway. As its nearest habitat is in Bohemia, it can only be supposed that some wading bird, in rapid flight from Bohemia to Norway, brought the seed with it; and, furthermore, that as the seed fell upon favorable soil, the plant grew up and had already begun to spread when the collection was made in 1842.

I have already ('05) endeavored to show that *Campanula barbata,* which occurs in a limited area on the mountains of central Norway, and is not again found until we come to the mountains of Central Europe, cannot be a glacial relic, but must have been accidentally introduced into Norway (by birds?) in recent times.

Judging from the distribution in the present day of a number of plants on the south and west coasts of Norway, it seems natural to assume that they have been brought directly over the sea from the nearest country, Denmark or England. It was thus not necessary for them to move step by step by the long route through Sweden, or even round the Kristiania Fjord, to reach their present habitats. The latter is all the less probable from the fact that certain of them seem to have been imported quite recently, when the climatic conditions cannot have been very different from those which exist at the present time. The following are instances of these:

Aera setacea grows in Norway from Kristianssand to Stavanger. The species is common in Jutland in Denmark, but in Sweden is found only in the extreme south.

Airopsis praecox is found from Kragerö to Nordmöre. It occurs, it is true, in Sweden, from the south up to Vestergothland and Bohuslän; but from that region to Kragerö is considerably farther than from Jutland, where the plant is found in abundance.

Corydalis claviculata is found from Kristianssand to Haugesund. It grows wild in Denmark and England, but not in Sweden; I assume, therefore, that it immigrated from one of the former countries.

Galium saxatile is found from Kristianssand to Nordmöre. It grows in Sweden from Skaane to Bohuslän, but it is far more probable that it came from Jutland, where it is common.

Genista tinctoria is found only at Brevik, and must have been recently imported, as there are only a few specimens of it. It is found wild only in southern Sweden, but is common in Jutland.

Geranium columbinum is found in the district extending from Kragerö through the west of Norway to the Trondhjem Fjord. In Sweden it has an eastern distribution from Skaane to Upland. It is common in Denmark.

Heracleum australe is found from Kragerö to Söndfjord. It occurs in Sweden from the south right up to Vermeland, but the distance from this district to Kragerö is considerably greater than that from Jutland, where it also occurs.

Hydrocotyle vulgaris grows here and there from Larvik to Bergen. In Sweden it does not extend farther than to Dalsland, but it is exceedingly common in Jutland.[1]

Hypericum pulchrum grows in the region extending from Larvik through the west of Norway to the Trondhjem Fjord. In Sweden it is found from Halland to Bohuslän, but it is more natural to suppose that it immigrated from Denmark or England, where it is common.

Luzula sylvatica grows along the coast from Arendal to Lofoten. It is found wild only in the south of Sweden, but is common in Jutland.

Rubus Radula is found from Kragerö to Mandal. In Sweden it is found from Skaane to Bohuslän, but is very common in Jutland.

Sarothamnus scoparius grows between Grimstad and Mandal. In Sweden it is wild only in the east. It is very common in Denmark.

Scirpus multicaulis grows at Arendal and in Jaederen. It is found in Sweden from Skaane to Vestergothland. It is common in Denmark.

Scirpus setaceus is found to the west of the Kristiania Fjord and more recently has been found also along the coast almost as far as Bergen. It is found in Sweden from Skaane to Bohuslän, but it can scarcely be supposed to have migrated thence to its most easterly occurrence in Norway, as the center of its distribution in Sweden lies farther south, and in Norway farther west. It seems, therefore, more probable that it has been brought to Norway directly from Denmark.

[1] Since writing the above, I have discovered *Hydrocotyle vulgaris* in a locality on Kirkeöen (Hvaler) in southeastern Norway. The locality lies about midway between the easternmost of the previously known Norwegian stations and the Swedish localities and might be looked upon as proof that the species in question had immigrated step by step through Sweden and not directly from Denmark. This, however, is not the case. On an excursion in 1907, I visited the exact spot where I later found *Hydrocotyle vulgaris* and I can maintain with certainty that *Hydrocotyle* was not growing there at that time. The plant has, therefore, been introduced into the locality in question since that date. My opinion, therefore, that *Hydrocotyle* has immigrated by leaps and bounds directly from Denmark into Norway, is only strengthened by this discovery.

Stellaria Holostea grows along the coast from Grimstad to Bergen. It is found in Sweden from Skaane to Bohuslän, but must have migrated into southern Norway from Denmark, where it is common.

Teucrium scorodonia is found from Lyngör to Flekkefjord. In Sweden it has probably only become wild, but in Denmark it is common.

Vicia cassubica is found from Kragerö to Kristianssand. In Sweden it is found from Skaane to Dalsland, but it is common in Denmark.

Vicia lathyroides grows along the coast from the Hvaler Islands farthest east off Norway, to Kristianssand. In Sweden, however, its distribution is easterly from Skaane to Upland, so it must be assumed that it migrated into Norway directly from Jutland in Denmark, where it is not uncommon.

It will be noticed that most of these plants which I assume to have immigrated directly from Denmark (Jutland) to the south of Norway, are either bog or leguminous plants, or are such as have small seeds or stone-fruits. The carriage across water surfaces of such plants as these one would imagine could most easily take place through chance transport by birds. The distance across the Skagerak from Denmark to Norway is about 93 miles, and according to J. A. Palmén ('76) there are regular lines followed by birds of passage from Jutland to Jaederen, as also one almost to Kristianssand and another to Risör, the very places which appear to be the center of the distribution of the majority of the above-named species which I assume to have come directly from Denmark.

It is still less probable that a number of plants that belong to the coast flora of Western Europe, and in Norway are found only in the extreme west, where the winter temperature is unusually mild (from +1 to +2°C.), should have immigrated from England via Denmark and Sweden, where they do not now grow, or at any rate grow only in the extreme south. If they did make such a journey, the climate must have been so much milder in the southeast of Norway that the warm period that is proved in the Stone Age would not have gone nearly far enough. A climatic change as violent

as this would have been, and that in a comparatively very recent geological period, is not probable, nor is it necessary to assume it in order to explain the occurrence of these plants in the west of Norway, if only one does not blindly adhere to the dogma that plants can migrate only step by step.

As instances of plants which I assume have migrated from England direct to the west of Norway, the following may be mentioned:

Asplenium Adiantum nigrum is rare from Jaederen to Kristianssund. It is found in England, but only in the very east of Denmark and the extreme south of Sweden; immigration from the two last-mentioned countries seems, therefore, to be out of the question.

Asplenium marinum grows in the west of Norway from Mosterö to Stadt. It is found in England, but neither in Sweden nor Denmark.

Erica cinerea grows on the outermost islands from Farsund to Söndmöre. It is found in England, but in neither Sweden nor Denmark.

Hymenophyllum peltatum grows in the outermost coast districts from Farsund to Nordfjord. It is found in England, but neither in Sweden nor Denmark.

Scilla verna grows in the extreme coast regions from Söndfjord to Söndmöre. It is found in England, but neither in Sweden nor Denmark.

Scolopendrium vulgare is found in two or three places between Hardanger and Söndfjord. It is common in England, but it is doubtful whether it has grown in Denmark, and in Sweden it is found only in the extreme east, in Gothland.

Vicia Orobus grows farthest west, from Lister and Jaederen to Söndmöre. It is common in England, but is not found in Sweden, and only here and there in Jutland. It might thus be supposed to have come from Denmark direct to Norway, but in that case it would probably grow a little farther south than it does. I consider it, therefore, most probable that it came over from England to the coast of Norway, and then spread

along the coast southward and northward to its present limits.

It also appears, according to I. Hagen ('12), that the case is similar with regard to a number of mosses, a direct migration from England to Norway being assumed. Hagen has so little faith, however, in the ability of these plants to migrate by leaps and bounds, that he supposes a post-glacial land connection with England, over which migration might gradually take place.

This land bridge between Norway and England was originally hypothetically constructed for the pre-glacial times by L. Stejneger ('07), who considers it necessary on zoögeographical grounds. At the conclusion of his paper he says:

> "I think I may safely claim to have made it appear probable:
>
> "1. That if the characteristic and important portion of the animals and plants of west Norway, called the 'Atlantic' biota, invaded that country from Scotland, it came by way of a land bridge connecting northern Scotland with western Norway north of 59° north latitude.
>
> "2. That this land bridge existed after the first (Scandinavian) great glaciation.
>
> "3. That part of this biota surely survived the second (Scandinavian) glaciation along the west coast of Norway, and that possibly the climate was not too severe for all to survive.
>
> "4. That there is a possibility of a reëstablishment of the land bridge during the 'Upper Forestian' stage with its congenial, more continental climate, during which the tenderer species may have immigrated, in case it should be proven that they could not have come with the hardier ones."

As will appear from the foregoing pages, I have also maintained ('05) that during the Last Glacial Period there was a stretch of coast in Norway that was free from ice, where some arctic plants, and, of course, also animals, were able to survive that period.

Since then Gunnar Andersson and Selim Birger ('12) have endeavored to give to the facts that favor this view the interpretation that the entire arctic flora element must have immigrated through Sweden, and followed the receding margin of ice. I consider their arguments on this point so unconvinc-

ing, especially in view of the most recent discoveries of fossil arctic plants, and my own observations of the rock formations in the west and north of Norway, that I have come to the conclusion that this iceless strip of coast was broader than I formerly supposed, and extended to the extreme southern point of Norway. In this respect my view is thus in perfect accordance with that of Stejneger.

As to whether there was an interglacial direct land connection between England and Norway, as Stejneger assumes, I cannot express an opinion, but I do not, in any case, consider it necessary for botanical reasons, although I am inclined to believe that the assumption of Stejneger will prove to be correct. On the other hand, I consider a post-glacial land connection between England and Norway, concerning which Stejneger himself is much in doubt, to be quite out of the question. There is nothing that can be brought forward to prove that previous to the post-glacial subsidence the land lay high enough for any real land bridge between Norway and England to exist. On the other hand, there are several facts that go to show that the southern part of the North Sea has lain higher than it now does, so that even considerable portions that are now under the sea were clothed with forest. This may possibly to some extent have diminished the distance between England and Norway; but the deep Norwegian Channel outside the coast of Norway has certainly been in existence ever since the Last Glacial Period.

But a land connection is not necessary to explain why the few species of plants that Norway and England have in common, and that must be assumed to have migrated over the North Sea, were able to come over in the course of the last 7,000 years. It must not be forgotten that according to J. A. Palmén ('76) there are two lines followed by birds of passage between England and the west of Norway; and that there may also have been other chance means of transport.

All things considered, I am inclined to believe that in trying to explain the distribution of vegetable species and the paths they have followed, we shall arrive at better results by studying the ways in which they spread at the present time than

by setting up hypotheses of tremendous convulsions of nature such as elevated and depressed land connections, climatic changes from cosmic causes, the oscillatory movement of the poles, etc., which can neither be proved nor disproved, as they lie beyond the spheres in which our present knowledge has a firm foundation on which to stand.

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THE PHYLOGENETIC TAXONOMY OF FLOWERING PLANTS

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I. General Discussion

Seventeen years ago in presenting a somewhat similar paper[1] to a smaller body of botanists, I began by saying that "it is as yet impossible to present a complete phylogeny of the angiosperms," and then a little later, "it will be many a year before the direct evidence we so much desire will leave no considerable gaps," and I am impelled to use the same words now as I begin this discussion to-day. For, while in this interval paleontology has uncovered many important facts whose significance is unmistakable, it is still true that there are "considerable gaps" in the record of the evolution of plants, both before and after the attainment of flower production. In other words, we are still in quest of direct testimony as to how flowers came into existence in particular, and as to the details of how and when they were modified afterwards. Yet we are not wholly without the direct testimony of the rocks in our inquiry as to the phylesis of the higher plants.

And I may be permitted here to enter a defense of such a discussion as I propose to make in this paper, in reply to those who think that since much of what I shall have to say is reached by a process of deduction, or, as it is more commonly called, speculation, it can have little scientific value. And I grant that in those fields where direct observation, experiment, and induction are possible there can be no defense of the exclusive deductive or speculative method. There are, however, many fields of botanical inquiry in which experiment is impossible, and observation is reduced to a minimum, and this

[1] Bessey, C. E. The phylogeny and taxonomy of angiosperms. (Address of the retiring president of the Botanical Society of America, at its third annual meeting, at Toronto, Canada, August 17, 1897.) Bot. Gaz. **24**: 145–178. *f. 1–3.* 1897.

is necessarily the case when we are dealing with questions which relate to periods of time long past, as must be those involving phylogeny.

Moreover, it must not be forgotten that what I propose to do is after all much like what is done in even those sciences which we sometimes call the exact sciences. The ether of space, the undulatory theory of light, the tentative hypotheses as to the nature of electricity and gravitation, the form and extent of the universe, and the constitution of matter itself, are a few of the familiar speculations which physicists, astronomers and chemists have made parts of the conceptions of their respective sciences. To be sure, one can go but a short distance indeed in any science without finding it necessary to erect a speculative framework upon which to arrange his observed facts. As Jevons has so aptly expressed it in his 'Principles of Science' (2: p. 131):

> "When facts are already in our possession, we frame an hypothesis to explain their mutual relations, and by the success or non-success of this explanation is the value of the hypothesis to be entirely judged. In the framing and deductive treatment of such hypotheses, we must avail ourselves of the whole body of scientific truth already accumulated, and when once we have obtained a probable hypothesis, we must not rest until we have verified it by comparison with new facts. * * * Out of the infinite number of observations and experiments which are possible at every moment, theory must lead us to select those few critical ones which are suitable for confirming or negativing our anticipations."

A little later (p. 137) he remarks:

> "The true course of inductive procedure is that which has yielded all the more lofty and successful results of science. It consists in anticipating Nature, in the sense of forming hypotheses as to the laws which are probably in operation; and then observing whether the combinations of phenomena are such as would follow from the laws supposed. The investigator begins with facts and ends with them. He uses such facts as are in the first place known to him in suggesting probable hypotheses; deducing other facts which would happen if a particular hypothesis is true, he proceeds to test the truth of his notion by fresh observations or experiments. If any result prove different from what he expects, it leads him either to abandon, or to modify his hypothesis; but every new fact may give some new suggestion as to the laws in action."

I may quote one more sentence from the Manchester logician (p. 138): "Agreement with fact is the one sole and sufficient test of a true hypothesis."

So I come with a general hypothesis of the evolution of living things, and of plants in particular. This hypothesis is based upon observed facts, which are here given such a uniform interpretation as will make my general hypothesis, and it is this latter that I wish to discuss to-day, making such application as will enable us to arrange the flowering plants in accordance with it.

I am going to confine my discussion pretty largely to the plants of the highest phylum, here restricted to those that bear flowers. Since the discovery of the pteridosperms, it is manifestly untenable to regard all seed-bearing plants as members of one phylum. In other words, the *Spermatophyta* of the books constitute not one phylum, but several phyla. Briefly, I shall exclude first of all the cycad phylum which began in the Paleozoic period with the pteridosperms, and has extended with many losses to the present. I shall also exclude the conifer phylum, related to but not included in the cycad phylum. These two phyla are commonly associated in a group under the name of gymnosperms, but I have no hesitation in keeping them as distinct phyla, the cycads lower, and the conifers higher.

The remaining seed-bearing plants, whose seeds are enclosed in carpels, constituting the old group of angiosperms, I regard as a distinct phylum, and because the flower is the dominant and characteristic structure, I designate them as the Phylum *Anthophyta,* and they are the flowering plants about which I speak to-day.

So in clearing the way for this discussion, let me show the relationship of these three phyla of higher plants by means of an analytic key, as follows:

A. Gametophyte generation larger, and longer-lived than the dependent sporophyte generation. Here are set off the liverworts and mosses.

B. Gametophyte generation smaller and shorter-lived than the independent sporophyte generation.

(a) Here we set off those plants in which both generations are mostly holophytic and independent of one another, the megagametophyte still containing chlorophyll, including ferns, calamites, and lycopods.

(b) Gametophytes hysterophytic, dependent upon, and nourished by, the sporophytes, the megagametophyte not containing chlorophyll.

(1) Megagametophyte a fully developed cellular mass before the formation of the eggs; microgametophytes few-celled; antherids basicidal; sperms ciliated and motile; megasporophylls open, in simple spirals to simple strobili; seeds fleshy; microsporophylls mostly multisporangiate; bundles tracheidal, in a small, little-enlarging cylinder; pith and cortex large; stems simple; leaves ample, mostly pinnate, persistent, veins parallel .....CYCAD PHYLUM

(2) Megagametophyte a fully developed cellular mass before the formation of the eggs; microgametophytes few (to one)-celled; antherid apicidal; sperms non-ciliated and not visibly motile; megasporophylls open, in well-developed strobili; seeds not fleshy; microsporophylls with few (2–8) sporangia; bundles tracheidal, in an enlarging cylinder; pith and cortex small; stems branched; leaves small, simple, persistent, veins parallel .....CONIFER PHYLUM

(3) Megagametophyte fully developed as a cellular mass (endosperm) only after the fertilization of the egg; microgametophytes one-celled; antherids apicidal; sperms non-ciliated and not visibly motile; megasporophylls closed (carpels), in floral strobili (flowers), often much reduced; seeds not fleshy; microsporophylls (stamens) with four sporangia; bundles fibrovascular, in an enlarging cylinder; pith and cortex small (or bundles scattered and stem non-enlarging); stems branched; leaves mostly large, simple to compound, persistent to deciduous, veins netted to parallel .....FLOWERING PLANT PHYLUM

In the foregoing analysis, I have emphasized the similarities rather than the dissimilarities between the plants of these phyla, and such a statement will serve to show that they are related, and yet no one can compare them and not be forced to the conclusion that they must have diverged from one another at an early period in their evolution. And this divergence is to be interpreted as involving the cycad phylum as the primitive group from which have sprung the conifers on the one hand and the flowering plants on the other.

Following the plan which I adopted in my earlier paper,[1] I may here designate a number of generally accepted principles of classification as they apply to the flowering plants. While generally accepted, these principles have rarely if ever been formulated by taxonomists or others, so that as here formulated they may create some surprise and perhaps some opposition.

For the sake of brevity I give them in the form of dicta, as follows:

A. GENERAL DICTA

1. Evolution is not always upward, but often it involves degradation and degeneration.

[1] *Loc. cit.*

2. In general, homogeneous structures (with many and similar parts) are lower, and heterogeneous structures (with fewer and dissimilar parts) are higher.
3. Evolution does not necessarily involve all organs of the plant equally in any particular period, and one organ may be advancing while another is retrograding.
4. Upward development is sometimes through an increase in complexity, and sometimes by a simplification of an organ or a set of organs.
5. Evolution has generally been consistent, and when a particular progression or retrogression has set in, it is persisted in to the end of the phylum.
6. In any phylum the holophytic (chlorophyll-green) plants precede the colorless (hysterophytic) plants, and the latter are derived from the former.
7. Plant relationships are *up and down* the genetic lines, and these must constitute the framework of phylogenetic taxonomy.

B. DICTA HAVING SPECIAL REFERENCE TO THE GENERAL STRUCTURE OF THE FLOWERING PLANTS

8. The stem structure with collateral vascular bundles arranged in a cylinder is more primitive than that with scattered bundles, and the latter are to be regarded as derived from the former.
9. Woody stems (as of trees) are more primitive than herbaceous stems, and herbs are held to have been derived from trees.
10. The simple, unbranched stem is an earlier type, from which branching stems have been derived.
11. Historically the arrangement of leaves in pairs on the stem is held to have preceded the spiral arrangement in which the leaves are solitary at the nodes.
12. Historically simple leaves preceded branched (''compound'') leaves.
13. Historically leaves were first persistent (''evergreen'') and later deciduous.
14. The reticulated venation of leaves is the normal structure,

and the parallel venation of some leaves is a special modification derived from it.

C. DICTA HAVING REFERENCE TO THE FLOWERS OF FLOWERING PLANTS

15. The polymerous flower structure precedes, and the oligomerous structure follows from it, and this is accompanied by a progressive sterilization of sporophylls.
16. Petaly is the normal perianth structure, and apetaly is the result of perianth reduction (aphanisis).
17. The apochlamydeous perianth is earlier and the gamochlamydeous perianth is derived from it by a symphysis of the members of perianth whorls.
18. Actinomorphy is an earlier structure than zygomorphy, and the latter results from a change from a similar to a dissimilar growth of the members of the perianth whorls.
19. Hypogyny is the more primitive structure, and from it epigyny was derived later.
20. Apocarpy is the primitive structure, and from it syncarpy was derived later.
21. Polycarpy is the earlier condition, and oligocarpy was derived from it later.
22. The endospermous seed is primitive and lower, while the seed without endosperm is derived and higher.
23. Consequently, the seed with a small embryo (in endosperm) is more primitive than the seed with a large embryo (in scanty or no endosperm).
24. In earlier (primitive) flowers there are many stamens (polystemonous) while in later flowers there are fewer stamens (oligostemonous).
25. The stamens of primitive flowers are separate (apostemonous), while those of derived flowers are often united (synstemonous).
26. The condition of powdery pollen is more primitive than that with coherent or massed pollen.
27. Flowers with both stamens and carpels (monoclinous) precede those in which these occur on separate flowers (diclinous).

28. In diclinous plants the monoecious condition is the earlier, and the dioecious later.

Let us now endeavor to apply these principles candidly in an attempt to secure a phyletic taxonomy of the flowering plants.

As a consequence, we begin with the plants that are primitively opposite-leaved, as shown by their first leaves ("cotyledons") that are always opposite. These are what we have known as dicotyledons. But this name, which was once significant, is no longer useful, and in fact has become somewhat misleading, so that I propose to substitute for it the name *Oppositifoliae* for the first class of the *Anthophyta.* Likewise for the other class, hitherto known as the monocotyledons, in which the leaves are alternate from the first, and continue so throughout the whole plant body, I propose the more appropriate name of *Alternifoliae.*

In considering these two classes, it is quite evident that the first is not only the larger in the number of its species, but also that it includes many more important modifications of structure than does the other. Yet there is much similarity in the kinds of modification of structure in the two classes, the larger class, from its very largeness, including many more details of modification and variation.

In both classes we begin with apocarpous plants, and proceed toward those that are syncarpous. So the *Ranales* on the one hand, and the *Alismatales* on the other, are near the point of beginning. In one class syncarpy is attained after the passing of a few hundred species (*Alismatales,* 409 species), while in the other it is not reached until much beyond the limits of the order *Ranales,* for it is well known that the syncarpy of many *Malvales* and *Geraniales* is distinctly incomplete, the coherence between the carpels being so feeble that they readily separate at maturity. All told, fully 10,000 species of this class are passed before complete syncarpy is attained.

The strobiloid flower structure, in which the axis is elongated, cylindrical, spheroidal, or flattened, bearing on its sur-

face the fertile and sterile sporophylls, prevails in the earlier orders of both classes, in the smaller, continuing through the *Alismatales, Liliales, Arales, Palmales,* and *Graminales,* and aggregating more than 11,700 species. In the larger class the strobiloid structure prevails throughout fourteen orders, from the *Ranales* to the *Lamiales,* and aggregating more than 53,000 species. In these strobiloid flowers, as a result of the dominance of the strobilar structure, we have what has been known as the hypogynous form of flower. In both classes the strobiloid flowers show progressive modifications involving the perianth (actinomorphy to zygomorphy, diplochlamydy to achlamydy), the stamens (polystemony to oligostemony), the carpels (polycarpy to oligocarpy), the ovules (multiovulate to rariovulate). In the larger class the perianth modifications proceed with such regularity that we may recognize lower (apopetalous), and higher (sympetalous) groups of orders, but this is not observed in the smaller class, where indeed sympetaly is never more than sporadic, and does not become a fixed structure.

In summary fashion I may now outline the taxonomy of the flowering plants:

The opposite-leaved class (*Oppositifoliae,* or dicotyledons) is the first to emerge from the cycadean phylum, appearing as the ranalean complex.

From this Ranalean type arises the alternate-leaved class of flowering plants (*Alternifoliae,* or monocotyledons) as apocarpous *Alismatales,* and these soon merge into the syncarpous *Liliales,* which are successively more and more modified in the *Arales, Palmales* and *Graminales.* From *Liliales* by a cotyloid modification the mostly actinomorphic epigynous *Iridales* are derived, and from these again the zygomorphic epigynous *Orchidales.*

Returning to the *Ranales,* we find that they give rise first to five apopetalous, polycarpellate orders with gradually increasing syncarpy, namely *Malvales, Geraniales, Guttiferales, Rhoeadales,* and *Caryophyllales.* From the last arise three orders of sympetalous, polycarpellate plants, the *Ebenales, Ericales* and *Primulales,* and the latter have developed the

dicarpellate orders *Gentianales, Polemoniales, Scrophulariales* and *Lamiales,* constituting a series which shows diminishing numbers of stamens, carpels and seeds, and increasing zygomorphy. This phyletic sequence from *Ranales* to *Lamiales* constitutes the sub-class *Strobiloideae,* or cone-flowers.

Returning again to the *Ranales,* we find that they give rise to the simpler, cotyloid, apopetalous, polystemonous, polycarpous, hypogynous *Rosales* (sub-class *Cotyloideae*), from which by the early deepening of the cotyloid structure we have the mostly polystemonous, polycarpous, epigynous *Myrtales, Loasales* and *Cactales* as a strongly developed side line. The oligostemonous *Celastrales* continue the main phyletic line with reducing numbers of stamens, carpels and seeds, and a gradual deepening of the cup, to the side-line of the *Sapindales,* which are eventually epigynous, and the mostly dicarpellate *Umbellales.* The sympetalous, epigynous *Rubiales* with reduced calyx, few carpels and few seeds, pass easily into the *Campanulales,* and the *Asterales,* the latter with but one seed in the dicarpellary, one-celled, one-seeded, inferior ovary, and with its calyx, when not obsolete, transformed into bracts, spines or bristles to form a "pappus" for the efficient distribution of the seeds.

II. Taxonomy of Flowering Plants

Phylum XIV. **ANTHOPHYTA**. The Flowering Plants.

Typically chlorophyll-green plants (a few colorless hysterophytes), ranging from small or even minute plants to great trees a hundred or more meters in height; alternation of generations obscured by the extreme reduction of the gametophyte to a condition of dependence upon the long-lived, leafy-stemmed sporophyte. Spores of two kinds (heterosporous), produced on sporophylls which are borne in modified, often much reduced strobili (flowers); microsporophylls (stamens) normally with four sporangia (pollen sacs); the microspores being set free (as "pollen") when mature; megasporophylls (carpels) folded lengthwise (constituting the "pistil") enclosing the sporangia (ovules) in which the megaspores

remain and develop the minute gametophyte; archegones very much reduced, including little more than the egg, which is

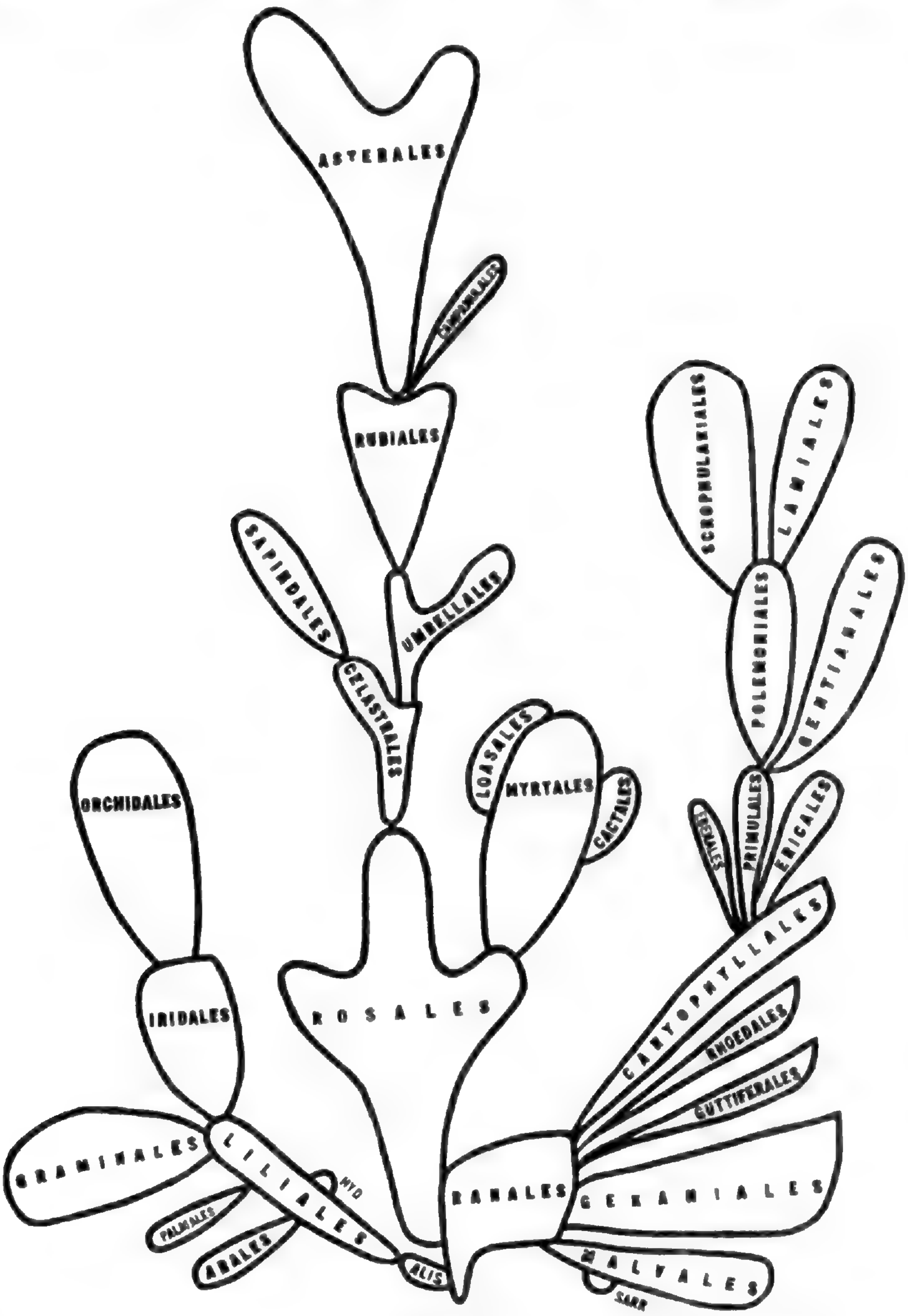

Fig. 1. Chart to show relationship of the orders. Relationship is indicated by position; the areas are approximately proportional to the number of species in the orders.

fecundated by the non-ciliated sperms (male nuclei) from the tubular antherids, resulting in the formation of an embryo

sporophyte; megasporangia surrounded by one or two enveloping indusial coats (seed coats); mature seed with or without endosperm (gametophyte tissue).

The flowering plants are here held to have sprung from cycadean strobiliferous ancestors, probably of the general type of the *Bennettitineae,* and as a consequence those anthophyta are considered to be primitive in which the sporophylls are many and distinct. Symphylly and syncarpy are later structural conditions than apophylly and apocarpy. So also, fewer sporophylls in the anthostrobilus is a later condition derived from the earlier polyphyllous structure. The symphysis of sporophylls is a mode of evolution, and so is their aphanisis.

The plants constituting this phylum are those commonly termed angiosperms, in contrast with the gymnosperms, including the cycads (*Cycadophyta*) and conifers (*Strobilophyta*). It appears to the writer, however, that these are more properly three pretty distinct phyla, and that the relationship of the gymnosperms to the angiosperms is so remote that the treatment here given them is more nearly in accordance with what is known as to their phylogeny.

There are two classes, *Alternifoliae* (monocotyledons) and *Oppositifoliae* (dicotyledons), of which the second was quite certainly the earlier, as it is now much the larger numerically. Indeed, it is becoming more probable that the monocotyledons are to be regarded as a peculiar side branch which sprang from the primitive dicotyledons after the latter had become well established. Yet the monocotyledons have not developed to as high a rank in any of their orders as have some of the dicotyledons.

Although I have here changed the technical names of these two classes, there is no objection to the retention of the old terms for the English names in popular usage: accordingly on the following pages I shall frequently make such use of the old names.

Class 32. ALTERNIFOLIAE (MONOCOTYLEDONEAE). The Monocotyledons. Leaves of young sporophyte

alternate; leaves of mature sporophyte alternate, and usually parallel-veined; fibro-vascular bundles of the stem scattered, usually not arranged in rings. (Species about 23,700.)

Sub-Class ALTERNIFOLIAE-STROBILOIDEAE. Axis of the flower from spheroidal to flattened, bearing on its surface the hypogynous perianth and stamens (or the stamens may be attached to the perianth), and the many or few, superior, separate or united carpels.

Order ALISMATALES. Carpels separate, superior to all other parts of the flower; endosperm scanty or none (species about 409). Related to and probably derived from the *Ranales* of the dicotyledons.

Family 1. **Alismataceae**. Water Plantains. Aquatic or paludose herbs with mostly radical, often large leaves; flowers small to large; perianth in two whorls of three leaves each (calyx and corolla); placenta sutural; ovules mostly solitary. *Alisma, Sagittaria.* (Pf. **2**[1]: 227.)[1]

Family 2. **Butomaceae.** Aquatic or paludose herbs, bearing narrow or broad leaves, with convergent veins; flowers large; perianth in two whorls, of three leaves each (calyx and corolla); placenta parietal; ovules many. *Butomus, Limnocharis.* (Pf. **2**[1]: 232.)

Family 3. **Triuridaceae.** Very small, pale, leafless plants growing in wet places in tropical countries. *Triuris.* (Pf. **2**[1]: 235.)

Family 4. **Scheuchzeriaceae.** Aquatic or paludose herbs with rush-like leaves, and small flowers, with a two-whorled perianth, each 4–6-parted. *Triglochin, Scheuchzeria.* (Pf. **2**[1]: 222.)

Family 5. **Typhaceae.** Cat-tails. Aquatic or paludose herbs, with linear, sheathing leaves and cylindrical-crowded flowers; pistil 1-celled; ovule 1. *Typha.* (Pf. **2**[1]: 183.)

Family 6. **Sparganiaceae.** Aquatic or paludose plants with creeping rootstocks and erect stems, bearing linear

[1] The abbreviation "Pf." has reference to Engler and Prantl's 'Natürlichen Pflanzenfamilien,' and the bold face, exponent, and Roman figures following refer respectively to "Abteilung," "Teil," and page of this publication.

leaves; flowers monoecious in dense globose heads. *Sparganium.* (Pf. **2**[1] : 192.)

Family 7. **Pandanaceae**. Screw-pines. Shrubs or trees with spirally crowded, narrow, stiff leaves on the ends of the branches; pistil 1-celled; ovules one or many. *Pandanus.* (Pf. **2**[1] : 186.)

Family 8. **Aponogetonaceae.** Aquatic plants with petioled, oblong, translucent leaves, with convergent veins; flowers small, spicate. *Aponogeton.* (Pf. **2**[1] : 218.)

Family 9. **Potamogetonaceae.** River-weeds. Aquatic or paludose herbs with mostly alternate stem-leaves; flowers mostly small and inconspicuous; perianth none, or of 1–6 leaves in 1 or 2 whorls. *Potamogeton, Zostera, Zannichellia.* (Pf. **2**[1] : 194.)

Order Liliales. Carpels united (usually 3), forming a compound pistil, superior; perianth (usually of 6 parts) in two similar whorls, delicate and corolla-like; endosperm copious. (Species about 3370.)

Family 10. **Liliaceae.** The Lilies. Pistil mostly 3-celled; stamens 6; perianth of two similar whorls, each of three similar leaves. *Lilium, Erythronium, Tulipa, Yucca, Asparagus, Allium.* (Pf. **2**[5] : 10.)

Family 11. **Stemonaceae.** Pistil 1-celled; stamens 4; perianth of two similar whorls, each of two similar leaves. *Stemona, Croomia.* (Pf. **2**[5] : 8.)

Family 12. **Pontederiaceae.** Aquatic herbs with 3 or 1-celled pistil; stamens 6 or 3; perianth of two similar whorls, each of three similar or dissimilar leaves. *Pontederia, Heteranthera.* (Pf. **2**[4] : 70.)

Family 13. **Cyanastraceae.** Tropical African rhizomatous plants. *Cyanastrum.* (Syllabus, 141.)[1]

Family 14. **Philydraceae.** Pistil 3-celled; stamen 1; perianth of two similar whorls, each of two dissimilar leaves. *Philydrium.* (Pf. **2**[4] : 75.)

[1] "Syllabus" has reference to Engler and Gilg's 'Syllabus der Pflanzenfamilien,' and the numbers following refer to pages of this publication.

Family 15. **Commelinaceae.** Spiderworts. Succulent herbs with 3 or 2-celled pistil; stamens 6; perianth of two dissimilar whorls of three similar leaves. *Commelina, Tradescantia.* (Pf. **2**^{4}: 60.)

Family 16. **Xyridaceae.** Rush-like plants with a 1-celled or incompletely 3-celled pistil; stamens 3; perianth of two dissimilar whorls, each of three similar leaves. *Xyris.* (Pf. **2**^{4}: 18.)

Family 17. **Mayacaceae.** Slender, creeping, moss-like plants with 1-celled pistil; stamens 3; perianth of two dissimilar whorls, each of three similar leaves. *Mayaca.* (Pf. **2**^{4}: 16.)

Family 18. **Juncaceae.** Rushes. Herbs with narrow leaves; pistil 1–3-celled; ovules solitary or many; fruit a dry 3-valved pod. *Juncus, Luzula.* (Pf. **2**^{5}: 1.)

Family 19. **Eriocaulonaceae.** Rush-like herbs with flowers in close heads; perianth segments 6 or less, small; pistil 3 or 2-celled; ovules orthotropous, pendulous. *Eriocaulon.* (Pf. **2**^{4}: 21.)

Family 20. **Thurniaceae.** South American herbs, with small, 1-nerved leaves, and small axillary flowers. *Thurnia.* (Syllabus, 139.)

Family 21. **Rapateaceae.** Tall, sedge-like marsh herbs with 3-celled pistil; stamens 6, in pairs; perianth of two dissimilar whorls, each of three similar leaves. *Rapatea.* (Pf. **2**^{4}: 28.)

Family 22. **Naiadaceae.** Slender, branching, wholly submerged aquatics, with sheathing, mostly opposite leaves, and monoecious or dioecious flowers. *Naias.* (Pf. **2**^{1}: 214.)

Order Arales. Compound pistil, mostly tricarpellary, superior; ovules one or more; perianth reduced to scales or entirely wanting; endosperm usually present. (Species about 1052.)

Family 23. **Cyclanthaceae.** Mostly herbaceous plants with broad, petioled leaves having parallel venation; pistil 1-celled; ovules many, on four parietal placentae. *Cyclanthus.* (Pf. **2**^{3}: 93.)

Family 24. **Araceae.** Arums. Mostly herbaceous plants with broad, petioled leaves, having reticulate venation; pistil 1–4-celled; ovules 1 or more. *Anthurium, Acorus, Monstera, Symplocarpus, Calla, Philodendron, Calocasia, Caladium, Arum, Arisaema.* (Pf. 2^3 : 102.)

Family 25. **Lemnaceae.** Duckweeds. Very small, floating, aquatic herbs; pistil 1-celled; ovules 1 or more. *Lemna, Spirodela.* (Pf. 2^3 : 154.)

Order Palmales. Compound pistil mostly tricarpellary, superior; ovule solitary; perianth reduced to rigid or herbaceous scales; endosperm copious. (Species about 1085.)

Family 26. **Palmaceae.** Palms. Trees or shrubs with pinnate or palmate leaves; pistil 1–3-celled; fruit a 1-seeded berry or drupe (rarely 2–3-seeded). *Phoenix, Chamaerops, Calamus, Oreodoxa, Cocos.* (Pf. 2^3 : 1.)

Order Graminales. Compound pistil reduced to 2 or 3 carpels; ovule solitary; perianth reduced to small scales or entirely wanting; endosperm copious. (Species about 5795.)

Family 27. **Restionaceae.** Rush-like herbs or undershrubs, with spiked, racemed, or panicled mostly diclinous flowers; perianth segments 6 or less, chaffy; pistil 1–3-celled; ovules orthotropous, pendulous. *Restio.* (Pf. 2^4: 3.)

Family 28. **Centrolepidiaceae.** Small rush-like herbs with mostly monoclinous flowers in spikes or heads; perianth none; pistil 1–several-celled; ovules orthotropous, pendulous. *Centrolepis.* (Pf. 2^4 : 11.)

Family 29. **Flagellariaceae.** Erect or climbing herbs with long narrow leaves, and panicled flowers; pistil 3-celled; ovules solitary, anatropous, ascending; fruit a 1–2-seeded berry. *Flagellaria.* (Pf. 2^4 : 1.)

Family 30. **Cyperaceae.** Sedges. Grass-like herbs with 3-ranked leaves; perianth segments bristly or none; pistil 1-celled; ovules anatropous, erect. *Cyperus, Scirpus, Fimbristylis, Rhynchospora, Carex.* (Species 1959.) (Pf. 2^2 : 98.)

Family 31. **Poaceae.** Grasses. Mostly erect herbs with hollow, jointed stems, and 2-ranked leaves; perianth segments

of 2–6 scales or vestiges; pistil 1-celled; ovules anatropous, ascending. *Bambusa, Bromus, Triticum, Bouteloua, Avena, Agrostis, Phalaris, Oryza, Panicum, Andropogon, Zea.* (Species 3545.) (Pf. 2^2 : 1.)

In the *Poaceae* the hypogynous, tricarpellary monocotyledons reach their culmination, as a highly specialized side line. In grasses the specialization involves plant-body, inflorescence, and flowers. Their nodose, mostly hollow, elongated stems, and long, narrow, tough leaves; the spreading paniculate arrangement of their spikelets; and their 1-celled, tricarpellary 1-ovuled pistils, producing caryopsis-fruits, are some of the more obvious indications of high specialization, suggesting the possibility that these plants, rather than the orchids, are the highest of the monocotyledons. With the *Poaceae* the hypogynous monocotyledonous phylum ends. Grasses have not given rise to other groups of plants.

Sub-Class ALTERNIFOLIAE - COTYLOIDEAE. Axis of the flower normally expanded into a cup, bearing on its margin the perianth and stamens (or the latter may be attached to the perianth). The carpels are thus inferior. Flowers from actinomorphic to zygomorphic.

Order HYDRALES. Flowers diclinous; compound tricarpellary pistil inferior to all other parts of the flower; perianth segments in each whorl alike in shape (flower regular); seeds without endosperm. (Species about 53.)

Family 32. **Vallisneriaceae.** Tape-grasses. Small aquatic herbs mostly inhabiting the fresh waters of temperate climates. *Vallisneria, Hydrocharis, Philotria.* (Pf. 2^1 : 238.)

Order IRIDALES. Compound tricarpellary pistil inferior; flower-leaves in each whorl mostly alike in shape (flower regular, actinomorphic); seeds with endosperm. (Species about 4419.)

Family 33. **Amaryllidaceae.** Amaryllises. Leaves narrow, or the blade broad, with longitudinal veins; pistil 3-celled; ovules many; stamens 6 or 3. *Amaryllis, Crinum, Narcissus, Agave, Hypoxis.* (Pf. 2^5 : 97.)

Family 34. **Haemodoraceae.** Leaves sword-shaped; pistil 3-celled; ovules 1 to many; stamens 6. *Haemodorum.* (Pf. 2^5: 92.)

Family 35. **Iridaceae.** Leaves sword-shaped; pistil 3-celled; ovules many; stamens 3. *Crocus, Iris, Tigridia, Sisyrinchium, Ixia, Tritonia, Gladiolus, Freesia.* (Pf. 2^5: 137.)

Family 36. **Velloziaceae.** Woody-stemmed, leafy plants, with a 3-celled pistil containing many ovules, stamens 6 or more. *Vellozia.* (Pf. 2^5: 125.)

Family 37. **Taccaceae.** Stemless herbs, with broad pinnately parallel-veined leaves; pistil 1-celled; ovules many; stamens 6. *Tacca.* (Pf. 2^5: 127.)

Family 38. **Dioscoreaceae.** Yams. Mostly twining herbs, with broad, petioled, longitudinally-veined leaves; pistil 3-celled; ovules 2 in each cell; stamens 6. *Dioscorea, Testudinaria.* (Pf. 2^5: 130.)

Family 39. **Bromeliaceae.** Pineapples. Leaves mostly rosulate; external perianth whorl calycine; pistil 3-celled; ovules many; stamens 6. *Tillandsia, Dendropogon, Ananas.* (Pf. 2^4: 32.)

Family 40. **Musaceae.** Bananas. Large herbs, the stem often composed of the sheathing leaf-bases; perianth petaloid of 6, often dissimilar segments; stamens 6; pistil 3-celled; ovules 1 to very many. *Strelitzia, Musa.* (Pf. 2^6: 1.)

Family 41. **Zingiberaceae.** Gingers. Perennial, medium-sized herbs, with creeping or tuberous rootstocks; perianth irregular; stamen 1, anther 2-celled, with several "staminodes"; pistil 3-celled; ovules 1 or more in each cell. *Curcuma, Zingiber, Amomum.* (Pf. 2^6: 10.)

Family 42. **Cannaceae.** Cannas. Perennial herbs of medium size, with simple pinnately-veined leaves; perianth irregular; stamen 1, anther 1-celled, with several "staminodes"; pistil 3-celled; ovules 1 to many. *Canna.* (Pf. 2^6: 30.)

Family 43. **Marantaceae.** Perennial herbs of variable habit; leaves parallel or pinnately veined; perianth irregular; functional stamen 1, with several "staminodes"; pistil 3-

celled; ovules 1 in each cell. *Calathea, Maranta.* (Pf. 2^6: 33.)

Order Orchidales. Compound tricarpellary pistil inferior; flower-leaves in each whorl mostly unlike in shape (flower irregular, zygomorphic); seeds numerous, minute, without endosperm. (Species about 7578.)

Family 44. **Burmanniaceae.** Flowers irregular; stamens 3 or 6. *Burmannia.* (Pf. 2^6: 44.)

Family 45. **Orchidaceae.** Orchids. Flowers irregular; stamens 1 or 2. *Cypripedium, Orchis, Platanthera, Vanilla, Spiranthes, Epidendrum, Dendrobium, Oncidium.* (Species 7521.) (Pf. 2^6: 52.)

In the *Orchidales,* and especially in the *Orchidaceae,* we have what is generally regarded as the highest development of monocotyledonous plants, and yet it must be acknowledged that many of their most striking flower structures are rather easily made entomophilous modifications of the perianth, the most mobile portion of the plant. In many ways the "grassy" plants (especially the *Poaceae*) show greater and more profound structural modifications than do the much more conspicuous orchids. With the orchids the epigynous monocotyledonous phylum ends.

Class 33. OPPOSITIFOLIAE (DICOTYLEDONEAE). The Dicotyledons. Leaves of young sporophyte opposite; leaves of mature sporophyte opposite or alternate, usually reticulate-veined; fibrovascular bundles of the stem in one or more cylindrical layers. (Species about 108,800.)

As indicated above the dicotyledons are here considered to have had their beginning earlier than the monocotyledons, which must be regarded as having diverged very early from the primitive dicotyledons, and developed into a relatively small lateral branch. The point of divergence of the monocotyledons from the dicotyledons must have been in the order *Ranales,* probably in the neighborhood of the *Ranunculaceae.* It is not probable that the early (woody) magnoliads or anonads gave rise to the monocotyledonous divergence; it is much more probable that this modification arose after the reduction had taken place from the ligneous to the herbaceous *Ranales.*

Here we have a possible explanation of the marked herbaceousness of monocotyledons as contrasted with the general tendency toward a more ligneous structure in dicotyledons.

Sub - Class OPPOSITIFOLIAE - STROBILOIDEAE. "Cone flowers." Axis of the flower normally cylindrical, spherical, hemispherical or flattened, bearing on its surface the hypogynous perianth, stamens and pistils (or the stamens may be attached to the corolla).

Super - Order STROBILOIDEAE-APOPETALAE-POLYCARPELLATAE. Carpels typically many, separate or united; petals separate. Flowers mostly actinomorphic. This super-order has much in common with the *Alismatales,* and also with the *Cotyloideae-Apopetalae.* In fact, these three groups appear to have diverged from a common point of origin.

Order RANALES. All parts of the flower mostly spirally arranged (acyclic), free (not united); carpels typically many, separate (or rarely united), rarely reduced to 1; stamens generally indefinite; embryo mostly small, in copious endosperm. (Species about 5551.)

The twenty-four families here included in the order *Ranales* naturally group themselves about three centers, the magnolias (*Magnoliaceae*), the anonas (*Anonaceae*), and the buttercups (*Ranunculaceae*). The plants in these centers are typically diplochlamydeous, polycarpellate, hermaphrodite, and actinomorphic, and the modifications in the surrounding families have been such as to result in an achlamydeous structure, which may be monocarpellate, diclinous, and even zygomorphic. Ranalean evolution has thus been one of more and more marked simplification of flower structure.

It is interesting to observe that while the families of *Ranales* have thus been evolved, the order has given rise to no less than five phyletic groups of full ordinal rank. One of these (*Malvales*) has produced a further modification (*Sarraceniales*), for three of them the evolutionary development came to a stand-still with the ordinal limits (*Geraniales, Guttiferales* and *Rhoedales*), while the virile *Caryophyllales* continued a development beyond its ordinal limits into the *Ebenales, Eri-*

cales and *Primulales*, and through the latter into *Gentianales*, *Polemoniales* and *Scrophulariales* to the end of this phyletic line in the *Lamiales*.

Family 46. **Magnoliaceae.** Magnolias. Petals present, usually many; receptacle usually elongated; shrubs and trees with alternate leaves and usually large flowers. *Magnolia*, *Liriodendron*. (Pf. **3**^{2}: 12.)

Family 47. **Calycanthaceae.** Petals present, usually many; seeds without endosperm; shrubs with opposite leaves. *Calycanthus*. (Pf. **3**^{2} : 92.)

Family 48. **Monimiaceae.** Petals absent; carpels many, 1-ovuled, embedded in the receptacle; trees and shrubs with opposite or whorled leaves, and diclinous flowers. *Kibara*, *Monimia*, *Siparuna*. (Pf. **3**^{2} : 94.)

Family 49. **Cercidiphyllaceae.** Trees with naked dioecious flowers, many stamens, and a single whorl of 2–5 free carpels. *Cercidiphyllum*. (Pf. **3**^{2} : 21.)

Family 50. **Trochodendraceae.** Trees and shrubs with naked flowers, many stamens, and a single whorl of 5 to many partly connate carpels. *Trochodendron*. (Pf. **3**^{2} : 21.)

Family 51. **Leitneriaceae.** Shrubs with alternate leaves and dioecious flowers in catkins; perianth minute or 0; pistil 1-celled, 1-ovuled; endosperm minute. *Leitneria*. (Pf. **3**^{1} : 28.)

Family 52. **Anonaceae.** Papaws. Petals present, in two whorls of 3 each; stamens and carpels many; endosperm ruminated; trees or shrubs with alternate leaves. *Asimina*, *Anona*. (Pf. **3**^{2} : 23.)

Family 53. **Lactoridaceae.** Much-branched shrubs of the South Pacific Islands, with alternate leaves, and apetalous flowers. *Lactoris*. (Pf. **3**^{2} : 19.)

Family 54. **Gomortegaceae.** Large trees of South America, with opposite evergreen leaves, and acyclic flowers; carpels 2–3, each with 1 ovule. *Gomortega*. (Pf. Nachträge zu Teil II–IV, 172.)

Family 55. **Myristicaceae.** Nutmegs. Sepals 3; petals absent; pistil 1 (or a second rudiment), 1-seeded; endosperm

ruminated; trees or shrubs with alternate leaves and small, inconspicuous, dioecious flowers. *Myristica.* (Pf. **3²**: 40.)

Family 56. **Saururaceae.** Rhizomatous marsh herbs, with alternate leaves; flowers perfect, small, spicate; perianth 0; carpels 3–4, more or less united. *Saururus.* (Pf. **3¹**: 1.)

Family 57. **Piperaceae.** Peppers. Herbs, shrubs, and trees with alternate (or opposite) leaves; flowers perfect or diclinous, mostly spicate; perianth 0; pistil 1-celled, 1-ovuled; endosperm present. *Piper, Macropiper.* (Pf. **3¹**: 3.)

Family 58. **Lacistemaceae.** Tropical American shrubs and trees with alternate leaves, and perfect flowers; perianth mostly 0; stamen 1; pistil 3 or 2-carpellary. *Lacistema.* (Pf. **3¹**: 14.)

Family 59. **Chloranthaceae.** No perianth whatever; pistil 1, with 1 ovule; mostly tropical trees and shrubs, with opposite leaves, and small flowers. *Chloranthus.* (Pf. **3¹**: 12.)

Family 60. **Ranunculaceae.** Buttercups. Petals present in one whorl, or absent; sepals mostly deciduous; stamens and carpels indefinite, the latter usually separate; mostly herbs with alternate leaves. *Myosurus, Ranunculus, Anemone, Clematis.* (Pf. **3²**: 43.)

Family 61. **Lardizabalaceae.** Petals and sepals 6 each; stamens 6; twining or erect shrubs, with alternate leaves. *Akebia, Lardizabala.* (Pf. **3²**: 67.)

Family 62. **Berberidaceae.** Barberries. Petals usually present, in 1–3 whorls; stamens few; carpel 1 (rarely more), with many ovules; mostly shrubs with alternate leaves and perfect flowers. *Podophyllum, Berberis.* (Pf. **3²**: 70.)

Family 63. **Menispermaceae.** Moonseeds. Petals present, in 2 whorls; carpels 3 or more; twining shrubs with alternate leaves and small dioecious flowers. *Menispermum, Cocculus.* (Pf. **3²**: 78.)

Family 64. **Lauraceae.** Laurels. Aromatic trees and shrubs with alternate simple leaves and small flowers; petals 0; carpel 1; ovule 1, pendulous; endosperm 0. *Cinnamomum, Persea, Ocotea, Umbellularia, Sassafras, Litsea, Laurus.* (Pf. **3²**: 106.)

Family 65. **Nelumbaceae.** Lotuses. Large aquatic herbs with peltate leaves, large acyclic flowers, with many stamens, and many separate carpels, the latter immersed in the flattish axis ("receptacle"); seeds 1 or 2, endosperm 0. *Nelumbo.* (Pf. $\mathbf{3}^2$: 1.)

Family 66. **Cabombaceae.** Water-shields. Small aquatic herbs with floating, sometimes peltate leaves, and few to many stamens, and separate carpels (not immersed); seeds 2 or 3; endosperm present. *Cabomba, Brasenia.* (Pf. $\mathbf{3}^2$: 2.)

Family 67. **Ceratophyllaceae.** Aquatic herbs with verticillate, divided leaves; flowers diclinous; perianth 0; stamens 12–16; carpel 1, 1-ovuled; endosperm scanty. *Ceratophyllum.* (Pf. $\mathbf{3}^2$: 10.)

Family 68. **Dilleniaceae.** Petals present, in one whorl; sepals persistent; stamens numerous, indefinite; carpels from many to 1, with 1 or more seeds; endosperm copious; mostly shrubs and trees with alternate leaves, and perfect flowers. *Dillenia, Actinidia.* (Pf. $\mathbf{3}^6$: 100.)

Family 69. **Winteranaceae.** Aromatic trees with alternate leaves; flowers perfect; sepals 4–5; petals 4–5 (or 0); stamens 20–30; pistil 2–5-carpellary, with as many parietal placentae; endosperm copious. *Winterana, Cinnamodendron.* (Pf. $\mathbf{3}^6$: 314.)

Order Malvales. Pistil usually of 3 to many weakly united carpels, with as many cells (sometimes greatly reduced); ovules mostly few; stamens indefinite, monadelphous, branched, or by reduction separate and few; endosperm present or absent. (Species about 3829.)

Family 70. **Sterculiaceae.** Trees and shrubs with alternate leaves; flowers perfect or diclinous, with or without petals; stamens monadelphous or polyadelphous, 2-celled; pistil 4–many-celled; endosperm present or 0. *Theobroma, Sterculia.* (Pf. $\mathbf{3}^6$: 69.)

Family 71. **Malvaceae.** Mallows. Herbs, shrubs, and trees with alternate leaves; flowers perfect, with petals; stamens monadelphous, 1-celled; pistil 5–many-celled; endosperm little

or 0. *Abutilon, Althaea, Malva, Hibiscus, Gossypium.* (Pf. **3**[6]: 30.)

Family 72. **Bombacaceae.** Tropical trees with alternate, palmate leaves; sepals and petals present; staminal column 5–8-cleft. *Adansonia, Bombax.* (Pf. **3**[6]: 53.)

Family 73. **Scytopetalaceae.** Trees of the southern hemisphere, with alternate leathery leaves; sepals small; petals much larger, valvate; stamens many. *Scytopetalum.* (Pf. Nachträge zu Teil II–IV, 242.)

Family 74. **Chlaenaceae.** Madagascar trees and shrubs with alternate leaves; inflorescence dichotomous; petals contorted. *Rhodochlaena, Leptochlaena.* (Pf. **3**[6]: 168.)

Family 75. **Gonystylaceae.** East Indian trees with leathery, evergreen leaves, pentamerous flowers, and a berry-like fruit. *Gonystylus.* (Pf. Nachträge zu Teil II–IV, 231.)

Family 76. **Tiliaceae.** Lindens. Trees, shrubs (and herbs) with mostly alternate leaves; flowers mostly perfect, with petals; stamens free, 2-celled; pistil 2–10-celled; endosperm present or 0. *Corchorus, Tilia, Grewia.* (Pf. **3**[6]: 8.)

Family 77. **Elaeocarpaceae.** Tropical trees and shrubs, with alternate or opposite simple leaves; sepals and petals present; stamens distinct, many; pistil of 2–several carpels. *Elaeocarpus, Aristotelia.* (Pf. **3**[6]: 1.)

Family 78. **Balanopsidaceae.** Australian trees and shrubs with alternate leaves; flowers dioecious, apetalous, the staminate in catkins, the pistillate solitary, producing acorn-like, 2-celled, 2-seeded fruits; seeds endospermous. This family is doubtfully given place here, and it may be that it should be placed near the *Fagaceae,* as is done by Baillon. *Balanops.* (Pf. Nachträge zu Teil II–IV, 114.)

Family 79. **Ulmaceae.** Elms. Trees and shrubs with alternate, simple leaves, small apetalous flowers, a 1-celled (rarely 2-celled) ovary, which develops into a samara, drupe or nut. *Ulmus, Celtis, Zelkova, Planera.* (Pf. **3**[1]: 59.)

Family 80. **Moraceae.** Figs. Trees, shrubs, and herbs, mostly with a milky juice, and alternate or opposite leaves;

flowers apetalous, diclinous (monoecious or dioecious); ovary 1-celled, 1-ovuled. *Morus, Toxylon* (*Maclura*), *Broussonetia, Dorstenia, Artocarpus, Castilloa, Antiaris, Ficus, Humulus, Cannabis.* (Pf. **3**[1]: 66.)

Family 81. **Urticaceae.** Nettles. Herbs, shrubs, and trees with alternate or opposite leaves; flowers mostly diclinous, apetalous; stamens few, 2-celled; pistil monocarpellary, 1-celled, mostly 1-seeded; endosperm none. *Urtica, Boehmeria.* (Pf. **3**[1]: 98.)

Order Sarraceniales. Pistil of 3–5 carpels united; placentae parietal or central; seeds small, numerous, endospermous; herbs with "insectivorous" leaves; related to the mallows, with which they should possibly be included. (Species about 66.)

Family 82. **Sarraceniaceae.** Pitcher-plants. Herbs with pitcher-shaped leaves, and perfect flowers; sepals 4–5; petals 5, rarely 0; stamens indefinite; pistil 3–5-carpellary. *Sarracenia, Darlingtonia.* (Pf. **3**[2]: 244.)

Family 83. **Nepenthaceae.** Pitcher-plants. Tropical undershrubs with pitcher-shaped leaves and dioecious flowers; sepals 4 or 3; petals 0; stamens 4–16; pistil 4–3-carpellary. *Nepenthes.* (Pf. **3**[2]: 253.)

Order Geraniales. Pistil of several (5–2) mostly weakly united carpels; ovules 1–2 (or many), mostly pendulous, attached at the inner angle of the carpel. (Species about 9268.)

Family 84. **Geraniaceae.** Geraniums. Herbs, shrubs, and trees, with opposite or alternate (compound or simple) leaves; torus elongated; stamens 10; pistil mostly 5-celled; ovules few; endosperm sparse or 0. *Geranium, Pelargonium, Erodium.* (Pf. **3**[4]: 1.)

Family 85. **Oxalidaceae.** Sorrels. Herbs, rarely shrubs or trees, the juice sour; leaves mostly 3 or more foliate; flowers pentamerous, regular; stamens 10; ovules many; endosperm fleshy. *Oxalis.* (Pf. **3**[4]: 15.)

Family 86. **Tropaeolaceae.** Nasturtiums. Succulent, prostrate or climbing herbs, with alternate, peltate leaves, and

irregular, long-peduncled, spurred flowers; stamens 8; ovary tricarpellary; ovules solitary; endosperm 0. *Tropaeolum.* (Pf. **3**[4]: 23.)

Family 87. **Balsaminaceae.** Touch-me-nots. Succulent herbs, mostly erect, with opposite or alternate leaves, and irregular, spurred axillary flowers; stamens 5; ovary pentacarpellary, ovules many; endosperm 0. *Impatiens.* (Pf. **3**[5]: 383.)

Family 88. **Limnanthaceae.** Succulent marsh herbs, with alternate, pinnate leaves; flowers pentamerous; stamens 10; carpels 5; endosperm 0. *Limnanthes.* (Pf. **3**[5]: 136.)

Family 89. **Linaceae.** Flaxes. Herbs and shrubs, with alternate simple leaves; pistil 3–5-celled; endosperm fleshy (or rarely 0). *Linum.* (Pf. **3**[4]: 27.)

Family 90. **Humiriaceae.** Trees with alternate simple leaves; pistil 5–7-celled; endosperm copious. *Humiria, Saccoglottis.* (Pf. **3**[4]: 35.)

Family 91. **Erythroxylaceae.** Shrubs and trees, with mostly alternate, simple leaves; flowers pentamerous; stamens 10; ovary 3–4-carpellary; fruit a drupe; endosperm fleshy. *Erythroxylon.* (Pf. **3**[4]: 37.)

Family 92. **Zygophyllaceae.** Herbs and shrubs with usually opposite, compound leaves; pistil lobed, 4–5-celled; endosperm copious (or rarely 0). *Zygophyllum, Guaiacum, Larrea.* (Pf. **3**[4]: 74.)

Family 93. **Cneoraceae.** Shrubs with alternate entire leaves, trimerous or tetramerous flowers; pistil 3 or 4-celled, each cell with one ovule; endosperm fleshy. *Cneorum.* (Pf. **3**[4]: 93.)

Family 94. **Rutaceae.** Oranges. Herbs, shrubs, and trees with glandular-dotted, opposite, simple, or compound leaves; pistil lobed, 4–5-celled; endosperm fleshy or 0. *Xanthoxylum, Ruta, Dictamnus, Ptelea, Limonia, Citrus.* (Pf. **3**[4]: 95.)

Family 95. **Simarubaceae.** Trees and shrubs with generally alternate, non-glandular, simple, or compound leaves; pistil lobed, 1–5-celled; endosperm fleshy or 0. *Simaruba, Quassia, Holacantha, Ailanthus.* (Pf. **3**[4]: 202.)

Family 96. **Burseraceae.** Balsamic trees and shrubs with alternate compound leaves; pistil 2–5-celled; endosperm 0. *Protium, Canarium, Bursera.* (Pf. **3**[4]: 231.)

Family 97. **Meliaceae.** Trees and shrubs with alternate compound leaves; pistil 3–5-celled; endosperm present or 0. *Swietenia, Melia.* (Pf. **3**[4]: 258.)

Family 98. **Malpighiaceae.** Trees and shrubs with usually opposite, simple or lobed leaves; pistil tricarpellary; endosperm 0. *Stigmatophyllon, Malpighia, Byrsonima.* (Pf. **3**[4]: 41.)

Family 99. **Trigoniaceae.** Climbing shrubs with opposite simple leaves and irregular flowers; pistil tricarpellary; seeds many, endospermous. *Trigonia.* (Pf. **3**[4]: 309.)

Family 100. **Vochysiaceae.** Shrubs and trees with opposite or whorled leaves; sepals 5; petals 1, 3, or 5; stamens several, usually but one fertile; pistil tricarpellary; seeds few; endosperm 0. *Vochysia, Qualea.* (Pf. **3**[4]: 312.)

Family 101. **Polygalaceae.** Herbs, shrubs, and trees with alternate leaves; flowers irregular; sepals 5; petals 3–5; stamens usually 8; ovary 2-celled; ovules solitary; endosperm present or 0. *Polygala, Xanthophyllum.* (Pf. **3**[4]: 323.)

Family 102. **Tremandraceae.** Small shrubs with alternate, opposite, or whorled leaves; flowers regular; sepals and petals 3, 4, or 5 each; stamens twice as many; ovary 2-celled; ovules mostly solitary; endosperm fleshy. *Tremandra, Tetratheca.* (Pf. **3**[4]: 320.)

Family 103. **Dichapetalaceae.** Trees and shrubs with alternate simple leaves; pistil 2–3-celled; endosperm 0. *Dichapetalum, Tapura.* (Pf. **3**[4]: 345.)

Family 104. **Euphorbiaceae.** Spurges. Herbs, shrubs, and trees, mostly with a milky juice and alternate or opposite leaves; flowers diclinous, with a perianth of 1 or 2 whorls, or wanting; stamens 2-celled, free or united; pistil usually 3-celled; ovules mostly solitary; endosperm copious. *Euphorbia, Pedilanthus, Phyllanthus, Croton, Mallotus, Acalypha, Ricinus, Jatropha, Manihot, Stillingia.* (Species 4319.) (Pf. **3**[5]: 1.)

Family 105. **Callitrichaceae.** Floating herbs with opposite sessile leaves; flowers diclinous, sessile in the leaf-axils; perianth none; stamens 1 or 2; ovary 2-celled; endosperm fleshy. *Callitriche.* (Pf. **3**^{5}: 120.)

Order GUTTIFERALES. Pistil mostly of 2 or more carpels, 2–several-celled, with axile placentae; stamens usually indefinite; endosperm usually wanting. (Species about 3138.)

Family 106. **Theaceae.** Teas. Trees and shrubs usually with alternate leaves; inflorescence various; petals imbricated; seeds few; endosperm scanty or 0. *Thea, Stuartia.* (Pf. **3**^{6}: 175.)

Family 107. **Cistaceae.** Herbs and shrubs with opposite (or alternate) leaves; sepals 3–5; petals 5; stamens many; pistil 3–5-carpellary, with as many parietal placentae; seeds usually many, endospermous. *Cistus, Helianthemum, Hudsonia.* (Pf. **3**^{6}: 299.)

Family 108. **Guttiferaceae.** Trees, shrubs, and rarely herbs, with opposite or whorled, glandular-dotted leaves; inflorescence often trichotomous, with flowers mostly diclinous; petals 2–6, or more, imbricated or contorted; stamens many; carpels mostly 3–5; endosperm 0. *Hypericum, Mammea, Clusia, Garcinia.* (Pf. **3**^{6}: 194.)

Family 109. **Eucryphiaceae.** Evergreen trees of the southern hemisphere, with opposite leaves; flowers large, tetramerous; stamens many; pistil many-celled; seeds endospermous. *Eucryphia.* (Pf. **3**^{6}: 129.)

Family 110. **Ochnaceae.** Tropical shrubs and trees with alternate, coriaceous, simple leaves; pistil lobed, 1–10-celled; endosperm fleshy or 0. *Ochna.* (Pf. **3**^{6}: 131.)

Family 111. **Dipterocarpaceae.** Tropical, resiniferous trees and shrubs with alternate leaves; inflorescence panicled; flowers regular, perfect; petals contorted; fruiting calyx enlarged, and wing-like; carpels few (3–1); seeds 2 in each cell; endosperm 0. *Dipterocarpus.* (Pf. **3**^{6}: 243.)

Family 112. **Caryocaraceae.** Tropical trees and shrubs, with alternate trifoliate leaves, large showy flowers, and many

long stamens; seeds solitary; endosperm scanty or 0. *Caryocar.* (Pf. **3**^{6}: 153.)

Family 113. **Quiinaceae.** South American trees and shrubs, with opposite or whorled simple leaves; sepals 4–5; petals 4–5; stamens 15–30. *Quiina.* (Pf. **3**^{6}: 165.)

Family 114. **Marcgraviaceae.** Tropical trees and shrubs, with alternate, simple leaves; sepals 2–6; petals as many; stamens as many or more; ovary 3–5-celled; seeds many; endosperm 0. *Marcgravia.* (Pf. **3**^{6}: 157.)

Family 115. **Flacourtiaceae.** Mostly tropical trees and shrubs with alternate leaves; sepals 2–15; petals 10–0; stamens indefinite; carpels 2–10; seeds endospermous. *Pangium, Flacourtia, Samyda.* (Pf. **3**^{6a}: 1.)

Family 116. **Bixaceae.** Tropical shrubs with alternate leaves; sepals 3–7; petals large; stamens indefinite; pistil bicarpellary; seeds endospermous. *Bixa.* (Pf. **3**^{6}: 307.)

Family 117. **Cochlospermaceae.** Tropical trees and shrubs with alternate lobed or compound leaves; petals large; stamens indefinite; pistil 3–5-carpellary; endosperm copious. *Cochlospermum.* (Pf. **3**^{6}: 312, and Nachträge zu Teil II–IV, 251.)

Family 118. **Violaceae.** Violets. Herbs and shrubs with alternate (or opposite) leaves; sepals and petals 5, irregular; stamens 5; pistil 3-carpellary with 3 parietal placentae; endosperm copious. *Rinorea, Hybanthus, Viola.* (Pf. **3**^{6}: 322.)

Family 119. **Malesherbiaceae.** South American branching herbs or undershrubs, with perfect, regular, pentamerous flowers; endosperm fleshy. *Malesherbia.* (Pf. **3**^{6a}: 65.)

Family 120. **Turneraceae.** Tropical herbs and shrubs with alternate leaves; flowers perfect; sepals and petals dissimilar; stamens definite; ovary tricarpellary; endosperm copious. *Turnera.* (Pf. **3**^{6a}: 57.)

Family 121. **Passifloraceae.** Passion flowers. Climbing herbs and shrubs (a few trees) with alternate leaves; flowers perfect, regular; sepals and petals similar, distinct; stamens definite; ovary free; endosperm fleshy. *Adenia, Passiflora.* (Pf. **3**^{6a}: 69.)

Family 122. **Achariaceae.** South African herbs and undershrubs, related to the *Passifloraceae;* but with the petals united. *Acharia.* (Pf. **3**[6a]: 92.)

Family 123. **Caricaceae.** Papaws. Succulent-stemmed tropical trees, mostly with palmate leaves and milky juice; flowers pentamerous; fruit a many seeded berry; endosperm fleshy. *Carica.* (Pf. **3**[6a]: 94.)

Family 124. **Stachyuraceae.** Asiatic shrubs and trees with alternate leaves; sepals 4; petals 4; stamens 8; endosperm fleshy. *Stachyurus.* (Pf. **3**[6]: 192.)

Family 125. **Koeberliniaceae.** Leafless, thorny Texan and Mexican shrubs, with tetramerous flowers; pistil bicarpellary; seeds many; endosperm scanty. *Koeberlinia.* (Pf. **3**[6]: 319.)

Order Rhoeadales. Pistil of 2 or more united carpels, mostly 1-celled, with parietal placentae; stamens indefinite or definite; endosperm none or copious. (Species about 2856.)

Family 126. **Papaveraceae.** Poppies. Mostly milky-juiced plants, with alternate leaves, and regular or irregular flowers; sepals 2–3; petals 4 or more (or 0); stamens indefinite; pistil many-carpellary; seeds usually many; endosperm fleshy. *Eschscholtzia, Sanguinaria, Argemone, Papaver, Bicuculla, Fumaria.* (Pf. **3**[2]: 130.)

Family 127. **Tovariaceae.** Annual herbs of the tropics, with alternate leaves; 8-merous flowers, and many seeds, with scanty endosperm. *Tovaria.* (Pf. **3**[2]: 207.)

Family 128. **Nymphaeaceae.** Water-lilies. Aquatic herbs with floating leaves, and regular flowers; petals present, in 1–many whorls (really acyclic); pistils closely united; seeds many, endospermous. *Victoria, Castalia, Nymphaea.* (Pf. **3**[2]: 1.)

Family 129. **Moringaceae.** Trees of the tropics, with decompound leaves and pentamerous, zygomorphic flowers, and producing bean-like tricarpellary pods; endosperm 0. *Moringa.* (Pf. **3**[2]: 242.)

Family 130. **Resedaceae.** Mignonettes. Herbs and shrubs with scattered leaves and zygomorphic flowers; sepals 4–8

(or 2 or 0); stamens 3–40; pistil 2–6-carpellary; seeds many; endosperm 0. *Reseda.* (Pf. **3**^{2}: 237.)

Family 131. **Capparidaceae.** Capers. Herbs, shrubs, and trees with alternate or opposite leaves, and regular or irregular flowers; sepals 4; petals 4 (or 0); stamens 4 (or many); pistil 2–6-carpellary, endosperm 0. *Cleome, Capparis.* (Pf. **3**^{2}: 209.)

Family 132. **Brassicaceae.** Mustards. Herbs, rarely shrubs, with alternate (or opposite) leaves, and regular flowers; sepals 4; petals 4; stamens 6 or 4; pistil 2-carpellary; endosperm 0. *Sinapis, Brassica, Raphanus, Bursa, Alyssum.* (Pf. **3**^{2}: 145.)

Order Caryophyllales. Pistil usually of 3 or more united carpels, mostly 1-celled, with a free-central placenta, and many ovules (sometimes reduced to a one-celled, one-ovuled ovary); stamens as many or twice as many as the petals; flowers regular; seeds mostly endospermous, usually with a curved embryo. (Species about 4330.)

The general arrangement of the families of the order *Caryophyllales* may be understood by placing the *Caryophyllaceae* centrally at the base; from this, one line runs off to the diplochlamydeous, hermaphrodite *Frankeniaceae* and *Tamaricaceae* to the achlamydeous, diclinous *Salicaceae,* while on the other hand another line passes from the diplochlamydeous, many-ovuled *Caryophyllaceae* to the apetalous, 1-ovuled *Amaranthaceae, Chenopodiaceae* and *Polygonaceae.*

Family 133. **Caryophyllaceae.** Pinks. Herbs (and shrubs) with opposite leaves; petals 3–5, stalked or not; ovules many on a central placenta; seeds endospermous. *Silene, Lychnis, Dianthus, Alsine, Paronychia, Illecebrum.* (Pf. **3**^{1b}: 61.)

Family 134. **Elatinaceae.** Small marsh herbs or undershrubs, with small, opposite or whorled leaves; inflorescence axillary; petals imbricated; stamens 4–10; endosperm 0. *Elatine.* (Pf. **3**^{6}: 277.)

Family 135. **Portulacaceae.** Purslanes. Herbs, or somewhat woody plants, usually somewhat succulent, with alternate or opposite leaves; sepals usually 2; petals 4–5; seeds many, endospermous. *Claytonia, Portulaca.* (Pf. **3**^{1b}: 51.)

Family 136. **Aizoaceae.** Herbaceous or shrubby plants with mostly opposite or verticillate, often fleshy leaves; calyx tetramerous or pentamerous; corolla often wanting; ovary mostly 2–5-celled with few to many ovules in each cell; seeds endospermous. *Mollugo, Sesuvium, Mesembrianthemum.* (Pf. 3^{1b}: 33.)

Family 137. **Frankeniaceae.** Herbs and undershrubs with opposite leaves, and perfect flowers; petals 4–5, long-stalked; ovules many, on 2–4 parietal placentae; seeds endospermous. *Frankenia.* (Pf. 3^{6}: 283.)

Family 138. **Tamaricaceae.** Tamarixes. Shrubs and herbs with minute, alternate, deciduous leaves and mostly racemose, perfect flowers; petals 5; ovules many, on 2–5 parietal placentae; seeds hairy-tufted; endosperm 0. *Tamarix.* (Pf. 3^{6}: 289.)

Family 139. **Salicaceae.** Willows. Shrubs and trees with large alternate leaves and racemose flowers; perianth 0; ovules many, on 2–4 parietal placentae; seeds hairy-tufted; endosperm 0. Here regarded as reduced, dioecious, apetalous, *Tamaricaceae. Salix, Populus.* (Pf. 3^{1}: 29.)

Family 140. **Podostemonaceae.** Riverweeds. Small aquatic, sometimes thallose, plants; flowers perfect or diclinous; perianth 0; pistil 1–3-celled; ovules many, centrally attached; endosperm 0. *Podostemon.* (Pf. 3^{2a}: 1.)

Family 141. **Hydrostachydaceae.** Large tuber-forming Madagascar plants, with naked, dioecious flowers, single stamens, and numerous ovules on 2 parietal placentae; endosperm 0. *Hydrostachys.* (Pf. 3^{2a}: 22.)

Family 142. **Phytolaccaceae.** Pokeweeds. Herbs, shrubs, and trees with usually alternate leaves; petals 0 (or 4–5); carpels several, distinct or nearly so, 1-ovuled; seeds endospermous. *Phytolacca.* (Pf. 3^{1b}: 1.)

Family 143. **Basellaceae.** Herbaceous climbing plants, with mostly alternate leaves; calyx dimerous; corolla pentamerous; stamens 5; ovary tricarpellary, 1-celled, with one ovule; endosperm scanty. *Basella, Boussingaultia.* (Pf. 3^{1a}: 124.)

Family 144. **Amaranthaceae.** Amaranths. Herbs, shrubs (and trees) with opposite or alternate leaves, and regular, mostly perfect flowers; perianth of scarious sepals; petals 0; ovules 1 or more, basal, campylotropous; endosperm copious. *Celosia, Amaranthus, Froelichia.* (Pf. **3**[1a]: 91.)

Family 145. **Chenopodiaceae.** The Goosefoots. Herbs, shrubs (and trees) with mostly alternate leaves, and regular, perfect or imperfect flowers; perianth of herbaceous sepals; petals 0; ovule 1, basal, campylotropous; endosperm fleshy. *Beta, Chenopodium, Spinacia, Atriplex, Sarcobatus, Salsola.* (Pf. **3**[1a]: 36.)

Family 146. **Polygonaceae.** Buckwheats. Herbs, shrubs, and trees with mostly alternate leaves and regular, perfect flowers; perianth often petaloid; petals 0; pistil tricarpellary, 1-celled; ovule 1, erect, orthotropous; endosperm copious. *Eriogonum, Rumex, Rheum, Polygonum, Fagopyrum, Coccoloba.* (Pf. **3**[1a]: 1.)

Family 147. **Nyctaginaceae.** Four o'clocks. Herbs and rarely shrubs and trees, with opposite or alternate leaves; flowers mostly perfect; petals 0; sepals often petaloid; pistil seemingly monocarpellary; ovule 1, erect; endosperm copious to scanty. *Mirabilis, Bougainvillea, Allionia.* (Pf. **3**[1b]: 14.)

Family 148. **Cynocrambaceae.** Annual, succulent herbs, with petioled leaves, opposite below, alternate above; flowers monoecious, apetalous, small, axillary; pistil monocarpellary; endosperm fleshy. *Cynocrambe.* (Pf. **3**[1a]: 121.)

Family 149. **Batidaceae.** Maritime shrubs with opposite fleshy leaves and small, dioecious flowers; petals 0; ovary 4-celled; ovule solitary, erect; endosperm 0. Very doubtfully placed here. *Batis.* (Pf. **3**[1a]: 118.)

Super-Order Strobiloideae-Sympetalae-Polycarpellatae. Carpels typically many, united; petals united. Flowers actinomorphic.

Order Ebenales. Flowers regular, perfect, or diclinous; stamens mostly isomerous with, and opposite to, the corolla-lobes, or in several series; ovary 2–many-celled; seeds mostly

solitary or few, usually large, centrally attached. (Species about 1136.)

Family 150. **Sapotaceae.** Sapodillas. Tropical trees and shrubs with a milky juice, and mostly alternate leaves; flowers mostly perfect; sepals and petals 4–8 each; stamens in 2–3 whorls, attached to the corolla; ovary superior, several-celled; endosperm from fleshy to 0. *Achras, Sideroxylon, Chrysophyllum, Mimusops.* (Pf. **4**[1]: 126.)

Family 151. **Ebenaceae.** Ebonies. Tropical and subtropical trees and shrubs, with very hard wood, and mostly alternate leaves; flowers mostly dioecious; sepals and petals 3–7 each; stamens usually many and free from the corolla; ovary 3–many-celled, superior; endosperm copious. *Diospyros, Maba.* (Pf. **4**[1]: 153.)

Family 152. **Symplocaceae.** Tropical and subtropical trees and shrubs, with mostly perfect flowers; sepals usually 5; petals usually 5; stamens many, attached to the base of the corolla; ovary 2–5-celled, inferior; seeds few, endospermous. *Symplocos.* (Pf. **4**[1]: 165.)

Family 153. **Styracaceae.** Styraxes. Trees and shrubs of warm climates with alternate leaves; flowers mostly perfect, sepals and petals 5 each; stamens usually many, attached to the base of the corolla; ovary 3–5-celled, usually inferior; seeds few, endospermous. *Halesia, Styrax.* (Pf. **4**[1]: 172.)

Family 154. **Fouquieriaceae.** Mexican shrubs with small leaves (becoming thorn-like), and panicled tubular flowers; sepals 5; petals 5, united into a tube; stamens 10–15, free; ovary tricarpellary; placenta central; seeds few; endosperm scanty. This small family is given place here with some confidence that it is much more closely related to these families than to those of the *Caryophyllales* and *Polemoniales,* with which it has been associated. *Fouquieria.* (Pf. **3**[6]: 298.)

Order Ericales. Flowers regular, perfect, pentamerous or tetramerous; stamens alternate with the corolla-lobes, and as many or twice as many; cells of the mostly superior ovary (or placentae) 2 to many; seeds minute. (Species about 1730.)

Family 155. **Clethraceae.** White alders. Shrubs and trees of warm climates, with alternate deciduous leaves and pentamerous flowers; stamens 10; pistil tricarpellary; endosperm fleshy. *Clethra.* (Pf. **4**[1] : 1.)

Family 156. **Ericaceae.** Heaths. Shrubs and small trees with mostly evergreen alternate or opposite leaves; ovary typically superior (sometimes inferior), 2–10-celled; anthers usually dehiscing by an apical pore; endosperm fleshy. *Rhododendron, Kalmia, Gaultheria, Arctostaphylos, Gaylussacia, Vaccinium, Calluna, Erica.* (Pf. **4**[1] : 15.)

Family 157. **Epacridaceae.** Shrubs and small trees (mostly Australian) with mostly alternate evergreen leaves; ovary superior, mostly 2–10-celled; fruit capsular or drupaceous; anthers dehiscing by a slit; endosperm fleshy. *Epacris.* (Pf. **4**[1] : 66.)

Family 158. **Diapensiaceae.** Low undershrubs, with alternate evergreen leaves; ovary superior, 3-celled; fruit a capsule; anthers dehiscing by a slit; endosperm fleshy. *Diapensia, Shortia.* (Pf. **4**[1] : 80.)

Family 159. **Pirolaceae.** Wintergreens. Low evergreen, or chlorophylless herbs, with pentamerous or tetramerous (rarely hexamerous) flowers; stamens twice as many as the petals; ovary 4–6-celled; endosperm fleshy. *Pirola, Chimaphila, Monotropa.* (Pf. **4**[1] : 3.)

Family 160. **Lennoaceae.** Parasitic, leafless herbs; ovary superior, 10–14-carpellary, 20–28-celled; ovules solitary; anthers dehiscing by a slit; endosperm copious. *Lennoa.* (Pf. **4**[1] : 12.)

Order Primulales. Flowers regular, mostly perfect and pentamerous; stamens epipetalous, mostly opposite to the corolla-lobes; ovary pluricarpellary, mostly 1-celled, with a free-central placenta. (Species about 1581.)

Family 161. **Primulaceae.** Primroses. Herbs with alternate or opposite leaves; stamens attached to the upper portion of the corolla tube; pistil 2–6-carpellary, one-celled; ovules many; fruit a capsule dehiscing longitudinally from the apex,

or circumscissilely; endosperm fleshy. *Primula, Androsace, Lysimachia, Cyclamen, Dodecatheon.* (Pf. **4**[1]: 98.)

Family 162. **Plantaginaceae.** Plantains. Herbs with clustered radical leaves, or alternate or opposite stem leaves; stamens alternate with the petals; ovary mostly 2-celled; ovules many; placenta axile; fruit a capsule dehiscing circumscissilely; endosperm fleshy. *Plantago.* (Pf. **4**[3b]: 363.)

Family 163. **Plumbaginaceae.** Leadworts. Herbs with alternate or clustered leaves; stamens opposite the petals; pistil 5-carpellary, one-celled, with one basal, anatropous ovule; fruit capsular; dehiscence valvate or irregular; endosperm copious. *Plumbago, Armeria.* (Pf. **4**[1]: 116.)

Family 164. **Myrsinaceae.** Trees and shrubs with mostly alternate leaves; stamens attached to the lower part of the corolla tube; ovules usually few; fruit a drupe or berry; endosperm fleshy. *Myrsine, Ardisia.* (Pf. **4**[1]: 84.)

Family 165. **Theophrastaceae.** Tropical trees and shrubs closely related to the preceding family, and sometimes included in it, but with many ovules. *Theophrasta, Jacquinia.* (Pf. **4**[1]: 88.)

Super-Order Strobiloideae-Sympetalae-Dicarpellatae. Carpels typically two, united; petals united. Flowers mostly perfect, from actinomorphic to zygomorphic.

Order Gentianales. Corolla actinomorphic (regular), mostly pentamerous; stamens alternate with the corolla-lobes, and usually of the same number and attached to the tube; leaves opposite (rarely alternate). (Species about 4664.)

Family 166. **Oleaceae.** Olives. Shrubs and trees (rarely herbs) with mostly opposite leaves, and tetramerous flowers; corolla-lobes mostly valvate or 0; stamens 2 (or 4); ovary 2-celled; ovules 1–3; endosperm present or 0. *Syringa, Olea, Jasminum, Fraxinus.* (Pf. **4**[2]: 1.)

Family 167. **Salvadoraceae.** Mostly tropical shrubs and trees, with opposite undivided leaves, and tetramerous or pentamerous flowers; corolla-lobes imbricated; stamens 4; ovary 2-celled; ovules 2; endosperm 0. *Salvadora.* (Pf. **4**[2]: 17.)

Family 168. **Loganiaceae.** Herbs, shrubs, and trees with mostly opposite simple leaves and pentamerous or tetramerous flowers; corolla-lobes imbricated or contorted; stamens mostly 4–5; ovary 2-celled (rarely 4-celled); ovules 1–many; endosperm fleshy. *Gelsemium, Logania, Spigelia, Strychnos.* (Pf. **4**^{2} : 19.)

Family 169. **Gentianaceae.** Gentians. Mostly herbs, with usually opposite undivided leaves and pentamerous or tetramerous flowers; corolla-lobes contorted, valvate, or induplicate; stamens 4–5; ovary bicarpellary, usually 1-celled; ovules many; endosperm copious. *Erythraea, Gentiana, Eustoma, Menyanthes.* (Pf. **4**^{2}: 50.)

Family 170. **Apocynaceae.** Dogbanes. Milky-juiced trees, shrubs, and herbs, with opposite or whorled, simple leaves and mostly pentamerous (rarely tetramerous) flowers; corolla-lobes contorted or valvate; stamens 5 (or 4), with granular pollen; ovary 2-celled or the carpels separating; ovules many; endosperm fleshy. *Vinca, Apocynum, Nerium.* (Pf. **4**^{2} : 109.)

Family 171. **Asclepiadaceae.** Milkweeds. Milky-juiced herbs and shrubs, with opposite, whorled (or alternate) leaves and pentamerous flowers; corolla-lobes contorted; stamens 5, with agglutinated pollen; ovary of two separated carpels with one discoid stigma; ovules many; seeds usually comose; endosperm fleshy. *Asclepias, Enslenia, Ceropegia, Stapelia, Hoya.* (Pf. **4**^{2} : 189.)

Order POLEMONIALES. Corolla actinomorphic, becoming somewhat zygomorphic in the later families; stamens alternate with the corolla-lobes, of the same number and attached to the corolla tube; leaves alternate (rarely opposite). (Species about 4112.)

The relationship of this order to the *Primulales,* and through it to the *Caryophyllales,* is so obvious as to make it scarcely necessary to point it out here.

Family 172. **Polemoniaceae.** Phloxes. Herbs (and shrubs) with alternate leaves (rarely opposite below); flowers pentamerous; corolla-lobes 5, contorted; ovary tricarpellary, 3-celled;

ovules 1 or more in each cell; endosperm fleshy. *Cobaea, Phlox, Gilia, Polemonium.* (Pf. 4^{3a}: 40.)

Family 173. **Convolvulaceae.** Morning-glories. Herbs (often climbing), shrubs (and trees) with alternate leaves and pentamerous flowers; corolla-limb more or less plicate (rarely imbricated); ovary 2 (3–5)-celled; ovules few; endosperm fleshy. *Evolvulus, Quamoclit, Ipomoea, Convolvulus, Cuscuta* (parasitic). (Pf. 4^{3a}: 1.)

Family 174. **Hydrophyllaceae.** Herbs with radical or alternate (rarely opposite) leaves and pentamerous flowers; corolla-lobes imbricated (or contorted); ovary 1 or incompletely 2-celled; ovules 2 or more; endosperm fleshy. *Hydrophyllum, Phacelia, Nama.* (Pf. 4^{3a}: 54.)

Family 175. **Borraginaceae.** Forget-me-nots. Herbs, shrubs, and trees with alternate leaves and pentamerous flowers; corolla-lobes imbricated (or contorted); ovary bicarpellary, 4-celled, 4-lobed; ovules solitary in each lobe; endosperm fleshy or 0. *Heliotropium, Cynoglossum, Oreocarya, Borrago, Myosotis, Mertensia, Lithospermum.* (Pf. 4^{3a}: 71.)

Family 176. **Nolanaceae.** Herbaceous or suffrutescent prostrate South American plants, with alternate, entire leaves; calyx 5-parted; corolla long funnel-shaped; stamens 5, inserted on the corolla; carpels 5, distinct or united; endosperm fleshy. *Nolana.* (Pf. 4^{3b}: 1.)

Family 177. **Solanaceae.** Nightshades. Herbs, shrubs (and trees) with alternate leaves and pentamerous, mostly regular, but sometimes irregular flowers; corolla-limb more or less plicate (rarely imbricated); ovary mostly 2-celled; ovules many; endosperm fleshy. *Lycium, Atropa, Hyoscyamus, Physalis, Capsicum, Solanum, Datura, Nicotiana, Petunia.* (Pf. 4^{3b}: 4.)

Order Scrophulariales. Corolla mostly zygomorphic (irregular or oblique); stamens fewer than the corolla-lobes, usually 4 or 2; ovules numerous; fruit mostly capsular (i. e., dehiscent). (Species about 7081.)

Family 178. **Scrophulariaceae.** Snapdragons. Herbs (or shrubs and small trees) with alternate, opposite, or whorled

leaves; ovary 2-celled with an axile placenta; seeds numerous, with endosperm. *Verbascum, Linaria, Antirrhinum, Maurandia, Collinsia, Scrophularia, Mimulus, Veronica, Digitalis, Gerardia, Castilleia, Pedicularis.* (Pf. **4**^{3b}: 39.)

Family 179. **Bignoniaceae.** Catalpas. Trees, shrubs (and herbs) with opposite or whorled leaves; ovary 1 or 2-celled with parietal or axile placentae; seeds numerous, without endosperm. *Bignonia, Catalpa, Tecoma.* (Pf. **4**^{3b}: 189.)

Family 180. **Pedaliaceae.** Mostly tropical herbs with generally opposite leaves; ovary 1, 2, or 4-celled with axile placentae; seeds 1–many, with but little endosperm. *Pedalium, Sesamum.* (Pf. **4**^{3b}: 253.)

Family 181. **Martyniaceae.** Mostly tropical herbs with generally opposite leaves; stamens 2 or 4; ovary 1-celled with projecting parietal placentae; endosperm 0. *Martynia.* (Pf. **4**^{3b}: 265.)

Family 182. **Orobanchaceae.** Broom-rapes. Leafless parasitic herbs; ovary 1-celled; placentae 4, parietal; ovules minute, numerous; endosperm fleshy. *Orobanche, Thalesia, Conopholis.* (Pf. **4**^{3b}: 123.)

Family 183. **Gesneraceae.** Tropical and subtropical herbs, shrubs (and trees) with usually opposite leaves; ovary inferior or superior, 1-celled, with 2 parietal placentae; seeds numerous; endosperm scanty or 0. *Streptocarpus, Gesnera, Gloxinia.* (Pf. **4**^{3b}: 133.)

Family 184. **Columelliaceae.** South American trees and shrubs with opposite, evergreen leaves and nearly regular flowers; stamens 2; ovary inferior, 2-celled, with an axile placenta; endosperm fleshy. *Columellia.* (Pf. **4**^{3b}: 186.)

Family 185. **Lentibulariaceae.** Bladderworts. Aquatic or marsh herbs with basal, entire or dissected leaves and irregular flowers; ovary 1-celled, with a globose basilar placenta; seeds numerous; endosperm 0. *Pinguicula, Utricularia.* (Pf. **4**^{3b}: 108.)

Family 186. **Globulariaceae.** Shrubs and undershrubs or evergreen herbs, with alternate leaves, and a terminal capitate

cluster of small irregular flowers; ovary 1-celled, with a single ovule; endosperm fleshy. *Globularia.* (Pf. 4^{3b}: 270.)

Family 187. **Acanthaceae.** Herbs (shrubs and trees) with opposite leaves; ovary 2-celled; placentae axile; fruit a dry pod which splits open vertically; seeds 2–many, without endosperm. *Thunbergia, Ruellia, Acanthus, Justicia.* (Pf. 4^{3b}:274.)

Order LAMIALES. Corolla mostly zygomorphic (irregular or oblique); stamens fewer than the corolla-lobes, usually 4 or 2; ovules mostly 2 in each carpel; fruit indehiscent. (Species about 4119.)

Family 188. **Myoporaceae.** Mostly Australasian shrubs and trees, with usually alternate leaves; flowers axillary; fruit a 1–4-seeded drupe; endosperm scanty. *Myoporum.* (Pf. 4^{3b}: 354.)

Family 189. **Phrymaceae.** Erect, perennial herbs, with opposite leaves, and small spicate flowers; calyx and corolla cylindrical, 2-lipped; stamens 4; ovary 1-celled, 1-ovuled; stigma bifid; endosperm 0. *Phryma.* (Pf. 4^{3b}: 361.)

Family 190. **Verbenaceae.** Verbenas. Herbs, shrubs, and trees, with usually opposite leaves; ovary of 2 carpels, but 2–8-celled, with 1 ovule in each cell; stigma usually undivided; endosperm scanty or 0. *Verbena, Lantana, Lippia, Tectona, Vitex.* (Pf. 4^{3a}: 132.)

Family 191. **Lamiaceae.** Mints. Mostly aromatic herbs, shrubs (and trees) with opposite or whorled leaves; ovary 4-celled, 4-lobed with 1 ovule in each cell; stigma usually bifid; endosperm scanty or 0. *Lavendula, Nepeta, Stachys, Salvia, Thymus, Mentha, Coleus.* (Pf. 4^{3a}: 183.)

With this order (*Lamiales*), and especially with this family (*Lamiaceae*), we attain the summit of the cone-flowers (*Strobiloideae*). We next return almost to the point of beginning, and there start on a new phyletic line.

Sub-Class OPPOSITIFOLIAE - COTYLOIDEAE. "Cup Flowers." Axis of the flower normally expanded into a disk or cup, bearing on its margin the perianth and stamens (or the latter may be attached to the corolla).

Super-Order Cotyloideae - Apopetalae. Petals separate. Carpels many to few, separate to united, superior to inferior. This super-order appears to have originated near the beginning of the *Strobiloideae,* and therefore the orders *Ranales* and *Rosales* are to be regarded as closely related. Their relationship to *Alismatales,* also, has already been pointed out.

Order Rosales. Flowers cyclic, usually perfect, dichlamydeous (rarely apetalous), actinomorphic to zygomorphic (regular to irregular) and mostly pentamerous; carpels usually several to many, separate or more or less united, sometimes united with the axis-cup (rarely reduced to 1); styles usually distinct. (Species about 14261.)

Family 192. **Rosaceae.** Roses. Herbs, shrubs, and trees with mostly alternate leaves; stamens usually indefinite, on the cup-margin; carpels several to many (rarely 1), free (but they may be enclosed in the deep cup); ovules usually 2, anatropous; endosperm 0. *Potentilla, Fragaria, Spiraea, Rosa.* (Species about 2700.) (Pf. $\mathbf{3}^3$: 1.)

Family 193. **Malaceae.** Apples. Shrubs and trees with alternate leaves; stamens usually many on the cup-margin; carpels few, more or less united, and adnate to the axis-cup, so as to be "inferior"; endosperm 0. *Sorbus, Pirus, Malus, Crataegus.* (Pf. $\mathbf{3}^3$: 1, 18.)

Family 194. **Prunaceae.** Plums. Shrubs and trees with alternate leaves; stamens many, on the cup-margin; carpel one, in the bottom of the deep cup, becoming a drupe; endosperm 0. *Prunus, Amygdalus.* (Species 150.) (Pf. $\mathbf{3}^3$: 1, 50.)

Family 195. **Crossosomataceae.** Southwest North American shrubs, with small leaves and a bitter bark; sepals and petals 5 each; stamens 20 or more; carpels 3–5; seeds many, reniform; endosperm scanty. *Crossosoma.* (Pf. Nachträge zu Teil II–IV, 185.)

Family 196. **Connaraceae.** Tropical trees and shrubs with alternate compound leaves; stamens definite (5–10); pistils mostly 5, free; ovules 2, ascending, orthotropous; endosperm fleshy or 0. *Connarus, Cnestis.* (Pf. $\mathbf{3}^3$: 61.)

Family 197. **Mimosaceae.** The mimosas. Mostly tropical trees, shrubs, and herbs, with alternate mostly compound leaves; flowers actinomorphic; stamens 10 or more, usually separate; carpel 1; fruit a legume; seeds mostly without endosperm. *Acacia, Mimosa.* (Species 1483.) (Pf. **3**[3] : 70, 99.)

Family 198. **Cassiaceae.** The sennas. Mostly tropical trees, shrubs, and herbs, with alternate mostly compound leaves; flowers zygomorphic; stamens 10 or less, usually separate; carpel 1; fruit a legume; seeds with or without endosperm. *Cassia, Caesalpinia, Gleditsia, Gymnocladus.* (Species 1172.) (Pf. **3**[3] : 70, 125.)

Family 199. **Fabaceae.** The beans. Mostly herbs of temperate climates, but with many shrubs and trees; leaves alternate, mostly compound; flowers zygomorphic; stamens 10 or less, usually more or less united; carpel 1; fruit a legume; seeds usually without endosperm. *Lupinus, Medicago, Trifolium, Robinia, Astragalus, Arachis, Vicia, Pisum, Phaseolus.* (Species 6948.) (Pf. **3**[3] : 70, 184.)

This family constitutes a well-marked side-line in the order *Rosales,* with zygomorphic, entomophilous flowers. It is not obvious what relation, if any, exists between this form of the flower, and the legume structure of the fruiting carpel.

Family 200. **Saxifragaceae.** Saxifrages. Herbs with alternate leaves, regular 4 or 5-merous mostly perfect flowers, with 8 or 10 stamens, and usually 2 more or less united carpels which are superior; seeds many; endosperm copious. *Saxifraga, Heuchera, Mitella.* (Pf. **3**[2a] : 41.)

Family 201. **Hydrangeaceae.** Hydrangeas. Shrubs and trees with mostly opposite leaves, and regular 4 or 5-merous mostly perfect flowers, with few (8) to many (40) stamens, and 2–5 united carpels, which are more or less overgrown by the axis-cup; seeds many; endosperm copious. *Philadelphus, Hydrangea.* (Pf. **3**[2a] : 41.)

Family 202. **Grossulariaceae.** Gooseberries. Shrubs with alternate leaves, regular 4 or 5-merous perfect flowers, usually 5 stamens, and 2 to several united carpels which are wholly

overgrown by the fleshy cup (ovary inferior); seeds few, endosperm copious. *Ribes.* (Pf. 3^{2a}: 41.)

Family 203. **Crassulaceae.** Stonecrops. Mostly fleshy herbs, with opposite or alternate leaves and perfect flowers; stamens definite (4–10 or many); pistils several, free or little united; ovules many; placentae central or axile; endosperm fleshy. *Sedum, Cotyledon, Crassula, Penthorum.* (Pf. 3^{2a}: 23.)

Family 204. **Droseraceae.** Sundews. Gland-bearing marsh herbs with perfect flowers; stamens mostly definite (4–20); pistil syncarpous, 1–3-celled, superior; ovules many, on basal, axile, or parietal placentae; endosperm fleshy. *Drosera, Dionaea.* (Pf. 3^{2}: 261.)

Family 205. **Cephalotaceae.** Pitcher-plants. Perennial Australian herbs with a rosette of elliptic, and pipe-shaped radical leaves, and a central, erect, spicate flowering stem; flowers regular, perfect, apetalous; sepals 6; ovules solitary; endosperm copious. *Cephalotus.* (Pf. 3^{2a}: 39.)

Family 206. **Pittosporaceae.** Trees and shrubs of the southern hemisphere, with alternate leaves; sepals, petals, and stamens 5 each; ovary 2-carpellate; endosperm copious. *Pittosporum, Marianthus.* (Pf. 3^{2a}: 106.)

Family 207. **Brunelliaceae.** South American trees, with opposite or whorled leaves and diclinous flowers; sepals and petals 4–5 or 7 each; stamens twice as many; carpels usually 4–5, free; endosperm fleshy. *Brunellia.* (Pf. Nachträge zu Teil II–IV, 182.)

Family 208. **Cunoniaceae.** Shrubs and trees, mostly of the southern hemisphere, with opposite or whorled leaves and small, perfect flowers; sepals and petals 4–6 each; stamens twice as many; carpels 2–5, united; endosperm fleshy. *Belangera, Cunonia.* (Pf. 3^{2a}: 94.)

Family 209. **Myrothamnaceae.** Small, rigid, balsamic South African and Madagascar shrubs, with opposite leaves, and dioecious, achlamydeous flowers; ovary tricarpellary; seeds many, with fleshy endosperm. *Myrothamnus.* (Pf. 3^{2a}: 103.)

Family 210. **Bruniaceae.** Heath-like shrubs of the southern hemisphere, with small leaves and small, perfect, regular, pentamerous flowers; stamens definite; pistil 2–3-celled, inferior or superior; ovules 1 to many, pendulous; endosperm copious. *Brunia.* (Pf. **3**^{2a} : 131.)

Family 211. **Hamamelidaceae.** Witch-hazels. Shrubs and trees with mostly alternate leaves and perfect or imperfect, mostly pentamerous flowers; stamens few or many; pistil bicarpellary, its ovary inferior; ovules solitary or many; endosperm thin. *Liquidambar, Altingia, Hamamelis.* (Pf. **3**^{2a} : 115.)

Family 212. **Casuarinaceae.** Beefwood trees. Shrubs and trees with striate stems bearing whorls of reduced scale-like leaves; flowers diclinous; petals 0; pistil bicarpellary, 1-celled; ovules 2, lateral, half anatropous; endosperm 0. *Casuarina.* (Pf. **3**^{1} : 16.) This family, which has puzzled botanists from the first, is doubtfully placed here, on the theory that these plants are leafless relatives of the *Hamamelidaceae.*

Family 213. **Eucommiaceae.** Chinese trees, with alternate leaves, and achlamydeous diclinous flowers; stamens 6–10; pistil bicarpellary, 1-celled, 2-seeded; endosperm present. *Eucommia.* (Pf. Nachträge zu Teil II–IV, 159.)

Family 214. **Platanaceae.** Plane-trees. Trees with alternate leaves, and monoecious flowers in globular heads; perianth 3–8-merous; stamens 3–8; pistils 3–8, each 1-celled, 1-ovuled; endosperm scanty. *Platanus.* (Pf. **3**^{2a} : 137.)

Order Myrtales. Flowers usually actinomorphic (regular) or nearly so, usually perfect; pistil of united carpels, usually inferior; placentae axile or apical (rarely basal); style 1 (rarely several); leaves simple, usually entire. (Species about 7323.)

Here again we shall soon reach the end of a phyletic sideline, consisting principally of the order *Myrtales,* with the *Loasales* and *Cactales* as the ultimate branches.

Family 215. **Lythraceae.** Herbs, shrubs, and trees usually with opposite leaves and 4-angled branches; flowers mostly 4–6-merous; stamens definite (8–12), or indefinite; pistil 2–6-

celled, free; ovules numerous, on axile placentae; endosperm 0. *Lythrum, Cuphea, Lagerstroemia.* (Pf. 3^7 : 1.)

Family 216. **Sonneratiaceae.** Tropical trees with opposite leaves; ovary sunken in the axis-cup, many celled (4–15); stamens many; endosperm 0. *Sonneratia.* (Pf. 3^7 : 16.)

Family 217. **Punicaceae.** Pomegranates. Small tropical and sub-tropical trees with opposite leaves and 5–7-merous flowers; stamens many; ovary inferior, 4–15-celled, producing a pulpy, many-seeded fruit; endosperm 0. *Punica.* (Pf. 3^7 : 22.)

Family 218. **Lecythidaceae.** Tropical trees, with alternate leaves and usually 4–6-merous flowers; stamens many; ovary inferior, 2–6-celled; endosperm 0. *Barringtonia, Napoleona, Lecythis, Bertholletia.* (Pf. 3^7 : 26.)

Family 219. **Melastomataceae.** Mostly tropical herbs, shrubs, and trees with generally opposite or whorled leaves; stamens usually double the number of petals; pistil 2–many-celled, inferior; ovules minute, numerous, on axile or parietal placentae; endosperm 0. *Melastoma, Osbeckia, Rhexia, Tamonea.* (Pf. 3^7 : 130.)

Family 220. **Myrtaceae.** Myrtles. Trees and shrubs with opposite or alternate leaves, and perfect, regular flowers; stamens many; pistil 2–many-celled, inferior; ovules 2 to many; plancentae basal or axile; endosperm 0. *Myrtus, Pimênta, Eugenia, Jambosa, Eucalyptus, Malaleuca.* (Species 2556.) (Pf. 3^7 : 57.)

Family 221. **Combretaceae.** Trees and shrubs often climbing, with opposite or alternate leaves; stamens usually definite (4–10); pistil 1-celled, inferior; ovules 2–6 or solitary, pendulous; endosperm 0. *Terminalia, Combretum, Laguncularia.* (Pf. 3^7 : 106.)

Family 222. **Rhizophoraceae.** Mangroves. Mostly tropical trees and shrubs with opposite leaves and regular, 4–8-merous flowers; stamens 2–4 times the number of petals; pistil 2–6-celled, usually inferior; ovules 2, pendulous; endosperm fleshy. *Rhizophora, Carallia.* (Pf. 3^7 : 42.)

Family 223. **Oenotheraceae.** Evening primroses. Herbs (shrubs and trees) with opposite or alternate leaves, and perfect, 2–3–4-merous, regular flowers; stamens 1–8, rarely more; pistil usually 4-celled, inferior; ovules 1 to many on axile placentae; endosperm scanty or 0. *Epilobium, Anogra, Oenothera, Meriolix, Gaura, Fuchsia, Circaea.* (Pf. **3**^{7} : 199.)

Family 224. **Halorrhagidaceae.** Aquatic or terrestrial herbs with opposite or alternate leaves and perfect or imperfect, sometimes apetalous flowers; pistil 1–4-celled, inferior; ovules solitary, pendulous; endosperm present. *Halorrhagis, Myriophyllum.* (Pf. **3**^{7} : 226.)

Family 225. **Hippuridaceae.** Aquatic perennial erect herbs, with whorled leaves, and small, reduced, axillary apetalous flowers; ovary 1-celled, 1-ovuled; endosperm scanty. *Hippuris.* (Pf. **3**^{7} : 237.)

Family 226. **Cynomoriaceae.** Parasitic rhizomatous fleshy plants with spicate, small, apetalous, diclinous flowers, each with a single ovule; endosperm fleshy. *Cynomorium.* (Pf. **3**^{1} : 250.)

Family 227. **Aristolochiaceae.** Dutchman's-pipes. Herbaceous or shrubby plants, with alternate leaves and large, apetalous, perfect, irregular flowers; stamens 6, rarely more; pistil 4 or 6-celled, inferior; ovules numerous, on axile (or protruding parietal) placentae; endosperm copious. *Asarum, Aristolochia.* (Pf. **3**^{1} : 264.)

Family 228. **Rafflesiaceae.** Fleshy, parasitic herbs, of warm climates, leafless, or nearly so, with mostly imperfect flowers; petals 0, or rarely 4; stamens 8 to many; pistil 1-celled or imperfectly many-celled, inferior; ovules minute, very numerous, on parietal or pendulous, folded placentae; endosperm present. *Rafflesia, Cytinus.* (Pf. **3**^{1} : 274.)

Family 229. **Hydnoraceae.** Parasitic, succulent, tropical herbs with perfect, 3–4-merous flowers; perianth single, valvate; stamens 3–4, but anthers many; seeds very numerous; endosperm copious. *Hydnora.* (Pf. **3**^{1} : 282.)

Order Loasales. Flowers usually actinomorphic, perfect or diclinous; pistil mostly tricarpellary, 1-celled, its ovary usually inferior; placentae parietal and with many ovules; styles free or connate; leaves ample, entire, lobed or dissected. (Species about 1392.)

Family 230. **Loasaceae.** Star-flowers. Herbs (rarely climbing) with opposite or alternate leaves; flowers perfect; sepals and petals dissimilar, mostly 5 each; stamens indefinite, 5–10 or more; ovary 3–7-carpellary, 1-celled; endosperm mostly 0. *Mentzelia, Loasa.* (Pf. $\mathbf{3}^{6a}$: 100.)

Family 231. **Cucurbitaceae.** Melons. Mostly climbing or prostrate herbs and undershrubs, with alternate leaves; flowers mostly diclinous and pentamerous; stamens definite (usually 3); ovary mostly tricarpellary; endosperm 0. *Melothria, Momordica, Luffa, Citrullus, Cucumis, Lagenaria, Cucurbita.* (Pf. $\mathbf{4}^{5}$: 1.)

Family 232. **Begoniaceae.** Begonias. Mostly erect herbs with alternate leaves; flowers diclinous, more or less zygomorphic; stamens indefinite and numerous, ovary tricarpellary, 3-celled, usually 3-angular; endosperm little or 0. *Begonia.* (Pf. $\mathbf{3}^{6a}$: 121.)

Family 233. **Datiscaceae.** Herbs or large trees, with alternate leaves; flowers small, and diclinous; stamens 4 to many; ovary 3–8-carpellary; placentae on the walls; seeds small, and many; endosperm scanty. *Datisca.* (Pf. $\mathbf{3}^{6a}$: 150.)

Family 234. **Ancistrocladaceae.** Climbing plants of tropical Asia, with alternate leaves, and small, regular, perfect flowers; petals 5; stamens 5–10; ovary 1-celled, many-seeded; endosperm present. *Ancistrocladus.* (Pf. $\mathbf{3}^{6}$: 274.)

Order Cactales. Flowers actinomorphic or very slightly zygomorphic, perfect; stamens many; pistil 4–8-carpous, inferior, 1-celled, with 4–8 parietal placentae; style single, with 2 to many stigmas; endosperm scanty or 0; embryo curved. Fleshy-stemmed plants with leaves mostly small or wanting. (Species about 1168.)

Family 235. **Cactaceae.** Cactuses. Mostly natives of the warmer portions of America; from small herbs to tree-like

dimensions. *Peireskia, Opuntia, Cereus, Carnegiea, Echinocactus, Melocactus, Cactus, Rhipsalis.* (Pf. 3^{6a}: 156.)

Order Celastrales. Receptacle often developing a glandular, annular or turgid disk, which is sometimes adnate to the pistil, in which case the pistil is more or less inferior; pistil 1 to many-celled (rarely apocarpous); ovules 1–3, pendulous or erect; endosperm present or 0. Flowers actinomorphic and mostly perfect. (Species about 2741.)

Family 236. **Rhamnaceae.** Buckthorns. Trees and shrubs often climbing, with alternate or opposite, simple leaves; petals present; disk more or less adnate to the 2–4-celled pistil; ovules 1 or 2, erect; endosperm fleshy. *Zizyphus, Rhamnus, Ceanothus, Phylica, Colletia.* (Pf. 3^{5}: 393.)

Family 237. **Vitaceae.** Grapes. Climbing shrubs (and trees) with alternate, simple or compound leaves; petals coherent, valvate; pistil superior, 2-celled, 2-ovuled (or 3–6-celled, 1-ovuled); endosperm often ruminate. *Vitis, Parthenocissus, Cissus.* (Pf. 3^{5}: 427.)

Family 238. **Celastraceae.** Bittersweets. Shrubs (often climbing) and trees, with usually alternate, simple leaves; petals present, imbricated; disk more or less adnate to the 2–5-celled pistil; ovules usually 2, erect or pendulous; endosperm fleshy. *Euonymus, Celastrus, Cassine.* (Pf. 3^{5}: 189.)

Family 239. **Buxaceae.** Boxes. Evergreen shrubs and trees, with alternate or opposite leaves, and usually monoecious, small, apetalous flowers; stamens 4; pistil tricarpellary, superior; endosperm fleshy. *Pachysandra, Buxus.* (Pf. 3^{5}: 130.)

Family 240. **Aquifoliaceae.** Hollies. Trees and shrubs, with alternate or opposite, simple leaves and small, perfect flowers; pistil superior, 3 to many-celled; ovule 1, pendulous; endosperm fleshy. *Ilex, Nemopanthes.* (Pf. 3^{5}: 183.)

Family 241. **Cyrillaceae.** South American evergreen shrubs or small trees, with alternate leaves; sepals 5; petals 5; stamens 5–10; carpels 2–5, united, superior; endosperm fleshy. *Cyrilla.* (Pf. 3^{5}: 179.)

Family 242. **Pentaphylacaceae.** Chinese trees, with alternate, leathery leaves and small, perfect flowers; sepals 5; petals 5; stamens 5; pistil superior, of 5 carpels, each 2-ovuled; endosperm scanty. *Pentaphylax.* (Pf. Nachträge zu Teil II–IV, 214.)

Family 243. **Corynocarpaceae.** New Zealand trees, with alternate, fleshy, leathery leaves; sepals 5; petals 5; stamens 5; pistil superior, of 2 carpels; endosperm 0. *Corynocarpus.* (Pf. Nachträge zu Teil II–IV, 215.)

Family 244. **Hippocrateaceae.** Tropical trailing and climbing woody plants with opposite leaves; sepals 5; petals 5; stamens 3 or 2 or 5; pistil of 3 carpels more or less adnate to the disk; endosperm 0. *Hippocratea, Salacia.* (Pf. **3**^{5} : 222.)

Family 245. **Stackhousiaceae.** Australian herbs and shrubs with simple alternate leaves and perfect flowers; petals 5; stamens 5; ovary 2–5-celled; ovule 1 in each cell, erect; endosperm fleshy. *Stackhousia.* (Pf. **3**^{5} : 231.)

Family 246. **Staphyleaceae.** Bladder-nuts. Erect shrubs and trees, with opposite, compound leaves and pentamerous perfect flowers; sepals 5; petals 5; stamens 5; pistil of 2–3 superior carpels; seeds few to many; endosperm fleshy or 0. *Staphylea, Turpinia.* (Pf. **3**^{5} : 258.)

Family 247. **Geissolomataceae.** South African evergreen shrubs, with opposite sessile leaves; sepals 4; petals none; stamens 8; pistil superior, of 4 carpels, each 2-ovuled; endosperm fleshy. *Geissoloma.* (Pf. **3**^{6a} : 205.)

Family 248. **Penaeaceae.** South African evergreen heath-like shrubs, with small, opposite leaves and regular, perfect flowers; petals 0; pistil superior, 4-celled; ovules 2–4, erect; endosperm 0. *Penaea.* (Pf. **3**^{6a} : 208.)

Family 249. **Oliniaceae.** African shrubs and trees, with thick, leathery, opposite leaves, and small, regular, perfect flowers; sepals 4–5, large; petals 4–5, very small; stamens 4–5; pistil inferior, of 3–5 carpels; endosperm 0. *Olinia.* (Pf. **3**^{6a} : 213.)

Family 250. **Thymelaeaceae.** Shrubs, small trees (and herbs), with alternate or opposite, usually coriaceous, simple

leaves and small petalous or apetalous, mostly perfect flowers; pistil superior, 1–5-carpellary, 1-celled; ovule 1, pendulous; endosperm fleshy, sparse, or 0. *Gnidia, Thymelaea, Daphne, Dirca.* (Pf. **3**^{6a}: 215.)

Family 251. **Hernandiaceae.** Tropical trees and shrubs, with alternate leaves; flowers perfect or monoecious, regular; sepals 4–10; petals none; stamens 3; pistil 1-celled, inferior; ovule 1, pendulous; endosperm 0. *Hernandia.* (Pf. **3**^{2}: 126.)

Family 252. **Elaeagnaceae.** Oleasters. White or brown-scurfy trees and shrubs, with alternate or opposite, simple leaves and perfect or diclinous flowers; petals 0; pistil 1-celled; ovule 1, ascending; endosperm 0 or scanty. *Elaeagnus, Lepargyraea.* (Pf. **3**^{6a}: 246.)

Family 253. **Myzodendraceae.** South American parasitic shrubs, with alternate, rather small leaves; flowers dioecious, apetalous; stamens 2–3; pistil 1-celled, inferior; endosperm fleshy. *Myzodendron.* (Pf. **3**^{1}: 198.)

Family 254. **Santalaceae.** Sandalwoods. Parasitic herbs, shrubs, and trees, with alternate or opposite, simple leaves and small, perfect, or diclinous flowers; epigynous; petals 0; pistil inferior, 1–5-carpellary, 1-celled; ovules 2–5, pendulous; endosperm present. *Santalum, Comandra, Thesium.* (Pf. **3**^{1}: 202.)

Family 255. **Opiliaceae.** Shrubs of tropical climates, with alternate leaves, and perfect flowers; sepals, petals and stamens 4–5 each; pistil superior, 1-celled, 1-ovuled; endosperm fleshy. *Opilia.* (Pf. Nachträge zu Teil II–IV, 142.)

Family 256. **Grubbiaceae.** South African shrubs with opposite leaves, and epigynous, apetalous flowers; ovary 2-celled; ovules 2; endosperm fleshy. *Grubbia.* (Pf. **3**^{1}: 282.)

Family 257. **Olacaceae.** Trees and shrubs, often twining, mostly tropical, with usually alternate, simple leaves and mostly perfect, apetalous flowers; pistil superior or inferior, 1–3-celled; ovules 2–3, pendulous; endosperm fleshy. *Olax.* (Pf. **3**^{1}: 231.)

Family 258. **Loranthaceae.** Mistletoes. Parasitic evergreen shrubs with opposite (or alternate) leaves, often re-

duced to bracts; flowers perfect or diclinous; petals 0; pistil 1-celled, inferior; ovule 1, erect; endosperm fleshy. *Loranthus, Viscum, Phoradendron, Razoumowskia.* (Pf. **3**[1]: 156.)

Family 259. **Balanophoraceae.** Parasitic, leafless herbs, all tropical, with much reduced, apetalous, monoecious or dioecious flowers; pistil 1-celled, inferior; ovule 1, pendulous; endosperm fleshy. *Balanophora.* (Pf. **3**[1]: 243.)

Order SAPINDALES. Flowers mostly actinomorphic, perfect, or diclinous; pistil 1 to several-celled, superior to inferior; ovules 1–2, erect, ascending, or pendulous; endosperm mostly 0. (Species about 2903.)

The *Sapindales* lie wholly in a phyletic side-line, and the order has been developed from some part of the intermediate order *Celastrales,* which constitutes a transition from the lower hypogynous cup flowers to those in which epigyny is fixed. In the lower *Sapindales* hypogyny still persists, but in the higher families this gives way to complete epigyny.

Family 260. **Sapindaceae.** Soapberries. Trees and shrubs, mostly tropical, with alternate (or opposite), mostly compound leaves and mostly perfect, irregular flowers; disk present or 0; petals 3–5 or 0; pistil 1–3-celled; ovules 1 or 2, ascending; endosperm usually 0. *Paullinia, Sapindus, Talisia, Litchi, Koelreuteria, Dodonaea.* (Pf. **3**[5]: 277.)

Family 261. **Hippocastanaceae.** Horsechestnuts. Trees and shrubs, with opposite, palmately compound leaves; flowers mostly regular; sepals 5; petals 4–5; stamens 8–5; pistil superior, tricarpellary; endosperm 0. *Aesculus.* (Pf. **3**[5]: 273.)

Family 262. **Aceraceae.** Maples. Trees and shrubs, with opposite, simple or compound leaves and small, regular flowers; sepals 4–10; petals as many or none; pistil superior, bicarpellary, winged in fruit; endosperm 0. *Acer.* (Pf. **3**[5]: 258.)

Family 263. **Sabiaceae.** Trees and shrubs of the tropics, with alternate, simple or compound leaves, and perfect or diclinous flowers; petals 4–5; pistil 2–3-celled; ovules 1 or 2, horizontal or pendulous; endosperm 0. *Sabia, Meliosma.* (Pf. **3**[5]: 367.)

Family 264. **Icacinaceae.** Tropical trees and shrubs, with alternate or opposite leaves and regular, perfect or diclinous flowers; sepals 5; petals 5; stamens 5; pistil superior, 1-celled, and tricarpellary; endosperm fleshy. *Icacina.* (Pf. **3**^{5} : 233.)

Family 265. **Melianthaceae.** Tropical trees and shrubs, with alternate leaves, and pentamerous, mostly perfect, zygomorphic flowers; endosperm fleshy. *Melianthus.* (Pf. **3**^{5} : 374.)

Family 266. **Empetraceae.** Heath-like shrubs, with small alternate leaves; flowers small, regular, mostly dioecious, solitary or in heads; petals present; stamens 2–3, 2–3-celled; pistil 2 to many-celled; seeds solitary, endospermous. *Corema, Empetrum.* (Pf. **3**^{5} : 123.)

Family 267. **Coriariaceae.** Shrubs with opposite, sessile leaves and perfect or diclinous flowers; 5 sepals; 5 petals; 10 stamens; 5–10 carpels, slightly united; seeds few; endosperm scanty. *Coriaria.* (Pf. **3**^{5} : 128.)

Family 268. **Anacardiaceae.** Sumachs. Trees and shrubs, mostly tropical, with alternate, usually compound leaves and small, perfect flowers; petals 3–7 or 0; pistil 1–5-celled, superior, but surrounded by the fleshy cup; ovules solitary, pendulous (or erect); endosperm 0. *Mangifera, Anacardium, Schinus, Cotinus, Metopium, Rhus.* (Pf. **3**^{5} : 138.)

Family 269. **Juglandaceae.** Walnuts. Trees and shrubs, with alternate, compound leaves and small, diclinous, apetalous flowers; pistil bicarpellary, 1-celled, adnate to the fleshy cup, and so inferior; ovule 1, erect, orthotropous; endosperm 0. *Engelhardtia, Juglans, Hicoria.* (Pf. **3**^{1} : 19.)

Family 270. **Betulaceae.** Birches. Trees and shrubs, with alternate, simple leaves, and monoecious or dioecious flowers, which are in aments; petals none; calyx small or none; stamens 2–10; pistil inferior, bicarpellary, 1–2-celled; endosperm 0. *Carpinus, Ostrya, Corylus, Betula, Alnus.* (Pf. **3**^{1} : 38.)

Family 271. **Fagaceae.** Beeches. Trees and shrubs, with alternate, simple leaves and small, diclinous flowers; petals 0; pistil mostly tricarpellary, 2–6-celled, inferior; ovules 2 in each cell, erect or pendulous; fruit usually 1-seeded; endosperm 0. *Fagus, Castanea, Pasania, Quercus.* (Pf. **3**^{1} : 47.)

Family 272. **Myricaceae.** Bayberries. Shrubs and trees, with alternate, simple leaves and small, achlamydeous, diclinous flowers; petals 0; pistil free, bicarpellary, 1-celled; ovule 1, erect, orthotropous; endosperm 0. *Myrica.* (Pf. **3**[1]: 26.)

Family 273. **Julianaceae.** Dioecious, tropical trees, with alternate leaves; flowers small, apetalous, dioecious; stamens 4–8; pistil of 3–5 carpels; endosperm 0. *Juliana.* (Pf. Nachträge zu Teil II–IV, 335, and Syllabus, 161.) This family is given place here very doubtfully.

Family 274. **Proteaceae.** Shrubs, trees (and herbs) of the southern hemisphere, with mostly alternate, simple, usually coriaceous, evergreen leaves; flowers perfect or diclinous; sepals petaloid; petals 0; stamens 4; pistil monocarpellary, 1-celled; ovule 1, erect or pendulous; endosperm little or none. *Protea, Leucadendron, Grevillea, Hakea, Banksia.* (Pf. **3**[1]: 118.) This puzzling family is given place here very doubtfully.

Order UMBELLALES. Flowers actinomorphic (regular), usually perfect, 4–5-merous; calyx small to minute; stamens usually definite (4–5); pistil syncarpous, 1 to many-celled, its ovary inferior; ovules solitary, pendulous; styles free or united at the base; endosperm copious; embryo usually minute. (Species about 2809.)

Family 275. **Araliaceae.** Aralias. Trees, shrubs (and herbs), mostly tropical, with alternate leaves; flowers in umbels, heads, or panicles; ovary 2–15-celled; fruit a berry with a fleshy or dry exocarp. *Hedera, Aralia, Panax.* (Pf. **3**[8]: 1.)

Family 276. **Apiaceae.** Parsleys. Herbs (shrubs and trees), with alternate leaves; flowers small, pentamerous, mostly umbellate; ovary 2-celled; fruit splitting into two dry indehiscent mericarps. *Hydrocotyle, Sanicula, Eryngium, Coriandrum, Conium, Apium, Cicuta, Carum, Foeniculum, Angelica, Ferula, Heracleum, Daucus.* (Species 2177.) (Pf. **3**[8]: 63.)

Family 277. **Cornaceae.** Cornels. Shrubs and trees (rarely herbs), with usually opposite leaves; flowers larger, 4–5-

merous, umbellate, capitate, or corymbose; ovary 2–4-celled, fruit drupaceous. *Garrya, Nyssa, Cornus, Aucuba.* (Pf. **3**[8]: 250.)

Super-Order COTYLOIDEAE - SYMPETALAE. Petals united. Carpels few, united, inferior; stamens usually as many as the corolla-lobes, mostly attached to the corolla.

Order RUBIALES. Flowers 4–5-merous, actinomorphic (rarely zygomorphic); stamens 4–5, attached to the corolla; calyx small; ovary 2–8-celled; ovules 2 to many in each cell. (Species about 5063.)

Family 278. **Rubiaceae.** Madders. Trees, shrubs and herbs, mostly tropical, with opposite or whorled leaves; flowers usually perfect, and regular, with valvate, contorted, or imbricate corolla-lobes; carpels mostly 2; style simple, bifid, or multifid; fruit a capsule, berry, or drupe; endosperm from fleshy to 0. *Houstonia, Cinchona, Bouvardia, Cephalanthus, Randia, Coffea, Mitchella, Galium, Rubia.* (Pf. **4**[4]: 1.)

Family 279. **Caprifoliaceae.** Honeysuckles. Mostly woody plants with opposite leaves; flowers usually zygomorphic, with imbricate corolla-lobes; carpels 2–5, with 1 or more pendulous ovules; style usually with a capitate undivided stigma; fruit a berry; endosperm fleshy. *Sambucus, Viburnum, Linnaea, Lonicera.* (Pf. **4**[4]: 156.)

Family 280. **Adoxaceae.** Moschatels. Slender herbs with scaly rootstocks, bearing ternately compound leaves; flowers small, regular, greenish, in heads; stamens about 10; ovary 3–5-celled; fruit drupaceous; endosperm cartilaginous. *Adoxa.* (Pf. **4**[4]: 170.)

Family 281. **Valerianaceae.** Valerians. Herbs (and shrubs) with opposite leaves; flowers somewhat irregular, cymose, corymbose, or solitary; stamens 1–4, the anthers free; ovary 1–3-celled, the ovules pendulous; fruit with 1 fertile cell, 1-seeded; endosperm scanty, or 0. *Valerianella, Fedia, Valeriana.* (Pf. **4**[4]: 172.)

Family 282. **Dipsacaceae.** Teasels. Herbs (and shrubs) with opposite or whorled leaves; flowers zygomorphic, in

involucrate heads; stamens 2–4, the anthers free; carpels 2, but pistil 1-celled; ovule 1, pendulous; endosperm scanty. *Cephalaria, Dipsacus, Scabiosa.* (Pf. **4**^{4} : 182.)

Order Campanulales. Flowers actinomorphic to zygomorphic; stamens mostly free, their anthers free or connate; ovary 1 to several-celled; ovules 1–8. (Species about 1539.)

Family 283. **Campanulaceae.** Bellflowers. Mostly milky-juiced herbs (shrubs and small trees), with alternate (or opposite) leaves; flowers regular or irregular; stamens usually 5, free, or more or less united; carpels 2–5; ovules many; endosperm fleshy. *Campanula, Lobelia.* (Pf. **4**^{5} : 40.)

Family 284. **Goodeniaceae.** Mostly Australian herbs and shrubs, with alternate (or opposite) leaves; flowers usually irregular; stamens 5, free, or cohering above; ovary 2–4-celled; ovules many; endosperm fleshy. *Goodenia, Scaevola, Brunonia.* (Pf. **4**^{5} : 70.)

Family 285. **Stylidiaceae.** Mostly Australian herbs, with tufted, radical, or scattered and sometimes crowded stem-leaves; flowers usually irregular; stamens 3–2, mostly connate with the style; ovary 2-celled, many-ovuled; endosperm fleshy. *Stylidium, Levenhookia.* (Pf. **4**^{5} : 79.)

Family 286. **Calyceraceae.** South American herbs, with alternate leaves; flowers regular or irregular in involucrate heads; stamens attached to the corolla-tube, anthers free; ovary 1-celled; stigma capitate; ovule 1, pendulous; endosperm fleshy. *Boopis, Calycera.* (Pf. **4**^{5} : 84.)

Order Asterales. Composites. Flowers actinomorphic or zygomorphic, collected into involucrate heads; calyx small, and often forming a "pappus"; stamens 5, epipetalous, mostly with their anthers connate, dehiscing introrsely; carpels 2, united, inferior, with one style which is 2-branched above; ovule one, erect, anatropous; endosperm 0. An immense order (commonly regarded as a family) of about 14,324 species, which are usually distributed among fourteen tribes, all of which are here raised to families. In the following arrangement the *Helianthaceae* are regarded as the lowest, from which the two principal phyletic lines have arisen, cul-

minating on the one hand in the *Eupatoriaceae,* and on the other in the *Lactucaceae.* (Pf. **4**^{5} : 87.)

Family 287. **Helianthaceae.** Sunflowers. Calyx not capillary; receptacle chaffy; usually with ray flowers; mostly large and coarse plants, with leaves usually opposite. *Helianthus, Zinnia, Rudbeckia, Silphium.* (Species 1364.) (Pf. **4**^{5} : 210.)

Family 288. **Ambrosiaceae.** Ragweeds. Calyx not capillary; receptacle chaffy; without ray flowers; mostly large and coarse plants, with leaves usually alternate, flowers diclinous. *Ambrosia, Xanthium.* (Species 74.) (Pf. **4**^{5} : 220.)

Family 289. **Heleniaceae.** False sunflowers. Calyx not capillary; receptacle usually naked; with or without rays; anthers tailless; medium-sized plants with opposite and alternate leaves. *Helenium, Gaillardia.* (Species 449.) (Pf. **4**^{5} : 251.)

Family 290. **Arctotidaceae.** Gazanias. Calyx not capillary; receptacle naked; anthers tailless. South African plants with mostly alternate leaves. *Gazania, Arctotis.* (Species 278.) (Pf. **4**^{5} : 307.)

Family 291. **Calendulaceae.** Marigolds. Calyx not capillary; receptacle naked; anthers tailed. Old World plants, mostly tropical, with alternate leaves. *Calendula.* (Species 125.) (Pf. **4**^{5} : 303.)

Family 292. **Inulaceae.** Everlastings. Calyx from bracteose to capillary; receptacle usually naked; anthers tailed; usually rayless; mostly low plants, with alternate leaves. *Inula, Antennaria, Gnaphalium, Helichrysum.* (Species 1580.) (Pf. **4**^{5} : 172.)

Family 293. **Asteraceae.** Asters. Calyx from bracteose to capillary; receptacle naked; usually with rays. Medium-sized plants, with alternate leaves. *Aster, Solidago, Erigeron, Bellis.* (Species 1815.) (Pf. **4**^{5} : 142.)

Family 294. **Vernoniaceae.** Ironweeds. Calyx from bracteose to capillary; receptacle naked; without rays; style branches hispidulous. Medium-sized plants, with mostly alternate leaves. *Vernonia.* (Species 788.) (Pf. **4**^{5} : 120.)

Family 295. **Eupatoriaceae.** Blazing-stars. Calyx from bracteose to capillary; receptacle naked; without rays; style branches papillose. Medium-sized plants, with opposite and alternate leaves. *Lacinaria, Eupatorium.* (Species 944.) (Pf. **4**^{5}: 131.)

Family 296. **Anthemidaceae.** Camomiles. Calyx a short crown or wanting; involucral bracts with scarious margins; receptacle chaffy or naked; usually with white ray flowers. Medium-sized plants, with alternate leaves. *Anthemis, Chrysanthemum, Artemisia.* (Species 915.) (Pf. **4**^{5}: 267.)

Family 297. **Senecionidaceae.** Groundsels. Calyx capillary; involucral bracts mostly 1-seriate; receptacle naked; flowers mostly yellow, with or without rays. Medium-sized to large plants, with alternate leaves. *Senecio, Arnica.* (Species 1982.) (Pf. **4**^{5}: 283.)

Family 298. **Carduaceae.** Thistles. Calyx mostly capillary; involucral bracts multiseriate; anthers tailed; receptacle usually bristly (not chaffy); without rays. Mostly stout plants, with alternate leaves. *Carduus, Arctium, Cnicus.* (Species 1563.) (Pf. **4**^{5}: 312.)

Family 299. **Mutisiaceae.** Mutisias. Calyx mostly capillary; receptacle usually naked; flowers all two-lipped. Medium to large (even woody) plants, of tropical or warm regions, with mostly alternate leaves. *Mutisia, Chaptalia.* (Species 550.) (Pf. **4**^{5}: 333.)

Family 300. **Lactucaceae.** Lettuces. Calyx mostly capillary; receptacle usually naked; flowers all strap-shaped. Small to medium-sized plants, mostly with a milky juice, and with alternate leaves. *Lactuca, Hieracium, Cichorium, Leontodon,* (*Taraxacum*). (Species 1701.) (Pf. **4**^{5}: 350.)

THE BOTANICAL GARDEN OF OAXACA

C. CONZATTI
Director of the Botanical Garden of Oaxaca, Mexico

I. General

At the end of the year 1909, when I was at the head of the Teachers' Normal School of the State of Oaxaca, a post which I had held since the middle of 1891, I was asked by the Ministry of Improvements, Colonization and Industry, at that time under Sr. Lic Don Olegario Molina, to assume the management of the Botanical Garden which was to be established on the grounds of the Agricultural Experiment Station of the same state. This station is situated about four kilometers from the city and had been in operation for only a few months.

Professor Don Félix Foëx, the first director of the station, was entrusted with the establishment of the Garden. He had several interviews with me; however attractive the proposition appeared to me, I could not decide to accept it. Finally, after much hesitation, I accepted the new position, and since then I have devoted myself to it entirely, even though success is doubtful; without fear of being contradicted, I can say boldly that I have been everything in the Botanical Garden, laborer, manager, topographer, landscape gardener, clerk, gardener, excursionist, and a hundred other things besides.

At the beginning of 1910 there was a general suspension for several months of the activities of the Station. As soon as the work could be resumed I devoted, with the half dozen men that I had at my command, the rest of that year and the whole of 1911 to the preliminary task of levelling, cleaning and adapting, in general, the ground for the new branch of the Station. This was a mistake; I recognize it now when it is too late. I should have insisted that the Botanical Garden, which was to be established on the grounds of the Station, be absolutely independent of the latter, or else I should have refused its management. Unfortunately, I did neither, and to this date

I deplore the consequences of such a serious lack of forethought, since, depending on the wills of others with ideas differing from mine, the Garden will never be able to prosper, or will prosper with great difficulties on account of lack of freedom.

Having finished the preliminary tasks which I had undertaken, I proceeded to make a sketch of the Garden as shown in fig. 1, which is here reproduced as approved by the authorities. As may be seen in the sketch, the Botanical Garden of Oaxaca is still in the process of formation. The tract of land assigned to it consists approximately of nine hectares, an area extensive enough to contain all the most prominent specimens of the mundane flora and all the characteristic specimens of the national flora.

Of the three valleys of the Station to the east of the Oaxaca and Ejutla Railroad, the Garden occupies the middle one, which is the one best suited for that purpose and at the same time most accessible. At the beginning it was subdivided into five departments, somewhat unequal in size, together comprising a rectangle 400 meters in length (from north to south) by 200 meters in width (from east to west); but later this area was increased by an addition of 3,000 square meters, which was annexed to the southwest corner, and again by a sixth department, semilunar in outline, comprising 5,000 square meters, annexed at the middle part of the west side. Deducting from this total area about two hectares which will be taken up by the prospective lake, walks, and lanes, there remain not more than seven hectares of land which can be utilized for the cultivation of plants.

As I have shown in a recent work, the Botanical Garden of Oaxaca is the first and only one worthy of the name in the whole of the Republic. This fact alone, signifying a positive progress, should have been sufficient to enlist the support of the authorities, as well as the public in general; but contrary to what might be expected, its existence has been, especially recently, extremely neglected. I have made this clear in the opinion expressed in my reports to the higher authorities, as may be seen from the following:

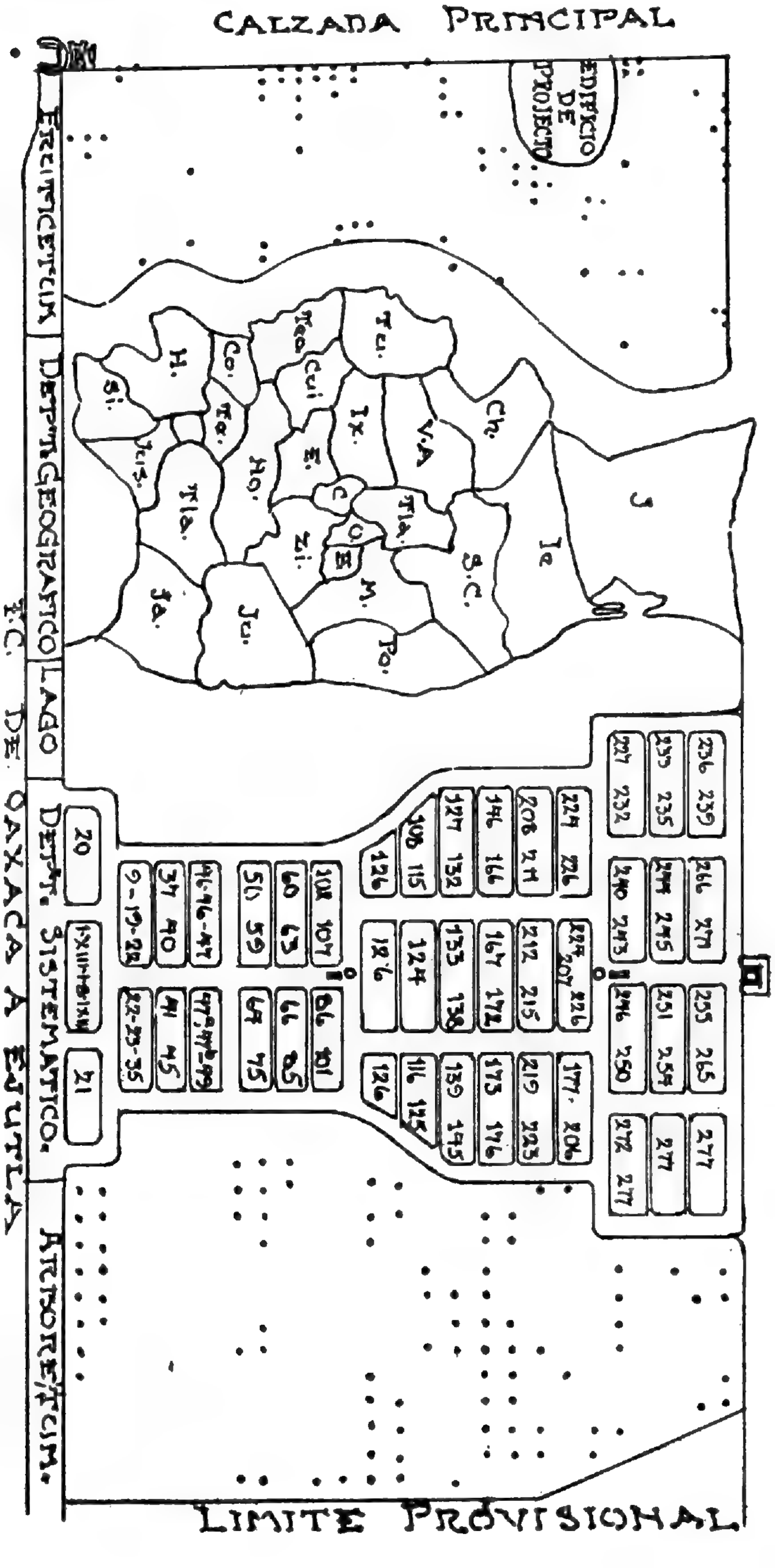

Fig. 1. Sketch of the Botanical Garden of Oaxaca in process of formation.

'I am not at all satisfied with the progress of the Botanical Garden, especially during the second half of the fiscal year, 1913–1914.

Receiving no encouragement, lacking entirely means and workmen, its existence has been extremely difficult, so much so that it would be practically impossible for it to continue under the same conditions for any length of time without failing for want of support. I must not cherish any illusions in this respect, and I consider it my duty to make this clear with all frankness.'

In the same report I point out:

'Such a difficult situation is due especially to the deplorable conditions which have depleted the Public Treasury, and that as soon as the present sad state of affairs disappears (which, fortunately, seems to be already taking place), all the branches of the administration will again receive that encouragement of which they are in such great need.'

And this I believe sincerely, since I have faith in the movement which is being started for the salvation of the country and for the restoration of peace.

After all, this is the history of the development of every new idea; it is obliged to struggle on its own merits—with danger of being suppressed—against all kinds of difficulties. One of these, and certainly not the least which I have encountered, has been the predominating instability everywhere, due to the political disturbances which have been ravaging the country for a long time. This circumstance and the absolute lack of means have prevented me from making the trips which I had planned in order to bring to the Garden some living plants, which to-day constitute the most pressing need of our institution. I am convinced that the life of the Botanical Garden depends essentially on providing it with plants. Since the departments are really well prepared, the essential thing now is to fill them with plants, preferably with the greatest possible number of specimens of the Mexican flora which are found in the mountains; and the only effective way of obtaining them is to go and get them. As long as this cannot be done, the work of the Garden must be limited to the routine work of preserving what is already there.

II. Detailed Description

At the end of 1913, according to the compilation made at that time, the Botanical Garden contained the following

plants: 1,099 in the systematic department, 101 in the arboretum, 1,158 in the propagation department, and 1,035 in the geographical department and the fruticetum, or a total of 3,393 specimens. For reasons already mentioned, the Botanical Garden from then until now has not only remained stationary, since it has received no appreciable additions, but it has also deteriorated a great deal, partly because a great number of plants have dried up from lack of water, and partly because its personnel—reduced to only four workmen—is insufficient to attend to the varied duties which are required. In fig. 1 some of the plants are indicated by black dots as occurring in the outer departments, arboretum and fruticetum, neither of which have any particular shape.

GEOGRAPHICAL DEPARTMENT

This department, on the contrary, is meant to represent in its main outlines the political map of the State of Oaxaca, the divisions of which are marked with the initial letters of the districts which constitute it. These districts at present are grouped, primarily on the basis of their climatic conditions, into six natural regions, as follows: Central, Cuicateca, Serrana, Istmica, Costena, and Mixteca, separated from one another by lanes two meters in width. The edges of these regions have already begun to receive—as a kind of an enclosure—the typical plants of each region, while the interior of each will receive the most characteristic vegetable productions of the exuberant soil (see fig. 2).

In accordance with this plan, the central region (fig. 2), which consists of the districts (see fig. 1) E—to the right of O—(Etla), Zi (Zimatlan), M (Miahuatlan), E—to the left of C—(Ejutla), Tla (Tlacolula), and O (Ocotlan), all bordering on, or similar by their products to, district C (Center), shows now on its perimeter 121 specimens of *Ceanothus azureus*, a vigorous and elegant shrub of the hills which surround the Capitol.

The point corresponding to Santa Maria del Tule, a small village in the same region and situated about two leagues east of Oaxaca, is planted with a shrub "Sabino del Tule"

(*Taxodium distichum*) two meters in height and a direct offspring—by seed—from its historic parent. Among other things, it has the merit of being the oldest member of the department.

The Cuicateca region, consisting of the districts Cui (Cuicatlan), Teo (Teotitlan), and Tu (Tuxtepec), is limited now to 65 specimens of *Vallesia glabra*, or "Tree of the Pearls," native of the Canyon of Tomellin. This small collection is characterized by its exuberant growth and uniform size. Of the districts which constitute this region, only Cuicatlan has received a supply of plants—twenty-two different specimens from Quiotepec. Among these are six plants of *Bursera sucedanea* from Linaloé, called "Palo Hediondo" (fetid stick) by the natives of that place.

Three districts form the Serrana region, Ix (Ixtlan), V. A. (Villa Alta), and Ch (Choapam); only very recently I have planted around these, 81 specimens of *Cerocarpus fothergylloides*, a beautiful rustic little tree which is native of this region.

The perimeter of the Istmica region, composed of the districts J (Juchitan) and Te (Tehuantepec), was also planted in a similar manner with some 34 specimens of an arboreal *Pereskia*, new to science, from the coast of Salina Cruz. In the district of Tehuantepec I have planted 30 plants coming from the same region and belonging to about a dozen species in several genera—*Stemmadenia, Pedilanthus, Mimosa*, etc., and in the district of Juchitan species of several genera of the *Cactaceae—Opuntia, Cereus, Mamillaria, Selenicereus, Echinocactus*, etc.—have been planted.

On the southern side of this department there are planted 40 palm-trees, species of *Phoenix*, about two meters high, bordering a walk which bears the name of the famous Brazilian botanist, Barbosa Rodrigues; while on the north side runs another walk, five feet wide, called "Andres Cesalpino," along the edges of which we have planted 148 specimens of *Poinciana Conzattii* Rose, brought from Tehuantepec.

Finally I shall mention the collection of Mexican agaves

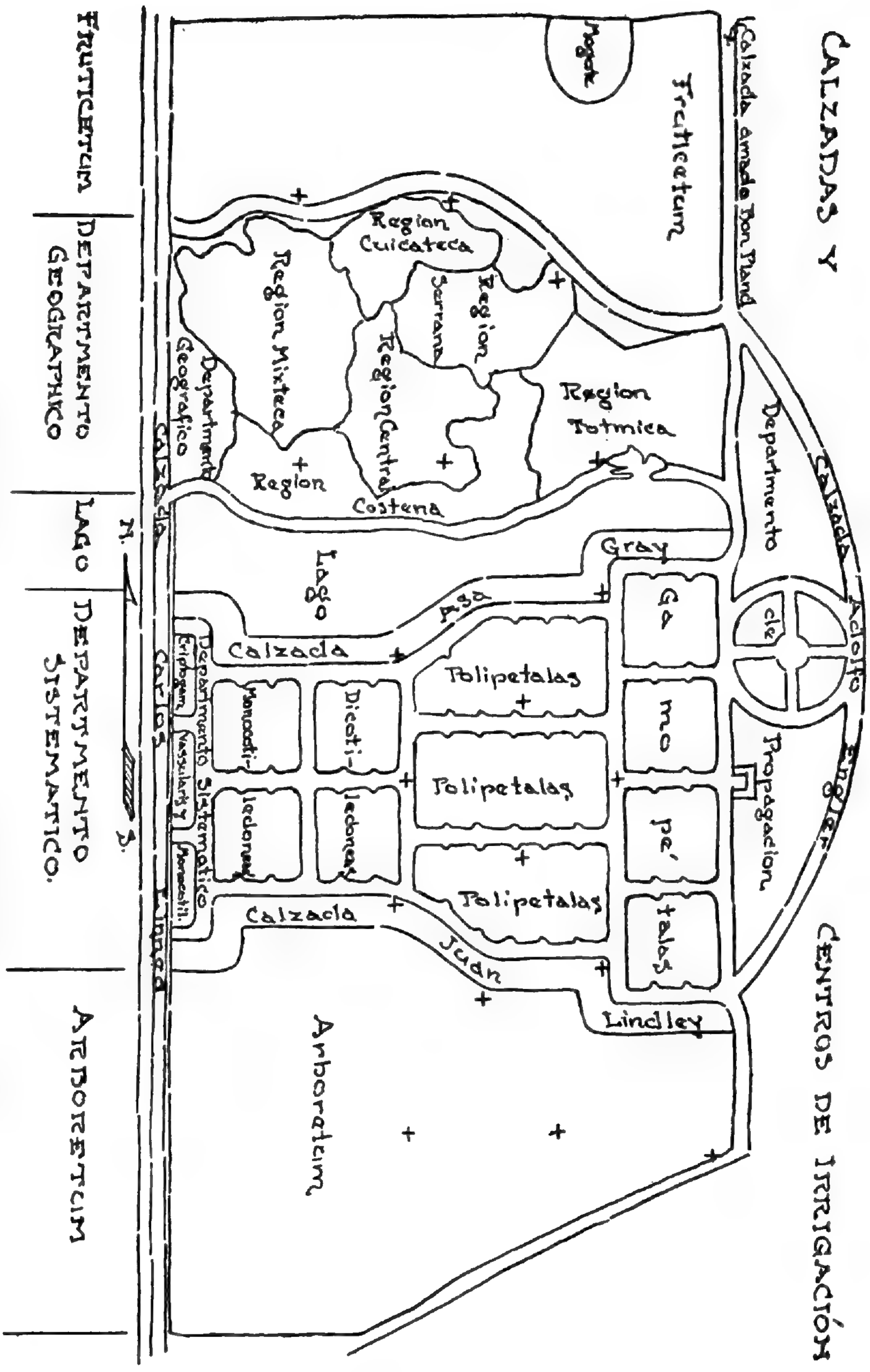

Fig. 2. Walks and irrigation centers in the Botanical Garden of Oaxaca.

which are in the district H (Huajuapam) of the Mixteca region, as well as the fact that it is planned to introduce into

this department various groups of practically useful plants —industrial, tinctorial, poisonous, medicinal, etc.

DEPARTMENT OF PROPAGATION

This department is situated in the middle eastern part of the Botanical Garden and comprises an area of not more than half a hectare. Its shape is that of a semicircle bounded on its convex side by the Adolf Engler walk; this is the name of the famous author of the classification adopted by the Garden, with few very slight exceptions suggested by the 'Lexicon Generum Phanerogamarum' of von Post and O. Kuntze. The sides of this walk are planted for the time being with various specimens of *Melia Azedarach,* but in the near future these will be replaced by specimens of "Rosa-Cacao," an imposing pyramid-like tree with horizontal and vertical branches.

As indicated by the name, this department is devoted to the propagation of plants for this Garden and similar establishments in this and other countries.

WALKS AND IRRIGATION CENTERS

Of the walks of the Garden, the one called "Carlos Linneo" forms the western boundary line of the Garden and serves it, so to speak, as a base. It is a straight line 420 meters long, running from north to south, parallel to the Oaxaca and Ejutla Railroad, and throughout its length there are, five feet apart, 84 specimens of *Casuarina stricta* about three meters in height. Two other walks worth mentioning on account of their width (10 meters) are the Asa Gray and the John Lindley walks; these run along the outer side of the systematic department and have as a border 105 laurels from India, as yet rather small.

One of the far-reaching improvements for the progress of the Botanical Garden has been the establishment of a practical irrigation system, which was first introduced at the end of 1913 and developed later as shown in fig. 2.

For this purpose we first laid under the ground 400 meters of $2\frac{1}{2}$-inch pipe through the center of the Garden from the large circular tank, situated on the southern slope, to the wide

avenue leading from the Station building on the north. This was the main artery and at fixed points, which were carefully selected beforehand, crosses were placed to mark the respective connections. These consisted of lateral ramifications of smaller pipe which were to carry the water to the 35 irrigation centers, 50 meters apart, into which the Garden is subdivided.

All these centers must have nozzles, and at present there are 18 of them in working order; these are marked with crosses in fig. 2. To install them we have used 500 meters of smaller piping, so that a similar amount, if not a little more, would be required to complete the network. Of these irrigation centers eight belong to the arboretum, twelve to the systematic department, seven to the geographical department, five to the fruticetum, and three to the propagation department. As soon as the Botanical Garden has completed its irrigation system and has a sufficient supply of water for all seasons, we shall be able to consider its existence as assured.

SYSTEMATIC DEPARTMENT

Together with the two preceding departments, the geographical and propagation departments, the systematic department constitutes the central part of the Garden, and from the botanical point of view is the most interesting of them all. Many plants have already been planted in it, as may be seen in pl. 3, which represents the central part of the department; but the empty places are still numerous, and the need of having them planted is great. The shape of this department is that of an immense cup, 200 meters long and measuring 145 meters at its widest part.

As I have shown in a previous paper, which was published some time ago in the 'Memorias y Revista de la Sociedad Cientifica "Antonio Alzate,"' of Mexico, and to which I now refer for a better presentation of this subject, 'its interior is subdivided into 45 large squares approximately equal, among which are distributed the 277 phanerogamic families of the "Syllabus" of Dr. Engler.' The plants in this department, therefore, are arranged strictly in the order of affinity,

namely, vascular cryptogams and monocotyledons at the base, followed in order by the dicotyledonous groups, *Apetalae, Polypetalae,* and finally the *Gamopetalae.* With the latter the lineal series is closed, since according to the consensus of modern opinion they constitute the most highly differentiated group of flowering plants.

In the preceding lines I have endeavored to condense the most prominent features relative to the life of the Botanical Garden of Oaxaca. They are totally without pretense on my part, although they would wish to carry to the minds of all those who may read them the same high concept which I myself have formed of such a progressive institution.

In spite of the discouragement that I often feel about the Garden, I have confidence in its final success. Everything indicates that to-day the Republic is approaching rapidly a better era, which will be effected through organic peace and progress in its truest sense, since the horizon appears already free from the dark clouds.

In concluding, I wish to say that the Botanical Garden of Oaxaca, after showing itself in the preceding lines in all its smallness, has the honor of sending its older brother, the Missouri Botanical Garden of St. Louis, its most cordial congratulations for the Twenty-fifth Anniversary, wishing it long life and abundant prosperity.

Explanation of Plate

PLATE 3

General view of the Botanical Garden of Oaxaca, Mexico, particularly of its Systematic Department.

CONZATTI—BOTANIC GARDEN OF OAXACA

THE ORIGIN OF MONOCOTYLEDONY

II. Monocotyledony in Grasses

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Recently Dr. Land and I published[1] the results of an investigation suggested by a specimen of *Agapanthus umbellatus*, one of the South African *Liliaceae*, possessing two good cotyledons. It seemed to us that if the seedlings of the same species are indifferently monocotyledonous or dicotyledonous, there must be some evident relationship between the two conditions. These two conditions of the seedling of *Agapanthus* were compared critically, and *Sagittaria* was included in the investigation because it has stood, along with *Alisma*, for the typical monocotyledonous embryogeny, in which the terminal cell of a filamentous proembryo is said to give rise to the single cotyledon, in contrast with the dicotyledonous embryogeny, in which the corresponding terminal cell produces the stem tip, and the cotyledons are distinctly lateral. No contrast would seem sharper and less capable of being confused with intergrades.

The result of the investigation, as recorded in the paper referred to, was to show us that there are no such rigid categories for cotyledony; that the cotyledonary apparatus is always the same structure, arising in the same way, and varying only in the details of its final expression. Briefly stated, the situation is as follows: In the embryogeny of both monocotyledons and dicotyledons, a peripheral cotyledonary zone gives rise to two or more growing points, or primordia; this is followed by zonal development, resulting in a cotyledonary ring or sheath of varying length. If both growing points con-

[1] Coulter, John M., and Land, W. J. G. The origin of monocotyledony. Bot. Gaz. 57: 509–519. *pl.* 28–29. 1914.

tinue to develop equally, the dicotyledonous condition is attained; if one of the growing points ceases to develop, the continued growth of the whole cotyledonary zone is associated with that of the other growing point, and the monocotyledonous condition is attained. In like manner, polycotyledony is simply the appearance and continued development of more than two growing points on the cotyledonary ring. It follows that cotyledons are always lateral structures, arising from the peripheral zone developed at the top of a more or less massive proembryo. This reduces cotyledony in general to a common basis in origin, the number of cotyledons being a secondary feature. The constancy in the number of cotyledons in a great group is no more to be wondered at than the same constancy in the number of petals developed by the petaliferous zone. This is a brief statement of the thesis of our previous paper, detached from the evidence upon which it was based.

It was our purpose to extend the investigation far enough to include all of the representative regions of monocotyledons, so that the conclusion could be tested sufficiently to lead either to its abandonment or to its establishment. This second paper deals with a study of the embryos of grasses, which have been examined more extensively, perhaps, than the embryos of any other monocotyledonous group. As a result of this extensive study there are available many accurate records in the form of good figures, giving the details of embryogeny in such a way that interpretation is almost as satisfactory as it would be from the actual material. Of course this use of illustrations has been checked by the direct inspection of more or less material.

The embryo of grasses early attracted special attention because it does not seem to conform to the plan of the ordinary monocotyledonous embryo. Certain structures appear that could not be accounted for, but they enriched terminology. As a consequence, the nature of scutellum, epiblast, and coleoptile became subjects of discussion. It was to be expected that

the embryo of grasses, with all of its unusual structures, would be interpreted in terms of a rigid conception of the monocotyledonous embryo; in other words, that the conventional monocotyledonous embryo would be read into the grass embryo. There is no better illustration of the compelling power of a preconception than this treatment of the grass embryos, for it so happens that they show all the intermediate stages between dicotyledony and monocotyledony.

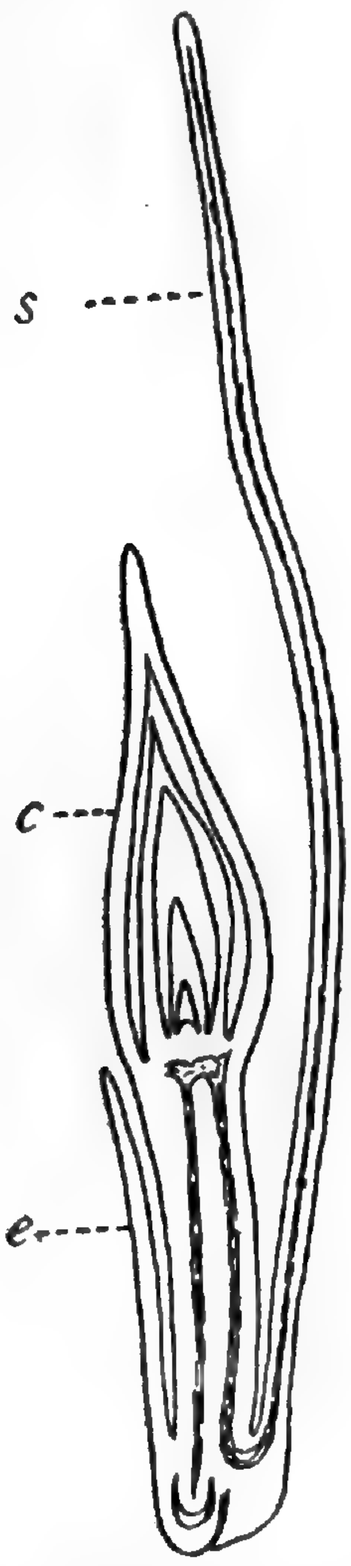

Fig. 2. Embryo of *Zizania aquatica*: *s*, scutellum; *e*, epiblast; *c*, coleoptile; × 11. — After Bruns.

Very early in the history of this subject, the scutellum came to be recognized as a cotyledon. The corollary to this proposition, however, was that it must be recognized also as a terminal structure. Any one who has seen the vascular system of the embryo of corn (fig. 1), the most highly specialized of all grass embryos, with its distinct axial cylinder, made up of stem cylinder and hypocotyl cylinder, and the cotyledonary strands leading off from the intermediate cotyledonary plate, just as do the strands of any lateral cotyledons, will understand the great difficulties in the way of interpreting this cotyledon as a terminal structure.

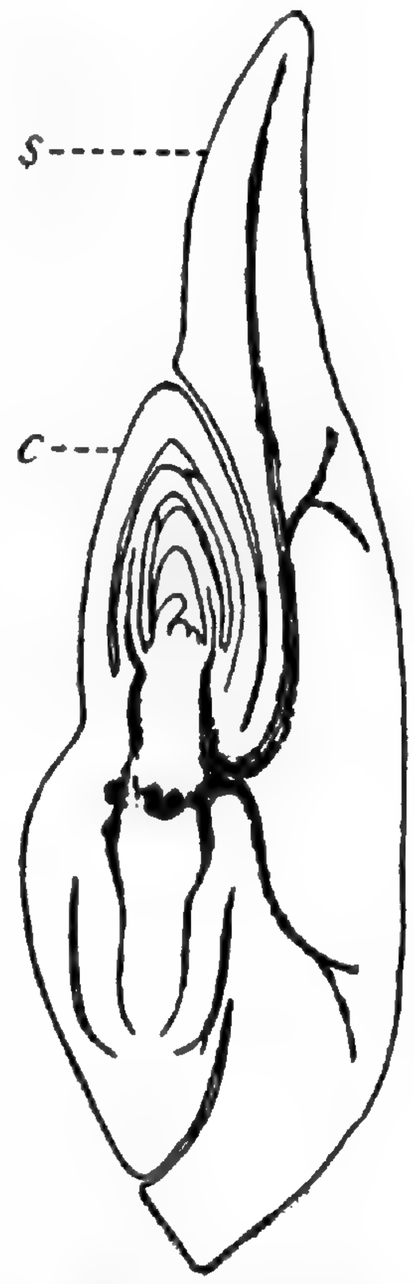

Fig. 1. Embryo of *Zea Mays*: *s*, scutellum; *c*, coleoptile; the vascular cylinder of the embryo is shown, made up of stem cylinder and hypocotyl cylinder, also the lateral origin of the cotyledon (scutellum) from the cotyledonary vascular plate; opposite the vascular connection of the cotyledon there appears a group of procambium cells, marking the origin of another cotyledonary strand connected with the suppressed second cotyledon (epiblast); ×18.

The structure which presented the greatest difficulty, however, was the epiblast, usually defined as a small scale "opposite" or "over against" the

cotyledon. The definition is accurate, for the epiblast occupies exactly the place of a second cotyledon opposite the large and functional one (fig. 2). If some one had found an epiblast vigorous enough to establish vascular connections, this debated structure would long since have been accepted as a second cotyledon, for the definition of it always emphasized the fact that it is a scale in the right position for a cotyledon, but with "no vascular strands."

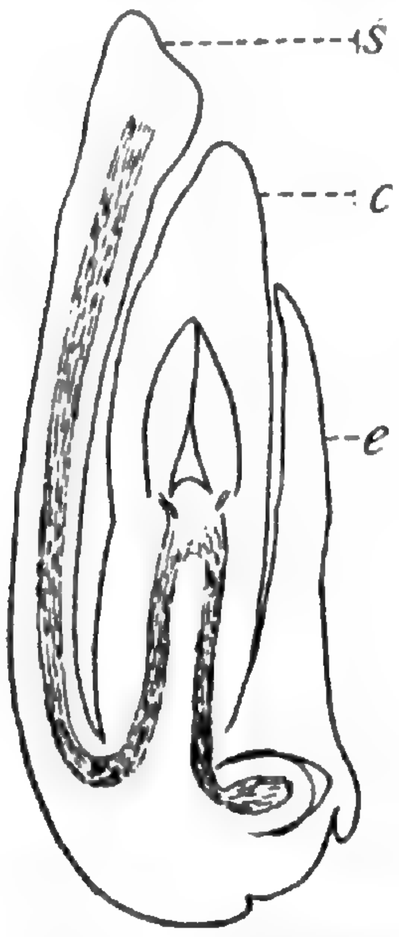

Fig. 3. Embryo of *Leersia clandestina: s*, scutellum; *e*, epiblast; *c*, coleoptile; × 44. — After Bruns.

So obvious is the interpretation of the grass embryo when an epiblast is developed that Porteau in 1808, Mirbel in 1809, Turpin in 1819, and Bischoff in 1834, all called the epiblast a rudimentary cotyledon. The submergence of this idea seems to have been due to Schleiden, who in 1837 dissented from this view, and it disappeared from literature. It reappeared in 1897, when Van Tieghem, in his paper on the embryo of grasses and sedges,[1] reiterated it, based chiefly upon the study of vascular connections.

Any series of sections, cross or longitudinal, through the embryos of grasses, shows the following facts: the so-called scutellum or functional cotyledon arising from the peripheral cotyledonary ring or sheath which surrounds the apex of the embryo, and establishing vascular connections laterally with the cotyledonary plate; the epiblast in a similar relation to the cotyledonary ring on the opposite side, and varying in development from a structure somewhat smaller than the large cotyledon, to complete suppression; and the apex of the

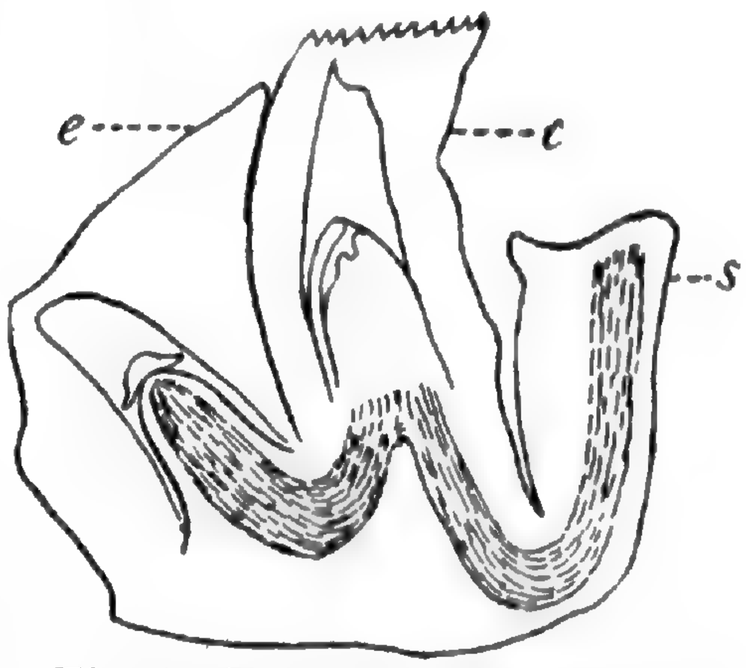

Fig. 4. Embryo of *Oryza sativa: s*, scutellum; *e*, epiblast; *c*, coleoptile; ×22.—After Bruns.

[1] Van Tieghem, Ph. Morphologie de l'embryon et de la plantule chez les Graminées et les Cypéracées. Ann. d. Sci. Nat., Bot. VIII. 3: 259–309. *pl. 14–16.* 1897.

embryo, continuing beyond the cotyledonary ring or sheath, and producing a variable number of leaves.

The early appearance and rapid development of these leaves seems to account for the abortion of one of the growing points. I am convinced that if grass embryos had been the only monocotyledonous embryos studied, we should never have heard of terminal cotyledons.

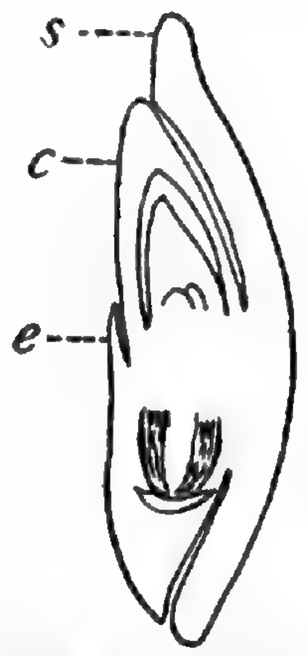

Fig. 5. Embryo of *Spartina cynosuroides: s*, scutellum; *e*, epiblast; *c*, coleoptile; ×13.— After Bruns.

Some common grasses, whose embryos have been figured by Bruns,[1] may be used to illustrate stages in the abortion of the second cotyledon. The abortion always is accompanied by the diversion of the growth of the whole cotyledonary zone in connection with the growing point that remains active; so that growing tissue is not suppressed, but develops as one structure rather than as two.

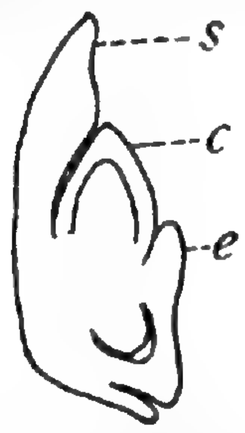

Fig. 6. Embryo of *Leptochloa arabica: s*, scutellum; *e*, epiblast; *c*, coleoptile; × 44. — After Bruns.

In *Zizania aquatica* (fig. 2), the so-called epiblast is very conspicuous, arising as distinctly from the peripheral cotyledonary ring as does the so-called scutellum, and attaining at least one-quarter to one-third of its length. This unusual development of the second cotyledon is associated with the fact that the stem axis above the cotyledons develops a long internode, so that the first leaves begin to appear at an unusual distance from the origin of the cotyledons. In fact, in this case the length of the second cotyledon is approximately the length of the first internode, and where the leaves begin this cotyledon ends.

Fig. 7. Embryo of *Triticum vulgare: s*, scutellum; *e*, epiblast; *c*, coleoptile; ×22.— After Bruns.

In *Leersia clandestina* (fig. 3), the second cotyledon (epiblast) approaches the large cotyledon in length even more

[1] Bruns, Erich, Der Grasembryo. Flora 76: 1–33. *pl. 1–2.* 1892.

than does that of *Zizania,* and all the connections of the various organs show a lateral origin for the cotyledons, and a terminal origin for the "coleoptile," a structure made up chiefly of leaves arising from an indistinctly differentiated stem-tip region.

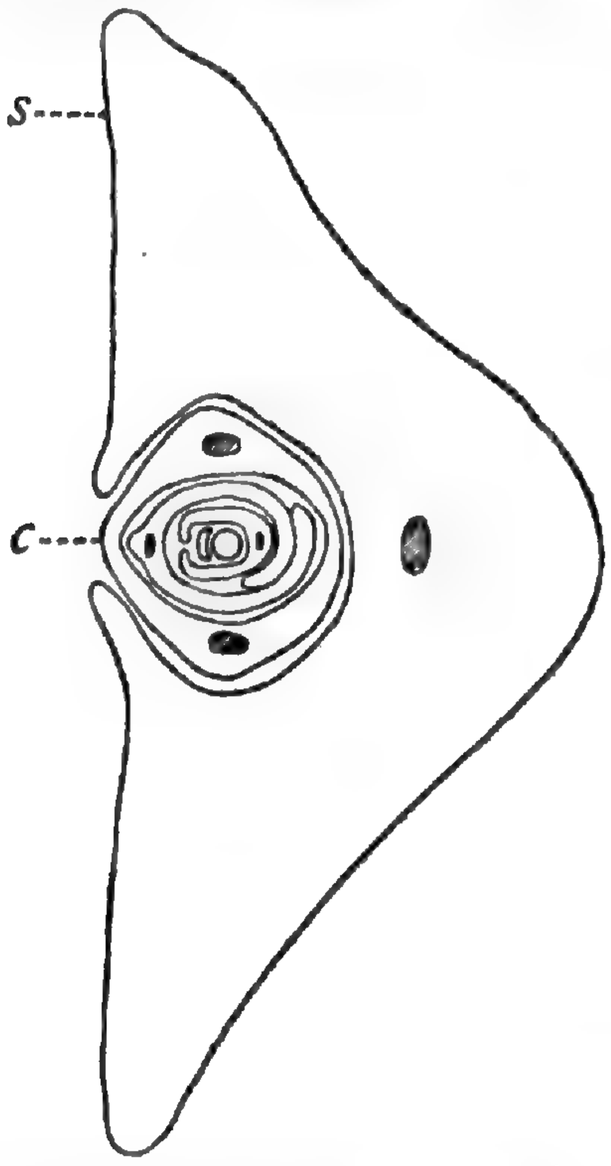

Fig. 8. Transverse section through cotyledon (*s*), showing it embracing the plumule (*c*) of *Zea Mays:* the plumule shows three distinct leaves and the terminal stem tip; the succession of opposite vascular bundles indicates that a bundle opposite that of the cotyledon is missing, but its rudiment is evident in a lower section; ×20.

Oryza sativa (fig. 4) is interesting in the relation of the parts of the embryo, the "scutellum" and "epiblast" being opposite and well-balanced structures, between which the prominent plumule (a name expressing the real character of the "coleoptile") is evident.

In *Spartina cynosuroides* (fig. 5), the small cotyledon (epiblast) is less prominent, but its relation to the functioning cotyledon, and the relation of both to the plumule are evident.

In *Leptochloa arabica* (fig. 6) and in *Triticum vulgare* (fig. 7), the epiblast remains very small, but the significant connections are evident.

It is in the embryo of *Zea Mays* that this reduction series reaches its extreme expression in the complete disappearance of the epiblast or second cotyledon (fig. 1), whose position is indicated merely by more or less protuberant

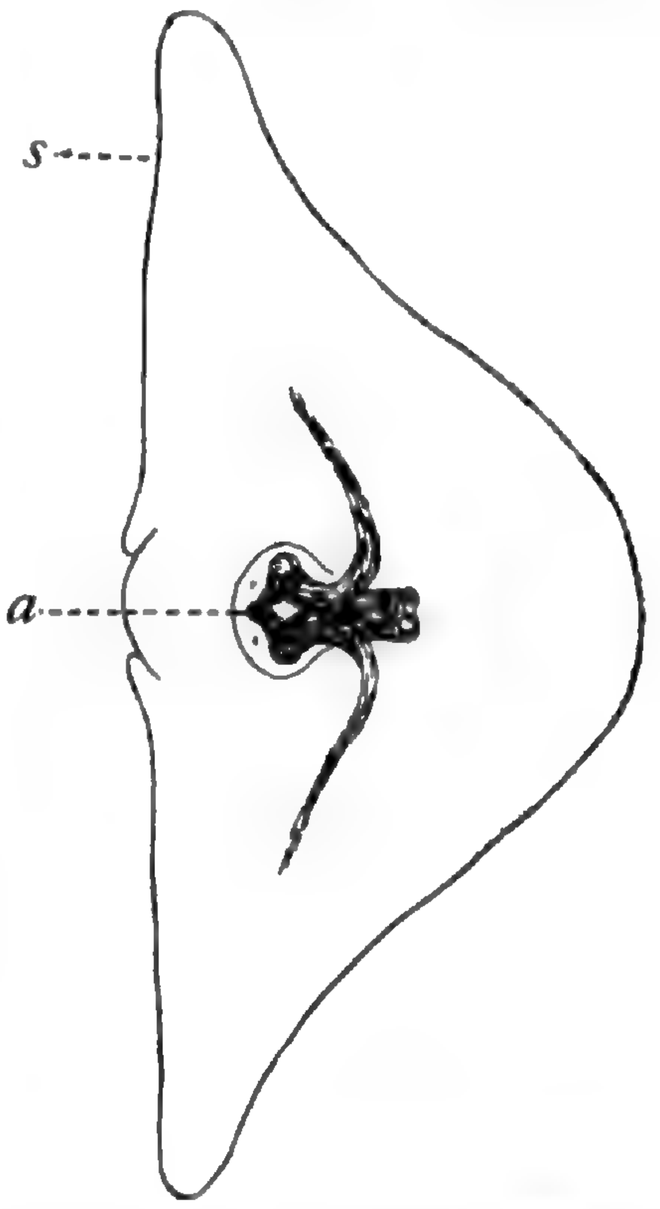

Fig. 9. Transverse section through the cotyledonary plate of *Zea Mays:* the functioning cotyledon (*s*) does not overlap a small protuberance, which represents the site of the missing cotyledon (epiblast), as indicated also by the appearance of a procambium mass (*a*), which is the rudiment of a former vascular connection; ×20.

tissue and by the very obvious vascular relations. A cross-section of this very specialized embryo is instructive (figs. 8 and 9). The large functional cotyledon is seen originating on one side, embracing the vascular axis of the embryo and more or less overlapping the other side, where in most grasses the second cotyledon (epiblast) appears. Moreover, in the section of the centrally placed plumule, with its succession of leaves, a section of the stem tip may be seen, clearly representing the axis of the embryo, with no suggestion of a lateral origin. A transverse section through the cotyledonary plate (fig. 9) shows some tissue developed at the site of the missing cotyledon (not overlapped by the functioning cotyledon). This is emphasized by the appearance of a mass of procambium at the base of the protuberance, which in other grasses develops into the epiblast. This procambium is distinctly a rudiment of a former vascular connection.

Some idea of the frequency with which the second cotyledon appears among the grasses may be obtained from the excellent work of Bruns on the grass embryo, published in 1882, and from the work of Van Tieghem, already cited, published in 1897. Bruns examined 82 genera, representing 12 tribes. In 29 of these genera epiblasts were present, and the genera represented 9 of the 12 tribes. The tribes in which no epiblasts were found were *Oryzeae, Agrostideae,* and *Aveneae.* The situation in the *Agrostideae* is noteworthy, for 13 genera were examined, and no trace of an epiblast found. *Festuceae* may be mentioned, for 20 of its genera were examined, and only 4 of them were found to possess epiblasts. Taking Bruns' results as a whole, they indicate that approximately 40 per cent of the grasses still develop a second cotyledon to a stage that enables it to be recognized under ordinary inspection as a definite structure.

The work of Van Tieghem included a somewhat wider range of forms, 91 genera being examined, and 61 of these showed epiblasts. This suggests that perhaps in as many as two-thirds of the grasses a second cotyledon is more or less obvious. In any event, it is certain that the grasses as a whole exhibit a remarkable number of transition stages from dicoty-

ledony to monocotyledony; and this fact strongly supports the view that grasses are a comparatively primitive assemblage of monocotyledons.

It is not difficult to explain the prolonged misconception concerning monocotyledony. When the first detailed studies of monocotyledonous embryogeny were made by Hanstein, and supplemented by Famintzin, a form (*Alisma*) with a filamentous proembryo was selected. If a form with a massive proembryo had been selected for these early investigations, there would probably have been no misconception, for in such proembryos the peripheral (that is, lateral) cotyledonary zone is so evident that it could hardly have escaped recognition. Since that time, embryogeny that starts with a filamentous proembryo has been regarded as the typical embryogeny, and all other kinds of proembryos have been dismissed as exceptions. In the case of this filamentous proembryo, it was observed that the terminal cell passed into the quadrant and octant stages, and later a terminal cotyledon appeared. It seemed safe to conclude that the terminal cell had developed the terminal cotyledon. The inference was true so far as it went, but it failed to recognize the fact that the terminal cell develops other structures as well. With the origin of the terminal cotyledon disposed of, the conclusion was confirmed by the appearance at its base of a notch, from which arose the stem tip. What could be more obvious than that the stem tip is lateral in origin, and therefore must arise from the cell of the proembryo behind the terminal one? In this way the conventional embryogeny of monocotyledons was established, and the relation of monocotyledony to dicotyledony became completely obscured.

The facts not observed in these earlier investigations are as follows: The terminal cell of the proembryo forms a group of cells; the peripheral cells of this group develop the cotyledonary ring or sheath, on which two growing points appear. One of these growing points soon ceases to be active, and the whole zone develops in connection with the other growing point; but at the base of the growing cotyledon a notch is left by the checking of the other growing point. This notch

is really the space between the two very unequal cotyledons, which surround the real apex of the embryo. The apex of the embryo is at the bottom of the notch, and not at the tip of the large embryo. This apex soon begins to form leaves, and the so-called stem tip appears issuing from the bottom of the notch, in a relation apparently lateral only because the two cotyledons are so unequal. Furthermore, when the stem tip is examined, it is found not to be a stem tip, but a cluster of leaves whose rapid development has aborted one of the growing points on the cotyledonary zone. All this is very obvious in grasses, and is equally obvious in any massive proembryo, but it escaped the earlier observers of filamentous proembryos.

The general conclusion is that monocotyledony is simply one expression of a process common to all cotyledony, gradually derived from dicotyledony, and involving no abrupt transfer of a lateral structure to a terminal origin.

This paper was prepared in collaboration with Dr. W. J. G. Land, who also supplied the material and made the illustrations.

THE HISTORY AND FUNCTIONS OF BOTANIC GARDENS

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There are three things which have stimulated men throughout the ages to travel far and wide over the surface of the globe, and these are gold, spices and drugs. It is to the two latter of these universal needs of man that we may trace the origin and foundation of botanic gardens.

The value of spices has led to the foundation of more than one botanic garden in the tropics, while to the necessity for drugs must be attributed the formation of the earliest botanic gardens in Europe.

Before entering more fully into the history of the founding of the various botanic gardens it may be pointed out that progress in the science of botany and the establishment of gardens were by no means contemporaneous. To the Greeks, for instance, we owe the foundation of our knowledge of the classification of plants, and these early botanists were assiduous in collecting plants from all available sources and in drawing up accurate descriptions.

Little interest, however, would appear to have been aroused in them to cultivate the plants they so carefully described, and the only record we have of the existence of anything of the nature of a botanic garden is the mention of Aristotle's Garden at Athens which he bequeathed to Theophrastus, by whom it was newly equipped and improved.

Prior to the interest displayed by the Greeks in the vegetation of the earth and quite independent of their influence we find evidence of the formation of gardens in Egypt, Assyria, China, and subsequently in Mexico—gardens not strictly botanic in our more modern sense but enclosures[1] set apart

[1] See Greene, E. L. Landmarks of botanical history. Smithsonian Misc. Coll. 54[1]: pp. 56–57. 1909. No doubt Theophrastus (370–286 or 262 B. C.) gained his intimate knowledge of plants very largely from the specimens cultivated in this early Athenian garden.

for the cultivation of plants of some definite economic or aesthetic value.

In considering the history of this subject we look back to the earliest history of mankind, with which gardening in some form is inseparably connected, for, as Francis Bacon reminds us:

> "God Almightie first planted a Garden and indeed it is the Purest of Humane Pleasures. It is the greatest refreshment to the spirits of man; without which Buildings and Palaces are but grosse Handyworkes: and a man shall ever see that when ages grow to civility and elegancie men come to Build stately sooner than to garden finely as if gardening were the greater Perfection."

We are still exercised to seek out and grow "every tree that is pleasant to the sight and good for food," and the "tree of life" also in the midst of the garden is ever the object of our inquiries. It would be well indeed if at this present time we could discover that tree whose leaves were to be "for the healing of the Nations."

The earliest garden of which we have any representation is the Royal Garden of Thotmes III of about the year 1000 B. C., which was planned by Nekht, head gardener of the gardens attached to the Temple of Karnak.[1] This Royal Garden, rectangular in outline, with its rows of date and branched doum palms and with its vine pergola and lotus tanks, was probably in the nature of a pleasure garden, while those attached to the temples may well have been of more economic importance. The Chinese,[2] however, should, as might be supposed, be credited with being the real founders of the idea of botanic gardens, since it is clear that collectors were despatched to distant parts and the plants brought back were cultivated for their economic or medicinal value. The semi-mythical Emperor Shen Nung, of the twenty-eighth century B. C., is considered to be the Father of Medicine and Husbandry and is said to have tested the medical qualities of herbs and discovered medicines to cure diseases. If this be

[1] See Holmes, E. M. Horticulture in relation to medicine. Roy. Hort. Soc., Jour. **31**: pp. 44–45. *f. 11*. 1906.

[2] Bretschneider, E. Botanicon sinicum. China Branch Roy. Asiatic Soc., Jour. N. S. **25**: p. 24. 1893.

correct, it was but a repetition of history which led to the foundation of the monastic herb gardens in the ninth century A. D., and the subsequent institution of botanic or herb gardens in connection with the medical faculties of the earliest European universities.

We learn from Bretschneider also that the Han Emperor Wu Ti (140–86 B. C.) planted a number of rare herbaceous plants and trees brought from the southern regions in the garden of his palace and the following plants have been identified from the list enumerated: *Nephelium Litchi, N. logan, Areca Catechu,* the banana, *Quisqualis indica, Canarium album, C. Pimela, Cinnamomum Cassia, Canna indica,* and sweet oranges. He also despatched officers to the northwestern frontiers of China, who brought back reports on the productions of this region. Ancient Chinese authors ascribe to Wu Ti the introduction of the vine, pomegranate, safflower, common bean, cucumber, lucerne, coriander, walnut, etc.

It is a fact of no small interest in this connection to remember that the modern world has turned to China and that her vast botanical treasures have only recently been seriously explored through the enterprise of British, French, and American botanists for the enrichment of our botanic gardens and pleasure grounds.

The establishment of gardens in Mexico is a noteworthy fact—though we have but little information about them—since their origin must have been autochthonous and independent of such institutions in the Old World. Prescott[1] tells us, and we have reason to believe his account to be true, that Montezuma had extensive gardens filled with fragrant shrubs and flowers and especially with medicinal plants. New Spain, indeed, furnished more important species of medicinal plants perhaps than any other part of the world, and their virtues were understood by the Aztecs, who are credited with having studied medical botany as a science. The gardens at Iztapalan[2] and Chalco[3] are said to have been stocked with

[1] Prescott, W. H. Conquest of Mexico **2**: pp. 110, 111. 1847. [3rd ed. London.]
[2] *Ibid.* pp. 60 and 61.
[3] *Ibid.* **3**: p. 37. 1847; Clavigero, D. F. S. Stor. del Messico **2**: p. 153.

trees and plants scientifically arranged, and the gardens at Chalco, which were preserved after the Conquest, furnished Hernandez with many of the specimens described in his book.[1]

The cases cited, however, have little more than an academic interest for us and have in no way influenced the foundation of modern botanic gardens. These we can trace back to monastic institutions and probably to the famous injunctions of Charlemagne,[2] the direct outcome of which was the establishment, among others, in the ninth century, of the "hortus" at St. Gall with the attendant "herbularis," or Physic Garden, this latter being the precursor of the physic gardens established in connection with the medical faculties of the Italian and other universities in the sixteenth century.

It is fortunate that we have preserved to us exact details of the "hortus" and "herbularis" at St. Gall, with lists of the plants cultivated therein.[3] The hortus was an oblong enclosure containing eighteen rectangular beds, while the Physic Garden, or herbularis (see fig. 1), formed a square set with similar beds and having the doctor's house close at hand.

The monks being bound to live on pulse, vegetables and fruits and to gather the same for themselves, the garden and its cultivation were of especial importance in the monastery. To the fostering care of the monks and to their knowledge of drugs, horticulture and botany, in common with other arts and sciences, we owe a debt the magnitude of which it is difficult to estimate.

We do well to recall at this point the services rendered in recent years to the biological sciences by the labors of Gregor Mendel in the monastic garden at Brunn, if only to emphasize how widespread and far-reaching are the functions involved in the true idea of the botanic garden.

The fourteenth and fifteenth centuries, as is well known, were times of a great revival and interest in learning, and

[1] Hernandez, F. Nova plantarum animalium et mineralium Mexicanorum historia. Rome, 1651.

[2] Holmes, E. M. Horticulture in relation to medicine. Roy. Hort. Soc., Jour. **31**: p. 50. 1906.

[3] Archaeological Inst., Jour. **5**: p. 113; see also Amherst, A. History of gardening in England p. 5. 1896. [2nd ed.]

the science of botany received its due share of attention. Unfortunately, energy was chiefly employed in attempting to identify the plants named by the Greek writers with those of Western Europe and progress in the science was only fitful. The compilation of herbals was the main occupation

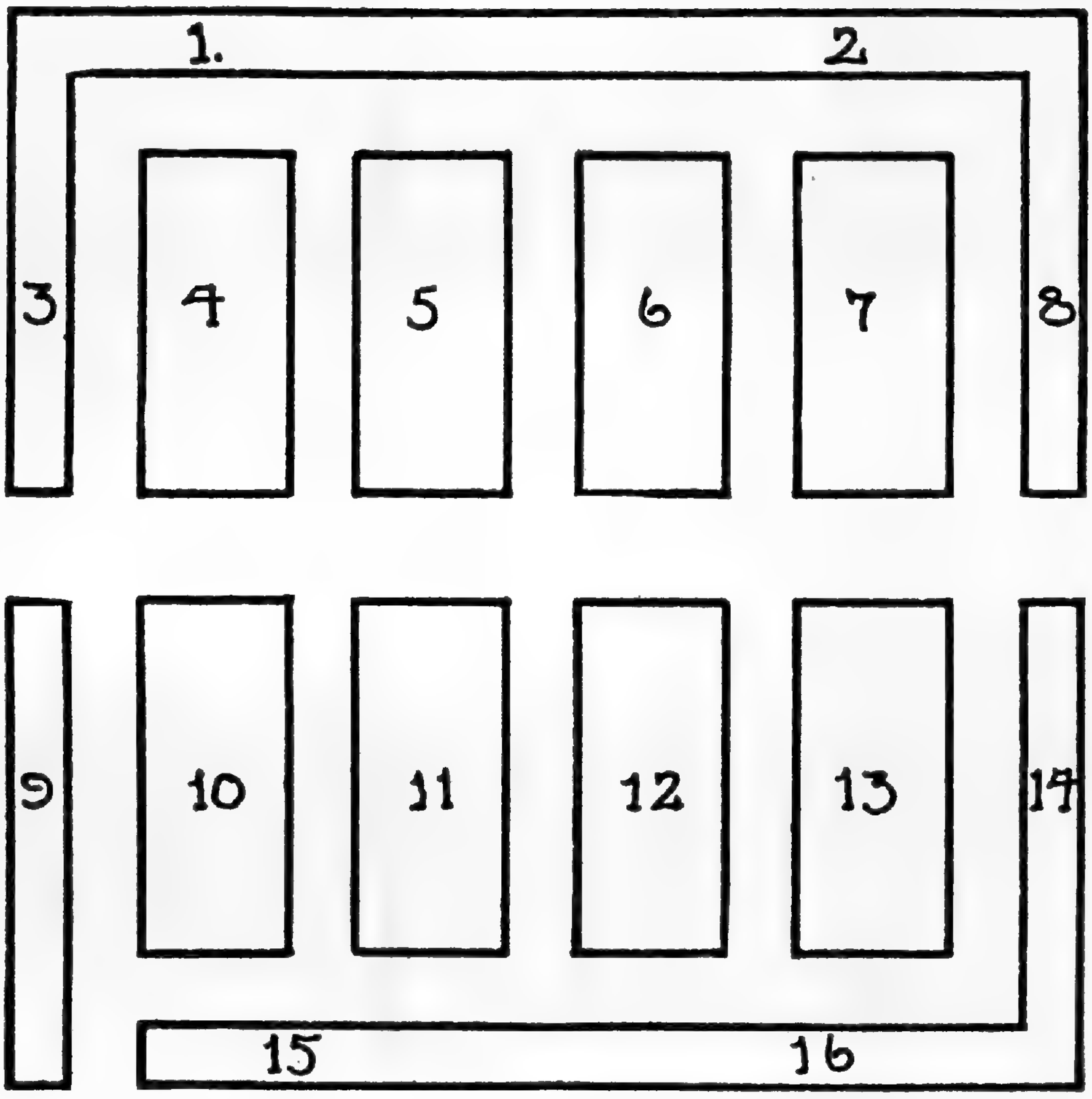

Fig. 1. Monastery of St. Gall. Physic Garden: *1*, Fasiolo; *2*, Sataregia; *3*, Rosas; *4*, Sisimbria; *5*, Cumino; *6*, Lubestico; *7*, Feniculum; *8*, Costo; *9*, Lilium; *10*, Salvia; *11*, Ruta; *12*, Gladiola; *13*, Pulegium; *14*, Fenugraeca; *15*, Mentha; *16*, Rosmarino. The Cemetery contained apples, pears, peaches, mulberries, plums, laurels, figs, hazelnuts, service, chestnuts, medlars, quinces, almonds, and walnuts.

of industrious botanists and many of these works, though of little botanical value to-day, can be treasured by us as storehouses of artistic beauty.

With the real growth in the knowledge of plants and their uses there grew up also a mass of superstitious information,

partly founded on old tradition, increased with the importation of strange drugs,[1] and partly no doubt invented by the herbalists and drug-sellers to prevent any infringement of their monopoly in plants of real or supposed medicinal virtue, and to frighten the ignorant from attempting to collect the plants for themselves.

The faint resemblance of the mandrake root to the human form, for instance, probably suggested its use as a remedy for sterility; it is still sold to-day in Egypt as a charm. Its use may have led to the discovery of its anaesthetic qualities since it was used in ancient times for this purpose, and the legends which abounded as to the danger of death to those who gathered the root may have been circulated in order to try to prevent its use for criminal purposes.

It was largely owing to the need of protecting the doctor and apothecary against the drug-sellers that the growing of "simples" in recognized gardens had its origin. As the seats of the medical profession were established in the universities and monasteries, these institutions set apart definite enclosures for the cultivation of medicinal herbs, the "simplicia" or "simples" from which the "remedia composita" were prepared by the apothecaries.

Since the universities and monasteries were generally situated in towns, their physic gardens were usually small, and on the continent of Europe we still see these ancient gardens, which have been gradually transformed into the botanic gardens of the universities.

In connection with the growth of learning and increase of observation which is noticeable in the arts and sciences at this time of renaissance, it is strange that biology was still so largely under the thrall of superstition and curious invention. Reference to the early herbals, such as the 'Buch der Natur' (1475), the 'Herbal of Apuleius' (1484), and the 'Grant Herbier' (1526), shows both as regards text and illustration a persistent state of ignorance of facts, which could easily have been remedied by observation, and possibly does not represent

[1] Medicinal plants were imported from the Continent in a dry state, hence the English word "drug," which is part of the Anglo-Saxon verb "drigan," to dry.

the true state of the knowledge of the more competent medical botanists of the period. The herbal of Brunfels (1530), with its beautiful and accurate illustrations but indifferent text, and those of Bock, Fuchs, Cordus, and many others, may be taken as evidence of the rapid advance that was taking place in the knowledge of plants, though the fabulous and mythical still found adherents even amongst the most learned.

Private physic gardens, as distinct from the monastic herbaries, existed towards the end of the fifteenth century, and some of these developed into municipal gardens for the growing of "simples." The botanic garden at Padua, which appears to have been one of the earliest of these gardens, was founded in 1545 on the exact spot which it now occupies near the church of S. Antonio and S. Giustino. The garden owes its origin to the sound suggestion put forward at the end of the year 1542 by Francesco Bonafede, who in 1533 had founded the chair of "simples" (Lectura Simplicium)—the first in Europe—at the University of Padua.

This garden is of especial interest, as not only have we an excellent account of it written by de Visiani,[1] but also because it is preserved very largely in its original condition. The circular wall by which it is enclosed, though not the original one built in 1551, occupies the same site, and was rebuilt between 1700 and 1707; within the wall the garden is laid out in numerous little beds with stone edgings. The garden underwent many vicissitudes and fell into considerable decay, but in the year 1837 it was thoroughly restored, and the arrangement of the beds may well be a restoration of the original condition of the garden. In any case it affords an excellent example of the type of geometrical garden illustrated in horticultural books published at the end of the sixteenth and beginning of the seventeenth centuries,[2] which for so long a time dominated garden design on the Continent.

[1] de Visiani, R. Dell' origine ed anzianita dell' orto botanico di Padova. Padua, 1839. Saccardo, P. A. L'orto botanico di Padova nel 1895. *pl. 1–8. f. 1.* Padua, 1895.

[2] See illustrations of the gardens of De Vries, 1580–1583, reproduced by Sir F. Crisp in 'Illustrations of some mediaeval gardens,' 1914; and cf. Mariani, Florilegium renovatum et auctum. Frankfurt, 1641.

It is to be regretted that the principal features have been somewhat obscured by the growth of trees, but the ground plan fortunately remains unaltered. Pisa in 1544, Bologna in 1547, and others,[1] quickly followed the lead given by Padua. We are fortunate in possessing an elaborate plan of the Pisan garden published in Tilli's catalogue[2] of 1723 with a list of the plants cultivated in the various beds and enclosures, the latter being here reproduced.

EXPLICATIO
PROSPECTUS
HORTI PISANI

1. Topiarium magnum instar Tentorii, Cupressinis Arboribus flexilibus, & ferreis catenis circumdatum.
2. Umbraculum primum venustum, opere topiario, Citris Arboribus, ac Citroidibus poma suaveolentia ferentibus instructum, & fontibus ornatum.
3. Umbraculum alterum Citroidibus Florentinis repletum.
4. Vaporarium pro Plantis Americanis.
5. Vaporarium gestatorium.
6. Locus pro Plantis Aegyptiis aquam respuentibus.
7. Vaporarium cum laminis vitreis fixum ad semina vegetanda.
8. Paries per totam longitudinem Aurantiorum Olyssipponensium, aliarumque: Arborum poma sustinens.
9. Fenestrae Hypocausti.
10. Fenestrae Hybernaculi.
11. Platea cum variis Aloës Plantis.
12. Nemus exoticarum, & indigenarum Arborum.
13. Hydrophylacia, seu Castella.
14. Locus pro Plantis montanis, & Sylvestribus.
15. Laboratorii Chimici, in quo Anthlia Pneumatica reperitur, pars externa Hortum respiciens. Supra verò extat infundibulum ad pluviam recipiendam, de qua fusè D. G. Derham in suis transactionibus, ac etiam in Demonstr. cap. iii. pag. 23. mentionem facit; eadem pars externa variis fontibus, ac lapidibus figuratis est ornata; ibi scilicet reperiuntur Astroites, qui in Metallotheca Mercati pag. 235. & Corallites, Placentae, Lapis Lumbricatus cap. 55. quorum etiam aliqui sunt Lapides Cerebriformes, an huc allati sint ex Sicilia, vel Sardinia, aut ex Jamaica, ut Rayus Hist. Tom. iii. pag. 5. ex Sloanis verbis, adhuc nescimus.

[1] Botanic gardens were founded in Zurich, 1560; Bologna, 1568; Leyden, 1577; Leipzig, 1579; Montpellier, 1598; Paris, 1597, known as Jardin des Plantes after 1635; Heidelberg, before 1600; Giessen, 1605; Strasburg, 1620; Oxford, 1621; Jena, 1629; Upsala, 1657; Chelsea, 1673; Berlin, 1679; Edinburgh, 1680; Amsterdam, 1682. See also foot-note, p. 209.

[2] Tilli, M. A. Catalogus plantarum Horti Pisani. Florence, 1723.

16. Pergulae Laurorum.
17. Prunorum diversae Arbores murum tegentes.
18. Aurantiorum Arbores.

Divisiones Plantarum secundum earum propriam naturam, areolis contentarum.

19. Locus Herbis tantum Hortensibus repletus.
20. Locus Acanaceis Plantis.
21. Locus Plantis Umbelliferis.
22. Locus Plantis Palustribus.
23. Locus Plantis Venenatis.
24. Locus Plantis Odoratis.
25. Locus Plantis Bulbosis.
26. Florilegii locus.
27. Vaporarium fixum, ac fimo equino repletum, ubi Ananas, & similes Plantae exoticae aluntur.
28. Ostium primum.
29. Ostium Laboratorii Chimici, ubi Anthlia reperitur, aditum respiciens.[1]
30. Ostium alterum Horti publici: intus insignium Botanicorum Virorum effigies visuntur.
31. In Tecto Infundibulum pluviam recipiens.
32. Paries Aurantiis Hermaphroditis ornata.
33. Platea.
34. Ubi Muscae odoratae D. Chimentelli oriuntur.
35. Aditus qui ad ostium Viae publicae ducit: ibi Balenae, & Physeteris ossa suspensa, ut pagina 4. hujus Catalogi, ubi de Agarico agitur.
36. Fenestrae Domus Custodis.
37. Fenestrae Musei In earum medio Inscriptio haec legitur.

The beds at Pisa are arranged on the geometrical plan and the picture of the garden shows a perfect specimen of the typical formal garden of the end of the sixteenth century. The plants were grouped chiefly according to their properties and morphological characteristics: Thus one finds beds for poisonous plants, prickly plants, smelling plants, bulbs and marsh plants. "Aloes" (*Aloe, Gasteria,* etc.) were also grown and are figured in the catalogue and there was a "vaporarium pro plantis Americanis."

The lectures on "simples" delivered at the early Italian universities were not at first accompanied by demonstrations upon living specimens, but the growing of the plants in

[1] This and the remaining buildings, etc., are shown on a separate plan which is not reproduced here.

definite gardens led to the establishment of demonstrations upon living specimens of the medicinal plants, and at Padua sixteen years after the foundation of the garden, a separation was made of the "Lectura" from the "Ostensio simplicium," or demonstration of living plants.

Botany, however, in all these early universities to which gardens were attached was merely ancillary to medicine. At Montpellier, for instance, the same professor taught anatomy in winter and botany in summer, and as late as 1773 anatomy, surgery and botany formed the subjects for one and the same professor at Jena.

Very soon after the founding of the gardens at Padua and Pisa, plants other than those of strictly medicinal value were introduced into the physic gardens. This was due to the revival of interest in the plant world which took place about the middle of the sixteenth century and to the desire for travelling and interest in collecting which then sprang up. Conrad Gesner, writing in 1561 in the 'Horti Germaniae,'[1] mentions that in botanic gardens not only medicinal herbs were cultivated but also other plants, especially rare ones, for the purpose of observing and admiring nature:

> "Hortorum alii vulgares sunt, utilitatis tantum gratia confiti: in quibus olera, legumina, vites, fructus qui edendo sint, & gramen, usum homini aut pecori praebent. Alii medicinales, ut Medicorum & Pharmacopolarum: in quibus non hortenses tantum stirpes, sed etiam sylvestres omnis generis, & peregrinae quoque coluntur, propter remedia quae ex ipsis earúmve partibus homini fiunt. Alii similes istis, sed magis varii, in quibus non solium plantae remediis nobiles, sed aliae etiam quae uis rariores praesertim coluntur, propter admirationem & contemplationem naturae."

John Ray visited both Padua and Pisa early in 1664; referring to the garden at Padua, he says: "Here is a public Physick garden, well stored with simples but more noted for its prefects, men eminent for their skill in Botanics." The Pisan garden at this time would not appear to have been in a very flourishing condition since Ray merely remarks, "*The*

[1] Gesner, Conrad. Horti Germaniae p. 237 verso. Strasburg, 1561.

Physick Garden at our being there but meanly stored with simples.''[1]

In particular, Gesner[2] alludes to several gardens at Padua and mentions the one under the charge of Anguillara, which was no doubt the Botanic Garden, as having a fine collection of plants with representatives from Syria, Crete and other distant places. He refers in the first place to the Garden of Caspar à Gabrielis "vir inter nobiles Patavinos longe nobilissimus," and then to "Priulanus hortus magnificus," which was under Aloisius Anguillara (Romanus). Gesner's account is as follows:

> "Ibidem Priulanus hortus magnificus, plantis variis & raris e Syria etiam accersitis admirationi est. Omnes vero omnium, ni fallor, hortorum magnificentia simul, & stirpium in eo variarum omnis generis, e Creta etiam & aliunde peregrinarum, numero laudes facile vincit publicus ille Patavii in medicorum gratiam inclyti Senatus Veneti liberalitate institutus hortus, cui hoc tempore Aloisius Anguillara Romanus, vir in stirpium historia nostro seculo exercitatissimus atque peritissimus omnium, magna cum laude praeest."

According to Saccardo,[3] Luigi Squalermo (detto Anguillara) was the first prefect "dell 'orto padovano ed ostensori dei semplici" from 1546 to 1561.

From this time onwards, no doubt, the tendency was to grow as many plants as possible, and a healthy rivalry commenced between the various botanical establishments as to who could show the greatest number of different species in cultivation.

[1] Ray, J. Travels through the Low Countries 1: p. 182. 1738. [2nd ed.] Ray mentions the following eminent men at Padua: Aloysius Mundella, Aloysius Anguillara, Melchior Guilandinus, Jacobus Antonius Cortusus, Prosper Alpinus, Joannes Veslingius.

Saccardo, *loc. cit.* p. 7, gives the following list of Prefects of the Paduan Garden:

1546–1561	Luigi Squalermo (detto Anguillara).
1561–1589	Melchiore Guilandino.
1590–1603	Giacom' Antonio Cortuso.
1603–1616	Prospero Alpini (o Alpino).
1616–1631	Giovanni Prevozio (Prevot).
1631	Giovanni Rhodio, iosto rinunciatario.
1631–1637	Alpino Alpini.
1638–1649	Giovanni Veslingio.

[2] Gesner, C. De Hortis Italiae. *Loc. cit.* p. 239 verso.

[3] *Loc. cit.* p. 7.

In the botanic garden at Paris, for example, in the year 1636, there were about 1,800 species under cultivation and the number had risen in 1640 to 2,360, and in 1665 to as many as 4,000 species.

With the interest aroused in the collection and cultivation of plants came also the interest in their description and illustration, and many bulky and costly works were produced to illustrate the plants grown in botanic gardens.

In Great Britain the foundation of the botanic gardens at Oxford, Chelsea, and Edinburgh, was preceded by the establishment of several interesting private gardens devoted to the cultivation of medicinal herbs and plants of botanical interest, catalogues of which were published. The Rev. William Turner (1510–1568), who has been called the "Father of English Botany," had a garden somewhere at Kew and afterwards a renowned garden at Wells, when he was Dean of the Cathedral. Then there was the noted physic garden of John Gerard (1545–1612) in Holborn, at that time the most fashionable district in London, the catalogue of which—published in 1596—enumerates 1,030 plants and is of interest as being the first complete catalogue ever published of the contents of a single garden. His 'Herball,' published in 1597, was not his own work, but was simply a translation by a certain Dr. Priest of the 'Stirpium Historiae Pemptades' of Dodoens, which Gerard adopted and published as his own. On the title page of the edition of 1597, a garden is figured which has been generally considered to represent Gerard's own garden in Holborn, but as Sir Frank Crisp[1] points out, he obviously borrowed his illustration from an engraving by A. Collaert, representing a garden of A. D. 1590, in April, much in the same unscrupulous manner as he borrowed his text.

Among other early private physic gardens of interest in connection with the history of such institutions in England may be mentioned the garden of Thomas Johnson, M.D., the apothecary who had a garden on Snow Hill, in 1633—he it

[1] Guide for the use of visitors to Friar Park, Henley-on-Thames, Pt. II. Illustrations of some mediaeval gardens p. 87. 1914.

The illustration reproduced by Gerard is to be found on the title page of Tabernaemontanus, J. T. Kreuterbuch. [eds. of 1664 and 1687.]

was who brought out the improved and enlarged edition of Gerard's 'Herball' in 1638. The garden of John Parkinson (1567–1650), apothecary to James I, and King's Herbalist in Long Acre, and that of John Tradescant (died 1638) the elder, at Lambeth, are also worthy of particular mention.

John Tradescant, his father and his son were all of them botanists, collectors, and travellers. Tradescant the elder, who was gardener to various noblemen and also to Queen Elizabeth, was appointed Gardener to Charles I and founded a garden at Lambeth. This garden, after that of Gerard, was probably the most important early botanic or physic garden in England, and a catalogue of the plants therein was published in the 'Museum Tradescantianum' by his son in 1656. In addition to the garden, the Museum is worthy of notice in passing, since the curiosities it contained were bequeathed by the younger Tradescant to Mr. Ashmole, and formed the nucleus of the collection in the Ashmolean Museum at Oxford.[1]

Parkinson was created King's Herbarist, "Botanicus regius primarius," by Charles I. He was a horticulturist rather than a pure botanist, and his well-known book on garden plants, 'Paradisi in sole Paradisus Terrestris,' published in 1629, probably did much to stimulate interest in the cultivation of new and rare ornamental plants. Parkinson it was who had the boldness to depict the Garden of Eden on the title page of his 'Paradisus,' and includes among other remarkable products, the "Vegetable Lamb," a pineapple, and an opuntia, the two latter plants being, as far as we are aware, unknown in the Eastern Hemisphere before the discovery of America.

Reference need only be made in passing to garden illustrations from 1580 and onwards, and to such works as the 'Hortus Floridus' of Crispian de Passe, published in Holland in 1614, and to the numerous herbals that were being produced to show the great strides that had been made in horticulture and botany in Elizabethan and early Stuart times.

The establishment of a botanic garden in Oxford in the year 1621, the nineteenth year of the reign of James I, is an

[1] See Johnson, G. W. History of English gardening p. 98. London, 1829.

important landmark in the history of botanical progress in England and follows the lead already given by the founding of university botanic gardens on the Continent.

Like them, it was "primarily founded for a Nursery of Simples, and that a professor of Botanicey should read there and shew the use and virtue of them to his auditors."

The founding of the Oxford Garden[1] was due to the munificence of Henry, Lord Danvers, Earl of Danby, who acquired the lease of five acres of meadow land by the River Cherwell, near Magdalen College, and arranged that the University should lease the ground from the College, to whom it belonged. The land was considerably raised to prevent flooding, at great expense, and was surrounded by a wall which was completed about 1632.

Access to the Garden was by means of the Danby gateway, the foundation stone of which was laid with all fitting ceremony on St. James' Day, 1621, by the Vice-Chancellor of the University.[2] The following is taken from Vines and Druce:[3]

"*Botanic Lectures.*

"The next Lecture that must be mentioned is that of Botanicey: but before I speak anything of its institution and settlement, I think it convenient that somewhat should be said of the Physic Garden, because 'twas primarily founded for a Nursery of Simples, and that a Professor of Botanicey should read there, and shew the use and virtue of them to his Auditors.

"Henry Lord Danvers therefore, Baron of Dauntsey in the County of Wilts and Earl of Danby in Yorkshire, sometime a Gent. Com. of Christ Church, being minded to become a Benefactor to the University, thought that his money could not be better laid out than to begin and finish a place whereby learning, especially the Faculty of Medicine, might be improved. At length selecting a place without the East Gate of Oxford, near the river Cherwell, which was then meadow ground, and

[1] Daubeny, C. The Oxford Botanic Garden, popular guide. Oxford, 1850; Günther, R. T. Oxford Gardens. Oxford, 1912; Vines, S. H., and Druce, G. C. An account of the Morisonian Herbarium, etc. [Introduction.] Oxford, 1914.

[2] The date of the founding of the Garden has usually been incorrectly given as 1632, the year of the completion of the gateway, and in the account given by Wood of the foundation of the Garden there is a mistake of 1622 for 1621, but in their interesting epitome of the history of the garden, Vines and Druce show clearly that 1621 is the correct date when the ground was handed over and delegates were appointed.

[3] *Loc. cit.* pp. IX–X.

had in ancient times been a Cemitery for the Jews of Oxon, gave to the University £250 to make a purchase of it. Upon the receipt of it they bought out the present possessor thereof, Mar. 27, 19 Jac. Dom. 1622; and not long after the University took a lease of the said ground from Magdalen College (for to them it did belong) in their own name July 28 following, by paying yearly for it 40*s*. Afterward much soil being conveyed thither for the raising of the ground to prevent the overflowing of the waters, the first stone of the fabric was laid on the day of St. James the Apostle (July 25) an. 1622, after this manner: About two of the clock in the afternoon, the Vicechancellor with certain Heads, Doctors, and both the Proctors, went solemnly from St. Mary's Church to that place; where being settled, Mr. Edward Dawson, a Physician of Broadgates, spoke an elegant Oration; which being done, Dr. Clayton, the King's Professor of Medicine, spake another. Afterward the Vicechancellor laid the first stone with the offering of money thereon, according to the ancient custom; then several Doctors and both the Proctors; which being done, the Vicechancellor concluded with a brief Oration.

"Afterward the said Earl proceeding in building and encompassing it with a stately free-stone wall; which being almost finished, set up in front thereof, next to the East Bridge, a comely Gatehouse of polisht stone; on which for the perpetuation of his name, he caused this Inscription to be engraven on the out and inside thereof:

GLORIAE DEI OPT. MAX.
HONORI CAROLI REGIS
IN USUM ACAD. et REIPUB.
HENRICUS COMES DANBY D. D. MDCXXXII.

In the year 1633 all the wall being finisht, and soon after the floor raised, which cost the Earl £5,000 and more, he caused to be planted therein divers simples for the advancement of the Faculty of Medicine. All which and several hundred more may now compare with any in the kingdom or elsewhere."

An interesting plan of the Garden by Loggan, made in 1675, shows four main enclosures within the boundary wall, each containing four series of geometrically arranged beds according to the formal arrangements then in vogue.

Thomas Baskerville[1] gives the following description of the early condition of the Garden (about 1670–1700):

"Amongst ye severall famous structures & curiosities wherewith ye flourishing University of Oxford is enriched, that of ye Publick Physick Garden deserves not ye last place, being a

[1] Account of Oxford Collectanea (c. 1670–1700).

> matter of great use & ornament, prouving serviceable not only to all Physitians, Apothecaryes, and those who are more immediately concerned in the practice of Physick, but to persons of all qualities seruing to help ye diseased and for ye delight & pleasure of those of perfect health, containing therein 3,000 seuerall sorts of plants for ye honor of our nation and Universitie and service of ye Commonwealth."

A further interesting piece of information given by Baskerville is as follows:

> "Anno 1670. Here was built by the Income of the money given by the ffounder a fair greenhouse or Conservatory to preserve tender plants and trees from the Injury of hard winter."

This conservatory covered with a roof of stone slates is shown in Loggan's plan and was of sufficient solidity to be transformed early in the eighteenth century into the herbarium, library, and professorial residence, but it was subsequently demolished.

The conservatory was heated in severe weather by means of a four-wheeled fire-basket, or wagon filled with burning charcoal, which was drawn backwards and forwards along the path by a gardener.[1]

Similar conservatories, or orangeries, were common in English gardens, and the building now used as a Museum (No. III) at Kew, was erected as an orangery in 1760.

The first wooden greenhouses ever made were those erected at Oxford, in 1734, on either side of the Danby Gate.[2]

Although the Garden was founded in 1621, it appears that some twenty years elapsed before Jacob Bobart was appointed the first gardener, owing probably to delays caused in preparing the site. Under his supervision the Garden attained a considerable reputation and was visited by many distinguished people, including Evelyn and Pepys. Bobart's catalogue of the plants cultivated, published in 1648, enumerates 1,600 plants, 600 of which were British, and many Canadian; it may be taken as evidence of his successful management of the Garden.

[1] See Gardeners' Chronicle N. S. **23**: 732. *f. 163.* 1885. The figure is reproduced in Günther, R. T. Oxford Gardens p. 92. Oxford and London, 1912.

[2] See engraving in Oxford Almanac, 1766; reproduced in Günther, *loc. cit.*, plate facing p. 153.

Owing to the outbreak of the Civil Wars and the death of the Earl of Danby, in 1644, his intention to provide the University with a Professor of Botany as well as with a physic garden and a gardener, was long delayed, and the first professor, in the person of Dr. Robert Morison, was not elected to fill the office until December 16, 1669. Morison's first lecture was given in the Medicine School on September 2, 1670, and on September 5, he "translated himself to the Physic Garden where he read in the middle of it (with a Table before him) on herbs and plants for five weeks space, not without a considerable Auditory."[1]

Space does not permit us to follow the fortunes of the Oxford Garden or to make mention of the many distinguished professors associated with it since its foundation, but it is of interest to remember that Sir Joseph Banks was a student at Christchurch, from 1760 to 1763, in the days of Sibthorp's professorship, a time when no lectures on botany were given and the subject was much neglected in the University.

Banks was so keenly interested in botany that he applied to Sibthorp for permission to procure a qualified lecturer to be paid entirely by the students. This request being acceded to and a sufficient number of students having been obtained, Banks went to Cambridge and secured the services of a Mr. Lyons, a botanist and astronomer, for the purpose.[2] The assistance rendered by the sister university in the botanical education of one who was to achieve such great things for the science and to have so large a share in directing the fortunes of the Royal Gardens at Kew, is worthy of more particular notice since botany was not officially recognized in Cambridge until 1724, when a professor was appointed, and there was no botanic garden there until the year 1762.

The Botanic Garden at Edinburgh, which now claims attention, has had a somewhat involved history, as the present Royal Botanic Garden is the sixth and only remaining botanic garden in the Scottish capital, though in the early years of

[1] Vines, S. H., and Druce, G. C. *loc. cit.*, p. XXIV.

[2] Anonymous, Sir Joseph Banks and the Royal Society p. 62. London, 1844.

the eighteenth century there were three distinct gardens in Edinburgh.

The original Edinburgh Garden was founded by Sir Robert Sibbald and Sir Andrew Balfour, physicians, for the cultivation of medicinal plants in order "to safeguard the Practitioner against the Herbalist and to enable him to have a correct knowledge of the plants which were the source of the drugs he himself would have to compound."[1]

For this purpose they acquired the lease of a small area of ground near Holyrood, and James Sutherland was secured to look after it and instruct the apprentices and lieges in botany. Such success attended the venture that a piece of the Royal Flower Garden at Holyrood was assigned to the cultivation of medicinal plants and this with the title of Physic Garden became the Royal Botanic Garden in Scotland.

In 1767 the same physicians acquired from the Town Council of Edinburgh a lease of the Garden of Trinity Hospital and adjacent ground—a site now partly occupied by the Waverley Station—and Sutherland was appointed to lecture on botany as Professor in the Town's College, now the University, and to be in charge of this new Physic or Town's Botanic Garden. Then in 1702 another botanic garden was established by the University—the College Garden—of which Sutherland was also placed in charge. The distance of the two existing gardens being too great from the University, Sutherland resigned the care of the Town's Garden and College Garden in 1706, but remained King's Botanist, retaining the Keepership of the Royal Botanic Garden, and the Town Council appointed a professor to take charge of the Town and College Gardens. There were thus two rival botanical schools with their gardens in Edinburgh, and it was not until the year 1739 that the rivalry was terminated by the appointment of Dr. Charles Alston, the then Keeper of the Royal Botanic Garden, to the University Chair—a combination which holds to the present day by consent of the Crown and the University.

[1] Balfour, I. Bailey, History of the Royal Botanic Garden, Edinburgh. Notes of the Roy. Bot. Gard., Edinburgh 4: 1904. Historic Notice. pp. v-viii.

Between the years 1760 and 1786 a new site was found for a botanic garden and the other gardens were abandoned. This new garden, formed during John Hope's keepership, eventually became unsuitable owing to the growth of the town, and the present site (twenty-seven acres) was selected about 1820, during the keepership of Professor Graham.

The Edinburgh Garden, through the University, still retains its connection with the Medical School, and the instruction of the medical student is one of the functions of the Professor and his staff. With its fine collections of living plants, its herbarium, library, laboratories, and remarkable series of specimens in the museums, the Edinburgh institution may well serve as an example of the ideal botanic garden.

The Chelsea Physic Garden,[1] which next claims attention, was founded as the Garden of the Society of Apothecaries[2] in London in the year 1673. The earlier garden of the Society had been at Westminster, but this had no river frontage, and the ground at Chelsea was leased from Charles Cheyne, in 1673, as a convenient spot for building a barge house for their processional barge in which they attended city functions, as was customary for city companies.

In 1676 the plants at Westminster were moved to the Chelsea Garden, which had already been suitably enclosed with a wall. The freehold of the Manor of Chelsea, including the Physic Garden, was purchased in 1712 by Dr. (afterwards Sir Hans) Sloane, who in the year 1722 conveyed the Garden by deed to the Society of Apothecaries. The conveyance was made "to the end that the said garden might at all times thereafter be continued as a Physick Garden, and

[1] Field, H., and Semple, R. H. Memoirs of the Botanic Garden at Chelsea. London, 1878.

[2] The Society of Apothecaries itself was formed in 1617 "that the ignorance and rashness of presumptuous Empirics and unexpert men might be restrained, whereby many discommodities, inconveniences and perils do daily arise to rude and incredulous people." See Blunt, R. Cheyne Walk and thereabout p. 99. London, 1914.

Certain continental botanic gardens, such as the ancient garden at Salzburg were founded in connection with local pharmaceutical schools and have had no connection with any university.

for the better encouraging and enabling the said Society to support the charge thereof, for the manifestation of the power, wisdom, and glory of God in the works of the creation, and that their Apprentices and others might better distinguish good and useful plants from those that bore resemblance to them, and yet were hurtful and other the like good purposes.''[1]

The utilization of the Garden for the sole purpose of growing medicinal plants to be converted into drugs for the Society's use was prohibited by Sir Hans Sloane's deed of gift, and he definitely encouraged the science of botany by making it a condition that fifty specimens of distinct plants, well dried and preserved, which grew in their garden that same year, with their names and reputed names, were to be delivered yearly to the President and Fellows of the Royal Society of London, ''until the number of two thousand had been attained.'' He also enjoined that the plants so presented in each year were to be specifically different from those presented in every former year; and this injunction was more than faithfully carried out by the Society.[2]

The Garden achieved some notoriety in having been the first garden in England where the Cedar of Lebanon was planted; the final survivor of the four placed there in 1683 was only removed in the year 1904.

John Evelyn, who visited the Garden in 1685, was impressed by the heating arrangement of the greenhouses, then quite an innovation. ''What was very ingenious,'' he remarks in his diary, ''was the subterranean heate conveyed by a stove under the conservatory, which was all vaulted with bricks, so as he[3] has the doores and windows open in the hardest frosts, secluding only the snow.'' An arrangement far more efficient and useful than the remarkable open fire-baskets formerly in use at Oxford.

[1] Perrédès, P. É. F. London Botanic Gardens. Wellcome Chemical Research Laboratories, London, Publ. 62: p. 57. London, 1906 (transferred from the present to the past tense).

[2] Johnson, G. W. History of English gardening p. 150. London, 1829.

[3] John Watts, appointed gardener in 1680.

The appointment of Philip Miller,[1] in 1723, as Head Gardener, is an important event in the history of the Garden, both for the value of his services to the Garden itself and for his widespread influence on botany and horticulture.

At the time of Miller's appointment, exotic plants were pouring in from every clime under the patronage of a general taste for their acquisition. Hothouses were multiplying and their inhabitants accumulating to a hitherto unheard-of extent, and a man of Miller's practical skill and botanical knowledge was needed not only to demonstrate his skill, but also to impart his knowledge for the use of others. From his 'Dictionary' it can be seen that many plants were grown and flowered at Chelsea for the first time under cultivation.

William Aiton (1731–1793), the first Curator of the Royal Gardens at Kew, was a pupil under Miller at Chelsea, nor must Nathaniel Bagshaw Ward, Examiner to the Society of Apothecaries from 1836 to 1854, the inventor of Wardian cases, be forgotten. His invention made possible the introduction of the tea plant to India by Robert Fortune (Curator of the Chelsea Garden, 1846–1848), of *Cinchona* from South America to Kew by Markham, and thence to India, and of many other valuable products to botanic gardens which have subsequently been disseminated for the use of mankind. Not the least useful of the activities of the Chelsea Physic Garden were the herborizing excursions around London, under the charge of the Demonstrator of Plants, which were maintained for some two hundred years. The Physic Garden has suffered many vicissitudes in the course of its existence, and towards the end of the last century almost ceased to exist, but fortunately a new arrangement for its maintenance was made in 1899.[2] Reorganized under the new scheme and with its modern greenhouses and laboratory, the Chelsea Garden has entered on a sphere of usefulness in connection with the teaching of botany and the provision of material and opportunity

[1] Charles Miller, son of Philip (who had aided in the selection of the site), was made first Curator of the original Cambridge University Botanical Garden founded in 1762.

[2] The Chelsea Physic Garden. First Report of Committee of Management, 1905, with plan of the Garden in 1753.

for botanical investigation as great if not greater than at any time in the past.

The origin of the Royal Botanic Gardens, Kew, was due to the interest in botany displayed by Princess Augusta, Princess Dowager of Wales, under the guidance of Lord Bute, an enthusiastic botanist; and a piece of the Royal Garden attached to Kew House was set apart in 1760 for the purpose of forming a physic garden.

> "The space allotted consisted originally of nine acres, enclosed by walls (the ornamental building now standing, called the Temple of the Sun, being then nearly the centre of the Garden), which was laid out and scientifically planted in two divisions, one containing a collection of herbaceous plants, arranged according to the Linnean system, then in its infancy, but with which Aiton had become well acquainted while serving under Miller. This division was called the Physic Garden.
>
> "The second division was called the Arboretum, containing all the then known introduced hardy trees and shrubs scientifically arranged. Within the area were several Glass houses, and in 1761 a large hothouse, 110 feet long, was erected by Sir Wm. Chambers . . in after years known as the Great Stove. In the same year an Orangery, 130 feet long, was also erected."[1]

No doubt several of the old and interesting trees now standing near the Temple of the Sun were planted in Princess Augusta's arboretum soon after the foundation of the Garden.

William Aiton was placed in charge of the Garden under the direction of Lord Bute, and was Chief Gardener from 1759 to 1793. Sir W. Chambers, the designer of the Pagoda and most of the Temples still to be seen in Kew, gives the following account of Princess Augusta's Physic Garden:

> "The Physic or exotic garden was not begun before the year 1760; so that it cannot possibly be yet in perfection; but from the great botanical learning of him who is the principal man-

[1] Smith, John. Records of the Royal Botanic Gardens, Kew. p. V. 1880. See also Kew Bull. Misc. Inf. **1891**: 289–294. 1891.

The Great Stove stood near the Temple of the Sun and was removed in 1861. Its site is marked by an old wistaria, trained on an iron cage which grew upon its walls. The method of ventilating the house was designed by William Hales, the physiologist, who described his method in a letter to Linnaeus written in 1758. The method is in use at Kew to-day and was devised independently by Sir W. T. Thiselton-Dyer.

The Orangery is now Museum No. III.

> ager and the assiduity with which all curious productions are collected from every part of the globe without any regard to expense, it may be concluded that in a few years this will be the amplest and best collection of curious plants in Europe."[1]

With the death of Princess Augusta in 1772, George III inherited the Kew property and united the gardens of Kew House with those lying contiguously, which formed the gardens of the Palace of Richmond, and so produced the extensive domain now occupied by the Royal Botanic Gardens. To the great benefit of Kew, George III chose Sir Joseph Banks as his botanical adviser, and for forty-eight years Sir Joseph directed the affairs of the Gardens. During his term of office the practice of sending out collectors was established, a practice fraught with discoveries of wide-spread interest and value for horticulture and botany. Of the many Kew collectors[2] it is well to mention in particular the following: Francis Masson, the famous collector of Cape plants; David Nelson, assistant botanist on Cook's third voyage, who subsequently died from exposure after the mutiny of the Bounty; Archibald Menzies, who travelled in Australia and Chili and introduced *Araucaria imbricata;* William Ker, the collector in China, who in 1812 became Superintendent of the Royal Botanic Garden, Ceylon; and Allan Cunningham, whose travels took him to Brazil, the Cape, Australia, Tasmania, New Zealand and Norfolk Island. Cunningham returned to Australia, in 1836, to fill the post of Superintendent of the Botanic Garden at Sydney.

The days of Sir Joseph Banks were indeed the Golden Age of Kew, and under his direction the Royal Gardens became a center of botanical exploration and horticultural experiment unparalleled before or since. The well-known lines of Erasmus Darwin[3] refer to the Kew of Sir Joseph Banks' day, enriched by the labors of her collectors:

[1] Chambers, Sir W. Plans, elevations, sections and perspective views of the gardens and buildings at Kew in Surrey, the seat of Her Royal Highness, the Princess Dowager of Wales p. 3. Brentford, 1765?

[2] For the complete list of Kew collectors, see Kew Bull. Misc. Inf. 1891: 295–311. 1891.

[3] The Botanic Garden. 1791.

"So sits enthroned, in vegetable pride,
Imperial Kew by Thames' glittering side;
Obedient sails from realms unfurrow'd bring
For her the unnam'd progeny of Spring;
Attendant Nymphs her dulcet mandates hear,
And nurse in fostering arms the tender year;
Plant the young bulb, inhume the living seed,
Prop the weak stem, the erring tendril lead;
Or fan in glass-built fanes the stranger flowers,
With milder gales, and steep with warmer showers.
Delighted Thames through tropic umbrage glides,
And flowers antarctic, bending o'er his tides;
Drinks the new tints, the sweets unknown inhales,
And calls the sons of Science to his vales."

George III and Sir Joseph Banks both died in 1820, and for some twenty years the Royal Gardens gradually fell into a condition of sad neglect. In the early years of the reign of Queen Victoria, however, the Royal Gardens were restored to their proper position as the National Botanical Garden, thanks to the devoted labors of the committee of which John Lindley and Sir Joseph Paxton were the distinguished members, and Sir William Hooker was appointed Director of the Royal Botanic Gardens in 1841. Thence onwards, under Sir Joseph Hooker, and Sir William Thiselton-Dyer, the history of Kew has been one of steady progress and usefulness and the Royal Botanic Gardens have played a prominent part in connection with all matters of botanical enterprise in the British Colonies.[1]

[1] The establishment at Kew comprises: I. The Botanic Gardens and Arboretum (288 acres); II. The Herbarium and Library; III. The Museums devoted to (i and ii) dicotyledons and monocotyledons and their economic products, (iii) exotic timbers and conifers, (iv) British forestry, and (v) The North Gallery of paintings by Miss Marianne North; IV. The Jodrell Laboratory for scientific research; V. The Pathological Laboratory; VI. Director's Office.

The more important books dealing with the history of Kew and its collections are:

1. Aiton, W. Hortus Kewensis, 3 vols. London, 1789.
2. Aiton, W. T. Hortus Kewensis, 5 vols. London, 1810–13. [2nd ed.]
3. Scheer, F. Kew and its Gardens. Richmond, 1840.
4. Historical account of Kew to 1841. Kew Bull. Misc. Inf. **1891**: 279–327. 1891.
5. Royal Botanic Gardens, Kew, Reports on progress and condition. 1855–1882.
6. Perrédès, P. É. F. London Botanic Gardens. Wellcome Research Laboratories, London, Publ. 62: 17–40. 1906.
7. Bean, W. J. The Royal Botanic Gardens, Kew. London, 1908.
8. Popular Official Guide to the Royal Botanic Gardens. Kew, 1912.
9. Kew Bull. Misc. Inf. **1887**.
10. Kew Plant Lists and Museum Guides.
11. Smith, J. Records of the Royal Botanic Gardens, Kew. London, 1880.

Kew, having no connection with any university or educational establishment,[1] differs markedly in this respect from the botanic gardens to which allusion has been made. Her sphere of usefulness is largely concerned with the economic aspect of botany, and it is her aim and object to encourage and assist, as far as possible, scientific botanists, travellers, merchants and manufacturers, in their varied botanical investigations.

Space does not permit of more than a brief mention being made of the new Berlin Garden at Dahlem and of many other important gardens on the Continent and in Great Britain and Ireland. The Berlin Botanic Garden[2] was founded in 1679 in the heart of the city, and in 1801 it was reorganized and improved. The removal of the Garden to its present site at Dahlem was completed in 1909. The new Garden with its geographical and ecological arrangements of the plants and the splendid Botanical Institute and Museums, now forms one of the finest schools of botany in the world. In her aims and objects she compares more closely to Kew than to any other botanic garden.

The following notes refer to other important gardens not specifically mentioned in the text:

The Upsala Garden (founded 1655-57) was injured by the great fire in 1702, and remained neglected until 1741. The restoration was begun by Rosen and energetically taken up by Linné. (See Swerderus, M.B. Botaniska Tragarden, Upsala, 1655–1807. Falun, 1877.) The Imperial Botanic Garden of Peter the Great, Petrograd (St. Petersburg), was founded in 1713 (see Kew Bull. Misc. Inf. 1913: 243–252. 1913), and that of Vienna in 1754.

The Cambridge Botanic Garden was founded in 1762 by Richard Walker, D.D., formerly Vice-Master of Trinity College. The Garden was transferred to its present site in 1846 and occupies about twenty acres. It is in close connection with the Botany School at Cambridge and provides abundance of material for research work and for the teaching purposes of the Botany School. The Garden is also fitted with a small laboratory. Some eighteen acres are available for extension.

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[1] Lectures and demonstrations in chemistry and physics, general botany, systematic and geographical botany, economic botany, plant pathology and on soils and manures are given in the Gardens to the young gardeners at Kew.

[2] See Urban, I. Geschichte des Königl. botanischen Gartens und des Königl. Herbariums zu Berlin, nebst einer Darstellung des augenblicklichen Zustandes dieser Institute. Festschr. naturwiss. u. med. Staatsanst. Berlin, 1881.

Engler, A., and others. Der Kgl. bot. Garten und das Kgl. bot. Museum zu Dahlem. Berlin, 1909.

The Royal Botanic Gardens, Glasnevin, Dublin, were founded in 1790, through the influence of Dr. Walter Wade and the Hon. Dublin Society, and in 1877 were transferred to the Science and Art Department. The Botanic Garden of Trinity College, Dublin, was established in 1806–08. (See Notes from the Botanical School of Trin. Coll., Dublin 1: p. 3. 1896.)

The garden at Breslau was founded in 1811. The Geneva Garden, founded in 1817, has recently been transferred to a new site. The Munich Garden was founded in 1822 (see Martius, Hort. Bot. R. Acad. Monacensis p. 5. 1825.) It is now one of the most interesting gardens on the Continent and forms an integral part of the new and magnificently equipped Botanical Institute.

The Glasgow Botanic Garden was established in 1817, having been preceded by an earlier Physic Garden; in 1841 the garden was moved to its present site and now occupies about forty acres (see Sherry, C. The Glasgow Botanic Gardens. Glasgow, 1901).

The botanic gardens whose history has been sketched in the preceding pages can all trace back their origin to the herb gardens of mediaeval times and the physic gardens of the early universities. Their *raison d'être,* the growing of simples for the medical profession, has resulted in the exploration of the globe for the useful, the beautiful, and the curious in the vegetable kingdom. A few other botanic gardens, however, remain to be considered, whose origin must be traced to a different motive. These gardens lie within the tropics, and the desire to participate in the valuable trade in spices, then a monopoly of the Dutch, led to the establishment of gardens for the cultivation of various spices and other important economic plants during the latter part of the eighteenth century.

The credit of establishing economic gardens in the tropics belongs to Great Britain, and the experiment, started with the founding of the botanic garden in the Island of St. Vincent, in 1764, has been continued, at times somewhat intermittently, until at the present day a botanic garden or station is to be found in almost every British dependency and possession.

The lead given by Great Britain has been followed by other nations and several notable achievements have resulted. Foremost among these must be mentioned the Botanic Gardens at Buitenzorg, Java,[1] probably the most complete and exten-

[1] The complete institution at Buitenzorg, known as "Lands Plantentium," is divided into nine Departments: I. Herbarium and Museum; II. Botanical

sive botanical establishment in the world. The garden was founded in 1817 at the suggestion of Reinwardt,[1] and Dr. C. L. Blume was appointed the first Director when Reinwardt left Java to become Professor at Leiden. The first Curator, James Hooper, had been trained at the Royal Gardens, Kew. The valuable scientific researches in pure and applied botany carried out at Buitenzorg are too well known to require detailed description, and allusion need only be made to the important encouragement given to the cultivation of *Cinchona*, rubber, coffee, and other economic products in Java, through the medium of the Botanic Gardens.

The earliest tropical botanic garden appears to have been that founded in the West Indies at St. Vincent, in 1764.[2] A garden of about forty acres was established with Government House in the center, as a place where plants "useful in medicine and profitable as articles of commerce might be propagated and where nurseries of the valuable productions of Asia and other distant parts might be formed for the benefit of His Majesty's Colonies." Plants intended for the West Indies were lost owing to the mutiny of the Bounty in 1790, but three years later Captain Bligh succeeded in landing a valuable consignment of plants from the Pacific, including the bread fruit, and a few years after, nutmegs, cloves, and other spice plants were introduced.

Until 1815 the Garden flourished, when interest was shifted to Trinidad, where a garden was formed in 1817, and many

Laboratories; III. Agricultural and Experimental Garden (151 acres) with laboratory for agricultural chemistry; IV. Pharmacological Laboratory; V. Botanic Garden (145 acres), Mountain Garden (77 acres and 700 acres virgin forest), and Laboratory; VI. Office, Library, and Photographic Laboratory; VII. Forest Flora collections; VIII. Laboratory for the study of Deli tobacco; IX. Coffee Experiment Station (the two last are partly private institutions).

[1] It is possible that the original idea of founding a botanic garden at Buitenzorg was made by Sir Stamford Raffles, when Governor of Java, during the few years (1811–17) that Java was a British possession. Near the entrance there is a small monument to the memory of Lady Raffles, who died in Java during the British occupation of the island.

[2] Guilding, Rev. Lansdown. An account of the botanical garden in the island of St. Vincent. Glasgow, 1825. See also Kew Bull. Misc. Inf. **1892**: 92–104. 1892.

of the plants were removed thence from St. Vincent. The St. Vincent Garden was restored in 1890 and now, fortunately, there is a botanic garden or station in every West Indian island of importance. These serve as centers for the distribution of economic plants and of scientific information, and have also become gardens of peculiar charm for the refreshment and recreation of the inhabitants.

The gardens of the East, however, are preëminent among tropical botanic gardens owing to the vastness of the territory over which they exercise their influence. Foremost among these, after Buitenzorg, is the Calcutta Botanic Garden, founded in 1786 on the suggestion of Lieut. Col. Robert Kyd.

This garden was intended to be the source of botanical information for the possessions of the East India Company, and also the center to which exotic plants of economic interest could be imported for experimental cultivation and thence distributed.[1]

It was hoped at first that the spices which rendered the trade of the East India Company with the Moluccas, etc., so lucrative, might be cultivated in Bengal, and Kyd's earliest efforts were directed to the introduction of cloves, nutmegs, cinnamon, and pepper vines, but the climate of northern India proved unsuitable. Much was attempted and, despite numerous failures, much accomplished in the way of new introductions in the early days, the failures possibly being as important as successes since it was soon evident what could or could not be grown in Bengal. The Calcutta Gardens, however, despite the failure in their original intention, have under their distinguished superintendents achieved notable results. The introduction of tea to India—one of Kyd's original ideas—was mainly carried out through the instrumentality of the Gardens, and potato growing, the introduction of mahogany, jute, sugar-cane, and the improvement of Indian cotton cultivation, may be counted among its many benefits to the people of India.

[1] King, George. Guide to the Royal Botanic Garden, Calcutta. 1895.

But most important of all was the part played by the Garden in the introduction of *Cinchona*[1] from South America to India with the coöperation of Kew, and the subsequent cultivation of Peruvian bark in the Sikkim Himalaya. The Calcutta Garden in this particular has retained the ancient connection of botanic gardens with medicine perhaps more than any other similar institution. The cultivation of the quinine-yielding cinchonas has been carried to such a successful issue in the plantation and factory at Sikkim under the superintendents of the Garden, notably Sir George King, that government hospitals and dispensaries have for years been supplied from this source with all the quinine required for them; while 5-grain doses of the same drug can be purchased for a pice each (equal to about ¼d. English) at every post-office in the Province.[2]

Associated with the Garden are the valuable herbarium and the economic museums, the whole forming an institution capable of responding fully to the botanical requirements of the Indian Empire.

The history of botanic gardens would be incomplete without reference being made to the foundation of such institutions in Malaya and Ceylon. At Penang[3] the Hon. East India Company decided to start spice gardens with a view of breaking down the Dutch monopoly. Living plants of nutmegs and cloves were collected in the Moluccas in 1796, and the first nutmegs were produced in Penang in 1801.

The Gardens, however, were destroyed[4] in 1805, and refounded in 1822 at the instance of Sir Stamford Raffles. He it was who founded the Singapore Gardens in 1823, and intro-

[1] See Markham, Sir C. R. Peruvian Bark. London, 1880.

[2] Guide to Royal Botanic Garden, Calcutta p. 6. 1902. [Revised ed.]

[3] Ridley, H. N. The abolition of the Botanic Gardens of Penang. Agr. Bull. Straits and Fed. Malay States 9: p. 97. 1910.

[4] *Ibid.* p. 104.

	founded	abolished
First Penang garden	1800	1805
Second Penang garden	1822	1826
Third Penang garden	1884	1910
First Singapore garden	1823	1829
Second Singapore garden	1878 and still existing.	

duced nutmegs, cloves, and cacao, but the Garden was unfortunately abolished in 1829.

The botanical enterprise of this remarkable man in Java, Malaya, and Sumatra, deserves an honorable place in our botanical history, and no more fitting memorial of his genius could be found than the present beautiful garden at Singapore, founded in 1878, which has so ably upheld the best traditions of the founder of the original garden.

The first botanic garden established in Ceylon[1] was created by the Dutch on Slave Island, near Colombo, but this was neglected when the island passed into the possession of Britain, and it was not until 1810, when Sir Joseph Banks suggested a site, that a new garden was established, also on Slave Island at a place still known as Kew. William Ker was transferred from Canton, in 1812, and appointed superintendent. The Garden was not a success, owing to its situation, and in 1821, during the superintendence of Alexander Moon—who had been sent out by Banks—the Garden was transferred to Peradeniya. In its new site its history has been a record of prosperity, and its usefulness has been considerably increased by the formation of additional gardens in different parts of the island suitable to the varied climatic conditions of the country.

The scientific researches in pure and applied botany, in tropical mycology and chemistry, and the cultural experiments which have been carried out in the Gardens and laboratory in Ceylon have thoroughly justified the existence of the institution at Peradeniya, and prove, if proof were needed, the inestimable value of scientific botanical establishments in the tropics.

The colonizing of Australia soon led to the foundation of botanic gardens, and those at Sydney[2] have the honor of being the first to be founded in the Australian Continent.

[1] Trimen, Henry. Hand guide to the Royal Botanic Gardens, Peradeniya. Colombo, 1885.

[2] Sydney Botanic Gardens. Kew Bull. Misc. Inf. 1906: 205–218. 1906.
Maiden, J. H. Presidential address to the Royal Society of New South Wales, 1912. Roy. Soc. N. S. Wales, Jour. and Proc. 46: 1–73. 1912. [See p. 49.]

These Gardens occupy the site of the Government Garden established in 1788, and here the first exotic plants were installed in the same year. Owing to the great demand for New Holland plants, due largely to the interest taken in them by Sir Joseph Banks, a vigorous exchange in plants soon grew up between the Sydney Gardens and the outside world, to the great profit of the institution, which appears to have been definitely founded as a botanic garden in the year 1816.

Sydney is now fully equipped for botanical work with its renowned Botanic Gardens, its university department of botany, and museum.

Other well-furnished botanic gardens are to be found at Brisbane, Melbourne, Adelaide, Hobart, and Tasmania; at Melbourne and Adelaide their value is enhanced by association with the botanical departments of the universities.

Flourishing botanic gardens are also established in New Zealand, at Wellington, Dunedin, Napier and Christchurch.[1]

Before leaving the subject of botanic gardens in British Dominions, mention must be made of the foundation only last year (1913) of the National Botanic Garden of South Africa, at Kirstenbosch,[2] which, though the most recent of such gardens, bids fair to take a place in the front rank of the botanic gardens of the world, both on account of the admirable nature of the site and the remarkable character of the South African flora. The predecessor of this garden was the Cape Town Botanic Garden, founded in 1848, which became the Municipal Garden of Cape Town in 1892, after a somewhat chequered career.[3]

The Municipal Gardens at Durban, Natal, established in 1853 as the Natal Botanic Garden, have played an important part in botanical enterprise in South Africa and at no time more than under the directorship of Dr. J. Medley Wood. It

[1] The Botanic Gardens at Hong Kong with their herbarium form a valuable center for Asiatic botany, nor must the Gardens at Tokyo and other important Japanese centers of botanical activity be omitted. Botanic gardens have been established also in Fiji, Seychelles, Mauritius, etc.

[2] Kew Bull. Misc. Inf. **1913**: pp. 309–314, and p. 373. 1913; Nature **93**: 190–191. 1914.

[3] Kew Bull. Misc. Inf. **1892**: 10–14. 1892.

would be a most unfortunate occurrence should the activities of this important garden, small though it is, be in any way curtailed or its functions abrogated by the change in its administration or owing to the establishment of the new National Garden.[1]

In America,[2] botanic gardens have been in existence since the year 1728, when John Bartram founded a botanical garden in Philadelphia. Though no longer a botanic garden, the plot of ground still remains and serves as an interesting landmark in the history of North American botany.[3] The foundation of the Elgin Botanic Garden by Dr. David Hosack, in 1801, was an important advance and the Garden of some twenty acres was gradually stocked with a large and valuable collection of plants.[4] In 1810 it became the Botanic Garden of the State of New York and was subsequently granted to Columbia College. It has ceased to exist as a garden, but it will be always held in remembrance from its association with the work of its founder, of Amos Eaton, John Torrey, and Asa Gray.

The founding of the New York Botanical Garden, as a result of the untiring energy of Dr. N. L. Britton and the Torrey Botanical Club, may be regarded as a worthy monument to the memory of these pioneers in American botany. Furnished as it is with the Torrey Herbarium, the value of which has been enhanced by vast acquisitions—including the Chapman and Meisner herbaria—, the library, museum, and laboratories, the New York Botanical Garden, in association with the Department of Botany of Columbia University, rivals

[1] Other botanic gardens and stations in Africa have been established in Uganda, in the British and French West African Colonies and at Victoria in the German Cameroons. In Algeria there is the fine old "Jardin d'essai" at Algiers.

[2] In Canada there is a botanic garden at Ottawa in connection with the Agricultural Department, and a small garden at Montreal belonging to the botanical department of McGill University.

[3] Bartram, through Peter Collinson, appears to have received seeds from Philip Miller of the Chelsea Physic Garden. See Wilbert, M. I. Some early botanical and herb gardens. Am. Jour. Phar. **80**: 412–427. 1908. [See p. 416.]

[4] Hosack, David. A statement of facts relative to the establishment and progress of the Elgin Botanic Garden, etc. New York, 1811.

Wilbert, M. I. *Loc. cit.* p. 423.

in its completeness, if it does not already excel, any botanical institution in the Old World.[1]

The Botanic Garden of Harvard University, which was founded in 1805, next claims attention. The garden itself is small, but in combination with the herbarium containing Gray's collection, the museums, library, and laboratories, it forms a botanical institution singularly complete and efficient.

With the Arnold Arboretum situated close at hand, Harvard has become a Mecca for botanists all the world over. The Arboretum,[2] founded by Mr. James Arnold, covers at present about two hundred and twenty acres, and the collection of trees and shrubs brought together by the remarkable industry of Professor Sargent is unrivalled, and it stands to-day for one of the most interesting and valuable developments of the principles of a botanic garden. To Professor Sargent, as well as to such enlightened men as the de Vilmorins and the firm of Veitch, the gardening world also owes a great debt of gratitude for the introduction of countless new hardy plants for the enrichment of our gardens.

Important work is being performed by the United States Department of Agriculture, at Washington, in the introduction of new plants, nor should the part played by the herbarium of the United States National Museum be forgotten in this connection. Allusion may also be made at this point to the Desert Laboratory at Tucson, and to the importance of the experimental work which is being undertaken in Hawaii, Cuba, and the Philippine Islands.

Other botanic gardens are those of the Michigan Agricultural College (1877), the University Botanic Garden at Berkeley, California, the Botanic Garden of the University of Pennsylvania at Philadelphia, of Smith College at Northampton, and the Buffalo Botanical Garden. These each and all are of recent foundation and have been established in response

[1] Britton, N. L. Botanical Gardens. N. Y. Bot. Gard., Bull. **1**: 62–77. 1897; Underwood, L. M. The department of botany and its relation to the New York Botanical Garden. Columbia Univ. Quart. **4**: 278–292. 1903; Britton, N. L. Botanical Gardens. Bull. Torr. Bot. Club **23**: 331–345. 1896. [See pp. 341–345.] See also Britton, N. L. *Loc. cit.* pp. 72–77.

[2] Kew Bull. Misc. Inf. **1910**: 261–269. 1910.

to the need of such institutions for teaching and research in botany.

Finally there is the Missouri Botanical Garden,[1] founded in 1889 by the munificence of Henry Shaw, in pious memory of whom this Twenty-fifth Anniversary Celebration is being held.

Founded on broad lines and generously endowed, the Garden has already established itself as one of the important botanic gardens of the world. With its herbarium, library, and laboratories, and the close relationship with the Shaw School of Botany of Washington University, the future of the Missouri Botanical Garden cannot fail to be one of ever-increasing usefulness.

It is a matter of regret to all botanists that South America, so rich a storehouse of botanical treasures, should contain so few important botanic gardens. The magnificent Garden at Rio de Janeiro,[2] founded in 1808, the Botanic Gardens at Santiago in Chili,[3] at Georgetown, British Guiana, and at Buenos Aires represent the measure of botanical enterprise in the continent.

The botanical possibilities at Rio de Janeiro are very great, and the Garden, in addition to its collection of living plants, possesses the herbarium of Martius, a library and laboratories. When the interest in botanical science becomes fully aroused in Brazil, a striking development of the botanic garden may be confidently expected.

[1] Trelease, W. The Missouri Botanical Garden. First annual report of the Director, for 1889. Mo. Bot. Gard., Rept. 1: p. 91. 1890.

Trelease, W. The Missouri Botanical Garden. Pop. Sci. Month. 62: 193–221. 1903.

[2] Rodrigues, J. B. Hortus Fluminensis. Rio de Janeiro, 1894.

[3] Philippi, F. Vorgeschichte des botanischen Gartens von Santiago. Gartenflora 31: 6–9. 1882. The date of the foundation of this garden is uncertain. herbarium and museum attached to the University. See also Philippi, F. It contains a very interesting collection of plants and trees, and there is a good Memoria i catalogo de las plantas cultivadas en el Jardin Botanico. Santiago de Chile, 1884.

Functions of Botanic Gardens

The varied functions performed by botanic gardens in the course of their history have been indicated to some extent in the preceding pages, and the gradual change in function from that of the purely medicinal garden for the growing of simples to the fuller conception of the true botanic garden has been traced.

With the increase in knowledge and interest in botany, new plants were brought into cultivation from all sources and gardens threatened to be overwhelmed by unarranged masses of material. Classification, therefore, became a necessity and various systems began to be put forward in response to the demand. To these we cannot do more than make brief allusion. After the efforts of Caesalpino came Morison's system of classification, which did not receive general acceptance and was absorbed into that of Ray, and neither system found many adherents as regards the disposition of plants in the botanic gardens.

The two early systems which really dominated plant arrangement were those of Linnaeus and Jussieu, the latter finding acceptance in France, where the Linnaean system never became established.

To France, in consequence, we must look for the evolution of the natural system of classification, and, with its adoption, botanic gardens gradually developed into a means of providing a synoptical illustration of the whole vegetable kingdom.

It was in the Trianon gardens that Bernard and A. L. de Jussieu, towards the close of the eighteenth century, evolved the idea of grouping plants according to a system based on natural affinities, and the Trianon system was quickly imitated and elaborated in course of time by Gärtner, De Candolle, Robert Brown, and others.

With the revival of interest in plant collecting a new development took place, and plant geography came to the front as a basis of plant arrangement in botanic gardens. Thus collections were made to represent the floras of definite regions, such as that of New Holland or The Cape, and af-

forded instructive and useful aids to the study of botany and plant distribution in particular.

These two tendencies in botanic garden arrangement hold good at the present day, and gardens may be found adhering to one or the other plan. Both systems have their merits, and where possible both may be followed with due regard to local conditions, but a slavish adherence to the one or to the other tends to court disaster and produce confusion rather than edification.

There is much to be said for the older ideas of separating "herbaceous plants" from "trees and shrubs," and for making an independent arrangement of the two classes, mainly on the ground of cultural requirements.

The natural system in plant houses, again, is almost certainly doomed to failure, and an arrangement on geographical or ecological lines must perforce be adopted.

How instructive such an arrangement may be is shown by an arrangement of plants from alpine regions or by a collection of xerophytes representative of some particular desert area of the globe.

Plant physiology affords another basis for plant arrangement and perhaps is fruitful of greater educational value than almost any other system. It has the further advantage that it lends itself to adoption in the smaller garden where a complete conspectus of the vegetable kingdom is an impossibility.

In some botanic gardens on the Continent, particularly at Berlin, and to a smaller extent at Geneva and elsewhere, the flora of mountain regions is arranged with an attempt at actual verisimilitude as to soil conditions and altitudinal distribution of the zones of vegetation. The idea is an excellent one, but its realization is liable to be far from perfect since the limiting factors of altitude and climate are absent and the plants of the mountain tops, deprived of their natural restrictions, tend to usurp more than their proper share of available space.

In whatever manner the main garden may be arranged, there should always be special portions set apart for certain well-marked plant types, such as alpine and rock plants, suc-

culents, bulbous plants, halophytes, bog and water plants, and the like, and if possible there should also be a definite economic and medicinal garden. Plant houses should also be set apart for economic plants where such as are of definite medical and economic values may be studied in connection with their products displayed in the museums.

The exact determination of plants of economic value, especially in connection with the vegetation of the tropics, is a matter of such importance that the necessity of a well-furnished herbarium and museum, in connection with a botanic garden of any pretension, needs no demonstration. With the aid of the herbarium, also the correct determination of all plants cultivated in a botanic garden should be ensured.

Just as necessary for the complete botanical establishment is the possession of a laboratory both for the examination and analysis of plants, and also for the study of such problems in mycology, plant physiology, plant hybridization, etc., as can be studied nowhere at greater advantage than in a botanic garden.

A somewhat unexpected exhibition in a botanic garden is an arrangement of fossil plants in the open, such as may be seen in the Breslau Botanic Garden,[1] where the coal measure series of strata have been built up and characteristic fossil plants have been arranged to form a kind of fossil rock-garden. Such an exhibition as this in close connection with the collection of living plants, is probably of greater educational value than a similar display would be within the four walls of a museum and may be assumed to justify its formation.

How numerous are the possibilities of arrangement in the modern botanic garden has been fully realized by the enlightened botanists of the present day. The difficulty, however, which is being somewhat acutely felt in many institutions, is that of lack of space, not only for the vast numbers of new plants being introduced to cultivation — particularly from China—but also for new and important developments

[1] Göppert, H. R. Der Königliche Garten der Universität Breslau, Führer. 1875.

made necessary by the progress of the science of botany both for teaching purposes and for research.

Experiments in plant breeding, for instance, which are a legitimate development of botanic garden research, demand an amount of space which many gardens are unable to afford, and in the tropics in particular such work has had to be relegated to definite experiment stations. In England work of this character is being carried on mainly in connection with agricultural institutions and at the newly-founded John Innes Horticultural Institution at Merton, under the direction of Mr. Bateson, while in the United States such lines of inquiry are being pursued with laudatory vigor by the United States Department of Agriculture and by many other public and private institutions.

Another function of botanic gardens of first importance is the opportunity they afford for the training of men; and in work of this character Kew has probably played a larger share than any other garden. From Kew, in the course of her long history, her sons have gone out either as collectors or gardeners to bring home plants of interest and of economic value, or to take charge of the botanical establishments in the British Colonies and Dependencies. A glance at the Kew roll will also show how many of her young men are helping to propagate the art and science of horticulture in the United States of America.

With some of our larger institutions one of the most important functions in the past has been the distribution of plants of economic importance. The distribution of cotton seed, in 1732, by Philip Miller from the Chelsea Garden to Georgia (the parent stock of upland cotton), the introduction of Para and other rubber plants, and of *Cinchona* from South America through the agency of Kew, of tea into India by the Calcutta Botanic Garden, may be cited as a few among innumerable cases. There are those who have expressed the opinion that this function of botanic gardens is now obsolete, but it does not require much reflection to perceive how wide is the field of usefulness still open in the direction of the introduction and distribution of plants.

Our smaller botanic gardens then may rest content with the attempt to develop their resources on lines best calculated to stimulate interest and promote sound learning, both as centers of education and of research, while it falls to the lot of the larger institutions to display as far as possible the complexity and variety of the vegetable kingdom. The latter, with their herbaria, museums, and laboratories, are responsible to the world for the correctness of the information they supply, since in cases of economic plants incorrect determinations or injudicious advice may involve incalculable harm to the planting community, whose interests they serve.

The magnitude of this responsibility has been fully appreciated, and the results achieved amply serve to demonstrate the success which has attended the efforts of the distinguished botanists who have guided the destinies of our botanic gardens.

> "The people will tell of their wisdom and the congregation will shew forth their praise."

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2. Britton, N. L. Botanical gardens. Bull. Torr. Bot. Club **23**: 331–345. 1896. Also in N. Y. Bot. Gard., Bull. **1**: 62–77. 1897.
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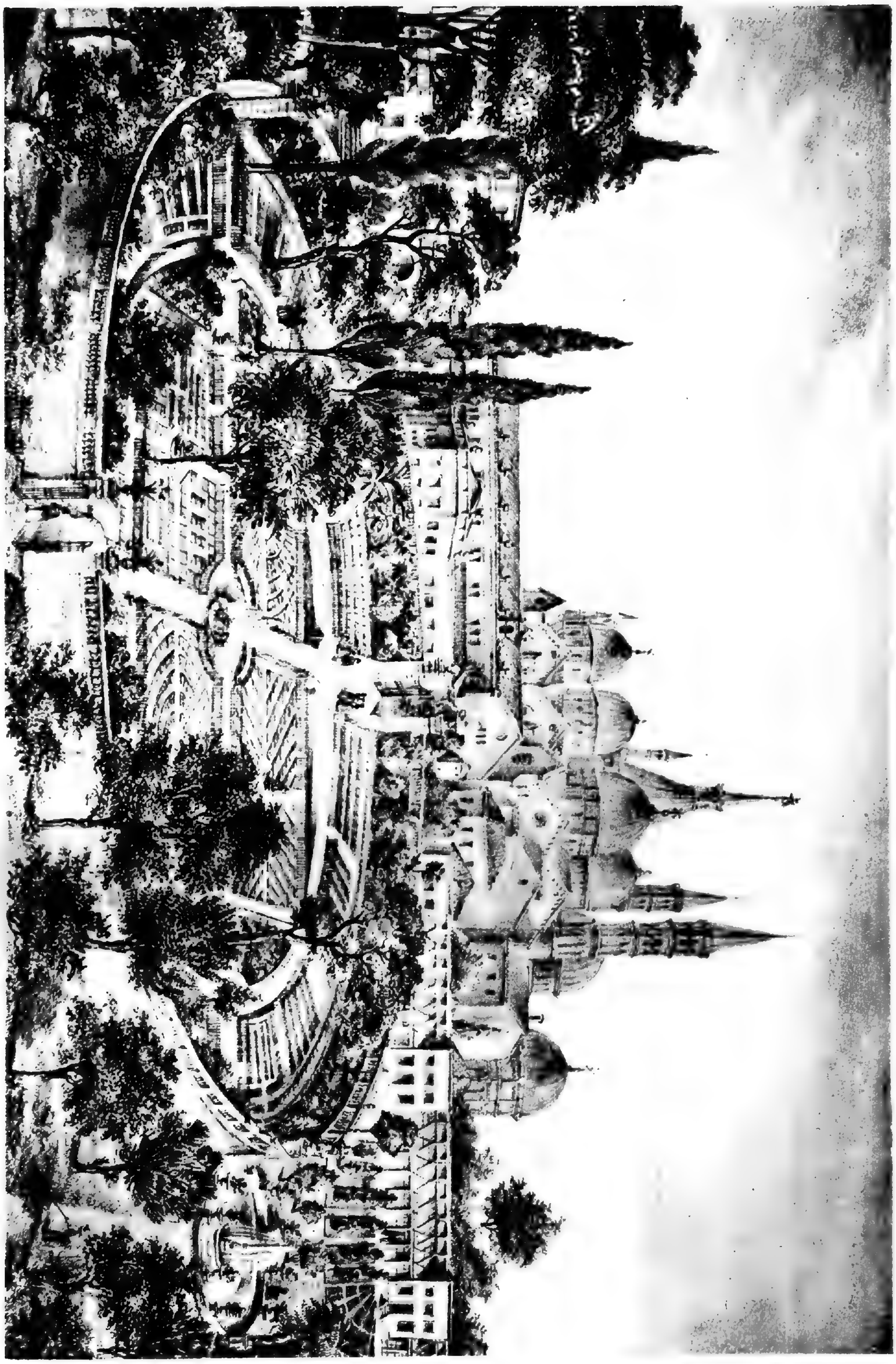
4. Holmes, E. M. Horticulture in relation to medicine. Roy. Hort. Soc., Jour. **31**: 42–61. 1906.
5. Johnson, G. W. A history of English gardening. London, 1829.
6. Kerner von Marilaun, Anton. Die botanischen Gärten, ihre Aufgabe in der Vergangenheit, Gegenwart und Zukunft. Innsbruck, 1874.
7. Maiden, J. H. Functions of a botanic garden, etc. Roy. Soc. N. S. Wales, Jour. and Proc. **46**: 1–73. 1912. [See pp. 49–73.]
8. Philippi, F. Los jardines botanicos. Santiago de Chile, 1878.
9. Pulteney, R. Sketches of the progress of botany in England. 2 vols. London, 1790.

EXPLANATION OF PLATE

PLATE 4

Padua Botanic Garden.

Photograph of plate in de Visiani's 'Dell' origine ed anzianita dell' orto botanico di Padova.' Padua, 1839. (See p. 191.)



HILL—BOTANIC GARDENS

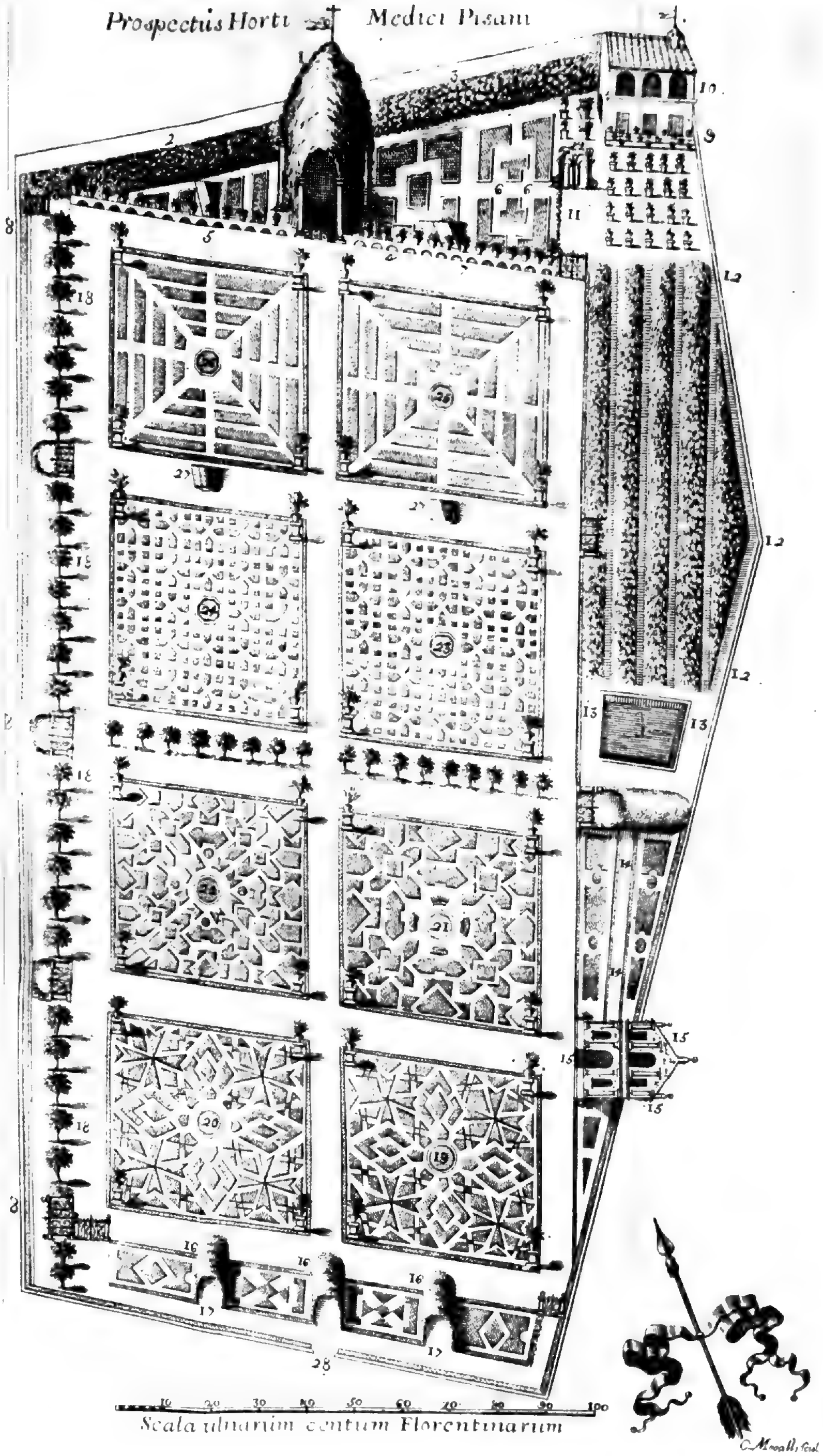
COCKAYNE, BOSTON

Explanation of Plate

PLATE 5

Pisa Botanic Garden.

Photograph of plate in M. A. Tilli's 'Catalogus Plantarum Horti Pisani.' Florence, 1723. (For explanation see p. 192.)



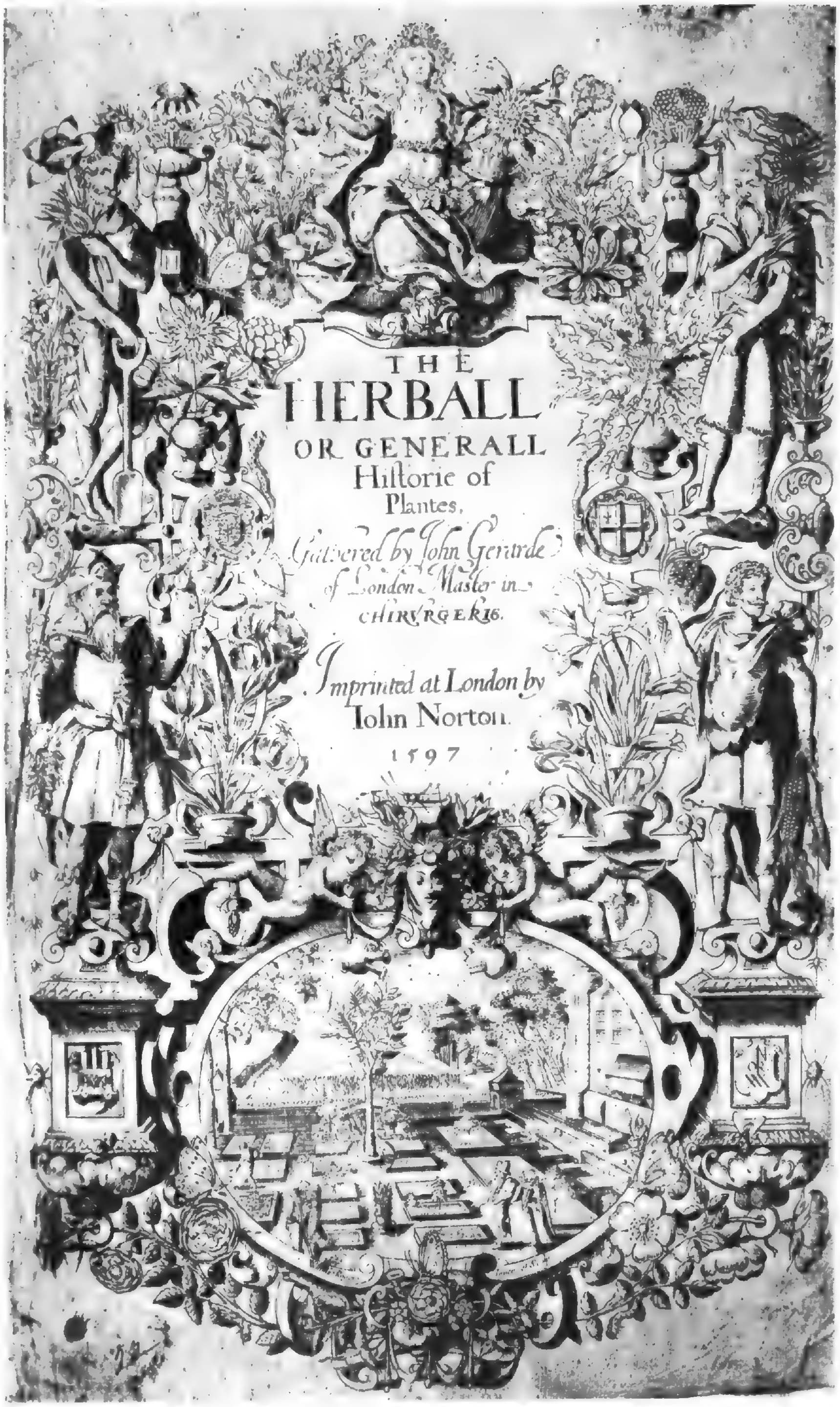
HILL—BOTANIC GARDENS

COCKAYNE, BOSTON

Explanation of Plate

PLATE 6

Photograph of title page of Gerard's 'Herball.' 1597. (See p. 196.)



HILL—BOTANIC GARDENS

COCKAYNE, BOSTON

EXPLANATION OF PLATE

PLATE 7

Photograph of title page of Parkinson's 'Paradisi in sole Paradisus Terrestris.' 1656. [2nd ed.] (See p. 197.)

HILL—BOTANIC GARDENS

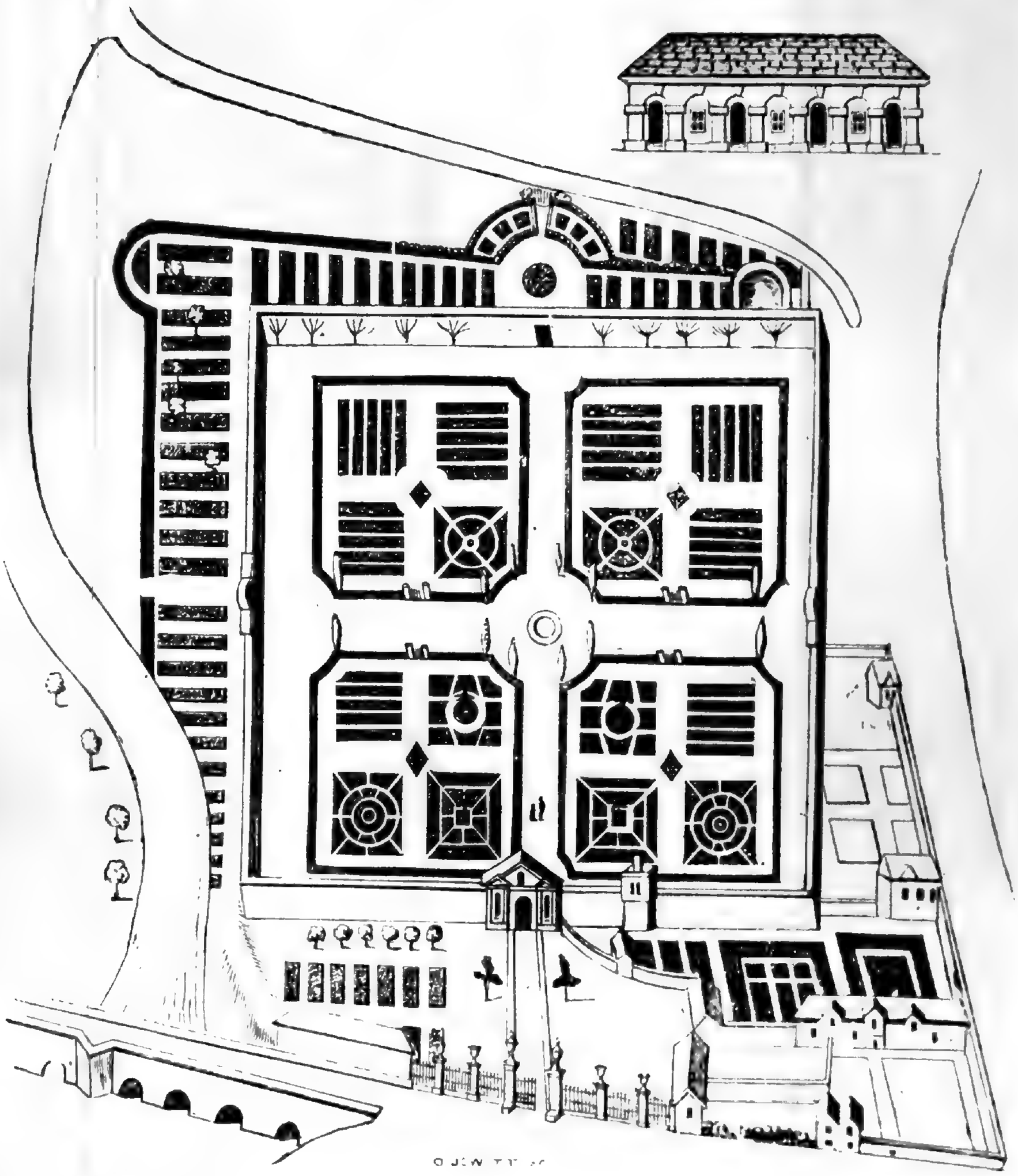
COCKAYNE, BOSTON

Explanation of Plate

PLATE 8

The Oxford Botanic Garden, founded 1621. Reproduced from Loggan's plan of the Garden in 1675. (See p. 197.)

South Elevation of the Conservatory



East Bridge

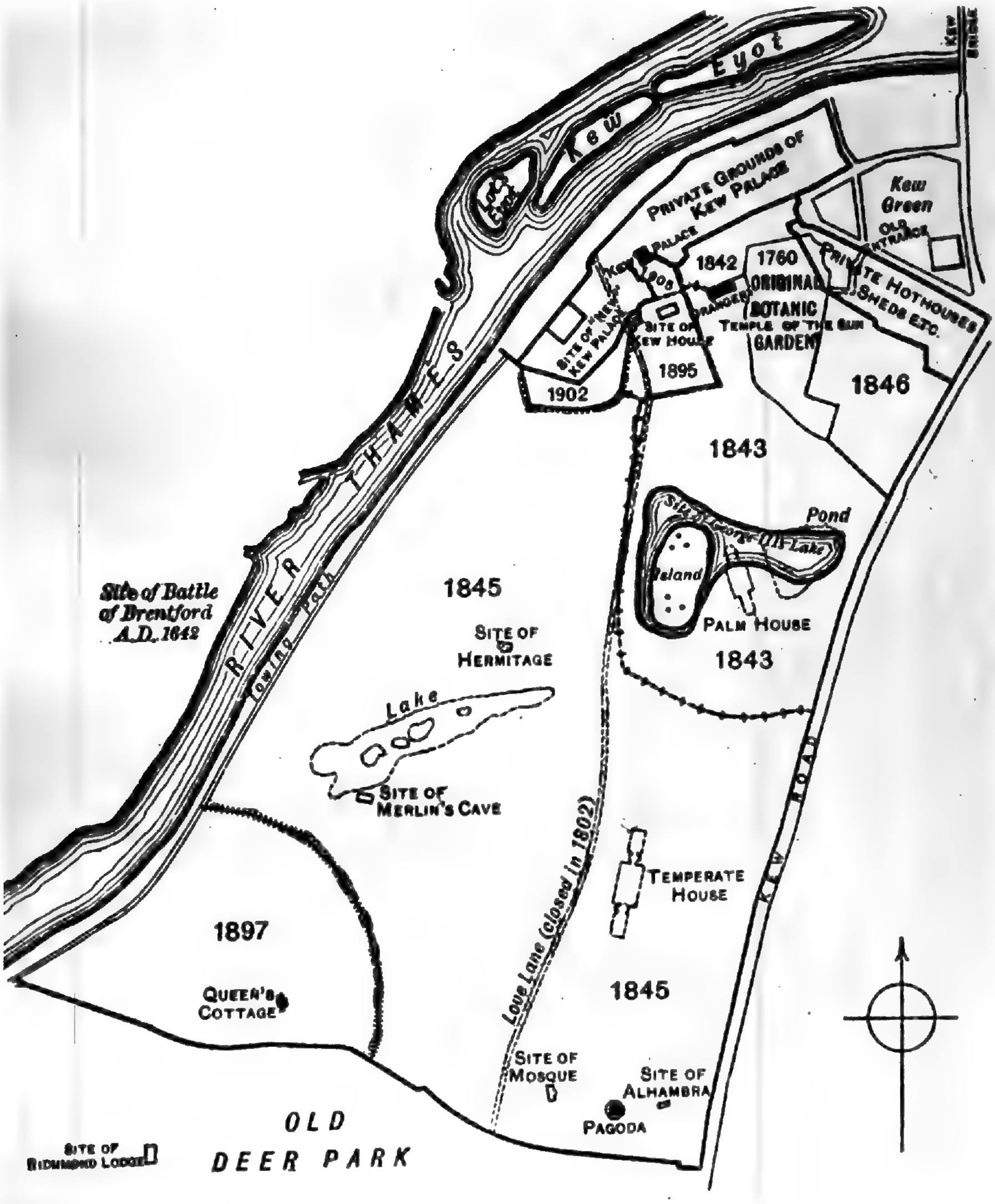
HILL—BOTANIC GARDENS

COCKAYNE, BOSTON

Explanation of Plate

PLATE 9

Royal Botanic Gardens, Kew, showing dates and extent of successive additions to the area open to the public and site of the original Botanic Garden of 1760. Photograph of plan in W. J. Bean's 'The Royal Botanic Gardens. Kew,' London, 1908. (See p. 206.)—Published by permission of Cassell & Co., Ltd. London, England.



HILL—BOTANIC GARDENS

COCKAYNE, BOSTON

Explanation of Plate

PLATE 10

The Herbaceous Ground, Royal Botanic Gardens, Kew, showing beds arranged according to the natural orders.

HILL—BOTANIC GARDENS

COCKAYNE, BOSTON

Explanation of Plate

PLATE 11

The Rhododendron Dell, Royal Botanic Gardens, Kew.

HILL—BOTANIC GARDENS

COCKAYNE, BOSTON

Explanation of Plate

PLATE 12

The Lake, Royal Botanic Gardens, Kew.

HILL— BOTANIC GARDENS

COCKAYNE, BOSTON

RECENT INVESTIGATIONS ON THE PROTOPLASM OF PLANT CELLS AND ITS COLLOIDAL PROPERTIES

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I have the honor of publicly congratulating the Representatives of the Missouri Botanical Garden upon the Twenty-fifth Anniversary of Henry Shaw's magnificent foundation,—the unique memorial of a magnanimous citizen of this great metropolis.

I shall endeavor to show to the members of this splendid assembly how plant physiologists at present attempt to reach a satisfactory understanding of the wonderful mechanism which in never-ceasing variation is unfolded to us in myriads of phenomena characteristic of nutrition, reproduction, adaptation, growth, and stimulation, in the lower as well as in the higher plant organisms.

Wherever science is following these various processes to their mysteriously hidden roots, the physiologist has to face the complex problems associated with the living content, the so-called protoplasm of the plant cell. Without this singular matter plant cells are mere dead bodies able neither to grow, to take up food, nor to assimilate their nutriment.

It was not until 1841 that Hugo von Mohl, the well-known botanist of Tübingen, discovered the important fact that all phenomena in cell life are strictly confined to the thin layer of slimy material which clothes the inside of each growing and living plant cell. He stated that this protoplasmic slime was stained deeply yellow by means of iodine, and he expressed the opinion that protein substances in particular were the constituents of this living material, from which all other parts and organs of the cell were believed to take their origin.

We shall not be surprised to learn that biologists felt inclined to suppose that the protoplasm might contain some

peculiar and highly complex proteins constituting the living matter in the proper meaning of the word, whose chemical qualities we should have to make responsible for the whole complex of life phenomena. Therefore, it appeared a most attractive problem to subject protoplasm to a thorough chemical investigation. The names of Reinke and Rodewald are connected with this work. These two botanists, in 1880, then in Göttingen, analyzed the protoplasmic mass, the so-called plasmodium, of *Fuligo septica,* a common species of the *Myxomycetes.* The result was that a part, about three-quarters, of the material was recognized to belong to the protein group in the widest sense; while 25 per cent was a mixture of diverse carbohydrates, fatty bodies, organic acids, and inorganic materials. No evidence of the presence of any peculiar protoplasmic substances was found. Reinke, therefore, laid emphasis on the point that protoplasm could not be regarded as a single chemical body of peculiar qualities, but that it should be considered as a mixture of various substances, of which not even one was unknown to the chemists. The consequence of this view was that Reinke inclined to the hypothesis that the peculiarities of protoplasm were not due to its chemical nature but rather to its peculiar structure. The stuff-hypothesis had to be replaced by a structure-theory of protoplasm.

At present, however, we can scarcely accept all conclusions drawn by Reinke from his famous analysis of protoplasm. Reinke thought that all the vital properties of living protoplasm were destroyed when cells were killed, in the same way as the mechanism of a watch is destroyed by grinding it down in a mortar. The chemical substances, however, may remain unchanged while the mechanism is forever destroyed. The first experiments which proved that Reinke's simile is not quite an exact one were obtained from studies on the various enzyme effects which continue in a mass of finely comminuted tissue. Among those effects we know a series of processes which undoubtedly belong to the complex of vital metabolism, —as, for example, to those of respiration and digestion. And these effects may be followed for weeks and for months after

trituration of the cells, if precaution is taken to prevent change in the material by bacterial action. But the essential difference between such autodigestion and the life-process consists in the fact that the first is not ruled by the laws of correlation and regulation, which are so peculiar to life processes. Nevertheless, we cannot say that the whole of the life-mechanism is destroyed by grinding down living organs. At least a part of it cannot immediately be transformed by this type of disintegration. From this we may draw the conclusion that there are certain chemical substances present in protoplasm which are responsible for certain activities of the living tissue. Such substances are the enzymes, which are entirely unknown in inanimate nature, and absolutely distinctive of cell protoplasm. Further, we cannot suppress some scruple that in Reinke's analysis there were examined not the original protein-bodies of protoplasm, but only substances artificially produced during the treatment of the original material.

Our chief objection against the "Engine-Theory" of protoplasm is that no mechanism has hitherto been known which may be destroyed by heat as easily as is protoplasm, whilst on the other hand one cannot immediately and entirely destroy it merely by pounding to an impalpable pulp. Besides this, recent investigations on the proteids of animal organs—in which great care was taken to dry the pulp quickly at a temperature as low as possible—have shown that there really exist highly compounded protein bodies of hitherto unknown constitution which have to be considered as real constituents of protoplasm.

Can such discoveries in some way explain the vital properties of the cell? It seems as if we may not understand the wonderfully accurate working-together of all organs in cells without supposing trans-microscopical structural qualities; but we need not assume any mysterious new forces or structures. Most of the well-known characteristics of protoplasm can be understood by considering further the colloidal state of the constituents of the cells.

The first naturalist who turned his attention to the great importance of colloidal substances in cells was Bütschli, the zoölogist of Heidelberg. A great number of his admirable papers deals with the microscopical features of cell plasma, which he described as a framework of jelly-like substances containing interstices, or meshes filled with fluid substances. Bütschli emphasized the view that the foam structure described by him is not peculiar to living matter, because a mixture of oil and gelatin solution shows the same microscopical structure which he attributed to protoplasm and to all colloids.

But later on it became more and more probable that such a foam structure in protoplasm indicates nothing more than certain gross features which are by no means identical with the real colloidal structure of plasmatic constituents. Not even in gels, or solid colloids, apparently, is the foam structure a dominant characteristic. Zsigmondy's recent work on gelatinous structure clearly showed that while forming the gel the colloidal particles, which are distinctly visible in the ultramicroscope, do not arrange themselves in a network, but settle quite irregularly; so that we cannot assume that meshes are formed in the precipitation of colloids. On the other hand, biologists of rank, as Lepeschkin, after a careful study of the microscopical structure and the physical properties of protoplasm, have arrived at the conclusion that we should not regard it as a foamy mass, or jelly-like substance, but rather as a liquid colloid with the characteristics of protein sols of certain higher concentrations. We can easily confirm the observation that protoplasm, examined by means of the highest power of the microscope, often appears merely as a homogeneous liquid, or transparent mass, sometimes moderately turbid from the presence of small distinct drops or corpuscules which are collectively known under the name of "microsomata." Even though we do not accept Bütschli's idea with respect to specific structure, we fully share his more general point of view that living protoplasm owes its peculiar activities to colloidal qualities. And this represents our attitude to-day towards protoplasmic investigation.

The chemistry of colloids is not a descriptive science. To the utmost extent it has to use experimental physical methods. So we cannot advance in knowledge of protoplasm by mere microscopical observation, but mainly by experimental investigation.

A long time even before colloidal chemistry became dominant as the basis for the physiology of protoplasm, a memorable epoch in plant physiology had opened, developing from the ingenious work of Pfeffer and De Vries on the osmotic properties of living cells. These investigations unveiled the fundamental fact that living protoplasm alone is in possession of those peculiar properties of permeability which are responsible for the whole complex of nutrition. Dead protoplasm behaves quite differently. Since, however, differences in respect of the penetration of different solutions can be detected to a certain extent in colloidal membranes, it became probable that the so-called semipermeability of living protoplasm is a colloidal phenomenon, due to the constituent colloids in living protoplasm; whilst after the death of the cells the coagulation of these colloids completely changes the peculiar permeability of the protoplasmic layer.

It was, however, Ernest Overton, in 1899, then at Zurich, who acquired the merit of placing colloidal chemistry in fundamental relation to the phenomena of diosmosis in living cells. The well-known theory of Overton consists in the hypothesis that fatty substances play an important rôle as constituent elements in the protoplasmic matrix. It is due to such substances, generally comprised under "lipoid bodies," that living cells show quite distinctive diosmotic qualities. Overton's hypothesis is founded upon the fact that only those substances which readily dissolve in fatty oils are easily diffusible in living cells; whilst all substances which are insoluble in oily media, as sugar or mineral salts, easily produce plasmolysis, because they penetrate into cells only very slowly.

The leading physical idea in this theory was the so-called "Partition-Rule" of Berthelot and Jungfleisch. This law states the fact that there exists a constant relation between the quantities of a certain solute dissolved in two immiscible

solvents. Overton considered the endosmosis of dissolved substances into living cells as merely a question of solubility. It is known how fertile this idea has proved in physiology, particularly in the phenomenon of narcosis, where it is still the leading hypothesis in animal physiology.

But recently experimental work, including my own, has shown that it is scarcely quite correct to consider the endosmosis of solutions into living cells as a typical solution phenomenon. According to Loewe even the partition of methylene-blue or of chloroform between oil and water cannot readily be explained by means of the principle of Henry and Berthelot. Rather, the oily solution of such substances is not a true solution, but only a colloidal solution; so it is not ruled by the laws of osmotic pressure, but by the laws of adsorption.

A striking fact was discovered by Traube and by myself in studying the effects of alcohols and other capillary-active substances on living cells. Their injurious action clearly and exclusively depends upon the relative capillary activity. Every one of these substances kills the cells at a concentration corresponding exactly to a certain value of surface tension. The main importance of this observation consists in the evidence that in narcotic effects capillary phenomena must be a dominant factor. This cannot be interpreted by the supposition that the entrance of narcotics into cells is due to true solution phenomena. The observed capillary effects distinctly show that the factor of real moment is to be found in alterations of contact-surface; but such surface-phenomena are met with only in colloids and in their adsorption.

A prominent feature of our experiments involves the fact that cells of higher plants are constantly killed by concentrations of narcotics such that the capillary activity reaches about two-thirds of the surface tension of pure water in contact with air. It is remarkable that saturated and neutral emulsions of triolein or other typical fats always show approximately the same surface tension value. This result I tried to explain by means of the hypothesis enunciated in the following sentences: Alcohol and other narcotics are taken up by ad-

sorption into living protoplasm. According to the theorem of Willard Gibbs the surface in liquid systems which consist of different fluids and contain some capillary-active substances is always occupied by those substances which show the greatest reduction in the surface tension of the medium. If subsequently another substance with greater capillary activity is added to the system it displaces all other substances from the surface. Narcotics may displace certain plasmic substances in an analogous way, provided that the surface tension of the concentration applied is just a little lower than the surface tension of the plasmatic substances referred to. The fact that the fatal narcotic pressure value coincides with the maximum surface tension in fat emulsions may be explained by the hypothesis that fatal effects of alcohols on living cells consist in destroying the emulsion structure of protoplasm, by displacing some fatty substances. So our experiments to a certain extent uphold the view that the surface layer of protoplasm really contains fat, and thus far is in accordance with Overton's hypothesis.

In the course of time the lipoid-theory of Overton has met with sharp criticism. Among other renowned physiologists, Ruhland strongly denied the presence of fatty bodies in the plasmatic membrane of plant cells. On the other hand, we are aware that animal physiologists, such as Fühner, Höber, and Vernon still firmly adhere to the old lipoid-theory. However, since according to Overton sugars and mineral nutrient salts are believed to penetrate only poorly into the living cell, it is obvious that Overton's hypothesis stands in direct contrast to the common experiences in respect to plant nutrition. The substances referred to are materials which the cells have to take up as among their most important nutrients. Nevertheless, there have been developed some supplementary theories which permit us to lessen the difficulties of the lipoid-theory, for example, that of Nathansohn, according to which the lipoid membrane of protoplasm is not a continuous film of fat, but a kind of mosaic of fat and protein which is able to permit the penetration of both fat-soluble substances and mineral salts.

Ruhland's experiments especially were not at all favorable to the lipoid-hypothesis. They show decidedly the error of the opinion that only those aniline dyes penetrate into living cells which are soluble in oil. Many aniline dyes have been found which are easily taken up by cell protoplasm in spite of their insolubility in fat, while other coloring matters which easily dissolve in fat do not penetrate at all through the living plasmatic layer. Ruhland, as well as Küster, drew from such experiments the convincing conclusion that substances readily soluble in lipoids may not always be readily taken up by the living cells. But in other respects it seems as if Ruhland had gone too far when he denied that protoplasm possesses any fat content. He emphasized that he never could detect any microscopical trace of plasmatic substances which may be stained by means of such aniline dyes as are readily stored by fat.

Since our own experiments seem to be in some accord with the view that fatty matter really is present in protoplasm, I wanted to compare some chemical systems which are entirely free from fat with protoplasm in respect to its behavior toward alcohols. It could be taken as a proof of the view that protoplasm does not contain fatty bodies, if there were noticed no difference between the effects of alcohols on the physical properties of such systems and on protoplasm. The investigations of Mr. Geo. H. Chapman in our laboratory were begun in order to examine the influence of different narcotics on enzymes. Surprisingly, the results were opposed to the above-mentioned view of similar action with respect to these systems. This work clearly showed that the capillarity-rule which is so distinctive of the effects of narcotics on living protoplasm does not apply to the effects of narcotics on enzymes. While the deleterious influence of methyl, ethyl, and propyl alcohol gradually increases with the molecular weight of these homologous substances, the higher members such as butyl and amyl alcohol act considerably less on enzymes, and both heptyl and octyl alcohol have practically no weakening influence on these ferments. In respect to their coagulation by diluted alcohol protein solutions show relations corresponding to

those just discussed. In consequence of this result we can hardly explain the effects of narcotics on protoplasm by the view that only plasmatic protein bodies are influenced by such toxic agents. Besides this, for the coagulation of protein bodies there is required not less than five mols of ethyl alcohol while a little more than two mols is sufficient to kill living protoplasm. Therefore, some other substances in protoplasm besides the protein bodies must be affected by the alcohols, and these substances must differ from the latter in their physical properties. So it seems that the view according to which the plasmatic membrane is constructed exclusively of hydrocolloids, viz., proteins, as Ruhland believes, cannot be considered to be quite satisfactory. Our attention must be directed anew to the possibility that some lipoids play the part of important constituents of the protoplasmic membrane.

On the other hand, I have to state that several lines of experimental work have led us to the conclusion that the endosmose of solutions into living cells never does take place by way of plasma lipoids, but only through hydrocolloidal constituents of the cell plasma. The work of Mr. Krehan, which dealt with the influence of highly diluted hydrocyanic acid on plant cells, distinctly showed that in the presence of this agent the permeability of cells to certain salts, such as sulphates, and to sugar, is raised, so that the threshold of plasmolysis for these substances is raised. When the effects of different salts on plasmolysis were compared it became manifest that just those salts causing the greatest rise of the plasmolytic limit, are those which were strongly adsorbed, and which display a most marked effect on the precipitation or coagulation of albumen. Such salts are sulphates, citrates, tartrates—by their anionic effects, and the salts of ammonium, calcium, and magnesium—by their cationic effects. These phenomena are only to be understood upon the supposition that hydrocolloids are the media through which different substances must pass when taken up by the living cell plasma. There has been discovered not the faintest indication that

lipocolloids can play an important part in endosmose, as Overton originally suggested.

If there really are plasmatic lipoids present, they probably have no significance as the path of nutrient substances into cells. But, on the other hand, lipoids certainly participate in narcotic effects, because the more soluble is this narcotic in fat the more of the narcotic substance is stored by the plasmatic substances. Consequently, the higher members of the series of alcohols are more injurious for cells than the lower, because the lipoid constituents of protoplasm become saturated with the narcotic and can discharge these narcotics only slowly. So the protoplasm succumbs to the influence of the narcotic agent. On this point I share the opinion of Böeseken and Waterman.

The capillarity-rule can scarcely be explained otherwise than by the hypothesis that lipoids are present in the surface layer of protoplasm. So we are forced to continue our work as an exploration designed to determine if lipocolloids are present in protoplasm. A plan was devised and a decision was sought in the following manner: Emulsions of pure triolein or of olive-oil were prepared which had about the same surface tension value as have solutions injurious to protoplasm. To a series of samples arranged from such a fat emulsion alcohol in gradually increasing amount was added. The question now was whether there were effects produced on the emulsion in some way comparable to the action of alcohol on cells. Cell plasma contains also protein bodies and mineral salts. So our model of emulsion had to be compounded by adding a solution of mineral salts, as a physiologically balanced mixture, and by adding also albumen solution. The mineral salts were added as in the Van't Hoff mixture in 0.1 molar concentration. An alkali is indispensable, so that 0.1 mol of sodium carbonate was used in order to produce a fine and stable emulsion upon shaking the mixture with oil. The results were in brief the following: When a fat emulsion from olive oil was prepared by mixing only oil, water, and sodium carbonate, the decomposing effect of alcohol on the emulsion was noticed at a concentration of 3 mols, i. e., about 15 per

cent. When concentrations higher than this were used then the emulsion, examined capillarimetrically, did not differ from a mixture of pure alcohol and water of the same concentration (but without oil). Then we added to the emulsion Van't Hoff's solution 0.1 mol instead of water. The decomposition of the emulsion by ethyl alcohol was now observed at 2 mols, i. e., about 10–11 per cent. This is just the concentration of alcohol which kills cells of the higher plants. The addition of sodium chloride 0.1 mol instead of Van't Hoff's liquid showed the critical concentration of alcohol to be 3 mols, about the same concentration as in the absence of mineral salts. On the other hand, the addition of magnesium chloride induced the fatal effect of alcohol at 1 mol, much lower than in living cells. Magnesium sulphate showed the same effect as magnesium chloride, and the sulphate of sodium the same as the chloride. Therefore, it does not seem probable that the differing solubility in alcohol is responsible for the various effects of the salts. One may endeavor to explain these phenomena in the following way: Emulsions are only stable when the droplets of the emulsified fat remain suspended in a soap solution of approximate concentration. Substances which alter the limiting surface between the soap solution and the suspended oil must prove fatal as soon as their capillary activity surpasses the capillary effect of the soap solution. Bivalent cations, such as Mg and Ca, which form insoluble salts with fatty acids, lower the concentration of soap, so that alcohol must exhibit a decomposing action on the emulsion, even in lower concentrations.

From such experiments it seems as if the critical concentration of alcohol for living cells would not be so sharply determined by proteins contained in protoplasm as by the mineral salt and the lipoid constituents of the protoplasm. Since we suppose that the various mineral salts in protoplasm are present in about the same concentration as they are found in sea water, or as they are mixed together in Van't Hoff's solution, we have to face the question whether the destructive effect of alcohol on living cell plasma consists in some decomposition of colloidal fat emulsoids in protoplasm.

That protein bodies are not primarily affected by alcohol and other narcotics seems to be sufficiently proved by the fact that ethyl alcohol coagulates protein solution at a concentration not lower than 5 mols, and that while the higher alcohols show fatal effects on living cells, they do not produce any protein coagulation.

So we are brought, I think, by several facts to the conclusion that living protoplasm must be considered as a colloidal emulsion of lipoids in hydrocolloidal media, the latter containing proteins and mineral salts. For the endosmotic passage of dissolved substances the fatty constituents of protoplasm have no significance. The narcosis, however, and the deleterious effects of alcohols clearly show how lipoids, more than the protein constituents of the surface layer of protoplasm, participate in such phenomena. The more we advance in the disclosure of the details regarding colloidal mixtures and structures in living protoplasm, the more indispensable it is to be reserved when applying the new results to the various problems to which an approach is so tempting to the physiologist.

Many may feel inclined to be disappointed when they observe how much time and mental energy are needed to study only so small a question as that about the presence of fat in protoplasm. But now after some years' work on this subject it may be seen how important a part is to be attributed even to the combination of mineral salts contained in the plasma colloids. And so we may hope that in the progress of research new and unexpected paths may become visible and open to the indefatigable investigator. Further, we shall not be discouraged if when after long and patient work some results and ideas are won which subsequently are proved untenable. We are all common soldiers in the great battle for truth in science, and we know that few will attain the happiness of planting the flag of victory upon the battlements of the conquered fortress.

THE EXPERIMENTAL MODIFICATION OF GERM-PLASM

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The doctrine of an inviolable germ-plasm has formed the foundation of many imposing edifices in biological thought, and facilitated many advances in genetics and heredity during the last two decades. The authors who have rigidly adhered to the principles of the hypothesis and reasoned from its tenets have exposed many fallacies which have been offered in explanation of problems in evolution.

This prevalence of theoretical considerations over mistaken experiences has laid the foundation for an unreasoning devotion to the idea of an independent germ-plasm, carrying agents which may not be seen, measured, or tested in any practicable manner, and which might consequently be termed "idealoplasm" with attributes approaching the supra-physical.

The desperate straits of those who voluntarily consign themselves to the bondage of such a conception is well exemplified by the group of writers who subscribe to the conclusion that all evolutionary movement is due simply to recombination and rearrangement of qualities or factors already present in the protoplasm. An additional illustration of the futile extremes to which this view may be pushed is to be found in the recent utterances of Bateson, who has arrived at the conclusion that evolution is mainly and essentially loss of inhibitors, and release of activities previously latent or suppressed, an hypothesis which predicates premutation.

If it be allowed that the non-appearance of a character is a direct loss of its determiner and that the appearance of a new feature is the loss of a retarder or inhibitor which held it in abeyance, then the answer to the question as to the method by which organisms have arrived at their present condition is obvious, but of a simplicity that is metaphysical instead of actual and hence of little value, even tentatively, as a frame-

work on which new concepts in biological science may be formulated. The group of problems with which we are endeavoring to make headway are in the domain of physiology and their solution may be reached only by experimentation, the results of which are to be interpreted in terms of physico-chemical activities and their correlated functional manifestations in the living organism.

That phylogenetic advance in the main lines of descent in the plant kingdom at least reflects, or harmonizes with, the expectancies of somatic experience is tacitly admitted on all hands, but that the direct response of a shoot to the environment, or conversely stated, that the impression on the soma made by environic agencies is communicated to successive generations in a constant manner has not been demonstrated, although it seems fairly established that certain experiences of individual plants are reflected directly or indirectly to the next generation, and in lesser degree to the next or second generation. How are lasting or permanent changes brought about?

Functional adequacy and architectural suitability present themselves on every hand, yet about all of our reliable evidence is against anything like a direct or functional adaptation becoming hereditary or continuously transmissible.

Two methods of experimental attack on the problem are available. Species showing measurable features and of simple genetic constitution may be taken from their habitual or known environment to other localities in which the climatic and soil characters may be calibrated and the response of the organism, somatically and hereditarily, determined. Hundreds of thousands of introductions and acclimatization operations have been carried out in agriculture, horticulture, and especially in botanic gardens during the last century, yet neither the genetic constitution nor the response of the organism has been followed by trained observers who compared the plants in their different habitats. The exposure of the organism to any climatic complex, of course, might affect the germ-plasm directly, and any departure detected in such experimentation must be evaluated by controlled cultures under

laboratory conditions in which both the nature of the reaction and the identity of the inciting agent may be found. The most notable series of experiments of this character which have as yet been carried out are those of Tower with the potato beetles.

Over two hundred species of seed-plants selected for their suitability and promise of response have been taken into the series of cultures of the Department of Botanical Research on mountain top, desert, and at the sea-shore, less than eighty of which have survived and about a score continue in all three locations. The most notable feature in the behavior of these plants put under stress in unaccustomed habitats consists in divergences in sexual reproduction and seed-formation. Conjointly with this decrease of the sexual reproduction, vegetative propagation assumes a greater importance. Shoots are variously affected. The measurement of these departures and their fate when the *n* th generation is returned to the original habitat, or to a place in which the habital tension is changed, will be necessary to determine whether or not permanent impress on the species has been made.

The second method would include all forms of experimentation in which inciting agents would be applied directly to the reproductive bodies, in which case any deviation from the usual or typical would be more clearly attributable to changes in the germ-plasm.

It is pertinent to call attention to the necessity for new viewpoints and new standards in the evaluation of any results which may be obtained in such manner. We are not likely to go far or progress easily into the region of the unknown if we attempt to interpret these effects too directly, with the idea that determiners, inhibitors, genes, etc., are ultimate or even penultimate units. In brief, the time has come for testing the performances of lineal series of organisms by methods in which attention will be centered upon the physico-chemical complex and an open eye will be kept for cleavage lines which may cut across directly or obliquely the limits of all of the arbitrary concepts of alternate inheritance. The house of the living thing is inclusive of walls, doors, roofs, windows, floors,

ceilings, rafters, and plumbing, but the materials used may be bricks, stones, metals, sand, lime, boards, glass, and paint. Our present needs lead us to experiments with these components rather than to trials of the possible combinations and inhibitions, possibilities and impossibilities of sets of builders' blocks, no matter how complete or full these may be.

Living material is a colloidal complex with its enmeshed reactions highly fluctuant, its combinations unstable and its types of energy transformation multifold. It is concrete, however, and amenable to experimentation of many kinds. Its physical qualities and form undergo changes of phase which have some correspondence with the mechanism of morphogeny, reproduction, and heredity. Thus, for instance, in the higher plants the germinal protoplasm in the earlier stages of the individual is in the form of meristematic tracts made up of highly distended plasts in which absorption of water, hydratation, auxetic enlargement, and division of the separate elements is very marked and rapid. Elements at the peripheries of these masses are separated which undergo differentiation and pass into the permanent tissues of the individual. These separating cells may be modified to an enormous extent by external agencies; thus conditions of aridity acting upon an individual may cause the tissues formed from its embryonic tracts to make such structures as to give the organs which they make up a xerophytic aspect.

This final xerophytic or other character of the soma, however, is in the permanent tissue, and the modifications which have resulted in its specialization ensued after the cells were pushed away from the meristem, and there seems to be no reflection of the final fixed qualities back to the embryonic tract, although there are many promising possibilities to be considered. Of these none are more interesting than the regenerative processes by which highly specialized cells reassume embryonic activity and reproduce members or individuals vegetatively. Actual tests of the transmission and permanence of the specializations under these conditions have not yet been made with that exactitude which would allow any serious conclusion to be formulated. At certain stages of the

ontogeny, generally much later in the plant than in the animal, and this is a matter which may be determined by the environic agencies, the germ-plasm or meristem tract undergoes such change of phase that instead of all of its separating elements passing into somatic cells a few become reproductive masses from which sexually specialized elements may be differentiated, and in which the number of chromosomes, the metabolic balance, degree of hydratation, auxetic energy and mechanism of division suggest physico-chemical conditions widely different from those of somatic elements; furthermore, the reproductive elements are highly individualized. The meristem in its myriad cells may at any moment present all of the phases of growth and differentiation. The egg nucleus or the fertilized egg, a single element of the plasma, may include the fate of the individual and its unending line of progress, and it may be affected in its entirety by agencies impinging upon it. The reaction of such specialized cells to external agencies would of course be different from those of the meristem tracts, which are made up of plasmatic units of the most generalized form.

The experiments of Tower with the *Leptinotarsae,* which have been carried on under widely diverse conditions in southern tropical Mexico, in the arid semi-tropical climate of the Desert Laboratory, and under controlled conditions at the University of Chicago, furnish a great series of cultures of these beetles in which it is possible to demonstrate logically by exclusion and analysis that certain climatic features, notably moisture, may affect the germ-plasm, or the entire organism when the germ-plasm is in a certain stage, in such manner as to induce disturbances in hereditary lines. These experiments show the vulnerability of the germ-plasm.

That the germ-plasm is directly responsive to the action of foreign substances which are introduced into the embryo-sac was demonstrated when (early in 1905) I was so fortunate as to hit upon an experimental method of treatment of the ovaries of seed-plants which resulted in the formation of embryos developing into individuals not entirely identical with the parental types. The essential feature of the discovery

consisted in the successful introduction of various substances into the neighborhood of the embryo-sacs at the time that fertilization was imminent, and when the first trials were made I had two main purposes in mind: first, to ascertain whether or not foreign substances could be introduced into ovaries in such manner as to affect the ovules with a minimum of traumatic effects, so that the ovaries might reach maturity; and secondly, to ascertain whether or not such changes could be produced in an early stage of sexual specialization, before the development of the embryo-sac or after the union of the sexual elements in fertilization.

The first results were obtained with pure strains of *Oenothera biennis* and *Raimannia odorata* at the time mentioned, but the transfer of my activities from the New York Botanical Garden to the Desert Laboratory made it impossible to carry out cultures of the progeny or to repeat similar experiments upon this material. Meanwhile, Col. R. H. Firth, of the Royal Medical Corps of Great Britain, duplicated[1] my general results with *Raimannia* and other plants in 1908, although the fact that I had previously done this work was unknown to him.

New material was selected from the vicinity of the Desert Laboratory and the tests were begun anew in 1906. The difficulties to be overcome in such experiments are fully commensurate with the importance of the problem upon which they bear. It is a necessary preliminary that the plants chosen for the operations should be an elementary strain, a matter which may need two or three years for determination, if not already known. Next, not all ovaries will withstand the shock and injury inflicted in the operations. The chances of ultimate success will be greatest in many-seeded ovaries in which the number, however, does not extend much beyond that of ovules which may be affected by a single operation, giving some opportunity for differentiation of effects and not entailing large cultures. Lastly it is advantageous to deal with perennial species which come quickly to maturity. This gives

[1] Firth, R. H. Roy. Med. Corps, Jour. **16**: 497–514. 1911.

the operator opportunity to preserve the original material alive and to have it for comparison with succeeding generations.

The numerous cacti in the vicinity of the Desert Laboratory lead them to be selected for some tests, and the mechanical conditions for operation which they offer are unexcelled. As much as 1 cc. of solution may be introduced into the ovary of an opuntia without traumatic effects, but as all are under suspicion as to their genetic complexity, and as they germinate and develop slowly, the investigator must wait the greater part of a decade to obtain decisive results. Striking departures were obtained with *Echinocereus Fendleri,* a small cylindrical form native to southern Arizona, and the changed characters grouped in one derivative have not been obtained in nature or in cultures of the original. This derivative has been obtained a second time. The species, however, presents such a complexity of characters that definite conclusions are difficult.

Similar conditions were encountered in *Penstemon Wrightii,* about which an announcement was made in 1909. Some of these, however, furnished material from which the greatest sources of error might be eliminated.

The search for suitable subjects for experimentation was continued and the results with *Penstemon* led to a closer examination of other members of the *Scrophulariaceae.* Finally, an undescribed species of *Scrophularia* from the pine-forest area on the Santa Catalina Mountains in Arizona was brought into the environic series of the Laboratory of this Department in 1909. Rootstocks were taken to the Coastal Laboratory, and seeds were germinated at various localities. After having seen many hundreds of plants taken from various parts of its range and having followed them thoroughly two and three generations, it was found that the species is a simple one and not readily separable into elementary forms or strains. The only noticeable feature suggestive of complications was the fact that the broad-bladed nepionic leaf-forms are sometimes carried nearly to the summits of stems grown under certain conditions, giving the appearance of a robust race.

Another feature that received attention was the fact that branches formed in the closing part of the cycle of development of shoots bear leaves very much smaller than those arising from the median part of the main stem during the first part of the season. The flowers borne on these branches are also much paler than those on the more robust branches. Peloric flowers sometimes appear near the apices of the inflorescences in this as well as in other species of the genus. It is to be noted also that the divisions of the corolla are variously and irregularly incised on individuals at times during the season, but these are not heritable and do not appear in any regular manner.

This scrophularia appearing to offer some promise, several ovaries of a plant at Carmel were treated with solution of potassium iodide, one part in forty thousand, in July, 1911, and the ripened capsules were collected in September of that year. No record was made as to the time of day (see page 268) and nothing may therefore be said as to the possibilities of the action of the reagent on egg or pollen nuclei, singly, together, or after fertilization. No other species of *Scrophularia* grew near the cultures at that time.

The seeds were sown in suitable pans of screened soil, and in February three plantlets had survived. In May these were set in the open and their development followed. One formed a shoot fairly equivalent to the normal, finally producing flowers in which the anthocyans of the flowers were of a noticeably deep hue. The two remaining plantlets were characterized by a succulent aspect of the leaves, and by a lighter or yellow color of the leaves and stems. Inflorescences were matured late in 1912, and the flowers on one of the derivatives, as they may be called, were so completely lacking in color as to be a cream-white, this derivative being designated as *albida*, while the other showed some marginal color and a rusty tinge, and was designated as *rufida*.

Some disturbance of the relative velocities of development of the fibrovascular elements and mesophyll had taken place in both forms, so that the leaves were variously bowed and convexed and the two halves of the laminae were unequal and the

whole blade was more oblique in outline. The elongation of the lamina had been checked and the ratio of width to length of the leaves was greater than in the parental stock. If correspondent leaves of *rufida* and the originals were laid side by side it could be seen that the basal veins on the side away from which the tips were curved were different in the two cases, the derivative showing two strong veins in the place in which one lateral with a thin branch occurred in the original (fig. 1). The water relations of derivatives and normal were not identical, and when young shoots or branches developed

Fig. 1. *O*, branching lateral vein in parental *Scrophularia; D*, branching vein replaced by two laterals in leaf of modified *Scrophularia*.

under similar conditions were detached, those of the derivatives flagged and wilted much more quickly than those of the normal.

The auxetic departures noted above also extended to the inflorescences, which in the original show a fairly regular basipetal development into thyrses. The derivatives, however, exhibited a rather irregular maturation of clumps of buds and the thyrses were very irregular, not reaching the spread of the parental forms. The fragility of the leaves does not seem to extend to the flowers, which opened very slowly, and in some cases the distended corolla persisted for a few days. The amount of color in the corolla was largely a matter of illumination, but under equivalent circumstances the derivatives always showed less than the parental form. As noted above the color persists to some degree in the deriva-

tives along the margins of the uppermost lobes of the corolla, while that on the broad upper surface disappears. It is to be recalled that it is the color of this region which is variously disposed in other species of the genus.

The corolla lobes were irregularly incised in the flowers of the first and second seasons of the F_1, as they have been seen to be in the original, but in the second generation of both derivatives cultivated at the Desert Laboratory this effect persists as a regular wedge-shaped incision of the lower lip only, and is not seen in every individual of both derivatives, although the seeds were from plants which may have been pollinated by the parental form.

Seedlings from the original stock grown from seeds gathered on the Santa Catalina Mountains in Arizona were sowed early in 1910 at the Desert Laboratory and the plantlets preserved on April 15 furnished the data:

First pair of leaves smaller than in the derivative, being only 13–15.5mm. wide and 16–18mm. long, obscurely dentate with not more than two or three blunt teeth showing on each side. The petioles were 12–16mm. long. The third pair of leaves above the cotyledons, which probably were not quite mature, had petioles 20mm. long, and laminae 22–25x50–52mm. Marginal stalked glands were so numerous that 15–20 appeared in the field of the microscope at one time, and these structures were very numerous on the petioles. It is to be noted that differences in the last-named feature between this original and the derivatives disappear in the adult, or on the leaves appearing in the later stages.

Seeds from the original two derivatives matured at Carmel late in the summer of 1913 were sowed in the greenhouse at Tucson in November, 1913. But one plant of *albida*, the extremest departure, survived, while four of *rufida* were secured. These, of course, represented the F_2 of the departures. The measurements of *rufida* correspondent with those of the original are as follows: First three leaves deeply incised, five or six teeth on a side, abruptly pointed. Petioles 18–22mm. long, laminae 21–26mm. wide and 41–45mm. long. Mature leaves on sixth, seventh and eighth internodes, with petioles

36–45mm., and laminae 36–56x85–100mm. Marginal glands showing 6–10 in field, few on the petioles.

The single plantlet of *albida* bore leaves, the first pair of which were not deeply cut, the three or four teeth on each side being abruptly but sharply pointed, the petioles 15mm. long, and the laminae 24–26x35–38mm. The leaves from the sixth, seventh and eighth internodes had petioles 30–40mm., and laminae 45–51x90–100mm. Not more than four stalked glands might be seen in the field at any one time. These trichomes were very sparsely distributed over the under surface of the petioles only. The greater relative width of these leaves was correlated with a greater angle of divergence of the lateral veins from the midrib, a feature which, as will be shown later, was to be observed in adult plants.

The three plants representing the progeny of the treated individual were established in a row within a half meter of each other at Carmel in 1912. Irregular clusters of long thickened roots were formed, and these, as is customary with the species, bear buds and are a means of propagation of the plant. The three plants were taken up in November, 1913. While the main clumps could be identified, yet broken fragments of roots were preserved which could not be assigned to any one of the three, and although these were and are still preserved they are not taken into account here.

Albida was divided in May and June, 1914, and portions were sent to coöperators in New York, St. Louis and Chicago, but all failed to survive this unseasonable transplantation, so that at the present time this strain is represented by only two clumps, one of which is at the Desert Laboratory and the other at the Coastal Laboratory. The single plant of *albida* bloomed at Tucson early in the year, while the one at Carmel reached that stage too late to mature seeds.

Rufida was divided into three clumps and reset in the garden at the Coastal Laboratory in November, 1913. The shoots from these began to open flowers in July, 1914, which corresponded in all essential particulars with those of the previous seasons except that they were more highly regular. Two were enclosed in small glass cages for protection and to insure

close pollination, a strong individual of the original being similarly enclosed for purposes of control. Conditions being favorable for a minute comparison of these plants with the parental type, colored illustrations of flowers and buds and diagram of structure were prepared. The inequality of the leaves was recorded by direct prints. The dimensional relations noted above were again seen. The readiness with which the leaves flag was noted and in these organs, as well as in the stems, it was seen that rigidity is maintained by turgidity rather than by stiffness of the mechanical tissues. The development of the bast-fibers is less marked in the derivative,

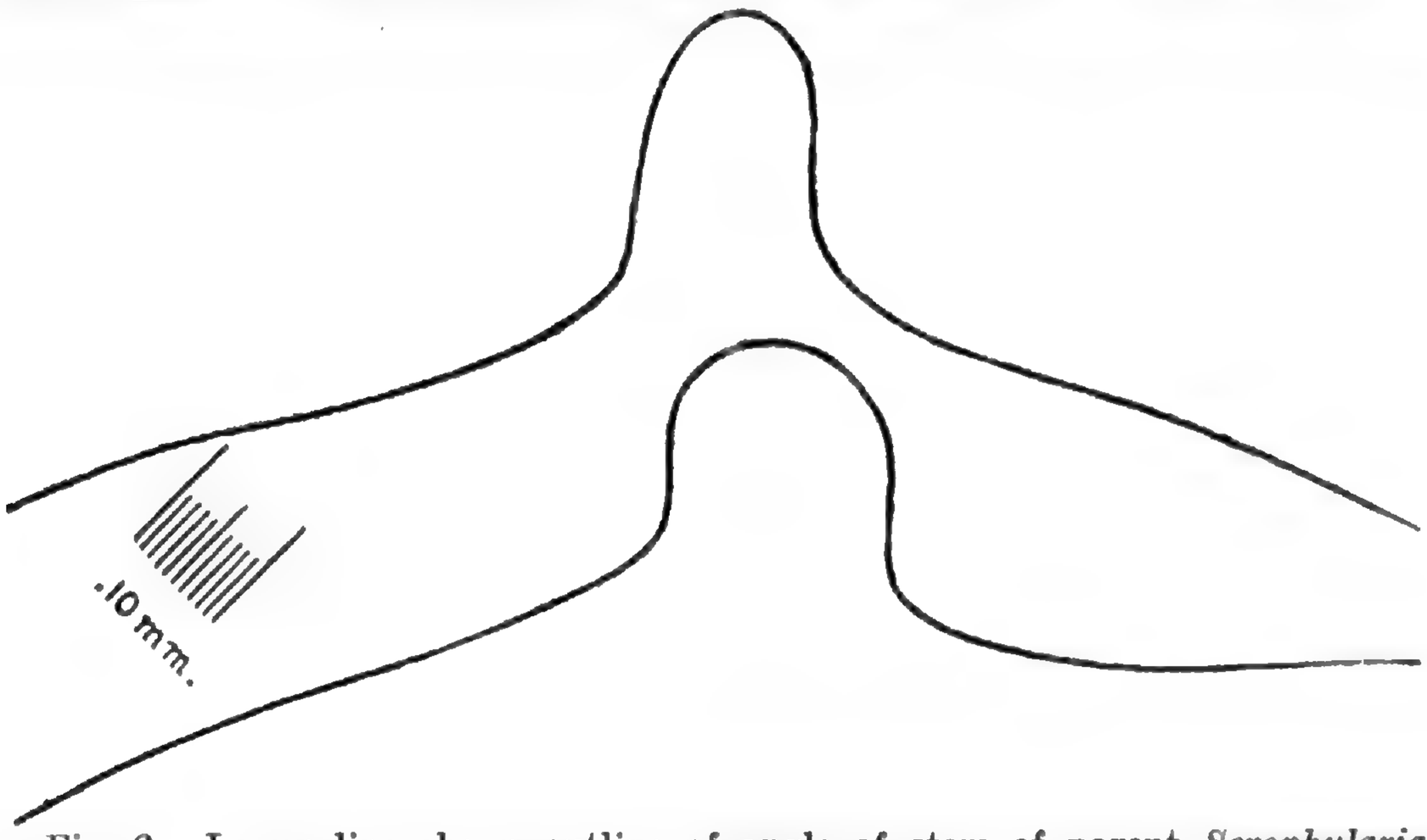

Fig. 2. Lower line shows outline of angle of stem of parent *Scrophularia;* upper line outline of same feature in derivative.

and a similar deficiency of wood-formation is noted. A correspondent difference is apparent in the wings of the angles of the stems, which are thick with their sides parallel in the original, while in the derivative these decrease in thickness gradually toward the margin, with the effect in cross-section seen in fig. 2. The actual value or importance of these differences is not a matter of moment in the present connection. The chief interest lies in the fact that recognizable effects have been produced by the introduction of foreign substances into ovaries and that the differences shown by the first generation, F_1, are borne by the second generation, F_2. The original observations with the plant in which this was demonstrated

began in 1909, the treatments were made in 1911, and now first and second generations of the derivatives are alive, as well as the original stock.

Much irrelevant comment and inconclusive experimentation has followed the original announcement of the discovery of the methods used in this work. The necessity for a careful genetic analysis of the material for treatment has already been noted, and it may be well to call attention to some of the features of operation which might appear simple, yet are not easily carried out. No better way has yet been found for introducing solutions into the region of the embryo-sac than by injection into ovaries with an all-glass syringe fitted with gold needles (14 karat). The wounding of the ovary produces abortion in some species, and in almost all treatments some of the ovules are crushed. This, however, is a matter of no moment if some reached by the reagent survive and come to maturity. The extent and mode of diffusion of the reagent is in fact one of the most important features of the treatment, and the experimenter will do well to make control tests for the purpose of finding out whether or not there is some possibility of success.

A test of the ovaries of *Carnegiea* previously described showed that the liquid was taken up by the placental vessels and conducted to a point near the egg cell in a very short time if the reagent were introduced into the ovaries of flowers fully open and mature. Operations made at an earlier stage resulted in the accumulation of the reagent in the inner walls of the locule, in the integument of the ovule and especially at the micropylar orifice. The pollen tube would be subject to the action of the accumulated substance in the micropyle and integument in this case.[1]

It being my present intention to extend experimentation in the *Scrophulariaceae,* tests have been made with methylene blue in the ovaries of *Penstemon Torreyi,* the solution being one part of the dye to ten thousand of distilled water.

[1] MacDougal, D. T. Alterations in heredity induced by ovarial treatments. Bot. Gaz. **51**: 241–256. 1911.

Three hours later but little of the color could be found in sections of the ovary. Next, five ovaries of *Oenothera* 3.21

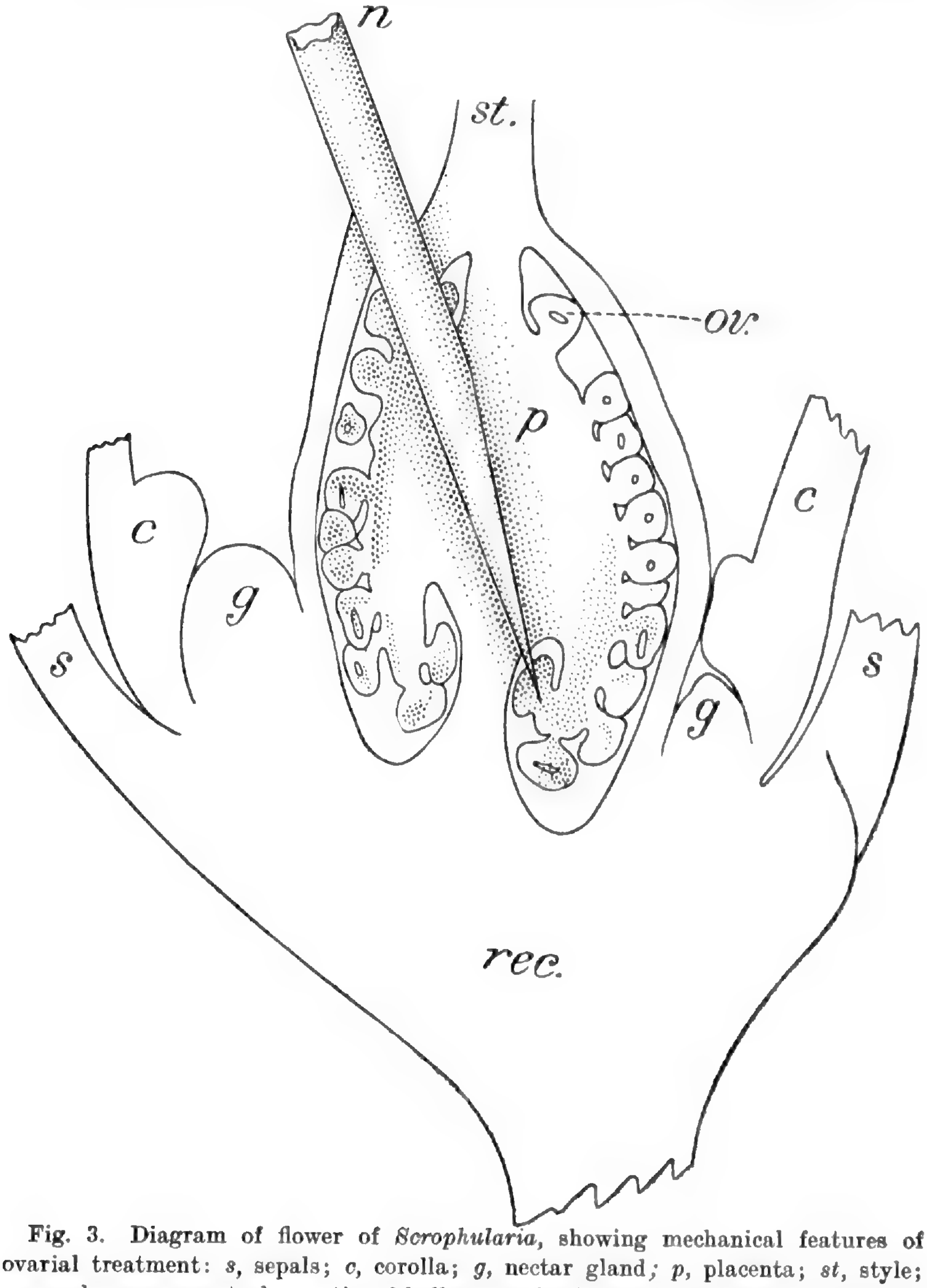

Fig. 3. Diagram of flower of *Scrophularia*, showing mechanical features of ovarial treatment: *s*, sepals; *c*, corolla; *g*, nectar gland; *p*, placenta; *st*, style; *ov*, ovule; *rec*, receptacle; *p*, tip of hollow needle thrust through the ovarial wall and penetrating the placenta. The stippling shows the diffusion of a solution of methylene blue introduced by the needle.—Drawn by F. E. Lloyd.

(a stable cruciate hybrid) were injected with a solution of one

part in a thousand. Fifteen to forty ovules had been touched by the color in young flowers not yet open. A much larger number had been colored in the ovaries of mature flowers. This solution was introduced into ovaries of the scrophularia under examination (fig. 3). Young ovaries in this plant showed very few ovules affected, none in a few cases. Older ovaries in which fertilization had probably taken place showed as many as 15–20 colored ovules. Probably only a small proportion of the ovules affected would have survived and developed into viable seeds, so that many of the treated ovaries would have yielded nothing but normal seeds. This condition is to be taken into account by those who do not recognize the technical difficulties in the way of duplication of any particular treatment.

The recent results of Churchman and Russell[1] in securing stimulation of the growth of animal tissues with methylene blue suggest that this substance might produce some effects on the embryo-sacs of plants, and also the advantage of using a reagent the diffusion and penetration of which are visible and obvious.

It was desirable to use this dye in obtaining some knowledge of the probable action of other solutions in *Scrophularia,* so tests were made with this plant. A number of ovaries on a detached shoot in the laboratory were placed in a solution of one to a thousand at 9:30 a. m. Material was taken for examination at suitable intervals.

The placental walls and funicles were stained in part within a half hour. Two hours later the color had advanced well along the conducting tract in the funicular stalk. Five hours after treatment a notable amount of the dye had been carried clear to the embryo-sac, where it stained the nucellus and the antipodal region deeply. It is to be noted that the material was still alive and that this material if left attached to the plant would have developed some mature seeds in all probability (fig. 3).

[1] The effect of gentian violet on protozoa and on growing adult tissue. Soc. Exp. Biol. and Med., Proc. **2**: 124. 1914.

Professor F. E. Lloyd, of McGill University, who kindly came to my aid in this matter, now made a brief study of the intra-vitam staining in the ovules of *Scrophularia* and found that the reagent accumulated throughout the embryo-sac inclusive of the egg cell, demonstrating the possibility of the direct action of introduced solutions on the entire egg apparatus as well as upon the endosperm. The micropylar orifice was closed and was not stained in the ordinary treatments and took up only a small amount of the dye when laid separately in a solution of it. Professor Lloyd also showed me preparations in which pollen tubes deeply stained had entered the micropyle and had elongated, reaching the egg.[1] These experiments made clear the immediate possibility of reagents reaching the egg apparatus through the funicle and of the staining of the pollen tube and nucleus in the cavity of the ovary before fertilization. It is also possible that the pollen tube might be affected by reagents which had accumulated in cells through which it penetrates to the egg nucleus (fig. 4).

These facts would make it probable that treatments before pollination has taken place would affect the embryo-sac and its inclusions only, while introductions of solutions at a later stage would be likely to affect the pollen tubes and nuclei. These generalizations are to be taken to be applicable to *Scrophularia,* and to species which present similar arrangements for reproduction. The egg in ovules in which the micropyle is open might be even more readily exposed to the action of a reagent, and if the ovule is porogamous the pollen tube would also inevitably be affected, and still many other combinations may be encountered which need not be enumerated at this time.

It is of course to be understood also that not all of the ovules in any pistil are in equivalent stages of development at any given moment, and this applies also to the penetration by the pollen tubes. Pollination of *Scrophularia* takes place in the morning, and substances introduced before mid-forenoon

[1] See Lloyd, F. E. The intra-vitam absorption of methylene blue in ovules of Scrophularia. Report of the department of botanical research for 1914. Carnegie Inst. Washington, Yearbook 13: 77–81. 1914.

would be taken up and diffused through the tissues, especially through the funicle before the pollen tubes had reached the cavity of the ovary. Introductions timed to meet the elongat-

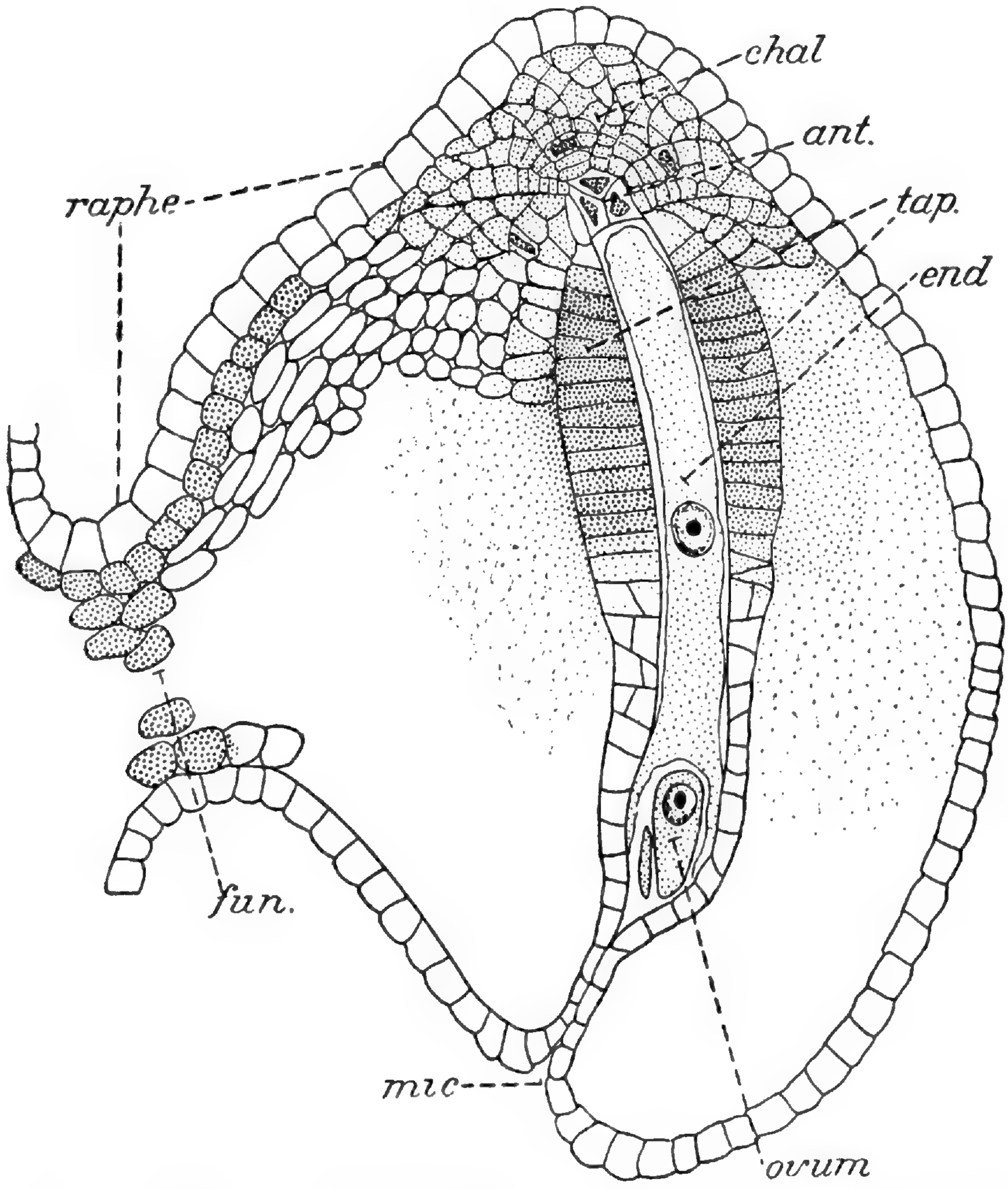

Fig. 4. Diagram of longitudinal section of ovule of *Scrophularia: fun,* funicle; *chal,* chalaza; *ant,* antipodal cells; *tap,* tapetum; *end,* endosperm; *mic,* micropyle. The shading shows the course of a solution of methylene blue diffusing through the funicle from the placenta (see fig. 3) and its selective fixation in the tapetum and nucellus. The solution finally reaches the ovum.

ing pollen tubes would of course be more liable to affect the pollen nuclei, and a number of lots of seeds matured in ovaries

treated at various stages of development now await germination and test.

The differences between the two surviving derivatives of *Scrophularia* described in this paper may well be due to such differential action. It is to be seen that if egg or sperm were affected singly the resultant seed into which these elements might enter would be hybrid. Even if both were acted upon, it is by no means to be taken for granted that the effects in the two would be equivalent. The F_2 of *rufida* was identical in the cultures described, while the F_2 of *albida* presented some modifications, the status of which is not yet established, as both were open pollinated in the F_1. Very little information as to hybrids in *Scrophularia* is available. Goddijn and Goethart[1] report that *S. Neesii* Wirtg. × *S. vernalis* L. is a unified, stable, intermediate type and that the reciprocal is of a similar character.

The behavior of the original stock, and the facts of fertilization, yield nothing suggestive of parthenogenesis, and the derivatives may be taken to be produced by a typical fertilization. No cytological examination has yet been made for the purpose of ascertaining possible differences induced in the chromosomes.

This discussion may be fittingly brought to an end by a brief reconsideration of the salient ideas which have been touched upon. The point of view taken throughout all of the work which has been described is one in which the conception of a theoretical or idealized germ-plasm has been relegated to secondary position, and attention has been concentrated upon the concrete germ-plasm of the higher plants. This physical basis of heredity is seen to present two distinct phases. In one it takes the form of a meristem or embryonic tract of highly distended cells in which auxesis and division are both rapid and the elements which are separated from it pass by differentiations into the permanent tissues of the soma. Environic agencies affect only the development of the somatic cells which are being formed from the meristem, and the ex-

[1] Ein künstlich erzeugter Bastard Scrophularia Neesii Wirtg. × S. vernalis L. Van's Rijks Herb., Mededeel. **1913**[15]: 1–9. 1913.

perience of these cells are not reflected back to the embryonic tract, so far as available facts may be considered. Sexually specialized reproductive elements with a reduced number of chromosomes are developed from the embryonic tracts in a late stage of the ontogeny, and these elements present a metabolic balance different from that of the meristem stage, the colloids having a greater density, and some of the energy transformations having altered velocities.

The embryonic tract or meristem of a higher plant at any given moment includes an enormous number of primitive or initial cells and of separating elements in all stages of division, growth, and differentiation toward the specialized tissues which are derived from it. The tract as a whole could therefore not react in a unified manner to any climatic or environic agency which would impinge upon the plant. Such forces, as a matter of fact, visibly affect only the manner in which the differentiation of the resting tissues takes place. The rejuvenescence of such differentiated cells might carry the effects into the organ or individual produced by the regeneration, but no test has yet been made of this matter, or of the transmission of such supposititious characters to a second sexually produced generation; neither has the proposal, that repeated or long continued exposure of the germ-plasm to any environic stimulus may result in the fixation of effects, been tested out. The continuation of introduced species in the mountain, desert, and coastal plantations of the Department of Botanical Research for the term of years during which any one person might conduct such experiments, may not be taken as an adequate test of this phase of the matter, although these cultures are carried on for the express purpose of determining what permanent changes may be induced by the tension of unusual environic complexes. So far these have been confined to alterations in sexual and asexual reproductive procedure, and to alterations in structure and aspect of the shoot, while no tests have been made upon the fixity of the changes.

Aberrant behavior of the chromosomes in certain determinative or initial cells may possibly be responsible for bud-mutations or bud-variations, and theoretically it is conceivable

that special stimuli might be applied to such cells in a manner that might bring about similar results. Practically, however, it would be enormously difficult to localize initial cells with sufficient certainty so as to give any slight chance of success.

The second stage of germ-plasm in which it is in the form of sexually specialized elements offers far more promising conditions for experimental modification of the genetic content of the species which it represents. Solutions may be introduced into the ovaries in such manner as to affect the egg bearing the entire group of qualities of the species, and furthermore the direct action of such reagents may be ascertained to some extent.

The present-day aspect of the mechanism of heredity is one which increases momentarily in complexity. The greater part of the researches in genetics during the last fifteen years has been devoted to the interaction of factors, determiners, inhibitors, or qualities in the organism. If these conceptions may be taken to be the expression of the reactions of either chemical groupings or to rest upon a physico-chemical foundation of any kind, the reagents which have been used have not been of a selective character, but would affect practically the entire colloidal mass of the protoplast in some manner and to varying extent, neutralizing or coagulating proteins, and their general tendency would be to inhibit or check energy transformations. In the case of the iodine treatments the free ions from potassium iodide or the iodic acid formed would cause a neutralizing effect, as it does not seem from the results of Czapski and Adler[1] that this element would form any compound with the proteins.

The experimenter is dealing with an actual physico-chemical complex of highly unstable compounds in which many types of energy transformation are occurring. Introduced substances may slow down or inhibit some of these, and accelerate others or start new reactions. The morphological possibilities in any given strain of plants are somewhat limited, however, and in this sense the direction of the departures is al-

[1] Beiträge zum Chemismus der Jodwirkung. Biochem. Zeitschr. 65: 117. 1914.

ready determined. This limitation of the possibilities of morphogenesis is the chief one in any expectancy of duplication of results in successive treatments, outwardly mechanically identical.

The variables in any experimental setting are many, and the briefest consideration of the physical effects consequent upon the introduction of a foreign solution to the vicinity of the embryo-sac, reveals at once the lack of probability of exact repetitions in a mechanism so complex. The conditions are much different from those which would be presented if free floating eggs or sperms were immersed in a solution. If we are able to induce other changes in *Scrophularia* besides those shown, they will be quite as important in demonstration of the fact that germ-plasm had been modified as if they were exact repetitions of previous inductions. If previous results were exactly recalled there might be some suggestion of premutation.

It is evident that the experimenter who wishes to proceed with the greatest precision and least loss of effort will first test the genetic strictness of his living material, ascertain the rate and manner and diffusion of solutions in the ovary and ovules, the time of pollination and the rate of development of the tube in reaching the egg. Next, the structure and number of ovaries and the traumatic reactions of the entire pistil are to be taken into account. Having also traced out the simpler features of pollination and fertilization, the operator should test the effects of various reagents which may neutralize proteins, including enzymes, or act as excitators or catalyzers. Without enlarging too much upon the difficulties to be encountered in the experiments described in this paper, they may be illustrated by the fact that over fifty operations upon *Scrophularia* in July, August and September, 1914, at Carmel, California, were total failures, as the ovaries perished before reaching maturity.

Finally, many present interests in phylogeny and genetics will be concerned with the nature of the evolutionary movement which is simulated by the alterations which have been induced experimentally by the method described. Some of

these would unquestionably be designated as of a retrogressive character, such, for example, as the defection of a part of the color pattern of the corolla; others, such as the accentuated incision of the leaves and corollas and the development of the venation, as progressive alterations; while still others may not with any substantial reason be assigned to either class. With reference to taxonomic criteria, it may be said that the divergent individuals are distinguishable at sight from the parental stock, but the real test of the characters presented is not their degree or kind of departure, but their stability and permanence indicative of actual modifications of the germplasm.

THE RELATIONS BETWEEN SCIENTIFIC BOTANY AND PHYTOPATHOLOGY

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The ever-increasing importance of phytopathology is the result of the steady development of agriculture, forestry, and horticulture. In this way phytopathology has become a part of each of these sciences.

In former times well-known botanists, such as Gleditsch, Martius, Caspary, de Bary, and Sachs did not estimate themselves too highly to concern themselves at times with phytopathological problems. In modern times, however, it is not often that a university professor of botany occupies himself with such problems. This is due partially to the specialization which has become a necessity in modern science. Above all, however, this is due to a peculiar conception which looks upon the applied branches of applied natural science as something inferior to the pure natural sciences. It must, however, be said that we find exceptions even here, if we think of such scientists as Brefeld and De Vries.

Agriculture has within a short time presented many problems to phytopathology, and of these the principal ones have been those of disease control. These problems were often solved in a hasty way, which, I must admit, lacked scientific thoroughness. But even in the solution of these problems many interesting facts were brought to light. But with the progress in working out these questions it became more and more evident that many of these problems could not be ultimately solved unless investigated in a thoroughly scientific manner.

In criticising the plant pathologists it should not be forgotten that most of them are for the greater part autodidacts. Until recent times there were no places where scientific phytopathology was taught. In Germany it was only the

University of Munich, in which von Tubeuf has been and is still teaching the subject. In Austria, Hecke has been giving lectures for some years. In the United States there has been much progress in this line, due, no doubt, to the fact that plant diseases are of greater importance here than in any other country. As the number of chairs in phytopathology in our institutions of learning increases, however, the relation between scientific botany and phytopathology will become more and more intimate.

Among the factors which favor unusual ravages by vegetable and animal parasites, I wish to mention the rapid development of agriculture by way of growing the same varieties or races over vast areas, the great fertility of the previously uncultivated soils, which often induced people to crop the soil and neglect rotation, and lastly the favorable climatic conditions, which not only favor the cultural plants but also their parasites.

One of the oldest problems of phytopathology is the smut-problem. Since ancient times smuts have been among the most important plagues of our cereals, and long before we knew the cause of these diseases people tried to control them. But rational measures of control could not be developed before the cause of the disease was known. Julius Kühn succeeded in clearing up the life-history of the stinking smut. This was the first distinct step in advance, but here, unfortunately, progress ceased for some time, principally because of the lack of knowledge concerning the taxonomy of the smut-fungi. All loose smuts of oats, wheat, barley, and the close smuts of oats and barley were united under the single species *Ustilago carbo*. This prevented the investigations of the biology of the smuts, and it was not until the fact was demonstrated that various species of smuts were concerned that the way was opened for the proper investigation of the biology and subsequently also of the control of the parasite.

The development of our knowledge of the smuts was due to the biological facts demonstrated by Brefeld and Hecke. They discovered that infection takes place through the

flowers. This fact pointed out the way of control. The problem was to kill one organism, the smut-fungus, within another organism, the grain seed, without doing damage to the latter. Jensen by his empirical work had demonstrated that such a procedure was possible. The correct method of control, however, could not be worked out because of the lack of knowledge concerning the fundamental scientific facts involved. In order to establish such a firm basis, I, together with my assistant, Riehm, studied the resistance of the smut-fungi to external conditions, primarily to the effects of temperature. When the mycelium was grown in water and other substrata we demonstrated the fact that the thicker-celled mycelium as well as the spores are more resistant to external influences than is the vigorously growing mycelium. However, not only the smut but also the grain is more resistant in the resting period than when germinating. Therefore, we tried to bring the infected grain seed under conditions which cause the fungus to grow and which at the same time do not allow the seed to germinate. We succeeded in doing this by allowing the seeds to remain for about four hours in water at 25-30°C. If one then subjects the seeds to a temperature at which the mycelium is killed but which does not yet induce germination in the grain, it is possible to kill the mycelium in the seed without injuring the latter.

In these investigations the key to the so-called hot water and hot air treatment was found, and it was then only a technical problem to build apparatus with which the desired results could with certainty be realized. For our conditions in Germany this latter problem has also been solved. We have constructed several pieces of apparatus of this sort, and the treatment of grain against loose smut has been introduced on many farms.

But the smut-problem has not been solved for all cases. This is especially true in the case of the stinking smut in the United States. This disease is of the greatest importance in the wheat districts of Idaho. In Germany *Tilletia Tritici* is spread by the seeds and is controlled by seed disinfection. In Idaho it occurs so generally in the soil that disinfection is

of no avail. Losses of 25 per cent of the crop are not uncommon. The solution of this problem seems possible only by the breeding of disease-resistant varieties. It is certain that smut-resistant races of wheat exist. The problem is to find these varieties and, in case they are not sufficiently productive, to cross them with other varieties until races which combine the desired characteristics are obtained. In the districts where smut occurs every year it is possible to find these races in an empirical way. But in general it is my opinion that all work of selecting and breeding should be prosecuted along fundamental scientific lines.

It is therefore first of all necessary to determine to what characters the plant owes its disease-resistant qualities. When this has been accomplished it is next necessary to determine to what extent the characters are heritable, that is to say, whether they appear in crosses as dominant or recessive. The great advantage of this method lies in the fact that it makes it possible to recognize resistant races (by the presence of the specific characters to which resistance is due) without infection experiments, which are uncertain owing to the influence of external and unknown conditions.

I have shown to you by this example that in the solution of a single phytopathological problem such diverse branches of botany as taxonomy, biology of the flower, fungus-biology, and inheritance are involved. The following examples will show that in addition other branches of botany are of importance in phytopathology.

In exact phytopathological investigations it is a primary factor that one know the host plants and the parasites in detail. This information must be based upon thorough systematic knowledge. This seems to be very easy in cultivated plants, the species of which are generally well distinguished. Some cases, however, are more complicated. When we want to make studies of cereal rusts, it is not sufficient to know the races of cereals by their agricultural names. We must know to what botanical species they belong; our cultivated wheats, for instance, comprise species of different susceptibilities.

Much more difficult are the systematic relations of the fungi. Many experiments and publications are valueless because the identity of the fungus was not made sure of in every single case. These difficulties are greater in case the fungi in question belong to the *Fungi Imperfecti*, where very often only the name of the genus has been determined, while the species name was simply made from the name of the host. Moreover, the descriptions of these imperfect fungi are often so insufficient that it is impossible to identify the fungi afterwards, especially when they occur on other plants or on a different or unrecognizable substratum. Within a genus that is rich in species there have sometimes been erected so many species that there is no possibility of identification. We find an instance of this in the genus *Fusarium*. Several hundreds of species have been described; which of these are identical has not yet been made clear, and in many cases this may never be possible. We cannot always solve the problem by making use of the exsiccata of the author of the species. Moreover, on one species of host several species of *Fusarium* may be harbored, and the author has often considered them identical. It is further often impossible to find what fungus was the type of the author's description. In such a case the only alternative is a thorough reworking of the taxonomy. How extensive a work this may often involve is instanced by the genus *Fusarium*. To establish the fundamental facts regarding the taxonomy within this genus required four years of work on my part as well as on the part of my assistant, Dr. Wollenweber, who devoted all of his time to the subject.

Even after the establishment of these fundamental facts, only a very small part of the species had been determined, and for another two years Wollenweber has been working up the remaining species. I wish only to point out in addition that there exist more genera of this type: *Botrytis, Gloeosporium,* and *Alternaria* and its relatives.

Modern taxonomy of fungi cannot limit itself to the morphology of the species casually collected. It must have the help of pure cultures on various media, for in artificial culture additional differences show themselves. These differ-

ences are not only biological, such as color formation and changes in the culture media, but also morphological, such as the form of the "Fuszellen" or basal cells of species of *Fusarium,* and even gross, as, for instance, differences in form of colonies, etc.

In the first place, artificial culture is of enormous value as it furnishes the proof of the presence or absence of a relation between different forms of fungi. This knowledge not only gives us a better insight into the development of the organism, but also gives us most important information as to the methods of control.

In the identification of bacteria cultural methods are absolutely necessary as these organisms cannot be determined otherwise. The determination of the host and its enemies is not only desirable on the ground given above, but also because it gives us opportunity for ecological observations. A disease occurs only when conditions are favorable to its development, and these conditions are often pointed out by the composition of the flora of the locality, of which my studies upon the dying-out of alder trees in Germany give you a clear proof. In different localities these trees are killed by a fungus, *Valsa oxystoma.* The fungus grows into the wood through wounds, especially where branches or twigs are broken off, and kills out parts of the cambium and the bark. The parts into which it does not penetrate remain alive. There was no doubt about the fungus being the cause of the disease, but there were groups of trees which, though the fungus was present, were not quite killed out, the damage done in these localities being much smaller. I hit upon the correct explanation of this condition through a study of the special character of the flora under the trees. It was a typical flora of pastures, in which occurred specimens of *Iris pseudacorus* and retreating areas of *Carex paniculata.* These two plants are typical inhabitants of the peats, or water borders. It was clear that the locality had been formerly of a peaty character. I could determine that recently the water level had been lowered for the formation of artificial meadows. Without a knowledge of the flora this relation would never have been found, as these meadows

were situated behind a chain of hills. The depth of the ditches had changed the water level and prepared the right conditions for an attack of *Valsa oxystoma.*

In another paper I have shown the importance of the work of E. Münch.[1] This work is a model as to the manner in which investigations of plant diseases upon a scientific basis should be prosecuted. And, therefore, I wish to come back in a more detailed way to the work of Münch. The fungous diseases of our trees belong, in general, to the most important diseases, and we yearly lose millions on their account. But we did not know the factors upon which the appearance of such diseases rested until these were demonstrated by the work of Münch. It was known that many fungi attack woody plants under definite conditions. Sometimes closely related species of one genus of hosts behave differently and sometimes only definite tissues are attacked. Lastly these relations vary in different years or seasons in different localities. The difficulty has been that the cause of this variability was sought in the different soil conditions which might have an influence on the constitution of the tissues of the host, in external injuries—such as sunburn or frost, and in the period of development of the fungus. These factors, however, are not of fundamental importance in the question of the production or suppression of a fungous attack.

Münch has proved through numerous experiments that the content of air in the tissues is the determining factor. The greater part of the wood-decaying fungi have a large air requirement and are able to grow only when a maximum of air is furnished. In the first place the content of air is dependent on the quantity of water, and the occurrence of this large class of plant diseases depends upon the water supply. Similarly, the quantity of solid substance may be of influence. Specimens with narrow annual rings are more resistant than those with broad ones, because there is less room for air in the former. The different annual rings of the same wood

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[1]Untersuchungen über Immunität und Krankheitsempfänglichkeit der Holzpflanzen. Naturwiss. Zeitschr. f. Forst- u. Landw. 7: 54–75, 87–114, 129–160. 1909.

may be attacked differently, which is supported by the evidence of many observers. Not infrequently do we find tree trunks in which only some annual rings have been infected, or in which the same ring is diseased on one side and healthy on the other. The decayed rings are always the broad ones. The same varieties have a different air content in different localities. In the neighborhood of water sprouts or vigorous branches, the tissues are rich in water and poor in air, and infections very often do not penetrate into such regions. We know now that poorly fed and crippled specimens are likely to be attacked; on the other hand, it seems clear that fruit trees which are richly fed with nitrogen are very susceptible to canker. An abundance of nitrogen induces the development of a very loose tissue, which during drought is more subject to diseases than a firm tissue. We recognize the periodicity in the occurrence of many plant diseases, for we know the fluctuations in the water content of a tree. The air content of the healthy bark of beeches in winter-rest is 19–20 per cent, and diminishes at the time of budding to 11 per cent, rising afterwards. This is correlated with the fact that the canker, which in Europe is caused by *Nectria ditissima,* does its damage from autumn until spring, while this damage ceases during the vegetative period. This was pointed out by Aderhold, who, however, failed to recognize the cause.

If once we know the absolute percentage of air necessary for fungous growth in the different kinds of wood, we may decide through direct investigation whether in certain localities the danger of infection is large or small. We may test the different varieties and try to avoid the danger. By this method the control is not directed against the fungus, but against the conditions which make its growth possible. In other words, we use instead of direct control, measures which prevent the outbreak of epidemic diseases.

You see by this example what an exactly planned scientific investigation may do, and you can recognize the application of these facts to the American conditions. In the irrigated districts the fruit trees have but few die-back diseases due

to species of *Valsa* and other fungi. When, however, such diseases occur, you will find the cause in defective irrigation methods, which may be remedied by changing the irrigation system. It is of the greatest importance that the land be irrigated at the time the trees contain less water and plenty of air, and that the next irrigations be made in time to prevent an excessive decrease of the water in the tissues.

Not all fungi, however, are dependent upon the air contained in the wood. This is, for instance, the case with *Armillaria mellea,* where the rhizomorphs bring a sufficient quantity of air into the inner tissues. Whoever has cultivated the fungus artificially knows that after a short time rhizomorphs are formed which grow deep into the medium. But the rhizomorphs are not formed on all kinds of trees and it may be possible that the fungus in these cases depends on the air already in the wood.

Another question of great importance for American conditions is the question whether the growth of bacteria, principally of *Bacillus amylovorus,* is dependent upon the air content of the host or not. These experiments must be supported by thorough physiological investigations. That manner of control which seeks to remove the bacteria by cutting out the branches does not guarantee success for the future. I have been convinced of this in my trip through the United States, where I visited districts in which this control measure was thoroughly carried out.

It may be possible that not only trees, but also herbaceous plants, show relations between fungous growth and air content. I think it must be so for the organisms which cause the wilt diseases and the rhizoctonia disease of the potato, both of which have a high air requirement. On media poor in air these fungi grow only on the surface and absorb very eagerly the oxygen of hydrogen peroxide. The growth of *Rhizoctonia* in the well-aërated peat soil of the Stockton Delta and the forest soil of Germany is more marked in the dry years than in the years when the plants get a sufficient supply of water. In the United States these diseases are wide-spread, principally through the irrigated lands. In my trip I came to the

conclusion that these diseases are not to be controlled by fighting the fungi, but by influencing the potato plant. Though caused by a fungus, the production of the conditions favorable to the progress of the disease is attributable to irrigation. In many cases the root system was poorly developed, the different kinds of irrigation showing an influence upon the growth of the underground parts of the plants. We know very little of the conditions of growth of the potato in spite of a few publications on this subject by Müller-Thurgau, De Vries, and Vöchting. Moreover, we know nothing about transpiration and water requirements in these plants or about their ability to form roots, or the factors that influence these processes. It is, therefore, very important that Shantz, of the Department of Agriculture, has actually undertaken the investigation of these problems. Others must follow him as soon as possible to solve these questions for the irrigated lands.

The chemical-physiological side of the phytopathological questions also needs more attention, as has been pointed out recently by me and others in work upon the freezing problem. For a true judgment of the resistance to frost, in the case of cereal diseases, Gossner has apparently found the right way. The earlier stated fact that the cells of small pieces of tissue floating on a sugar solution are less quickly killed by frost than when floating in water, made it probable that the young plant is protected by sugar against frost injury. The investigation of the winter and summer rye shows that the sugar content of the former is several per cent greater than of the latter. The same is the case for frost-susceptible races of wheat. We may thus find out the relative frost resistance of closely related races of plants by determining the sugar content.

But other phases of chemistry are of importance in phytopathological investigations, as, for instance, the chemistry of colloids, which, as Ruhland showed in his work, is of great value. The microchemical reactions are also of great importance. We know today that cork formation in the potato is a protection against bacterial invasion. I could show by using the reaction of Tisson that the deposition of

cork in the cell walls near the places of infection occurs earlier than the formation of cork plates.

Of special interest is the physiology of inheritance. In this lecture I wish merely to emphasize that the inheritance of the unit characters and their behavior in the next generation is one of the fundamentals of breeding resistant races.

Finally, I must speak of anatomy. The necessity of the examination of series of sections oblige the pathologist to make use of the latest discoveries in histology. It is by way of anatomy that we shall approach the problem of leaf-roll of the potato. Onemjer has shown that the sieve tubes, which have the function of providing the plant with albumen, are destroyed in the leaf-rolling plants, similar symptoms occurring in plants which suffer from other diseases only when the plants are nearly dead. In leaf-rolling plants, however, we find these changes from the very beginning, and we may use them in diagnosis. Anatomy, likewise, points out relations between external disease symptoms and inner changes of structure. For instance, the three inner diseases of the potato, leaf-roll, wilt, and bacterial ring disease, have distinguishable anatomical characters; the leaf-roll is a disease of the phloem; wilt, of the secondary wood vessels; and bacterial ring, of the spiral vessels. A thorough anatomical knowledge is of primary importance in all investigations concerning the inner structure of healthy and diseased plants, the formation of excretions and tyloses, and the different ways of recovery.

I hope that it has been possible for me to show you that phytopathology has many fundamental relations to scientific botany, and that it further presents many important problems for scientific investigation which deserve attention from the botanical departments of universities.

Should I have succeeded hereby in winning new friends to phytopathology in this sense it would be a source of genuine satisfaction and pleasure to me.

THE LAW OF TEMPERATURE CONNECTED WITH THE DISTRIBUTION OF THE MARINE ALGAE

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What I have to bring before you is simply a preliminary consideration of the general subject of the geographical distribution of the marine algae together with some inquiry into the conditions immediately affecting such distribution and as possibly effecting a segregation into the larger units. In accordance with such an intention, I have started a tabulation of all the marine species and varieties, which is far from being completed as yet, but which has, however, reached a stage at which certain general statements may be made as to probable results.

The geographical distribution of the marine algae has been treated of in various ways and in many papers. It is more or less customary to make a comparison between a particular flora and other more or less corresponding floras in comparative tables, percentages of common and endemic species, etc. Certain speculations, based on such data, as to the origin of certain algal floras have also been indulged in. The result is that we have certain geographical areas fairly well marked out and certain others more or less indistinctly outlined or surmised. Certain ecologic classifications have been proposed, particularly as to zonal occurrence in varying depth, influence of varying degrees of salinity, character of the substratum, influence of surge, quiet waters, etc. Very little attention, however, has been paid to general factors controlling distribution over larger areas. We speak broadly of tropical species, or of arctic or antarctic species, of temperate species, etc., but no attempt has been made to survey the distribution of marine algae in general throughout the oceans and seas of the world and to attempt to determine the limiting factors segregating one large area from another. An attempt to determine how far our present knowledge of

species and their distribution may further such an inquiry is the object of the present paper.

Among the more general discussions, there are to be mentioned first those connected with the geographical distribution in the Arctic Ocean. Kjellman's extensive and fundamental paper 'Algae of the Arctic Sea' ('83) led the way and placed at the disposal of future students a very considerable amount of data and brought forward certain fundamental points of view as to a division of the arctic marine flora into provinces, as well as a consideration of the conditions underlying this division. This work was the result of the working over of very considerable collections of the various Swedish expeditions into the Arctic Ocean and a careful examination of all other existing data.

Later, Rosenvinge ('93, '98, '98[a], '98[b]) published a series of papers dealing with the marine flora of Greenland, and Jónsson ('03, '03[a], '04, '12) has also published on the same subject as well as on the algae of Iceland and Jan Mayen.

Finally, somewhat over twenty years after Kjellman's paper, Simmons ('05) surveyed the whole matter, revised all tabulations of the Arctic flora and brought forward further views together with a full discussion of all literature bearing upon the subject.

In these various papers and others not referred to specifically, the North Polar Sea is defined and delimited from the Northern Atlantic and Northern Pacific Oceans. The conditions under which marine algae occur in the Polar regions as well as the differences between the conditions of the various portions of its waters are also determined and discussed.

The North Atlantic has also been treated of, but more floristically than as to uniformity, or differences, of physical conditions affecting the flora. A considerable part of the discussion regarding the North Atlantic Ocean has centered about the Faeröes. Simmons ('97), Börgesen ('02, '05), Porsild and Simmons ('04), and Börgesen and Jónsson ('05), have discussed the marine flora of these islands together with its relation to other North Atlantic floras and ocean currents. Reinke ('89), Svedelius ('01), and Kylin ('06, '07),

have considered the algal flora of the Baltic Sea and its relation to that of the North Atlantic from points of view both floristic and as to physical conditions. Harvey ('58), Farlow ('81), and Collins ('00), have dealt similarly with the algal flora of the northeastern coast of North America, and Börgesen and Jónsson ('05) have made an extended floristic comparison between the floras of the North Atlantic and those of the polar or arctic seas.

For the antarctic and subantarctic regions, the work even of floristic comparison is still hampered by incomplete knowledge. The foundations were laid by Hooker ('45) in the 'Cryptogamia Antarctica' in which there are scattered notes on distribution. Skottsberg ('06) published his 'Observations on the Vegetation of the Antarctic Sea' and later ('07) the first part of his antarctic and subantarctic work. The latter has only floristic details with notes on distribution. Gain ('12) has given a detailed discussion of the distribution of the marine algae thus far credited to either the antarctic or the subantarctic regions of the western hemisphere. Murray and Barton ('95) have given a comparison between the arctic and antarctic marine floras, and Mme. Lemoine ('12) has made a similar comparison limiting it, however, to the species of crustaceous *Corallinaceae.*

The distribution of marine algae in the warmer portions of the oceans, Atlantic, Pacific, and Indian, has not been so much considered as that of the colder portions, although very considerable floristic work has been done. Murray ('93) published a comparison of the marine floras of the warm Atlantic, Indian Ocean, and the Cape of Good Hope. Yendo ('02) has made definite statements about the distribution on the coasts of Japan. Saunders ('01) and Setchell and Gardner ('03) have dealt with the northwest coast of North America, and Schmitz ('96) and Schroeder ('12) have called attention to the relations between the marine flora of East Africa and those of the East Indies and of the central Pacific Ocean.

Various papers and floras have considered distribution, such as bathymetric zonal distribution or according to varying substratum, salinity, etc., within limited regions, prov-

inces, or districts, but no general paper has as yet appeared dealing with the distribution over the oceans in general or any definite suggestions as to the factors concerned.

The nearest approach to an attempt to account for the general facts of distribution is my own attempt (cf. Setchell, '93) to explain the main facts of the geographical distribution of the *Laminariaceae*. The plants of this family are rather inhabitants of the colder than of the warmer waters, proceeding, as it were, from the poles towards the equator, but lacking in strictly tropical waters. It was found that the *Laminariaceae* flora changed its facies with every increase or decrease of 5°C. of summer temperature, thus forming latitudinal zones controlled by temperature relations. This idea was extended to explain the demarcations of the floras of the west coast of North America by Gardner and myself (cf. Setchell and Gardner, '03) with apparent adequate reason.

In attempting to discuss the more general facts of distribution we first necessarily consider the various marine floras and their subdivisions. While the term flora has been used in all sorts of senses, both wider and narrower, to include any aggregation of plants of any region under discussion, whether larger or smaller, it generally carries a certain idea of uniformity of composition with it when used in connection with the floristics of distribution. This uniformity may, however, be only as regards region. It is desirable, here, to use the word for the aggregation of species of marine algae found in a certain region, province, or district, having a certain fairly considerable percentage of species in common throughout its extent, even of the more extended region.

The world's surface, whether land or water, is usually divided into zones of temperature, these in turn into regions, the regions into provinces, and the provinces into districts. For marine floras, the districts must be still further divided into formations, and these in turn into bathymetric or littoral belts. The bathymetric belts, in their turn, show different algal associations.

Considerable work has been done in the description of various floristic associations occurring in various depth belts and of various formations, and the special ecological relationships have been discussed and made reasonably plain. My intention, however, is to discuss the broader distribution and segregation of floras, particularly as to regions and perhaps provinces and to attempt to determine the factor, or factors, governing these.

In attempting to mark out the various floristic regions and their provinces, we are met with certain difficulties. The flora of the Arctic or Boreal region is fairly definite and has been the most carefully studied and tabulated. The provinces of the Arctic region are the Asiatic, the American, that of West Greenland, and the extended province of Spitzbergen (cf. Simmons, '05). The North Atlantic Ocean as distinguished from the Arctic has five regions, viz., those of Northwestern Europe, Southwestern Europe, and the Mediterraneo-Northwest African region on the east and Northeastern North America and Middle eastern North America on the west. The Antarctic or Austral region possesses a fairly consistent flora and is not so readily divided into provinces, but the Antarctic-Magellanic province may be contrasted with the Indo-Pacific province. The South Atlantic Ocean has a flora as yet little understood, but, for the present at least, may be considered to have the regions of Southwest Africa and Southeast South America. The Northern Pacific has Bering Sea probably representing a province of the Arctic or Boreal region. Otherwise it is divided into five regions, viz., those of Northwest North America, Middle West North America, and Southwest North America on the east and the Ochotsk-Yeso region and that of East and West Honshu (or Nippon) on the west shores. The South Pacific Ocean has five regions, viz., those of Southwest South America, Middle West South America on the east and those of New Zealand and South and Southeast Australia on the west coasts. The southern portion of the Indian Ocean has two regions, viz., that of Southwest Australia and the South Africa or Cape region. The tropical waters may probably be divided into two regions, viz., the

Tropical Atlantic and the Indo-Pacific regions with their proper subdivision into provinces. Concerning these various regions, it may be said that some seem to possess very distinct and characteristic species content while others are more or less related to one another. However, it is expected that there will be a possibility of discussing this segregation at another time in more extended fashion.

Of particular interest and importance in connection with the marking off of floristic regions, are the points or areas of demarcation. Some of these are well established while others may be only more or less accurately surmised. One of these much referred to in the literature (cf. Harvey, '58; Farlow, '81; etc.) is Cape Cod on the eastern coast of Massachusetts which divides so clearly and so accurately the flora of northern New England from that of southern New England. Cadiz in Spain appears to be another point of demarcation, or possibly indication of an area, where the flora of the Southwestern European region stops, or mingles with that of the Mediterranean-Northwest African region. At Clare Island on the west coast of Ireland (Cotton, '12, p. 160) the flora "resembles that of the southwest of England," but it has elements also of a distinctly northern character. It is probably in or near a demarcation area. Similarly southern Norway and the west coast of Sweden (Kjellman, '02, '06; Svedelius, '01; Kylin, '06, '07) have a mixed flora and are in a transition region.

In Japan Cape Inuboi on the east coast of Honshu (cf. Yendo, '02, p. 181) is a demarcation point and the Strait of Sangar (cf. Yendo, '02, p. 182) is also a region of demarcation or transition. On the opposite side of the Pacific Ocean, along the western coast of North America, Cape Flattery or just south of it, Point Conception, and the region about the mouth of the Gulf of California are demarcation points or indicate transition areas (cf. Setchell, '93, p. 370; Saunders, '01, p. 393; Setchell & Gardner, '03, p. 170). In the southern hemisphere the marine flora of the Cape Region is definitely delimited both to the southwest and to the northeast and in

Australia the marine flora of the southeastern region is definitely set off from that of the southwestern region.

These various points and regions will doubtless become more definite and more of them will become established as careful investigations of the floras are made. They undoubtedly indicate that thereabouts are changes in the conditions regulating the separation of the general flora into its larger divisions and are of great importance in any inquiry as to the general factors affecting the distribution of marine algae.

Along with the mapping out of floras into regions, provinces, etc., it seems best to consider, next, the factors which seem to regulate the distribution. These have been considered by Kjellman ('83) and by others, and are summed up by Oltmanns ('05). Particularly is it desirable to consider which may be chiefly responsible for the limiting of the species within the regions or provinces.

The substratum exercises an important influence on the attached flora or benthos and that is particularly the part of the marine flora I intend to limit this paper to, since the plankton brings in certain particular factors having to do with its floating habits. Of course, benthos can only exist on its proper firmer substratum and different species differ in the nature of this. However, it is sufficiently evident that the character of the substratum limits species only locally and can by no means be considered as a factor in controlling floral regions or even floral provinces.

The motion of the water is a limiting factor in distribution, some algae preferring quiet water, some flowing, some surge, etc., but this factor, too, is clearly a local and not a general one in the distribution of the marine algal benthos.

The specific gravity of sea-water varies and with it, of course, its salt content. This variation, so far as marine algae are concerned, varies from water only slightly brackish to that (in case of exposed and shallow tide pools) of an almost concentrated solution. There is a latitudinal zonal difference here also, but it is not so great as may be found in localities at no considerable distance from one another. It

certainly seems impossible that this can be a general factor. Its local effect, however, may be very considerable.

Light varies from the equator, where it is most intense, to the poles where it is least. It very decidedly limits the distribution as to depth. Marine algae of the benthos need light and are, therefore, limited to the neritic portion of the photic zone as to their general distribution. Outside of this general limitation, however, it does not appear that the varying intensity of light can be considered as a prime factor in limiting floral regions and floral provinces, i.e., not alone.

Varying temperature, however, does act directly upon algae to limit their distribution, both locally and generally. It can easily be recognized to be the one most important factor in controlling the distribution of benthos over wide areas as well as, at times, in smaller districts or spots. We recognize that, in general, the species of the frigid zones, of the temperate zones, and of the tropical zones are sufficiently different to give an entirely different facies to each. Yet, in considering general regions, we find that they are not marked out by the same parallels as are used to mark these zones geographically. These geographical zones, however, are established more particularly as regards direction of the sun's rays and the temperature of the air rather than that of the water.

The waters concerned with the life and persistence of the algae, even of the benthos, are, relatively speaking, the surface waters, since algae seldom grow lower than at a depth of 100 meters and for the most part cease at 20-30 (or at times 40) meters. The normal decrease in temperature at such depths is slight even in temperate waters, although, at times, sufficient to account for special sporadic anomalous distribution. The range in temperature under which algae, in general, may carry on their full course of vegetative and growth activities is from —2°C. up to the neighborhood of 90°C., but that for marine algae is only from —2°C. up to 30°C. (or possibly 32°C.), this being the extent of ranges for all surface waters of the ocean.

A comparison between charts in which the isotherms for surface temperature of the water of the oceans are laid off

shows a definite correspondence between certain of these lines and the boundaries of different marine floral regions as previously laid out and indicated in this paper.

From the point of view of the distribution of the marine benthos, so far as algae are concerned, it is found by practice to be satisfactory to divide the surface waters of the ocean into nine zones, as follows: Upper Boreal, Lower Boreal, North Temperate, North Subtropical, Tropical, South Subtropical, South Temperate, Lower Austral, and Upper Austral. The limiting isotherms of surface temperature chosen are those of the summer month or maxima, viz., the isotheres, which are those of February (or possibly March) for the southern hemisphere and those of August (or possibly September) for the northern hemisphere. These lines are laid down with approximate accuracy in the charts of the atlases of the different oceans published by the "Deutsche Seewarte" of Hamburg ('92, '96, '02). These isotherms are more accurate and explicit for the open ocean than for the neritic zone where the algal benthos occurs, but, with certain allowances, the zones as indicated are sufficiently accurate.

Each of the zones I have proposed covers 5°C. range of surface temperature with the exception of the Upper Boreal and the Upper Austral, each of which includes a range of 10°C. or slightly over. The zones, then, more or less arbitrarily adopted, are the Upper Boreal and Upper Austral, between the isotheres of 0°C. (or even —2°C.) to 10°C., Lower Boreal and Lower Austral between the isotheres of 10°C. and 15°C., North Temperate and South Temperate between the isotheres of 15°C. and 20°C., North Subtropical and South Subtropical between the isotheres of 20°C. and 25°C., and the Tropical between 25°C. and 30°C. (or above).

These 5°C. zones are thus laid out according to the 5° isotheres, because on inspection these isotheres approach most closely or touch the shores at the division points of floras and principal floral provinces. They have been determined empirically, and indicate, as it seems from experience in working with them, that they coincide with floral boundaries the oceans over more exactly than do any of the

winter isotherms or isocrymes, or any of those in the intermediate seasons.

For example the isothere of 20°C. passes somewhat south of Cape Cod to the eastern end of Long Island, but the shallow and more or less protected waters of Long Island Sound, Narragansett Bay, Buzzard's Bay and Vineyard Sound carry a higher temperature eastward even to the Cape Cod region. At exposed points, however, the somewhat colder waters of the ocean outside exist and exercise their influence at exposed points or in deeper waters.

Again at Cadiz, the isothere of 20°C. abruptly curves up to the coast. At Cape Inuboi, Japan, the isothere of 25°C. touches land and at the Strait of Sangar, that of 20°C. The Cape Region of South Africa is included between the isotheres of 20°C. and 25°C. Similar relations hold good on the coast of Ireland, for the 15°C. isothere comes in just north of Clare Island at about Annagh Head. On the south coast of Australia, the isothere of 20°C. touches the east coast just above Cape Howe and the south coast about Cape Arid, thus leaving the southeastern coast below 20°C. of average summer temperature and the southwestern coast above it. Although the western coast of North America has its temperature relations very much disturbed, as I shall indicate later, yet there is a fairly definite relationship to the isotheres of 10°C., 15°C., 20°C., and 25°C. The arctic or boreal floristic region has a definite southern boundary in the 10°C. isothere and the subarctic in that of 15°C., while those of the North Atlantic are bounded to the south by that of 25°C. The strictly tropical species are found almost entirely between the isotheres of 25°C. and 30°C. (or 32°C.). It is expected that a later paper will deal more definitely and in more detail with the reasons for selecting the isotheres as bounding lines for the temperature zones.

Two seeming disturbances of those zonal areas may be noted in passing; one is that the polar zones (Upper Boreal and Upper Austral) are for 10°C. interval rather than 5°C. This is in accordance with what is known of the distribution of the marine flora in the higher Arctic and the higher Ant-

arctic regions, where there seems to be no useful purpose served in segregation by assuming two zones rather than one. The second disturbance of zonal areas is through the occurrence of local areas, of greater or less extent, of water of a higher or lower temperature than is normal for the general zone. Colder waters occurring among warmer waters are found along the west coasts of North and of South America, of northwestern and southwestern Africa, and of northeastern Africa. These are due to currents or to upwellings of cold water. Their existence is well substantiated but their cause is still a matter of discussion among oceanographers. When warm waters exist among colder waters, they occur as "spots" or small areas where the higher temperature is due to comparatively local factors apart from general oceanographic conditions. Such disturbances as upwellings and spots may bring about a puzzling discontinuity in the distribution, very puzzling, indeed, until the immediate cause is discovered.

Another matter causing seeming disturbance of the limits of temperature zones proposed is the seasonal variation of the temperature of the surface waters. This is variable, but in general may be considered to hold true as follows: The seasonal surface temperature variation as platted for 2° squares is least in the Upper Boreal, Upper Austral and Tropical zones, where it is not over 5°C. in range; is greatest in the Temperate zones where it averages nearly 15°C. and may be as great as 27 or 28°C., and is medium in the Subtropical zones and in the Lower Boreal and Lower Austral zones where it approximates 10°C.

These, then, are the principal features of temperature distribution with which we may be concerned.

In connection with the empirical establishing of the temperature zones previously outlined, I have attempted to arrange each and every species of marine algal benthos thus far described in the zone or zones to which it has been accredited. The work is not as yet by any means completed, but a general view has been obtained for the *Rhodophyceae, Phaeophyceae, Chlorophyceae,* and *Myxophyceae,* and the greater part of the

Rhodophyceae have been worked out in fair detail, although no percentages of absolute accuracy can be given at present. The general results are as follows:

(1) The greater part of the species are known from one zone of temperature.

(2) A considerable number of species are known from two zones of temperature.

(3) A comparatively small number are credited to three zones of temperature.

(4) Species credited as occurring in four or five zones of unlike temperature are extremely few and almost always doubtfully so accredited.

(5) There is a change of facies of the flora in each successive zone, i.e., with every increase or decrease of 5°C., excepting in the cases of the Upper Boreal and the Upper Austral.

This means that most species are, so far as known, confined to zones of amplitude of 5°C. of summer temperature, that certain species extend over zones representing 10°C. amplitude, while a few may extend over zones representing 15°C. amplitude of summer temperature, and extremely few definitely known in zones covering over 20°C. amplitude of summer temperature.

To mention the results of the preliminary survey of the marine *Rhodophyceae* so far listed and checked, may give approximate conditions which also seem to exist in other groups. The species and varieties thus far accredited to this group number about 3,350. Of these the northern hemisphere has about 34 per cent in its extratropical waters, the southern hemisphere approximately 44 per cent, while the tropical waters have approximately 22 per cent. Of the entire number, approximately 71 per cent are confined to one zone of temperature; about 21 per cent extend over two successive zones of different temperature; about 6 per cent are accredited to three successive zones of different temperature; while between 1 and 2 per cent are accredited, but with more or less, generally very considerable, doubt, to four, or even to five, successive zones of different temperature.

Commenting on the above, it may be surmised that the percentage in one zone is high on account of many new or little known species which have been collected only once, while the percentage of species occurring in two successive zones of different temperature is low because of our incomplete knowledge. Concerning the species credited to three zones, the percentage is small but perhaps not much lower than will be found on final careful revision. Here seasonal occurrence and "spot" distribution will undoubtedly be found to be concerned in the overlapping, as it will be also in the case of overlapping in two zones. Concerning the occurrence in four or five successive zones of different temperatures the percentage although small will, with very little doubt, be decidedly decreased or even entirely erased when the doubtful cases are investigated and cleared up. There may be a fraction of one per cent still left, however, and if there is, I doubt not that some fairly simple physiological explanation of their toleration of such an extreme range of temperature will be found. The disturbances in the uniformity of regular increase or decrease in the temperature of surface waters, as referred to latitude, have already been mentioned as due to cold upwellings and spot variation according to local physical peculiarities. These disturb, of course, the zonal distribution. Where such intrusive areas of colder or warmer water are extensive, the distribution in those areas must be considered in connection with the nearest zone of similar temperature. Spot distribution also, may be so referred but only in general considerations of distribution. Otherwise it must be considered specially.

The disturbance of regular zonal distribution which must have special consideration from the zonal point of view is that which arises from seasonal variation in the surface temperature accompanied by seasonal occurrence of a certain element of the flora in some district or province of a region of the particular zone.

Seasonable amplitude varying on an average from about 5°C. to 15°C. in extent, as I have mentioned before, is found in the various temperature zones. Seasonal duration, or, at

least increased seasonal vigor in certain elements of the flora is found in all zones, a phenomenon of mixed dependence upon light and temperature. It is most marked in the Temperate zones but is to be found in the Subtropical, Lower Boreal and Lower Austral zones as well. In the Upper Boreal and Upper Austral zones its appearance is perhaps more associated with varying intensity of light than with temperature, and it is least pronounced in the Tropical zone, where it seems to be wholly dependent upon light variation.

It is certain that many boreal summer species appear as winter or early spring species in the Temperate zone and likewise certain temperate species appear during the colder season in the Subtropical zone. There is some, but apparently not very much, overlapping between the upper portions of the Subtropical zones and the Tropical zone. From the very incomplete studies thus far made, it seems that most species range through from 5 to 10°C. of temperature, that each zone has its own characteristic species and that extensions up to 15°C. for active growth and reproduction are few, if at all existent. More careful examination, however, is necessary to satisfactorily demonstrate this last point.

While the limits of the temperature zones have been founded on the isotheres or lines of average daily summer temperature, seasonal phenomena cause us to consider also the isocrymes or lines of average daily winter temperature, especially as to overlapping or transitions between the zones. The isocrymes are of especial importance in those portions of certain zones where, especially on account of strong currents, the seasonal variation is extreme, e.g., on the eastern coast of North America and on the eastern coast of Asia. In such regions there may be expected extreme expression of seasonal change of flora.

The disturbances of distribution due to upwellings cause confusion in the tabulated results unless they are to be definitely accounted for. This confusion is greatest at present in connection with the species of the central coast of California. Spot distributions also cause the species concerned to be tabulated in more than one, or, if combined with seasonal disturb-

ance, over three zones. Spot distributions are less easy to detect than other anomalous distributions but enough are sufficiently known to make apparent their influence and importance in any scheme of representation of geographical distribution.

While the distribution of any particular species of plant depends upon a complex of conditions controlling continued existence, both vegetative and reproductive, certain more general factors may be distinguished as prevailing over larger areas, while others, less general, may account for local and usually discontinuous distribution within particular provinces and districts, and as components of various formations, bathymetric belts, and associations.

Temperature has come to be considered as one of the most important of the conditions controlling, or governing, the distribution of plants and animals (cf., e.g., Merriam, '94, '98, etc.; Livingston and Johnson, '13; and others). Any biologic factor has, of necessity, two variables (cf. Livingston and Johnson, '13, p. 351), intensity and duration, and these two variables present considerable range, especially in the case of land plants. For marine plants, particularly for those species constantly submerged, the amplitude of these variables is less than for the land plants. The surface waters of the ocean, while influenced by the temperature of the air, change slowly and only within certain limits. More considerable is the variation through the influence of varying, especially seasonal, currents or upwellings. Yet on the whole the temperature variables are seemingly, at least, much less in amplitude than are those of the land. For those plants exposed during tidal changes the temperature variables may be considerable in amplitude. Yet such exposures are only occasional and of short duration, except, perhaps, for the plants of the uppermost tide limits. One matter of importance as to all factors in plants submerged entirely or for the greater portion of the time, is the uniformity of exposure to the same conditions. While the land plant may have its roots buried in the soil of one temperature and its aerial organs exposed to a considerably different temperature, the entire

surface of the submerged plant is exposed to one and the same temperature. The problem, therefore, of temperature as a physiological factor in controlling the distribution of algae, in general, and of marine algae in particular, is, as compared with that of land plants or of land animals, comparatively simple.

Any attempt to unravel the physiological basis for the control of distribution must be, at this point of the progress of the work, lacking sufficient data for conviction. The statements presented merely represent approximate optimal conditions for the duration, succession, and, therefore, continued persistence of the species of the various life zones. It seems certain that the coefficients for continued existence vary among the different species, but are restricted in the case of each species to about 10°C. in amplitude. There must be for each species a certain minimum and a maximum of optimal temperature for continued life and reproduction. It is possible that certain species may continue to exist outside these, especially if they possess powers of vegetative reproduction.

Thus far, it has been in mind to attempt to determine coefficients of efficiency as Livingston and Johnson have suggested in the case of climatic factors controlling the distribution of land plants, but no real beginning has, as yet, been made. The interval of 10°C. certainly suggests the working of the van't Hoff-Arrhenius principle as applied to vital phenomena. Taking the variation of 10°C. as the controlling interval of temperature and regarding it as an index to the summation of temperature, it may be possible in a later paper to definitely estimate the coefficients of temperature-efficiency in a fashion similar to that already suggested by Livingston and Johnson ('13) for land plants.

If the rate of the vital activities are, in general, doubled or nearly so with each increase of 10°C., then, judging from the results of the *Rhodophyceae,* thus far tabulated, it would seem that marine algae cannot endure an acceleration greater than 2, that each species has its own definite initial temperature for efficient vegetative and reproductive activity and that such initial efficient activity may be accelerated up to the

doubling point, but not beyond it. In this way may be explained the fact that from 0°C. (or —2°C.) to 10°C. of mean summer temperature marks the limits of the Upper Boreal and Upper Austral zones. The marine algae inhabiting these zones are subjected to a range of not over 10°C. at any, or all, times. The species of the Temperate zones, enduring a mean summer temperature of 10°C. to 15°C. have a range of 10 to 12°C., probably not over, at any or all times. Similarly those of the Subtropical and Tropical zones endure a range of not over 10°C. If, therefore, tentatively, a temperature efficiency coefficient be estimated according to the formula of Livingston and Johnson ('13, p. 365) but modified by leaving out the assumption of an initial temperature higher than 0°C., viz., $u = 2\,\frac{t}{10'}$ the efficiency coefficient in the case of the Upper Boreal and the Upper Austral zones (0 to 10°C.) will be unity to 2, in case of the Lower Boreal and also the Lower Austral (10 to 15°C.), will be 2 to 3, for the Temperate zones (15 to 20°C.), the coefficients will be 3 to 4; for the Subtropical zones (20 to 25°C.), the coefficients will be 4 to 5, and for the Tropical zones (25 to 30°C.), the coefficients will be 5 to 6. Incidentally to carry out this idea of temperature efficiency coefficients, it may be said that the application to the case of thermal algae, where I find the 10°C. amplitude rule also to apply, would carry the coefficient index up as high as 16, i.e., in the case of those species enduring highest temperatures (80°C.), and even to 18 in the case of thermal bacteria (90°C.).

In conclusion, I may say that while much detail remains to be considered and brought into order before the final data and conclusions may be published, I have reason to believe that the statements and conclusions I have either made or brought forward in this preliminary account, will probably not need be changed, at least to any great extent.

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PHYTOPATHOLOGY IN THE TROPICS

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Tropical life is a luxurious life. Nowhere does plant and animal life show itself in such variety and abundance as on the equator.

As the conditions in those regions are uncommonly favorable to plant growth, it would appear that the plant parasites also have a good chance of living. In several tropical countries plant diseases have been studied in a more or less extensive way, but the general features of plant diseases in the tropics, unlike those of the temperate regions, have hardly been touched. I have been for some time studying plant diseases in our colonies of the East Indies, the so-called Malayan Archipelago, and I wish to give you some general impressions on fungous diseases in those countries. My remarks can be only suggestions, as thorough investigations on these tropical problems have never, so far as I know, been made.

The Malayan Isles have an average temperature of 30°C. in the lower parts, accompanied by a humidity of 80–100 per cent. The climate is a monsoon climate. In the time of the wet season it pours every afternoon, but in the dry time the rains are very scarce in the lowlands but not infrequent in the forest-covered mountains.

One would be inclined to think that this combination of high temperature and moisture would be extremely favorable for fungous growth, and that therefore fungous diseases would play a large part in the culture of economic plants. This, however, is not the case. We find that insect troubles prevail, and that, compared with our temperate regions, few diseases exist. We would not conclude these facts from the literature, as a large number of diseases caused by fungi have been described. But in visiting the countries it struck me that only a few diseases are of real importance; a great

many of those described must have been found occasionally, and have had no serious influence upon the cultivation of plants.

Not only among the cultivated plants do we find little fungous growth, but also in the natural vegetation. In the virgin woods the trees have few enemies among the fungi, and even the flora of mushrooms on the ground, so characteristic of our woods, is absent. Everything seems to point to the conclusion that conditions are unfavorable to fungous growth.

Why is this so? As has already been said, there are two conditions which characterize a tropical climate: (1) a high temperature which is about equal through all seasons, and (2) a high humidity, the latter varying somewhat in the different monsoons, but being altogether much higher than in our climates.

It seems to me that the tropical temperature is too high for many fungi. I cultivate in my laboratory over 600 fungi, and this collection shows clearly that the temperature of optimum growth of the greater part of the fungi lies beneath 30° C., often under 25°C. An exposure to high temperature prevents many parasites from forming their spores or fruiting bodies, whereas others require a change of temperature for normal growth. The *Polyporaceae,* for instance, bear exposure to frost very well, but many of them scarcely develop at 30°C. High temperature very often gives rise to an abnormally abundant mycelial growth, combined with an absence of spores. On the other hand, the high moisture content of the air must be favorable to fungous development.

But every fungous disease of plants involves two organisms, the parasite and the host, and the same conditions may influence these two in a very different way. The heavy rainfalls, combined with the abundant transpiration—owing to the intense heat, must cause a high water-content and a small air-content, of the wood-vessels of the trees, thereby making a substratum poor in air. We know that this is an important factor in fungous growth. This fact, combined with the high temperature, would explain the rare occurrences of *Hymenomycetae* and other wood-destroying fungi in the tropics.

I shall begin the consideration of the different groups of fungi which cause plant diseases in the tropics by mentioning one biological group of hymenomycetous fungi the members of which attack tropical cultivated plants. These are the so-called root fungi. It is certain that the root parasites belong to different species of *Hymenomycetae,* and that one species of host-plant may be attacked by a number of species of these fungi. Several of the latter, if not all, are characterized by the peculiar mycelium characteristic of the *Hymenomycetae;* in many cases, however, fruiting bodies have never been found. Practically all cultural woody plants —tea, coffee, rubber, quinine, cacao, coca—may suffer from the attacks of root-fungi, these attacks occurring mostly on virgin soil. The fungi develop on the decaying stumps of the forests, grow through the soil, and reach the roots and stem bases of the young tea, coffee, or quinine plant. The bark is penetrated and the mycelium destroys both bark and wood (the mycelium strands can be very clearly seen between bark and wood). Whereas young plants up to three or four years old nearly always are killed, older ones may resist; different species of plants, however, behave differently in this respect. In some districts the fruiting bodies of *Fomes semitostus* appear on the dying plant or on the dead roots, but in others fruiting bodies have never been found.

A second biological group of fungi, so common in our latitudes, has only a few representatives in the tropics under discussion. I am speaking of those ascogenous or imperfect fungi which cause the die-back diseases of our orchard, forest, and park trees, e.g., *Valsa, Diplodia,* and others. These fungi kill the branches by penetrating into the bark and sometimes into the wood. They appear on our trees when these are in a dry condition, and in dry climates or in dry years such diseases are of importance. Not so, however, in the tropics. The only die-back disease which is common is caused by *Corticium javanicum,* which, however, belongs to the *Hymenomycetae* and forms red layers on twigs, branches, and even trunks of all cultural woody plants, e. g., rubber, coffee, quinine, tea, cacao, coca, and fruit trees. We find the disease

mostly in very moist valleys, where the wind has no free play. The fruiting bodies of many *Ascomycetae* develop in dry air, and it is not remarkable that that type of disease is found in some parts of the West Indies, which have a drier climate.

A group which has no representative in the tropics is that of the powdery mildews (*Erysiphaceae*). These fungi occur only in colder climates. The so-called false mildews or *Peronosporaceae,* on the other hand, are of considerable importance, these fungi seeming to thrive well under the moist and hot weather conditions. We find the canker of rubber and cacao (caused by *Phytophthora Faberi*) of far-reaching importance. In both the rubber and the cacao the disease attacks the bark and, in the case of the cacao, also the fruit. The growth of this fungus depends upon a very moist air. This is proved by the fact that when the trees are cut back severely so that the trunk is exposed to sun and wind, the wounds often heal and the disease is stopped. A plantation in which the trees are planted far apart also suffers less.

Another fungus—*Phytophthora Nicotianae*—belonging to the *Peronosporaceae* is the cause of a dangerous tobacco disease. The parasite kills the seedlings in the beds, the plants "melt," and even the mature tobacco plants are attacked. The fungus penetrates into the pith of the lower part of the stem and the "tobacco-tree" falls. A third member of this family destroys a large part of the Indian corn, so widely grown by the natives. It is *Peronospora Mayidis,* unknown, so far as I am aware, in the large corn areas of the United States. The exceedingly moist climate, combined with the excessive heat, evidently favors the attack by the fungus. In the potato fields of the mountain districts of Java we find a friend of our countries, *Phytophthora infestans.* Potatoes are grown in the tropics between 1500 and 6000 feet altitude. In the lower areas we find phytophthora-infected regions only rarely, but the higher we ascend, the lower the temperature (frosts may even occur in the nights) and the more destructive the phytophthora becomes. The spores of the fungus (it has been proved) cannot germinate at a high temperature, which explains the occurrence of the disease only in the higher

altitudes. It is very remarkable that in the tropics tubers are never, so far as I observed, affected. This fact might help us to discover the cause of the difference in susceptibility of the tubers of different potato varieties in our climate.

Speaking of potatoes, I wish to point out another disease of our regions which I found in the tropics and which has the greatest influence upon tropical potato culture. I am speaking of the internal brown spot, the nature of which has not been recognized. Nearly every potato tuber shows this disease and in a much more striking way than in the temperate regions. The brown spot is accompanied by a soft consistency of the tuber and a small amount of solid substance. As far as we know to-day, this trouble is a physiological one, caused by particular conditions of "climate and soil," the nature of which is unknown to us. The cause of the disease may be different in the tropics and in our regions, but a careful study of it in warm climates might give us an indication as to what conditions favor it.

Among the large group of rust-fungi, there is only one representative which is of importance to tropical agriculture. This is the coffee-leaf disease, due to *Hemileia vastatrix,* a rust which to a considerable degree ruined a large part of the coffee culture of Eastern Asia, and obliged the growers to introduce other species, which, unhappily, are of poorer quality. On other cultural plants, however, no rust of any importance occurs. The important cereal crop of the tropics, the rice, has no rust enemy. The rust of the sugar-cane is of no consequence in cane growing. The same is true of the smut diseases. Rice smut is found exceptionally, and smut of sugar-cane is a rarity; smut of corn is even rarer than in our regions.

Leaf spot diseases, belonging to ascogenous or imperfect fungi, are much less frequent than in Europe or the United States. The leaf spots of sugar-cane (*Leptosphaeria Sacchari, Cercospora Sacchari,* and *Cercospora Kophei*) are widely spread but have little influence on cane production. They are of more importance in the moist western part of Java than in the drier east. The tea blights (*Pestalozzia palmarum* and

Laestadia Theae) cause but small losses of tea leaves in our colonies.

The sugar-cane evidently is the crop which is most subject to the attack of fungi. This becomes clear when we look upon the method of propagating the saccharum. Small pieces of the cane stem are used as cuttings, which are put into the soil. The soft pith, rich in sugar, is an ideal substratum for fungous growth, and we must not be astonished that even saprophytes enter it. *Thielaviopsis ethaceticus* and *Colletotrichum falcatum* are two typical destroyers of sugar-cane cuttings.

Bacterial diseases are scarcely to be found. I will admit that more bacterial diseases may be discovered, but up to the present time the only bacterial disease of importance is the tobacco wilt due to *Bacillus Solanacearum,* the same trouble which occurs in the United States. The same bacillus also causes a disease of peanuts. Probably the gum-disease of sugar-cane is also caused by bacteria. It is curious that algae in some cases (*Cephaleuros virescens*) cause diseases of tea and coffee plants, as they kill not only leaves but, as is true in the case of tea, also the twigs.

Here I have come to the end of the list of fungous troubles. Compared to the fungous diseases of the United States and even to those of Europe, those of the tropics are smaller in number. Tropical agriculture might be compared to the agriculture of the United States more than to that of the Old World. Vast areas are covered with one crop and often with one variety of a crop, so far as we know anything definite about varieties and races of tropical plants. In the subtropical regions of the United States, where at certain times the temperature equals that of the tropics, the air is much drier and there is a certain change of temperature, even in the region of eternal spring in California, which is foreign to the tropical climate. In the tropics of Asia and the subtropics of the United States insect troubles have assumed immense proportions, but as to fungous diseases, these are of more importance in the subtropics of the New World.

Different groups of fungi are much less restricted in their geographical distributions than are phanerogams. Up to the present time, no special tropical families among the fungi are known, and, as far as I know, the only fungus group that has no representatives in the tropics is that of the *Erysiphaceae*. The secondary part which fungi play in the plant diseases of the tropics is not caused by the absence of fungi, but by the particular conditions which influence both the host and the parasite, and their relations to each other. To establish the exact nature of these influences is a problem for the future.

PHYLOGENY AND RELATIONSHIPS IN THE ASCOMYCETES[1]

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Part I. Argument

Perhaps there is no other large group of plants whose origin and phylogeny have given rise to such diametrically opposed hypotheses as the fungi. The presence of chlorophyll and the synthesis of carbohydrates from inorganic materials are such general and dominant characteristics of plants, that many students regard them as the fundamental traits which primarily marked the divergence of plant from animal life. According to this hypothesis all plants possess chlorophyll or were derived from chlorophyll-bearing ancestors.

No one questions the origin of the chlorophylless seed plants from chlorophyll bearing ones by the loss of chlorophyll and reduction of photosynthetic organs.[2] What is more natural then, than the hypothesis that the fungi have been derived from chlorophyll-bearing ancestors? It is not my purpose to discuss the question as to whether or not the *Phycomycetes*, or lower fungi, had an independent origin, or were derived from one or several different groups of the green algae. I wish to consider some of the evidence which points to the origin of the *Ascomycetes* from fungus ancestry, rather than from the red algae.

[1] The first part of this paper is the abstract or argument as read at the anniversary proceedings. Because of the brief character of the abstract which renders many of the statements more or less categorical, while some therefore will appear dogmatic, the subject is further elaborated, and illumined by examples in a series of *Notes* which follow as an appendix in Part II.

[2] The chlorophylless seed plants constitute comparatively small, isolated groups of separate origin from different families or orders of the spermatophytes. They do not constitute a phylum. The situation is quite different with the *Ascomycetes*, which make up a great phylum with ascending and diverging lines, as well as descending branches. They do not give evidence of many isolated groups derived by degeneration from many separate families of the red algae.

In this abstract the statements must be more or less categorical, and some will therefore appear rather dogmatic.

1. The phylogenetic relation of the oöblastema filaments of the red algae, and the ascogenous threads of the sac fungi.—The nuclear history in the two structures is very different. In the red algae there is a single fusion of one pair of sex nuclei in the egg, forming a true diploid nucleus which multiplies by division in the oöblastema filament providing the primary nucleus for each cystocarp. The oöblastema filament fuses with vegetative auxiliary cells to furnish attachment and base for food supply of the cystocarp, but the diploid and haploid nuclei of the fusion cell repel each other. The attempt to show a phyletic relation between the copulation of short oöblastema filaments with cells of the procarp, or the fusion of the procarp cells, after the union of haploid gametic nuclei, in some groups of red algae, and the communication of functional archicarp cells of certain sac fungi, as well as entertaining the notion that fusions of approximate cells of the ascogenous hyphae are phyletically related to the fusion of oöblastema filaments and auxiliary vegetative cells, introduces additional confusion into a doctrine already overburdened with questionable hypotheses. The oöblastema filaments and ascogenous threads are parallel developments. They present an example of morphological homology or analogy, not of phylogenetic affinity.

2. The phylogenetic relation of the ascus and carpospore, or tetrasporangium (see Part II, Notes II and III).—There are two horns to the dilemma here, and either one requires several additional supporting hypotheses. The origin of the ascus from a coenocytic zygote, in some cases by reduction, in others terminating a progressive splitting of the same, is far more comprehensible. The nuclear fusion in the ascus is not vegetative (see Note III). It takes place in all forms thus far investigated and is to be considered the final stage of the sexual act, however modified this may be. Were it merely vegetative fusion there would be no need of conjugate division in the ascus hook to avoid the union of sister nuclei. The nucleocytoplasmic relation, or balance, would be just as easily at-

tained by fusion of sister nuclei, or even by contemporaneous growth of nucleus and cytoplasm, such as is well known to occur in many other cases, for example in sexual cells, gonotokonts, etc.

3. The phylogenetic relation of the ascocarp and cystocarp.—If this principle of the resemblance between different types of cystocarp and ascocarp has any force, it would mean that the sac fungi had as many points of origin from the red algae as there are points of resemblance between their fruit structures. I presume no one at the present time holds any such view of the polyphyletic origin of the *Ascomycetes*.

4. The phylogenetic relation of the trichogyne and sexual apparatus of the Ascomycetes and those of the red algae.—The sexual apparatus of some of the *Ascomycetes*, particularly the trichogyne, and the so-called spermatia, is generally conceded to be the strongest evidence in support of their phyletic relation to the red algae. This theory, however, requires a jump from the simple trichogyne, a continuous prolongation of the egg of the red algae, to the complex, multiseptate one of the *Ascomycetes*. It requires further the reduction of this trichogyne to a unicellular one, and then to the simple gamete. It also requires the transition from free antheridia, or spermatia, to fixed ones, and from this specialized condition to the simple gamete, thus finally attaining the generalized condition of the copulation of simple gametangia. This appears to me to be a rather strained backward reading of the evidence.

ORIGIN OF THE ASCOMYCETES FROM FUNGUS ANCESTRY

Although Sachs' suggestion of the relation of the *Ascomycetes* to the red algae was received with favor by many students at that time, and the doctrine has received a fresh impetus in recent years, it was not accepted by some of the foremost students of the fungi at that time (Winter, '79; deBary, '84). DeBary plead for the application of the theory of descent which had come to be used as the basis of classification for the higher plants. As a result of his extensive studies of development in the *Phycomycetes* and *As-*

comycetes he was led to the conclusion that the *Ascomycetes* were derived from the *Phycomycetes*. This doctrine is based chiefly on the evidence of a phyletic relation between the sexual organs of the two groups. In spite of the persistence of the belief in the origin of the sac fungi from the red algae, deBary's doctrine of their descent from the *Phycomycetes* has had many adherents. Nowhere in deBary's writings have I been able to find any statement which can be construed as favoring the origin of the sac fungi from the red algae. The esteem in which his judgment is held, even at the present day, has led to the republication of a rumor of an *ante mortem* statement by deBary to the effect that he was inclined to the view that the procarps of the two groups pointed to the origin of the *Ascomycetes* from the *Rhodophyceae!*

Our present knowledge of the cytology of the ascus would not perhaps favor such close contact between the *Ascomycetes* and *Phycomycetes* as would appear from the knowledge possessed in deBary's time. Unfortunately we are not yet in possession of any cytological knowledge of spore production in the zygote of the *Phycomycetes* which we can use for comparison. But at any rate, the difficulties in this relation are no greater than are met with in attempting to derive the ascus from the carpospore or tetrasporangium of the red algae.

Origin of the ascogenous threads.—The ascogenous threads are outgrowths of the zygote or oögonium and represent one method of splitting up and proliferation of the same in accordance with recognized principles of progression in the same direction of increase in the output of spores following the sexual process, or its equivalent, and terminating the diploid phase.

One of the most instructive forms suggesting a mode of transition from the *Phycomycetes* to the *Ascomycetes*, is *Dipodascus*. Its sexual organs are strikingly like those of certain *Mucorales* or *Peronosporales* in their young stages. The sexual organs, which can be recognized as antheridium and oögonium, arise either from adjacent cells of the same thread, or from different threads. After resorption of the wall at the point of contact, the fertilized oögonium (or zygote) grows

out into an elongate stout "ascus" or zygogametangium with the production of numerous spores. While all phases of the nuclear phenomena have not yet been made clear, the gametes are multinucleate, and multiplication either of the sex nuclei, or of the fusion nucleus, takes place in the generalized "ascus." This so-called ascus is an outgrowth of the undifferentiated oögonium or ascogonium. The splitting up of such a generalized ascus by filamentous outgrowths, the ascogenous threads, which branch and produce terminal asci containing fewer spores, would be a very natural course in progressive evolution, specialization, and increase in spore output.

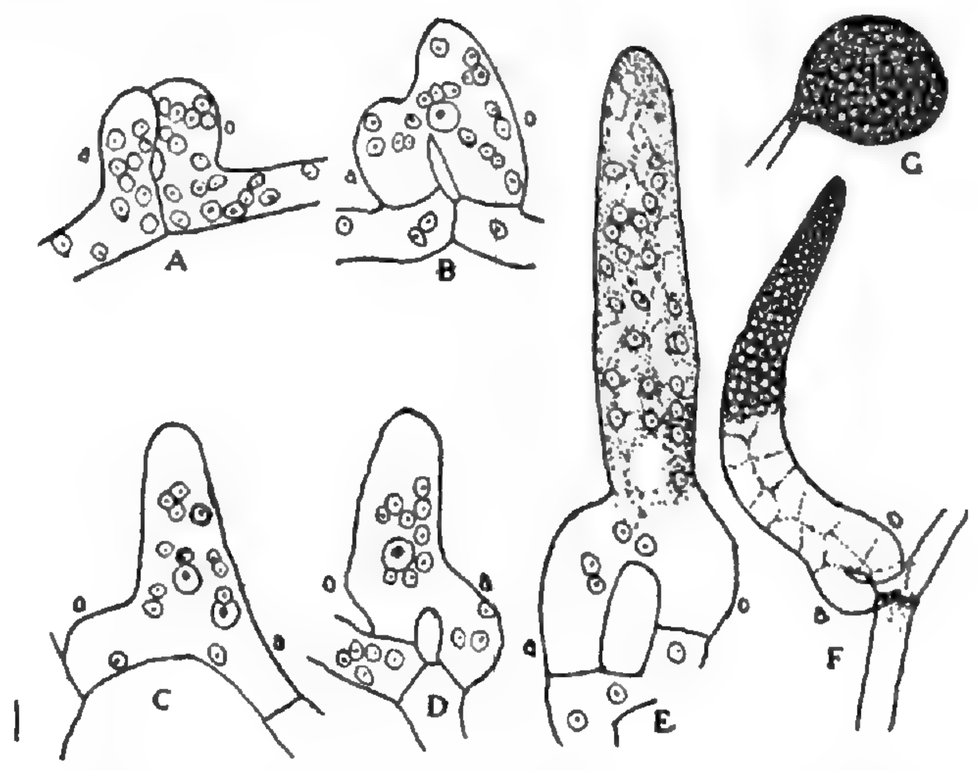

Fig. 1. *Dipodascus albidus: A*, copulation of gametangia; *B*, communication established between antheridium and oögonium; *C*, the two sex nuclei approaching each other; *D*, fusion nucleus large, vegetative nuclei small; *E*, growth of generalized ascus from oögonium side of copulating gametes, early stages of, in *C* and *D*; *F*, generalized ascus with numerous spores; *G*, spore mass crowded out of end of ascus. *a*, antheridium; *o*, oögonium.—*A–E*, after Juel; *F* and *G*, after Lagerheim.

Origin of the ascus in the Endomycetaceae.—The tendency of generalized forms to split up in different directions, often giving rise to divergent lines or series, is a well founded principle in the doctrine of descent. These series are often of different character in respect to numbers and diversity of forms, as well as to progression or reduction in one or more structures. One of the directions in which descent from such a generalized, coenocytic, germinating zygote (or ascus) as represented by *Dipodascus* has taken place is that of reduction in size of the generalized ascus and in the number of spores. Evidence of this reduction is furnished by *Dipodascus* itself; for, as the culture ages the asci become smaller and smaller and the spores fewer in number. In this way by reduction in number of spores to 8 and 4, just permitting the meiotic nuclear divisions, forms like *Eremascus* and *Endomyces* have

arisen. Further reduction of one of the gametes, or of the vegetative stages, would result in apogamous forms of *Endomyces,* the *Exoasceae,*[1] the *Saccharomycetes,* or yeasts, etc. By reduction and loss of one of the gametes without reduction in size of the generalized "ascus," such forms as *Ascoidea, Protomyces, Taphridium,* etc., may have arisen.

Origin, progression and sterilization of the so-called trichogyne.—There is no well developed trichogyne-like structure in any of the known *Phycomycetes.* But there is evidence in a few of the forms, like certain species of *Cystopus,* of a tendency of the oögonium, probably under chemotactic stimulation and a softening of the wall, to develop a short process directed toward the antheridium. This has been suggested by a number of students (Lotsy, '07, p. 468) to be an indication of the origin of the trichogyne in the *Ascomycetes.* It does not mean that *Cystopus*[2] is to be regarded as an ancestral form of the *Ascomycetes,* though certain species do possess a number of peculiarities which may be attributed to such a hypothetical form. This peculiar feature of the oögonium of some species of *Cystopus* is, however, of importance as it indicates one probable method of origin of the trichogyne in the *Ascomycetes.* The trichogyne is not a character possessed by all *Ascomycetes,* even of those which still retain two functional gametangia. This, I believe, is strong evidence of the independent origin of the trichogyne in the *Ascomycetes.*

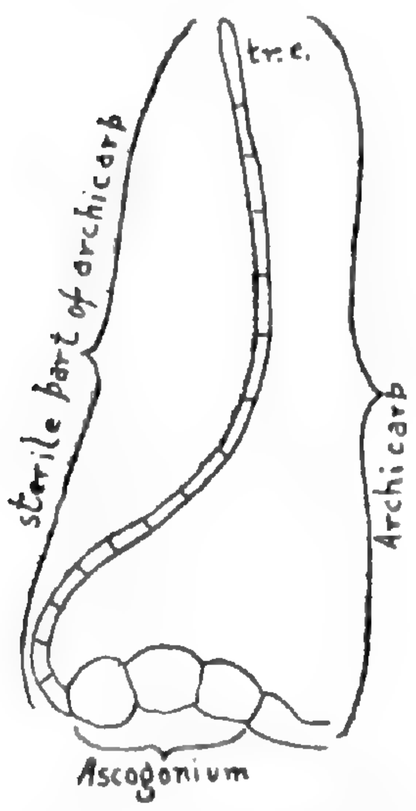

Fig. 2. Diagrammatic representation of the archicarp of lichens and many other *Ascomycetes.* The fertile part is the ascogonium; the sterile portion is the so-called "trichogyne"; *tr.c,* trichogyne cell.

It arose as a copulating process or beak from the oögonium

[1] Such an origin for the *Exoasceae* is more comprehensible than the theory that their mycelium may represent ascogenous hyphae which have migrated from the condition of parasitism in the vegetative portion of a former ascocarp, to parasitism on their present hosts, as suggested by Harper ('00, p. 392).

[2] One of these features is the generalized character of the sexual organs, which are polyenergid, but particularly the great variation in number of functional egg nuclei in different species as described by Stevens ('99, '01).

under chemotactic stimulation, combined with a transverse splitting of the oögonium or archicarp.

The failure of the antheridium to perform its function in the sexual process, its reduction or loss, are well known features in the life history of a number of *Ascomycetes*. In many cases where the antheridium or its supposed equivalent, the spermatium, is to all appearance potentially functional, its failure to function appears to be due to the sterilization of the terminal portion of the archicarp.[1]

Analogous situations are known in the seed plants. I need only cite the case of *Elatostoma acuminatum* (see Strasburger, '09). The nucleus of the embryo sac mother cell enters the preliminary phases of the heterotypic division. After synapsis the further stages of the heterotypic division are inhibited, and by typic or "vegetative" division the eight-nucleated embryo sac is formed. The egg, therefore, ripens with a diploid nucleus, and, without fertilization, develops the embryo. The walls of the inner integument grow together at the micropylar end of the ovule and harden, thus forming an effectual barrier to the entrance of the pollen tube (Treub, '05; Strasburger, '09). While great disturbances occur in pollen development and most of the pollen grains are empty or undeveloped, some pollen is formed which appears normal. In some cases the mother cell, which usually forms the diploid embryo sac, undergoes a true reduction division forming a row of four cells, the lower one of which forms a normal embryo sac with a haploid egg. The few male plants of this species, Strasburger thinks, result from fertilization of such

[1] While the "trichogyne" or terminal portion of the archicarp assumed vegetative characters in an increasing degree, it seems that it did not in every case lose all of the features appropriate to a receptive organ. It appears in a few cases at least to still respond to chemotactic or analogous stimuli, seeking the fixed spermatia as in *Collema pulposum* (according to Bachmann, '13) and *Zodiomyces vorticellarius* (Thaxter, '96). In a number of cases there seem to be receptive areas on the trichogyne where the free sperms become fixed, where fusion of sperm and trichogyne takes place. The perforation of the transverse walls of the trichogyne, which is said to occur after fusion with the sperm, also appears to be another example of the retention of an ancestral character of the archicarp which primarily permitted the passage of sperm nuclei through the terminal segment, or the association of nuclei of different segments as parthenogenesis or apogamy was introduced.

haploid eggs by sperms from the normal pollen.

This sterility of the archicarp, I believe, has been brought about by its assumption more and more of a vegetative character. The formation of septa at the base of the "trichogyne" in such forms as *Pyronema* and *Monascus,* which primarily may have been the beginning of a transverse splitting of the oögonium, would make more difficult the fertilization of the basal portion of the archicarp. In *Aspergillus repens* the so-called "trichogyne," or terminal cell of the archicarp, sometimes gives rise to ascogenous hyphae[1] (according to Miss Dale, '09). The basal portion of the two-celled archicarp, or the basal or central portions of the several-celled archicarp, seem to be the portions which have retained the function of ascogenic cells where that function still resides in the archicarp. As the archicarp becomes longer, the sterile portion, which is non-ascogenic, becomes longer and more septate. This only increases the difficulties of the passage of the sperm nuclei.

The increasing vegetative character of the terminal portion of the archicarp has given rise to the long, simple, multiseptate "trichogyne" of the lichens and many *Pyremomycetes* and *Discomycetes,* as well as to the profusely branched multiseptate trichogyne of certain *Laboulbeniales.*[2] It is an interesting fact that in many of the cases of the extraordinary vegetative development of the terminal portion of the archicarp (the "trichogyne"), antheridia and spermatia are entirely wanting.[3]

The degeneration changes of the sterile portion of the archicarp (multiseptate and often also much branched "trichogyne") which are described as taking place after connection of the spermatium with the receptive terminal cell (for lichens see

[1] It is worthy of note in this connection that Olive's studies ('05) of *Monascus* led him to regard the "trichogyne," or terminal cell of the archicarp, as the ascogonium, and the second cell, or ascogonium according to others, as a nurse cell.

[2] Thaxter ('96) says that when the spermatia do not become attached to the receptive cell of the trichogyne the vegetative growth of the trichogyne is greatly increased.

[3] (*Lachnea cretea,* according to Fraser, '13; in *Teratomyces actobii,* Thaxter, '96, was not able to find antheridia.)

Stahl, '77, Baur, '98, Bachmann, '13; for the *Laboulbeniales,* Thaxter, '96, p. 225), may be classed as secondary or accompanying sexual phenomena. It does not necessarily follow that the sperm nucleus reaches the egg or fertile portion of the archicarp. The trichogyne changes taking place after the entrance of the sperm into, or its connection with the receptive terminal cell, are not dependent on the final fate of the sperm, i. e., whether it reaches the egg or not. They are antecedent phenomena and in no sense a proof that fertilization has taken place. These disintegration changes, initiated, it would seem, by the influence of the sperm on the receptive cell of the archicarp, terminate the vegetative growth of the archicarp and thus the reflex upon the fertile portion at the middle or base releases the ascogenic cells from the inhibiting influence of the vegetative phenomena, and they then proceed with the modified sexual process among the ascogonial nuclei which may be now associated in sexual pairs, or this pairing be postponed to some period in the development of the ascogenous hyphae.

Origin of spermatia in the Ascomycetes.—The presence of the so-called spermatia in many lichens and other *Ascomycetes,* associated at the same time in numerous instances with the trichogyne-like termination of the archicarp, is one of the major pieces of evidence brought forward in supporting the doctrine of the red algal origin of the sac fungi. If we accept this doctrine, then in the *Ascomycetes* we must read the history of the antheridia in the following order: They appeared first as free structures, spermatia, abjointed from spermatiophores, large numbers of which were crowded in highly specialized receptacles.

At the next step there were few, imbedded, isolated antheridiophores to which a few spermatia remained attached, until finally the stage was reached where spermatium and antheridiophore were merged into the simple antheridium. This doctrine also requires that along with the change from free spermatia to the simple antheridium, there was a transition from the condition in which the spermatia do not function to

that where the sperm nuclei of the simple antheridium are functional.

Notwithstanding this interesting course of evolution of the antheridium and of sexuality which we trace if the red algae are accepted as the source of the *Ascomycetes*, I believe, just as in the case of the archicarp and trichogyne, the evidence warrants us rather in reading it in just the opposite direction; and that in the last stages of progressive development of the sexual apparatus in the *Ascomycetes*, the resemblances to the sexual apparatus of the red algae are merely those of morphological homology and analogy, not phylogenetic homology and affinity.

According to this view, then, the ancestral forms of the *Ascomycetes* were fungi with well developed, simple but generalized gametangia. This condition is retained in a number of existing *Ascomycetes*, in many of which true sexuality exists.[1]

In connection with the specialization of the antheridium and the origin of the spermatia of the *Ascomycetes*, *Monascus* is an extremely interesting form. The antheridium is an elongate terminal cell of a hypha. The archicarp arises as a branch below the septum. It curves closely against the antheridium, bending it over more or less at right angles, and copulates at any point along the side of the antheridium, there being no portion of the latter especially selected as a copulation place. The conidia in *Monascus* are formed in chains by constriction and septation of terminal portions of hyphae similar in diameter to the antheridium. The archicarp sometimes copulates with a conidium of the chain before their final separation (Barker, '03). A chain of conidia is thus homologous with the antheridium, and a conidium with any section of the antheridium. It would be but a step from this condi-

[1] Examples of generalized, simple (non-septate) gametangia are found in *Dipodascus* and *Gymnoascus*. Examples of simple specialized gametangia, i. e., uninucleate gametangia, are found in the powdery mildews (*Erysiphaceae*) and *Eremascus*. A second stage is presented in forms where the antheridium remains simple and generalized, but there is a beginning of specialization in the archicarp where it is split transversely into two cells, the terminal one (trichogyne) functioning as a copulating organ and migration tube for the sperm nuclei. Examples are found in *Pyronema* and *Monascus*.

tion to the copulation of the archicarp with free conidia. The situation in *Collema pulposum* (Bachmann, '13), *Ascobolus carbonarius* (Dodge, '14), and *Zodiomyces vorticellarius* (Thaxter, '96), is similar where the trichogyne copulates with spermatia (conidia) still attached to the spermatiophore. These cases are very strong evidence suggesting the homology of conidia (or pycnospores as the case may be) and spermatia[1] in the *Ascomycetes*.

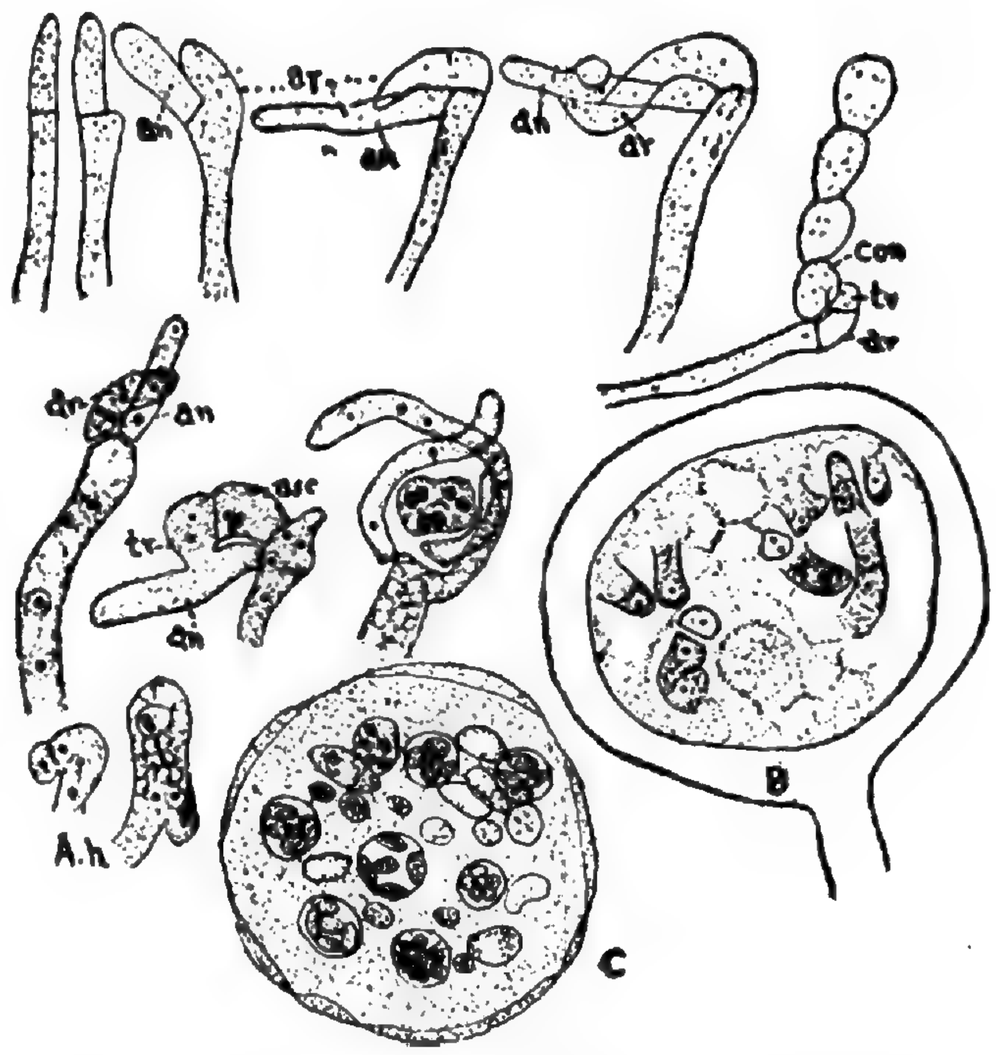

Fig. 3. *Monascus*, showing development of sexual organs and fruit. *an*, antheridium; *ar*, archicarp; *tr*, trichogyne; *asc*, ascogonium; *con*, conidium with which trichogyne is copulating; *A.h*, ascus hooks or croziers; *B*, young fruit showing ascogenous hyphae within, at left is a very young fruit body showing ascogonium becoming surrounded by the enveloping filaments; *C*, mature fruit body with asci and ascospores.—Upper row of figures after Barker; lower group after Schikorra.

Progression in the direction of multiplication of antheridia, or spermatiophores, and their association in groups followed from the simple and more or less isolated situation, progressing along the same course which is recognized in the association and massing of conidiophores into bundles, cushions, or pycnidia. It is the same course which is universally recognized as a striking indication of progression in other groups of plants, a *cephalization* of fruiting or reproductive structures, as in the bryophytes, lycopods, conifers, and angiosperms. In the latter it has given us the flower, and further cephalization of the flower has resulted in the head of the com-

[1] Their function in the ancestral or early forms may have been generalized enough to permit of their performing as conidia or sperms, as in the case of *Ectocarpus, Prostosiphon, Ulothrix*, etc. Strasburger ('05, p. 25) has expressed the idea that the pycnospores of the *Ascomycetes* might have been spermatia, and that the process of fructification now presented by these fungi is a secondary adaptation in place of the erstwhile fertilization by spermatia.

posites, the highest stage of phyletic evolution in the plant world.

In conclusion, the *Ascomycetes* present a very rich variety of form, structure, and adaptation with very marked diverging series. Some of these series present evidences of progression from simple, generalized forms to highly specialized forms, while others indicate descent by reduction. The evidences of progression are of the same kind and value as are generally recognized in other groups of plants.

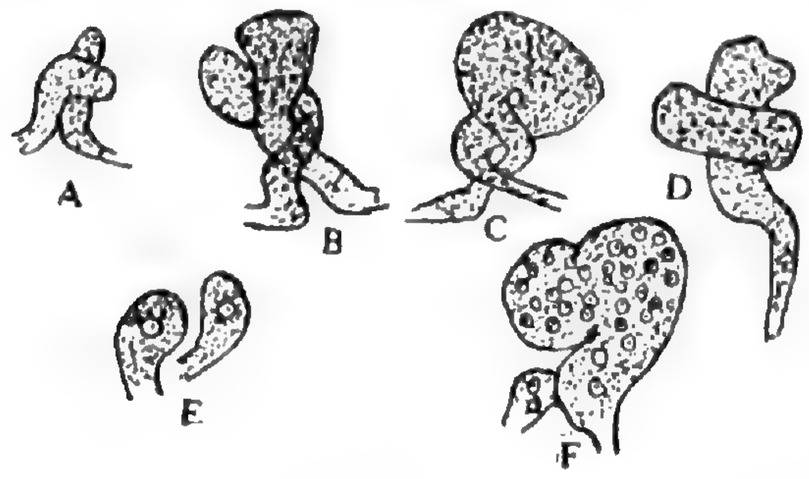

Fig. 4. *Gymnoascus Reessii: A–D,* formation of sexual organs, fusing at *C; E,* sexual organs in uninucleate condition; *F,* fusing sexual organs in multinucleate stage.—After Dale.

Sachs, in his later writings, agreed with deBary in recognizing the *Ascomycetes* as a distinct phylum, with an ascending series from simple and generalized forms to complex and specialized ones. He never mentioned the trichogyne as evidence of their phyletic relation to the red algae. But his theory was based on the presence of a *procarp* whether with or without a trichogyne. He selected *Gymnoascus,* where the sexual apparatus consists of simple copulating gametangia, as the simplest ascomycete known at that time. It is only in recent years that the trichogyne has been seized upon as evidence of the phyletic relation of the two groups and has forced this anomalous backward reading of the history.

PART II. ELUCIDATION

NOTE 1

The red algae are remarkable for the great constancy in the form of the procarp (procarpic branch, carpogonial branch, etc.) and the very great divergence in the processes subsequent to the fertilization of the egg (terminal cell of the procarp, carpogonium) and ending in the production of the carpospores. The general character of this divergence may be shown by a brief presentation of several types, as follows:

1. The simplest type of cystocarp development occurs in the *Nemalionales* where the carpogonium, or egg cell, after fertilization, gives rise to several branched sporogenous threads in a compact cluster, bearing terminally the carpospores (*Nemalion, Lemanea,* etc.), or in some species the sporogenous threads are more widely extended in the thallus, the branches producing separated clusters of carpospores (*Dermonema dichotomum,* see Schmitz and Hauptfleisch, '97). Fertilization by the fusion of a sperm nucleus with the egg nucleus after entrance into the trichogyne and migration down into the carpogonium has been described in *Nemalion* (Wolfe, '04) and in *Batrachospermum* (Schmidle, '99; Osterhout, '00).

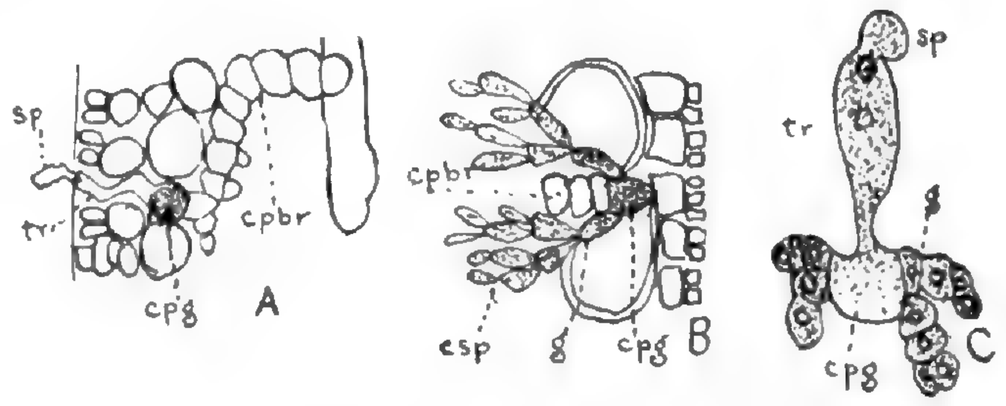

Fig. 5. *A* and *B*, *Lemanea; C*, *Batrachospermum: cpbr*, procarp or carpogonial branch; *cpg*, carpogonium or egg; *tr*, trichogyne; *sp*, spermatium; *g*, gonimoblast; *csp*, carpospores. —*A* and *B*, after Atkinson; *C*, after Davis.

2. In *Polysiphonia* (*Rhodomeniales*) the procarp branch of four cells is curved around so that the carpogonium is in contact with an auxiliary cell lying between the carpogonium and the pericentral cell which gave rise to the procarp. After fusion of the sperm and egg nucleus in the carpogonium, the fusion nucleus divides once. The carpogonium now connects with the auxiliary cell mentioned, which fuses with the pericentral cell. The two diploid nuclei migrate into the pericentral cell, the carpogonium separates from the auxiliary cell, while it and the remaining cells of the procarp degenerate. The pericentral cell now fuses with several other auxiliary cells, which arose from it as a branch, forming the central cell. The diploid nuclei remain in the upper part of the central cell, while the haploid nuclei from the auxiliary cells, some having divided, now degenerate (Yamanouchi, '06).

3. A somewhat different situation exists in *Erythrophyllum delesseroides* (*Gigartinales*). The oöblastema filament from the fertilized egg connects with the auxiliary cell which is the basal cell of the seven or eight-celled pro-

carp. This in turn fuses with the two other large cells of the basal portion of the procarp, thus forming the large fusion cell from which the gonimoblasts, or sporogenous threads arise (Twiss, '11).

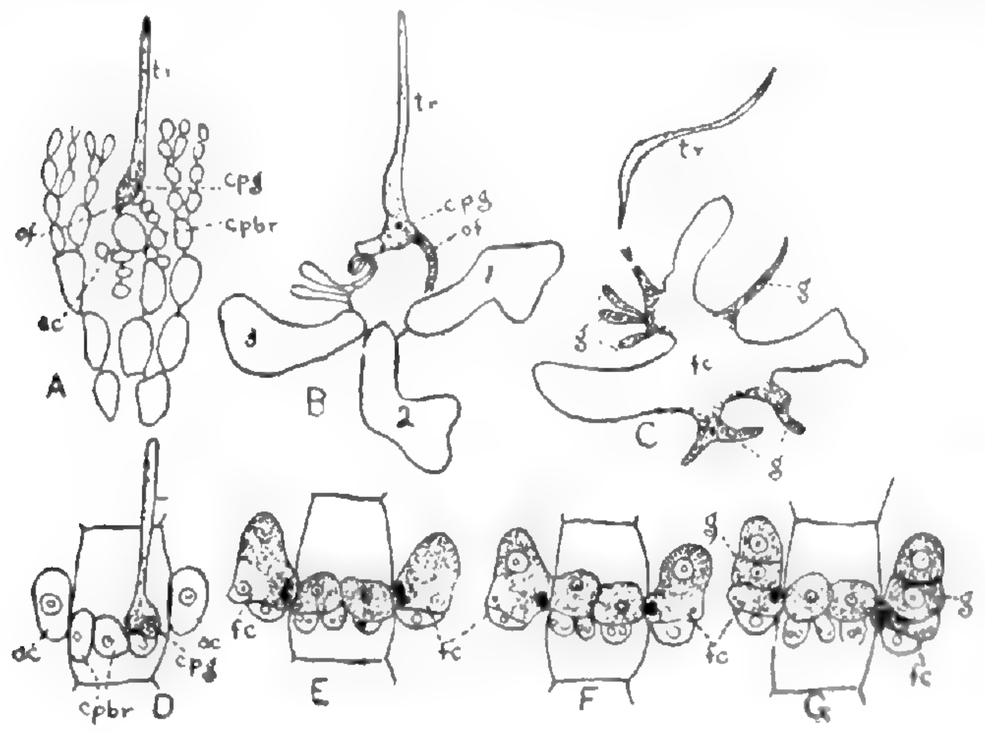

Fig. 6. ***A, Harveyella mirabilis; B*** **and** ***C, Erythrophyllum delesseroides; D, E, F,*** **and** ***G, Callithamnion corymbosum: cpbr,*** carpogonial branch; ***cpg,*** carpogonium; ***tr,*** trichogyne; ***of,*** oöblastema filament; ***ac,*** auxiliary cell; ***g,*** gonimoblast; ***fc,*** fusion cell. ***1, 2,*** **and** ***3*** are the three large basal cells of the procarp in *Erythrophyllum* which fuse with the oöblastema filament to form the fusion cell. Shaded portions are diploid; note that in the fusion cell of *Callithamnion* the vegetative nucleus (haploid) remains at a distance from the diploid nucleus.—***A,*** after Sturch; ***B*** and ***C,*** after Twiss; ***D, E, F,*** and ***G,*** after Oltmanns.

4. In *Harveyella mirabilis*,[1] a large cell which gives rise to the four-celled procarp is the auxiliary cell. A short oöblastema filament from the egg connects with the latter, which becomes the central cell.

5. In *Callithamnion* (*Ceramiales*) the fusion (diploid) nucleus in the egg divides into two. Two short oöblastema filaments proceed from the carpogonium, each containing a diploid nucleus, and fusing with an auxiliary cell at the side of the base of the procarp. Each of the two auxiliary cells now contains two nuclei. A wall divides each cell into two. The upper daughter cell contains the diploid nucleus and becomes the central cell, giving rise to the sporogenous threads, while the haploid nucleus in the lower cell degenerates (Oltmanns, '04).

6. The most complicated type may be represented by *Dudresnaya purpurifera* (*Cryptonemiales*) where several oöblastema filaments arise from the sterilized egg cell. These fuse with auxiliary cells which are either certain cells of the procarp branch, or terminal cells of its branched system, or of more distant "secondary procarp branches." An oöbla-

[1] *H. mirabilis* is parasitic on certain species of *Polysiphonia*, and is devoid of chlorophyll. For this reason it is regarded by some as indicating a step in the direction of an ascomycete.

stema filament after fusing with one auxiliary cell may grow forward and fuse with another and so on. The diploid nucleus formed in the egg multiplies by division in the oöblastema filaments. In the fusion cell, resulting from the union of the filament and auxiliary cell, the diploid and haploid nuclei repel each other so that the former lies on the filament side while the latter lies in the base of the auxiliary cell. An outgrowth

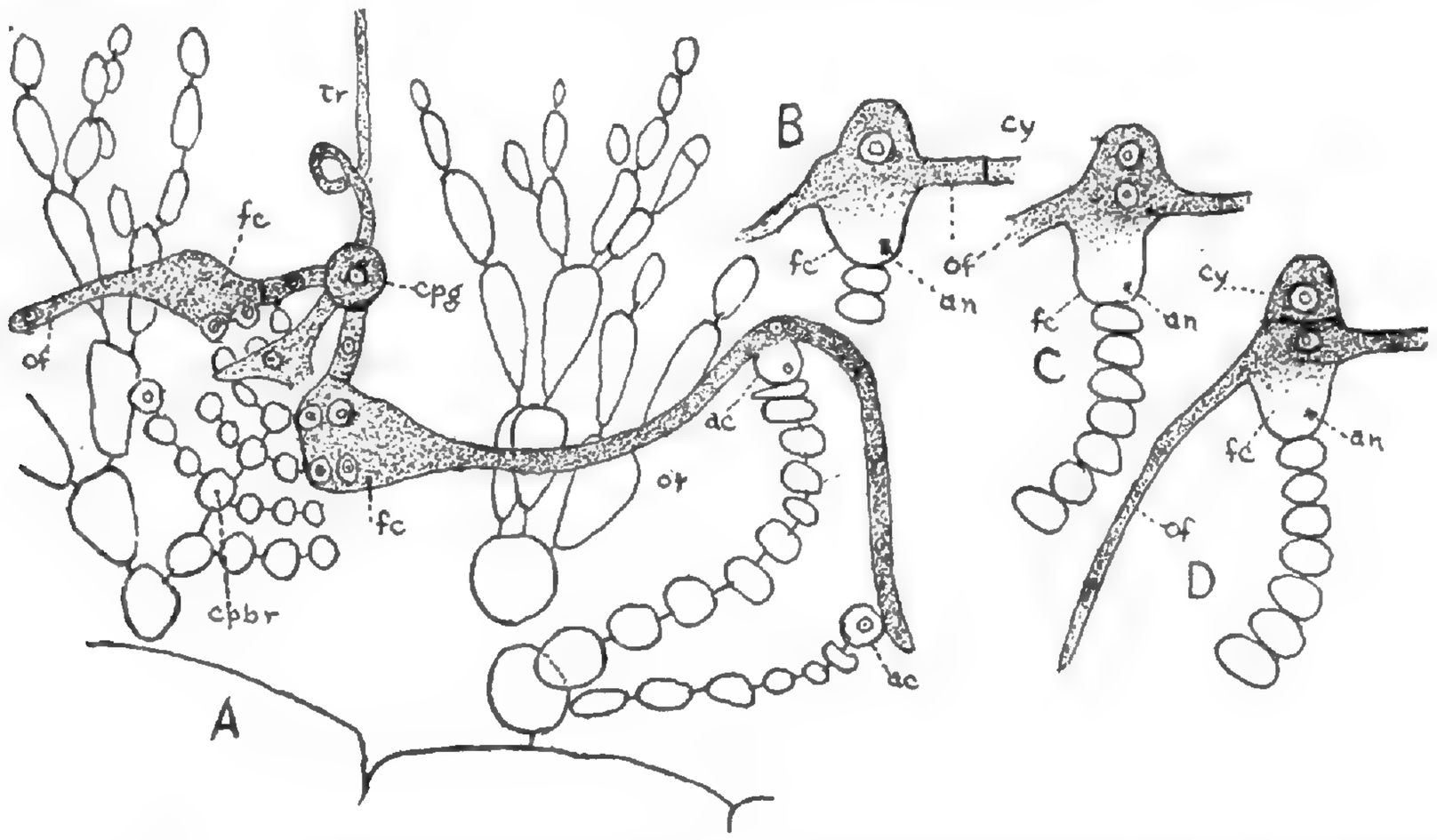

Fig. 7. *Dudresnaya purpurifera: A*, oöblastema filaments fusing with auxiliary cells; *B*, *C* and *D*, outgrowth from the fusion cell to form the central cell; *C*, diploid nucleus dividing; *D*, central cell of cystocarp separated by a wall. Note that the nucleus of the auxiliary cell remains distant from the diploid nucleus of the oöblastema filament. Shaded portions are diploid. *cpbr*, carpogenic branch; *cpg*, carpogonium; *tr*, trichogyne; *of*, oöblastema filament; *fc*, fusion cell; *ac*, auxiliary cell; *an*, auxiliary cell nucleus; *cy*, central cell of cystocarp.—After Oltmanns.

arises from the oöblastema filament at the point where the diploid nucleus lies. The latter divides, one nucleus migrating into the outgrowth, while a wall separates it from the fusion cell. This new cell with its diploid nucleus becomes the central cell (Oltmanns, '04).

7. In *Cruoriopsis cruciata* the situation is similar. The oöblastema filament by coursing widely through the thallus, fuses with the terminal cell (auxiliary cell) of "secondary procarp branches." Each of these fusion cells, or auxiliary cells, then gives rise to one or two simple rows of 2–4 spores (Schmitz, '79, '83), or a single 2–4-celled spore chain (Oltmanns, '04).

Relation between the fusions of procarp and auxiliary cells, and those of archicarp cells.—Several persons have made the interesting suggestion that certain similarities between the events which take place in the fusion of one or more of the middle or basal cells of the procarp with an outgrowth from the carpogonium, either direct, or through the medium of an auxiliary cell, as represented in *Erythrophyllum, Harveyella, Callithamnion,* etc. (third, fourth and fifth types mentioned above), and those occurring in the fusion among themselves of the middle or basal cells of the archicarp prior to the formation of the ascogenous threads, may be evidence of a phylogenetic relationship between the red algae and *Ascomycetes.* Thus Baur ('98) suggests that the first fertile cell of the several-celled ascogone of *Collema crispum* may be the egg cell, that this may be fertilized by the entrance of the sperm nucleus and its fusion with the egg nucleus. This fusion nucleus may now divide. The other cells of the ascogone below the egg are conceived of as auxiliary cells into each one of which a nucleus resulting from the division of the fertilized egg nucleus migrates after pore formation in the intervening walls.

In an interesting paper on the morphological relationships of the *Florideae* and *Ascomycetes,* Dodge ('14) emphasizes this theory by pointing to a number of cases in the lichens and other *Ascomycetes* where fusion, or pore connections, are known to occur between the ascogenous cells of the archicarp where more than one cell gives rise to ascogenous hyphae. Examples among the lichens are *Collema crispum* (Baur, '98), *Physcia pulverulenta* (Darbishire, '00), *Anaptychia ciliaris* (Baur, '04), and *Collema pulposum* (Bachmann, '13), while among the other *Ascomycetes* may be mentioned the following: *Ascobolus* (Harper, '96. Here there is but one ascogenous cell which gives rise to the ascogenous hyphae, but pore formation in intervening walls permits intercommunication between several adjacent cells in the middle of the archicarp. The species is not given), *Ascophanus carneus* (Cutting, '09), *Lachnea cretea* (Fraser, '13), *Polystigma rubrum* (Nienburg, '14).

Now as to the suggested relationship between the phenomenon of broad or narrow pore formation in the walls of certain cells near the middle or base of the archicarp in certain lichens and other *Ascomycetes*, and that shown in the communications taking place between the carpogonium and auxiliary cells (often including one or more of the other procarp cells), it may be said (1) that in the red algae this communication of the carpogonium (terminal procarp cell) with other procarp cells when it does take place is not direct, but by a roundabout method, either through a distinct outgrowth from the carpogonium, or through the medium of one or more auxiliary cells, or by a combination of both, to form the central cell; (2) no evidence of any similar roundabout method has been observed in the archicarp of the sac fungi. The intercommunication between the middle or basal cells of the archicarp is always direct, and no communication in the multicellular archicarp occurs by means of which either a fertilized nucleus, or a sperm nucleus has been observed to migrate from the terminal cell to the middle or basal cells; (3) that in a number of the fungi where pore formation occurs between cells of the fertile portion of the archicarp, the "trichogyne" is either absent, or admittedly degenerate, or the antheridium is absent. Examples are: *Ascobolus,* studied by Harper ('96), antheridium and trichogyne absent; *Ascophanus carneus,* antheridium absent, trichogyne doubtful or degenerate; *Lachnea cretea,* no antheridium observed, trichogyne not functional; *Polystigma rubrum,*[1] trichogyne not functional, from a multicellular cell at base of archicarp one nucleus migrates into the adjacent uninucleate archicarp cell, which is regarded as the ascogonium (Nienburg, '14). In none of the lichens has a sperm or other nucleus been observed to move down into the fertile part of the archicarp. Pore formation in the archicarp of the *Ascomycetes* has no phyletic relation to the fusions of auxiliary cells among themselves or with a short oöblastema thread or the egg cell. It occurs in-

[1] Blackman and Welsford ('12), who earlier investigated the cytology of *Polystigma rubrum,* are of the opinion that the "spermatia" as well as the archicarps degenerate, and that certain vegetative cells become transformed into ascogones.

dependently in different groups of the fungi as a means of permitting the association of nuclei, often in conjunction with the association of sex nuclei or their equivalent modified sex nuclei (see the situation in *Basidiobolus,* Eidam, '86; Raciborski, '96; Fairchild, '97; Olive, '07; Woycicki, '04).

Relation of oöblastema filaments and ascogenous hyphae.—In the *Ascomycetes* the processes in the growth of the zygote or ascogenic cell present to a certain extent a somewhat analogous course of progression to that of the carpogenic cell of the red algae. In the less complicated process, as shown in the *Laboulbeniales,* the carpogenic cell may undergo a few divisions, the subterminal cell of the series forming the ascogonium. The ascogonium then usually divides to form two or four ascogenic cells, or without division forms the single ascogenic cell (Thaxter, '96; Faull, '12). The ascogenic cells give rise directly, by budding, to the asci. They are, therefore, somewhat comparable or analogous to the gonimoblasts of the red algae. In *Sphaerotheca* (Harper, '95[a], p. 475) there is a single short ascogenous thread of a few cells (arising from the one-celled oögonium or ascogonium) forming a single ascus from the subterminal cell. Where the process is more complex, as in *Pyronema* (Harper, '00; Claussen, '12), several long ascogenous hyphae arise from the large single-celled zygote or ascogonium, giving rise ultimately to numerous terminal asci. In other forms the ascogonium is several-celled, a number of the cells developing ascogenous hyphae (*Collema,* Stahl, '77; Baur, '98; Bachmann, '12, '13; *Anaptychia ciliaris,* Baur, '04; *Physcia pulverulenta,* Darbishire, '00; *Ascophanus carneus,* Cutting, '09; *Lachnea cretea,* Fraser, '13; etc.).

Some of the chief objections in the way of accepting the theory of a phylogenetic relation between the oöblastema filaments of the red algae and the ascogenous threads of the sac fungi are as follows:

1. The fusion of a free sperm and the egg nucleus in the single uninucleate oögonium or carpogenic cell. So far as we know this is universal in the red algae. In the *Ascomycetes* the oögonium is usually multinucleate or multiseptate. In no

case has fertilization by a free sperm been determined, and in forms with a multiseptate "trichogyne," or oögonium, the so-called spermatia, or antheridia, do not, so far as we know, play the usual rôle in fertilization, not even a modified rôle by association with the oögonial nuclei.

2. The individual nuclei of the oöblastema filaments are of the usual diploid character, and there is no fusion of these nuclei prior to the formation of the carpospores. The individual nuclei of the ascogenous threads, or ascogenic cells, are probably haploid in character, and sooner or later form the so-called synkarion, an association of two nuclei, together equivalent to a diploid nucleus. Fusion of the paired nuclei takes place before the formation of the ascospores.

3. It has been suggested that the complex processes in the extensive migration, branching and fusions of the oöblastema filaments with auxiliary cells as is known to occur in the *Cryptonemiales* (as in *Dudresnaya, Cruoriopsis, Gloeosiphonia,* etc.), may furnish still more important evidence of the ancestry of the *Ascomycetes* than that suggested in the fusions of procarp and auxiliary cells on the one hand, and archicarp cells on the other (Dodge, '14). The fusions of the oöblastema filaments with auxiliary cells and the production of sporogenous threads from the central cells thus formed, are supposed to be represented by the fusions which are known to occur between the ultimate and antepenult cells of the ascus hook prior to the formation of additional asci. The processes in both groups result in the multiplication of spore origins and consequently in an increase in spore output. Perhaps the nearest analogue to the process in the *Ascomycetes* which results in the formation of the ascus with its four to eight spores, is found in *Cruoriopsis,* where one or two spore chains of two to four spores each are produced as a result (Schmitz, '79, '83; Oltmanns, '04). The theory of "second sexual fusions" in the red algae was founded on the discovery of these fusions of the oöblastema filaments with auxiliary cells, since it was supposed that a fusion occurred between the nucleus of the oöblastema filament (derived from the diploid nucleus of the fertilized egg) and the nucleus of the vegetative auxiliary cell

(Schmitz, '83). Recent cytological work on the red algae has not confirmed this theory, but, on the other hand, has discredited it, since in the cases examined the diploid nucleus of the oöblastema filament and the haploid nucleus of the auxiliary cell are said to repel each other and no fusion between them occurs. It should be emphasized that the fusion of the oöblastema filament and the auxiliary cell is a fusion of a diploid structure with a haploid one, that it is probably of a nutritive, or parasitic, nature comparable to the fusion of the moss sporogonium with the tissue of the gametophyte, a physiological, nutritive requirement in the absence of other means of nourishing the moss sporogonium. The fusions occurring between cells of the same ascogenous hypha are fusions between cells of the same phase and serve to bring into association nuclei of more or less remote ancestry, but each endowed with the same number of chromosomes (probably the 1x number).

Thus, while there are somewhat analogous variations in the splitting up of the ascogonium in the sac fungi, and of the carpogonium in the red algae, with progress in the direction of increasing the output of spores, it seems fair to conclude, that, so far as the evidence at present in hand is concerned, the relation between the fusion of oöblastema filaments and auxiliary cells in the red algae, and those between the ultimate and antepenult cells of the ascus hook (of the ascogenous hyphae), however interesting it may be, has no phylogenetic significance, and is at best a rather strained parallel.

Ascogenous hyphae, gonimoblasts, oöblastema filaments, the several fertile cells of certain ascogonia which communicate by resorption of the intervening septa, the fused procarp, may be considered as morphological equivalents, as suggested by Dodge ('14, p. 174), but there is no evidence of a phyletic relation between the ascogenous hyphae and fusing ascogonial cells, and their morphological equivalents in the red algae. They illustrate different modes of increase of spore output by splitting up of the oögonium.

NOTE II

The fundamental difference in the method of development of ascospores and carpospores is one of the great barriers in the

way of the descent of the *Ascomycetes* from the *Florideae*. Some (Bessey, E., '13, p. 151) have attempted to overcome this difficulty by suggesting the homology of the ascus and tetrasporangium. But this effort leads to so many suppositions and supporting hypotheses because of the fundamental difference between the process of spore formation in the ascus, and the processes of carpospore or tetraspore formation, that the descent of the ascus fungi from the red algae would require a far more labyrinthian course than would be necessary in deriving them from the *Phycomycetes*.

NOTE III

IS NUCLEAR FUSION IN THE ASCUS OF A VEGETATIVE OR SEXUAL NATURE?

It is unfortunate that there is such great divergence of opinion in the interpretation of the nuclear phenomena in the archicarp and ascogenous threads. These conflicting results are probably, in a large measure, due to the difficulties presented in the minute size of the nuclei. The divergence of opinion relates primarily to the question as to whether the fusion nucleus of the ascus is the result of two successive nuclear fusions, the first taking place in the ascogonium and the second in the ascus, or whether the nuclear fusion in the ascus is the only one.

The principle of a single nuclear fusion, that in the ascus, interprets this act as the final stage in the process of fertilization, by the fusion of two nuclei of more or less remote ancestry. At some time prior to ascus formation these two nuclei may possibly become associated in pairs into a synkarion and multiply in the ascogenous threads by conjugate division, or the synkarion and conjugate division may be postponed to the ascus hook and the complicated series of fusions between the ultimate and antepenult cells of the crozier, or proliferations of the young ascus with accompanying conjugate divisions of the synkarion.

Dangeard ('94) first described the presence of two nuclei in the young ascus, and their fusion, in several species (*Borrera ciliaris, Peziza vesiculosa, Helvella ephippium, Geoglossum*

hirsutum, Acetabula calyx, Exoascus deformans, and some lichens). The origin of the ascus was correctly described in a number of cases, but in the majority of cases at that time he thought the young ascus arose by the copulation of two unicellular gametes according to a method similar to the formation

Fig. 8. *Pyronema confluens: A*, section of mature discocarp; *B*, group of archicarps copulating with antheridia by means of the slender prolongation (trichogyne) of the ascogonium which is separated as a distinct cell; *C*, pair of sexual organs copulating by means of the trichogyne cell, ascogonium at left, antheridium at right; *D*, showing multinucleate condition of sexual organs and communication of antheridium and trichogyne. *a*, antheridium; *b*, trichogyne; *c*, ascogonium. *E*, older stage of a similar group of sexual organs after the antheridial nuclei have entered the ascogonium and the trichogyne nuclei have degenerated; also showing early stage of growth of ascogenous hyphae from the ascogonium; *F*, showing relation of ascogonia, ascogenous hyphae, asci, and paraphyses in mature fruit body.—After Harper.

of the ascus in *Eremascus*, so that the ascus appeared to be supported on two stalks. Frequently, however, in *Peziza vesiculosa* and *Helvella ephippium* he observed the origin of the ascus from a single hypha curving at the end in the form of a hook or crozier. The four nuclei resulting from the division of two were so situated in the crozier that after the formation of two cross walls the ultimate and antepenult cells each contained one nucleus, while the penult cell contained two nuclei. The association of two nuclei in the young ascus and their fusion he interpreted as a sexual act, and the young ascus was looked upon as an oögonium. Later, Dangeard found that the crozier method of ascus formation was the usual one in the forms studied and that in no case in these higher forms did the ascus arise immediately from the conjugation of two different hyphae.

This important pioneer work by Dangeard was a great stimulus to further studies which has led to a more or less clear knowledge of the history of the nuclei from the archicarp through the ascogenous hyphae to the ascus, while the origin of the ascogenous hyphae from the fertile cells of the archicarp was first described by Janczewski ('71) in *Ascobolus*, and later by Kihlman ('83) in *Pyronema confluens*. Harper first demonstrated the origin of the ancestral ascus nuclei in the archicarp of *Sphaerotheca castagnei* ('95[a]) and *Pyronema confluens* ('00) and their migration in the ascogenous hyphae, though he does not give the nuclear history in the ascogenous hyphae, except the later stages at the time of formation of the ascus. Their archicarp origin has been abundantly confirmed by several investigators in a number of different forms, both among the lichens and other *Ascomycetes*.

The different opinions in regard to the significance of nuclear fusion in the ascus rest upon the interpretation by different investigators of the behavior of the nuclei in the archicarp, or ascogenous cells, before they begin to move into the ascogenous hyphae. Some maintain that there is a fusion, in pairs, of the sex nuclei (1) in the archicarp when fertilized

by an antheridium (Harper in *Sphaerotheca castagnei,*[1] '95[a], '96; *Erysiphe,* '96; *Pyronema confluens,* '00; *Phyllactinia,* '05; Blackman and Fraser in *Sphaerotheca,* '05; Claussen in *Boudiera* [=*Ascodesmis*], '05); or (2) in the archicarp where the antheridium is functionless or absent (Blackman and Fraser, '06, in *Humaria granulata;* Fraser, '07, in *Lachnea stercorea*). In *Aspergillus herbariorum* Miss Fraser (07, p. 420) finds that the antheridium often degenerates and did not observe disappearance of the intervening wall when fusion with the trichogyne took place. She *nowhere* describes or figures fusion in pairs of the ascogonial nuclei. She merely assumes it, for, in the summary ('07, p. 428) she says: "It seems probable that normal fertilization occurs in some cases, and that in others it is replaced by a fusion of ascogonial nuclei in pairs"; Welsford ('07) in *Ascobolus furfuraceus;* Dale ('09) in *Aspergillus repens;* Cutting ('09) in *Ascophanus carneus* believe in the fusion of archicarp nuclei in pairs; or (3) of nuclei in vegetative cells where the archicarp is wanting or functionless (Fraser, '07, '08, in *Humaria rutilans,* fusion of the nuclei said to take place soon after entering the ascogenous hyphae; Carruthers, '11, in *Helvella crispa;* Blackman and Welsford, '12, merely found evidence of nuclear fusion in vegetative cells of *Polystigma rubrum*).

[1] Dangeard ('97) claims that the antheridium is functionless and that the single nucleus in the oögonium divides into two. After his study of *Pyronema* Claussen ('12) is inclined to question the fusion of the two sex nuclei in the oögonium of *Sphaerotheca, Erysiphe, Phyllactinia,* and *Pyronema* as described by Harper ('95[a], '96, '00, '05), and by Blackman and Fraser ('05) in *Sphaerotheca* as well as in the case of *Boudiera* (= *Ascodesmis*) studied by him in 1905. In respect to his work on *Boudiera* he now says: "My own statements upon the nuclear fusion in the ascogone of *Boudiera* (*Ascodesmis*) are clearly wrong." He points out that in none of these cases is the history of the nuclei in the ascogenous hyphae known, and thinks that a reinvestigation will show paired nuclei here. A question to be considered, says Strasburger ('05, p. 24), is whether the chromosomes of the nuclei united in the oögonium do not remain in separated groups in the ascogenous hyphae, in order to fuse as individual nuclei in the ascus. Lotsy ('07) has expressed a somewhat similar view in an attempt to harmonize the situation in the *Ascomycetes* and *Basidiomycetes.* The fusion nucleus in the oögonium remains for a time a 2x nucleus but some time prior to ascus formation the 2x nucleus separates into two individual 1x nuclei in the ascogenous hypha, forming a synkarion. Conjugate division now takes place with ascus formation occurring immediately or after several successive conjugate divisions.

Others maintain with equal assurance that there is no fusion of the sexual nuclei in the archicarp. There is merely an association of sex nuclei.

(1). In forms with a functional antheridium and archicarp may be mentioned *Monascus*[1] (Schikorra, '09) and *Pyronema confluens* (Claussen, '07, '12).

(2). In forms where the antheridium is absent or functionless may be mentioned *Pyronema confluens* (Brown, W. H., '09, antheridium functionless), *Lachnea scutellata* (Brown, W. H., '11, antheridium absent). In both of these examples, cases of division of the nuclei in the ascogonium were observed which might be mistaken for fusion. Since no divisions of nuclei in the ascogonium have been described by authors in the forms where they believe sexual fusions of nuclei to take place, W. H. Brown ('11) suggests that they may have had before them division stages. In *Ascophanus carneus* and *Ascobolus immersus* the antheridium is absent, but association of the nuclei in several of the multinucleate ascogonial cells occurs after pore formation in the walls. Most of these nuclei become paired and remain paired as they migrate in the ascogenous hyphae to the ascus hooks, where conjugate division takes place. The only fusion of nuclei is that in the ascus, except in badly fixed preparations or in degenerating nuclei in the ascogonium (Ramlow, '14). In *Leotia* (Brown, W. H., '10) the ascogenous hyphae

Fig. 9. *Pyronema confluens: A*, *B*, and *C*, conjugate division of nuclear pairs in the ascogenous hyphae; *D*, conjugate division in ascus hook; *E*, tips of branched ascogenous hyphae with ascus hooks, young asci, and beginning of conjugation of the ultimate and antepenult cells of the ascus hooks; *F*, completed conjugation of the ultimate and antepenult cells of the hook and association of their nuclei as a pair. *Ascog*, ascogonium; *asc. h*, ascogenous hyphae with paired "sexual" nuclei.—After Claussen.

[1] Barker ('03) ascribed his failure to find a fusion of nuclei in the ascogonium of *Monascus* to the absence of proper stages in his material.

are supposed to arise from an ascogonium in the base of the ascocarp, but the nuclei are believed to arise from a haploid nucleus. Conjugate division occurs in the ascus hooks, the majority of which are formed by proliferation of the binucleate penult cell and from fusions of the ultimate and antepenult cells of croziers, so that many conjugate divisions of the haploid nuclei take place, and the first nuclear fusion is in the ascus. In *Laboulbenia chaetophora* and *L. Gyrinidarum* (Faull, '11, '12) fusion of nuclei does not occur in the ascogonium, the mature binucleate ascogenic cell develops the asci by budding, each ascus bud being preceded by a conjugate division of the nuclear pair. In *Polystigma rubrum* (Nienburg, '14) no fusion in the ascogonium occurs. In *Collema pulposum* (Bachmann, '13) the nuclei in the ascogenic cells were often found in pairs, but no cases of fusion were observed.

(3). Forms in which an archicarp is absent or functionless, and certain vegetative cells take on the function of ascogenic cells, in which the authors believe nuclear fusion does not take place except in the ascus: *Gnomonia erythrostoma* (Brooks, '10); *Helvella elastica* (McCubbin, '10) in which the "ascogenous hyphae" form an intricately interwoven subhymenial layer of threads each with two nuclei in the end. The ends of these hyphae form croziers with conjugate division of the two nuclei followed by about six repeated proliferations of the young ascus and crozier formations, accompanied by fusions of the ultimate and antepenult cells and crozier formation, resulting in many successive conjugate divisions of the haploid nuclei, with fusion first in the ascus. In *Xylaria tentaculata* (Brown, H. B., '13) the ascogenic cells which appear to be derived by the separation of the cells of "Woronin's hypha" are uninucleate and soon become multinucleate by nuclear division. The nuclei multiply also in the ascogenous hyphae.

The theory of a vegetative fusion in the ascus arose from the belief on the part of some students that sexual fusion of the nuclei occurred in the ascogonium, that the nuclear fusion in the ascus must be a second fusion with no relation to the

sexual process, and, therefore, it must be of a vegetative nature. If a second fusion of the nuclei occurred it would call for a triple division of the fusion nucleus in order that the haploid condition should be again reached.

The universal occurrence of the triple division in the ascus in the formation of the spores is by some ascribed to a "quadrivalent character" of the chromosomes in the fusion nucleus, and rendered necessary in the return to the univalent condition (Harper, '05; Overton, '06), and Overton states, "that all these divisions persist, no matter how many spores are to be produced, which shows their necessity in the process of reduction."[1] *Eremascus* controverts this statement since there is certainly but one fusion (Stoppel, '07; Guilliermond, '09) and yet triple division occurs in the ascus.

The results of cytological investigations by different students in connection with the triple division show considerable variation. Thus Harper ('00, '05) finds the same number of chromosomes in all three divisions (10 in *Pyronema,* 8 in *Phyllactinia*). The two ascus nuclei "fuse with all their corresponding parts" (Harper, '05, p. 67), so that the quadrivalent nature of the chromosomes in the fusion nucleus is not to be seen, though he conceives it to exist. Synapsis occurs in the first division.

Miss Fraser ('07, '08) describes *Humaria rutilans* as having 16 chromosomes in the first division where synapsis occurs (heterotypic) which split transversely and the daughter nuclei have each 16 chromosomes which appear on the nuclear plate in the second division. In the second division the chromosomes split longitudinally (homöotypic) and 16 chromosomes pass to each daughter nucleus. In the third division the 16 chromosomes are supposed to separate at the nuclear plate without division, 8 going to each daughter nucleus. This division she terms "brachymeiotic". A similar situation is described by Fraser and Welsford ('08), Fraser and Brooks ('09), and Carruthers ('11). Faull ('05) finds the same num-

[1] Polysporous asci resulting from several to many nuclear divisions may be the retention of an ancestral character, the number of divisions being reduced to three in most forms.

ber of chromosomes in all three divisions, in some species 4 or 5 (*Hydnobolites*), in others 8 (*Neotiella*).

More recently Claussen ('12) after a very thorough study of *Pyronema confluens* finds the same number of chromosomes (about 12) in all three divisions. The first division is heterotypic accompanied by synapsis, diakinesis and a splitting of the chromosomes. The second is homöotypic, while the third is typic. Faull ('12) in a recent study on *Laboulbenia* also finds that the two first divisions in the ascus agree with the usual phenomena accompanying reduction in spore mother cells, the first being heterotypic, while the second follows "very swiftly on the heels of the first." He concludes that "probably the only nuclear fusion in the life cycle is that in the ascus," and that conjugate divisions of nuclei are an important phase in the sexual phenomena of the *Ascomycetes*.

The evidence from recent investigations, therefore, supports more and more the interpretation of nuclear fusion in the ascus as a process of exactly the same significance as the nuclear fusion in the basidium of the *Basidiomycetes*, and in the teleutospore of the *Uredinales*, i. e., it is the fusion of a pair of nuclei of a longer or shorter history of conjugate divisions from a pair of ancestral nuclei of more or less remote association. This association of nuclei arises in a variety of ways and at different periods in the ontogeny just as it does in the *Basidiomycetes* (Maire, '02; Ruhland, '01; Harper, '02; Nichols, S. P., '04; Kniep, '13), and *Uredinales* (Sappin-Trouffy, '96; Maire, '99, '01; Blackman, '04; Christman, '05, '07; Blackman and Fraser, '06; Olive, '08; Hoffmann, '12; Werth und Ludwigs, '12). The association is accomplished in some cases through the copulation of two gametangia (*Pyronema, Monascus, Gymnoascaceae,* and the *Erysipheae*). Such an association represents nearly, if not quite exactly, the true type of sexuality. The other methods of association represent a variety of modified types of sexuality (see Note 1) where the archicarp is present and the antheridium absent, or functionless, or where the archicarp is absent and vegetative cells, either with or without the migration into them of nuclei

from adjacent vegetative cells, give rise to the ascogenous threads.

The results of recent work tend more and more to show that there is no fusion of the associated nuclei in the ascogonium, or ascogenic cells, whether certain of the nuclei have been derived from an antheridium (*Pyronema,* Claussen, '12; *Monascus,* Schikorra, '09), or not. Conjugate division in the ascogenous threads has been abundantly proven, though in some cases it may occur only one or a few divisions prior to the formation of the ascus.

What the peculiar features of nuclear fusion in the ascus are which characterize it as vegetative, seem to rest more on an *ex parte* judgment of a fusion of nuclei in the ascogonium than upon any well established idea of the nature of vegetative nuclear fusion. Thus, Miss Fraser ('08, p. 37) states that in *Humaria rutilans* the two nuclei in the ascus enter independently upon the prophases of the first division, fusing in the spirem stage. This she regards as evidence in disproof of the sexual nature of the fusion of nuclei in the ascus ('08, p. 44). Harper ('05) raises a similar objection. On the other hand, it seems to me that it is excellent evidence that it is not of a vegetative nature. It is well known in a number of cases that the egg and sperm nuclei, lying side by side in the egg, undergo the prophase stages of division up to the formation of the chromosomes before fusion of the two takes place. I cite certain examples in the *Abietineae: Pinus sylvestris* (Blackman, '98); *P. strobus* (Miss Ferguson, '01, '04); *Tsuga canadensis* (Murrill, '00).

In support also of the supposed vegetative nature of the fusions in the ascus Miss Fraser ('13, p. 559) cites "vegetative nuclear fusions" in the quadrinucleate ascus of *Humaria rutilans* and her work on this plant in 1908. But she nowhere describes or figures the fusion of the four nuclei in such asci. She says ('08, p. 41) "trinucleate (Fig. 50) and quadrinucleate (Fig. 51) asci are sometimes formed; their fate could not be determined." It is very likely that such tetranucleate young asci found by Miss Fraser in *Humaria* result from further conjugate division prior to the prolifera-

tion of the young ascus to form branches and further croziers resulting in an increase of asci as shown to take place in *Pyronema confluens* by Claussen ('12, p. 25, fig. 6, III).

It has been suggested by some who regard the fusion in the ascus as a second fusion of nuclei (Harper, '05; Overton, '06) that if the synkaryophytic condition of the terminal portion of the ascogenous hyphae in *Pyronema,* and far back in those of *Galactinia succosa* (Maire, '03, '05), could "work back until the egg cell was reached," an apogamous condition might result similar to that in the *Hymenomycetes.* Certainly those who have suggested this theory have not thought far enough ahead, for how would the univalent condition of the spore nucleus pass to the bivalent condition of each nucleus prior to the paired (= quadrivalent) condition in the ascogenous hyphae of the next generation unless this were preceded by a nuclear fusion. Such a condition would not be apogamy. The quadrivalent character of the fusion nucleus of the ascus, or of the synkarion in the ascogenous threads, demands two successive nuclear fusions, if the triple division in the ascus brings about the reduction of a quadrivalent nucleus to a univalent one as maintained by the adherents of this theory. As to such an apogamous condition being similar to that in the *Hymenomycetes* it must be remembered that there are only two divisions in the reduction process in the *Hymenomycetes,* so that when two univalent nuclei become associated in cells of the mycelium or basidiocarp the bivalent condition of these cells is attained.

In a very interesting and scholarly argument Harper ('05) has attempted to explain the inclusion and fusion of two nuclei in the young ascus on the basis of the nucleo-cytoplasmic relation or balance in the cell. The abundance of food material in the tips of the ascogenous hyphae inhibits cell wall formation so that two nuclei are enclosed in one cell. Rapid growth of the ascus and cytoplasm follows in order to balance the relation of the latter with the nuclear mass. The fusion of the nuclei and growth of the fusion nucleus again overbalance the cytoplasm, which then by growth increases again

in mass. The process is thus a reversible one, and by a sort of see-saw growth of nucleus and cytoplasm the ascus cell is pushed up to the large size characteristic of spore mother cells.

It is very true that the "regulative function is a reversible one," that an active cell with a large amount of cytoplasm demands a correlative amount of nuclear substance, that the increase in one may result in the increase of the other. Also it is very true that the ascus belongs to the category of spore mother cells, which are characterized by relatively large nuclei and cytoplasmic mass compared with most vegetative cells, but this does not explain why, when ascus or spore mother cell formation is about to take place, cell division does not occur at a period when the food relation would permit the formation of young uninucleate asci if these nuclei are bivalent in nature. The regulative functions accompanying growth and maturity of such a young gonotokont would assure sufficient size, sufficient food material, and the necessary equilibrium. The fact that asci in different species and groups vary so greatly in size shows this, and also that there is no general standard of mass in relation to surface area which would demand two nuclei at the origin of the ascus.

In fact it is very clear, from the morphological processes which take place in the tip of the ascogenous hyphae of most of the forms studied, that cell division, or cell wall formation, is more likely governed by the last division of the two nuclei so that the cell walls are laid down between the daughter nuclei. If the inclusion and fusion of two nuclei in the young ascus were controlled entirely by nutritive and cyto-regulative processes, why are not sister nuclei included? Surely the purely cyto-regulative functions would be just as well satisfied. It appears that in rare cases sister nuclei may be included in the ascus (Brown, W. H., '10, in *Leotia chlorocephala*).

Of the four nuclei resulting from the two successive divisions of the zygote nucleus in *Spirogyra*, Chmielewski ('90) states that two fuse to form the nucleus of the single germling which is usually formed in the *Zygnemaceae*. Harper inter-

prets this as a vegetative fusion in support of his interpretation of vegetative fusion in the ascus. Karsten ('08) describes the divisions of the zygote nucleus into four nuclei in *Spirogyra jugalis,* but does not state the relation of the nuclei to the germling (second division sometimes omitted). Tröndle ('07) interprets the process in *Spirogyra Spréeiana* as presenting but a single division of the zygote nucleus. Results of this nature, so divergent from expectations based on the normal history in many other organisms in widely separated groups, are usually received with considerable reserve, particularly where they are pioneer investigations in a group not yet studied. Recently Kurssanow ('11) in a thorough study of nuclear division and germination of the zygote in two species of *Zygnema* (*Z. cruciatum* and *Z. stellinum*) has shown that the process is normal, there being two successive divisions, three of the nuclei usually degenerating, while one becomes the nucleus for the single germling characteristic of the *Zygnemaceae.* Occasionally only two of the nuclei degenerated, but then two germlings were formed, an interesting case showing a tendency to retain what is believed to be the ancestral condition where four germlings are formed as in the *Mesotaeniaceae,* while in the desmids two germlings are regularly formed.

Other cases cited as examples of vegetative nuclear fusion and classed with nuclear fusion in the ascus, are those of the endosperm nucleus with the second sperm nucleus in seed plants (Harper, '05), and (Fraser, '13) nuclear fusions in paraphyses and in hairs of the excipulum of certain discomycetes. Such cases, however, cannot be legitimately compared to fusion in the ascus, since those nuclei are shut off from further participation in the line of successive ontogenies.

The example cited by Harper of Boveri's ('88) experiment in shaking sea urchin's eggs after fertilization, resulting in the production of an abnormally large larva with 72 instead of 36 chromosomes, is in a different class from most of the other examples of vegetative fusion given. This is equivalent to a true double fertilization and it is quite within the bounds of possibility that among many such larvae some

might under favorable conditions be the starting point of a new ontogeny which would be similar to certain mutants. The case of *Oenothera gigas* (see De Vries, '03, '13) a mutant from *Oe. Lamarckiana* with double the number of chromosomes is similar.[1] Other tetraploid mutants are known (see Gates, '13), the diploid gametophyte and tetraploid sporophyte of the mosses produced experimentally by Marchal ('09, '11) is interesting in this connection.

Now, the possibility of a similar double fertilization in an ascomycete is not, a priori, excluded. There might be an isolated example. But the normal expectation is that it would have afterward a nuclear history in its ontogeny similar to others with one nuclear fusion and one reduction from 2x to 1x. But it is not likely that the entire group of sac fungi is founded on such a mutation, followed by a double reduction with triple division and then double fertilization again and so on. The several cases where it has been quite well established that there is no nuclear fusion prior to the ascus, together with the great uniformity of the ascus nuclear phenomena in the group, controverts the idea of any such origin for the sac fungi.

All of these facts go to prove that the inclusion and fusion of two nuclei in the young ascus is of a very different and far greater significance than a vegetative one. The process of nuclear fusion in the ascus does not comprise in itself the entire series of events generally accepted as belonging to the process of fertilization, for in most organisms nuclear fusion occurs in the same cell where nuclear association takes place. It is generally conceded that before the haploid condition of the nucleus is again established important processes take place which we call reduction phenomena, the full significance of which we perhaps are as yet ignorant of. These processes, including synapsis, cannot take place unless nuclear fusion has occurred, and some students see in

[1] Just how the doubling arose in this instance is of course difficult to determine. Stomps ('12) suggested that it arose through the union of two unreduced diploid gametes, while Gates ('09, '13) thinks it arose through "suspended mitosis of a megaspore mother cell" having (4x) 28 chromosomes, and its apogamous development.

them the real act of fertilization (Strasburger, '00, '04, '05).

Remarks on the origin of the specialized ascus.—In the direction of progression from the generalized ascus by splitting up of the zygote, the diploid phase has been prolonged and the number of spores multiplied. The filamentous outgrowths of the zygote, or its equivalent, provide numerous terminal cells of restricted size suitable for the production of a small number of spores in each, following the meiotic divisions of the fusion nucleus which terminate the diploid phase.

The situation in species with polysporic asci, where the spores result from numerous divisions of the fusion nucleus, is interpreted by some as a germination phenomenon (Overton, '06), but it seems to me more comprehensible to regard it as a retention of a primitive feature existing in certain phycomycetous ancestors, and characteristic also of primitive *Ascomycetes* like *Dipodascus.*

The formation of internal non-motile spores through free cell formation in the zygote, under conditions adapted for dispersion by ejection from either the generalized or specialized ascus, may be sufficient to account for the distinctive processes of spore formation in the sac fungi. In the oögonium of *Saprolegnia,* functional nuclei in the oögonium are very similar to the nuclei of the ascus preceding ascospore formation. The nucleus is provided with a prominent central body at its pointed end from which kinoplasmic radiations extend (Hartog, '95; Claussen, '08; Mücke, '08).

In most of the *Ascomycetes* the cytoplasm in the ascus is differentiated into epiplasm and spore plasm, the former assisting in the ejection of the ascospores. This separation of the plasm may have been one of the direct causes of the peculiar method of ascospore formation.

NOTE IV

THE PHYLOGENETIC RELATION OF THE TRICHOGYNE AND SEXUAL APPARATUS OF THE ASCOMYCETES AND THOSE OF THE RED ALGAE

The sexual apparatus of the *Ascomycetes,* particularly the trichogyne and the so-called spermatia, is generally conceded to be the strongest evidence in support of their phylogenetic

relation to the red algae. The analogy at least between the trichogyne of the red algae and that of the *Ascomycetes* is very striking. The evidence brought forward by Stahl ('77) and others of the relation of the trichogyne to the ascogonium in the lichens, together with the fusion of spermatia to the trichogyne, followed by the gradual and peculiar degeneration of the latter and the subsequent development of the ascogenous threads, was generally accepted as proof of fertilization in the ascogonium by a spermatium. Also the early studies of *Polystigma rubrum* (Fisch, '82; Frank, '83) and *Gnomonia erythrostoma* (Frank, '86) in which similar structures and phenomena were observed at that time, were generally accepted as indicating a well developed condition of sexuality. These studies gave a great impetus to the theory suggested by Sachs ('96) that the *Ascomycetes* had their origin from the red algae, or that the two groups had ancestors in common. This theory has taken very deep root and probably is accepted by a majority of botanists even at the present time, especially by those who are not special students of the fungi. It should be stated also that a number of our foremost students of the fungi, perhaps a majority of them, are firm disciples of this theory.

Recent investigation, however, including a cytological study of several of the now classic types, including *Collema* (Bachmann, Miss F. M., '12, '13), *Polystigma rubrum* (Blackman and Welsford, '12; Nienburg, '14), *Gnomonia erythrostoma* (Brooks, '10) have failed to furnish any evidence of a real sexual function on the part of either the trichogyne or spermatia in any of the species of fungi possessing these two structures. Pairing of nuclei in the oögonium, or the pairing of these with nuclei from adjacent cells of the ascogonial branch or archicarp, furnish the synkaria, or the synkaria are organized at different stages in the development of the ascogenous hyphae (see Note III). In some quarters these results have led to a loss of confidence in the sexual significance of the trichogyne and spermatia of the *Ascomycetes*. Some have therefore attributed to the trichogyne a physiological significance of another kind, that of a respiratory organ for

example (Brooks, '10), or a boring organ, a terebrator (Lindau, '99). Zukal ('89) interpreted the trichogyne of *Pyronema confluens* as a haustorium to provide food for the large ascogonium with its numerous ascogenous threads.

Recent investigations on *Collema pulposum* (Bachmann, F. M., '13) have revealed an interesting departure in the relation of the trichogyne and spermatia from that thus far found in other lichens, and is in strong contrast with the condition found by Stahl in *Collema*. The "spermatia" are not free and are not formed in large numbers in superficial receptacles, but are imbedded in the thallus and remain attached to the supporting hypha. The trichogyne does not extend to the surface but migrates through the interior of the thallus, seeks the spermatia and fuses with one. Then the trichogyne undergoes the usual deterioration, but no evidence was obtained of the migration of the nucleus of a spermatium to the ascogonium, although a nucleus supposed to be the sperm nucleus appears to have been observed in the terminal cell of the trichogyne.

In the red algae the only variations and progression in the trichogyne is in variations in length to meet the requirements of thin or thick cortex, some more or less sinuous or spirally wound, and a few stout and blunt. It is universally a continuous, enucleate,[1] prolongation of the oögone, i. e., not septate nor a separate cell. So far as we know the sperm always functions in the red algae. In the sac fungi, there is great variation and marked morphological progression from an oögone without a trichogyne through short one-septate trichogynes to long, simple, several-celled ones, and also to profusely branched, multi-septate trichogynes. It is more comprehensible to regard this progression and variation in the light of evolution from the simple to the complex, in the ascomycete phylum, independent of the red algae, than to con-

[1] Davis ('96) describes the trichogyne of *Batrachospermum* as having a nucleus of its own, but it is not separated from the egg nucleus by a wall until just prior to the development of the gonimoblasts from the egg. He also states that the sperm nucleus never passes out of the trichogyne into the egg. However, Schmidle ('99) and Osterhout ('00) find no trichogyne nucleus and describe a real fertilization by fusion of sperm and egg nucleus.

ceive the long septate trichogyne of the highly specialized *Collema* to be derived directly from the simple trichogyne of the red algae, and then degenerate to the simple gamete of lower more generalized *Ascomycetes*.

NOTE V

MODIFICATION OF SEXUAL PROCESS ALONG WITH STERILITY OR LOSS OF THE ANTHERIDIUM AND STERILIZATION OF THE ARCHICARP

Sterility or loss of the antheridium.—Several species are known in which the antheridium, though present, does not function. In such cases sexuality is modified in such a way that sex differentiation occurs among the nuclei in the ascogonium or in the ascogenous hyphae. Several examples may be cited as follows: In *Pyronema confluens* (Brown, W. H., '09) the antheridium sometimes fuses with the trichogyne but there is no migration of its nuclei; in other cases it may not connect with the trichogyne. The antheridial nuclei degenerate. In still other cases the antheridium is absent. In *Lachnea stercorea* the antheridium fuses with the terminal cell of the archicarp but its nuclei degenerate (Fraser, '07). In *Aspergillus herbariorum* (Fraser and Chambers, '07) and *A. repens* (Dale, '09) a similar situation exists. In those numerous examples where spermatia (mostly free "antheridia") are present it is very likely that the sperm nuclei no longer play a rôle in fecundation due to such extensive sterilization of the terminal segments of the archicarp, but the cytology of only a few species has been determined. They no longer perform the function of fecundation in *Polystigma rubrum* (Blackman and Welsford, '12; Nienburg, '14), *Gnomonia erythrostoma* (Brooks, '10), and in *Collema pulposum* (Bachmann, '13) the sperm nucleus has not been traced through the long succession of sterile segments of the archicarp, and it is very probable that it does not reach the ascogonial cells. The spermatia are entirely absent in a number of species where archicarps are present, as in *Laboulbenia chaetophora* (Thaxter, '96; Faull, '12).

Sterilization of the terminal portion of the archicarp and differentiation of sex nuclei in the ascogonium or ascogenous

hyphae.—A moderately large number of species, in which more or less extensive sterilization of the terminal portion of the archicarp has occurred, have been examined by cytological methods and in most cases a reduced or modified sexual condition has been found.

In *Pyronema confluens* great variations occur in the sexual nature of the ascogonium. In what may be called normal cases, antheridial nuclei enter and become associated with the ascogonial nuclei (Harper, '00; Claussen, '07, '12). Under cultural conditions the antheridium may be normal, rudimentary or absent, but the ascogonium develops in a normal manner (van Tieghem, '84). Different strains may also behave differently. In some the antheridium does not fuse with the trichogyne, while in others it does (Brown, W. H., '09). In some cases even when the antheridium fuses with the trichogyne, its nuclei do not pass into the ascogonium (Dangeard, '07), but degenerate *in situ* (Brown, W. H., '09). In these cases where the antheridium does not function the sexuality of the ascogonium is modified in as much as its nuclei are differentiated sooner or later so that in pairs they perform the function of sperm and egg nuclei. According to W. H. Brown ('09) in cases where the origin of the pair of nuclei in the ascus hook could be determined, they were sisters. After the one conjugate division in the hook the two nuclei in the ascus, or penult cell, are "cousin" nuclei.

The archicarp of *Lachnea scutellata* (Woronin, '66; Brown, W. H., '11) consists of about nine cells. No antheridial structure has been observed. The penultimate cell functions as the ascogonium (Brown, W. H., '11). It is multinucleate and no fusion of nuclei in pairs takes place here. The nuclei are increased in numbers by division, not only in the ascogenous threads where they do not appear to be paired or show conjugate division, but also in the ascus hook where conjugate division takes place. The numerous fusions of the terminal and basal cells of the ascus hook result in numerous successive conjugate divisions. In *Leotia,* although the archicarp has not been clearly observed, it would appear from the account (Brown, W. H., '10) that the antheridium is absent (or

if present, functionless) and that the ascogonium consists of a single coenocytic cell. Conjugate division takes place in the ascus hook, and the subsequently fusing cells, so that in most cases rather distantly related pairs of nuclei form the fusion nucleus in the ascus. In *L. chlorocephala* (Brown, W. H., '10), it appears that the pair of ascus nuclei are sometimes sisters. This would indicate an extreme case in the modification of sexuality, the distance of relationship between the sex nuclei being reduced to the minimum. It recalls the very close relationship of the sex nuclei in many of the lower algae, particularly in certain diatoms[1] (Oltmanns, '04), and in the species of *Spirogyra* having buckle-joint conjugation (Chodat, '10). In the case of *Spirogyra* it is not known whether the pair of sex nuclei in this type of conjugation are cousins or sisters, or whether now one and then another of these possibilities exists. Such species of *Spirogyra* in which certain threads present scalariform as well as buckle-joint conjugation offer an interesting parallel to the variation in distant relationship of the fusing nuclei in the young ascus.

In some other species where the antheridium is functionless or wanting, sex differentiation is said to take place among the nuclei in the ascogonium. This indicates a sex differentiation much earlier than that which is supposed to occur in the species just cited. This differentiation in sex nuclei has been described in *Humaria granulata* (Blackman and Fraser, '06).

Another species in which similar phenomena are described is *Lachnea stercorea* (Fraser, '07). Here the archicarp consists of several coenocytic large cells and the terminal trichogyne of 4–6 smaller coenocytic cells. The unicellular coenocytic antheridium fuses with the terminal cell of the trichogyne, but its nuclei do not reach the single-celled ascogonium, among whose nuclei sex differentiation is said to take place.

For a number of years *Polystigma rubrum*, a parasite on cherry leaves, as the result of studies by Fisch ('82) was regarded as an example of fertilization of an ascogone coil by

[1] In *Achnanthes subsessilis*, the protoplast divides into two parts along with nuclear division. The two uninucleate protoplasts now immediately unite in auxospore formation.

sperm nuclei from spermatia after passing through a long succession of cells constituting the trichogyne or sterile portion of the archicarp. The trichogyne, or sterile portion of the archicarp, is very long and branches into two portions, one extending to either surface of the leaf. But according to Nienburg ('14) sex differentiation has occurred between the basal cells of the archicarp and a nucleus from the basal cell migrates into the adjacent cell, which becomes the ascogonium or ascogenic cell, but nuclear fusion does not take place here.

Loss of function by the archicarp or its disappearance.— A number of examples are known in which the archicarp has either lost its function as a sexual organ or ascogone, or has disappeared. In such cases differentiation of sex occurs in special vegetative cells, sometimes by the migration of a nucleus from certain cells into adjacent ones. In *Gnomonia erythrostoma,* although Frank ('86) described coiled ascogone-like structures with trichogynes, and believed that the coils were fertilized through the agency of the spermatia, recent cytological work (Brooks, '10) on this species appears to show that the tufts of hair-like structures emerging through the stomates of cherry leaves, on which this species of *Gnomonia* is parasitic, are not now connected with the coiled hyphae deeper in the tissue. It appears also from the same work that the ascogenous hyphae do not arise from the coils, but from one or more slightly differentiated hyphae in the center of each coil.

A similar example is found in *Xylaria polymorpha* (Fisch, '82), where an extensively coiled hypha ("Woronin's hypha") occurs in the early stages of the formation of the ascocarp, but later disappears and certain vegetative cells give rise to the ascogenous hyphae.

In *Humaria rutilans* (Fraser, '08) no archicarp or ascogone coil is discernible, but certain vegetative cells function as ascogenic cells following the migration into them of nuclei from adjacent cells.

MORPHOLOGY OF THE ARCHICARP

If the history of the *Ascomycetes* is correctly read from the simpler and more generalized forms to the complex and

highly specialized ones as Sachs ('74, '96), de Bary ('81, '84), and many other students have advocated, the female organ or archicarp first appeared as a "unicellular" or continuous organ, not differentiated into an oögonium or fertile portion, and a trichogyne. The presence of a "procarp," whether consisting of one or several cells, which ultimately gave rise to the asci or ascogenous threads was the predominant character which led Sachs in 1896 to believe in the phyletic relation of the sac fungi and red algae, although earlier he had regarded the morphology of the ascocarp and cystocarp of greater importance in showing relationship. No known red alga possesses a procarp simple enough to represent the prototype of the two groups. *Gymnoascus* was selected by Sachs as representing the simplest *Ascomycetes*. The archicarp of *Gymnoascus* is a continuous structure more or less coiled around the antheridium from which it copulates directly without the intervention of a trichogyne.

After copulation the ascogonium divides into several cells which give rise to the ascogenous hyphae. In some forms the splitting up of the ascogonium by transverse division occurs at an earlier period, before copulation. There is some evidence which indicates that the "trichogyne" in the *Ascomycetes* primarily was a prolongation of the "unicellular" oögone (or carpogone), and that when it was first separated as a distinct cell it was still a fertile part of the archicarp. In *Aspergillus repens* the terminal cell, or "trichogyne," sometimes gives rise to ascogenous hyphae (Fraser, '08).

The terminal cell became merely a trichogyne when it ceased to give rise to ascogenous hyphae, and acted as a transport tube for the sperm nuclei from the antheridium to the ascogonium, as in *Pyronema* and *Monascus*. The septum between the terminal cell and the functional ascogonium was an impediment to the passage of the sperm nuclei, as well as the fact that when they entered the terminal cell of the archicarp they did not meet with functional egg nuclei. This situation very likely favored the assumption of sperm and egg functions by the nuclei of the functional ascogonial cell. The variations in *Pyronema* where the antheridium may or may

not be present, and often when present and fused with the trichogyne its nuclei degenerate and the ascogonium is still functional producing ascogenous hyphae and asci, is in support of this interpretation.

Further sterilization of the terminal portion of the archicarp proceeds as it becomes longer and more septate, the fertile ascogonial cell or cells being near the center or base. All of the sterile portion of the archicarp distal to the ascogonial cells is usually interpreted as the trichogyne. I believe it would be more in harmony with the historical origin of the archicarp, and with the real homologies, if only the terminal sterile receptive cell of the archicarp were called the trichogyne, the other portions to be regarded as sterile portions of the archicarp or ascogonium. This would be in harmony also with Thaxter's ('96) interpretation of the archicarp of the *Laboulbeniales*.[1] In this group the inferior and superior supporting cells are sterile cells of the archicarp derived by a transverse splitting of the ascogonium. Even with this interpretation of the trichogyne of the *Ascomycetes*, it would be a different structure from that of all the red algae where it is merely a continuous prolongation of the egg cell.

NOTE VI

The coenocytic character of the mycelium of the *Phycomycetes* has been presented as an obstacle to the derivation of the sac fungi from the sporangium fungi (Bessey, E. A., '13); this character can, however, have very little or no significance, for many of the *Ascomycetes* are coenocytic. As in most of the fungi, cell wall formation is delayed so that new portions of filaments are often multinucleate, the cell walls being laid down subsequently, sometimes enclosing one nucleus, sometimes several in a cell. There are the monoenergid and polyenergid species of sac fungi. In the *Phycomycetes* cell wall formation is usually longer delayed or does not occur except where reproductive cells are formed. In the *Mucorales* old mycelium frequently becomes multiseptate. It should be noted that in *Basidiobolus* (Eidam, '86; Raciborski, '96; Fair-

[1] Except in the case of the multiseptate branched trichogynes.

child, '97, and others) the cells are uninucleate. The variation in coenocytic character of mycelium probably is due in some measure to the usually fundamental difference between cross wall formation in dividing cells, in the thallophytes and the higher groups of plants, where the fibers of the inner spindle play a part and the cell wall development is centrifugal, while in most thallophytes the spindle fibers do not play such a part, wall formation being centripetal, like a closing iris diaphragm.

The strong plasma connections between the protoplasts of the *Laboulbeniales* (Thaxter, '96) present a very striking resemblance to those in the red algae. This feature is regarded by some as very strong evidence of a phylogenetic relation between the *Laboulbeniales* and the red algae. But intercellular plasma connections are a common feature in all groups of plants, though in many plants these connections are very minute. The single central pore in the wall of the *Laboulbeniales* is perhaps the result of incomplete closing of the ring-forming wall, and in the *Laboulbeniales* would seem to be of physiological rather than of phylogenetic significance. The firm cell walls which are characteristic of the members of this group bear a very definite relation to their habit as external parasites of insects. Standing out free from their bodies and thus having no other means of support than their own rigidity, thick cross walls would interfere with transport of food material, while the prominent plasma connections permit easy passage of nutrients.

NOTE VII

BRIEF OUTLINE OF SOME OF THE THEORIES AS TO THE PHYLOGENY OF THE ASCOMYCETES

I. *Descent from the Rhodophyceae.*—Sachs ('74, p. 287) regarded the resemblances between cystocarp and ascocarp as the most important character indicating a relationship between the red algae and sac fungi, although the form of the sexual organs, particularly the carpogonial branch, was also believed to point in the same direction. In his 'Lehrbuch der Botanik' he did not even suggest that the *Ascomycetes* were derived from the *Florideae*. The relationships were based

on the principle of morphological homology, which he believed were great enough to justify their inclusion in the same class. To justify his arrangement in one large group of plants with such diverse aspects and habitats, he cites the inclusion of the *Lemnaceae* and palms in the great group of the monocots. We could not then interpret his inclusion of the sac fungi and red algae in one class, the *Carposporeae,* as indicating that the former were derived from the latter.

Sachs says ('74, p. 288) that in order to find the relationships between plant divisions one must compare the simplest, not the highest forms. By this method he finds that the *Coleochaetaceae* and *Characeae* are linked, on one hand to the simplest *Florideae,* and on the other to the simplest *Ascomycetes.* Each of these series, he says, has developed in its own peculiar manner to higher forms, so that if one compared the most complete *Ascomycetes* with the coleochaetes only very slight resemblances are to be found. From this it is very clear that Sachs, at that time, had no thought of the derivation of the *Ascomycetes* from the *Florideae.* There is nothing to indicate that he believed the *Ascomycetes* descended from the charas and simplest coleochaetes, to which he says the simplest *Ascomycetes* are most closely related. Nor would his theory require a common ancestor for the two groups. Because of the morphological resemblance between cystocarp and ascocarp, he would have united the *Ascomycetes* and *Florideae* into a higher group even had he believed that the former were derived from the *Phycomycetes.*

It has been said by Sachs ('96, p. 204) that the fungi as a whole cannot be valued as an architype because, as apochlorates, they must be descended from green plants. The bacteria he would derive from the *Cyanophyceae,* the *Phycomycetes* from the *Siphoneae,* and the *Ascomycetes* (or at least the *Discomycetes*) from the *Rhodophyceae.* The predominant feature indicating the descent of the sac fungi from the red algae he now sees in the procarp of both groups ('96, p. 205).

The chlorophylless seed plants have only a slight form-producing power or motive, as Sachs has pointed out ('96, p. 205), since they occur mostly as small plant groups within certain

green leaved families and show very plainly the morphological characters of their antecedents. But he says it is quite otherwise with the fungi. The simplest primitive forms of the *Ascomycetes, Phycomycetes* and *Basidiomycetes* have given rise independently to an enormously high state of differentiation. Now Sachs in 1896 (and earlier, '74, p. 310) recognized *Gymnoascus* as belonging to the simplest *Ascomycetes,* the sexual organs of which are a simple carpogone and pollinode. It is very clear then that Sachs would not derive the *Ascomycetes* from any primitive form at all like any known red algae, much less through such forms as the highly specialized *Collema* or *Polystigma.* This warrants us in concluding that Sachs had in mind a primitive hypothetical ancestor of the sac fungi and red algae, which possessed simple copulating gametes. With the knowledge we possess to-day of such forms as *Dipodascus, Eremascus,* etc., where the zygote becomes the ascus (generalized or simple) I believe he would have recognized in the *Phycomycetes,* as we know them to-day, a situation very closely approximating an "Urform" for the *Ascomycetes,* particularly in view of the fundamental difference in the cytology of the red algae and sac fungi.

But whether the fungi represent one or several architypes it by no means follows that, because of the absence of chlorophyll, they *must* be derived from green plants, or that each great series must be derived separately from different groups of algae.

The appearance of the higher fungi (*Eumycetes*) was, in the opinion of Vuillemin ('12, p. 223), contemporaneous with the emergence of sea-shore, which abandoned certain red algae to a terrestrial life. This new environment introduced the change, which, accompanied by loss of chlorophyll, gave rise first to the *Pyrenomycetes,* from which the other higher fungi (*Uredinales, Basidiomycetes*) have originated. The saprophytic forms represent the productive and progressive stock. Parasitic groups, like the *Uredinales, Laboulbeniales,* lichens, etc., are composed of highly specialized and uniform members, their progressive potentialities being suppressed, but they retain their hold on existence because of their specialized hab-

itat. The first *Pyrenomycetes,* according to his view, were some of these depatriated red algae, losing their pigments while preserving the structure, the sexual organs and the general evolution. But he recognized no known member of the red algae as a prototype of the *Pyrenomycetes.* Primitive trichogyne-bearing algae gave rise to the red algae on one hand, and to the *Pyrenomycetes* on the other, the now known colorless red algae (like *Harveyella mirabilis, Choreocolax alba*) being recently reduced forms having no significance in the origin of the sac fungi. But the *Pyrenomycetes* with well developed trichogyne and spermatia are chosen as the primitive forms, the simplest represented by *Polystigma* (in his "*Polystigmales*") the higher ones (his "*Pyreniales*") giving rise successively to the *Hysteriales* and *Phacidiales.* From the *Polystigmales* three other lines arose, their simplest forms being represented by first, *Gymnoascus;* second, *Pyronema;* and the third line represented by the *Laboulbeniales* (see Vuillemin, '12, pp. 338-341).

Bessey ('14) regards the *Discolichenes* as the most primitive *Ascomycetes.* This theory is based on the supposed phyletic relation of the multiseptate trichogyne of the lichens (*Collema,* for example) to the trichogyne (a mere tubular, continuous, prolongation of the egg) of the red algae. Certain of the red algae became parasitic on blue-green algae and on simple members of the green algae, forming a lichen thallus. It is supposed that this parasitism may have had its origin while both kinds of organisms still lived in the water, but finally the lichen assumed the land habit. The improbability of such a derivation of the sac fungi as suggested in the above theories has been fully discussed in the preceding pages.

II. *Descent from the Phycomycetes.*—De Bary ('81, '84, '87), as already stated in the first part of this paper, believed the *Ascomycetes* were derived from the *Phycomycetes,* particularly through such forms as the *Peronosporales.* The criterion for the *relationship* is the close homology and morphological resemblance of the sexual organs, though he suggested that *Eremascus* might have been derived from the *Mucorales* through some such form as *Piptocephalus* where

the zygote is the outgrowth from the fusion point of two equal gametangia.

Brefeld ('89, '91) also derived the *Ascomycetes* from the *Phycomycetes* but interpreted the ascus as the phyletic homologue of the sporangium, the ascus representing a specialized structure derived from the generalized sporangium in one direction, while the conidia were regarded as reduced one-spored sporangia. But the nuclear fusion and reduction phenomena in the ascus are so fundamentally different from any known cytological processes in the sporangium, that its phyletic relation to the sporangium is doubtful.[1] The conjugation of the gametangia he interpreted as ordinary fusion of hyphae which occurs in numerous instances devoid of all sexual significance. *Protomyces, Ascoidea* and *Thelebolus,* with numerous spores in the ascus, were interpreted as representing an intermediate condition between the generalized sporangium of the *Mucorales* and the specialized ascus. In *Thelebolus* it has been found that the development of the ascus follows the type with crozier formation and that it is closely related to *Ascobolus* and *Rhyparobius* (see Ramlow, '06; Dangeard, '07). As for *Protomyces* and *Ascoidea* they probably represent forms with reduced sexuality while retaining the ancestral character of many divisions of nuclei to form numerous spores.

Zukal ('89), influenced by Brefeld, derived the hymenial *Ascomycetes* (like *Ascobolus, Pezizales,* etc.) through *Thelebolus* and *Monascus;* the stromatic *Ascomycetes* (whether *Pyrenomycetes* or *Discomycetes*) from the *Uredinales;* the *Gymnoascales* and others with asci arising directly from the mycelium, from another ancestral type.

Lotsy ('07, p. 469) sees no difficulty in deriving the polyenergid forms like *Pyronema* from the *Phycomycetes.* The forms with spermatia, which are usually monoenergid, it would seem rational, he thinks, to derive from the red algae, and this raises the question as to whether the *Ascomycetes* are of polyphyletic (or biphyletic) origin. The great uniformity of the

[1] The nuclear phenomena in the "germ" sporangium (from the zygote) are not known.

ascus in the entire group is a great obstacle in the way of accepting a polyphyletic origin for the group. All things considered he is inclined to accept de Bary's view of their phycomycetous origin.

The origin of the *Ascomycetes* from the *Phycomycetes* is recognized by Dangeard ('07) through such forms in which there is still a union of gametangia. *Dipodascus* and *Eremascus* represent such forms in his scheme. The generalized ascus resulting from the union of the gametangia of *Dipodascus* he terms a "sporogone." From *Eremascus,* by reduction, forms like *Endomyces* arose, while the *Ascomycetes* with ascogenous hyphae were derived from such forms as *Dipodascus* by delayed nuclear fusion and the proliferation of the gametangium into what he terms "gametophores" (= ascogenous hyphae). The gametes then are formed in the nuclear pair which fuses in the ascus. This terminology arises from his persistent belief that the ascus is the egg. Shorn of the change in terminology and his, perhaps, unfortunate insistence on homologizing the ascus with the egg, his interpretation of the relation which such a form as *Dipodascus* bears to the *Ascomycetes,* has much merit.

Nienburg ('14) suggests the origin of the *Ascomycetes* from the *Phycomycetes* through some such form as *Monoblepharis.* He would find the evidence for this in the homology of the archicarp of *Polystigma rubrum* with such forms of *Monoblepharis* in which the stalk cell of the oögonium is an antheridium, and where the oögonium is terminated by one or more sterile cells. The archicarp of *Polystigma* he interprets as having two fertile cells at the base and prolonged into a long sterile septate portion (so-called trichogyne) which forks, sending a branch to either surface of the leaf. The basal multinucleate cell is the antheridium. After pore formation one nucleus migrates into the unicellular egg. Interesting as this suggestion is, forms of *Pythium* (see de Bary, '81, '84; Atkinson, '95) with intercalary oögonia and stalk antheridia present a closer analogy to the archicarp of *Polystigma* as described by Nienburg, but it is extremely doubtful if the point of contact is to be sought through such structures.

Brief comparative summary of the above views on the phylogeny of the Ascomycetes.—The adherents to the doctrine of the red algal origin of the *Ascomycetes* interpret the point of contact in three different ways: *first,* sac fungi with highly developed "trichogyne" (sterilized archicarp) of the *Collema* type with red algae like certain of the existing forms, *Nemalion,* or some of the higher forms in the vicinity of *Harveyella,* etc.; *second,* sac fungi with highly developed "trichogyne" (= sterilized archicarp) of the *Polystigma* type with hypothetical trichogyne algae representing the common stock for the origin of both groups; *third,* sac fungi with simple generalized copulating gametes of the *Gymnoascus* type with hypothetical algae having a simple procarp representing the stock from which both groups originated.

According to the two first interpretations the sac fungi have been derived through highly developed and specialized forms from either quite highly developed and specialized red algae, or both groups from a common trichogyne algal stock, and then by degeneration have slid backward from complex and specialized structures to simple, generalized and primitive ones. The third view which recognizes a simple procarp, without regard to a trichogyne, as the important character of the hypothetical stock, is far more comprehensible.

But if we must go back to some hypothetical ancestor, which cannot be represented by any known red alga, for the source of the sac fungi it is far more reasonable to search for one in another fungus line, where, in the light of present-day knowledge, there are known forms with sexual organs very much like the sexual organs of simple, known forms of the *Ascomycetes.* But we are not yet in a position to name any known phycomycete[1] as a probable ancestor of the *Ascomycetes,* though it appears very likely that the ancestral stock possessed phycomycetous characters.

[1] Lotsy ('07) suggests *Cystopus;* Miss Dale ('03) in her study of *Gymnoascus* suggests *Basidiobolus;* Nienburg ('14), *Monoblepharis;* while Dangeard ('07) suggests *Myzocytium vermicolum* as the prototype of the higher fungi.

PROVISIONAL ARRANGEMENT OF MAIN LINES OF DEVELOPMENT IN ASCOMYCETES

For those who are interested in the suggestions as to the phylogeny and relationships of the *Ascomycetes* presented in this paper, a diagrammatic arrangement of the principal series or lines which will illustrate the relationships tentatively held by the writer may be acceptable. It is with considerable hesitation that this arrangement is presented. The writer trusts that it will be accepted as provisional and in the nature of a working hypothesis which he hopes will further stimulate investigation, suggestions and criticisms on the ideas embodied in this paper, all of which, for or against, will be gladly welcomed.

Dipodascus, a primitive form, cells of mycelium polyenergid, gametogenous branches large, unequal, polyenergid. Ascus is elongated, broadened zygospore, zygote germinating immediately forming a broad germ tube in which spores are formed. Since the process does not go on to the formation of a sporangium, a different mode of internal free cell-formation then arose in connection with the precocious formation of spores in the zygote and retention of epiplasm which assists in discharge of spores. *Dipodascus* retains tendency of gamogenic branches to copulate early before they become strongly differentiated as gametangia, just as in *Mucorales.*

I. Protoascomycetes are derived by descent and degeneration from some such primitive ascomycete form as *Dipodascus.* The ascus when of sexual origin is the zygote, except in *Nadsonia.*

Endomyces Magnusii is the nearest known form to the generalized condition seen in *Dipodascus.* Cells of mycelium usually polyenergid, those of stout mycelium are polyenergid. Formation of ascus in *Endomyces Magnusii* repeats formation of zygospore in *Zygorhynchus.* Gamete branches in both are multinucleate, but when cell wall is laid down delimiting the gametangia all but one nucleus in each gametangium of *E. Magnusii* are excluded. After contact of the two sexual branches the male gametangium is formed by enlargement of its tip, into which protoplasm and the one nucleus migrates,

exactly as male gamete of *Zygorhynchus* is formed, except the latter is multinucleate. By disappearance of the separating wall, ascus is formed of the two gametes.

Endomyces series, then, derived from *Dipodascus*-like ancestors, with *Endomyces Magnusii* the lowest and most generalized.

Developmental tendencies from here in four, five, or six different directions:

1. *Eremascus,* both gamogenic branches uninucleate, ascus more definite and specialized in shape. Loss of conidial formation. *Endomyces fibuliger* indicates step toward *Eremascus* (*E. fertilis*) in small size of gametes.

2. *Endomyces* diverging into the two series, one chiefly with sprout conidia, the other chiefly with oidia; the latter preserves the *E. Magnusii* character, the former takes on sprout conidia in addition to oidia (*E. fibuliger* and *E. capsularis* form both oidia and sprout conidia); oidia formation the more primitive and generalized condition in *Ascomycetes.*

3. *Saccharomycetes.* Still more specialized and reduced than in *Endomyces fibuliger* and in this same line. *Schizosaccharomyces* may have come from same line with dropping of sprout conidia, or may be descended from form near *Endomyces Magnusii.*

4. *Exoascaceae.* From *Endomyces*-like ancestors. Nuclear phenomena not well known. Diploid young ascus may have arisen in connection with cell wall formation, two nuclei being retained in ascogone instead of one as in *E. Magnusii,* where all but one are excluded at time of wall formation, i. e., ascus fundament may have retained the polyenergid character of the most primitive forms like *E. Magnusii.* Tendency to form hymenia may be controlled by host since asci in all, except *Taphrina laurencia,* come to surface to mature.

5. *Ascocorticium,* saprophytic on wood where food is not so rich, tendency to drop conidial formation (?), association of asci in hymenium, highest development of the *Endomyces* series, or of the *Protoascomycetes.* Series is terminated early, tendency in *Endomyces* line to specialization of zygote into one ascus with reduced number of spores, and line soon terminated.

6. *Ascoidea, Protomyces, Taphridium,* etc., probably represent forms derived by reduction and loss of distinct sexual organs but preserving primitive feature of many divisions of nucleus in the generalized ascus.

II. Euascomycetes. Lowest forms with generalized archicarp. Similar to *Monascus, Gymnoascus,* etc.

1. *Tendency* to late copulation of gamogenic branches, so that archicarp becomes large and many-nucleate, or tendency to elongate, or both.

2. As it elongates *tendency* to septation, first a single terminal cell ("trichogyne"), and later longer and multiseptate "trichogyne," or rather sterilization of terminal portion of archicarp. One of the early tendencies in connection with elongation of the archicarp may have been the origin of a receptive terminal portion under chemotactic or similar stimulation; such a condition suggested in *Cystopus*.

3. This made the passage of antheridial nuclei increasingly difficult, and resulted in early *tendency* to sterilization of antheridium or failure to function because of functionless condition of "trichogyne." Led in many cases to modified sexuality by differentiation of sex among nuclei in ascogonium, vegetative cells, or ascogenous threads.

4. *Progressive tendency* to multiplication of spores by postponement of nuclear fusion and spore formation; conjugate division of sex nuclei, and multiplication of the specialized structures (asci) in which spores are formed, so that spore formation and distribution is extended over greater period of time. This most advantageously attained by sprouting of zygote (ascogone), branching of threads, and terminal formation of specialized asci.

Diverging lines from *Gymnoascus* and *Monascus*-like ancestors or related prototypes in which asci are irregularly arranged but associated in groups with imperfect envelope.

1. A line with interwoven asci, *Plectascales* as a highly specialized lateral group, with *Gymnoascaceae* at base. *Aspergillaceae* a progressive line, with *Perisporiales* an offshoot, or *Perisporiales* direct from *Monascus*-like ancestors.

2. *Elaphomycetaceae,* asci interwoven in groups but separated by sterile walls.

3. *Pezizales,* asci remaining in groups not interwoven in mycelium, but spaced by sterile threads (paraphyses). *Pyronema* represents one of the generalized, lower forms. The *Helvellales,* etc., are probably derived from the *Pezizales.*

4. The *Microthyriales*[1] have usually been placed among the *Perisporiales* with which they have little in common. I believe they

[1] Recent studies by several authors, particularly by von Höhnel ('10) and by Theissen ('12, '13, '14) have greatly increased our knowledge of these interesting fungi, partly by the discovery of new forms but especially by uncovering many forms from the clouded situation in which they have been placed for lack of an adequate study of their structure.

represent reduced forms derived on the one hand from the *Phacidiales* and perhaps on the other from the *Sphaeriales* and possibly some from the *Perisporiales.* The formation of the characteristic shield has rendered superfluous the perithecial wall as a protective structure. The genus *Diplocarpon,* the structure and development of which was investigated by one of my former students (see Wolf, '12), I believe is an excellent illustration of a form on the way (by reduction of the perithecial wall in conjunction with the formation of the shield) from the *Phacidiales* to the condition presented by many members of the *Microthyriales.*

The above provisionally suggested relationships may be represented by the following five or six series, or lines of development, with the accompanying diagram (fig. 10):

1. Apocarp line — from *Dipodascus*-like forms and by reduction.
2. Plectocarp line — from *Dipodascus*-like forms, perhaps similar to *Monascus.*
3. Perispore line — arising from *Monascus*-like prototype, before splitting of archicarp, or from *Aspergillaceae.*
4. Pyrenocarp line — arising near *Monascus*-like prototype. *Laboulbeniales* side line near base, and some of the *Mycrothyriales* as reduced from *Sphaeriales.*
5. Discocarp line — from *Dipodascus*-like forms near *Monascus,* but lower (it is not improbable that some of the members of the stock of primitive *Euascomycetes* showed considerable variation in the strength of the ascocarp envelope, also in its presence or absence in forms where it is more or less rudimentary[1]); and some of the *Microthyriales* as reduced forms from *Phacidiales.*

Or a 6th line also, *Laboulbeniales* from *Monascus*-like ancestor.

[1] This variation sometimes occurs in existing forms. Zukal ('89) describes an abnormal case in *Eurotium* (*Aspergillus*) *herbariorum* where the antheridial branch and envelope are wanting, the mass of asci being exposed. In this connection it is worthy of note that Fraser and Chambers ('07) regard *Aspergillus* "as representing a primitive ascomycetous type from which most others can be derived." This suggestion was based on the assumption that the red algae were the ancestors of the sac fungi. On the basis of the counter theory (phycomycetous origin) *Gymnoascus* and *Monascus*-like forms are more comprehensible as primitive *Euascomycetes.*

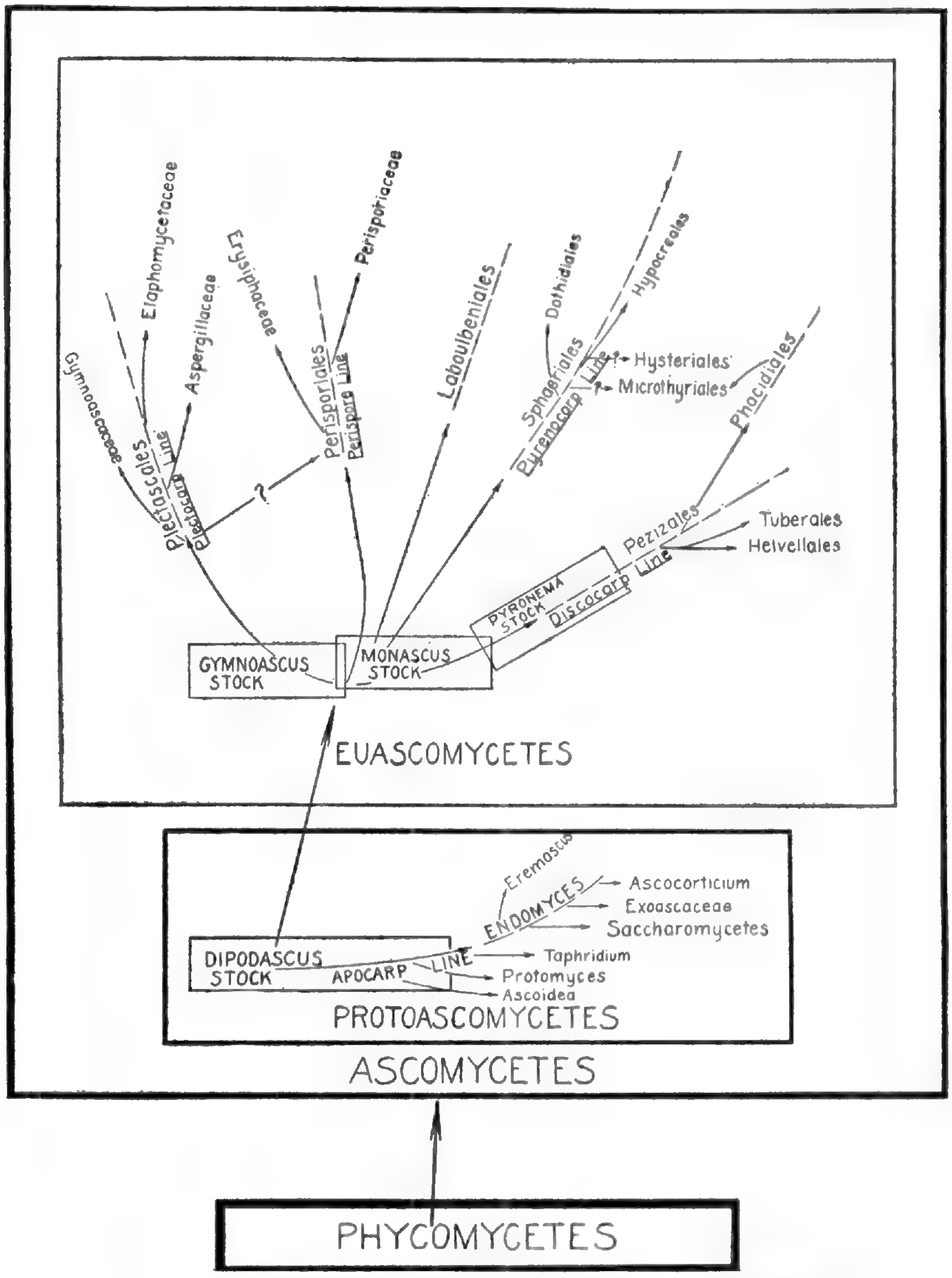

Fig. 10. Chart showing suggested phylogeny of the *Ascomycetes*.

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A CONSPECTUS OF BACTERIAL DISEASES OF PLANTS

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All our knowledge of these diseases has come within a generation. It began thirty-six years ago with the announcement of the bacterial origin of pear blight by Professor T. J. Burrill of the University of Illinois, who is with us to-day. During the first half of that period progress was slow and doubt universal, especially in Europe.

It is now eighteen years since I ventured the statement,[1] that "there are in all probability as many bacterial diseases of plants as of animals." This statement was received with much skepticism, not to mention active opposition, but time has more than borne out my statement, and there is now no one left to dispute it. To-day I will venture another, and broader generalization, to wit: It appears likely that eventually a bacterial disease will be found in every family of plants, from lowest to highest. This prediction is based on the fact that although the field is still a very new one, with no workers in most parts of the world, such diseases have been reported from every continent, and are already known to occur in plants of one hundred and forty genera distributed through more than fifty families.

DISTRIBUTION

Following Engler's arrangement, I will list these families that you may see how wide is the distribution of bacterial diseases in plants and how utterly wrong were those who said that there were no such diseases, and also those who conceded a little but said that they were very rare and restricted to the soft underground parts of a few bulbous and tuberous plants, and generally preceded by fungi. In this list, I have included only the flowering plants, but some of the cryptogams are also

[1] Am. Nat. **30**: p. 627. 1896.

subject to bacterial attack. The number following the family name indicates the number of bacterial diseases known within the limits of the family. The total of the figures, however, will not give the number of bacterial parasites, because some of the diseases overlap.

TABLE I

SHOWING THE FAMILIES OF FLOWERING PLANTS ARRANGED SERIALLY FROM LOWEST TO HIGHEST. THOSE CONTAINING GENERA SUBJECT TO BACTERIAL DISEASES ARE UNDERSCORED, AND WHEN SEVERAL DISEASES HAVE BEEN RECOGNIZED THEIR NUMBER IS ALSO GIVEN

1. Cycadaceae
2. Ginkgoaceae
3. Taxaceae
4. Pinaceae 2
5. Gnetaceae
6. Typhaceae
7. Pandanaceae
8. Sparganiaceae
9. Potamogetonaceae
10. Naiadaceae
11. Aponogetonaceae
12. Scheuchzeriaceae
12. *Juncaginaceae*
13. Alismaceae
14. Butomaceae
15. Vallisneriaceae
15. *Hydrocharitaceae*
16. Triuridaceae
17. Poaceae
17. *Gramineae* 7
18. Cyperaceae
19. Phoenicaceae
19. *Palmae*
20 Cyclanthaceae
21. Araceae
22. Lemnaceae
23. Flagellariaceae
24. Baloskionaceae
24. *Restionaceae*
25. Centrolepidaceae
26. Mayacaceae
27. Xyridaceae
28. Eriocaulaceae
29. Rapateaceae
30. Bromeliaceae
31. Commelinaceae
32. Pontederiaceae
33. Philydraceae
34. Juncaceae
35. Stemonaceae
36. Melanthiaceae
37. Liliaceae 3
38. Convallariaceae
39. Smilacaceae
36.
37.
38.
39. } *Liliaceae*
40. Haemodoraceae
41. Amaryllidaceae
42. Velloziaceae
43. Taccaceae
44. Dioscoreaceae
45. Iridaceae
46. Musaceae
47. Zingiberaceae
48. Cannaceae
49. Marantaceae
50. Burmanniaceae
51. Orchidaceae
52. Casuarinaceae
53. Saururaceae
54. Piperaceae
55. Chloranthaceae
56. Salicaceae 2
57. Myricaceae
58. Balanopsidaceae
59. Leitneriaceae
60. Juglandaceae 2
61. Betulaceae
62. Fagaceae
63. Ulmaceae
64. Moraceae
65. Urticaceae 4
66. Proteaceae
67. Loranthaceae
68. Myzodendraceae
69. Santalaceae
70. Grubbiaceae
71. Opiliaceae
72. Olacaceae
73. Balanophoraceae
74. Aristolochiaceae
75. Rafflesiaceae
76. Hydnoraceae
77. Polygonaceae 2
78. Chenopodiaceae 4
79. Amaranthaceae
80. Nyctaginaceae
81. Batidaceae
82. Theligonaceae
82. *Cynocrambaceae*
83. Phytolaccaceae
84. Aizoaceae
85. Portulacaceae
86. Basellaceae
87. Silenaceae
87. *Caryophyllaceae* 2
88. Nymphaeaceae
89. Ceratophyllaceae
90. Trochodendraceae
91. Ranunculaceae
92. Lardizabalaceae
93. Berberidaceae
94. Menispermaceae
95. Magnoliaceae
96. Calycanthaceae
97. Lactoridaceae
98. Annonaceae
99. Myristicaceae
100. Gomortegaceae
101. Monimiaceae
102. Lauraceae
103. Hernandiaceae

104. Papaveraceae
105. Brassicaceae
105. *Cruciferae* 5
106. Tovariaceae
107. Capparidaceae
108. Resedaceae
109. Moringaceae
110. Sarraceniaceae
111. Nepenthaceae
112. Droseraceae
113. Podostemonaceae
114. Hydrostachyaceae
115. Crassulaceae
116. Penthoraceae
115. } *Crassulaceae*
116. }
117. Cephalotaceae
118. Saxifragaceae
119. Hydrangeaceae
120. Escalloniaceae
121. Grossulariaceae
118. }
119. }
120. } *Saxifragaceae*
121. }
122. Pittosporaceae
123. Brunelliaceae
124. Cunoniaceae
125. Myrothamnaceae
126. Bruniaceae
127. Hamamelidaceae
128. Platanaceae
129. Crossosomataceae
130. Rosaceae
131. Malaceae
132. Amygdalaceae
130. }
131. } *Rosaceae* 6
132. }
133. Connaraceae
134. Mimosaceae
135. Caesalpiniaceae
136. Krameriaceae
137. Fabaceae
134. }
135. }
136. } *Leguminosae* 5
137. }
138. Geraniaceae 2
139. Oxalidaceae
140. Tropaeolaceae 3
141. Linaceae
142. Humiriaceae
143. Erythroxylaceae
144. Zygophyllaceae
145. Cneoraceae
146. Rutaceae
147. Simaroubaceae
148. Balsameaceae
148. *Burseraceae*
149. Meliaceae
150. Malpighiaceae
151. Trigoniaceae
152. Vochyaceae
152. *Vochysiaceae*
153. Tremandraceae
154. Polygalaceae
155. Dichapetalaceae
156. Euphorbiaceae
157. Callitrichaceae
158. Buxaceae
159. Coriariaceae
160. Empetraceae
161. Limnanthaceae
162. Anacardiaceae
163. Cyrillaceae
164. Pentaphylacaceae
165. Corynocarpaceae
166. Aquifoliaceae
167. Celastraceae
168. Hippocrateaceae
169. Stackhousiaceae
170. Staphyleaceae
171. Icacinaceae
172. Aceraceae
173. Aesculaceae
173. *Hippocastanaceae*
174. Sapindaceae
175. Sabiaceae
176. Bersamaceae
176. *Melianthaceae*
177. Impatientaceae
177. *Balsaminaceae*
178. Rhamnaceae
179. Vitaceae 3
180. Elaeocarpaceae
181. Schizolaenaceae
181. *Chlaenaceae*
182. Gonystylaceae
183. Tiliaceae
184. Malvaceae 2
185. Tripiochitonaceae
186. Bombacaceae
187. Sterculiaceae
188. Scytopetalaceae
189. Dilleniaceae
190. Eucryphiaceae
191. Ochnaceae
192. Caryocaraceae
193. Marcgraviaceae
194. Quiinaceae
195. Theaceae
196. Hypericaceae
197. Clusiaceae
196. }
197. } *Guttiferae*
198. Dipterocarpaceae
199. Elatinaceae
200. Frankeniaceae
201. Tamaricaceae
202. Fouquieriaceae
203. Cistaceae
204. Bixaceae
205. Cochlospermaceae
206. Koeberliniaceae
207. Canellaceae
208. Violaceae
209. Flacourtiaceae
210. Stachyuraceae
211. Turneraceae
212. Malesherbiaceae
213. Passifloraceae
214. Achariaceae
215. Papayaceae
215. *Caricaceae*
216. Loasaceae
217. Datiscaceae
218. Begoniaceae
219. Ancistrocladaceae
220. Cactaceae
221. Geissolomaceae
222. Penaeaceae
223. Oliniaceae
224. Thymelaeaceae
225. Elaeagnaceae
226. Lythraceae
227. Blattiaceae
227. *Sonneratiaceae*
228. Crypteroniaceae
229. Punicaceae

230. Lecythidaceae
231. Rhizophoraceae
232. Combretaceae
233. Myrtaceae
234. Melastomataceae
235. Onagraceae
236. Trapaceae
236. *Hydrocaryaceae*
237. Haloragidaceae
237. *Halorrhagidaceae*
238. Cynomoriaceae
239. Araliaceae 2
240. Apiaceae
240. *Umbelliferae* 3
241. Cornaceae
242. Clethraceae
243. Pyrolaceae
244. Monotropaceae
243, 244. } *Pyrolaceae*
245. Lennoaceae
246. Ericaceae
247. Vacciniaceae
246, 247. } *Ericaceae*
248. Epacridaceae
249. Diapensiaceae
250. Theophrastaceae
251. Myrsinaceae
252. Primulaceae
253. Plumbaginaceae
254. Sapotaceae
255. Diospyraceae
255. *Ebenaceae*
256. Styracaceae
257. Symplocaceae
258. Oleaceae 2
259. Salvadoraceae
260. Loganiaceae
261. Gentianaceae
262. Menyanthaceae
261, 262. } *Gentianaceae*
263. Apocynaceae
264. Asclepiadaceae
265. Convolvulaceae
266. Cuscutaceae
265, 266. } *Convolvulaceae*
267. Polemoniaceae
268. Hydrophyllaceae
269. Boraginaceae
270. Verbenaceae
271. Menthaceae
271. *Labiatae*
272. Nolanaceae
273. Solanaceae 9
274. Scrophulariaceae
275. Bignoniaceae
276. Pedaliaceae
277. Martyniaceae
278. Orobanchaceae
279. Gesneriaceae
280. Columelliaceae
281. Pinguiculaceae
281. *Lentibulariaceae*
282. Globulariaceae
283. Acanthaceae
284. Myoporaceae
285. Phrymaceae
286. Plantaginaceae
287. Rubiaceae
288. Caprifoliaceae
289. Adoxaceae
290. Valerianaceae
291. Dipsacaceae
292. Cucurbitaceae 3
293. Campanulaceae
294. Goodeniaceae
295. Candolleaceae
296. Calyceraceae
297. Cichoriaceae
298. Ambrosiaceae
299. Asteraceae
297, 298, 299. } *Compositae* 3

The widest gap, it will be observed, is between *Cruciferae* and *Rosaceae,* but I believe this represents nothing more than lack of knowledge.

Also I should like to list the genera within the limits of which one or more species are now said to be subject to attack, because many of these genera contain plants of great economic importance. Where I have some personal knowledge of the subject I have italicized the genus name, and in what follows the reader will naturally expect me to draw illustrations principally from the diseases most familiar to me.

TABLE II

SHOWING GENERA OF FLOWERING PLANTS SUBJECT TO DISEASES OF BACTERIAL ORIGIN

Macrozamia	Bromus	*Avena*	Phleum
Pinus	*Zea*	*Saccharum*	Poa
Dactylis	*Andropogon*	*Triticum*	*Cocos*

Oreodoxa	*Beta*	Prosopis (?)	*Syringa*
Richardia	*Amaranthus*	Erythrina	*Olea*
Amorphophallus	*Dianthus*	Geranium	*Fraxinus*
Hyacinthus	*Delphinium*	*Pelargonium*	Strychnos
Allium	*Papaver*	*Tropaeolum*	*Nerium*
Lilium	*Brassica*	Citrus	Tectona
Iris	*Raphanus*	Cedrela	*Verbena*
Ixia	Cheiranthus	Manihot	Capsicum
Gladiolus	Matthiola	*Mangifera*	*Solanum*
Musa	Amelanchier	*Euonymus*	*Lycopersicum*
Zingiber	Sorbus	*Vitis*	*Nicotiana*
Dendrobium	Eryobotrya	*Gossypium*	*Physalis*
Cattleya	*Pyrus*	Malva	*Petunia*
Oncidium	*Cydonia*	Sterculia	*Datura*
Odontoglossum	*Prunus*	Elodea	Calceolaria
Cypripedium	*Rubus*	*Begonia*	*Sesamum*
Phalaenopsis	*Crataegus*	*Opuntia*	*Pavetta*
Vanilla	Fragaria	Eucalyptus	Psycotria
Salix	*Rosa*	Oenothera	*Benincasa*
Populus	Heteromeles	*Aralia*	*Cucumis*
Juglans	*Dolichos*	*Hedera*	*Cucurbita*
Castanea	Lathyrus	*Carota*	*Citrullus*
Corylus	Indigofera	*Pastinaca*	*Sicyos*
Morus	Kraunhia (?)	Levisticum	*Echinocystis*
Pouzolzia	Lupinus	*Apium*	Ageratum
Cannabis	*Mucuna*	*Arbutus*	*Chrysanthemum*
Acalypha	*Phaseolus*	*Vaccinium*	*Lactuca*
Humulus	*Vigna*	*Ardisia*	Blumea
Ficus	*Pisum*	Crispardisia	Synedrella
Rheum	*Trifolium*	Amblyanthus	*Tragopogon*
Polygonum	*Medicago*	Amblyanthopsis	*Bellis*
Atriplex	*Arachis*	Diospyros	Aster
Spinacia	Acacia	Ligustrum	

PERIOD OF GREATEST SUSCEPTIBILITY

In certain diseases the brief seedling stage of the plant is the one most subject to attack, e. g., Stewart's disease of maize due to *Bacterium Stewarti,* and brown rot of tomato and tobacco due to *Bacterium Solanacearum,* but many bacterial diseases of older plants are also rather strictly time-limited. In both groups it is a question of abundant immature tissue. To the latter class belong the numerous leaf-spots, fruit-spots, and blights, e. g., black spot on the plum and peach, due to *Bacterium Pruni,* and fire-blight of the pear, apple, quince, etc., due to *Bacillus amylovorus.* In such cases, so far at least as they occur in temperate climates, the disease appears in

the spring and the greater part of it occurs during a brief period in the early summer, in which growth of roots, leaves and shoots is proceeding rapidly and there are many young and succulent parts. The cause of the disease may and often does remain on the plant over winter in a latent or semi-latent condition (walnut blight, pear blight, plum canker), but the active period is limited to three months, more or less, of actively growing weather in which developing tissues, subject to infection, are abundant. With definitive growth and the hardening of the tissues in late summer and autumn, the disease is checked and disappears, or remains as a slow canker to appear again on other parts the following spring. It is a very instructive experiment to see, for example, inoculations of *Bacillus amylovorus* on ripening fruits and shoots of the pear wholly fail toward the end of July, which were eminently successful on the same trees at the beginning of June. The difference in this case is not due to lessened virulence on the part of the organism, but to changes in the host-plant, making it non-susceptible. Similar changes leading to non-susceptibility occur in the Japanese plum subject to *Bacterium Pruni;* the young fruits are very susceptible, the maturing fruits cannot be infected.

Other parasites on the contrary are able to attack, disintegrate and destroy matured tissues, e. g., the pith of cabbage stems, turnip roots, the ripened tubers of the potato, well developed roots of sugar beets, the bulbs of onions and hyacinths, full-grown melon and cucumber fruits.

In both of these types the action of the parasite is expended chiefly on the parenchyma, although in some cases (the plum disease, Appel's potato rot) there is more or less bacterial invasion of the local vessels. Vascular occupation is not a special characteristic.

In the typical vascular diseases the case is reversed. Here parenchyma is also destroyed, more or less, but the most conspicuous and destructive action is on the vascular bundles themselves, which are occupied for long distances, to the death, or great detriment, of the whole plant. In maize attacked by *Bacterium Stewarti,* it is not unusual, indeed one might rather

say it is customary, to find the vessels of the stem filled with the bacteria continuously for a distance of 3–6 feet from the point of infection, i. e., from the surface of the earth to the top of the full-grown plant. In cucurbits attacked by *Bacillus tracheiphilus* and in sugar-cane attacked by *Bacterium vascularum* the same thing occurs, and many of the vessels are filled solid with the bacterial slime to a distance of 8 or 10 feet from the place of infection. In such cases infection has taken place generally near the base of the plant, which continues to grow for some weeks or months.

Transitions, of course, occur. *Bacterium Stewarti,* for example, is confined much more strictly to the vascular bundles of the maize stem than is *Bacterium Solanacearum* to those of the tomato, potato, or tobacco stem, although it also is a vascular parasite; that is, following infection of the vessels we do not find in the maize stems that extensive breaking down of the pith and phloem into vast cavities which is so common, for example, in tobacco and tomato stems.

WHAT GOVERNS INFECTION

Within the plant we may suppose, from certain indications, that abundant juiciness is the chief factor governing the infection of immature tissues. To this may be added an abundant well-adapted food supply and, in some cases, probably the absence of inhibiting substances, which may appear later. As the parts approach maturity the water content becomes less. Along with this, acids, sugars, amids, proteids, etc., are consumed and converted into substances less well adapted to the needs of the meristem-parasites, if not wholly inimical. In young shoots of potato and tomato, or of pear and apple, as contrasted with old ones, or in the roots of carrots as compared with the leaves, or in rapidly-growing cabbages, as compared with slow-growing ones, we know that there is an excess of water, and this alone appears to be sufficient to explain the difference in behavior of their respective parasites in old versus young parts. When, however, we come to ripening fruits, such as the pear and the plum, it would seem that they are still juicy enough to favor the growth of almost any

bacterium, and we are forced to the hypothesis of chemical changes within the fruits to account for the failure of inoculations. As a rule (there are striking exceptions), parasitic micro-organisms are rather sensitive to changes in their environment, e. g., to drying, exhaustion of food supplies, multiplication of their own by-products, conversion of an easily assimilable substance into one less assimilable or actually harmful, appearance of esters, new acids, etc. But why speculate! Much additional experimenting must be undertaken before we shall have precise and full data. We are still largely in the observational stage.

The parasites of ripened tissues do not require so much water, are able to convert starch into sugar, or have a special liking for some other element of the plant tissue.

Externally, a number of factors favor infection. One of these is excessive shade, either of clouds or of foliage. Another is high temperature. When these two factors are accompanied by excessive rainfall, wet earth, and heavy dews, the conditions are ideal for the rapid dissemination and the destructive prevalence of a variety of bacterial diseases of cultivated plants. The bean spot due to *Bacterium Phaseoli,* the black spot of plum due to *Bacterium Pruni,* and the larkspur disease due to *Bacterium Delphinii,* are all favored by heavy dews and by shade. In hot, wet weather in July pear blight due to *Bacillus amylovorus* often bursts out like a conflagration and sweeps over whole orchards. In warm, moist autumns bacterial diseases of the potato may destroy almost or quite the entire crop over extensive districts.

HOW INFECTION OCCURS

As I have already described elsewhere how infection occurs,[1] I will only dwell for a moment on it here, offering a few examples.

The commonest way of infection is probably through wounds.

[1] Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27[2]: pp. 51–64. 1911.

In Italy, the olive tubercle due to *Bacterium Savastanoi* has been observed to begin very often in wounds made by hail-stones. In South Africa, crown-gall is said to be disseminated in the same way. In this country and also in Sumatra, *Bacterium Solanacearum* enters the plant more often than otherwise through broken roots. A tomato or tobacco plant with unbroken roots will thrive in a soil deadly to one that has been root-pruned. I have myself observed this. We may suppose that substances attractive to the particular bacteria diffuse into the soil from the broken roots, following which they enter the plant. Resistant plants may be supposed to diffuse indifferent or repellant substances. All infections must be chemotactic.

More interesting perhaps are those diseases which begin in natural openings, i. e., in places where the protective covering of the plant gives place to special organs such as nectaries, water-pores, and stomata.

All the pome fruits subject to fire-blight are liable to blossom infection. The bacteria multiply first in the nectaries of the flower, passing down into the stem by way of the ovary and pedicel. Blossom blight of the pear is a very conspicuous and common form of the disease as everybody knows. Thousands of blighted blossom clusters may be seen in any large orchard subject to this disease.

In the black rot of the cabbage due to *Bacterium campestre,* the majority of the infections begin in the water-pores. These are grouped on the margins of the leaf at the tips of the serratures. From this point the bacteria burrow into the vascular system of the leaf and so pass downward into the stem and upward into other leaves.

In the black spot of the plum, almost or quite all of the infections are stomatal. A large proportion of them are also stomatal in the leaf-spot of cotton, and other leaf-spots.

TIME BETWEEN INFECTION AND APPEARANCE OF THE DISEASE

As in animal diseases, the period of latency may be very short or surprisingly long. Some time must be allowed the parasitic organism to multiply inside the plant before it does

damage serious enough to be recognized externally as a *disease*. This is the so-called "period of incubation," during which the parasite is growing and its enzymes and toxins are becoming active. The microscope shows it to be present in the tissues, but the latter have yielded only a little in the immediate vicinity of the bacterial focus. This time is short or long depending on whether the parasite or the host has the first advantage. If the host is growing rapidly it may either entirely outstrip the parasite, or be only so much the more subject to it. All depends on whether the parasite finds the initial conditions entirely suited to its needs, or by means of its secretions and excretions can quickly make them so, and consequently can from the start make a rapid growth, or must first slowly overcome obstacles of various sorts, such as inhibiting acids and resistant tissues. The plant may show signs of infection within as short a time as one or two days after inoculation (various soft rots), or it may be as long a time as one to two months before they appear (Cobb's disease of sugar-cane, Stewart's disease of sweet-corn). In the latter, infection generally occurs in the seedling stage and the maize plant may be three months old and six feet tall before it finally succumbs. Of course, as in case of bacterial animal diseases, the greater the volume of infectious material the shorter the time. I have seen many instances of that law. In general, the period of latency may be said to vary from one to three weeks (yellow disease of hyacinth, black rot of cabbage, black spot of plum, cucurbit wilt, pear blight, angular leaf-spot of cotton, sorghum leaf-stripe, etc.).

RECOVERY FROM DISEASE

Mention has already been made of the self-limited spot diseases and blights. As the actively growing season draws to a close such diseases cease their activity.

Also in some plants well developed signs of vascular disease may be suppressed (squash, maize, sugar-cane) or remain in abeyance for a longer or shorter period, according to the varying fortunes of the host and the capabilities of the parasite. The tomato plants inoculated with *Bacterium Sol-*

anacearum (Medan III) and photographed for Volume III of 'Bacteria in Relation to Plant Diseases' (plate 45 D), entirely outgrew the disease, as did also certain sugar-canes (series VI) inoculated with *Bacterium vascularum*.[1] Also, I have seen tomato plants recover only to develop a second and fatal attack of the vascular brown rot three months after the first attack, during which period they had made an extensive healthy-looking growth.[2]

Recovery from disease may depend on *loss of virulence* on the part of the parasite. This often occurs when bacteria are grown for some time on culture-media, and it occurs also in nature, but its cause is obscure.

AGENTS OF TRANSMISSION

These may be organic or inorganic. In many cases the plant itself harbors the parasite indefinitely, carrying it over from year to year on some portion of its growth.

Seeds, tubers, bulbs, grafts, or the whole plant may be responsible for the appearance of the disease the following year in the old localities, and through the agency of seedsmen, nurserymen, or whoever disseminates plants, for outbreaks in regions hitherto exempt.

There is good reason to believe that the black rot of cabbage and Stewart's disease of sweet corn have been disseminated broadcast in the United States in recent years by ignorant and unscrupulous seedsmen. Both diseases are transmitted to seedling plants from the seed. The yellow disease of hyacinths is carried in the bulb. Potato tubers from diseased fields may infect healthy fields. Apple grafts have transmitted crown-gall. Slightly infected trunks and limbs of trees (hold-over pear blight, walnut blight, canker of the plum) may infect shoots, leaves, blossoms, or fruits the following season. The soil around the infected plant may serve for years as a source of infection to other species (crown-gall), or to other individuals of the same kind (various leaf-spots). Occasionally, however, a parasite seems to die out of certain soils (*Bac-*

[1] Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27[3]: p. 33. 1914.

[2] *Ibid.* p. 179.

terium Solanacearum). The pear blight organism probably dies out of soils quickly as it does in a majority of the blighted branches. Pear blight by soil infection is not known.

Among extraneous agents, wind and water have been suspected. I have never seen any clear indications of wind-borne infection, not even when conditions seemed to invite it, but water often carries parasites and furnishes conditions favorable to infection. Horne has shown that the olive tubercle in California is transmitted in this way. Honing, in the tobacco fields of Sumatra, has traced infection several times to the watering of plants from infected wells, and has cultivated the parasite from the water. I have discovered experimentally that to obtain several sorts of bacterial leaf-spots (bean, cotton, peach, plum, carnation, larkspur, sorghum, geranium) the surface of the leaves must be kept moist to the same extent they would be in case of prolonged dews or frequent light showers. Such conditions are necessary to enable the bacteria to penetrate the stomata and begin to grow. In case of water-pores, however, the plant itself furnishes the water necessary for infection, if the nights are cool enough, i. e., if the air remains near enough to saturation to prevent for some hours the evaporation of the excreted water from the leaf-serratures. Every plant with functioning water-pores awaits its appropriate bacterial parasite. The genus *Impatiens* is a good example. I have looked on it for one in vain but I am sure it must occur.

Man and the domestic animals, especially through the agency of the dung-heap, infallible repository of all sorts of discarded refuse, undoubtedly help to spread certain bacterial diseases of plants (potato rots, black rot of cabbage, etc.).

Birds probably transmit some of these diseases on their feet or in other ways. In connection with the bud-rot of the coconut palm in the West Indies, I suspect the turkey-buzzard, but the evidence is not complete. Long since, Mr. Waite obtained (once in Florida, once in Maryland) the strongest kind of circumstantial evidence going to show that pear blight may be spread by birds.

Respecting insects, molluscs, and worms, the evidence is complete. They often serve to carry these diseases. I have summarized our knowledge in another place[1] and will here content myself with a brief statement calling renewed attention to the subject.

We had very good evidence of the transmission of one bacterial disease of plants by insects long before the animal pathologists awoke to the importance of the subject,[2] but it cannot be said that they have ever paid much attention to it, although it antedates by two years the work by Theobald Smith and Kilborne showing that Texas fever is transmitted by the cattle tick (*Ixodes bovis*). That discovery also belongs to the credit of the U. S. Department of Agriculture, and the two together may be said to have laid broad and deep the foundations of this most important branch of modern pathology. Waite isolated the pear blight organism, grew it in pure cultures, and proved its infectious nature by inoculations. With such proved cultures he sprayed clusters of pear flowers in places where the disease did not occur and obtained blossom-blight, and later saw this give rise to the blight of the supporting branch, found the organism multiplying in the nectar, and reisolated it from the blighting blossoms. On some trees he restricted the disease to the sprayed flowers by covering them with mosquito netting to keep away bees and other nectar-sipping insects. On other trees where the flowers were not covered he saw bees visit them, sip from the inoculated blossoms and afterwards visit blossoms on unsprayed parts of the tree which then blighted. Finally he captured bees that had visited such infected blossoms, excised their mouth parts, and from these, on agar-poured plates, obtained *Bacillus amylovorus,* with colonies of which he again produced the disease. These experiments were done in several widely separated localities with identical results. I saw them and they made a great impression on me.

[1] Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27[3]: p. 40. 1911.

[2] Waite, M. B. Results from recent investigations in pear blight. Bot. Gaz. 16: 259; Am. Assoc. Adv. Sci., Proc. 40: 315. 1891.

The writer has since proved several diseases to be transmitted by insects, notably the wilt of cucurbits, and here the transmission is not purely accidental, but there appears to be an adaptation, the striped beetle (*Diabrotica vittata*), chiefly responsible for the spread of the disease, being fonder of the diseased parts of the plant than of the healthy parts. This acquired taste, for it must be that, works great harm to melons, squashes, and cucumbers. Whether the organism winters over in the beetles, as I suspect, remains to be determined. Certainly the disease appears in bitten places on the leaves very soon after the spring advent of the beetles.

In 1897 I showed that molluscs sometimes transmit brown rot of the cabbage, and last year I saw indications in Southern France which lead me to think that snails are responsible for the spread of the oleander tubercle, i. e., I saw them eating both sound and tubercular leaves, and found young tubercles developing in the eroded margins of bitten leaves.

Parasitic nematodes break the root tissues and open the way for the entrance of *Bacterium Solanacearum* into tobacco and tomato, as was first observed by Hunger in Java and later by myself in the United States. One of the serious problems of plant pathology is how to control *Heterodera radicicola*, not only because of its wide distribution on a great variety of cultivated plants and the direct injury it works, but also on account of the often very much greater injury it causes through the introduction into the roots of the plant of bacterial and fungous parasites. The man who shall discover an effective remedy will deserve a monument more enduring than brass. Our Southern States in particular are overrun with this parasite.

Much remains to be done before we shall know to what extent fungous parasites function as carriers of parasitic bacteria. H. Marshall Ward sought to explain the presence of bacteria in diseased plants by supposing that they must enter the plant through the lumen of fungous hyphae. In this he was wrong, certainly if it be stated as a general proposition, but it appears to be clear that in some cases the two types of parasites work together, the fungus invading first, and the

bacterium following hard after and often doing the major part of the damage. The reverse of this also occurs, the bacterium entering first and the fungus following.

Parasitic bacteria are soon followed by saprophytic bacteria which complete the destruction of the tissues, and, if the disease is somewhat advanced, cultures from the tissues may yield only the latter (potato rots). Also, as in animals, one parasitic disease may follow another and the second be more destructive than the first, e. g., fire-blight following crown-gall on the apple.

EXTRA-VEGETAL HABITAT OF THE PARASITES

Here is perhaps the place to say a few words about the non-parasitic life of the attacking organisms.

All are able to grow saprophytically, i. e., on culture media of one sort or another, and probably all live or may live for a time in the soil. Very few, however, have been cultivated from it. The vast mixture of organisms present in a good earth rather discourages search. In some of the unsuccessful attempts failure may have been due to not having undertaken isolations at exactly the right time, or in just the right place, or on just the proper medium, but more often probably to the swamping tendency of rapidly growing saprophytes. How long a parasite is able to maintain its virulent life in a soil must depend largely on the kind of competitors it finds. I have used the term *virulent,* because it is conceivable that an organism might remain alive in a soil long after losing all power to infect plants, just as we know it can in culture media. *Bacterium Solanacearum* causing brown rot of *Solanaceae, Bacillus phytophthorus* causing basal stem rot and tuber rot of the potato, and *Bacterium tumefaciens* causing crown-gall, certainly live in the soil, and the soundest plants when set in such soils, especially if wounded, are liable to contract the disease, if they belong to susceptible species. The root-nodule organism of *Leguminosae,* which I have not considered here, also lives in many soils, as every one knows.

MORPHOLOGY AND CULTURAL CHARACTERS OF THE PARASITES

Most of the plant bacteria are small or medium sized rod-shaped organisms. Very few parasitic coccus forms are known. In fact, none are very well established. Some of these bacteria are Gram positive, others are not. All take stains, especially the basic anilin dyes, but not all stain with the same dye or equally well. Most of the species are motile by means of flagella—polar or peritrichiate. A few are non-motile, genus *Aplanobacter*.[1] Some develop conspicuous capsules, others do not. Few, if any, produce endospores. Grown pure on culture media in mass, they are either yellow, pure white, or brownish or greenish from the liberation of pigments. Red or purple parasites are not known. We formerly supposed that there were no green fluorescent species capable of parasitism, but now several are known, e. g., the organism causing the lilac blight of Holland, with pure cultures of which the writer obtained typical infections at Amsterdam in 1906, and afterwards in the United States (now first recorded). Some species produce gas, liquefy gelatin, consume asparagin, destroy starch, and reduce nitrates; others do not. Their fondness for sugars and alcohols is quite variable. Some are extremely sensitive to sunlight and dry air (*Bacillus carotovorus, Bacillus tracheiphilus*). Others are remarkably resistant, remaining alive and infectious on dry seeds for a year (*Bacterium campestre, Bacterium Stewarti, Aplanobacter Rathayi*). Some are strictly aerobic, others can grow in the absence of air, if proper foods are available. Some are very sensitive to acids, alkalies and sodium chlorid, others are not. Some have wide ranges of growth from 0°C. upwards. Some will not grow at or near 0°C., others will grow at or above 40°C. Very few, however, will grow at blood temperature, certain ones even in plants or on culture media are killed by summer temperatures, and none are known definitely to be animal parasites.

[1] Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington. Publ. 27[1]: p. 171. 1905; *Ibid.* 27[3]: pp. 155, 161. 1914.

ACTION OF THE PARASITE ON THE PLANT

In some cases it is hard to draw the line between parasitism and symbiosis or mutualism. Probably we shall find more and more of these transition states. I have included *Ardisia* in my list of genera and have excluded the genera of legumes subject only to root nodules. But a nodule on the root of a legume, so far as the local condition is concerned, is a disease as much as a leaf-spot, and, if Nobbe and Hiltner's statements are to be credited, the general effect of the root-nodule organism on the plant may be excessive and injurious and not to be distinguished from a disease.[1]

In the tropical East Indian *Ardisia,* which is one of the strangest cases of mutualism known to me, and on which Miehe has done such a beautiful piece of work, we perhaps have something akin to what occurs in the root nodules of legumes. Here the bacterial injury is local and internal. There are no superficial indications of disease. The bacteria are most abundant in the leaf-teeth where they form pockets or cavities and multiply enough to make the leaf serratures appear blanched or yellowish and slightly swollen, but never enough to kill them. In smaller numbers the bacteria occur in other parts of the plant including the inner parts of the seed from which they are transmitted to the seedling, whose leaf serratures, infected through their water-pores, in turn become the chief focus of the bacterial multiplication. Apparently the bacteria are always present, and we do not know what would happen to *Ardisia* plants grown without them, nor do we know how to obtain such plants. It would be an interesting experiment to see if they could be produced and to watch their behavior.

The action of such organisms as I have mentioned differs probably from the behavior of active parasites in that they liberate much weaker toxins and enzymes, can attack only very actively growing parts, and also give off compensating nitrogenous substances. Not yet proved for *Ardisia.*

[1] Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27[2]: p. 131, last paragraph. 1911.

The active parasites produce toxins freely, poisoning the tissues, and enzymes converting starches into sugars, complex sugars into simpler ones, and so on, for their nutrition. They also neutralize and consume plant acids, and feed upon amido bodies and other nitrogenous elements of the host. As a result of their growth, many of them liberate both acids and alkalis to the detriment of the plant. The solvent action of their products on the middle lamellae separates cells and leads to the production of cavities in the bark, pith, phloem and xylem. There is also, or may be, a mechanical splitting, tearing or crushing due to the enormous multiplication of the bacteria within confined spaces. The whole intercellular mechanism may be honeycombed and flooded in this way, and if the cavities are near the surface the tissues may be lifted up or the bacteria may be forced to the surface through stomata in the form of tiny beads or threads (pear, plum, bean, maize, sugar-cane, etc.), or by a splitting process. The splitting in the black spot of plum fruits and peach fruits, however, results from local death of the attacked tissue with continued growth of the surrounding uninjured parts.

A majority of the forms known to cause plant diseases are extra-cellular parasites occupying chiefly the vessels and intercellular spaces, causing vascular diseases, soft rots, spot diseases, etc. But intra-cellular parasites also occur, e. g., *Bacterium Leguminosarum* causing root-nodules on legumes, and *Bacterium tumefaciens* causing crown-gall. The former multiplies within the cell myriadfold, prevents its division, destroys its contents including the nucleus, and enormously stretches the cell wall so that the cell becomes much larger than its normal fellow cells and is packed full of the bacteria. The latter does not multiply abundantly within the cell, does not enlarge it, does not injure its viability, and would be a harmless messmate were it not for the fact that it exerts a stimulating effect on the cell nucleus, compelling the cell to divide again and again.

THE REACTION OF THE PLANT

We now come to the reaction of the plant. What response does it make to this rude invasion? Ten years ago we might

have said, "With rare exceptions, the plant is passive or nearly so," but that would have been a superficial observation.

In every disease we must suppose that the plant makes some effort to throw off the intruder, although often its forces are paralyzed and overcome very early in the progress of the disease.

One of the most conspicuous results is lessened growth. In some of my plants recovering from brown rot due to *Bacterium Solanacearum*,[1] a month after external signs of the disease had disappeared the check plants were twice the size of the inoculated ones, and there was still a very decided difference after more than two months. I do not know how to explain this checked growth unless it be the response to absorbed toxins.

On potato plants attacked early by *Bacterium Solanacearum* the tubers remain small. On maize attacked by *Bacterium Stewarti* the ears are imperfect. Olive shoots inoculated and infected by *Bacterium Savastanoi* are always dwarfed, and the crown-gall dwarfings are frequently very conspicuous. The dwarfing of melon and squash plants attacked by *Bacillus tracheiphilus* is also conspicuous. Uninoculated sugar-cane stems soon surpass in height and vigor those successfully inoculated with *Bacterium vascularum*.

Changes in color are also conspicuous. The attacked parts may become greener than normal, or fade to yellow, red, brown or black. In tomato fruits there is often a retarded ripening on the attacked side with persistence of the chlorophyll. Crown-galls on daisy are greenish. In certain leaf-spots also the leaf green persists in the vicinity of the spot while the rest of the leaf becomes yellow (bean-leaf spot). The male inflorescence of maize attacked by *Bacterium Stewarti* ripens prematurely and becomes white.

Distortions of various kinds appear (leaves of bean, lilac, larkspur, hyacinth, mulberry, Persian walnut). The leaves of tomato plants attacked by *Bacterium Solanacearum* are bent downwards; so are the fronds of the coconut palm when

[1] Smith, E. F. Bacteria in relation to plant diseases. Carnegie Inst. Washington, Publ. 27[3]: *pl. 45–D.* 1914.

attacked by the bacterial bud-rot. Knee-shaped curvatures of the culms appear on *Dactylis* attacked by *Aplanobacter Rathayi,* and in the buds of the sugar-cane attacked by Cobb's disease.

Organs may be developed in excessive number or out of place, as roots in hairy-root of the apple, witch-brooms on *Pinus,* and incipient roots on the stems of tomato, tobacco, chrysanthemum, nasturtium, etc. Hunger found a bud on a tomato leaflet which he attributed to the stimulus of *Bacterium Solanacearum.*

In various diseases the plant removes starch from the vicinity of the bacterial focus which it endeavors to wall off by the formation of a cork barrier, and in this effort it is sometimes successful if the parasite is growing slowly.

The most conspicuous response of the plant is in the form of pathological overgrowths,—cankers, tubercles, and tumors. Some of these are very striking, e. g., those on the ash, olive, pine, oleander, and on a multitude of plants attacked by crown-gall. In some of these growths there is a great reduction of the vascular system, and a great multiplication and simplification of the parenchyma. There are also various other phenomena nearly related to what takes place in certain insect galls. In crown gall cell division under compulsion proceeds at such an abnormally rapid rate that the cells are forced to divide while still immature, and in this way masses of small-celled unripe (anaplastic) tissue arise. These develop tumor-strands on which secondary tumors arise.

PREVALENCE AND GEOGRAPHICAL DISTRIBUTION

Economically considered, bacterial diseases of plants may be classed as major or minor. Most of the leaf-spots would fall into the latter class. Various soft rots, blights and vascular diseases, being wide-spread and destructive to plants of great economic importance, may be classed as major diseases. Cankers and tumors would fall midway in such a grouping. Occasionally a minor disease, e. g., lettuce rot, celery rot, under favorable conditions may assume great importance.

It will be of interest to mention a few of these diseases with particular reference to their distribution and prevalence.

Dutch East Indies.—The tobacco disease of Sumatra and Java is probably the most destructive, if the Sereh of sugar-cane is not bacterial. Each of these diseases has caused enormous losses. Each threatens an industry. The tobacco disease occurs also in the West Indies, in the United States, and probably also in South Africa. If Janse's root disease of *Erythrina,* the coffee shade tree of Java, is also bacterial, as he supposed, then there is another great bacterial plague in that region, for hundreds of thousands of trees have died, and another species has been substituted as a shade tree.

West Indies.—Here the most destructive disease is the bacterial bud-rot of the coconut palm, which occurs all around the Caribbean, and threatens the entire destruction of a profitable industry in Cuba. There is also the bacterial disease of bananas and plantains, but the most wide-spread and destructive *Musa* disease of the Western Hemisphere is the Panama disease, due to a *Fusarium.*

Australia.—Cobb's disease of sugar-cane has probably attracted more attention in Australia than any other bacterial trouble, although bacterial rots of the potato are also very destructive. The cane disease in both Queensland and New South Wales has in many cases destroyed the output of whole plantations and greatly discouraged planters. This disease occurs also in Fiji, and probably in South America.

Japan.—Probably the tobacco wilt, which has destroyed many fields, is the worst Japanese disease. This is believed to be identical with the tobacco wilt of Sumatra and of the United States. Several other bacterial blights have been reported, including one of the basket willow.

India.—The brown rot of *Solanaceae* is common and destructive. Most of Asia is a *terra incognita.*

South Africa.—The mango disease in recent years has greatly reduced the exports. Potato and tomato wilts are common. There is a serious tobacco disease, probably bacterial. Crown-gall is common and injurious on shade and orchard trees. Other diseases occur.

South America.—There is a serious disease of sugar-cane in Brazil and another in Argentina, both of which I believe are of bacterial origin, and identical with Cobb's disease. Bondar has reported a destructive manihot disease. The bud-rot of the coconut occurs in the north.

United States and Canada.—Potato rots probably cause the greatest losses one year with another. Following these I should think pear and apple blight. Perhaps the latter should be placed first, for the destruction of an acre of potatoes would scarcely equal the value of a single fine pear tree, and thousands are destroyed every year. In California, which was free from pear blight until recently, the losses in the last fifteen years have been enormous, amounting to about one-third of all the full-grown orchards and to a money-loss estimated at $10,000,000 for the five years preceding the efforts for its restriction begun in 1905 by the U. S. Department of Agriculture. Very serious losses from this disease are experienced every year in the East, or were until growers became generally familiar with methods of control.

In our southern states the tobacco and the tomato wilt have made it impossible to grow these crops on many fields. In the northern United States the cucurbit wilt is wide-spread and destructive, but cucurbits are of course a minor crop.

The walnut blight has done much damage in California. This occurs also in New Zealand and Tasmania.

The bacterial disease of alfalfa has been serious in parts of the West. It is most injurious early in the season, i. e., on the first cutting.

Holland.—Here the yellow disease of hyacinths is always destructive and will eventually put an end to hyacinth-growing for export if means cannot be had for its control, since the land suited for hyacinths is limited in amount. Brown rot of cabbage occurs in Holland and Denmark, and is common now also in many parts of the United States. It was probably imported into the United States from Denmark on cabbage seed. Some years in nurseries about Amsterdam the lilac blight has been troublesome.

Great Britain and Germany.—Potato rots are probably the most destructive bacterial diseases.

France and Italy.—Potato diseases are common. Olive tubercle, common also in California, and all around the Mediterranean, is prevalent in spots. Vine diseases, especially Maladie d'Oleran and crown-gall, do considerable damage. Pear blight seems to be absent in France, but has been reported from several places in Italy. The destructive Italian rice disease, brusone, is not due to bacteria as reported, but to a fungus (*Piricularia*).

METHODS OF CONTROL

In conclusion, some words on prophylaxis will be in order. Until recently almost nothing was known. Unfortunately so far as regards most of these diseases, methods of control must still be worked out. But with rapidly increasing knowledge of the biological peculiarities of the parasites causing these diseases, and of the ways in which they are disseminated, light begins to dawn, so that before many years have passed we may confidently expect the more intelligent part of the public to be applying sound rules for the control of these diseases,—rules based on the individual peculiarities of the parasites and carefully worked out experimentally by the plant pathologist.

The little that we now know may be summarized in part as follows:

Waite has shown that pear blight winters over in exceptional trees on trunk and limbs in the form of patches which ooze living bacteria the following spring and are visited by bees and other insects, and that if these "hold-over" spots are cut out thoroughly over regions several miles in diameter (wide as a bee flies), the disease does not appear on the blossoms and shoots the following spring, except as it is introduced into the margins of this area from remoter uncontrolled districts. He has tried this method of control very successfully, both in Georgia and California. Sometimes only one tree in many carries over the disease, but such is not always the case, and the success of this method involves the inspection of every pome tree in a district with complete eradication

of every case of the hold-over blight, and this in great fruit regions requires a small army of trained inspectors. During the blighting period in late spring and early summer, if one would save his orchard, the trees must be cut over for removal of diseased material as often as every week, and in the worst weather oftener.

The introduction of diseases transmitted by way of seeds, bulbs, and tubers may be avoided by obtaining these from plants not subject to the disease. As this freedom cannot always be known, bulbs and tubers should be inspected critically before planting, and firm-coated seeds should be soaked for 15 minutes in 1:1000 mercuric chlorid water. In case of two plants (cabbage and maize) we know positively that the diseases are transmitted on the seed and this is probably true for several others—beans, sorghum, orchard grass. All shrivelled seeds should be screened out before planting.

The seed bed in case of tobacco, tomato, cabbage, and transplanted plants generally, should be made on steam-heated or fire-heated soil, or new earth which one has good reason to think free from the parasite in question.

Nematode-infected soil should be avoided.

Cuttings of carnations, chrysanthemums, roses, peaches, plums, apples, quinces, sugar-cane, etc., used for slips, buds, or grafts should be from sound plants. By following this practice, recommended in case of sugar-cane by Cobb, the more intelligent cane planters in New South Wales have overcome the disease due to *Bacterium vascularum*.

On badly infested soils a careful long rotation should be practised and the low places should be drained.

Certain diseases may be held in check by germicidal sprays. Pierce reduced the number of infections in walnut blight fifty per cent by this method. Scott and Rorer combated leaf-spot of the peach in this way, the sprayed trees retaining their leaves, the unsprayed ones becoming defoliated. ——— in Italy has recommended it and used it successfully on olive trees following hail-storms to keep out the olive tubercle.

When diseases are transmitted by insects the destruction of the latter must receive prompt attention.

Great care should be taken to keep the manure heap free from infection. Diseased rubbish should be burned or buried deeply. It must not be thrown into a water supply or fed to stock or dumped into the barnyard.

It has been found that some varieties of plants are less subject to disease than others (pear, apple, plum, maize, potato, tomato, sugar-cane, banana, cabbage, etc.), and there are also individual variations within the variety. These phenomena lead us to hope that by selection, or hybridization, valuable resistant strains may be originated. Meanwhile the resistant sorts when they are of any value commercially should be substituted for sensitive sorts in localities much subject to the disease. Unfortunately some of the resistant sorts have other less desirable qualities. A vast amount of experimental work must be done in this field before we shall have substantial results, and at least a generation or two will be required to learn even the boundaries of the field. But the problem offered is so enticing and has such immediately practical bearings that in the near future we may suppose many pathologists will devote themselves to it, and that long before the whole field is worked over, many useful results will be forthcoming. The labor involved is enormous and exacting to discouragement at times, the results come so slowly, so much must be done to be certain of so little, all because the organisms dealt with are very small—*how small,* we seldom realize!

Many a time in the past when downcast I have repeated to myself Seneca's rolling words, *Palma non sine pulvere per viam rectam,* and have had more or less encouragement out of them. They are a good motto for any man, since nothing is more certain than this, that without plenty of well-directed hard work there can be no worthy success in any field of human endeavor.

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RHIZOCTONIA CROCORUM (PERS.) DC. AND R. SOLANI KÜHN (CORTICIUM VAGUM B. & C.), WITH NOTES ON OTHER SPECIES

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The form genus *Rhizoctonia* was established in 1815 to include two parasitic species, both characterized in part by the production of a mat of violet mycelium investing the affected roots or other submerged members. The serious root diseases due to these organisms (later included in one species) have received consideration by many mycologists since that time. The demonstration is comparatively recent, however, that several important types of root and certain stem and other diseases of a variety of hosts are induced by two or more related species of this genus.

The literature of Rhizoctonia diseases has grown enormously in the past fifteen years, yet some unnecessary confusion and difference of opinion exist regarding the two main species or groups of species and their distribution and relation to disease in plants. This is in part due to the lack of comparative study and to the neglect or inadequacy of herbarium material. It seems well, therefore, to present a conspectus of the investigations relating to this subject, and to include such comparative data as are available.

In coöperation with Mr. F. C. Stewart of the New York (Geneva) Agricultural Experiment Station, I undertook, in 1898, a general study of the relation of *Rhizoctonia* to plant diseases in America. This joint investigation followed two

independent studies, one of a serious root disease of the sugar beet, the other of a destructive stem rot of the carnation. A preliminary report upon the investigations relating to *R. Solani* Kühn was published ('01), and it was arranged that in the further work one of us would undertake the morphological, cultural, and taxonomic aspects of the study, and that the other would assume responsibility for all cross inoculation and field work. Unfortunately for this purpose a change of position on the part of one of us and the demands of other work necessitated the abandonment of the plan as proposed. It is to be regretted particularly that the systematic inoculation experiments which had been carried forward for two seasons could not be continued and published. It is understood, however, that an extensive study in the relations of the culturable forms on different hosts has been carried forward both by cultural and inoculation experiments at the University of Illinois by Dr. George L. Peltier, who has already presented a preliminary report ('15), on the subject. It is mainly a general account of the diseases with notes on comparative morphology that I am able to include, but it is hoped that this may serve to clear up the more obvious difficulties and to suggest some problems requiring special investigation.

The writer wishes to acknowledge the assistance, mentioned in the text, of many mycologists who have furnished material during the progress of these studies, and especially the coöperation of Mr. F. C. Stewart, who contributed many of the American hosts during the earlier studies. To Prof. E. A. Burt I am also indebted for suggestions.

THE VIOLET ROOT FELT FUNGUS, RHIZOCTONIA CROCORUM (PERS.) DC.

EARLY PATHOLOGICAL STUDIES

The first mention of a plant disease which may be referred with certainty to *Rhizoctonia* as the causal agent is an important paper by Du Hamel (1728) read before the Paris Academy. In this paper he gives a careful description of a fungous disease of *Crocus sativus* (saffron) occurring in France. His description of general pathological features

leaves little to be desired, and one cannot mistake the fact that he was discussing the disease, later known to be due to *Rhizoctonia Crocorum*. He does not describe the more minute morphological features, but discusses the macroscopic appearance of the mycelium and sclerotial stages with such completeness that no doubt remains concerning the identity of the fungus. The illustration included would likewise confirm the description. He regarded the sclerotium, "tubercule," as the fruit body of a fungus allied to the truffles, and to this special form of body, assumed to bear the organs of reproduction, he gave the name "tuberoides." He likewise determined that a similar fungus is the cause of a disease found upon the roots of *Sambucus Ebulus, Coronilla varia, Ononis spinosa, Muscari* sp., and perhaps other plants.

It was more than fifty years later that Fougeroux de Bondaroy (1785), discussing primarily a disease of the saffron known as "tacon" gives further notes on the "mort du safran," recording the occurrence of this disease on asparagus when following (in the same soil) diseased crocus.

After a further considerable lapse of time De Candolle (1815) made a careful study of the pathology of a similar alfalfa (*Medicago sativa*) disease in the vicinity of Montpellier, but known throughout France. This led to the establishment of the genus *Rhizoctonia* as noted later. It is necessary to the pathological account to note here, however, that he recognized two species, *R. Crocorum* DC., primarily inhabiting the crocus, and *R. Medicaginis* DC., on the alfalfa and other hosts. He did not follow the development of the fungus on the saffron, where host characteristics render somewhat obscure the appearance of the fungus; and so for a long time the continuous violet felt of mycelium was associated primarily with *R. Medicaginis*.

Among other diseases of the carrot and beets in Germany, Kühn ('58) found typical rots of these root crops, accompanied in both cases by a red-violet mycelium with other characteristics indicating the alfalfa organism. He identified the fungus as *R. Medicaginis* and thus established the greater importance of Rhizoctonia diseases, and greatly extended the

range of the fungus. He found a somewhat similar disease of the potato, but clearly distinguished the fungus as another species, as further indicated in another part of this paper.

Chief among those who extended our knowledge of the pathology and distribution of the violet root felt fungus was Rostrup ('86), who observed the fungus in Denmark and described its effects on various hosts.

EARLY TAXONOMIC AND MORPHOLOGICAL ACCOUNTS

The fungi belonging to the genus *Rhizoctonia* received attention taxonomically from the earliest mycologists. Brief references should be made to the works of some of those who have presented synopses of the genus or who have contributed to the solution of the problem regarding the taxonomic position of these fungi. Bulliard (1791) evidently based his description of species upon the observations and data of Du Hamel and de Bondaroy; emphasizing therefore the sclerotium as the fruit body, and believing it homologous with the truffle he gave to this fungus on *Crocus sativus* the name *Tuber parasiticum.* He contributed nothing further to the morphology of the species. Persoon (1801) did not accept Bulliard's disposition of the fungus, but named it *Sclerotium Crocorum,* and gave a diagnosis which, while based on the observations of the earlier writers, did not confuse the sclerotium with a true fruit body.

De Candolle (1815[a]), in his first taxonomic discussion employed Persoon's name for the fungus, and then, after giving the characteristics and parasitism of the species on alfalfa more careful attention, he established (1815, 1815[b]) the genus *Rhizoctonia* to include two species, *R. Crocorum* DC. on crocus and other hosts and *R. Medicaginis* DC. on alfalfa. It will be noted that he adopts Persoon's specific name for the crocus fungus. De Candolle also considers a doubtful species, *R. Mali,* reported on apple.

Nees (1816) placed the crocus fungus in *Thanatophytum* under the name *T. Crocorum.* Fries (1823) assigns *Rhizoctonia* to the *Sclerotiaceae* just following his extensive genus *Sclerotium.* It is important to note, since Fries' work has been

made the starting point for mycological nomenclature, that he designates three species in the following order, (1) *R. Crocorum* DC., (2) *R. Medicaginis* DC., and (3) *R. muscorum* Fr., also giving *R. Mali* DC. among *species ignota.* The descriptions of the two species first mentioned leave no doubt that he is here defining the violet root felt fungus of crocus and of alfalfa. Moreover, Fries recognized *Sclerotium Crocorum* Pers. as a synonym of *R. Crocorum* DC. So far as has been ascertained no specimens of these species which he examined are still in existence. Link (1824) excluded the doubtful forms, added a species *R. strobilina,* and otherwise left the genus as constituted by De Candolle. Duby (1830) included among the species *Rhizoctonia Allii* Graves, arranging the genus close to *Sclerotium* in the *Scleroteae* of *Lycoperdaceae.* Fries later included in this genus *R. Batatas* Fr. on *Ipomoea Batatas* from America.

The most complete mycological account of the genus *Rhizoctonia* is that given by L. and C. Tulasne ('62). They reduce *R. Crocorum* DC. and *R. Medicaginis* DC. to a single species to which they apply a new name, significant of the appearance of the fungus, *R. violacea* Tul. This reduction to a single form was made after a most careful morphological study of the fungus in all stages. From the accurate descriptions and the excellent illustrations it is clear that they had under consideration material referable to the names above. The Tulasne brothers also refer to other species insufficiently known, as follows: *R. Allii* Graves, *R. Batatas* Fr., and *R.* (?) *Mali* DC. They were inclined to the view that the affinities of the genus would be found to be with the *Ascomycetes,* and, in fact, they considered certain minute cushions of hyphae, referred to in detail later, as immature perithecia. Successively, therefore, attention was drawn by mycologists (1) to the sclerotium as a fruit body (Du Hamel and Bulliard), (2) to the sclerotium as a sterile structure (Persoon), (3) to the strand-like habit of the mycelium (De Candolle), and (4) to the minute cushion-like sclerotia as suggesting perithecia (Tulasne, L. and C.).

NAME, SYNONYMY, AND MATERIAL EXAMINED

Since the investigations of the brothers Tulasne many mycologists have studied the violet root felt fungus on its various hosts, especially on crocus, alfalfa, and certain root crops. There is general, though not complete, agreement in confirmation of the view that the crocus and the alfalfa forms are identical, and that this species, *R. Crocorum,* occurs on numerous hosts. I shall indicate later some of the morphological details in which the two forms agree and give other evidence supporting the view of a single species. For the present it is necessary to anticipate this evidence in order to state that until a perfect stage is definitely established, it would appear that the correct designation of the violet fungus is *Rhizoctonia Crocorum* (Pers.) DC. As noted above, the specific name applied by Persoon was adopted by De Candolle when he established the genus. This name, perhaps unfortunately, has priority over *R. Medicaginis* DC. in that it is mentioned first by Fries (1823). Though necessary, it may seem unwise to call the fungus *R. Crocorum,* inasmuch as it is far more widely distributed on alfalfa; and, furthermore, because its dicotyledonous hosts are more numerous. *R. violacea* would be a most appropriate descriptive name, but it is obvious that this also would not conform to the rules. The following provisional synonymy has been collated:

Tuber parasiticum Bull. (1791),
Sclerotium Crocorum Pers. (1801),
Rhizoctonia Crocorum DC. (1815),
Rhizoctonia Medicaginis DC. (1815),
Thanatophytum Crocorum Nees. (1816),
Tuber Croci Duby (1830),
Rhizoctonia Rubiae Dcne. (1837),
Rhizoctonia Dauci Rabenh. (1859),
Rhizoctonia violacea Tul. (1862),
Rhizoctonia Asparagi Fckl. [non Fr.] (1869),
Hypochnus violaceus Eriks. (1913).

The identity of *Rhizoctonia Crocorum* DC. and *R. Medicaginis* DC. suggested by the brothers Tulasne ('62) and accepted by most taxonomists, has been confirmed by a study

of all the material I have been able to examine, and there is included below a list of the material identified as *Rhizoctonia Crocorum* (Pers.) DC.

Exsiccati: *Rhizoctonia Medicaginis* DC., Linhart, Fung. Hung. Fasc. 4: *400; Rhizoctonia Dauci* Rabenh., Rabenhorst, Herb. Mycolog. Fasc. 1: *74.* (*Helminthosporium rhizoctonum* Rabenh.); *Rhizoctonia Solani* Kühn, De Thuemen, Myc. Univ. Cent. 18 : *1797.*

European collections: (1) Material from Prof. Delacroix, Paris, 1901, as follows: on sugar beet; on sugar beet, obtained by inoculation from diseased beet; on potato; on potato, by inoculation from affected beet; on crocus; on crocus, by inoculation from affected beet; on alfalfa; on *Onobrychis sativus;* on asparagus; and on asparagus, by inoculation from diseased beet. (2) On crocus from bulb gardens, Pithiviers, France, 1901. (3) From Prof. Aderhold, Proskau, Germany, 1899, on carrot and on root of young apple tree. (4) From Prof. Sorauer, Berlin, 1900, on potato and on asparagus. (5) From Herr Weigand, Helmitzheim, Bavaria, 1899, on alfalfa. (6) From Prof. v. Tubeuf, Munich, 1899, on sugar beet. (7) From Prof. Hartig, Munich, on roots of young conifer. (8) From Prof. Cugini, Modena, Italy, 1899, on alfalfa. (9) Material which the writer was able to obtain fresh near Munich, 1905, on sugar beet and alfalfa.

In 1901 the writer was unable to find in the Kew Herbarium or in Paris any type material, and none was found in Montpellier in 1905.

American collections: (1) From Mr. P. W. Graff, Manhattan, Kansas, 1911, on alfalfa. (2) From Mr. F. D. Bailey, Laurel, Oregon, (sent by Dr. G. L. Peltier, Univ. of Ill.) 1915, on potato.

DISTRIBUTION

In Europe the violet root felt fungus is in general widely distributed, but its occurrence now and then in epidemic form on some one host would appear to indicate some locality or race influence. On *Crocus sativus* the fungus has been reported from France chiefly; on asparagus, more frequently from France, Belgium, and Italy; on *Medicago sativa* it would

seem to occur more commonly from southern France eastward to Bavaria and Hungary and southward to the Mediterranean. No information is available with respect to its occurrence in Russia. On the fleshy root crops and on the potato the fungus has often been reported from central France and Germany northward through Denmark, Norway and Sweden, and also on the sugar beet in Italy. In Denmark it appears to be found oftener on species of *Trifolium* than on alfalfa.

The root felt disease is certainly not unknown to market gardeners and others throughout England, yet there are relatively few references to it in pathological literature. It would appear that Güssow has observed the fungus in England, for in speaking of diseased tubers from a farm in Essex he says, "They were covered with a dull reddish-brown webbing, which was raised into numerous points, as if grains of sand were below it," but in view of his reference in the same article to the commoner potato fungus no definite statement should be made. Salmon's account ('08) of the disease of seakale, described as "a felted mass of violet spawn or mycelium," evidently refers to this species.

In the United States *R. Crocorum* was first reported from Nebraska by Webber ('90) on lucerne. He states that it was rare in the Nebraska flora at that time. Heald ('06) lists the fungus as among disease-producing organisms prevalent in Nebraska during 1905. The record is as follows: "Root rot. *Rhizoctonia violacea* Tul. reported from a single locality: Platte County. Not common in that region." The complete observations made in 1906 were not reported until later, in which account, however, Heald ('11) fails to make note of Webber's earlier report of its occurrence. Freeman ('08) refers to the fungus as the cause of a well established disease of alfalfa in Kansas, and a specimen received by the writer in 1911 from that state indicates that it is identical with the European fungus. More recently it has been mentioned by Gandara ('10), and the inference is that it is found on alfalfa in Mexico. The first occurrence on potato in America is from a locality in Oregon (Bailey, '15). No well authenticated instance of the occurrence of this fungus in South America,

Australia, Asia, or Africa has come to my attention, yet the distribution of alfalfa growing throughout the world and the frequent interchange of seed might suggest that the distribution of the organism may be found to be much more general than is reported. It should be mentioned that Shaw ('13) reports the fungus from India, but he has obviously been misled regarding the fungus concerned, as will be shown later.

Du Hamel represented the violet root fungus as prevailing under a variety of soil conditions, but electing dry, gravelly, and acid localities. It is reported by the brothers Tulasne that while wet weather may give the fungus an advantage, still it is found in the driest situations permitting crop growth. In central Germany Kühn's studies led to the suggestion that on root crops and potatoes it is found more frequently in low and stagnant places. Frank and Comes concur in this view. The writer was able to observe the fungus in the vicinity of Munich in 1905 and in the fields examined, it was found under conditions which appeared to be favorable for the growth of the host. The very general occurrence of the fungus in southern Europe, especially in southern France and Italy, would seem to indicate that excessive moisture is not always an important factor. At the same time the fungus is of frequent occurrence in Scandinavia. It is not reported as one of the more serious diseases of any host in England. In the more humid regions of the eastern United States it is unknown, while two of the localities from which it has been reported are regions of lower humidity and lesser rainfall.

HOST PLANTS AND GENERAL SYMPTOMS

There is every reason to believe that the number of host plants for *Rhizoctonia Crocorum* is much greater than has been reported. The fungus has been observed upon many economic plants; and it has been reported in the agricultural press of Europe as occurring upon a variety of weeds, but these references are not always definite. Eriksson has made some observations regarding the plants attacked when culti-

vated in soil from a carrot field known to be infected, and the following weed hosts are noted: *Stellaria media, Myosotis arvensis, Galeopsis Tetrahit, Erysimum cheiranthoides, Urtica dioica.*

This would indicate that a careful study of any epidemic would confirm the view that the number of hosts is considerable. The following is a list by families of the host plants which have been reported in the more accessible literature:

Pinaceae
- Abies pectinata
- Picea alba
- Picea excelsor
- Pinus Laricio
- Pinus montana

Liliaceae
- Asparagus officinalis
- Crocus sativus
- Lilium sp.
- Muscari sp.
- Narcissus sp.
- Tulipa sp.

Urticaceae
- Ficus silvatica
- Humulus Lupulus
- Urtica dioica

Polygonaceae
- Rumex crispus

Chenopodiaceae
- Beta vulgaris
- Chenopodium album

Caryophyllaceae
- Spergula arvensis
- Stellaria media

Cruciferae
- Brassica campestris
- Brassica Rapa
- Crambe maritima

Rosaceae
- Crataegus oxyacantha
- Pyrus Malus

Leguminosae
- Anthyllis vulneraria
- Coronilla varia
- Medicago lupulina
- Medicago sativa
- Melilotus alba
- Onobrychis sativa
- Ononis spinosa
- Ornithopus sativus
- Phaseolus sp.
- Trifolium hybridum
- Trifolium pratense
- Trifolium repens
- Vicia Faba

Geraniaceae
- Geranium pusillum

Rutaceae
- Citrus Aurantium

Vitaceae
- Vitis sp.

Umbelliferae
- Daucus Carota
- Erysimum cheiranthoides
- Foeniculum vulgare
- Pastinaca sativa

Oleaceae
- Ligustrum vulgare

Convolvulaceae
- Convolvulus arvensis

Boraginaceae
- Myosotis arvensis

Labiatae
- Galeopsis Tetrahit

Solanaceae
- Solanum tuberosum

Rubiaceae
- Rubia tinctoria

Caprifoliaceae
- Sambucus Ebulus

Compositae
- Taraxacum officinale
- Sonchus arvensis
- Sonchus oleraceus

The difficulty in giving an accurate list of hosts compiled from the literature is, however, a serious one, since one cannot be certain that all the observations are carefully made. Again, some mycologists do not distinguish the two species of *Rhizoctonia* here discussed; thus Salmon ('08), after describing an interesting disease of seakale with all the characteristics of *R. Crocorum,* goes on to refer to carnation stem rot, damping off, and other diseases as if they were induced by the same fungus, doubtless, however, intended to have reference to another related fungus.

Regarding the above-ground symptoms of affected plants, it may be said that they are not striking, and were it not for the characteristic dead area in the field it would not be an easy matter to designate slightly affected plants. Generally, there is in alfalfa evidence of yellowing, sometimes marked chlorosis, while in beets and carrots there is merely a paler appearance of the foliage, followed by wilting. The critical period for affected alfalfa is usually about the time of the second cutting, and at this time considerable wilting may occur without preliminary indications of lack of health. In these main effects the disease is remarkably similar to the Texas root rot of cotton, alfalfa, and other plants. The unmistakable symptom is the relatively sudden dying of the plant affected.

The disease is generally though not necessarily fatal. Even a plant so susceptible as the alfalfa may recover from early injuries, usually with the loss of the tap root. Under certain conditions the disease incites the development of adventitious roots,—which may be a factor in recovery. The progress of the disease in the field is radial, and during the first year especially, circular dead areas mark its presence. The spread of the fungus during the season may be from a few feet to several rods. After the first year or two, considerable areas irregular in outline may be involved.

MYCELIUM AND SCLEROTIA

It would be difficult to confuse the mycelium of the violet root felt fungus with any other species, for when one is

familiar with it in the different stages of development it is at all times an organism with striking characteristics. Such differences in appearance as may be found in comparable stages on the various hosts may be regarded as causally related to the host substratum, or, at least they may be so regarded until adequate morphological differences or contrasting physiological relations are established. The general appearance of affected roots of asparagus, carrot, beet, or alfalfa are well expressed in some of the common names applied, such as red root, root felt disease, violet fungus, etc.

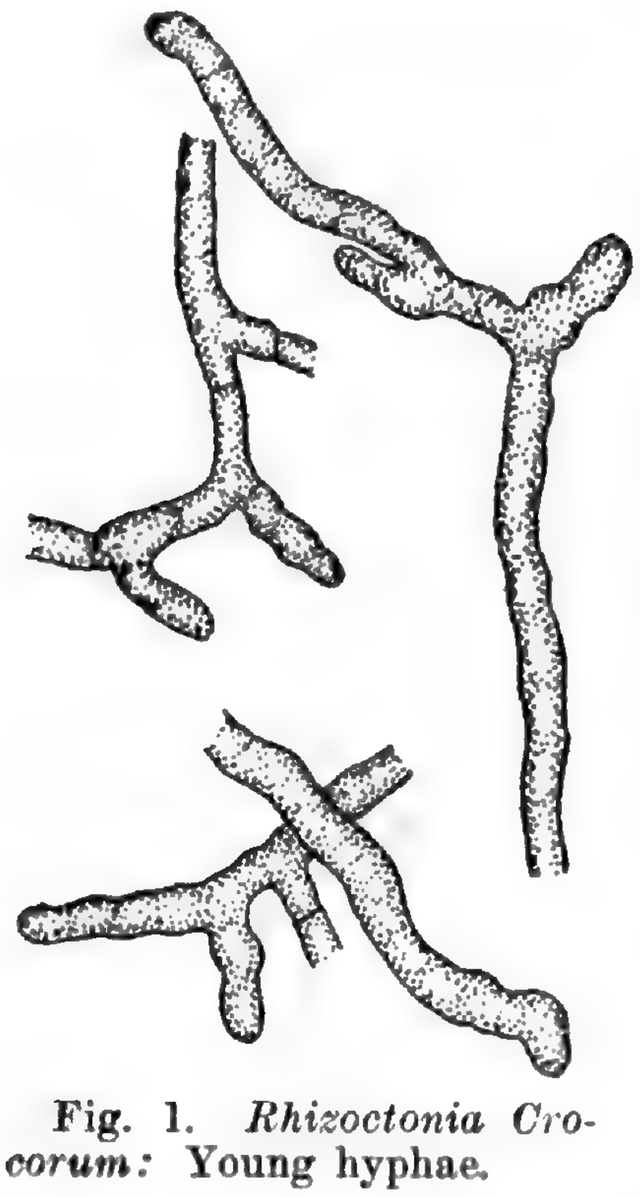

Fig. 1. *Rhizoctonia Crocorum:* Young hyphae.

With sufficient time for abundant growth the fungus completely invests the root or root system with a mantle, weft, or mat of hyphae of characteristic color. In the early stages of growth on the root the mycelium is pale buff to violaceous, but when the root is completely invested, the mycelium is red-violet to violet-brown, and always violet-brown with age or when densely matted. The numerous small darker papillae or "minute sclerotia" in the mantle of mycelium are in reality cushion-like mycelial bodies described later.

In the following description the writer will not attempt to follow all changes in the development of the various mycelial conditions, but will endeavor to give briefly those developmental features of greatest interest and those diagnostic characteristics which may be applied to most herbarium material. For further morphological details the accounts of L. and C. Tulasne ('62) and Prillieux ('91) should be consulted.

The external, general hyphae are more or less different in form and appearance with age. The younger hyphae are usually dilutely violaceous with a pigment which may be decolorized by the application of acidulated water. The pro-

toplasm is dense towards the tips of branches and vacuolated farther away. The hyphae are somewhat flexuous, branched (sometimes closely), with the branches arising at right angles to the main hypha, and with a partition wall laid down at not over 10 μ distant (fig. 1). With age the hyphae become rigid, somewhat less in diameter, 4–8 μ, the branching is distant, and these branches readily break off at the first partition wall (fig. 2). At the point of union the diameter is uniform with the main hypha. The partition walls are distant,

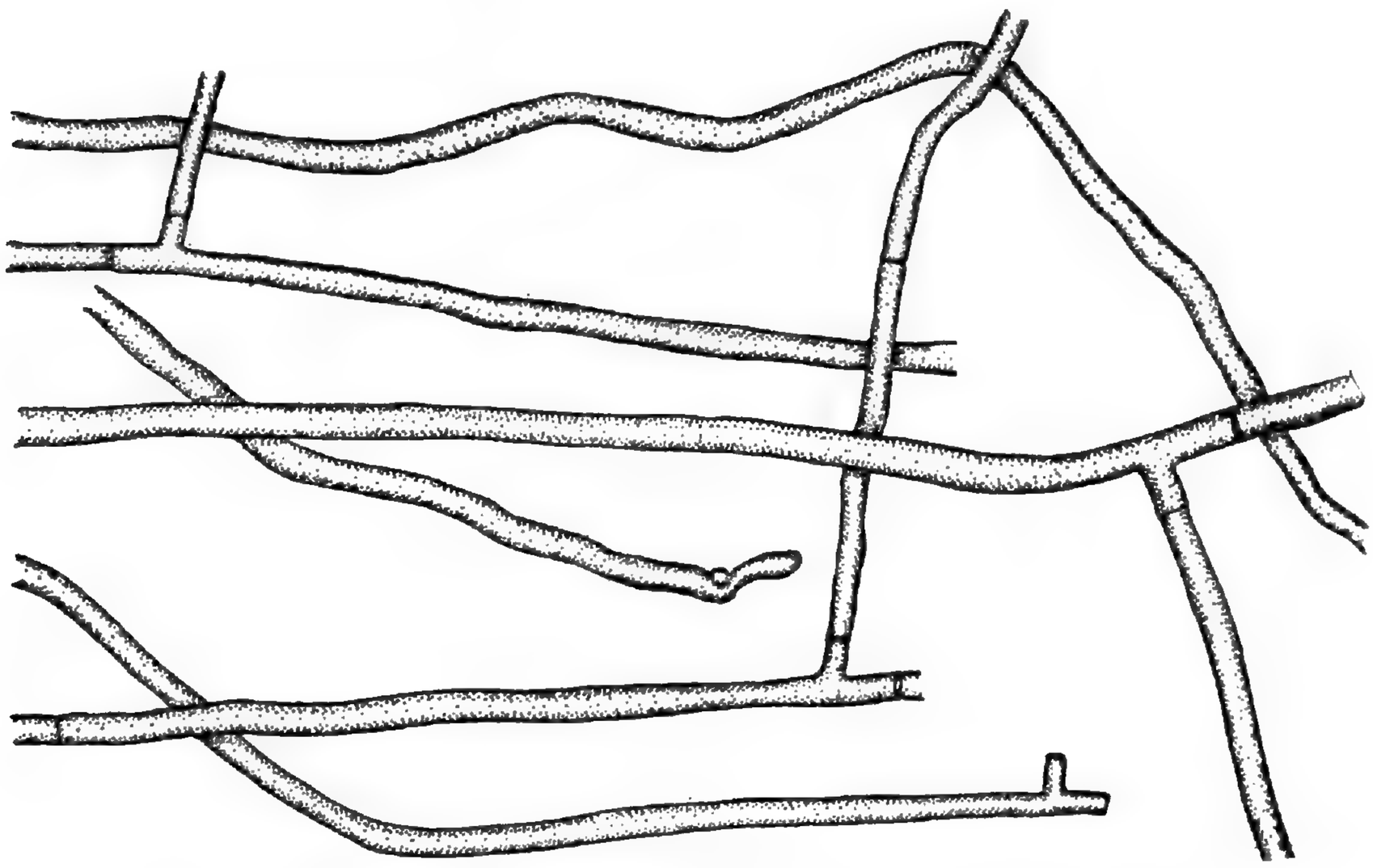

Fig. 2. *Rhizoctonia Crocorum:* Mature root-investing hyphae.

often 120–200 μ apart. The walls now possess the violet-brown pigment and in the lumen little or no protoplasm is observable.

The internal mycelium is likewise branched, septate, often associated into loose strands, passing between the cells or traversing them. In the early stages of the disease, so far as reported, these internal hyphae are nearly colorless; Prunet reports that there are sometimes areas of brown mycelium in the attacked tissues, and this I find particularly true of asparagus. The internal hyphae are generally of less diameter than those constituting the external mat.

Disregarding for the time the small cushions already men-

tioned, the hyphae constituting the external mantle may be uniformly distributed, as is the case usually when the fungus attacks fleshy roots or tubers, or they may also form a number of aggregates having the appearance of loose or root-like strands. The strands are developed later rather than early in the progress of the disease. They are conspicuous on such hosts as alfalfa and sainfoin. These strands course along the whole root system; they also pass out into the soil, apparently beyond the minutest rootlets, and doubtless attack plants in the vicinity. Upon the larger strands sclerotia may be formed, and thus the sclerotia are connected with the mantle of hyphae.

Infection Cushions.—Small stromatic bodies distributed amongst the hyphae were noted by several of the early observers. Kühn ('58) calls special attention to them on the carrot and the potato. The brothers Tulasne ('62) studied and described them in some detail and came to the conclusion that these were the early stages in the development of the perithecial form. Search for the reproductive phase was in this way transferred from the sclerotium to the bodies in question. Sorauer ('86) among others accepted the view of the perithecial nature of this structure. Prillieux ('91) seems to have been the first to point out that the "corps miliaires," as he termed them, are in reality special mycelial cushions having the important function of effecting the penetration of the host. He regarded them as the main, if not the sole, seats of tissue invasion, and his studies included a comparison of these bodies and of the penetrating strands in alfalfa, sugar beet, and crocus. After mentioning these cushions as one type of sclerotia, Prunet designates them more specifically as minute "corps noirâtres," .2 to 1.2 mm. in diameter with a brown hyphal cortex and a colorless medullar. He indicates that these as well as the larger sclerotia send out filaments which enter the soil and extend the fungus. These bodies have also been figured by Bailey ('15) in the case of the occurrence of the fungus on the potato in Oregon and particularly well by Salmon and Crompton ('08, pl. 25). The writer is of the opinion that Prillieux's notion is in general correct,

and while they are not the only means of penetration they are most important in this connection.

The hosts upon which the writer has had the opportunity to examine the infection cushions in best condition are alfalfa, carrot, and asparagus. The cushions are distributed over infected roots, often 1 mm. apart in alfalfa, .5 mm. in carrot, and 3 mm. in asparagus. The external hyphae are for the most part similar to those of the general mycelium, but there occur also branches in which the cells are short and swollen, sometimes resembling a short chain of spores. This form of hypha may have given the suggestion of a conidial stage (see Kühn ('58), Sorauer ('86), and others. The medullary portion of younger cushions is made up of finer, almost colorless hyphae, and it is this type which enters—strand-like—the cortical tissues of the root, destroying particularly the cambium and younger phloem regions. In the later stages of development it will be found that the cushions seem to extend considerably into the cortex, and more of the hyphae are colored.

In this connection it is well to call attention briefly to some gross changes in the affected roots. By the time the host (alfalfa) reaches the critical stage, the bark slips readily from the root. The disintegration may continue further, however, through the spread of the fungus to the medullary rays and all other parenchyma, so that the root shreds or crumbles when lifted. The late stages of destruction may be assisted by saprophytic organisms. It is difficult to determine if the fungus continues its growth for a short time after the death of the root. At any rate, the fungus rapidly disappears with the further decay of the roots.

In the case of asparagus the cushions are largely superficial and the main affected tissues are beneath the shell of thick-walled cells constituting the periphery of the host. In the carrot the invading strands are large, and the host cells in the vicinity rapidly collapse and darken. I have been fortunate in obtaining affected asparagus roots at intervals after the disease had run its course. In no case could any evidences of spore forms be found which gave promise of genetic connection. On the contrary, the fungus gradually disappears,

first the mantle of mycelium, and then the cushions, so that when the root is reduced to a mere shell there are only vestiges of the cushions remaining.

Sclerotia.—The true sclerotia are flattened or rounded bodies varying in diameter from a few millimeters to several centimeters. When mature they are of a deep violet-brown

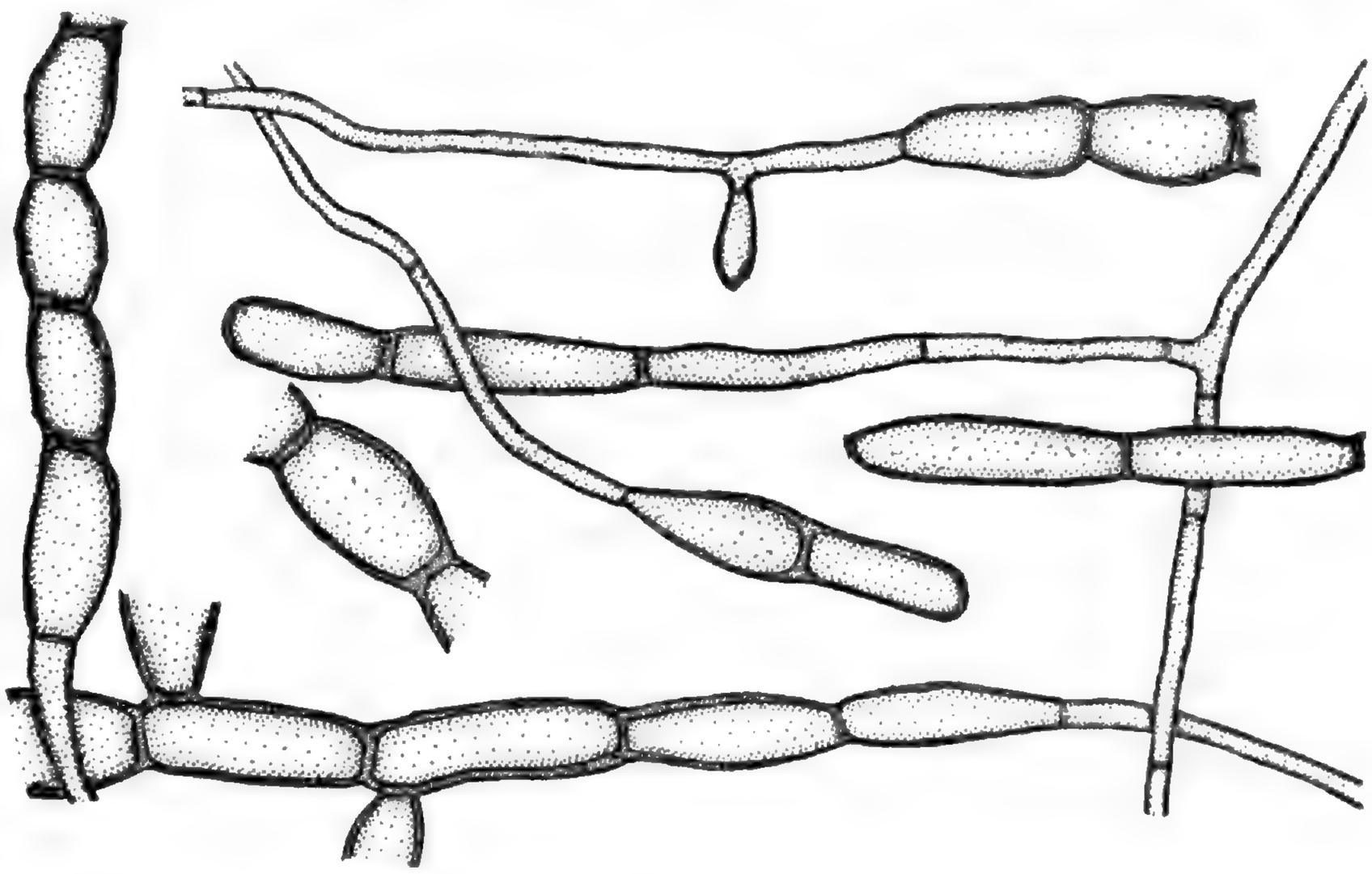

Fig. 3. *Rhizoctonia Crocorum:* Cells characteristic of the tufted growth covering the surfaces of the large sclerotia and to a certain extent of the "infection cushions."

and are thickly clothed with a persistent velvety felt, externally of the same color as the root-investing hyphae, but darkening further in. Among the surface hyphae of the sclerotia as well as of the "infection cushions" are found chains of enlarged cells (fig. 3) quite distinct from the enlarged cells of *R. Solani.* The sclerotia, as noted previously, are always connected with the root felt by large hyphal strands. In the saffron disease the sclerotia are formed both in contact with the shriveling bulb and also in the adjacent soil. On affected alfalfa roots they often occur below, and in the angles of, the larger branches, but often one finds no sclerotia in immediate contact with the host. In connection with diseased carrots, beets, and potatoes, they are not so frequent, unless perhaps they are then formed at greater

distances from the plant. Most herbarium material, unfortunately, with the exception of crocus specimens, does not include sclerotia.

In section a sclerotium consists of fairly compact tissue made up of cells often considerably branched and sometimes curiously lobed (fig. 4).

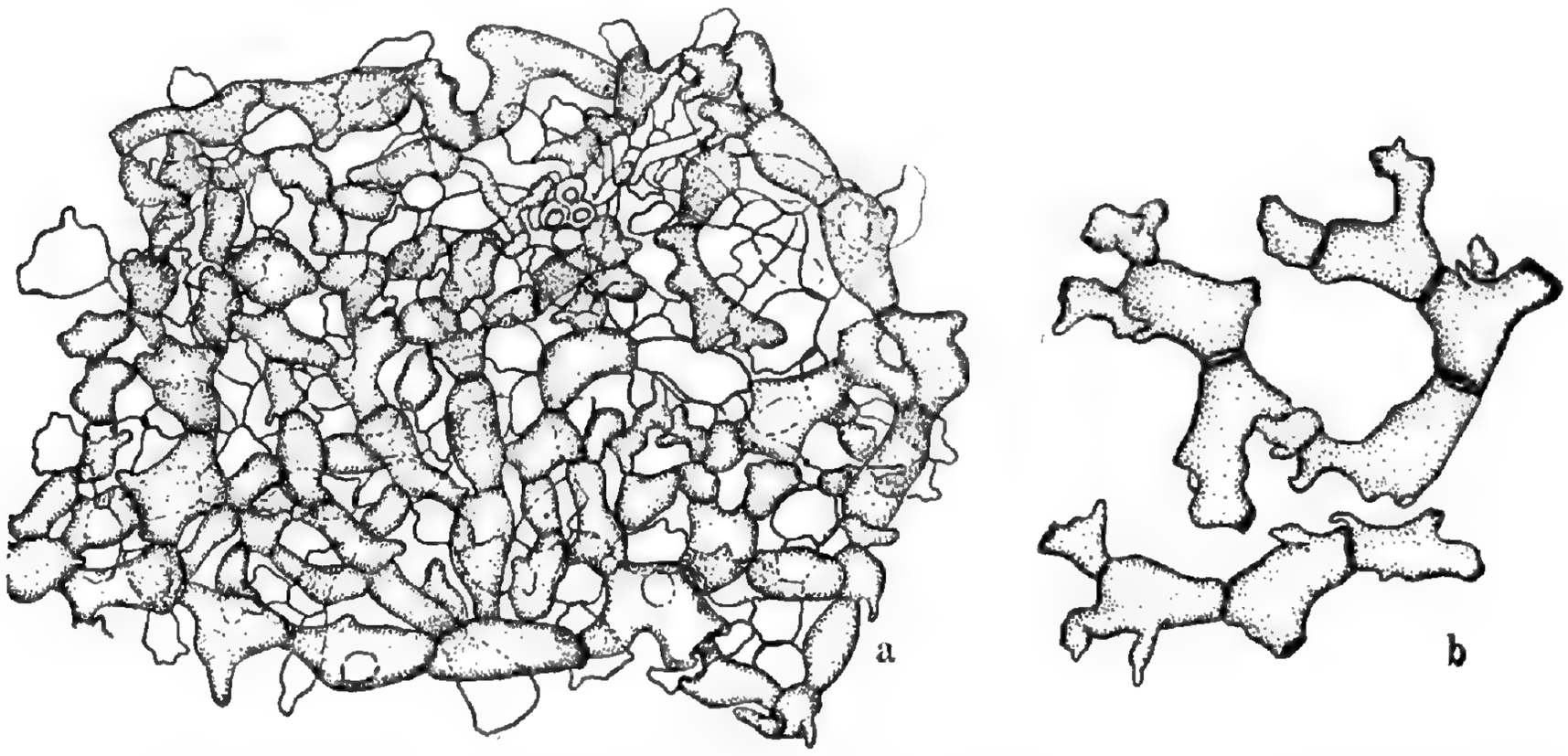

Fig. 4. *Rhizoctonia Crocorum:* a, from a section of a large sclerotium; b, extreme forms of cells isolated from a macerated sclerotium.

SUGGESTIONS REGARDING THE PERFECT STAGE

It has been noted that Du Hamel and other early observers stated that the affinities of the violet fungus were with the truffles. Persoon, Fries, and others placed the genus near *Sclerotium*. Tulasne considered the small sclerotia as probably a stage in the development of an ascomycete (pyrenomycete). This suggestion of Tulasne has apparently influenced many mycologists, and a search in this direction for the perfect stage has continued practically until the present time. Fuckel suggested that *Lanosa nivalis* Fr. might be considered the first or conidial stage of this fungus and he believed that the minute sclerotia or penetration cushions gave rise during the latter part of the season to pycnidia. With the more complete disintegration of the affected tissues he reported the development of a perithecial stage, and this fungus he called *Byssothecium circinans* (*Leptosphaeria circinans* (Fckl.) Sacc., *Trematosphaeria circinans* (Fckl.) Wint.). It will be noted that Winter regarded this

view of the genetic relation to *Rhizoctonia* as improbable; and Saccardo, who at first accepted the relationship, subsequently changed his opinion. Prunet ('93) states that he made certain inoculation experiments from which he was convinced that Fuckel was correct; but we possess no indications as to how these experiments were conducted. The writer in 1899, at Leipzig, germinated the spores of *Leptosphaeria circinans* and obtained a mycelium bearing no resemblance to the Rhizoctonia hyphae. The idea that *Leptosphaeria* constitutes a perfect stage of the *Rhizoctonia* has had no support recently, although Comes ('91) incorporates it in an extreme form in his treatment of the genus.

Rostrup ('86) found in the spring on the old roots of affected plants a pycnidial stage which he considered to be connected with the Rhizoctonia hyphae; and on the old roots of *Ligustrum* he found reddish filaments and scattering perithecia; the latter he identified as a species of *Trichosphaeria*. His assumption, however, has received no encouragement. When Hartig ('80) discovered a *Rosellinia* as the perfect stage of his *Rhizoctonia Quercina* there was a temporary revival of interest in the quest for one of the *Ascomycetes* as the perfect stage of *R. Crocorum*.

Frank ('97) reported observing the violet fungus on the grape, and associated with it he found a species of the *Thelephoraceae*. This he regarded as the perfect stage, and to the fungus he applied the name *Thelephora Rhizoctoniae*. This observation has failed of confirmation.

Eriksson ('13) has recently presented an extension of his earlier account ('03[a]) of diseases produced by *Rhizoctonia*, and in this he records a new "*Hypochnus*," *H. violaceus* (Tul.) Eriks. as the perfect stage of "*Rhizoctonia violacea*, Tul." In this he was stimulated by the observations of Rolfs ('03) and others in America, and Pethybridge ('11) in Ireland, on the occurrence of the basidial stage (*Corticium vagum* B. & C. or *Hypochnus Solani* Prill. & Del.) of *Rhizoctonia Solani* Kühn, resulting in a reëxamination of some material of the violet fungus on roots and stems of certain wild plants. This material had been preserved in alcohol thirteen

years earlier. The result of his study is reported as follows:

> "D'après ces renseignements, il faut—du moins pour ce qui concerne les formes du champignon qui envahissent les Carrottes—considérer comme résolue la question tant débattue de savoir à quel groupe rapporter le mycélium stérile connu sous le nom de *Rhizoctonia violacea.* Dans ce qui suit, je vais indiquer le nom scientifique qu'il faut donner, ainsi que les caractères diagnostiques du champignon autant que j'aie pu en juger sur les documents conservés que j'avais à ma disposition."

On the basis of these observations he creates the *Hypochnus* mentioned. No adequate diagnosis is given, but the important part of the account is as follows:

> "Ensuite le champignon forme autour des tiges de la même plante ou d'autres espèces de plantes immèdiatement au-dessus du sol, une enveloppe annulaire, membraneuse, d'un rose tendre, qui, montant souvent sur les tiges jusquà une hauteur de 5 à 15 mm. et s'étalant parfois sur la surface du sol comme une feuille toute mince, produit des basidiospores. C'est le stade *Hypochnus.*"

This apparently refers to material on *Stellaria media, Myosotis arvensis, Galeopsis Tetrahit, Erysimum cheiranthoides, Urtica dioica,* and *Sonchus arvensis,* which hosts he would regard as harboring the Hypochnus stage of that form of the violet fungus attacking the carrot, and for this reason the names just given appear in the list of hosts.

In the writer's opinion he properly considers it remarkable that the fructification stage should attack hosts other than those producing the sterile stage. In view of the character of the material, the incompleteness of the account, and the possibility of confusion with *Corticium vagum* B. & C. it would appear necessary to await confirmation of the observation that a *Corticium* (*Hypochnus*) may represent the perfect stage of the fungus here discussed, although, reasoning from the apparent relationship of this species to *R. Solani,* a Corticium stage might well be assumed. The writer has been unable thus far to secure any of the material mentioned.

In a footnote Eriksson expresses himself thus: "Quant à la Rhizoctone de la Luzerne, je suis porté à croire, d'après les

observations de cette année (1912), quelle doit être rapportée à un groupe d'Ascomycètes." This suggestion is both interesting and surprising since Eriksson adopts the Tulasnes' name for the *Rhizoctonia* on carrot and this would seem to concede the identity of the carrot and alfalfa forms. It is also in a measure inconsistent with his inoculation results, as reported later.[1]

CROSS INOCULATION AND CULTURAL STUDIES

The amount of cross inoculation work yet reported is not considerable, and for this, doubtless, the inability to cultivate the organism is largely responsible. Throughout the early literature numerous indications are offered showing that following a severe outbreak of the disease on any crop, it may appear on susceptible plants grown in the affected area—observations which tend to establish the identity of the fungus on different hosts. Among later observations may be mentioned those of Güntz ('99) who records that in a field where alfalfa and red clover had been seriously affected, beans, potatoes, and tuberous artichokes were planted; the potatoes subsequently developed the disease in serious form, and the other plants showed indications of its presence. In England it is reported (Bd. of Agr., '06) that potatoes are affected by the violet felt fungus, especially when following alfalfa; and under similar conditions the fungus appears upon clover, carrots, beets, and mangolds.

Eriksson ('13) undertook some cross inoculation work employing, in zinc cylinders, soil from diseased carrot fields (eight cylinders) in contrast with soil taken from areas free from the disease (two cylinders). At the same time, to the diseased soil he added pieces of carrots affected by the fungus. The cylinders were permitted to stand over winter

[1] Since obtaining proof of this paper I have received from Prof. Eriksson an advance reprint of his paper, "Fortgesetze Studien über Rhizoctonia violacea DC." Arkiv för Bot. 14 (Art 12) : 1–31. *f. 1–13.* 1915. It is impracticable to include here a full discussion of this paper. It is necessary to state, however, that he treats at length *Rhizoctonia Medicaginis* DC. and *R. Asparagi* Fckl., and includes inoculation experiments indicating form differences. After germinating the spores of *Leptosphaeria circinans* he comes to the conclusion that, in spite of his earlier work on *Hypochnus violaceus*, the pyrenomycete mentioned is the perfect stage of *R. Medicaginis*. Prof. Eriksson has also furnished material of *R. Asparagi* and of the *Leptosphaeria*.

and the following spring were planted to several varieties of carrots, to beets, mangolds, red clover, and alfalfa. At the time of harvest, the carrots were all more or less severely affected, while the sugar beets and alfalfa showed very light attacks, and the clover none at all. Continuing the work in subsequent seasons he obtained evidence in one case—that of the sugar beet—pointing to an increased virulence of the fungus with adjustment to that host. On the contrary, in the second year the alfalfa exhibited greater resistance, thus rendering a decision as to the existence of physiological races hazardous. He also reported, that on placing diseased soil and diseased carrots in a box in which various weeds were permitted to grow, the fungus appeared on eight species of weeds (representing several families), apparently a considerable proportion of those present. This also would seem to discourage the idea of marked host specialization.

Attempts to cultivate the violet fungus on artificial media have been made by several investigators without success. While in Leipzig, 1900, I obtained particularly good material on alfalfa from Bavaria. Dilution cultures were attempted both on various kinds of agar and on gelatin, but no growth of the fungus was secured in any case. Further trials were made with material from France in 1902, and again upon receiving comparatively fresh material from Kansas in 1911. Bailey ('15) reports an endeavor to cultivate the organism in Oregon, also without success. It is quite possible that special conditions are essential to its growth in artificial culture, but we should not assume that it is incapable of growth in this way. It would appear that the presence of contaminating organisms is not the sole cause of the difficulty, since isolated hyphae in the dilution cultures remain free from the growth of contaminating organisms, and yet themselves fail to develop a colony of growth. It will be recalled that Atkinson[1] found difficulty, but ultimate success, in growing *Ozonium omnivorum* (Lk.) Shear, the cause of the southwestern root rot of cotton. The writer also found that this organism is not readily cultured, but obtained a satisfactory

[1] Bot. Gaz. **18**: 16–19. 1893.

growth on cotton decoction starch paste in 1902. Since in general pathology and physiology the cotton *Ozonium* and the violet *Rhizoctonia* have much in common, a further careful investigation of their life relations would doubtless yield interesting results.

PREVENTION AND CONTROL

Relief measures respecting the violet fungus are very largely limited to the practices of good culture, good drainage, and sanitation. The early pathologists have generally recommended pulling up diseased plants and burning them. It is well to point out, however, that after a careful examination of the distribution of the fungus on the smallest fibrous roots, it has been found to invest these to a considerable depth in the case of alfalfa, and therefore a very small measure of security may be expected unless one carries out this recommendation in a far more thorough manner than is practicable in the field. The further suggestion has been made that where the diseased areas are few, small, and clearly defined, trenches may be dug to prevent the further spread of the disease; but if this should prove feasible under any conditions, it would be advisable only in connection with a thorough disinfection of the isolated areas by formaldehyde or sulphuric acid—the former disappearing from soil in time, and the latter being easily neutralized by liming. The rotation of crops is undoubtedly desirable, but complete immunity from the disease cannot be expected if we may trust the statements of Du Hamel and other observers to the effect that the fungus may remain alive in the soil for periods of from three to twenty years. The fact that many hosts are affected also complicates the practice of rotation.

THE COMMON RHIZOCTONIA, R. SOLANI KÜHN (CORTICIUM VAGUM B. & C.)

EARLY STAGES

In addition to his discussion of the violet *Rhizoctonia* on beets and carrots Kühn ('58) described a disease of potatoes, of which the causal organism was recognized as a species of

Rhizoctonia differing notably from the violet organism, and to this potato fungus he gave the name *R. Solani.* The life history of the fungus and the symptoms of the disease induced were very imperfectly known at the time, so that the description could not be complete. As a result, those who subsequently discussed the genus *Rhizoctonia* have sometimes recognized *R. Solani,* while others have referred the organism to *R. Crocorum* (*R. violacea*), and still others have assumed that *R. Solani* Kühn was also the cause of another disease of beets and of carrots mentioned by Kühn without identifying the causal organisms. After a study of certain diseases in America induced by *Rhizoctonia,* I was keenly aware of this confusion, so when opportunity presented itself in the winter of 1899–1900 I conferred with Professor Kühn regarding those diseases, and also endeavored to obtain satisfactory specimens of the fungi. There has been no earlier opportunity to utilize the information obtained in connection with a general discussion of the genus.

Kühn laid special stress upon a scab ("Schorf oder Grind," later termed "Pockenkrankheit") of potatoes, sometimes followed by deeper seated injuries and decomposition ("als Räude und Krätze bezeichnet"). The symptoms are clearly those that we now know as one type (cf. McAlpine, '12) of the potato diseases ascribed to *R. Solani* Kühn (*Corticium vagum* B. & C.). It has been noted that the fungus was not so well described as might be wished, and the spores mentioned were evidently those of contaminating organisms, or else the oval cells of the tufted stage of the fungus; but when we use in connection with this general description Kühn's comparison of this plant with the violet fungus (Kühn, '58, p. 248) it is convincing that the fungus on the potato which he had under consideration was not *Rhizoctonia Crocorum.*

The sclerotia were also inadequately described and figured. With reference to that point, however, Professor Kühn stated that while a common form of the fungus on the tubers consisted of irregular superficial sclerotia, this form did not lead to serious consequences and therefore received less attention from him. Material of this superficial sclerotial stage was

furnished the writer by Professor Sorauer in 1900 (for a photograph see Duggar, '09, p. 477, fig. 219), and, subsequently, from other points in Germany. It is clearly the "black speck" form of the disease now generally recognized. Professor Kühn also identified cultures of the American fungus on sugar beets (Duggar, '99) as very close to, if not identical with, his *R. Solani.* In 1858 Kühn was obviously unaware of the fact that the violet fungus also occurs on potato in Germany; and, in fact, he told me in 1900 that it was subsequent to 1858 when he first collected specimens of the violet fungus on this host. "The violet fungus produces no serious epidemics of the potato in Germany," he declared. Professor Kühn was unable to locate type material of *R. Solani,* and such material is doubtless unavailable. Before presenting still other indications pointing unmistakably to their identity, I shall proceed on the basis that it is correct to refer the sterile stages of the commoner American *Rhizoctonia* on potato and other plants to *R. Solani* Kühn, and once studied comparatively there can be no confusion of this plant with *R. Crocorum* (Pers.) DC.

A disease of carrots was also described by Kühn with which no fungus was positively associated. The indications are insufficient to determine whether this was a fungus or a bacterial disease. So far as the writer is aware no disease of carrots in Europe due to *R. Solani* has since been reported, though in 1900 Professor Kühn stated as his opinion that carrots as well as beets in Germany were affected by a fungus similar to *R. Solani.*

The violet root felt fungus was clearly distinguished by Kühn ('58, see pp. 235–237, 243–249) in its occurrence on both beets and carrots. It is not possible to mistake his statements in which the organism on these hosts is referred to *Rhizoctonia Medicaginis* DC." Moreover, he nowhere suggests the combinations *R. Dauci* Kühn and *R. Betae* Kühn, which later crept into the literature of the subject. This fact makes it difficult to understand the nomenclature employed by Eidam ('87) and Comes ('91). In discussing a beet disease prevalent in Germany, Eidam refers the organism to *Rhizoctonia Betae* Kühn. He gives a description of the disease and of the fun-

gus, including its growth on culture media. It is clearly the beet disease now well known in America, and of which the causal fungus is referred to *R. Solani.*

Kühn did describe the symptoms of another disease of beets, and this last bears every indication of being the heart rot later known to be due to *Phoma Betae* (*Phyllosticta tabifica*), much discussed by Frank and others. Kühn's discussion of this other beet disease has been interpreted, also, in the way I have indicated by Prillieux and Delacroix ('91) and others outside of Germany. In my conference with him, Professor Kühn stated that the only Rhizoctonia diseases of beets and carrots which he knew in the vicinity of Halle in 1858 and earlier were those due to the violet fungus, and of these he exhibited specimens having the usual characteristics. From the evidence at hand, therefore, the Rhizoctonia disease of beets described by Eidam was new on that host. It would seem, then, that Eidam is the authority for the combination *R. Betae,* which he attributes to Kühn. In any case it becomes a synonym of *R. Solani* Kühn (*Corticium vagum* B. & C.).

In discussing the Rhizoctonia disease of potatoes in Europe Sorauer ('86) describes unmistakably the "black speck" or sclerotial form of the fungus, and while he, like many others, assumed that it would be found to belong among the *Ascomycetes,* it is obvious that the characteristics of this stage of Kühn's fungus were well recognized.

Among the forms of *Rhizoctonia* which he enumerated and discussed Comes ('91) includes *R. Dauci* Kühn, and *R. Betae* Kühn. In his discussion of the first-named he reviews Kühn's account of the violet fungus on carrots, already mentioned; but in the account of *R. Betae* Kühn he evidently refers both to Kühn's account of the heart rot of beets and to the Rhizoctonia disease of this host described by Eidam. Pammel ('91) was the first American pathologist to report in this country a disease now known to be caused by *R. Solani.* He, however, followed Comes and Eidam in referring to the fungus causing the beet rot as *R. Betae* Kühn.

Atkinson ('92, '95) studied a "sterile" fungus causing sore

shin or damping off in cotton, and ascertained that the same fungus was commonly associated with, and capable of, inducing damping off of various seedlings in the greenhouse.

Duggar ('99) also referred to the beet rot fungus in America as *Rhizoctonia Betae* Kühn, following Comes, and was able to determine that this beet fungus was identical morphologically (mycelium and sclerotia) with the damping off fungus found by Atkinson. The characteristics of the two organisms in culture were also identical, both forming on certain media a rich mycelium and finally numerous flaky or tufted centers of growth, some of which become irregular, often crust-like, sclerotia. Neither on affected seedlings nor on beets were sclerotia ordinarily produced (compare, however, Edson, '15, pl. 23).

Subsequently, Duggar and Stewart ('01) reported that several types of disease, on a variety of hosts, including the potato, were induced by *Rhizoctonia.* The account given was intended to be merely preliminary, and for this reason a few words of explanation are necessary. The account referred to did not (perhaps unfortunately) explicitly indicate that, as far as the studies had progressed, there was evidence that the organism, or forms of the organism (except in the case of the form on rhubarb, referred to later) exhibited morphologically and in culture the characters of the beet rot and damping off fungus. The authors were likewise convinced, after a study of European material of Kühn's fungus on the potato, of the identity of the American and European forms on this host. Cultural studies were being carried forward with *Rhizoctonia Solani* from many hosts, since there was the possibility of establishing definite forms or races, of finding the perfect stage, and of discovering other species. Again, specimens of the violet root felt fungus on various hosts had been obtained by one of us, and it was intended to include in a final paper a general account of the genus.

This failure to designate the form with which we worked has doubtless led to some misunderstanding (see Prillieux '97, Eriksson '13, p. 17). However, in a more recent account (Duggar, '09, pp. 477–478), it will be seen that the diseases

discussed are ascribed to *R. Solani* (*Corticium vagum* B. & C.).

DISTRIBUTION

Rhizoctonia Solani is distributed throughout the United States and Canada. There is every reason to believe that it exists as a saprophyte in most arable soils, and under certain conditions may attack many species of plants. It is perhaps most frequently noted as a damping off disease in greenhouses and seed beds, but this occurrence may be explained by the fact that here the conditions are probably more conducive to the pathogenicity of the fungus. On the potato it is likewise wide-spread, although, as noted later, the economic importance of the diseases induced varies in different sections of the country, probably in accordance with climatic and soil conditions. In all potato-producing states and regions it is a well-known disease. On the sugar beet it has been observed in many states. The fact that it is an important disease of one crop or another in every section of the country is alone sufficient indication of its general occurrence. *Rhizoctonia* has been mentioned in Brazil by Potel ('00), but it is not clear to which species he refers.

It is rather surprising to find that *R. Solani* has received relatively little attention in Europe. Although recognized as inducing a disease of the potato widely distributed in central Europe, and occasionally reported on the beet, yet little careful work has been bestowed upon the fungus. Eriksson ('13), seems to be unfamiliar with the fungus in Sweden. On this account we can gain no incidental information regarding *R. Solani* as a result of his extensive studies of the related species in that country. The following will express his attitude regarding *R. Solani:*

> "Il paraît très douteux, du moins si l'on en juge d'après les descriptions et les figures données, que les nouvelles formes de la Rhizoctone stérile signalées dans ces derniers temps par B. M. Duggar et F. C. Stewart sur une quantité de plantes différentes en Amérique (* * *) soient vraiment identiques aux formes du *Rhizoctonia violacea* qui ravage l'Europe."

We have very little data regarding its occurrence in other sections of continental Europe, although from conference

with Prof. Delacroix in Paris (Nov. 28, 1901) and from an examination of material furnished by him I learned that it is not uncommon throughout France on the potato. It will be recalled that the perfect stage was described by Prillieux and Delacroix ('91). Judging from the amount of the black speck disease observed on the potato in the markets of various cities in southern Europe during 1905–'06 the writer would infer that it is of more frequent occurrence than is reported. Pethybridge ('11) finds the fungus (including the Corticium stage) well distributed in Ireland, and it is reported from other parts of Great Britain.

McAlpine ('11) has reported this fungus on the potato from several points in Australia, and he states that it occurs upon a variety of economic plants. Since it has proved a serious disease in very few localities, it receives little attention, and is therefore freely disseminated by commercial intercourse. It is also known in New Zealand and Japan.

The investigations of Shaw ('13) suggest that *Rhizoctonia Solani* may be an important disease-inducing organism in some of the more humid regions of India. Reference is made later (pp. 448–450) to the fact that he has obviously misapplied this name, however, and also that other confusion has resulted. In spite of this, it seems certain that he has observed all stages of the fungus.

TYPES OF DISEASES INDUCED, SYMPTOMS

It is not my purpose to attempt a complete description of the more important diseases caused by this species, yet sufficient will be included to indicate the main types of diseases thus far investigated, their general distribution, and their striking pathological relations. By types of disease, I have reference to general effects or symptoms. The effect of the fungus upon the stems may occasion a different appearance from its action upon the root, and thus there arise the different types referred to. With respect to penetration and action upon the cell the behavior of the fungus may be the same in all cases. Moreover, as a result of the primary injury, secondary effects may occur, and sometimes such secondary phe-

nomena may be so striking in appearance as to dominate the primary injuries or lesions.

For convenience we may arrange the types of disease in the following categories: (1) damping off, (2) stem rot, (3) root rot, (4) leaf rot, (5) scab, and (6) such secondary effects as rosette, little potato, and leaf roll. Since more than one type of disease may occur upon a single host, and especially since one form of the disease may grade into another, it will be more practicable to discuss these under the following captions: (1) damping off, (2) potato diseases, (3) rot of fleshy roots, (4) stem and root rots of herbaceous plants, and (5) fruit and leaf injuries.

DAMPING OFF

It would appear that the first mention of a disease of seedlings caused by *Rhizoctonia* is that of beets, recorded by Eidam ('87), although he gives no complete account of the evidence. It is preferable to date our knowledge of damping off diseases caused by *Rhizoctonia* from the work of Atkinson ('92), who studied particularly sore shin of cotton, but he also found the "sterile" fungus to cause damping off of seedling beets, radish, lettuce, egg plants, cabbage, and other plants in the forcing house. The later identification of the fungus concerned (Duggar, '99) and its association with the damping off of various plants (Duggar and Stewart, '01) was only the beginning of the observations which have now served to direct our attention to the vast importance of this fungous disease throughout the United States both in the greenhouse and in the outside seed bed.

Among numerous instances in which damping off has been reported due (or in all probability due) to this fungus may be noted the following: (1). It has been found as a source of serious injury to ginseng in the seed bed (Van Hook, '04; Whetzel and Rosenbaum, '12). (2). Tobacco seedlings are so frequently injured that soil treatment has received special consideration in the case of this crop (Selby, '04; Cook and Horne, '05). (3). As a damping off disease of cotton (sore shin) it occurs not only in America but in Africa (Balls, '05, '06) and possibly in India (Shaw, '13) as well. (4). Tomato

seedlings seldom attacked by *Pythium* have been found to succumb to *Rhizoctonia* in Louisiana (Edgerton and Moreland, '13). (5). Alfalfa seedlings have been reported susceptible in one instance (Stewart, French, and Wilson, '08). (6). Seedlings of various species of conifers from a few days to nine weeks old have been reported attacked in several instances (Hartley, '12, Clinton, '13).

The majority of the instances reported above were under normal seed bed or field conditions. Many other cases of the damping off of seedlings might be included where seeds are grown in crowded condition in moist greenhouses. Again, damping off of cuttings by *Rhizoctonia* is now a well-known phenomenon in the propagating house, and special precautions are taken with respect to drainage and moisture in order to reduce the injuries to a minimum. It is safe to assume—since the fungus seems to be found in practically all soils—that it is in general the worst enemy of seedling plants. In fact, it may be anticipated that under conditions favorable for the fungus the damping off of seedlings of numerous species may be anticipated. So far as the writer has been able to ascertain there has been no report of the damping off of monocotyledonous plants under normal seed bed conditions.

While *Rhizoctonia Solani* may perhaps induce damping off in innumerable species regarding which observations are lacking, some of the host plants which have come to the writer's attention as particularly susceptible are the following: lettuce (*Lactuca sativa*), celery (*Apium graveolens*), beet (*Beta vulgaris*), cress (*Lepidium sativum*), tobacco (*Nicotiana Tabacum*), balsam (*Impatiens balsamina*), snapdragon (*Antirrhinum majus*), cotton (*Gossypium* spp.), cucumber (*Cucumis sativus*), squash (*Cucurbita* spp.), sunflower (*Helianthus annuus*), carrot (*Daucus Carota*), radish (*Raphanus sativus*), and phlox (*Phlox Drummondii*).

Since the phycomycetous damping off fungus *Pythium* has been known to pathologists much longer, and prior to 1895 was practically the only fungus to which this type of disease was ascribed, it is probable that much damage due to *Rhizoctonia* has been ascribed to *Pythium*. Moreover, unless

examined microscopically, there are no symptomatic differences between the effects of the two organisms.

Seedlings affected exhibit symptoms somewhat different with age. The youngest seedlings of all delicate plants show what may be called the usual damping off characteristics. Near the base of the stem an hygrophorus or translucent appearance is quickly followed by shrinkage of the tissues and weakness of the stem. The plants topple over, the fungus invades all parts, and spreads rapidly to the neighboring individuals. The cells of the sap-perfused tissues are flaccid and injured, some showing this even before the entrance of the hyphae into the cells. Somewhat older plants and the more robust seedlings of cotton, bean, etc., often exhibit characteristic lesions. Atkinson ('95) gives a description of its effect on cotton seedlings as follows:

> "The trouble is caused by the fungus growing first in the superficial tissues of the stem near the ground and disintegrating them before it passes to the deeper tissues; in other words the fungus never seems to penetrate far in the living tissues, but 'kills as it goes,' and the tissues become brown, depressed, and present the appearance of the plant having a deep and ugly ulcer at the surface of the ground. The fungus does not spread into the tissues either above or below the ulcer to any extent, but literally eats away at that point until it has severed the stem at the affected place or the plant has recovered from its effects."

DISEASES OF POTATOES

The potato is the most interesting of the host plants with respect to the parasitism of *Rhizoctonia* by reason of the many types of disease induced under diverse conditions. The conditions may be in part climatic and, in part perhaps, dependent upon the pathogenicity of the particular strain of the fungus or upon the stage and development of the host at the time of infection. It has been noted that when Kühn first described the disease of potatoes in Germany he laid emphasis upon a scab which was often followed or accompanied by decay. This form of the disease was probably less prevalent in the country as a whole at that time, and the more recent accounts indicate that the "black speck scab" or "black speck," properly the sclerotial stage, is the feature by which the main type

of the disease is now generally known. At present the following main types of injury are recognized for the potato: (1) black speck scab or sclerotial stage, (2) Rhizoctonia scab, (3) Rhizoctonia rot, (4) stem lesions and root rot, (5) rosette and leaf roll, and (6) little potato and aerial potato.

Black speck is a form of the disease most widely distributed and in itself scarcely merits consideration as a "disease" at all, since the sclerotia are superficial on the tuber, and it is merely the appearance of the potato which is affected. The sclerotia may lead to other types of disease which are more serious. The black specks show up most clearly when the potatoes are wet and it is only at this time that they present the appearance of being black, for, as indicated later, the normal color of the sclerotia is deep brown. It was this form of the disease which first gave evidence of the wide distribution of the fungus in America (Duggar and Stewart, '01), and it has been shown to exist in practically all potato-producing sections of the United States and Canada. It occurs throughout Europe, especially on the later varieties of potatoes. It is also reported from India, Africa, and Australia, so that it may be assumed to be world-wide in its distribution on this host. It is safe to say that this is the only form of the disease which does not result directly in serious injury and loss to the crop. In the United States, especially from Ohio westward, other forms of the potato disease assume a seriousness nowhere else attained. If all such forms of the disease mentioned below occur in the Atlantic states they are of little consequence. They are, moreover, far less frequent in Europe, India, and Australia.

The Rhizoctonia scab is believed to occur as a result of the penetration of hyphae during the early stages of sclerotial development, and occasionally it may be induced by a late growth of new hyphae from old sclerotia. The writer has had an opportunity of examining only casually this form of the disease. It is one of the types doubtless seen by Kühn. According to McAlpine ('11), when this disease occurs, practically every part of the tuber is affected, no normal skin remaining. In severe cases the scab areas may be thrown into folds or puckers and these rub off easily in the form of "cork dust."

It is reported that the irritating hyphae are then found at the bases of such scab formations. This scab has been reported fairly common in Europe and in Australia. Güssow ('05) seems to refer to the same type in England, and Rolfs ('03) describes it from Colorado. Specific scabs of the potato have been clearly defined and related to particular organisms. The capacity of the tuber to respond with cork formation to varied injuries suggests that in certain modifications of Rhizoctonia scab this fungus may accompany other active scab inducing agents.

The Rhizoctonia rot is a form of disease which appears relatively late in the season when certain conditions prevail, or possibly when the fungus has for one reason or another developed unusual virulence. The disease is supposed to originate either from stem infections, from sclerotia, or from scab areas. In any case penetration of the mycelium occurs to a considerable depth, and according to McAlpine ('11) there is produced in Tasmania a form of the disease known as brown rust, characterized in the early stages by dark spots in the tuber resembling certain symptoms of *Phytophthora*. It may also be associated more or less with the deeper form of the Rhizoctonia scab. During the latter part of the season a typical stem rot may occur which is not characterized by the definite lesions described later. Instead, the affected cortex slips readily from the wood and about the bark a considerable web of the yellow-brown hyphae may be found superficially, below and just at the surface of the ground, and the pith may be fairly stuffed with the mycelium. Plants only slightly affected with this form of the disease, especially when growing on rich garden or muck soil, have been found to yield the collar or *Corticium* stage.

It is not always easy to distinguish as separate forms of the disease, stem lesions, rosette, little potato, aerial potato, rolling, etc., for these types of injury are often associated. All of these types except stem lesions are properly secondary effects, and there is abundant evidence that all represent responses of the plant to disturbed condition or nutrition, sometimes associated with native weakness. It would not be

strange, therefore, if somewhat similar effects should characterize, as they do, purely "physiological" disturbances. Stem lesions are generally dark, sunken areas, clearly different from black leg, occurring at the surface of the ground or on any of the underground stems, or tuber-forming stolons. These lesions may result in the early death of the affected plants. Selby ('02, '03) maintains that generally the lesions upon young shoots are associated with stunted growth and the production of rosette-like clusters of the upper leaves, as well as with less marked modifications of habit, including slight leaf rolling. Drayton ('15) finds the hyphae in the lesions.

If the tuber-bearing stolons are the seat of injury, the food supply is cut off from the young tubers and there may result "little potato," a form of the disease which Rolfs ('04) has found to be an important cause of the potato failures in Colorado. Little potato in Australia is considered an evidence of underground injuries occurring late in the season. Injuries which effectually girdle the stem, especially if these occur during a moist season or when the crop is frequently irrigated, lead to the formation of aerial tubers. In the relation of *Rhizoctonia* to the various types of potato diseases much remains to be investigated, and Orton ('14) rightly suggests that inadequate attention has been bestowed upon the question of the predisposition of the tubers used as seed, since it is quite possible that these may yield offspring with tendencies toward rosetting, leaf rolling, and other morphological modifications.

ROT OF FLESHY ROOTS

The root rot of beet, apparently first described by Eidam ('87) in Germany, and shortly afterward found by Pammel ('91) in Iowa, was observed in New York (Duggar, '99) some years later. Since that time it has appeared epidemically in Nebraska (Lyon and Wianco, '02) and other western states. The fungus is most virulent during midsummer or later. Infection may take place at the bases of the leaves or on the fleshy root. The leaf bases blacken, the leaves become paler, and finally wilt. Pammel ('91) has drawn attention to the

fact that when fleshy root crops of this type are attacked by such fungi they die gradually, while herbaceous plants (cotton, alfalfa, etc.) wilt suddenly. This is probably closely related to the effect of the fungus on the conducting tissues. In the beet root the invaded tissues are pale brown, and often cracks or rifts occur, though rotting may take place without such lesions. Sometimes there is partial recovery after the cracks are formed, and in this case callous tissue is developed.

A soft crown rot of the radish induced by this fungus has apparently been reported only once (Duggar and Stewart, '01). A similar disease of the carrot was found in 1900 in New York and this is possibly the disease first reported by Kühn ('58, pp. 241–243), although he did not identify it as due to a *Rhizoctonia*.

STEM AND ROOT ROTS OF HERBACEOUS PLANTS

Rhizoctonia Solani produces serious stem and root rots of a number of economic herbaceous plants, among which the following are known to be important: carnation (*Dianthus caryophyllus*), Sweet William (*Dianthus barbatus*), bean (*Phaseolus vulgaris*), sweet-pea (*Lathyrus odoratus*), and violet (*Viola odorata*).

The carnation stem rot is one of the most destructive diseases occurring on this host and is wide-spread in the United States. The general symptoms of the disease on carnation and Sweet William are much the same. The stem is affected at or just below the soil level. The fungus penetrates and kills the cortex which may be readily slipped from the wood. Through the medullary rays the hyphae also enter the pith, which likewise decays. In later stages of the disease the wood shreds, due to the complete penetration by the fungus of all parenchymatic tissues.

Several important epidemics of *Rhizoctonia* on bean have been reported from different parts of the United States. In addition to the outbreak described by Duggar and Stewart ('01), Hedgcock ('04), a few years later, found the bean disease severe near St. Louis. The base of the stem and the larger roots bore characteristic ulcerations; pods were af-

fected, and through the sunken areas of these the hyphae penetrated the seed and produced small sclerotia on the seed-coats. The fungus was cultivated and typical Rhizoctonia hyphae and sclerotia were obtained. Fulton ('08) observed the disease in Louisiana on stems and pods, with the characteristic ulcerations, especially at the surface of the soil or just below. He proved the causal relation of the organism through cultures, and inoculations yielded positive results with the damping off of seedlings. McCready ('10) reported the bean disease as new to Ontario, where it was also characterized by stem and pod ulcers. In New York Barrus ('10) observed an epidemic of this host in which as many as 30 per cent of the plants were affected. He determined the fungus by cultural studies and proved its pathogenicity by inoculation. On the sweet-pea the disease is mainly a root rot, yet the base of the stem may also be considerably affected before the plant succumbs. On the violet it is primarily a crown disease, but where the plants are succulent and the conditions are moist, the leaves are considerably invaded.

FRUIT AND LEAF INJURIES

In discussing stem diseases the occurrence of *Rhizoctonia* on bean pods has been mentioned. Another case of fruit injury is described by Wolf ('14), who found a severe rot of egg plant fruits from which the fungus was obtained. The pathogenicity of the organism was determined by inoculations, and cross inoculation from tomato and potato led to the conviction that the organism was *Rhizoctonia Solani.*

Direct attacks of leaves by *Rhizoctonia Solani* are infrequent. From the habits of the fungus this would be expected. The one serious leaf disease reported is that of lettuce (Stone and Smith, '00), in which the fungus spreads over the whole surface, causing a moist rot. Sclerotia are frequently formed in connection with this affection. It would be anticipated, perhaps, that diseases of a similar nature might be found on other plants with the rosette habit. Leaf stalks are frequently invaded, or may be the regions of first attack, in the case of the beet disease. The disease of leaf stalks of rhubarb

reported by Duggar and Stewart ('01) is not due to typical *R. Solani.*

MYCELIUM AND SCLEROTIA

The morphological characteristics of the hyphae and sclerotia have been adequately described by several writers, but it may be well to summarize some of the more important features. Upon such hosts as the potato, sugar beet, carnation, and others there is more or less development of an external web, but never over the general root system such a complete investment of roots by a mantle of hyphae as characterizes the violet fungus. The external hyphae are somewhat colored, usually yellowish brown, and they are generally of two types. One type may be designated as purely vegetative and another as constituting the external tufts or masses when these occur. All hyphae are practically colorless when young, vacuolate, more or less irregular, septate with the septa at intervals of 100–200 μ. The diameter of vegetative hyphae is 8–12 μ. Branches arise, and when young these are inclined in the direction of growth and are invariably somewhat constricted at the point of union with the main hyphae (fig. 5). As the hyphae mature and become more deeply colored they are more uniform and rigid, the distances between cross walls are greater, the constrictions where branches arise less marked, and the branches are approximately at right angles to the main hypha.

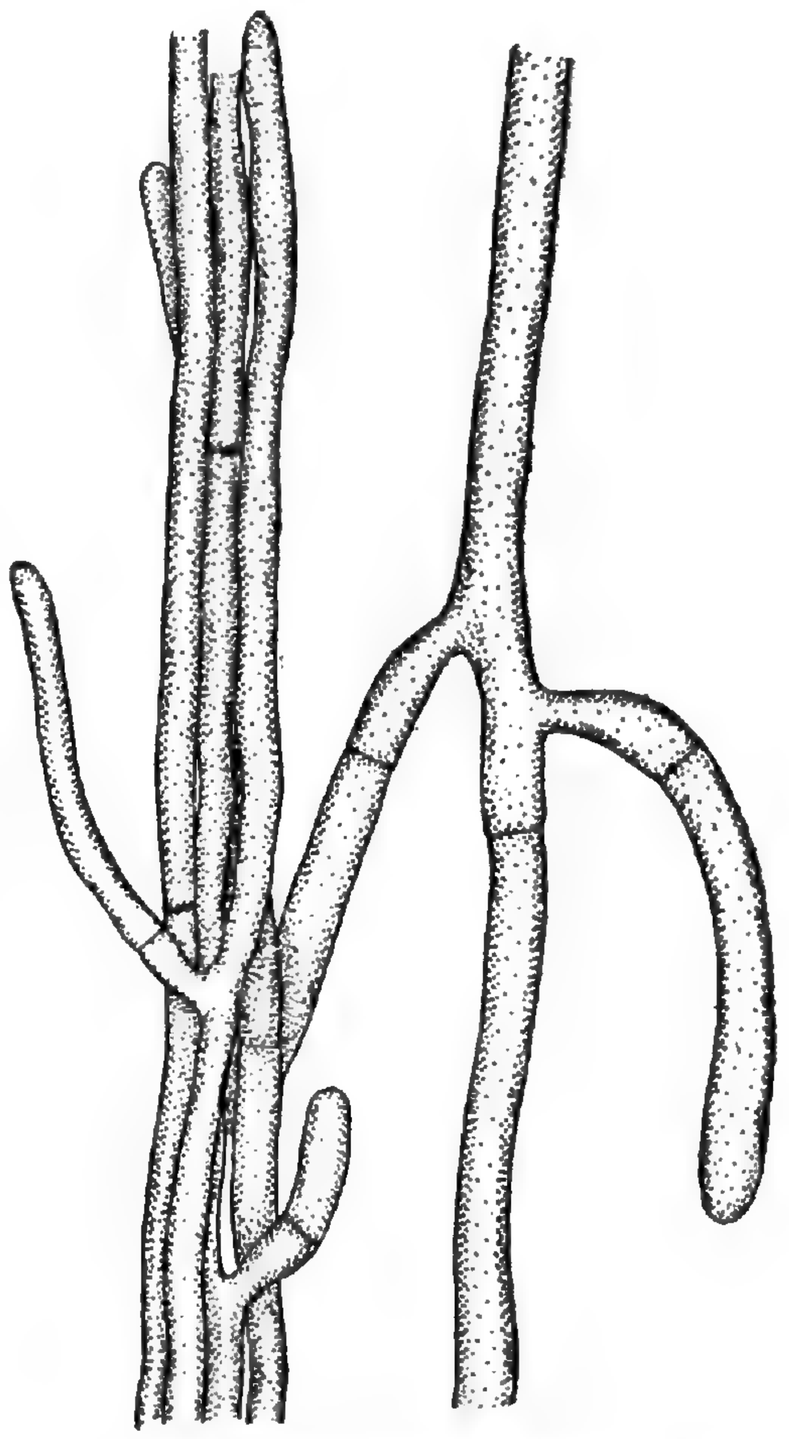

Fig. 5. *Rhizoctonia Solani* (*Corticium vagum*): A vegetative hypha and a small strand from artificial culture on potato.

On certain affected plants a short tufted or mealy growth occurs and this is made up of hyphae of very different characteristics. In the young condition threads are profusely

branched and lobed, sometimes botryoid, and they are ultimately divided into short, ovate cells, arranged in short chains, or elbowed, and producing branches in a more or less dichotomous fashion (figs. 7 and 8). In culture the denser

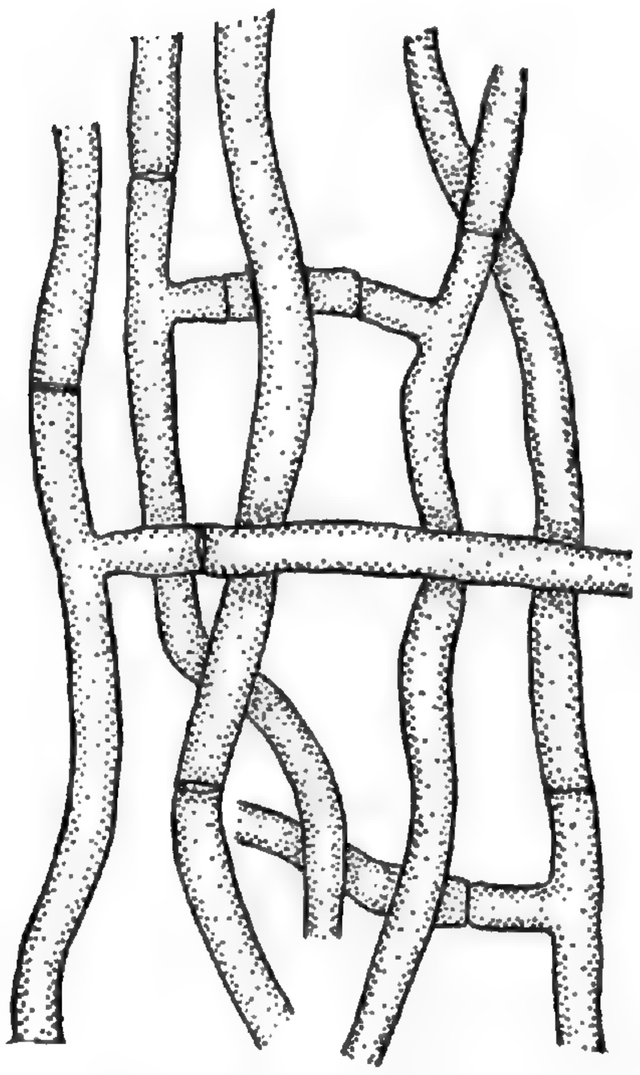

Fig. 6. *Rhizoctonia Solani:* Vegetative hyphae.

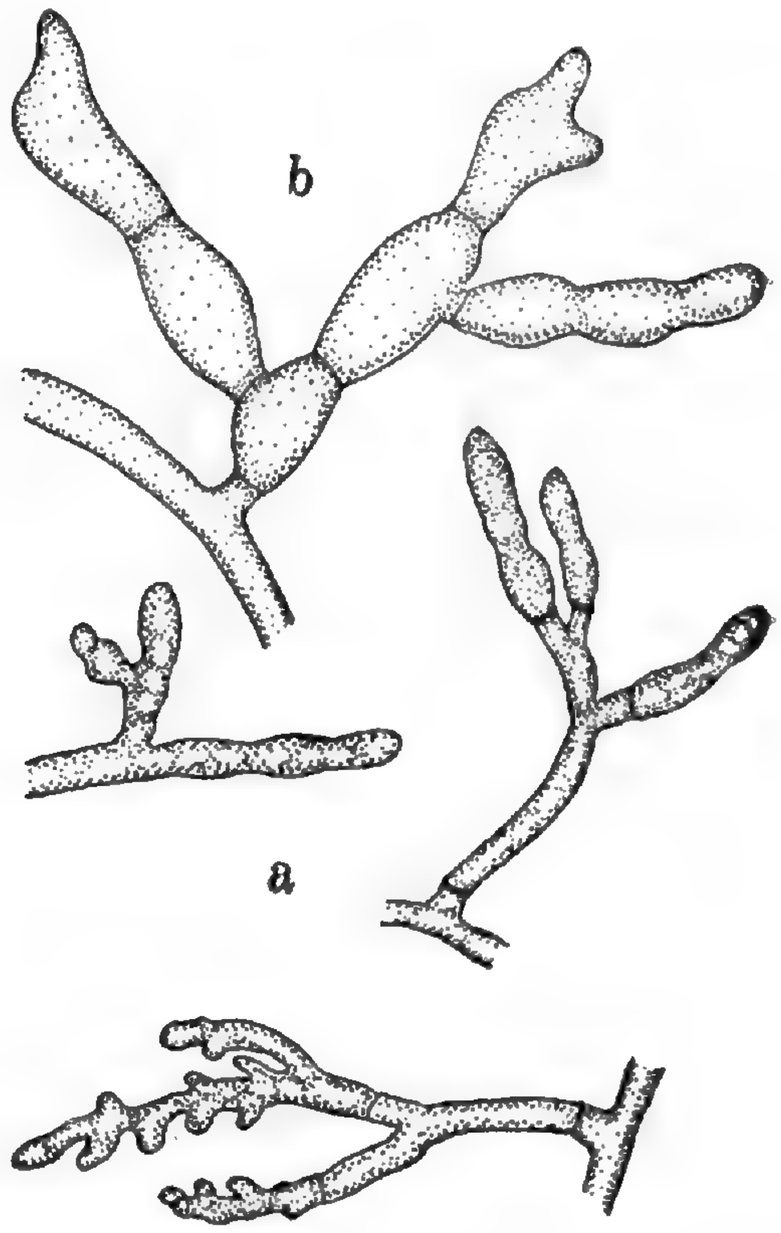

Fig. 7. *Rhizoctonia Solani:* a, young hyphae from young sclerotial tuft on lettuce; b, older cells from same source.

masses give rise to sclerotia. With maturity these hyphae become light brown in color, they break up readily into short hyphal lengths or single cells, the individuals of which bear some resemblance to conidia. However, they could not easily be mistaken for spores, although they may function as such, inasmuch as most of them may germinate within a few hours when placed under suitable conditions. I have previously described ('99) this process as follows:

"So far as observed, germination is always by the protrusion of a tube through a septum. When several cells are connected, a germ tube from one cell may pass into and through its neighbor, * * * *, and thus peculiar appearances may result. Some of the cells of the hyphal chains seem to be devoid of protoplasm, and from neighboring protoplasmic cells the germ

tubes seem to pass into such empty cells as readily as directly into the nutrient solution. When the germ tube is from 10 μ to 20 μ in length, it is invariably narrowed towards the outlet from the parent cell, and a septum forms at a short distance from this outlet."

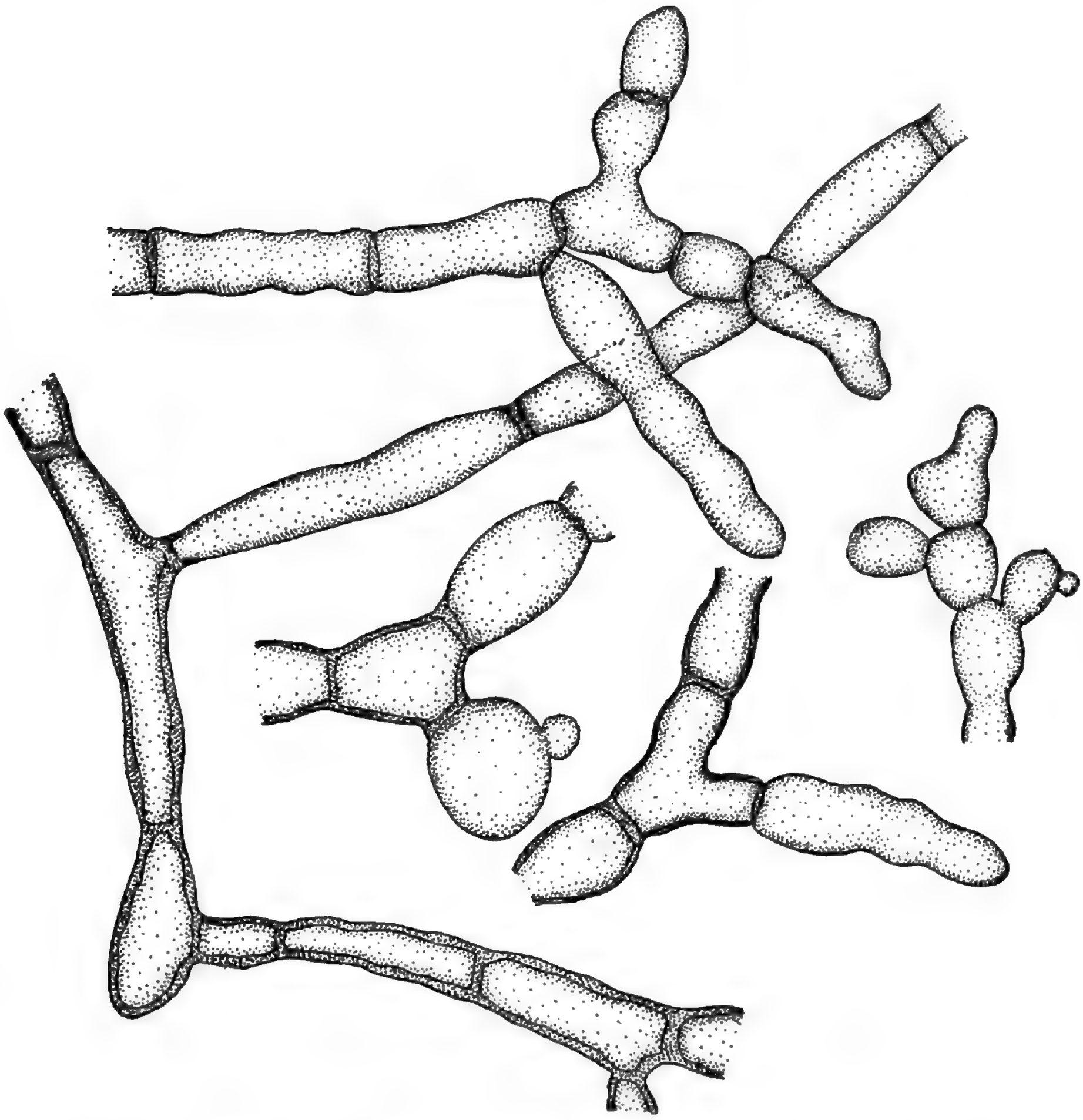

Fig. 8. ***Rhizoctonia Solani:*** **Lobulate, moniliform, and elbowed cells from tufted growth in artificial culture.**

The hyphae which penetrate the tissues remain colorless so long as they are in active growth, and while generally less in diameter they present much the same appearance as the young external hyphae. In the different strains which have been studied, originating from different hosts, certain minor modifications of the general habit of the fungus in culture have been observed. But these have not seemed to be suffi-

cient to be considered of specific importance, except in the case of the form on the rhubarb. In general, the differences referred to consist in a variable amount of the mealy or tufted growth, or of the amount of aerial growth; differences in the color of the colony are also observable; and the rapidity with which sclerotia are formed are all minor distinguishing features. The subject needs further investigation, but in general it is felt that these differences are such as might be due to permanent differences in the pathological strains, on the one hand, or may be regarded as temporary differences due to the recent environment, on the other. It may be pointed out that the appearance of the mycelium of the beet fungus from the damping off seedlings is not exactly comparable with that of the mycelium derived from the beet rot. When the organisms from both sources are grown in culture they are found to be identical. Strains do occur, however, evidence of which may persist for some time in the general appearance of the cultures.

The exact conditions under which sclerotia may occur on the various hosts affected have not been determined. It has been noted that affected potato tubers are the main seats of sclerotia formation when the fungus attacks that host. Upon this plant they are typical, and the numerous illustrations published are sufficient evidence that the appearance is much the same under a variety of conditions. Special attention may be called to the illustrations of Duggar and Stewart ('01), Rolfs ('02), Duggar ('09), McAlpine ('11), Pethybridge ('11), and Morse and Shapovalow ('14). On the majority of hosts, however, sclerotial formation is relatively rare.

From the various illustrations referred to it will be seen that the sclerotia vary in size from those so minute as to be scarcely visible, to others which may be a centimeter or two in diameter. They are generally more or less flattened, irregular, deep chestnut-brown, and generally smooth on the surface (that is, free from a looser growth of investing hyphae). Smoothness of sclerotia, which has been regarded by Kühn as of much diagnostic value, should not be considered

an important character except under natural conditions. Sclerotia which develop on fleshy organs in moist chambers as well as those which develop in culture show to a certain degree, a semi-persistent hyphal investment; but such investing hyphae are readily worn away, whereas in the violet fungus they are truly persistent.

Sections of the denser sclerotia exhibit a fairly homogeneous structure (fig. 9), with the cells more uniform in size and appearance than in *Rhizoctonia Crocorum.*

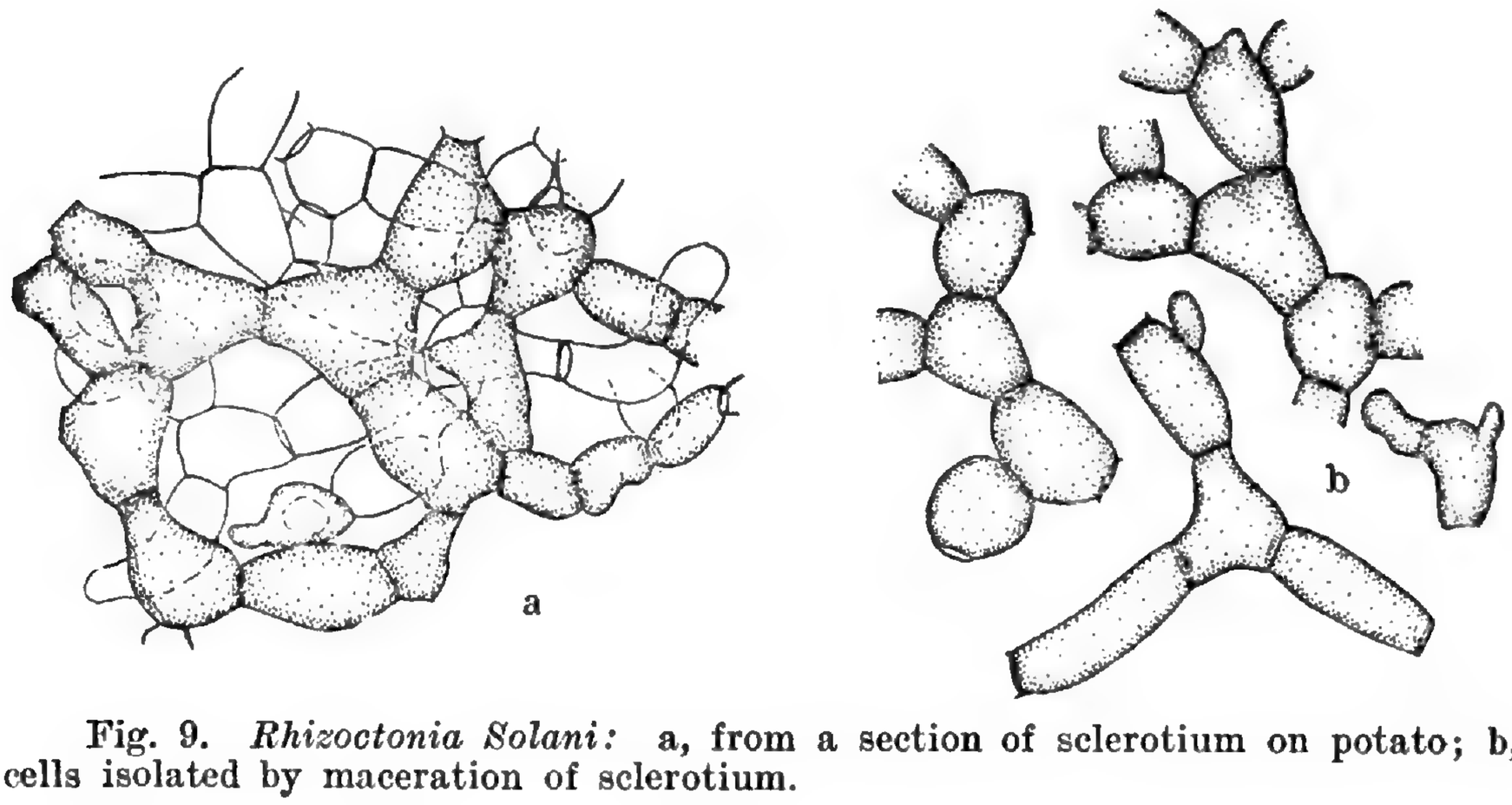

Fig. 9. *Rhizoctonia Solani:* a, from a section of sclerotium on potato; b, cells isolated by maceration of sclerotium.

THE BASIDIOSPORE STAGE, SYNONOMY, AND MATERIAL EXAMINED

Besides suggestions of a general nature no indications regarding the perfect stage of *Rhizoctonia Solani* were made prior to the discovery of the *Corticium.* Prillieux and Delacroix ('91) described *Hypochnus Solani* from potato stems, and although at this time the Rhizoctonia diseases were known in Europe no connection with this Hypochnus stage was suspected. The characteristic collar of mycelium was found surrounding the stem just above the surface of the ground, but they found nothing to indicate that the fungus had injured particularly the plant affected.

Rolfs ('03) found the collar fungus during his studies of potato diseases in Colorado. The material was determined by Prof. E. A. Burt as referable to the species *Corticium vagum* B. & C. On account of the parasitic habit, however,

it was considered advisable to make the fungus a variety of the Berkeley and Curtis species, so that it was written *Corticium vagum* B. & C. var. *Solani* Burt. Prof. Burt also recognized that it agreed closely with, and might be identical with, *Hypochnus Solani* Prill. & Del. This conclusion the writer accepts, but in view of the fact that Professor Burt is preparing a monograph of the *Thelephoraceae,* I shall not discuss this point; for the same reason I need only express doubt regarding the validity of Shaw's suggestion that *Hypochnus ochroleucus* Noack and *Corticium vagum* B. & C. are identical, although there is a certain similarity in the various stages.

Rolfs ('04) was able to germinate the basidiospores and to develop characteristic Rhizoctonia hyphae from these. Riehm ('11) also reported germinating the basidiospores and producing a characteristic Rhizoctonia mycelium together with the formation of sclerotia. Pethybridge ('15) gives a more complete account of mycelial production from spores.

The herbarium and fresh material which has been examined and found to agree with the authentic descriptions of *Rhizoctonia Solani* Kühn (*Corticium vagum* B. & C.) may be briefly enumerated:

Exsiccati: *Rhizoctonia Napaeae* nov. sp., Westendorp and Wallays, Herb. Crypt. Fasc. 5: *225.* (On decaying turnips which had been stored in a cave.)

American material: Hyphal stages on numerous hosts, many of which are mentioned in this paper, also others not included; sclerotia, on potatoes grown throughout the eastern and central United States, on potato stems (New York, 1900), on bean pods (New York, 1910), also on carnation stems, lettuce leaves, etc. Corticium stage from Prof. F. H. Rolfs, Colorado, 1901, on potato stems; from Dr. I. C. Jagger, Rochester, New York, 1914, on potato stems and on crown of carrot; from herbarium of Prof. E. A Burt, material on moist soil and decayed wood, collected by Prof. Farlow, Magnolia, Mass., 1903; from Herb. Mo. Bot. Garden, Nos. 44679, 44681, and 44682; collected by Dr. Geo. L. Peltier, Urbana, Ill., 1915.

European material: Sclerotia on potato tubers from Prof.

Sorauer, Berlin, 1900; from Prof. Magnus, Berlin, 1901; from Prof. Delacroix, Paris, 1901; and material secured on the markets of various cities, 1905–06.

As far as the writer has been able to determine, the following synonomy may be listed for *Corticium vagum* B. & C.:

Rhizoctonia Solani Kühn (1858).
Rhizoctonia Betae Eidam [non Kühn] (1887).
Rhizoctonia Napaeae West. (1846).
Rhizoctonia Rapae West. (1852).
Hypochnus Solani Prill. & Del. (1891).

PREVENTION AND CONTROL

Much the same situation confronts us regarding the prevention and control of *Rhizoctonia Solani* as in the case of *R. Crocorum.* The presence of the fungus in practically all soils serves to emphasize the importance of cultural methods including drainage and sanitation. In this case, however, since the fungus is of so much importance in the seed bed and in the greenhouse special preventive measures may be practised. Selby ('06) found that the treatment of the seed bed with formalin (1:160 to 1:200) proved satisfactory in most cases. In general, the best results have been obtained by steam sterilization, and where the facilities are at hand it is practicable to apply this to any type of greenhouse work, and, in certain cases, to seed beds outside. Liming has been recommended for the control of the disease in the field, but this has not been uniformly successful, and cultural studies have shown that the fungus is able to withstand a high percentage of alkalinity. Nevertheless, when liming results in the improvement of physical and sanitary conditions of the soil it undoubtedly assists in restraining the activity of the fungus in an indirect way, possibly by raising the resistance of the host.

Even though the fungus may be widely distributed, it is advantageous to plant clean "seed." This applies particularly to the case of the potato. The presence of the sclerotia upon the tuber makes possible the early spread of the fungus

to the young shoots. It has been positively determined that the more effective tuber treatment is the standard corrosive sublimate solution, as for potato scab. In all cases, however, it would be better to employ seed which are not infected, if this is possible.

CONCLUSIONS AND NOTES

In the account already given of *Rhizoctonia Crocorum* perhaps sufficient discussion of the occurrence and the characteristics of this form has been entered upon, except in the way of a direct comparison between this species and *R. Solani,* subsequently included. Further work upon the first named species should consider especially the culture of this organism, inoculation experiments, the development of the organism as it occurs on several hosts, the formation of sclerotia and infection cushions, and the confirmation or more definite declination of Eriksson's view that the fungus is referable to *Corticium* (*Hypochnus*). From the study of this organism thus far the following conclusions seem justified:

1. The views of L. and C. Tulasne that the forms of *Rhizoctonia* on crocus, alfalfa, and other hosts may be included in a single morphological species is confirmed.

2. The correct name of the violet root felt fungus, so long as a spore stage remains uncertain, is *Rhizoctonia Crocorum* (Pers.) DC.

3. This organism occurs throughout a considerable part of Europe and has been found in a few localities in America.

4. It attacks a variety of plants representing many families, mostly dicotyledonous.

5. The mycelium and sclerotia exhibit no important differences in equivalent stages on the different hosts, but large sclerotia which form freely in contact with crocus, and often near the affected roots of alfalfa, are seldom observed in connection with the attacks upon beets, carrots, and some other hosts.

6. The existence of distinct forms or races of this species requires further extended study.

7. The organism has not yet proved culturable with the usual laboratory methods.

8. At the present time there is insufficient evidence to determine what the perfect stage of this organism may be.

Obviously much still remains to be done regarding the physiological, pathological, and taxonomic relationship of the culturable forms which in the vegetative stage may be referred to the form-genus *Rhizoctonia*. The writer has grown in culture *Rhizoctonia* from twenty-three different American hosts, most of which are mentioned by Duggar and Stewart ('01). Most of these were grown upon a variety of culture media including prune juice, beet, and potato agar; also beans, stems and pods, celery, sugar beet and potato cylinders, and corn meal mush. With one exception (the organism from rhubarb) the cultural characteristics have been sufficiently similar, especially after protracted culture in the laboratory, to suggest a single species, with characteristics of the beet and cotton fungus, already sufficiently described (Atkinson, '92, '95; Duggar, '99). Moreover, these cultural studies have confirmed in all cases the conclusions tentatively arrived at from the preliminary microscopic examination of the fungus on the different hosts. Reasons have already been given to indicate why this species is properly *R. Solani*. It is recognized, however, that much culture and inoculation work is necessary to establish the point that the fungus on the various hosts is the same species, and to determine to what extent physiological forms may occur.

The following brief summary of conclusions may be presented with regard to *Rhizoctonia Solani:*

1. The common American species of *Rhizoctonia* is *R. Solani* Kühn.

2. This fungus is widely distributed in America and elsewhere, and would seem to occur on the potato in most regions of the world where this crop is a staple product.

3. The host plants represent many families of dicotyledons, *Asparagus Sprengeri* being the only monocotyledonous host thus far reported.

4. The types of disease induced are most diverse, damping off and root and stem rots being the most important direct effects. Secondary effects have been studied only in a few localities.

5. The mycelium and the sclerotia, as well as the general appearance on the host, readily distinguish the fungus from *Rhizoctonia Crocorum* (Pers.) DC.

6. The organism is readily culturable by the usual laboratory methods.

7. The evidence seems clear that the perfect stage of this organism is *Corticium vagum* B. & C.

It is to be regretted that the fungus causing a disease of rhubarb (Duggar and Stewart, '01) was lost before adequate study could be bestowed upon it. The fungus bore a close resemblance to *Rhizoctonia,* but the aerial hyphal cells were shorter and of greater diameter than those of *R. Solani.* No sclerotia were found on the host, and they did not develop in culture.

Shaw ('13) has contributed interesting notes on diseases of plants in India attributed to two species of *Rhizoctonia.* Unfortunately, however, he has added to the general confusion regarding this subject by a preliminary discussion which does not sufficiently designate the forms referred to, but more especially by the advancement of certain ideas regarding species which are made, apparently, without adequate study of material from other countries. The conclusions arrived at are necessarily at variance with our present knowledge of the forms of *Rhizoctonia.*

Of the organisms producing diseases in Indian crops he refers to *Rhizoctonia Solani* Kühn, a fungus which he found on jute, mulberry, cotton, groundnut, and cowpea. The mode of branching of young hyphae of his fungus is characteristic of *R. Solani,* but with this the resemblance apparently ceases. Basing an opinion wholly upon his descriptions and figures, the adult mycelium (Shaw, '13, pl. 7 and 8) differs from *R. Solani* (1) in being usually much finer; (2) in the abundant development of short "barrel-shaped" cells in the ordinary

vegetative mycelium, which would seem, from his figures, to have little in common with the chain-like, ovoidal, often branched or lobed cells (designated "barrel-shaped" by Balls) of *R. Solani* (see Atkinson, '92, '95; Balls, '05, '06; Duggar, '99; Duggar and Stewart, '01; and others); and (3) in the verrucose or warty, wall markings (Shaw, '13, pl. 8, figs. 2–3), all of which indicate some other fungus.

Again, the development of sclerotia (Shaw, '13, pl. 8, fig. 4) discloses a type of hyphal cell not characteristic of *R. Solani;* and the small discrete sclerotia themselves (Shaw, '13, pl. 2, fig. 3, pl. 8, fig. 1) convincingly indicate that another fungus was under consideration. I can find no record of a description of sclerotia resembling these in the literature of Rhizoctonia diseases. I am at a loss to understand how a fungus with such characteristics could be likened to Kühn's fungus on the potato, even though depending upon Kühn's imperfect description. On the other hand, neither in general appearance nor in structure (as described and figured by Shaw) am I able to find any resemblance to the "small sclerotia" or infection cushions of *R. Crocorum* (*R. violacea*).

In moist situations the sclerotia of *Rhizoctonia Solani* may occur on aerial organs (as on the pods of beans, Hedgcock, '04, on lettuce leaves, Stone and Smith, '00) but the frequent and apparently normal occurrence of minute sclerotia, fairly regularly arranged, on the dead tips of stems, as described by Shaw, finds no parallel in *R. Solani.* Again, in regard to the hyphae, it may be said that while there is a characteristic location of the septum when a branch is formed in a hypha of *Rhizoctonia,* this character alone is not sufficient to identify the fungus. It is necessary to take into consideration all of the mycelial characteristics which have been referred to, and if possible also the cultural characters. The writer finds that the "Rhizoctonia type" of branching is more or less similar to that found in the hyphae of certain species of *Sclerotinia, Morchella, Pleospora, Rosellinia,* and many others. It would be unwise to offer any definite suggestions regarding the fungus described by Shaw and referred to above. What relation it may bear to the fungus of "bangle blight" (Cunning-

ham, '97) must also remain, for the present, uncertain. It is possible that Shaw's fungus is one of the *Ascomycetes,* at least this is suggested by the figures of the sclerotia.

In my opinion Shaw has correctly referred to *Corticium vagum* B. & C. (accordingly to *Rhizoctonia Solani* Kühn, representing the vegetative phases of that species) another fungus which he also found in India on the groundnut and cowpea. Both the mycelium and the sclerotia of this second organism as described by him agree with *R. Solani* as we know it on carnation, beet, bean, lettuce, potato, etc., in America and elsewhere, as far as reported. The descriptions and measurements of basidia and spores are also in sufficient accord.

Shaw has even suggested that *Rhizoctonia violacea* Tul. is the vegetative stage of *Corticium vagum* B. & C. No such unfortunate confusion could result, however, had he been able to study that which is accepted as Kühn's organism on the potato together with the violet root felt fungus of Europe on any of its hosts. He has obviously failed to find material of the last named fungus in his studies thus far.

Between *Rhizoctonia Crocorum* and *R. Solani* in the vegetative condition some of the important and easily observed contrasting features as usually found are presented in the following table:

Rhizoctonia Crocorum	Rhizoctonia Solani
An external felt, or mantle, of investing hyphae, confined almost exclusively to underground organs.	External mycelium, if noticeable, only a web, or sometimes with flaky tufts, the formation of a "collar" occurring only at the time of fruiting.
Color of mycelial felt pink-red or violet to violet-brown with age.	Color of web, if evident, dirty yellow to yellow-brown.
Protoplasm of young hyphal cells soon develops a violet reddish pigment.	Young hyphal cells hyaline, and even when flavous later, pigment confined to walls.
Infection cushions conspicuous in the root-investing mycelium on most hosts.	Nothing comparable to infection cushions, though on potato sclerotia may serve as points of infection.

Sclerotia, when present, densely wooly with investing mycelium and filaments of short, ovoidal or elliptical hyphal cells. Internal structure not truly plectenchymatic, cells variable in size.	Sclerotia normally free from any definite or permanent investment of mycelium, or filaments of elbowed hyphal cells. Internal structure homogeneous in the larger, denser sclerotia.
Cultures difficult,—not yet obtained by usual methods.	Cultures readily obtained on any nutrient medium.
Typically a parasite, with perhaps the possibility of continuing existence only for a time saprophytically.	Grows rapidly saprophytically on the invaded host, and apparently on debris in the soil when conditions are favorable.

The following species may be excluded from *Rhizoctonia* as far as can be judged from reference to the descriptions and to the exsiccati material examined:

Rhizoctonia Allii Graves, de Thuemen, Myc. Univ. Fasc. 6: *600* (obviously not closely related to the forms here discussed). *R. bicolor* Ell. N. Am. Fung. Fasc. 10: *977* (with sclerotia like those of a Botrytis, e. g., *B. cinerea*). *R. Brassicarum* Lib., Libert, Pl. Crypt. Arduennae, Fasc. 3 : *240* (no characteristics of *Rhizoctonia*). *R. muscorum* Fr. Ellis, N. Am. Fung. Fasc. 13 : *1266;* Libert, Pl. Crypt. Arduennae, Fasc. 2 : *141.*

From the descriptions alone it would seem that the following species have insufficient affinities with *Rhizoctonia* to be included, but critical study of material is needed:

Rhizoctonia aurantiaca Ell. & Ev. on decaying wood of Acer; *R. Batatas* Fr. on *Ipomoea Batatas; R. placenta* Schw., and *R. radiciformis* Schw., on decaying wood (the three last mentioned are distributed in Schweinitz', Syn. N. Am. Fung., to which, however, the writer has not yet had access); *R. destruens* Tassi, reported parasitic on five species of *Delphinium,* and on *Lobelia laxiflora,* and *Hibiscus rosa-sinensis; R. moniliformis* Ell. & Ev. on branches of *Nyssa.*

Rhizoctonia Strobi Scholz ('97) on roots of *Pinus strobus* in Austria, is insufficiently described to warrant a suggestion; and *R. subepigea* Bertoni ('97) on coffee should be included in a further comparative study.

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SOME RELATIONS OF PLANTS TO DISTILLED WATER AND CERTAIN DILUTE TOXIC SOLUTIONS

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I. Introduction

In view of the extensive use of distilled water as a medium in which to grow control plants for comparative purposes in solution-culture work, there is well-grounded justification for the performance of considerable experimental work in order to determine more definitely the relations of plants to this medium. The subject is an important one, and it will require much experimentation for the ultimate solution of all phases of the problem involved. While the results herewith reported are only preliminary in their nature, the fact that they give positive indications along certain lines has been deemed sufficient warrant for their publication at this time. In addition to determining the growth relations of plants in this and other media, consideration has also been given to the effect produced by growing plants in this medium as determined by means of electrical conductivity measurements.

II. Historical Aspects of the Subject

The relation of plants to distilled water is a matter that has been under more or less serious consideration at different periods for a long time. Woodward (1699), who first employed the method of water culture in 1691–1692 in his interesting experiments, found that plants grew better in river water than in either rain water, spring water, or distilled water. The difference was of course due to the quantity of plant food contained in the medium, and this idea, coupled also with the character of the nutrients, has been the basis for a vast amount of physiological work since that time.

Coming down to more modern times, there has been a diversity of opinion among the investigators of the subject

in regard to the reason why plants and animals thrive so much better in natural water or aqueous media than in distilled water. Considering the period from about 1860 on down to the present, the most important explanations offered may be summed up under the following three heads:

1. Lack of essential nutrients;
2. The presence of deleterious substances;
3. Extraction of salts, or nutrient materials, from the organism immersed in the distilled water.

Holding each of these views there has been a formidable array of scientists at different periods, each group contending strongly to establish the correctness of its viewpoint.

Among the earlier workers in the field may be mentioned Boehm ('75), Dehérain ('78), and others, who believed that the lack of essential nutrients in the distilled water was responsible for the resulting poor condition of the organism. Boehm, for example, believed that calcium played a fundamental rôle in the metabolism of the plant, and that in its absence certain processes, notably that of starch formation, could not be carried on and that therefore deterioration resulted. He also believed that calcium was necessary for the transfer of the reserve materials from the cotyledons to the formative organs. Dehérain repeated Boehm's experiments and confirmed his results.

Owing to the fact that even distilled water, which had been unquestioningly regarded as pure, produced effects simulating toxicity, a great deal of attention has been given in the past to the chemical and other properties of water distilled from different kinds of apparatus and under various conditions. On the animal side, workers, among whom may be mentioned Kölliker ('56) and Nasse ('69), had early noticed the injurious effects on tissues when the same were placed in distilled water. Nasse, for example, found the deleterious effect of distilled water about equal to that of the following solutions: 2.5 per cent NaCl, 3.3 per cent NaBr, 3.7 per cent Na_2SO_4, and 5.0 per cent NaI.

Nägeli ('93), in his classical work published twelve years after his death, found that very minute amounts of toxic sub-

stances, notably copper, in solution produced injurious effects on organisms (*Spirogyra*), and to this phenomenon he applied the term "oligodynamik" action. This line of work was extended to include other substances and other organisms, and claimed the attention at different times of Aschoff ('90), Loew ('91), Locke ('95), Ringer ('97), Copeland and Kahlenberg ('99), Dehérain and Demoussy ('01), Lyon ('04), Bokorny ('05), Hoyt ('13), and others. It is of particular interest to note that Ringer in some of his earlier work ascribed the injury to the extraction from the organism of necessary nutrient materials; but after the publication of Locke's experiments ('95), which Ringer duplicated and confirmed, the latter concluded that the injury done in the particular case under consideration (*Tubifex*) was due to deleterious materials in the distilled water. He says: "Copper in even infinitesimal quantities will disintegrate tubifex whilst water free from copper or other heavy metals and without any salts such as calcium salts can sustain the life of tubifex."

In regard to the third idea pertaining to the effects of distilled water on organisms, early workers, both on the plant and animal side, found that salts were extracted from organisms placed in distilled water, even though their methods for determining the extraction were somewhat crude. Among the early investigators on the animal side may be mentioned Plateau ('83), Ringer and his school ('83, '84, '85, '94, '94[a], '94[b], '97), Loeb ('03), and others. The writer has another paper ready for publication in which is given a historical treatment of the subject of excretions from roots and other plant parts, so the discussion of certain phases of the plant work is reserved for that publication.

Upon the perfection and the employment of conductivity apparatus by physical chemists, it soon began to be used also by the various workers in the fields of soil, plant, and animal investigations. In this connection distilled water came in for its share of consideration. The determination of the purity of water by ascertaining its electrical conductivity speedily came into vogue, and it should be said that as far as elec-

trolytes are concerned it is a very accurate and excellent method and has deservedly come into more and more general use for this purpose in the fields of chemistry, physics, and biology.

Koeppe ('98), for instance, determined the electrical conductivity of water obtained from various sources and compared his results with those of other workers. He believed that distilled water has a deleterious effect which is partly due to a withdrawal of salts necessary to the organism, and partly to a swelling of the tissues. He was supported in his views by Oldham ('09), while Winckler ('04), Kobert ('05), and others argued in favor of the harmlessness of distilled water, especially in medical practice. Peters ('04) used the electrolytic conductivity method in his work on *Stentor* and found that there was an exosmosis of electrolytes when the organism was placed in distilled water, and he therefore concluded that the injurious effects noted were due to an extraction of salts. True and Bartlett ('12, '15, '15[a]) considered, for certain salts, not only the excretion but also the absorption of electrolytes under balanced and unbalanced conditions of the medium.

In a recent paper in which a historical discussion of the subject is also given, True ('14) concludes that over and above any injurious effects caused by deleterious substances in the distilled water there is still a "residuum of harmful action due to no known type of impurity." Because this harmful action seems to be most marked in water of least conductivity True believes that the withdrawal of electrolytes from the root tissues best accounts for the deleterious action, but that this withdrawal is "not due to the aggregate difference in osmotic pressure between the cells of the roots and the external medium." He chose lupine seedlings for his work because Frank ('88) had found them very sensitive to distilled water. Schulze ('91), however, after several years of experience with *Lupinus luteus,* claimed that distilled water produced no toxic effects upon those plants.

Both before and after the appearance of the recent contribution by True just referred to, I carried on the investi-

gations reported in this paper, which, as previously stated, are but preliminary in their nature, but which have given indications leading to the conception of an idea differing somewhat from the majority of those above mentioned regarding the relation between plants and distilled water. This conception will be briefly mentioned here, while the evidence and a further discussion will be given later; it is that pure distilled water is not harmful or injurious *per se*, but that because of the static condition forced upon them as a consequence of the absence of plant food, the growing cells become disorganized and thus become easy prey to bacterial and fungous action. Excretion of electrolytes does occur but this should be considered merely as a concomitant condition, or resulting effect of the conditions under which the plants are placed, and should not be considered as a *cause* of degeneration unless the electrolytes themselves be toxic.

III. Methods

(Germination, Culture, and Conductivity)

Canada field peas (*Pisum sativum*) and horse beans (*Vicia faba*), the small variety, were the plants selected, as both were known to be well adapted for growth in solution cultures. Of the various methods of seed sterilization tried out, the one in which the seeds were treated with 1–600 formalin-water for 15 minutes after being soaked for 24 hours in running water gave best satisfaction.

For germinating the seeds a modification of the method used by Boussingault ('74), and also by various investigators in the Bureau of Soils, was employed. This consisted in the use of ordinary enameled-ware pans about 12 inches in diameter and 3 inches in height, filled with tap water and covered with 6 × 6-mesh galvanized iron "hardware cloth," on which the previously soaked and sterilized seeds were placed. The seeds were then covered with filter paper or paper towelling which was kept moist throughout the germination process or until the radicles reached the water below. The germination was carried on in the greenhouse. In the

course of four or five days a splendid lot of vigorous, uniform seedlings which have serviceably straight radicles about 2 inches long with no laterals yet formed is obtained by this method; such seedlings are well adapted, both by their character and their accommodation to an aqueous medium, for solution-culture work. At this stage the plumules have grown to about one-half inch in length, and the plants are now ready for transfer to the culture medium, an operation which is easily and quickly done. This method of germination, which is shown in pl. 16 fig. 2, recommends itself both by reason of its simplicity and ease of operation and the certainty of securing excellent results. In the transfer process from the germinating pan to the culture medium, the entire seedling was always immersed and carefully rinsed in once-distilled and again in twice-distilled water; by this means the roots became free of any adhering impurities.

As containers for the cultures, ordinary glass tumblers were used, the sides of which were covered with black paper to prevent algal growth and the top covered with perforated paraffin paper. (For a complete description and illustration of the method see the paper by McCool, '13.) Ten plants were grown in most cases in each tumbler; exceptions to that number will be noted in each case when the series are discussed in detail. Galvanized iron wire supports were used to hold the plants upright when the seedlings had attained sufficient size to require them.

In all cases doubly distilled water was used, the second distillation being carried out in the laboratory with $KMnO_4$ added to the once-distilled water to oxidize any organic matter that might be present. Conductivity tests of this water showed it to possess a specific conductivity of 2.064×10^{-6}. The nutrient solution used was that of Pfeffer, redistilled water being the solvent for the necessary salts. Each tumbler was filled to a convenient level with either the water or the full nutrient solution as the case might be, approximately 250 cc. being required. To replace transpiration loss, doubly distilled water was added as needed.

In the early days of conductivity work on solutions,

measurements could be made only by means of a continuous current. Because of the resulting polarization effects, however, the resistance of the solution increased to such an extent as to introduce serious errors into the results. But thanks to the classical work of Kohlrausch and others, the alternating current method was devised and perfected, whereby the determinations became practically independent of polarization effects. A vast amount of work has since been done in the realm of physical chemistry on conductivity measurements, a review of which, however, is outside the scope of this paper. For a clear and concise discussion of this subject see Jones ('09), Walker ('10), or Findlay ('10).

In addition to the investigations already cited which deal with the practical applications of conductivity work, there might well be mentioned in this connection the work done by investigators in the Bureau of Soils of the U. S. Department of Agriculture: Whitney, Gardner, and Briggs ('97); Whitney and Briggs ('97); Whitney and Means ('97); and Gardner ('98). Heald ('02) used the Kohlrausch method for determining the conductivity of plant juices in order to get indications regarding the dissolved mineral substances in different parts of the plants under experimentation. Nicolosi-Roncati ('07), Bouyoucos ('12), Dixon and Atkins ('13, '13[a]) and others have also carried on conductivity determinations with different plants and under various conditions.

Sjöqvist ('95) was the first to use the conductivity method in enzyme investigations, which he did in his work on the action of pepsin on protein solutions. Similar work was done by Oker-Blom ('02), who also extended the applications of this method. Oker-Blom ('12) has recently given an account of his own and previous investigations in the field of bacteriology, wherein the electrical conductivity method was used. Various other investigators have also made use of it, among whom may be mentioned Bayliss ('07). Stiles and Jörgensen ('14) give a partial review of some of the historical aspects of this subject as it pertains to plant work.

For the conductivity work herein reported the following apparatus was used:

Wheatstone bridge (Central Scientific Co., catalogue number, 2475);
Resistance box, 11,110 ohms (Central Scientific Co., catalogue number, 2444);
Induction coil (Eimer and Amend, catalogue number, 4100);
Dry battery cells (Eimer and Amend, catalogue number, 592);
Conductivity cell, Freas (Eimer and Amend, catalogue number, 5202);
Telephone receiver (Central Scientific Co., catalogue number, 2355);
Thermometer graduated to 1/10°C;
Water tank holding 50 gallons, specially constructed for the purpose, pilot flame underneath; temperature regulated to 1/10°C;
Tiffany laboratory motor with which to operate a stirring apparatus in the tank.

In the method employed for the work the procedure given below was consistently followed: the tumblers were always filled to approximately the 250 cc. level with either the solution or redistilled water, depending on the culture. Before taking readings, doubly distilled water was added to bring the water or solution up to the original level, if the transpiration loss since the previous reading made the addition necessary. This was of course essential in order to keep the concentration factor under control. Readings in all cases were taken at 25°C. The control of temperature exactly to within 1/10°C. was comparatively easy by the use of the pilot flame underneath and the stirring apparatus in the tank of water.

For absolutely accurate and final quantitative determinations or ultimate values, as were required, for example, in the case of the standardization measurements for the cell constant with N/50 KCl, or the determination of the specific conductivity of the doubly distilled water, the greatest precautions possible were taken in regard to the conductivity cell and the concentration of its contents. But in making hundreds and even thousands of determinations, most of them as rapidly as accuracy permitted, due to the time factor involved, it was both impossible and unnecessary to dry the cell after each reading, since relative, and not absolute, values were

desired for the most part. The method employed, therefore, was to remove from the carefully stirred solution in the tumbler a 25 cc. sample with a pipette of the same capacity, the latter having previously been rinsed with the solution. Using exactly the same amount for each determination further reduced any possibility of error due to unequal dilution in the conductivity cell. Between readings the pipette was kept almost entirely immersed in redistilled water in a tall cylinder attached to a stand in the water bath. After carefully pouring the sample back into the tumbler, in case further readings were to be taken, the cell was rinsed twice with doubly distilled water and rapidly drained before taking the next reading, whether of the same or of a different culture. Any minute amount of doubly distilled water that might be present to dilute the next sample was a constant factor throughout all the readings and was of course inconsequential.

In using fresh batteries it was necessary to insert resistance coils between the battery and the induction coil in order to reduce the current. For this purpose German silver wire was used. While polarization phenomena may possibly be operative to a certain extent, such would be so small as to be practically negligible, especially in view of the fact that the effects from such a cause would be entirely relative and would therefore not affect the validity of the results.

Some of the conductivity results given in this paper are shown in tabular form and others are plotted as curves. In some instances the data are calculated as specific conductivity; in other cases the conductivity is represented by the value of x on the Wheatstone bridge. To make it clear what x actually represents, when the apparatus is set up as it was for the determinations, the following proportion is given:

$$R : R' :: x : 100—x$$

R is the resistance in ohms inserted in the resistance box; R′ is the resistance in ohms of the solution; and x is the number on the bridge wire (graduated in millimeters from 0 to 100 centimeters). As the position of x on the bridge varies with R and R′, the R for each series of curves or tables will be given (though in the great majority of cases it was 9,110),

from which R′ can then be calculated. Having these values, the specific conductivity can be calculated for any determined cell constant (the value of the cell used being .4088). For a fuller discussion see Findlay ('10).

IV. Recovery of Plants after being in Distilled Water for Varying Periods

The first question studied pertained to the recovery of plants in full nutrient solution after being kept in doubly distilled water for varying periods. To determine the comparative condition for optimum recovery, the distilled water and the full nutrient medium were renewed every four days in some cultures and left unrenewed in others, in such a way that for either condition of the medium of each set in a certain period the other medium would be both renewed and unrenewed so as to give all possible methods of combination. Examination of table 1 will make this clear. Thus, for example, with cultures 11, 12, 13, and 14 of the 10-day period in distilled water the doubly distilled water in Nos. 11 and 12 was unrenewed; but when these cultures were placed in full nutrient solution this medium was unchanged or unrenewed for No. 11 and was renewed for No. 12. The distilled water in Nos. 13 and 14 was renewed, and the full nutrient solution unrenewed and renewed respectively.

In series 1 the small variety of horse beans (*Vicia faba*) was employed, 8 plants being used to a culture. The condition of the media and duration of growth, the green weight of tops, and the dry weight of tops and roots of series 1 are given in table 1. On examining this table it is seen that even after the plants had remained for 20 days in distilled water, they recovered on being placed in the full nutrient solution, while those remaining for 10 days in distilled water produced practically as much growth when later placed in the full nutrient solution as did the plants which were in the latter medium during the entire period.

Of course, as would be expected, the cultures wherein the full nutrient solution was renewed every four days gave much better growth than did those in the unrenewed medium, due,

no doubt, to an increased amount of available nutrients. But an interesting comparison is manifest in connection with the effect of renewing the distilled water; the greater growth of both tops and roots may be noted in cultures 3 and 4, in which

TABLE I (Series 1)

EFFECT OF RENEWED VS. UNRENEWED MEDIA ON GROWTH OF HORSE BEANS

Culture no.	Length of period in dist. H_2O days	Dist. H_2O renewed or unrenewed	Length of period in full nutr. days	Full nutr. renewed or unrenewed	Green wt. of tops gms.	Dry wt. of tops gms.	Dry wt. of roots gms.
1	45	Unrenewed	.....	.....	2.15	.777	.124
2	45	Unrenewed	.....	.....	1.75	.666	.096
3	45	Renewed	.....	.....	4.40	.887	.272
4	45	Renewed	.....	.....	4.40	.870	.235
5	1	Unrenewed	44	Unrenewed	16.30	2.069	.485
6	1	Unrenewed	44	Renewed	27.00	3.069	.707
7	2	Unrenewed	43	Unrenewed	15.85	1.994	.429
8	2	Unrenewed	43	Renewed	32.51	3.543	.743
9	5	Unrenewed	40	Unrenewed	18.90	2.315	.463
10	5	Unrenewed	40	Renewed	26.25	2.895	.700
11	10	Unrenewed	35	Unrenewed	13.35	1.623	.382
12	10	Unrenewed	35	Renewed	26.35	2.928	.697
13	10	Renewed	35	Unrenewed	14.90	1.887	.463
14	10	Renewed	35	Renewed	22.90	2.376	.548
15	15	Unrenewed	30	Unrenewed	14.00	1.719	.388
16	15	Unrenewed	30	Renewed	18.05	1.880	.457
17	15	Renewed	30	Unrenewed	15.60	1.807	.417
18	15	Renewed	30	Renewed	21.20	2.403	.642
19	20	Unrenewed	25	Unrenewed	12.51	1.447	.300
20	20	Unrenewed	25	Renewed	11.40	1.247	.328
21	20	Renewed	25	Unrenewed	11.40	1.319	.284
22	20	Renewed	25	Renewed	15.50	1.670	.454
23	.....	.....	45	Unrenewed	14.60	1.975	.419
24	.....	.....	45	Unrenewed	14.70	2.044	.443
25	.....	.....	45	Renewed	27.85	2.925	.690
26	.....	.....	45	Renewed	27.05	3.025	.764

the distilled water was renewed every four days throughout the period, as compared with that of cultures 1 and 2, where the distilled water was not renewed, except, of course, for the occasional addition of water to replace the transpiration loss, which, however, was small. Furthermore, in noting the growth of cultures 11–22 inclusive, it is seen that in four of the six cases of comparison between the renewed and unrenewed distilled water, better growth of both tops and roots resulted where the distilled water was renewed. Considering cultures 1–4 and 11–22, inclusive, the total green weight of tops for the unrenewed distilled water as compared with the

renewed distilled water, and the same conditions for the dry weight of tops and roots, gave the results to be seen in table II. The total weight in all cases is therefore greater in the cultures in which the distilled water was renewed.

TABLE II (Series 1)

EFFECT OF RENEWED VS. UNRENEWED DISTILLED WATER ON GROWTH OF HORSE BEANS

(Summarized Results of Part of Table I)

Medium	Green wt. of tops in grams	Dry wt. of tops in grams	Dry wt. of roots in grams
Water renewed...	110.30	13.219	3.315
Water unrenewed	99.56	12.287	2.772

These results therefore indicate that the so-called injury to plants in distilled water cannot be entirely or even satisfactorily explained on the basis of extraction of solutes from the plant tissues. If that were the case we should have the greatest injury and least recovery in those cultures in which the distilled water was renewed, the periodically renewed water effecting *in toto* a greater exosmosis of the salts than the water which is not renewed. This statement will receive verification under the section on conductivity measurements. It would therefore seem that we must seek other explanations for the phenomena observed when plants are placed in distilled water. This phase of the subject will also be discussed later.

The points noted will be clear from an examination of pl. 13 figs. 1 and 2. Plate 13 fig. 1 shows the various stages of recovery after varying periods in the distilled water. The better growth is to be noted of both tops and roots of No. 2, in which the distilled water was renewed, as contrasted with No. 1, in which it was not renewed. It is interesting to observe how plants, even after 20 days in distilled water, will recover in full nutrient solution and then give even better growth than plants in unrenewed full nutrient solution the entire period, and that after 10 days in distilled water, plants will recover in renewed full nutrient solution and equal in

growth, plants grown the entire period in renewed full nutrient solution.

Plate 13 fig. 2 shows first (Nos. 1 and 2) the contrasted effect of renewing and not renewing the full nutrient solution. The remaining 8 cultures of the plate show the effect of renewing and of not renewing both the distilled water and the full nutrient solution. In cultures 3–10 the comparison should, of course, be made between the alternating numbers for the distilled water effect (renewed or not renewed), and between successive numbers for the effect of the renewal or the non-renewal of the full nutrient solution. While the culture represented by No. 7 of the plate gave greater growth than did No. 9, that excess was probably due to the individual hardihood of two plants. It is seen that a much more uniform and desirable growth was made by the plants of No. 9.

An interesting point in connection with the horse beans is that 16 days after setting up the series the tips of those plants still in distilled water were more or less blackened, probably as a result of enzyme (oxydase) action, and many of them were considerably inrolled. Such conditions were entirely absent from the cultures in full nutrient solution at that time. When the affected plants were later placed in full nutrient solution there was a gradual recovery from the blackening of the leaves, and this recovery was greater in the case of those cultures in which the distilled water had been renewed than in those in which it had not been renewed. Twenty days later Nos. 3 and 4 were in very much better condition than Nos. 1 and 2. There was much less blackening, some leaves not being blackened at all. The general height of the plants in Nos. 1 and 2 was $1\frac{1}{2}$–$2\frac{1}{2}$ inches; and in Nos. 3 and 4 it was $2\frac{1}{2}$–4 inches. A very noticeable feature at the end of the experiment was the condition of the medium, that of Nos. 3 and 4 being of course clear while that of Nos. 1 and 2 was milky, turbid, and opaque, indicating abundant fungous and bacterial action, a condition further emphasized by the hyphal threads and gelatinous coating on the roots.

The roots of the plants in Nos. 3 and 4 were also in much better condition at the end of the experiment than were those

of Nos. 1 and 2, especially as regards length and the amount of lateral root development. The root growth in No. 13 at the end of the experiment was also greater than that in No. 11; but in Nos. 12 and 14 it was about equal. The plants of No. 17 also showed greater root growth than did those of No. 15, and this difference was more marked than in the case of the tops. The lateral roots in No. 17 were produced all along the main roots, while in No. 15 they were practically confined to the upper or older portion of the main roots. Another interesting difference observed was that in No. 17 the main root tips were not permanently injured in the distilled water and when placed in the full nutrient solution they continued growth. This was not the case in No. 15. In general there was not much difference between the roots in Nos. 16 and 18; the plants in No. 18, however, had slightly greater growth of roots and showed less injury and some continuation of growth of the tips, whereas those in No. 16 did not. The same condition of the roots above noted for Nos. 15 and 17 held also in Nos. 19 and 21 respectively; but the difference in favor of the renewal of the distilled water though less marked was nevertheless evident. Likewise, Nos. 18 and 20 were similar to Nos. 16 and 18 respectively.

Strong evidence was therefore afforded by the cultures of horse beans that renewing the distilled water has a favorable effect upon the plants.

Series 2 is in every respect a duplicate of series 1 except that Canada field peas (*Pisum sativum*) were used instead of horse beans (*Vicia faba*), and that the dry weight of the tops was not determined; furthermore, the length of the experimental period was different. The condition of the media and duration of growth, the green weight of tops, and the dry weight of roots are given in table III, seven plants being grown in each culture. An examination of this table reveals results similar in many cases to those contained in table I; plants recovered even after 20 days in distilled water, but after 10 days in this medium the recovery was not so complete as in the case of the horse beans, for the plants so treated did not equal in growth similar ones which had remained in

full nutrient solution the entire period. However, plants which had been in distilled water only 5 days before being transferred to full nutrient solution subsequently equalled in growth other plants which had been in the latter medium from

TABLE III (Series 2)

EFFECT OF RENEWED VS. UNRENEWED MEDIA ON GROWTH OF PEAS

Culture no.	Length of period in dist. H_2O days	Dist. H_2O renewed or unrenewed	Length of period in full nutr. days	Full nutr. renewed or unrenewed	Green wt. of tops gms.	Dry wt. of roots gms.
1	47	Unrenewed	.....	.....	.80	.073
2	47	Unrenewed	.....	.....	.60	.076
3	47	Renewed	.....	.....	.45	.067
4	47	Renewed	.....	.....	1.30	.091
5	1	Unrenewed	32	Unrenewed	6.75	.400
6	1	Unrenewed	32	Renewed	11.05	.500
7	2	Unrenewed	31	Unrenewed	5.50	.401
8	2	Unrenewed	31	Renewed	12.90	.568
9	5	Unrenewed	28	Unrenewed	5.95	.263
10	5	Unrenewed	28	Renewed	12.35	.467
11	10	Unrenewed	23	Unrenewed	5.35	.254
12	10	Unrenewed	23	Renewed	7.90	.321
13	10	Renewed	23	Unrenewed	3.80	.160
14	10	Renewed	23	Renewed	6.07	.202
15	15	Unrenewed	18	Unrenewed	3.30	.144
16	15	Unrenewed	18	Renewed	4.40	.175
17	15	Renewed	18	Unrenewed	4.30	.162
18	15	Renewed	18	Renewed	4.15	.169
19	20	Unrenewed	13	Unrenewed	3.21	.124
20	20	Unrenewed	13	Renewed	2.52	.092
21	20	Renewed	13	Unrenewed	4.05	.139
22	20	Renewed	13	Renewed	4.43	.141
23	.....	.....	33	Unrenewed	5.50	.368
24	.....	.....	33	Unrenewed	6.94	.420
25	.....	.....	33	Renewed	9.60	.536
26	.....	.....	33	Renewed	13.45	.611

the start. The period between 5 and 10 days in distilled water is therefore a critical one, and will be discussed later in other connections.

Renewing the full nutrient solution again showed beneficial results, as might be expected. But the renewal of the distilled water did not produce such striking results in some respects as in the case of the horse beans; in other ways, however, the results were equally or even more striking. Where the plants remained in distilled water for 47 days the growth was better in one case and poorer in the other where the distilled water was renewed than where it was not renewed. The average

growth, however, of the two cultures in the renewed medium was better than that of the two in the unrenewed distilled water.

In Nos. 11–22, there was better growth of tops and roots

TABLE IV (Series 2)

EFFECT OF RENEWED VS. UNRENEWED DISTILLED WATER ON GROWTH OF PEAS

(Summarized Results of Part of Table III)

Medium	Green wt. of tops in grams	Dry wt. of roots in grams
Distilled water renewed. . .	28.55	1.131
Distilled water unrenewed.	28.08	1.259

in four cases where the distilled water was renewed and better growth in four cases where it was not renewed. Considering cultures 1–4 and 11–22 the results given in table IV were obtained, from which it is again evident that renewing the distilled water exercises no injurious influence, and the conclusion is reinforced that an exosmosis of mineral nutrients is not the fundamental basis of the injury which plants suffer in distilled water. Furthermore, the difference between the renewed and the unrenewed distilled water cultures was very marked if the plants remained for 20 days in distilled water before being changed to the full nutrient solution, the difference being greatly in favor of the cultures in which the medium was renewed.

Figures 1 and 2 of pl. 14 illustrate the points above mentioned. In pl. 14 fig. 2 should be noted the better growth of Nos. 9 and 10—which were in renewed distilled water for 20 days before transfer to full nutrient solution—as compared with Nos. 7 and 8, which had remained in unrenewed distilled water for the same length of time before transfer. The excess of growth in No. 4 over that in No. 6 is probably to be accounted for on the ground that since those cultures were in distilled water but 10 days neither the renewal nor the unrenewal of the medium exercised much effect. Hence the greater growth of No. 4 represents an individual variation.

At the expiration of the experimental period the following conditions prevailed in series 2: while the top growth in

cultures 1–4 was about the same in each case, the root growth in Nos. 3 and 4 was much better than that in Nos. 1 and 2, the roots of the former being whiter, cleaner, and having longer and more numerous lateral roots. In the case of those cultures grown in distilled water 10 days before removal to full nutrient solution, Nos. 11 and 12 were in somewhat better condition than Nos. 13 and 14, a difference which might readily be expected for the shorter periods in distilled water due to individual variation. After 15 days in distilled water and 18 days in full nutrient solution the benefits derived from renewing the former were markedly evident in the appearance of cultures 15–18, even though the actual weights did not show such difference. Nos. 17 and 18 were in better condition than Nos. 15 and 16 respectively, especially as regards the root growth; similarly, Nos. 21 and 22 were in better condition than Nos. 19 and 20 respectively.

Some special conditions which are of particular interest were observed when the cultures were examined carefully at the close of the experiment. The first point pertains to the method of recovery. After being in the distilled water only one or two days the top growth of such cultures when placed in full nutrient solution proceeds unhindered from the tips of the main stems, i. e., the tips of the stems remain uninjured and resume growth. But 5 days in distilled water almost marks the limit at which growth can be resumed at the tip of the main axis of the stem when such cultures are subsequently placed in full nutrient solution. After 10 days in distilled water the tips of the stems become injured so that the later growth in full nutrient solution is made from new lateral branches. Hence the period from 5 to 10 days in distilled water before removal to full nutrient solution may be considered a crucial period as regards the recovery and growth of the main stems.

Another point of interest is the delayed maturity which results in the case of the cultures which are grown for some time in distilled water and later are placed in full nutrient solution. Such plants remain in a green and growing condition much longer than do those which have been in full

nutrient solution for the entire period, or those which remained in distilled water for a shorter period before being transferred to the full nutrient solution. The growing season of the former is thus prolonged and the date of maturity delayed.

The foregoing series having given evidence of the recovery of plants in full nutrient solution after being in distilled water for 20 days, the question arose as to the maximum length of time plants might remain in distilled water without preventing recovery when subsequently transferred to full nutrient solution. Series 3 was therefore set up. This consisted of cultures of Canada field peas grown in distilled water for 10, 20, 30, 40, and 50-day periods before transfer to the full nutrient medium. The condition of the media and duration in each and also the results of the series (as shown by the green weight of tops) are given in table v, Nos. 1–20 inclusive. Renewals in this series also were made every four days. Nos. 21–28 under different conditions and concentration of nutrient solution are given for purposes of comparison. The maximum time limit in distilled water above referred to is thus seen to be approximately 30 days, and this was practically attained only in case of the cultures in renewed distilled water. After 40 days in distilled water, whether renewed or unrenewed, the recovery was almost nil, though somewhat better in the renewed, while after 50 days in either renewed or unrenewed distilled water all the cultures were dead.

In the 10 cases furnishing comparisons between cultures in which the full nutrient solution was preceded on the one hand by renewed and on the other by unrenewed distilled water, greater growth was attained in 7 cases where the distilled water was renewed. The total weight of green tops is more nearly equal in the two sets of cultures, however, being 24.20 grams in the case of those in the unrenewed and 22.38 grams in the case of those in the renewed distilled water. We thus see that no injurious effects attend the renewal of the distilled water when compared with the non-renewal of the same; on the other hand, positive benefits are derived from such a

renewal, especially in the case of plants approaching the maximum time limit of durability in distilled water—a period which enables the results of the two conditions to be more readily seen and compared.

TABLE V (Series 3)

GROWTH OF PEAS IN RENEWED AND UNRENEWED MEDIA FOR VARIOUS PERIODS UP TO THE MAXIMUM TIME FOR SURVIVAL. ALSO EFFECT OF ADDING WATER AT DIFFERENT INTERVALS TO MEDIA UNDER VARIOUS CONDITIONS

Culture no.	Length of period in dist. H_2O days	Dist. H_2O renewed or unrenewed	Length of period in full nutr. days	Full nutr. renewed or unrenewed	Green wt. of tops gms.
1	10	Unrenewed	42	Unrenewed	4.50
2	10	Unrenewed	42	Renewed	8.00
3	10	Renewed	42	Unrenewed	4.85
4	10	Renewed	42	Renewed	6.30
5	20	Unrenewed	32	Unrenewed	2.70
6	20	Unrenewed	32	Renewed	5.05
7	20	Renewed	32	Unrenewed	3.55
8	20	Renewed	32	Renewed	1.40
9	30	Unrenewed	22	Unrenewed	.55
10	30	Unrenewed	22	Renewed	1.30
11	30	Renewed	22	Unrenewed	1.90
12	30	Renewed	22	Renewed	1.90
13	40	Unrenewed	12	Unrenewed	.50
14	40	Unrenewed	12	Renewed	.55
15	40	Renewed	12	Unrenewed	.65
16	40	Renewed	12	Renewed	.72
17	52	Unrenewed	.....	.....	.60
18	52	Unrenewed	.....	.....	.45
19	52	Renewed	.....	.....	.56
20	52	Renewed	.....	.....	.55
21	Unrenewed full nutr. 42 days, dist. H_2O added every 8 days				6.40
22	Unrenewed full nutr. 42 days, dist. H_2O added every 4 days				6.00
23	Renewed full nutr. 42 days, the sol'n. renewed every 8 days				8.75
24	Renewed full nutr. 42 days, the sol'n. renewed every 4 days				18.50
25	Unrenewed 1/10 full nutr. 42 days, dist. H_2O added every 4 d'ys				2.90
26	Unrenewed 1/5 full nutr. 42 days, dist. H_2O added every 8 days				2.95
27	Renewed 1/10 full nutr. 42 days, sol'n. renewed every 4 days				10.10
28	Renewed 1/5 full nutr. 42 days, sol'n. renewed every 8 days				7.85

In pl. 15 fig. 1 some of the cultures are illustrated, the ones of special interest being Nos. 9–14. The exceptionally small or irregular growth of No. 8 is difficult to account for, because in the renewed full nutrient it should be greater than that of No. 7. Individual resistance is apparent, however.

V. Recovery of Plants after being in Toxic Solutions

Having thus ascertained the maximum time plants may remain in distilled water and then recover on being placed in full nutrient solution, we may turn our attention to toxic solutions. If distilled water in itself is toxic then it should be interesting to get quantitative data on its effects as measured by the power of plants so treated to recover. This power should furnish a good index regarding the extent of any injury suffered. By comparing the ultimate time limits for various media after which recovery in full nutrient solution is possible, we are able to get a basis on which to determine the relative toxicity of each medium. Almost simultaneously with series 3, series 4 was set up. The plan of the series and the green weight of tops and dry weight of roots of the plants in series 4 are given in table VI, while pl. 15 fig. 2 shows the actual condition of the plants in some of the media. The results obtained indicate the following relative toxicities of the substances used, the time expressed in days having reference to the longest period in the toxic solution after which recovery is possible:

Redistilled water	30–40 days
N/100 $MgCl_2$	4–8 days
N/1000 $MgCl_2$	about 20 days
N/1000 $CaCl_2$ & N/20 $MgCl_2$	about 16 days
N/12800 H_2SO_4	about 20 days
N/400 KOH	about 20 days

We thus see that as compared with the toxic solutions mentioned distilled water, if it be considered as a toxic agent at all, is much less so than either of the others given above. In this connection it is interesting to note that Kahlenberg and True ('96) found that N/12800 H_2SO_4 and N/400 KOH were approximately the critical concentrations for Lupinus roots. Hence, the fact that plants can remain much longer in distilled water than in these solutions and still recover would seem to indicate that as regards toxicity distilled water is only very slightly if at all deleterious. But the writer believes that it is entirely incorrect and misleading to speak of distilled water as being toxic. What is illustrated above for distilled water is not toxicity, therefore, but merely the length of time

TABLE VI (Series 4)

EFFECT ON GROWTH OF PLANTS OF VARIOUS PERIODS IN TOXIC SOLUTIONS

Culture no.	First sol'n. or medium	Length of period in first medium days	First medium renewed or unrenewed	Length of period in full nutr. days	Green wt. of tops gms.	Dry wt. of roots gms.
1	Dist. H_2O	32	Unrenewed		1.15	.116
2	Dist. H_2O	32	Renewed		1.55	.130
3	N/100 $MgCl_2$	32	Unrenewed		.35	.012
4	N/100 $MgCl_2$	32	Renewed		.40	.016
5	N/100 $MgCl_2$	1	Unrenewed	31	10.15	.428
6	N/100 $MgCl_2$	2	Unrenewed	30	8.40	.372
7	N/100 $MgCl_2$	4	Unrenewed	28	5.15	.132
8	N/100 $MgCl_2$	8	Unrenewed	24	.35	.018
9	N/100 $MgCl_2$	12	Unrenewed	20	.30	.020
10	N/100 $MgCl_2$	16	Unrenewed	16	.40	.016
11	N/100 $MgCl_2$	20	Unrenewed	12	.28	.012
12	N/1000 $MgCl_2$	32	Unrenewed		1.00	.085
13	N/1000 $MgCl_2$	32	Renewed		1.00	.038
14	N/1000 $MgCl_2$	2	Unrenewed	30	8.85	.385
15	N/1000 $MgCl_2$	4	Unrenewed	28	9.70	.384
16	N/1000 $MgCl_2$	8	Unrenewed	24	7.20	.305
17	N/1000 $MgCl_2$	12	Unrenewed	20	5.15	.192
18	N/1000 $MgCl_2$	16	Unrenewed	16	2.05	.121
19	N/1000 $MgCl_2$	20	Unrenewed	12	1.05	.093
20	N/1000 $CaCl_2$ and N/20 $MgCl_2$	32	Unrenewed		.75	.092
21	N/1000 $CaCl_2$ and N/20 $MgCl_2$	32	Renewed		.85	.099
22	N/1000 $CaCl_2$ and N/20 $MgCl_2$	1	Unrenewed	31	10.60	.409
23	N/1000 $CaCl_2$ and N/20 $MgCl_2$	2	Unrenewed	30	9.35	.388
24	N/1000 $CaCl_2$ and N/20 $MgCl_2$	4	Unrenewed	28	10.35	.384
25	N/1000 $CaCl_2$ and N/20 $MgCl_2$	8	Unrenewed	24	8.40	.294
26	N/1000 $CaCl_2$ and N/20 $MgCl_2$	12	Unrenewed	20	3.00	.144
27	N/1000 $CaCl_2$ and N/20 $MgCl_2$	16	Unrenewed	16	1.50	.117
28	N/1000 $CaCl_2$ and N/20 $MgCl_2$	20	Unrenewed	12	.75	.103
29	Full nutr. sol'n.	32	Unrenewed	32	8.95	.411
30	Full nutr. sol'n.	32	Renewed	32	18.50	.530
31	N/12800 H_2SO_4	32	Unrenewed		1.55	.130
32	N/12800 H_2SO_4	32	Renewed		1.25	.124
33	N/12800 H_2SO_4	2	Unrenewed	30	7.05	.318
34	N/12800 H_2SO_4	8	Unrenewed	24	7.45	.289
35	N/12800 H_2SO_4	16	Unrenewed	16	4.40	.236
36	N/12800 H_2SO_4	20	Unrenewed	12	1.95	.172
37	N/400 KOH	32	Unrenewed		1.25	.094
38	N/400 KOH	32	Renewed		1.50	.108
39	N/400 KOH	2	Unrenewed	30	8.60	.444
40	N/400 KOH	8	Unrenewed	24	6.60	.214
41	N/400 KOH	16	Unrenewed	16	2.55	.092
42	N/400 KOH	20	Unrenewed	12	2.60	.117

plants can survive in a medium without nutrient materials. That these plants could not survive for that length of time in the other media, however, shows that in those cases a real toxicity enters into consideration.

In addition to the actual time limits for recovery just tabulated, as well as the method of recovery and delayed maturity mentioned in the preceding section, another interesting point, which was very noticeable in the cultures and which can also be seen in the plates, is the character of growth of the rootlets in the boundary cultures, by which is meant those cultures which have remained in the inimical media nearly as long as their endurance would permit, and whose recovery in full nutrient solution is slower or more difficult than the normal unaffected plants. In the latter case the roots are short and compact and usually extend down only to about one-half the distance to the bottom of the tumbler. In the case of the first mentioned cultures, however, when transferred to full nutrient solution the rootlets develop a long, slender growth easily extending to the bottom of the tumbler.

VI. Effect of Sterilizing the Water During Growth of Plants

The foregoing series pointed, therefore, to factors other than extraction or loss of solute from the plant tissue as being responsible for the deteriorating phenomenon observed when growing plants are placed in distilled water. In the unrenewed water cultures in the previous series a brownish coloration developed and the roots appeared, in their gelatinized condition, to be covered by bacterial and fungous growths. Suspecting that these organisms played an important rôle, it was decided to grow additional cultures to test this point. Four cultures, each containing ten plants of *Pisum sativum*, were set up in distilled water: in one the medium was not renewed; in a second the water was renewed every four days; and in the remaining two the medium was sterilized every four days by boiling in a return condenser one-half hour. The results are given in table VII (series 5) and the cultures are shown in pl. 16 fig. 1. The full nutrient solution cultures

were grown for purposes of comparison. The duration of growth was 30 days.

Whether the beneficial effect of the sterilization was due to the destruction of the bacterial and fungous floras of the

TABLE VII (Series 5)

EFFECT PRODUCED ON GROWTH OF PLANTS BY STERILIZING THE WATER IN WHICH THEY ARE GROWN

Culture no.	Medium	Condition of medium	Green wt. of tops gms.	Dry wt. of roots gms.
1	Dist. H_2O	Unrenewed	1.55	.141
2	Dist. H_2O	Renewed	1.65	.150
3	Dist. H_2O	Sterilized	2.40	.225
4	Dist. H_2O	Sterilized	3.05	.233
5	Full nutr.	Unrenewed	10.30	.342
6	Full nutr.	Renewed	17.65	.507

medium, to a decomposition of any contained toxic substances (thereby rendering them less toxic), or to incidental effects such as aëration of the water by the boiling process, was not definitely determined. Neither was this effect compared with that produced by the addition of various bodies (tannic acid, pyrogallol, calcium carbonate, various hydrates, carbon black, and other substances mentioned by Livingston and his co-workers, '05, '07, Dachnowski, '08, '09, and others). In the last paper of Livingston and his co-workers referred to are given the results of boiling the aqueous extracts from soils containing toxic properties as determined by the growth of plants in the same. The boiling improved the extracts, but this effect was explained by "supposing the process of boiling to remove or change the toxic action of this extract, the toxic materials being perhaps partly volatile with steam." But since in our sterilization process a return condenser was used the removal of toxic substances by volatilization would not occur. A breaking down of toxic compounds into less toxic constituents may possibly be a condition induced by the boiling, however. It will be recalled that Lyon ('04) found the toxicity of tap water reduced by boiling.

While the oxidizing power of roots, due to enzymatic activity, may be an important factor in aiding in the decom-

position of vegetable matter in the soil, as pointed out by Schreiner and Reed ('07) and others, it is not believed that in the case under consideration the oxidizing power of the roots was altered to any appreciable degree by the boiling of the medium. Dachnowski ('12) mentions the effect of oxidation upon the toxic substances found in bog water. In the sterilization method by boiling under a return condenser, however, the aëration or oxidation phenomenon would no doubt play only a subsidiary rôle. The stronger line of evidence seems to favor the destruction of injurious bacterial and fungous agencies as the chief factor in the beneficial effect of the sterilization.

VII. Conductivity Measurements

The excellence of the electrical conductivity method for determining any change in the electrolyte content of an aqueous medium naturally led to its adoption for the experimental work described below. This phase of the investigation was especially concerned with determinations pertaining to the extraction of electrolytes — including the essential nutrient salts—from the roots of plants in distilled water. The generally beneficial results attendant upon a frequent renewal of the distilled water in which the plants were placed has already been noted, as well as the evidence in favor of the view that conditions other than extraction of essential salts constitute the underlying cause of the deterioration of plants in distilled water.

The next point to be determined was the relative amount of the total exosmosis in the renewed distilled water as compared with that in the unrenewed. In placing roots in distilled water it is pertinent to this subject to inquire whether all the exosmosis occurs during the first four days. If it does, we should have the same amount of extraction in both the unrenewed water and that renewed every four days. Or is there a renewal of the exosmosis of the electrolytes following the renewal of the water each time, thereby giving rise to a greater exosmosis than in the cultures in which the water was not renewed? If such a condition obtains and yet in

spite of it the renewal of the water shows no baneful effects, or indeed produces beneficial results, then may we well conclude, and with increasing assurance, that extraction of nutrient salts is in no way responsible for any injury plants undergo in distilled water. The results obtained strongly substantiate that conclusion.

A series of cultures (series 6) was set up in which healthy plants of Canada field peas were grown in full nutrient solution for about three weeks and then transferred, after carefully rinsing the roots, to doubly distilled water. In half of the cultures the distilled water was renewed at certain definite intervals for each culture, while in the other half of the cultures the water was not renewed. Conductivity determinations were then made of the water under both conditions—renewal and non-renewal—at certain regular intervals, varying for each set of cultures, for several days after the plants had been placed in this medium.

By numerous readings it was ascertained that with a resistance of 9,110 ohms in the resistance box the average value of x on the Wheatstone bridge for the water in the vessel after being rinsed and before placing the roots therein was approximately 6.0, rarely varying 1 cm. either way. Considering that figure, then, as the basis or the starting point for the exosmosis, and subtracting it from the different values found for the renewed, and from only the final value obtained for the unrenewed distilled water, we get the figures in the last column of table VIII.

The plan of the experiment with respect to renewal of the distilled water and the time of readings, the values of the individual readings, and the comparative amounts which represent the total exosmosis of the electrolytes under the various conditions of the experiment are all given in table VIII. The numbers given are the values of x on the Wheatstone bridge when the resistance inserted in the box was 9,110 ohms.

It is thus seen that by far the greater exosmosis was obtained in the case of those cultures in which the distilled water was renewed. Another point of interest was the reabsorp-

tion of electrolytes—as seen by the decrease in conductivity of the medium—in those cultures in which the distilled water was not renewed. The reabsorption of electrolytes has been observed to be a phenomenon characteristic of normal, healthy

TABLE VIII (Series 6)

COMPARATIVE EXOSMOSIS IN RENEWED AND UNRENEWED DISTILLED WATER

Culture no.	Water renewal	Conductivity Readings								Duration of treatment days	Total increase in conductivity
		Frequency	1st	2nd	3rd	4th	5th	6th	7th		
1	Every day	Every day	32.9	10.4	10.0	8.9	9.7	9.4	10.2	7	49.5
2	None	Every day	36.3	22.8	21.4	17.8	15.2	12.5	11.4	7	5.4
3	Every 2 days	Every 2 days	10.8	9.3	9.6	10.7	....	....	....	8	16.4
4	None	Every 2 days	25.0	14.3	13.6	11.0	....	....	....	8	5.0
5	Every 4 days	Every 4 days	12.9	15.0	16.1	16.1	....	....	....	16	36.1
6	None	Every 4 days	10.7	12.4	15.9	19.5	....	....	....	16	13.5

peas, when transferred from a full nutrient solution to distilled water, after being in the latter medium one or two days.

In order to obtain some additional information regarding the relations between the conductivity of the medium and the plants grown therein, series 7 containing 50 cultures was set up in full nutrient solution, ten Canada field pea plants to each culture. The nutrient solution was not renewed. At the end of each five-day period 5 of the cultures were taken down, the green weight of tops of the plants in each determined, and the conductivity of the solution measured; and from these results the average green weight of tops and the average conductivity of each set of 5 cultures were obtained. This was done throughout the entire period of 50 days. The results obtained are given in table IX and plotted as curves in fig. 1. In the latter the abscissa represents days, and the ordinate both specific conductivity and green weight of tops. The values given for conductivity should be multiplied by 10^{-5}

in order to get the specific conductivity values. In the case of the weights the numbers in the margin represent ten times the actual weight in grams, e.g., 40 in the margin = 4.0 grams.

From the results it is seen that both the increase in green

TABLE IX (Series 7)

GROWTH OF PLANTS AND CONDUCTIVITY OF FULL NUTRIENT MEDIUM FOR 50 DAYS

Cultures nos.	Length of period in full nutrient days	Av. green wt. of tops in each culture grams	Specific conductivity* at end of period		
			Minimum	Average	Maximum
1– 5	5	3.81	93.22	96.25	98.19
6–10	10	8.12	57.47	61.03	66.93
11–15	15	9.47	32.38	34.83	37.59
16–20	20	8.66	24.38	32.68	46.05
21–25	25	8.69	15.73	18.19	21.69
26–30	30	8.00	13.74	20.63	30.28
31–35	35	7.10	10.02	15.98	21.23
36–40	40	6.77	11.16	14.23	16.19
41–45	46	6.09	6.88	11.44	22.51
46–50	50	5.01	13.00	16.97	28.11

* The numbers in the three columns are to be multiplied by 10^{-5} in order to arrive at the specific conductivity values.

weight of tops and decrease in conductivity of the medium are most rapid and pronounced during the first 15 days. After that period both the green weight and the conductivity gradually decline, but the latter more slowly than the former. While the curves of the minimum, average, and maximum conductivity remain very close together during the first 15 days, they become more divergent after that time. The green-weight curve shows a gradual decline as the age of the plant increases, after a certain period, due to the drying of the tops and consequent loss of water. Different curves would, of course, have been obtained had the nutrient solution been renewed.

In table x and fig. 2 are seen the results of series 8, a similar experiment with distilled water, the same units being used as in the previous case. The green weight of tops increased during the first 10 days and then gradually declined to the end of the experiment. The conductivity of the water was practically the same on the 10th as it had been on the 5th day. Evidence from other experiments, however, indicates

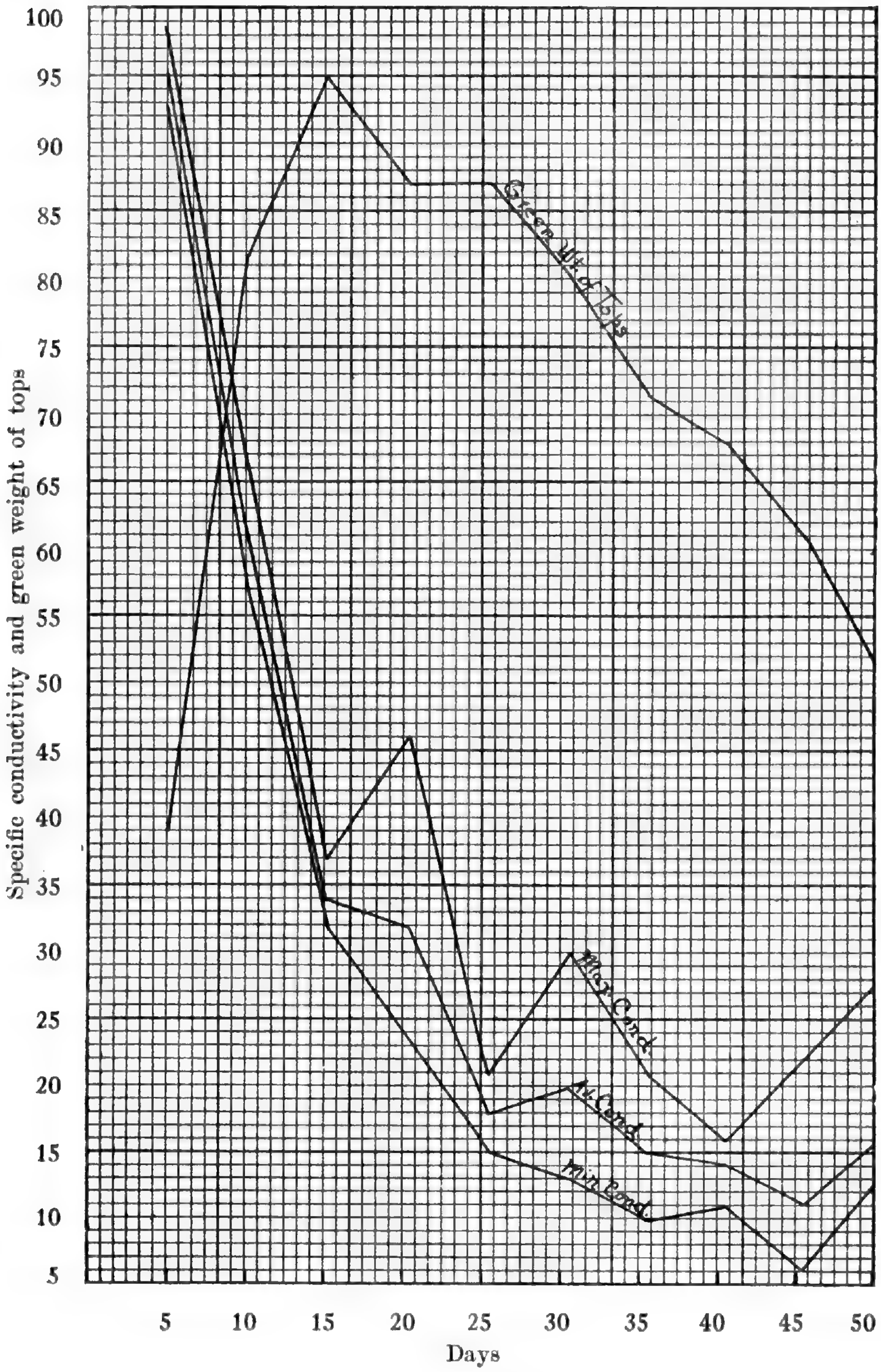

Fig. 1. The conductivity and growth curves for the full nutrient solution (Pfeffer's) in which plants were grown 50 days, the medium being unrenewed. (For complete explanation see the text.)

that in the interim the curve might have risen and fallen. After the 10th day the curve inclined with fluctuations. Here again are seen evidences that the 10-day period for seedlings in the distilled water may properly be considered a crucial one for the plants. After that time the growth declines and the conductivity increases markedly.

Suspecting that the question of injury to plants in distilled

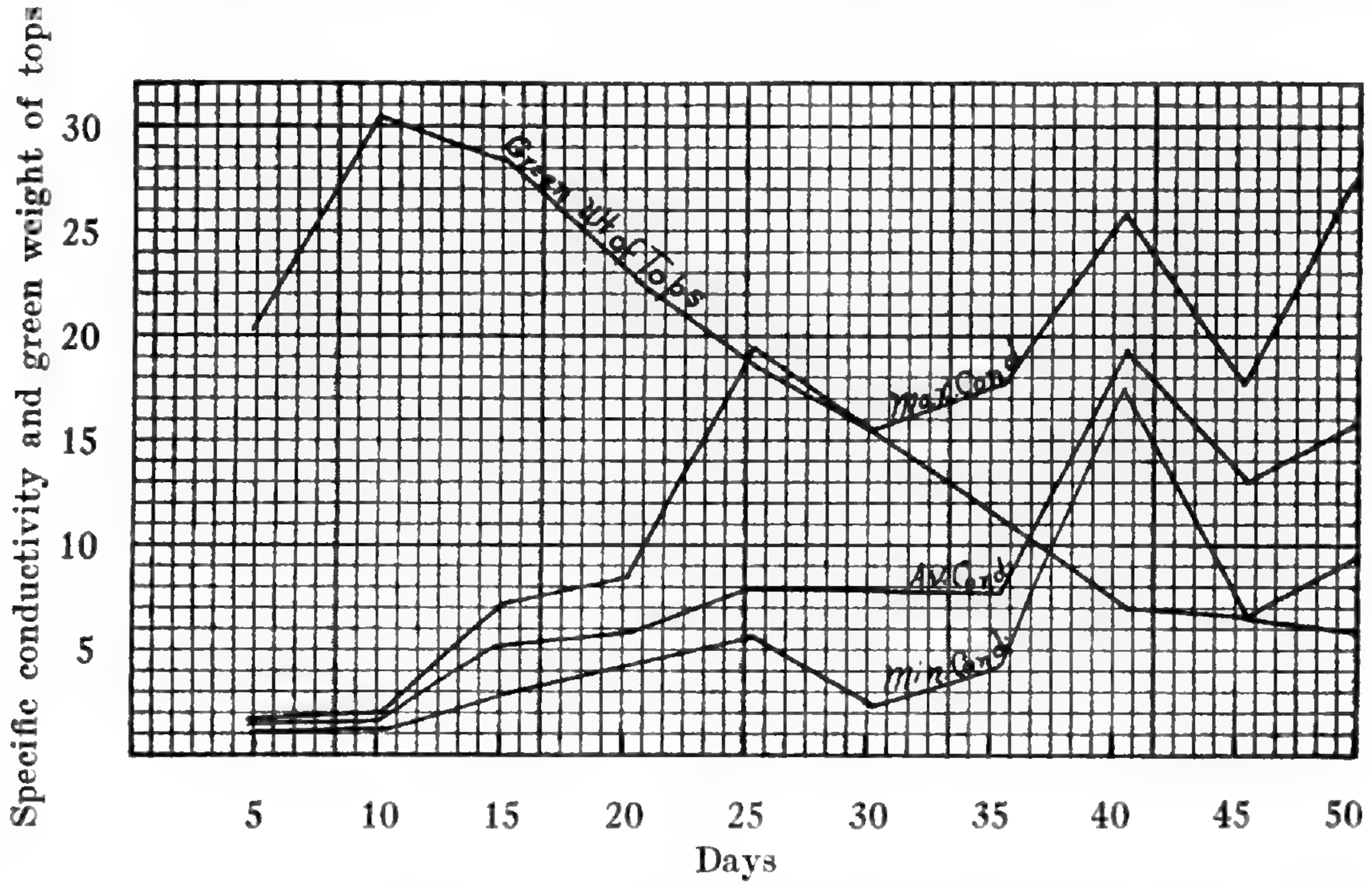

Fig. 2. The conductivity and growth curves for the unrenewed redistilled water in which pea seedlings were grown for 50 days. (For complete explanation see the text.)

water might be intimately bound up with that of lack of reserve food materials, the writer carried out an experiment bearing upon this matter. The experiment consisted, first, in placing some Canada field pea seedlings directly into redistilled water and determining the specific conductivity of the water at intervals for 20 days; and, next, in transferring some pea plants which had been grown in full nutrient solution for 1, 5, 10, 20, 30, and 40 days respectively to redistilled water, and determining the specific conductivity of the water at intervals for 20 days. The results are plotted as curves in fig. 3, the conductivity values being represented in terms of x on the Wheatstone bridge with a resistance of 9,110 ohms in the box. Four cultures of 10 plants each (except in the case

of the 20-day period in full nutrient solution in which 12 cultures were used) were grown under each of the specified conditions, and the curves represent the averages for the 4 (or 12) cultures under each condition. To determine how much

TABLE X (Series 8)

GROWTH OF PLANTS AND CONDUCTIVITY OF DISTILLED WATER MEDIUM FOR 50 DAYS

Cultures nos.	Length of period in dist. water days	Av. green wt. of tops grams	Specific conductivity* at end of period		
			Minimum	Average	Maximum
1– 5	5	2.04	1.46	1.54	1.66
6–10	10	3.07	1.01	1.34	1.81
11–15	15	2.89	3.04	5.43	7.41
16–20	20	2.34	4.34	5.92	8.63
21–25	25	1.89	5.66	8.15	19.77
26–30	30	1.55	2.60	8.26	15.82
31–35	35	1.15	4.43	7.80	17.95
36–40	40	.72	17.62	19.51	26.04
41–45	45	.68	6.87	13.32	17.95
46–50	50	.60	10.51	16.48	29.00

* The numbers in the three columns are to be multiplied by 10^{-5} in order to arrive at the specific conductivity values.

increase in conductivity was contributed by the glass tumblers in which the cultures were grown, 4 such containers filled only with redistilled water, and containing no plants, were used and the conductivity of the water determined at intervals for 20 days. It is seen that from the seedlings which had not been in full nutrient solution at all (Nos. 5–8) the highest conductivity resulted, while from those which were in the full nutrient solution longest before being placed in the distilled water (Nos. 37–40 and 33–36), the lowest conductivity was found at the end of 20 days. The other cultures at the end of 20 days were midway between the two extremes. It is also seen that, whereas the conductivity curve for Nos. 5–8 shows very little tendency to decline in the early stages, the curves for the cultures which had first been in full nutrient solution show that tendency to a considerable extent. And that tendency, as we have previously remarked, is a characteristic feature of normal plants transferred from full nutrient solution to distilled water.

Attention should be called to the difference in the character of the conductivity curves in fig. 2 and that of 5–8 in fig. 3. It

will be noted that both represent the conductivity curve of distilled water containing the roots of seedling peas. The difference mentioned no doubt finds its explanation in the different conditions under which the two series were grown (the series

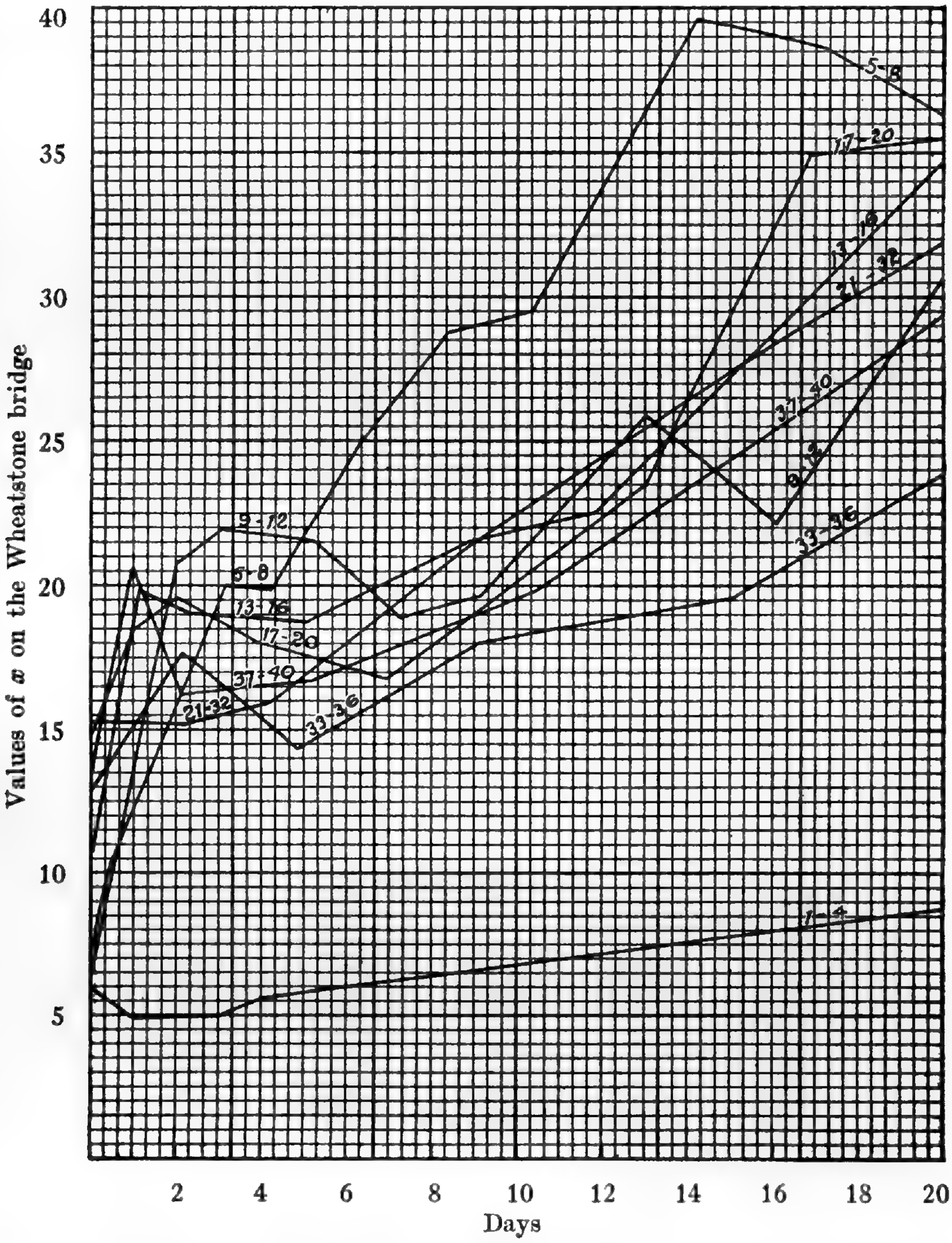

Fig. 3. The conductivity curves for cultures in distilled water 20 days—after growth in full nutrient solution for varying periods of time, as follows: Nos. 9–12, 1 day; Nos. 13–16, 5 days; Nos. 17–20, 10 days; Nos. 21–32, 20 days; Nos. 33–36, 30 days; Nos. 37–40, 40 days. Nos. 5–8 were grown only in distilled water, while Nos. 1–4 were without plants, consisting only of distilled water.

for fig. 2 being run in the fall when the seeds were fresh, and that for fig. 3 in the winter), in the vigor of the seeds, and in the difference in the units used in plotting the curves. It must be said, however, that various factors of the problem of exosmosis from the roots of plants remain as yet unknown.

The early drop in the curve of the conductivity of the controls (1–4) is an interesting feature which would seem to be explained by an adsorption of the electrolytes on the surface of the chemically clean glass tumblers.

At the end of 20 days in distilled water the roots of the plants which had not been in full nutrient at all showed marked deterioration (being badly decomposed and covered with a gelatinous coating), while the roots of those which had previously been in full nutrient solution for some time remained normal in every respect, even after 20 days in distilled water.

These results seem plainly to indicate that injury which plants sustain in distilled water is very closely related either to the lack of available nutrients in the medium or of reserve food material in the tissues. A seedling is in an exceedingly plastic state of growth. If no food materials become available the embryonic tissues which are in such an active condition of growth soon become disorganized, possibly suffering partial autolysis and becoming the prey to bacterial and fungous action. We would expect, therefore, that the larger the seeds (and hence also the supply of stored materials), the longer the seedlings could remain in distilled water before deterioration. Comparison of True's results on *Lupinus* with those here presented on *Pisum sativum* and *Vicia faba* seems to fulfill that expectation. We should also expect that the more nutrient materials the plant absorbed, the better it would be able later to withstand any deteriorating influences in the distilled water, and the experiment above noted seems to bear out that idea also.

In the light of what has been said we are led to believe that the conductivity curve of Nos. 5–8 is not a pure representation of exosmosis and that the products of bacterial and fungous action and cell decomposition account for at least a part of the conductivity. While the same condition may be

true of the other cultures to a certain extent, it no doubt plays a lesser, and real exosmosis a greater, part.

In connection with the above experiment it was thought desirable to determine whether a difference in the initial temperature of the water into which the roots were placed had any immediate or subsequent effect upon the exosmosis from the roots; plants which had been grown in full nutrient solution for 20 days were used for this purpose. Four cultures were prepared with distilled water at a temperature of 6.5°C., four at 17.2°C., and four at 35.0°C., and conductivity readings were taken after exactly one-half hour, and then at various intervals for 20 days. No attempt was made to keep the water at the initial temperatures and it therefore gradually returned to the temperature of the room. After one-half hour, when the first readings were taken, the respective temperatures were 8.9°C., 16.6°C., and 27.4°C.

The average conductivities of the water of these cultures are plotted for 20 days in fig. 4, the same units being used as in fig. 3. From these results it may be concluded that the initial differences of temperature can not be said to have exercised much, if any, effect. The results would probably have been different had the temperatures remained at the original point during the 20 days. Wächter ('05) has considered the rôle of the temperature factor in exosmosis.

VIII. Discussion and Conclusions

It is believed that the evidence furnished is sufficient to support the conclusion that pure distilled water *per se* is not toxic or injurious to plants, and that various other factors enter in to cause the deterioration noted when plants are placed in that medium.

Of course by qualifying the assertion to include *pure* distilled water only, we have thus eliminated the effect that may be produced by toxic substances in the distilled water, no matter from whence derived. The abundance of work that has been done on the toxicity of various substances to plant tissues would of course lead us to expect injurious effects if such substances were present in any quantity in the distilled

water. With that phase of the question we are therefore not much concerned at present. With a distilled water prepared as indicated, and with a specific conductivity which is approximately 2×10^{-6}, we have a water sufficiently pure for use in the consideration of other aspects of the question, and attention is directed to these.

The evidence presented has inclined us strongly to the view

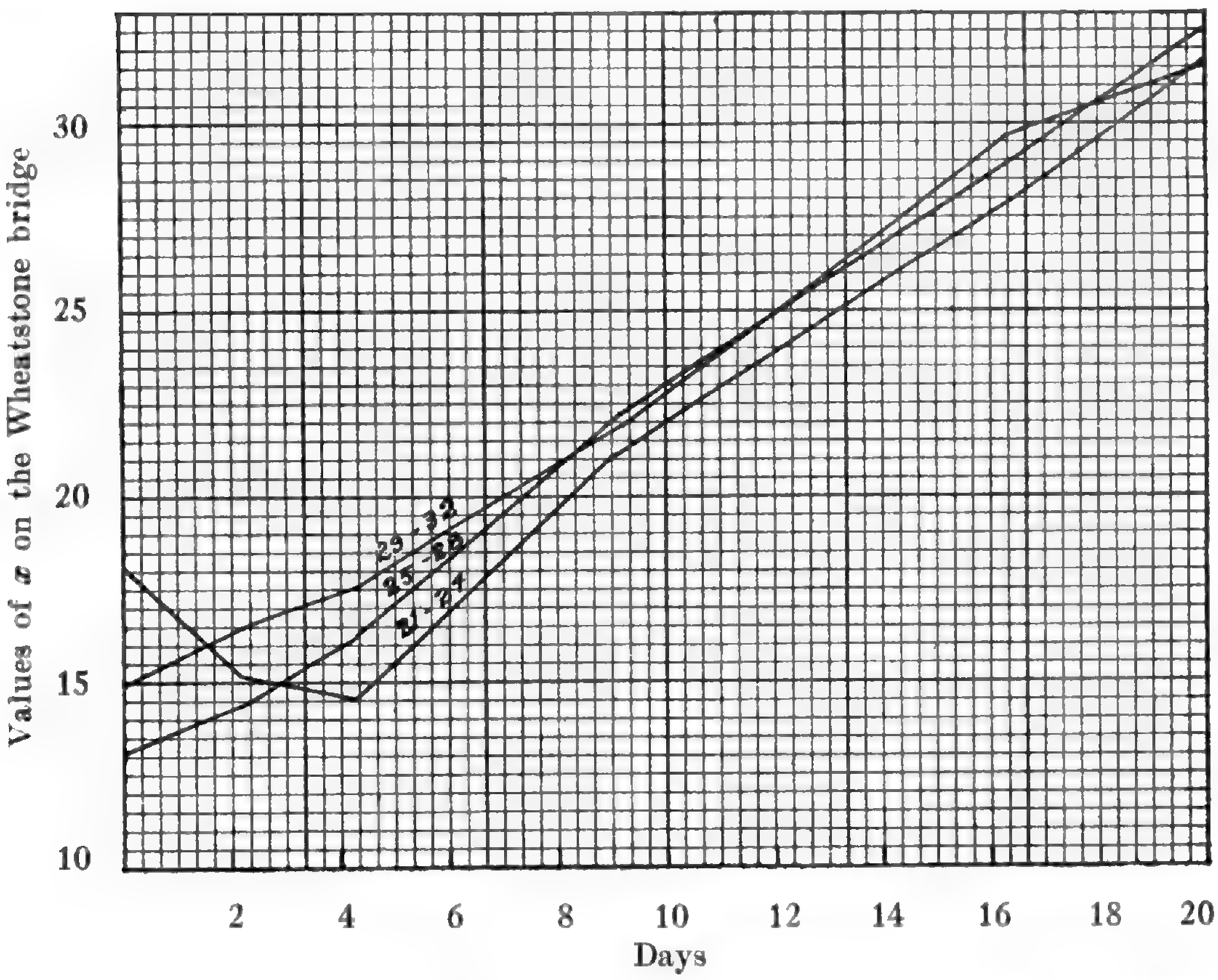

Fig. 4. The conductivity curves for cultures in distilled water 20 days—after growth in full nutrient solution for 20 days. The initial temperatures of the distilled water into which the roots were placed were as follows: Nos. 21–24, 6.5°C.; Nos. 25–28, 17.2°C.; Nos. 29–32, 35°C.

that the fundamental basis of the deterioration of plants in distilled water rests upon the food relations of such plants, but that, on the other hand, an exosmosis of food materials or nutrient salts is in no way responsible for the difficulty. It is considered that the question of the food relation plays an important rôle in the incipiency of the disorder, but that this is quickly followed by factors which have been initiated as a result of the inimical food or nutrient relation.

A plant must assuredly have food in order to thrive. The more food it has stored up in its tissues, the longer it can survive in a medium devoid of it. But because of the absence of available food it is believed that the tissues of the plant begin to become disorganized and in that condition fall a ready prey to bacterial and fungous action, which may then set in and play a very important part in the subsequent decomposition of the tissues.

While it may seem paradoxical to assert in one clause that absence of food is the fundamental basis of the injury which plants undergo in distilled water, and in the very next to say that exosmosis of nutrient salts plays no rôle, yet the results obtained have substantiated that idea. Furthermore, it is essential to consider the various other factors attendant upon these two conditions in order to arrive at the proper conclusions respecting their operation. Among such factors may be mentioned the decrease in conductivity after a short period coincident with exosmosis from normal tissues, the relation of sterilization to bacterial and fungous action, the recovery of plants under different conditions, and the numerous other questions already considered in the body of the article, all of which lend weight to the conclusions arrived at.

IX. Summary

A brief historical review is given in this paper of the views held in regard to the cause of injury to plants in distilled water.

The methods of work are outlined.

The experimental work is given and the results discussed, especially with reference to the conclusions of other workers.

A discussion is given of the results obtained in the experimental work and the conclusions derived therefrom are stated.

Some of the results obtained from the experimental work may be summarized as follows:

(a). Renewing the distilled water of the cultures every 4 days was in general beneficial, as shown by increased growth of both tops and roots. The plants were also able to survive longer in the renewed than in the unrenewed distilled water,

and continued growth better after being placed in a full nutrient solution.

(b). The period between 5 and 10 days in distilled water is a crucial one for plants; if they remain longer in this medium they are unable to recover normally or completely when subsequently placed in a full nutrient solution.

(c). By keeping the plants in distilled water a certain period before transferring to full nutrient solution the maturity of the plants is delayed.

(d). The longest period during which plants can be kept in distilled water and later recover on being placed in full nutrient solution was found to be 30–40 days. For certain dilute toxic solutions this period was much less, thus indicating that the so-called toxicity of distilled water is, if it exists at all, very slight.

(e). The lateral roots of "boundary cultures" were characteristically long and thread-like.

(f). Sterilizing the distilled water by boiling one-half hour every 4 days exercised a beneficial effect upon the growth of plants in that medium as compared with the growth of those in unsterilized distilled water.

(g). Greater total exosmosis was obtained in the renewed than in the unrenewed distilled water.

(h). Normal plants which have been grown for some time in full nutrient medium and then transferred to distilled water exhibit at first greater excretion than absorption of electrolytes. After one or two days, however, there is greater absorption than excretion and the conductivity curve declines. This condition may be maintained for a considerable period.

(i). The conductivity curve of the full nutrient solution in which plants were grown rapidly fell during the first 15 days or so; then it was more or less horizontal for a period, and finally began to incline after about 50 days. The growth curve was in general opposite in character to the conductivity curve.

(j). The conductivity of the distilled water in one series in which the roots of pea seedlings were placed was practically the same on the 10th as on the 5th day. After the 10th day

it rose considerably. The growth curve showed a rise the first ten days, then a decline.

(k). Higher conductivity in the distilled water after 20 days was caused by plants which had not previously been in full nutrient solution than by plants grown for a time in full nutrient solution before transference to distilled water. The former cultures also failed to give the decline in conductivity characteristic of normal plants transferred from full nutrient solution to distilled water.

(l). Greater deterioration of the roots in distilled water occurred if the plants had not previously been in full nutrient solution than in the case of plants which had been grown for a time in the latter medium.

(m). Initial difference of temperature of the distilled water produced no effect on the exosmosis of electrolytes.

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Explanation of Plate

PLATE 13

Figure 1.

Culture no.		Conditions of growth.
1	(2)	*Unrenewed distilled H_2O, 45 days.
2	(3)	Renewed distilled H_2O, 45 days.
3	(6)	1 day dist. H_2O, 44 days in renewed full nutr.
4	(8)	2 days dist. H_2O, 43 days in renewed full nutr.
5	(10)	5 days dist. H_2O, 40 days in renewed full nutr.
6	(14)	10 days dist. H_2O (renewed), 35 in renewed full nutr.
7	(18)	15 days dist. H_2O (renewed), 30 in renewed full nutr.
8	(22)	20 days dist. H_2O (renewed), 25 in renewed full nutr.
9	(23)	45 days in unrenewed full nutr.
10	(25)	45 days in renewed full nutr.

Figure 2.

1	(9)	5 days in unrenewed dist. H_2O, 40 days in unrenewed full nutr.
2	(10)	5 days in unrenewed dist. H_2O, 40 days in renewed full nutr.
3	(11)	10 days in unrenewed dist. H_2O, 35 days in unrenewed full nutr.
4	(12)	10 days in unrenewed dist. H_2O, 35 days in renewed full nutr.
5	(13)	10 days in renewed dist. H_2O, 35 days in unrenewed full nutr.
6	(14)	10 days in renewed dist. H_2O, 35 days in renewed full nutr.
7	(19)	20 days in unrenewed dist. H_2O, 25 days in unrenewed full nutr.
8	(20)	20 days in unrenewed dist. H_2O, 25 days in renewed full nutr.
9	(21)	20 days in renewed dist. H_2O, 25 days in unrenewed full nutr.
10	(22)	20 days in renewed dist. H_2O, 25 days in renewed full nutr.

* The numbers in parentheses correspond to the culture numbers of series 1. (See table 1.)

Fig. 1

Fig. 2

MERRILL—DISTILLED WATER

Explanation of Plate

PLATE 14

Figure 1.

Culture no.		Conditions of growth.
1	(2)	*33 days in unrenewed dist. H_2O at time picture was taken.
2	(3)	33 days in renewed dist. H_2O at time picture was taken.
3	(6)	1 day in dist. H_2O, 32 days in renewed full nutr.
4	(8)	2 days in dist. H_2O, 31 days in renewed full nutr.
5	(10)	5 days in unrenewed dist. H_2O, 28 days in renewed full nutr.
6	(14)	10 days in renewed dist. H_2O, 23 days in renewed full nutr.
7	(18)	15 days in renewed dist. H_2O, 18 days in renewed full nutr.
8	(22)	20 days in renewed dist. H_2O, 13 days in renewed full nutr.
9	(23)	33 days in unrenewed full nutr.
10	(26)	33 days in renewed full nutr.

Figure 2.

1	(9)	5 days in unrenewed dist. H_2O, 28 days in unrenewed full nutr.
2	(10)	5 days in unrenewed dist. H_2O, 28 days in renewed full nutr.
3	(11)	10 days in unrenewed dist. H_2O, 23 days in unrenewed full nutr.
4	(12)	10 days in unrenewed dist. H_2O, 23 days in renewed full nutr.
5	(13)	10 days in renewed dist. H_2O, 23 days in unrenewed full nutr.
6	(14)	10 days in renewed dist. H_2O, 23 days in renewed full nutr.
7	(19)	20 days in unrenewed dist. H_2O, 13 days in unrenewed full nutr.
8	(20)	20 days in unrenewed dist. H_2O, 13 days in renewed full nutr.
9	(21)	20 days in renewed dist. H_2O, 13 days in unrenewed full nutr.
10	(22)	20 days in renewed dist. H_2O, 13 days in renewed full nutr.

* The numbers in parentheses correspond to the culture numbers of series 2. (See table III.)

Fig. 1

Fig. 2

MERRILL—DISTILLED WATER

COCKAYNE, BOSTON

EXPLANATION OF PLATE

PLATE 15

Figure 1.

Culture no.		Conditions of growth.
1	(1)	*10 days in unrenewed dist. H_2O, 42 days in unrenewed full nutr.
2	(2)	10 days in unrenewed dist. H_2O, 42 days in renewed full nutr.
3	(3)	10 days in renewed dist. H_2O, 42 days in unrenewed full nutr.
4	(4)	10 days in renewed dist. H_2O, 42 days in renewed full nutr.
5	(5)	20 days in unrenewed dist. H_2O, 32 days in unrenewed full nutr.
6	(6)	20 days in unrenewed dist. H_2O, 32 days in renewed full nutr.
7	(7)	20 days in renewed dist. H_2O, 32 days in unrenewed full nutr.
8	(8)	20 days in renewed dist. H_2O, 32 days in renewed full nutr.
9	(9)	30 days in unrenewed dist. H_2O, 22 days in unrenewed full nutr.
10	(10)	30 days in unrenewed dist. H_2O, 22 days in renewed full nutr.
11	(11)	30 days in renewed dist. H_2O, 22 days in unrenewed full nutr.
12	(12)	30 days in renewed dist. H_2O, 22 days in renewed full nutr.
13	(13)	40 days in unrenewed dist. H_2O, 12 days in unrenewed full nutr.
14	(15)	40 days in renewed dist. H_2O, 12 days in unrenewed full nutr.

Figure 2.

1	(1)	†32 days in unrenewed dist. H_2O.
2	(2)	32 days in renewed dist. H_2O.
3	(20)	32 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$.
4	(22)	1 day in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 31 days unrenewed full nutr.
5	(23)	2 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 30 days unnewed full nutr.
6	(24)	4 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 28 days unnewed full nutr.
7	(25)	8 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 24 days unrenewed full nutr.
8	(26)	12 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 20 days unnewed full nutr.
9	(27)	16 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 16 days unrenewed full nutr.
10	(28)	20 days in unrenewed N/20 $MgCl_2$ & N/1000 $CaCl_2$, 12 days unrenewed full nutr.
11	(29)	32 days in unrenewed full nutrient solution.

*The numbers in parentheses correspond to the culture numbers of series 3. (See table V.)

†The numbers in parentheses correspond to the culture numbers of series 4. (See table VI.)

Fig. 1

Fig. 2

MERRILL—DISTILLED WATER

EXPLANATION OF PLATE

PLATE 16

Figure 1.

Culture no.		Conditions of growth.
1	(1)	*30 days in unrenewed distilled H_2O.
2	(2)	30 days in renewed distilled H_2O.
3	(3)	30 days in distilled H_2O, sterilized every four days.
4	(4)	30 days in distilled H_2O, sterilized every four days.
5	(5)	30 days in unrenewed full nutrient solution.
6	(6)	30 days in renewed full nutrient solution.

Figure 2.

Showing the method used for seed germination.

*The numbers in parentheses also correspond to the culture numbers of series 5. (See table VII.)

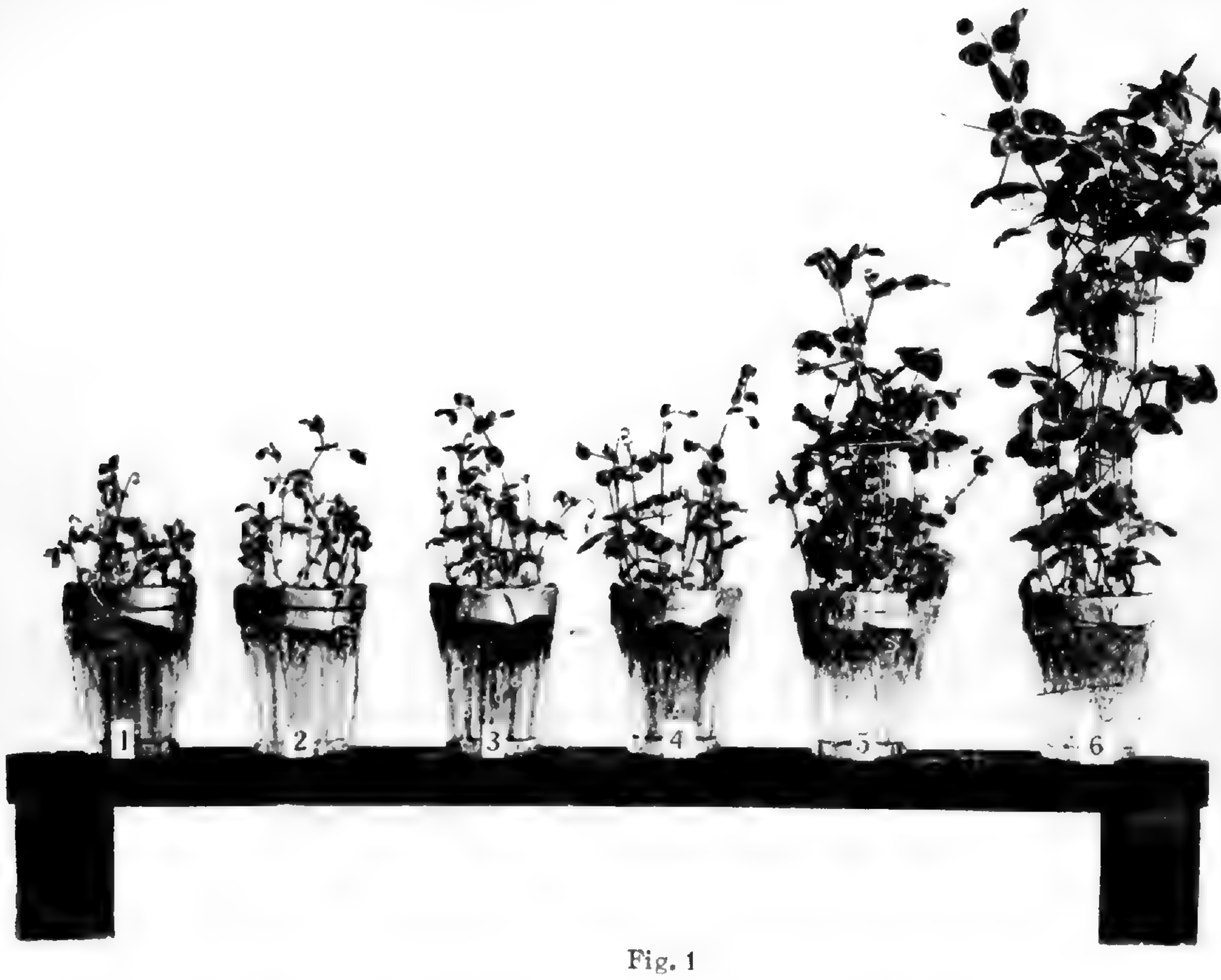

Fig. 1

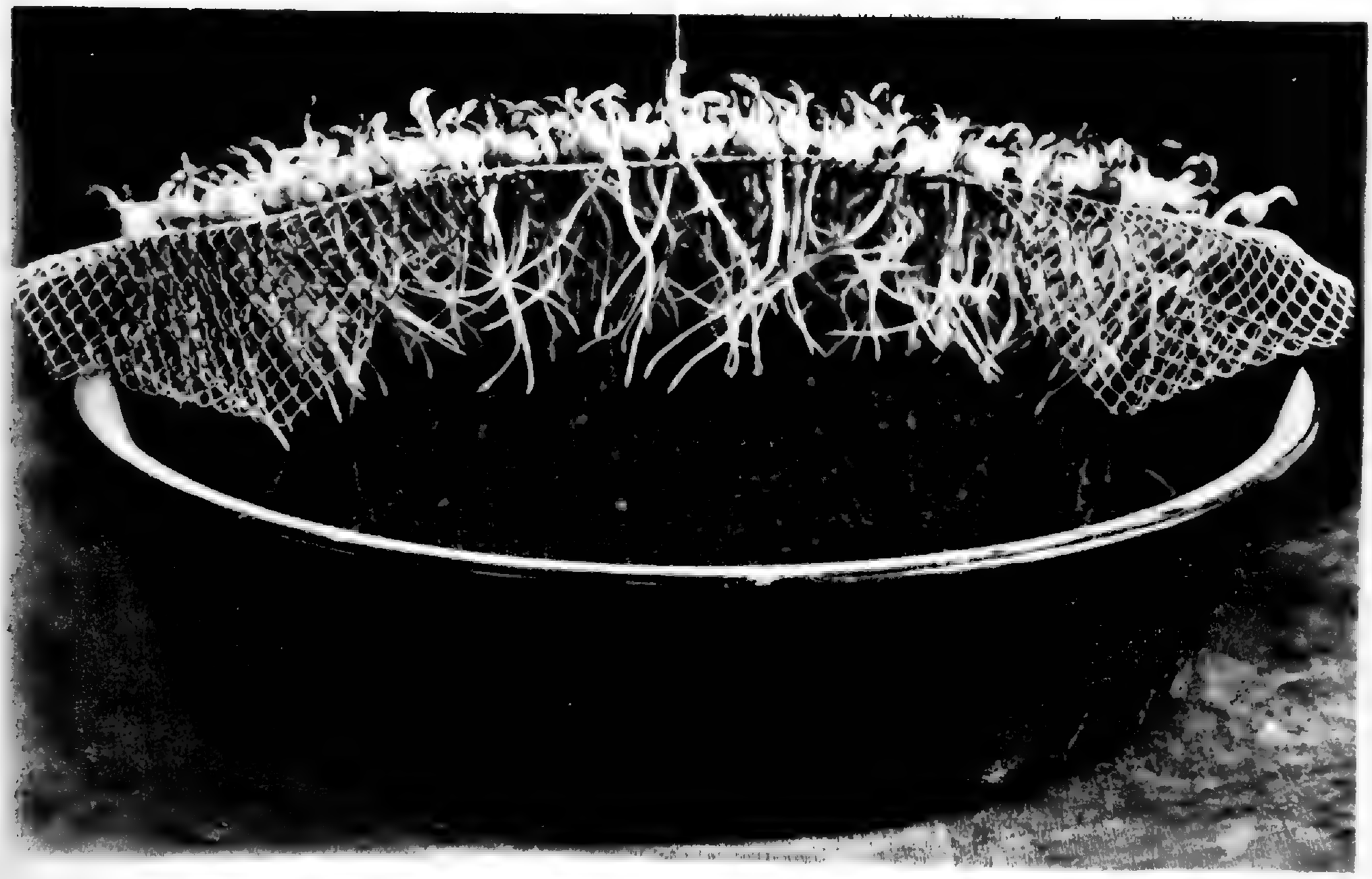

Fig. 2

MERRILL—DISTILLED WATER

COCKAYNE, BOSTON

ELECTROLYTIC DETERMINATION OF EXOSMOSIS FROM THE ROOTS OF PLANTS SUBJECTED TO THE ACTION OF VARIOUS AGENTS

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I. Introduction

In a previous paper the writer ('15) gave some results showing the exosmosis curves when normal growing plants are taken from a full nutrient medium and placed in redistilled water. Those results and the data herewith given show that exosmosis of electrolytes is a constant feature associated with the transfer of normal growing plants from a full nutrient solution to distilled water. In the paper above mentioned evidence was introduced indicating that such exosmosis was not a causal injury but that it was simply a concomitant condition or incidental effect and had but an indirect relation to the inimical condition of the plant in the distilled water. For convenience we might designate the agency or agencies causing such exosmosis as *passive* in their effects.

In this paper are given results on exosmosis in terms of the electrolytic conductivity of the medium when such excretion is caused, or at least is accelerated, by various factors or agencies which we may designate as *active* in their effects. Accordingly, plants have been treated by injurious agents or subjected to conditions of different kinds and the comparative effects on the exosmosis from the roots have been noted. By determining the conductivity of the medium at various intervals subsequent to the treatment, data have been secured for plotting the exosmosis curves shown in this paper. It has also been the aim to determine in each case the approximate boundary between the normal and the abnormal exosmosis by varying either the duration of application or the concentration of the substance applied, or both. Hence in most cases there will be found the two extremes with any given substance—at the upper end of the scale the curve of excessive exosmosis due to

cytolysis or death of the cells (though it should be noted here that excessive exosmosis from the roots may result even when those tissues are in an apparently normal condition), and at the lower end of the scale the curve of slight exosmosis that is in the region of the normal curve of exosmosis for untreated plants placed from full nutrient solution into distilled water. Between these two extremes lie various gradations depending on conditions.

II. Historical Review

The work that has been done on the problem of excretions from the roots of plants is very interesting from several standpoints and has been considered by various workers to be of great practical importance. Nearly a century ago De Candolle ('32) advocated a theory of crop rotation on the basis of root excretions in which he claimed that certain plants excreted from their roots substances which are harmful to succeeding crops of closely related plants, but not so to plants less closely related. This theory was based partly on his own observations and partly on the statements of earlier workers.

At De Candolle's suggestion Macaire ('32) performed some experimental work pertaining to root excretions. He took plants from the soil, washed the roots carefully, and placed them in rain water. After several days, during which the water was frequently changed, the water was yellow and had odor, taste, and chemical reactions indicative of contained exuded materials. By placing one part of the roots of a plant in a vessel of pure water and another part in a second vessel containing a solution of lead acetate and later finding the salt in the pure water, he concluded that a plant can excrete a poison which it has absorbed. The results of Macaire's experiments with water cultures led him to favor the theory of crop rotation on the basis of the excretions from the roots of plants, as advanced by De Candolle.

Braconnot ('39) repeated many of Macaire's experiments but was unable to convince himself that plants excrete toxic substances from their roots, and hence he did not look with favor upon De Candolle's theory. Braconnot believed that

capillary action played a rôle in Macaire's experiments whereby he obtained an excretion of lead acetate into distilled water, as noted above. Boussingault ('45) considered that under ordinary conditions radicular excretion is doubtful, and that any excretion from the roots in water is caused by disease. He also advanced various arguments opposing De Candolle's theory.

Gyde ('47) grew various agricultural plants in soil for a time and then, after carefully washing the roots, placed them in pure water. After 3–17 days, during which the plants continued in good condition for the most part, the water was evaporated. The finding of a residue of yellowish or brown matter, part organic and part inorganic, caused him to conclude that plants excrete both organic and inorganic substances in minute quantities, similar in composition to the sap. But he denied that root excretions have any injurious effect upon plants later grown in the same medium.

An examination of the literature on the subject of root excretions reveals the tendency among the workers of the particular period at which we have now arrived in our review, to pay more attention to the morphological and chemical aspects of root excretions, and perhaps not so much to the purely agricultural phases. Hence we find from this period on, considerable emphasis laid on the structure of the root and a more detailed account given regarding the chemical nature of the substances excreted from the roots, even though the experimental methods were somewhat crude in most cases. Furthermore, it should be said that opinion was divided on the question of whether or not there is an actual excretion from the roots.

Among those whose influence was felt in the development of the chemical aspects of the subject at this time Liebig should probably be mentioned first. In the American edition of his work ('41, p. 195) occurs the following statement: "It is evident that plants, also, by producing carbonic acid during their decay, and by means of the acids which exude from their roots in the living state, contribute no less powerfully to destroy the coherence of rocks." An appended note by Dr. Webster in the

same work ('41, p. 411) says that other chemists were unable to obtain results similar to those of Macaire. If they did, they were inclined to ascribe them to injury of the roots examined.

Various workers were thus attacking different phases of the problem. Chatin ('47) mentioned the excretions from roots and especially considered the elimination of toxic substances by them. Link ('48) held that the slimy drops found on root tips should not be considered as actual excretion inasmuch as they arise from the cast-off cap cells of the root. Garreau and Brauwers ('58) maintained a similar view in regard to the gummy, nitrogenous substance they found given off by the roots to the water in which they were placed. The observations of Liebig ('58) concerning the dissolving action of roots on limestone were later substantiated by the experimental work of Sachs ('60), which has been so much referred to since that time. Of the two possible explanations Sachs advanced —excretion of carbonic acid by the roots, and the liberation of acids by the decomposition of the cell walls of the roots—he inclined to favor the latter as being the best explanation for the marble etchings caused by the roots in his experiments. In his extensive series of experiments, Knop ('60, '61, '62) studied, among other things, the character and amount of root excretions from certain plants placed in distilled water, and the conditions governing the same. His analyses indicated that, in addition to other substances in small amounts, potassium, calcium, phosphoric acid, and some organic matter were excreted. The studies of Cauvet ('61) resulted in his declaring that physiologically sound roots do not excrete any substances, toxic or otherwise, and that all theories based on the ideas of root excretion advanced by De Candolle and Macaire were necessarily false. Sachs ('65) made further contributions along his line of work indicated above, while Liebig ('65) says:

"Wir haben allen Grund zu glauben, dass diese Absonderung an der ganzen Oberfläche stattfindet, wir beobachten sie nicht nur am Stamme, sondern auch an den kleinsten Zweigen, und wir müssen daraus schliessen, dass dieser Excretionsprocess auch an den Wurzeln vor sich geht. . . . . Eine Ausscheidung von Excrementen kann demnach bei den Pflanzen

> nicht geleugnet werden, wiewohl es möglich ist, dass sie nicht bei allen Pflanzen in gleichem Grade stattfindet."

Molisch ('87) branched out in a new direction as regards the subject of root excretions; he held that such excretions exercise an influence on organic bodies in the soil which is even more important than that exercised upon the inorganic constituents of the same, for he considered the latter merely a dissolving action but the former a real chemical transformation. His main work along this line pertained to a study of the ferments in the root excretions, and their reactions and properties. Johnson ('90), after considering Gyde's results above noted, says that "we may well doubt whether agricultural plants in the healthy state excrete any solid or liquid matters whatever from their roots," but that "under certain circumstances, small quantities of soluble salts or free acids may indeed *diffuse* out of the root-cells into the water of the soil. This is, however, no physiological action, but a purely physical process." Goebel ('93) found that after the roots of Hordeum and Lepidium plants had been in distilled water for six days the medium gave the reaction for formic acid.

We thus see that the early work on root excretions was characterized by contradictions and uncertainties. While the nature of the more recent work has been more exact and comprehensive, the subject, as we shall see, is still beclouded by a considerable degree of confusion.

A classic piece of experimental work was undertaken by Czapek ('96, '96[a]) to determine the exact chemical nature of the excreted substances from roots. In his report ('96[a]) he discussed the earlier work, especially with regard to the relation between excretion from injured cells and actual exosmosis. In his experimental work he found that root excretions are composed of soluble substances, partly organic and partly inorganic. Of the inorganic, he identified K, Ca, Mg, HCl, H_2SO_4, and H_3PO_4, only the first and last mentioned—in the form of the primary potassium phosphate—being excreted in any quantity. Of the organic substances he identified carbonic acid and also formic acid, the latter in the form of its potassium salt; oxalic acid was also isolated as a primary

potassium salt. Czapek believes the reddening of litmus paper by root excretions to be due ordinarily to the acid reaction of monopotassium phosphate, but in the case of hyacinth roots to the primary oxalate. The corrosion of marble he attributed to the dissolving effect of carbonic acid. While considering as possible the results obtained by Molisch ('87), who claimed that diastatic ferments were normally present in the root excretions, Czapek's own work in repetition of Molisch's experiments offered only negative results.

Prianischnikov ('04) performed some experimental work dealing with the action of organic acids on phosphates. It will be remembered that because the roots did not attack aluminum phosphate Czapek concluded that organic acids were not excreted by them, inasmuch as this substance is soluble in certain organic acids. Prianischnikov found that phosphates derived from different sources were utilized by various plants but in different degree, and he suggested that this might be correlated with a different amount of CO_2 excretion, in which case the presence of organic acids would not be necessary.

Kunze ('06) found that free mineral acids are not excreted from the roots of higher plants and concluded that any acidity in the excretions is probably not due to the presence of acid salts of mineral acids, but to excreted organic acids. These, however, were present in such minute amounts as to be below the sensitiveness of litmus. He held that a greater effect is produced on the soil by fungi than by the roots of the higher plants. Lemmermann ('07) held views similar to those of Kunze.

Stoklasa and Ernest ('08) disagree with the findings of both Czapek and Kunze. No potassium or phosphoric acid were ever found as a result of their determinations, and they maintain that in the economy of the plant the excretion of such useful or necessary substances is unthinkable. Only CO_2 was found to be excreted under conditions of normal aerobic respiration of the root system; no other free inorganic or organic acids were detected. In aerobic respiration of the root system, they believe the organic acids in the living cells would be split up to give CO_2 and H_2, the latter then being oxidized to H_2O.

They determined the amount of CO_2 excretion per gram dry weight of roots of wheat, oats, rye, and barley. The amount varied for the different plants but a correlation was found between the amounts of P_2O_5, K, and Na contained in the dry roots of plants grown on gneiss and basalt and the amount of CO_2 excreted.

We now come to the work of various soil investigators whose results have again focused attention during the past decade upon De Candolle's original theory. The essential features of this work have become so well known that for our purpose it is not necessary to do much more than merely mention it here. Though not considering directly the phases of the subject with which we are dealing, yet the much-discussed paper by Whitney and Cameron ('03) is historically important and bears an intimate relation to the later work of the investigators in the Bureau of Soils of the U. S. Department of Agriculture, the results of which led to the so-called toxic-excretion theory. Among the workers most prominently connected with the early studies along this line may be mentioned Livingston, Britton, and Reid ('05); Livingston, Jensen, Breazeale, Pember, and Skinner ('07); Schreiner and Reed ('07); Schreiner, Reed, and Skinner ('07); Schreiner and Reed ('07[a]); and others. As is well known, opinion is much divided on the various phases of this subject, however. Among those opposing the ideas or theories advanced along this line by the investigators named above should be mentioned Hopkins ('10); Hall, Brenchley, and Underwood ('14); and others.

That the question is one upon which investigations are still being pursued is shown by the publications from various quarters. As recent examples of these the work of Molliard ('13) and Prianischnikov ('14) may be cited. The former found that peas grown in water cultures in which previous crops of peas had grown produced a smaller growth than the original crops. This he attributed to the excretion of toxic substances in the medium by the earlier plants. The latter, from his own experimental work and from the results observed by him at the Rothamsted Experiment Station, is inclined to believe that the hypothesis of root excretion is not sufficiently demon-

strated. He says that other factors, as, for example, the physical nature of the soil, decomposition of roots, change in reaction of soil, etc., might be supposed to accomplish the same results as toxic excretions from the roots. In pure distilled water he found no decrease in either the size or quality of the crops of the second and third plantings, either where wheat followed wheat or where wheat followed oats. Experiments in sand, however, showed great decrease in the amount of the harvest of the second and third crops, but this, he believes, might be explained by the operation of the above-named factors.

So much for root excretions; we now come to a general consideration of exosmosis from living cells, both under natural conditions and under treatment of different kinds. While a great deal of attention has been given in the past to the intake, or endosmosis, of substances by the cell from its surrounding medium, comparatively little has been done on the opposite effect—the outgo, or exosmosis, of substances from the cell. It should be said, however, that the latter process, both in extent and in importance, is no doubt of much less significance in the plant's economy than the former.

Sachs ('60[a]) referred to the exosmosis of soluble material from germinating seeds when they remain for some time in distilled water. Knop ('64), in his studies on the absorption of salts by healthy seeds, also determined the quantities of the different salts which pass out of the seeds during the time they are swelling in distilled water. He found that both organic and inorganic substances were excreted. Hofmeister ('67) ascertained that when fresh pieces of sugar-containing plants were placed in water, no sugar passed out of the tissues into the medium. The much-cited experiments of De Vries ('71) showed that pieces of red beet placed in water for 15 days gave no trace of sugar or of colored material to the water during that time. In a NaCl solution of sufficient concentration, however, he obtained an exosmosis of both sugar and colored material. Turnips, beets, and the seedling roots of wheat, barley, and corn were used in the experiments of Boussingault ('74) but from none of them did he detect any

exosmosis of sugar into the water in which they were placed. Pfeffer ('76, '77) and Detmer ('79) also confirmed the results above noted regarding the absence of sugar in the water in which roots or other plant parts had been exposed for some time. Wilson ('81) found that in some cases (*Dionaea* and *Drosera*) the excretions may be influenced by external factors, e. g., partly by irritation caused by nitrogenous substances and partly by osmotic action. In general, he believed that the excretion of nectar is caused by the osmotic action of a fluid on the surface of the nectary. Pfeffer ('86) studied the effects of various organic acids (citric, picric, and tannic) and some inorganic compounds in causing the exosmosis of absorbed methylene blue from *Lemna, Trianea, Azolla,* and *Elodea.*

Wächter ('05) obtained considerable exosmosis of sugar, especially in the case of *Allium Cepa*; he found, however, that salts like NaCl and KCl tended to inhibit this exosmosis. He also investigated the effect of ether on this phenomenon. While he obtained greater exosmosis of sugar the first two days in a solution of ether alone than in one of ether and KCl, he attributed this increase to leaching from cells killed as a result of contact with ether, and believed that the ether itself has no effect on the actual process of exosmosis.

Lepeschkin ('06), from his experimental work on sporangia of *Pilobolus,* concluded that the exosmosis of water was due to an alteration of the plasma membrane caused by the anesthetics he used, provided the amounts employed were sufficient to be toxic. Small amounts of ether and chloroform, on the other hand, were found to decrease the exudation of water, and he believed this to be due to a decrease in permeability of the plasma membrane.

An interesting line of investigation was undertaken by Czapek ('10, '10[a], '10[b], '11) a few years ago to determine the surface tension relations of the plasma membrane. That work is especially pertinent to our discussion here because of the prominent part exosmosis played in his experiments. He used for the most part species of *Echeveria, Spirogyra,* and *Saxifraga,* in the cells of which is found a tannoid substance,

anthocyan, which is precipitated by caffein, giving a loose compound of tannin and caffein, called a "myelin-formation." Ammonia also gives this precipitate even in a solution as dilute as 1–15,000. Czapek investigated the effect produced by the application of a great variety of organic compounds and some inorganic acids in varying dilutions and for different periods of time, and determined the concentration at which exosmosis just occurred, i. e., the critical point. At the higher concentrations exosmosis of the tannoid substance readily occurred, as shown by the absence of the "myelin-formation" when caffein or ammonia was subsequently added. At the lower concentrations exosmosis did not occur and a precipitate was obtained, while at the critical point the precipitate was barely visible and usually in the form of fine particles.

By the use of his "capillar-manometer," Czapek was able to measure the surface tension exerted by the various concentrations, and found that, considering the surface tension of water as unity, that of the critical concentrations was approximately .68 in most cases. This lowering of the surface tension he considered as essentially a physical phenomenon which is intimately connected with the osmotic activities of the plasma membrane and is to be differentiated from the toxic action of injurious substances, e. g., anesthetics, whose action is chemical in large part, since even in very dilute solutions these caused marked exosmosis. Czapek used both aqueous and colloidal solutions and found that in general the critical concentrations had a surface tension of .68 in terms of water as unity. Inversely, he therefore concluded that the surface tension of the plasma membrane was also approximately .68 for the plant cells investigated. In his study of acids he found results coincident with those of Kahlenberg and True ('96) in that N/6400 was the critical concentration for exosmosis of the tannin bodies, just as those workers had found it to be the critical concentration for growth of Lupinus seedlings in solution culture.

In his later experimental work Lepeschkin ('11) obtained additional evidence tending to confirm and add to his previous results, as mentioned above. Thus he found that aniline dyes

penetrated cells of *Spirogyra* more slowly in the presence of one per cent chloroform than when the anesthetic was not used. If the cells were killed by the narcotic the rate was the same as for normal cells. He also used *Tradescantia discolor* and by the plasmolytic method found that the permeability to KNO_3 decreased during narcosis. This he explained on the assumption that the anesthetics (chloroform and ether) accumulated in the disperse phase of the plasma membrane which thereby leads to a hindrance of the solubility of KNO_3 and aniline dyes in the same. He considered that his results therefore showed that Nathansohn's hypothesis regarding the mosaic structure of the plasma membrane is not correct.

Another important piece of work dealing with the phenomenon of exosmosis from living tissue is that accomplished by Lillie ('09, '10, '11, '12, '12[a], '13, '13[a], '13[b]) and discussed at length in his various papers. Among other things he worked on the larvae of *Arenicola* and the eggs of *Arbacia,* each of which contains a pigment, and found that on placing them in NaCl or KCl solution (.55m) isotonic with sea-water, there was a rapid exosmosis of the contained pigment into the surrounding medium. When, however, the organisms were placed in the salt solutions to which had previously been added in a certain concentration any one of several anesthetics belonging to various classes (alcohols, esters, hydrocarbons, and miscellaneous compounds) a checking or possibly a complete prevention of exosmosis resulted. In general, all the anesthetics tried gave cytolysis in strong concentrations and therefore a rapid exosmosis of the pigment, while in weaker concentrations they showed a definite protective or anticytolytic action against the salt solution when used in conjunction with it. Lillie finds the explanation of the observed phenomenon in the relations of the plasma membrane, the salt solutions used having a permeability-increasing action which is offset or prevented by the temporary alteration of the membrane as the result of the action of the anesthetic. The alteration, he believes, is accompanied by an increase in the volume of the lipoid particles of the membrane.

In connection with the general subject of exosmosis it might

be well briefly to mention the results obtained by some of the earlier investigators working on the products excreted by the leaves of plants. De Saussure (1804) found that leaves immersed in distilled water soon lose a considerable amount of substance, composed for the most part of alkaline salts. Treviranus ('38) mentioned the results of various workers who studied the incrustation of minerals on the surface of leaves and found it to consist of calcium and silicon salts, especially of calcium carbonate. Gaudichaud ('48) and Payen ('48) both found that there is an alkaline excretion on certain parts of the leaves of some plants, yet they disagreed as to the extent of this phenomenon in nature. Sachs ('62) ascertained that drops of water on the leaves of certain plants soon become alkaline, which he considered to be the result of an outward diffusion of alkaline salts in the leaf. Volkens ('84) studied the deposit of calcium carbonate found on the leaves of various plants. Dandeno ('02) made a comprehensive study of the different phases of the subject. Among other things, he determined that the alkaline substances extracted from leaves by distilled water are largely potassium and calcium carbonates and probably potassium oxalate. He further found that the residue from the evaporation of dew drops, guttation drops, and of water used in drenching the leaves is practically the same, and is similar to the calcareous deposit found upon the leaves of certain plants. The above investigations may therefore be considered as tending to substantiate the idea of exosmosis from leaves.

III. Methods of Experimentation

The methods used for the electrolytic determination of exosmosis were the same as those described in the writer's paper referred to above. In that contribution (Merrill, '15) some of the curves were plotted on the basis of the specific conductivity. In the present paper, however, all curves are plotted on the basis of the values of x on the Wheatstone bridge when the resistance in the box is 9,110 ohms; as these values increase the specific conductivity also increases. In order to have a basis of comparison between the values of x

and the specific conductivity, the corresponding values of the latter for the values of x at 5, 10, 25, 50, 75, and 85 are given herewith:

Values of x on Wheatstone bridge for resistance of 9,110 ohms.	Corresponding values in terms of specific conductivity (to be multiplied by 10^{-5})
5	.23
10	.49
25	1.49
50	4.48
75	13.46
85	25.43

It is also advisable to have the conductivity values represented in terms of the concentration of some salt. The following are the values of the specific conductivity of NaCl solutions at 25°C. which had been determined by the writer for the concentrations indicated:

Concentration of NaCl	Specific conductivity (to be multiplied by 10^{-5})
N/16	686.13
N/32	353.94
N/64	181.93
N/128	93.25
N/256	47.79
N/512	24.54
N/1024	12.60

The correction for the specific conductivity of the water itself is not considered in the above values. Neither is that correction applied in any of the work here reported, since it is always a constant factor and only relative values are desired for the most part.

Plants of *Pisum sativum* were used. For the method of growing the seedlings, and other manipulations, see the writer's paper referred to (Merrill, '15). The plants were grown in full nutrient solution until a vigorous or well-developed condition was attained and then they were transferred to redistilled water[1] after rinsing the roots carefully and thoroughly in once-distilled water. Ten plants were grown in each culture. The treatment was always given when the plants were either in distilled water or in the solution, the effects of which on the plants were being studied. In all cases where the read-

[1] Hereafter, throughout this paper, whenever "distilled water" is referred to it will be understood to mean redistilled water with a specific conductivity of approximately 2×10^{-6}. If the ordinary distilled water is referred to, it will be specially designated as "once-distilled water" or some such distinguishing term.

ings were made in the distilled water, the resistance in the resistance box was 9,110 ohms. In some media other resistances were used; in such cases the values are given only in tables, and in terms of specific conductivity.

TABLE I

EFFECTS OF VARIOUSLY TREATED PLANTS ON THE DISTILLED WATER MEDIUM AS SHOWN BY GROWTH OF SECOND CROP

Culture no.	Kind and duration of treatment	Green wt. of tops of 2nd crop* grams
1 and 2	Controls—no treatment; full nutrient to dist. H_2O	2.90
3	Plant tops packed in ice 19 hrs.; dist. H_2O unchanged	2.80
4	Plant tops packed in ice 19 hrs.; dist. H_2O changed	
5	In gas incubator at 50°C., 3.5 hrs.	1.60
6	In gas incubator at 50°C., 3.5 hrs.	2.55
7 and 8	Inoculated with *Ascochyta Pisi*	2.80
9	Illum. gas under bell jar, 6 hrs.; dist. H_2O unchanged	2.75
10	Illum. gas under bell jar, 6 hrs.; dist. H_2O changed	2.25
11 and 12	N/1 $MgCl_2$ in full nutrient as the solvent, 7 hrs	5.20
13 and 14	.5% H_2SO_4 in full nutrient as the solvent, 7 hrs	2.30
15 and 16	1% KOH in full nutrient as the solvent, 7 hrs	8.45
17 and 18	Plants grown throughout in dist. H_2O; replaced by fresh seedlings in the unrenewed dist. H_2O	2.55
19 and 20	Same as Nos. 17 and 18, except that second crop was horse beans	6.85
21 and 22	Canada field peas in fresh dist. H_2O; no second crop	2.82
23 and 24	Horse beans in fresh dist. H_2O; no second crop	8.15

*The 2nd crop was 27 days old at time of weighing.

IV. Preliminary Experiments

In order to determine in a preliminary way whether the exosmosis from the roots of plants seriously affected by injurious agencies was sufficient to noticeably influence a new crop of seedlings in that medium (distilled water plus the excreted substances) as compared with control cultures in pure distilled water, the following series was set up. Canada field pea seedlings were grown in full nutrient solution until they were 15 days old, at which time they were about 8 inches high, and were green, vigorous, healthy, and in good condition. They were then treated in accordance with the plan given in table 1. In some cases, depending on the nature of the agent applied, the treatment was given after the plants had been transferred to distilled water. This was the case with Nos. 3, 4, 5, 6, 9 and 10. Cultures 7, 8, and 11–16 were treated while still in the

full nutrient medium, after which they were transferred to distilled water. In all instances, however, the roots were carefully rinsed before being placed in the water.[1]

To determine if any impurities had contaminated the distilled water in the cultures treated with ice, the distilled water in No. 4 was renewed after the operation. The resulting crop, however, was practically the same in cultures 3 and 4 and hence it may be considered that no plant food had entered from the ice. The distilled water was renewed in No. 10 a few hours after the treatment. The result of so doing was to discard the plant foods already excreted during, and immediately after, the treatment. This fact was evident from the better growth of the plants in No. 9 as compared with those in No. 10. Later work also showed that exosmosis caused by treatment with illuminating gas and other agents is comparatively rapid and immediate.

After the treatment the plants remained in the distilled water for 5–6 days, after which they were discarded. The distilled water level was then raised to the original height by adding fresh distilled water, and into this medium fresh Canada field pea seedlings were placed and the resulting growth determined. Cultures Nos. 17–24 are given in table 1 for comparison. After pea seedlings had been grown for 21 days in the unrenewed distilled water of cultures 17–20, the original plants were discarded and fresh seedlings of peas and horse beans were placed in the same distilled water. For comparison, cultures of these plants (Nos. 21–24) were set up at the same time in fresh distilled water.

Returning now to the effects of the treatments on the plants and noting the results given in table 1, we see marked differences evident. Neither the ice nor the inoculation with *Ascochyta Pisi*[2] produced any effect either on the plants or on the excretions from their roots, and hence these cultures are sim-

[1] The usual method of rinsing throughout this work was as follows: The solution to be discarded was thrown out, the tumbler filled twice with once-distilled water (the roots replaced and the whole thoroughly shaken each time), and then distilled water (redistilled) was added, the roots replaced, and the readings taken.

[2] Cultures of *Ascochyta Pisi* were kindly supplied the writer by Dr. R. E. Vaughan.

ilar and comparable to the untreated controls. Marked injury resulted in the case of the heat, illuminating gas, $MgCl_2$, and H_2SO_4, all in characteristic manner. The injury from KOH was rather slow in manifesting itself, but the coloration of the roots was a noticeable feature. An interesting condition to be noted here, which holds true also in the later experiments, is in regard to the effect of the heat and the illuminating gas. It should be borne in mind that during these treatments the roots remained in water. The tops only were affected and died; the roots remained white, turgid, and normal in appearance even though the exosmosis from them had been excessive, thus indicating a transfer of some electrolytes from the tops and down into the medium through the roots. Later experiments also substantiated the fact that abundant exosmosis sometimes occurs from roots which remain normal in appearance. The other agents ($MgCl_2$, H_2SO_4, and KOH) caused more or less injury to both tops and roots. The exosmosis of nutrients into the water from the affected plants is evident by the greater growth of fresh pea seedlings placed in such water as compared with the controls. Both peas and horse beans grew somewhat better in fresh distilled water than in distilled water in which pea seedlings had already been grown for 21 days.

Further preliminary experiments along this line gave similar results. Thus in another series, vigorous, thrifty plants of Canada field peas grown 10 days in full nutrient solution were transferred, after rinsing the roots, to distilled water, some being untreated and others treated. The treatment consisted in placing some of the cultures in an atmosphere of illuminating gas for 3 and 6 hours, and others in a gas-heated oven for 1 and 2 hours where it was not aimed to keep the temperature constant. For those cultures in the oven 1 hour the temperature at the outset was 53°C. and at the end 33°C., while for those remaining in the oven 2 hours the initial temperature was 60°C. and the final 33°C. The conductivity of the water was measured soon after the plants were placed in it but before the treatment, and again 5 days after treatment,

at which time the plants were discarded and a fresh lot of pea seedlings substituted.

The average reading (value of x) of the water for the 4 untreated controls at the beginning was 14.6 on the Wheatstone bridge, and with the same resistance in the box (9,110 ohms) it was 12.6 after 5 days. For the 4 cultures treated with illuminating gas (2 cultures for 3 hours and 2 cultures for 6 hours, the resultant effect being approximately the same for the two periods of exposure) the average initial reading was 17.0 for a resistance of 9,110 ohms, and at the end of 5 days it was 43.7 for a resistance of 1,000 ohms. In this case the increase in terms of specific conductivity was from 9.2×10^{-6} to 317.3×10^{-6}.

In the 4 cultures placed in the oven at the temperature designated there was no marked difference as regards variation in conductivity of the medium. The average initial reading was 17.2 and at the end (after 5 days) it was 12.4, the resistance in the box being 9,110 ohms in both readings. The rather high initial readings in the above cases are due to the fact that it was some hours after the roots were placed in the water before the readings were taken. In later work it was found to be advantageous to have the interval between placing the roots in the water and taking the first reading reduced to exactly one-half hour in order to obtain comparative data on the initial rate of exosmosis under different conditions.

We have, of course, no indication from the above regarding the exosmosis or conductivity curve during the 5-day interval. Subsequent work shows that it is very probable that the curve rose considerably in the case of the untreated and the oven-treated cultures and then fell, at the end of 5 days, to a position lower than that of the initial reading, due to the absorption being greater than the excretion after the first 2 or 3 days.

Let us turn now to the results obtained with the fresh seedlings grown in the same water in which the first crop had remained for 5 days under the conditions indicated above. After the second crop had been growing in this medium for just 15 days the green weight of tops of the 4 cultures in each group

was determined, with the following results, the figures representing the average green weight of tops in each culture:

Previous crop untreated	3.39 grams
Previous crop treated with illuminating gas	4.38 grams
Previous crop in oven 1 and 2 hrs. at 60–33°C	3.35 grams

V. Effects of Anesthetic Vapors

For this work the method used was to place the cultures (in some cases the medium also, in which instances the roots were in the water during exposure, and in other cases only the plants themselves, thus exposing the roots directly to the vapor) under bell jars into which the anesthetics were subsequently placed. In the case of ether and chloroform a meas-

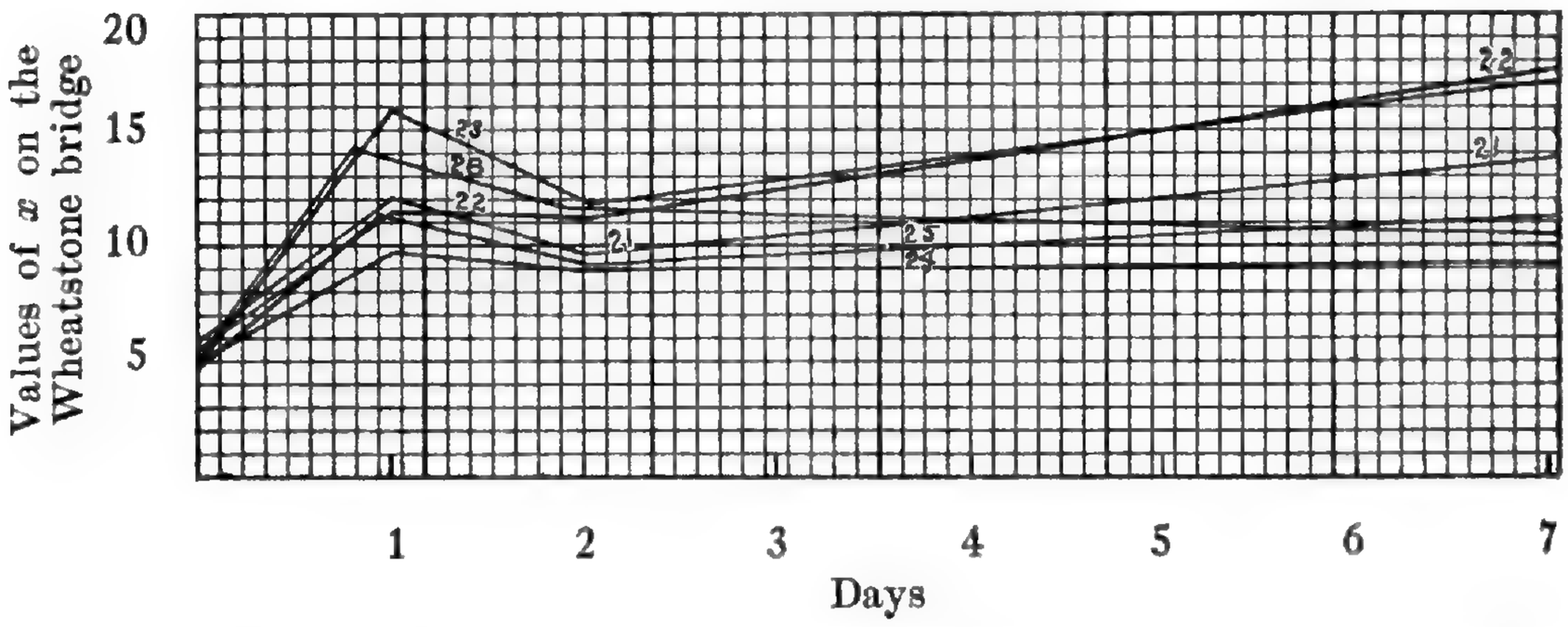

Fig. 1. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment with anesthetics, as follows: No. 21, ether vapor, 1 minute, roots exposed; No. 22, control—roots exposed under bell jar 1 minute; No. 23, ether vapor, 2 minutes, roots exposed; No. 24, ether vapor, 5 minutes, roots exposed; No. 25, ether vapor, 10 minutes, roots exposed; No. 26, ether vapor, 15 minutes, roots exposed. The plants used were 39 days old. The first reading in each case is of the distilled water before the roots were placed in it.

ured amount of these agents was placed in an open evaporating dish under the bell jar, and after the treatment the residue was measured to determine the amount which had evaporated; in the case of the illuminating gas, however, the agent was run in until the air in the bell jar was more or less completely replaced. Where the plants alone were placed under the bell jars they were carefully attached by cheese-cloth bands to the leg of an inverted tripod, over which the bell jar was then placed.

In figures 1 and 2 are shown the results of treatment with ether and illuminating gas for varying periods of time. The plants for this experiment were 39 days old at time of treatment and had roots in good condition and well developed. The

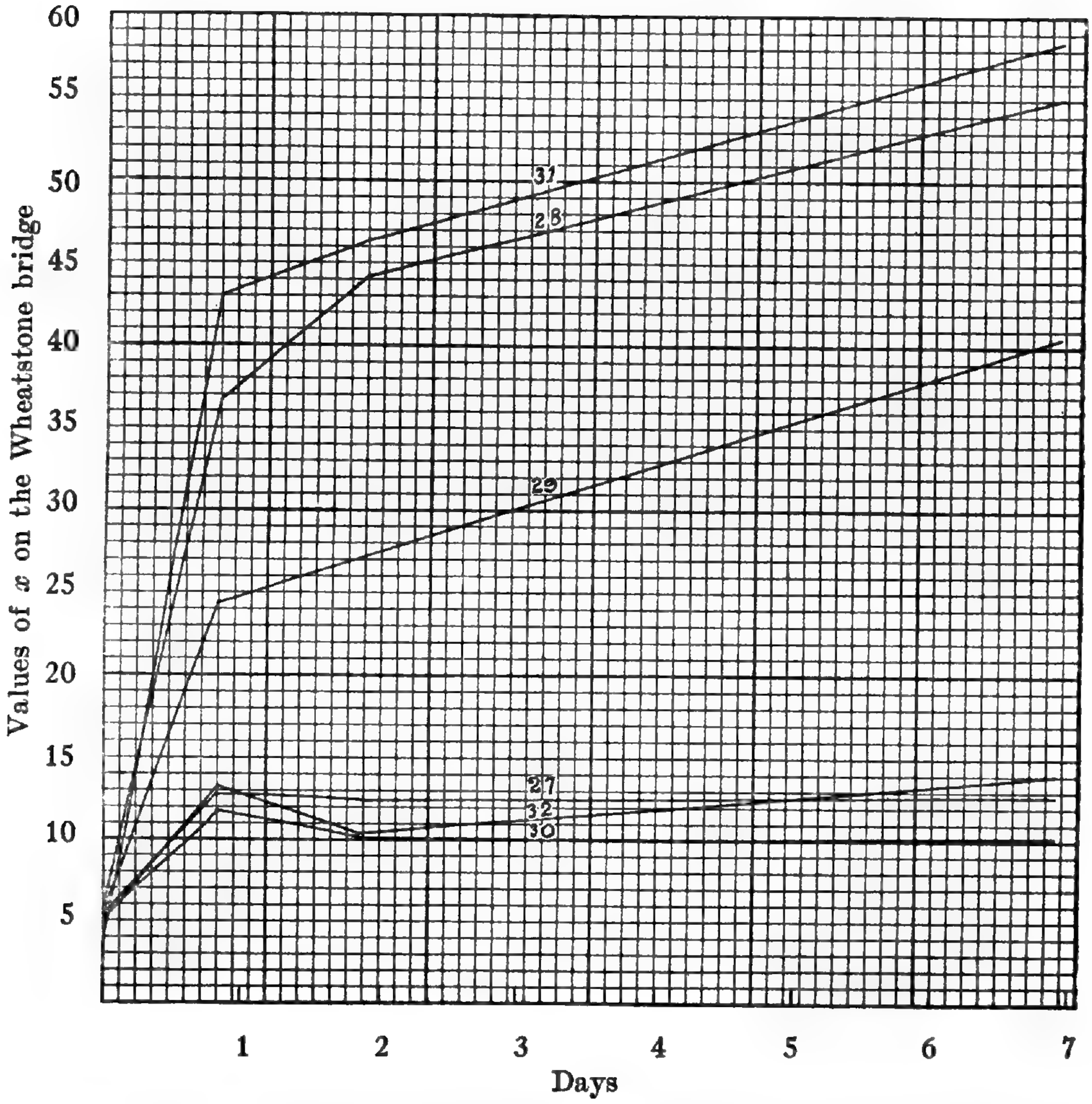

Fig. 2. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment with anesthetics, as follows: No. 27, illuminating gas, 5 minutes, roots exposed; No. 28, illuminating gas, 10 minutes, roots exposed; No. 29, illuminating gas, 15 minutes, roots exposed; No. 30, control—roots exposed under bell jar 15 minutes; No. 31, ether vapor, 3 hours, roots in tumbler; No. 32, control—under bell jar 3 hours, roots in tumbler. The plants used were 39 days old. The first reading in each case is of the distilled water before the roots were placed in it.

first conductivity readings of the water were taken before the plant roots were introduced. As seen from the plotted results the ether had no effect on the exosmosis when the duration of the exposure ranged from 1 to 15 minutes; after 3

hours exposure, however, the exosmosis was pronounced, even when the roots were not in direct contact with the vapor.

An exposure of only 5 minutes to illuminating gas produced no effect, but one of 10 or 15 minutes' duration caused considerable exosmosis. That the 15-minute exposure should result in less exosmosis than the 10-minute one is an interesting point which finds an analogy, we shall see, at different places throughout the work, where in isolated cases a briefer exposure or milder treatment results in greater conductivity of the medium than a somewhat more prolonged exposure or more severe treatment. Where such a condition exists it is usually found near the boundary line of noticeable effect, and not where the effect is either nil or very pronounced. At this critical point the individual hardihood of the plants themselves seems the most plausible explanation of the difference. As the manipulation methods were exactly similar for any given series it is altogether unlikely that difference in technique was responsible for the variation.

The only plants to sustain any injury were those of cultures 28, 29, and 31. The tops of those in No. 31 drooped immediately after the treatment and soon died, though the leaves remained green; the roots, however, remained entirely normal to all appearances and retained their turgor. This is an interesting point and was referred to above. After 7 days Nos. 28 and 29 plainly showed some injury, but it was slight, and its visible effects were slow in making their appearance. At that time the tops of these cultures showed greater yellowing and drying than did those in the controls, No. 29 being somewhat more affected than No. 28; the roots of both, however, remained normal in appearance.

The greatest contrast between the treated plants and the controls is seen in fig. 3. The effect on the treated cultures corresponds to the duration of treatment, the curves especially showing the difference in the speed of initial exosmosis. It will be seen that the conductivity curves of the controls rise rather high during the first day. This is no doubt due to the effect of rather prolonged exposure of the roots to the air in the bell jar, even though it was saturated with water vapor.

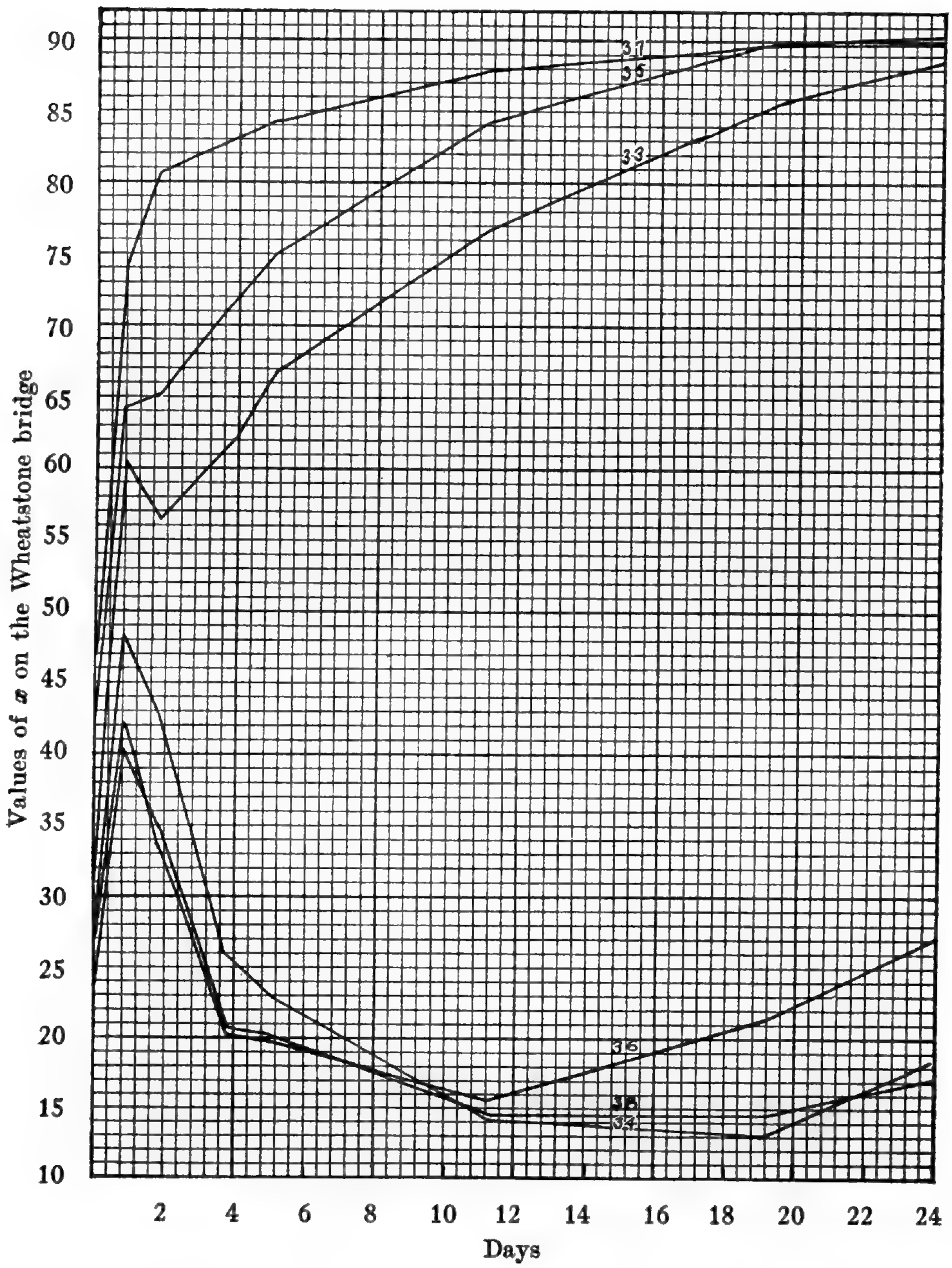

Fig. 3. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 33, illuminating gas, 15 minutes, roots exposed; No. 34, control—roots exposed under bell jar 15 minutes; No. 35, illuminating gas, 30 minutes, roots exposed; No. 36, control—roots exposed under bell jar 30 minutes; No. 37, illuminating gas, 1 hour, roots exposed; No. 38, control—roots exposed under bell jar 1 hour. The plants were 22 days old when treated. The first readings were taken in the various cultures after the roots had been in distilled water for the following periods: No. 33, 35 minutes; No. 34, 1 hour and 15 minutes; No. 35, 1 hour and 13 minutes; No. 36, 1 hour and 25 minutes; No. 37, 1 hour and 5 minutes; No. 38, 1 hour and 16 minutes.

The subsequent decline in the curve, however, is characteristic for normal root tissues. It is also seen here that the 15-minute exposure to illuminating gas resulted in a greater rise in the conductivity curve than did a similar exposure in the case of the cultures recorded in fig. 2. That this is due to the different ages of the plants in the two cultures was borne out by treatment of plants of different ages with other agents. The older the tissues the more resistant they become to the toxic substance. McCool ('13) was the first to point this out, in his experiments with manganese chloride, and we see that it here holds for anesthetics as well.

Figure 4 shows the effect of illuminating gas at different intervals when only the tops are exposed directly to the gas, the roots meanwhile remaining in distilled water. The plants were affected in proportion to the duration of treatment. The tops of No. 39 were only very slightly injured, so that there was practically no difference between them and the tops of the controls; No. 41 was affected more; and No. 43 still more, finally dying, after progressive drooping and yellowing. But here again the roots of the treated plants were in all respects similar to those of the controls and entirely unaffected, visibly, even though exosmosis was considerable. In such cases it was also presumed that the excreted substances came in part from the tops and that here we had an illustration of the downward flow of food materials which occurs in plants under natural conditions. This presumption was considered experimentally as follows:

Some cultures were placed under a bell jar and treated with illuminating gas as before, the roots meanwhile being in distilled water. The tops of one culture were not cut off, while those of another were removed just before treatment, and finally those of a third were removed just after treatment. The controls were not treated, but their tops were cut off immediately after the roots were placed in the distilled water. The treated plants all gave approximately the same exosmosis, which was considerably more than that from the controls. A point to be noted here is that even though the treated tops which were not cut off were very much affected,

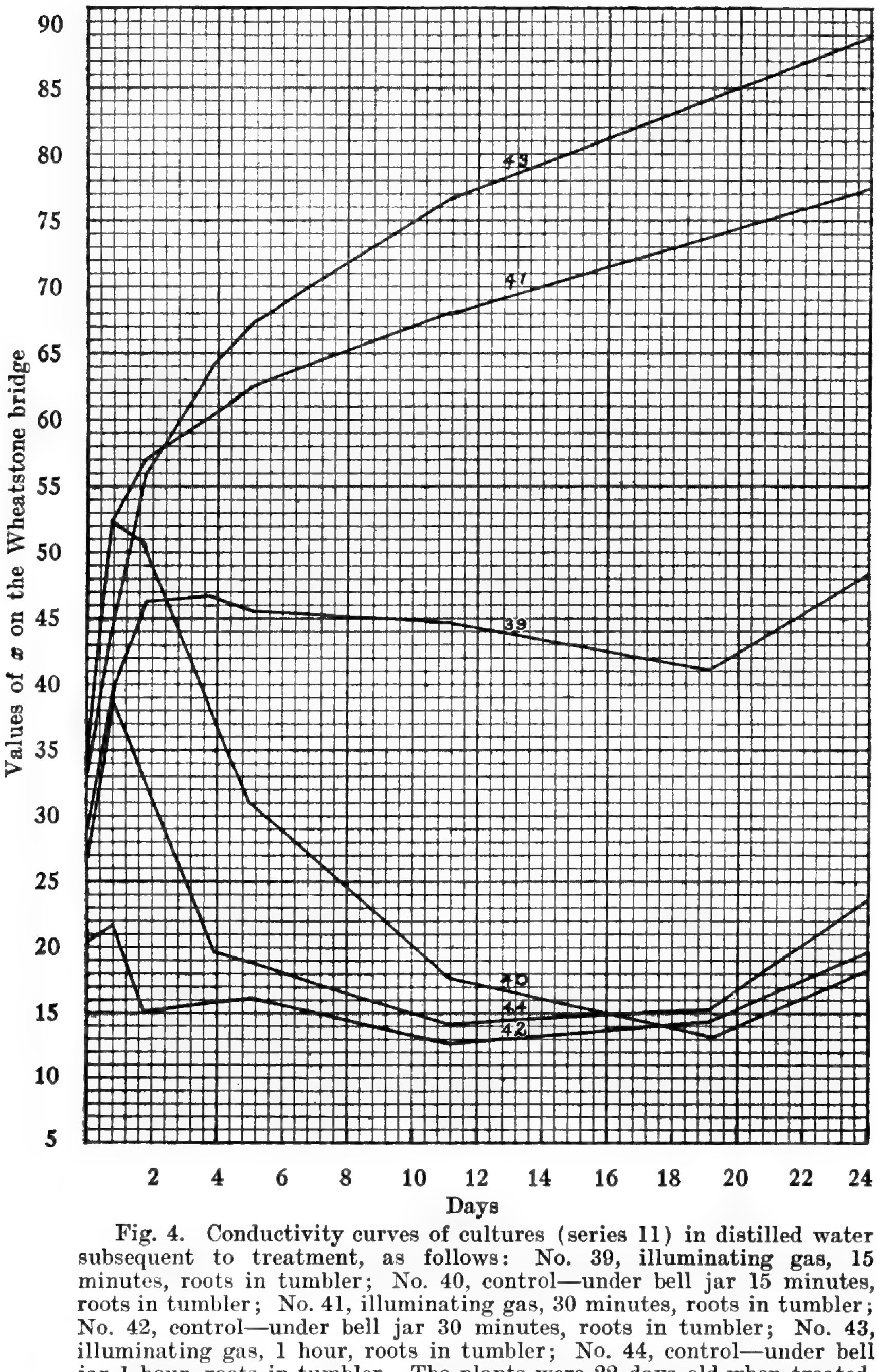

Fig. 4. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 39, illuminating gas, 15 minutes, roots in tumbler; No. 40, control—under bell jar 15 minutes, roots in tumbler; No. 41, illuminating gas, 30 minutes, roots in tumbler; No. 42, control—under bell jar 30 minutes, roots in tumbler; No. 43, illuminating gas, 1 hour, roots in tumbler; No. 44, control—under bell jar 1 hour, roots in tumbler. The plants were 22 days old when treated. The first reading was taken in the various cultures after the roots had been in the distilled water subsequent to the treatment for the following periods (but to these periods should be added the time the cultures were under the bell jar, for the roots were in the distilled water during that interval also): No. 39, 2 hours and 12 minutes; No. 40, 2 hours and 23 minutes; No. 41, 2 hours and 20 minutes; No. 42, 2 hours and 30 minutes; No. 43, 2 hours and 11 minutes; No. 44, 2 hours and 23 minutes.

the roots meanwhile remaining practically normal, transpiration no doubt still continued. It remains an open question, however, whether such transpiration caused lower conductivity readings, due to the consequent absorption of electrolytes, than would have been the case had there been no, or only slight, transpiration, as in the cases where the tops were removed. The roots in all the cultures remained turgid and practically

TABLE II

EFFECTS OF ILLUMINATING GAS ON THE EXOSMOSIS FROM THE ROOTS OF PLANTS UNDER VARIOUS CONDITIONS

Culture no.	Treatment	Interval in dist. H_2O before first reading	Conductivity Readings*			
			After first interval	After 24 hrs.	After 88 hrs.	Increase‡ over dist. H_2O after 88 hrs.
1 and 2	Controls in dist. H_2O, no gas treatment. Tops cut off immediately after placing roots in dist. H_2O....	10 hrs.	33.6	37.9	41.8†	35.8†
3	Illuminating gas 1 hr.; roots in tumbler. Tops not cut off.....	1 hr., 17 min.	18.4	38.9	56.7	50.7
4	Illuminating gas 1 hr.; roots in tumbler. Tops cut off immediately after exposure.....	1 hr., 23 min	23.4	46.6	61.6	55.6
5	Illuminating gas 1 hr.; roots in tumbler. Tops cut off just before exposure.....	1 hr., 28 min.	18.6	41.2	60.5	54.5

* Readings represent the values of x on the Wheatstone bridge, resistance in box being 9,110 ohms.

† After 99 hours.

‡ The average reading of the distilled water before roots were placed in it was approximately 6.0.

normal. The higher readings of the treated cultures whose tops had been removed, over those of the untreated controls are to be considered as due to the effect of the illuminating gas, even though in one case only part of the plants was exposed to the agent. The results of this experiment are given in table II.

The results of ether vapor treatment for different periods are seen in fig. 5. An interesting point in this connection is the decline in the curves of the treated plants comparable in

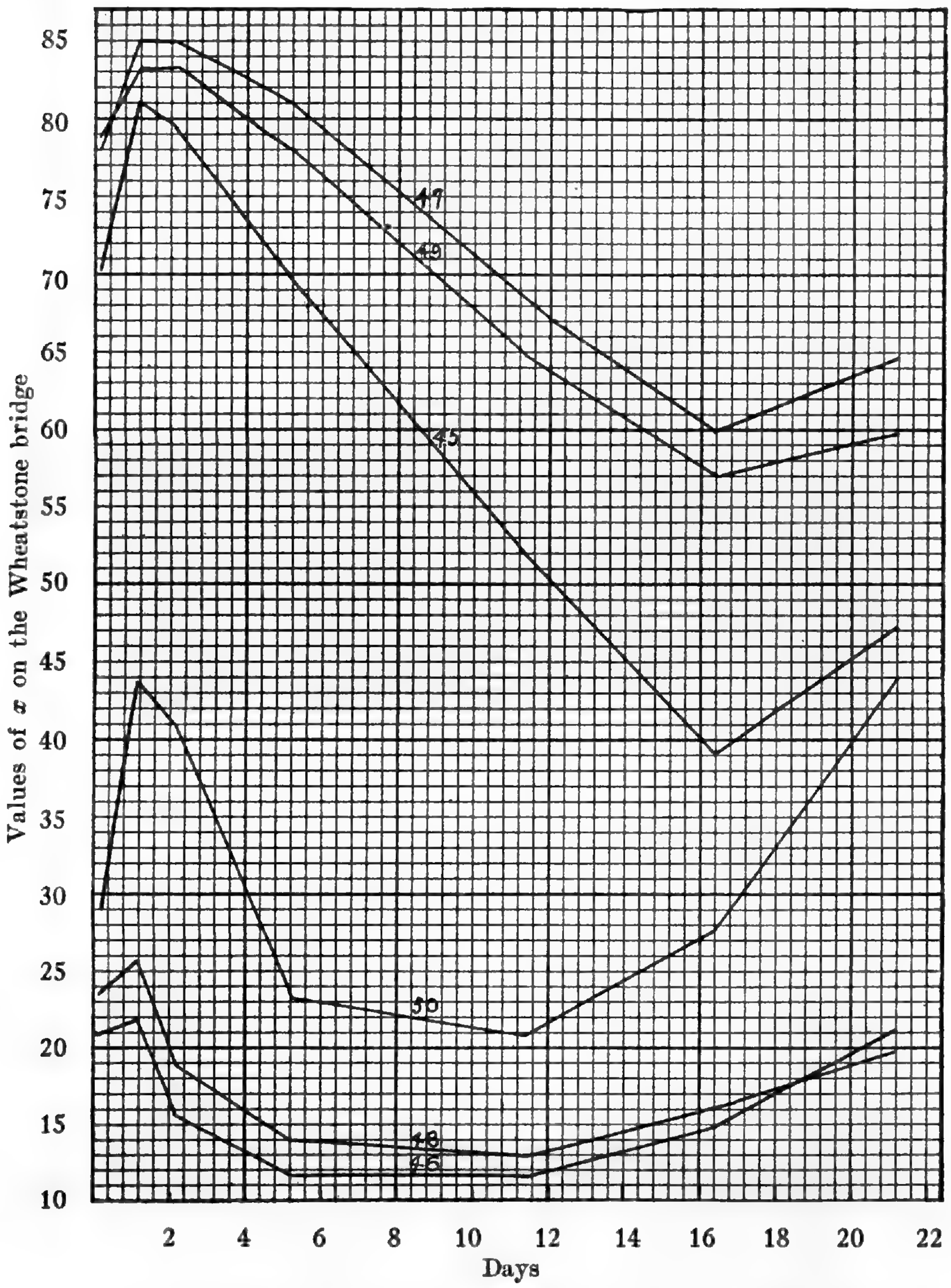

Fig. 5. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 45, ether vapor, 30 minutes, roots exposed; No. 46, control—roots exposed under bell jar 30 minutes; No. 47, ether vapor, 1 hour, roots exposed; No. 48, control—roots exposed under bell jar 1 hour; No. 49, ether vapor, 2 hours, roots exposed; No. 50, control—roots exposed under bell jar 2 hours. The plants were 25 days old at the time of treatment. In culture 49, 17cc. of the initial 50cc. of ether remained at the end of the 2 hours. The first reading plotted in each case was taken after the roots had been in the distilled water subsequent to the treatment for the following periods: No. 45, 1 hour and 1 minute; No. 46, 1 hour and 12 minutes; No. 47, 1 hour and 27 minutes; No. 48, 1 hour and 38 minutes; No. 49, 1 hour and 17 minutes; No. 50, 1 hour and 28 minutes.

some respects to that in the curves obtained from normal plants. A distinction should be made here, however, from the causal agency in this decline in conductivity and the anesthetic reversibility that Osterhout ('13) describes. The decline in the curve indicates that the absorption of electrolytes by roots occurs at a greater rate than they are excreted, for both processes, absorption and excretion, are undoubtedly going on and the curve represents the proportionate amounts of each for any given time. Thus if A represents the excretion and B represents the absorption, the curve declines when B is greater than A, and inclines when A is greater than B. Hence the curve may be represented as $A - B = C$, where C represents the number of ions or charge-carriers in the solution. The tops of the treated plants showed no visible effects whatever when compared with the controls. The roots of No. 45 were very slightly affected, but those of Nos. 47 and 49 were considerably so and to about an equal degree, as shown by flaccidity, root coloration, and the colored and turbid appearance of the medium; the tops, however, continued normal for 21 days after the treatment. Hence the metabolic processes no doubt proceeded unimpaired in many respects, as did also transpiration. The decline of the conductivity curve therefore represents merely a partial return to normal conditions. But the higher conductivity of the medium shows greater exosmosis than from the normal plants. This is due to the unalterable and invariable (and not reversible) effect of the anesthetic upon certain cells. Culture 50 shows in the higher position of its curve, as compared with the other controls, an effect that is no doubt due to the 2-hour exposure of the roots to the air in the bell jar.

As seen in fig. 6 no marked results followed the ether application for one-half to two hours when the roots were in the water during the treatment, though a slight rise is evident for the culture exposed 2 hours. No visible effects were produced on either the tops or roots.

Comparing the effects on plants of an ether vapor-saturated atmosphere with those produced by an illuminating gas-saturated atmosphere, it is thus seen that illuminating gas is much

more injurious than is ether vapor under the conditions of the experiment. Equal amounts of each might give different results, however. The gas used was a mixture of water- and coal-gas with a specific gravity of .62 as compared with air;

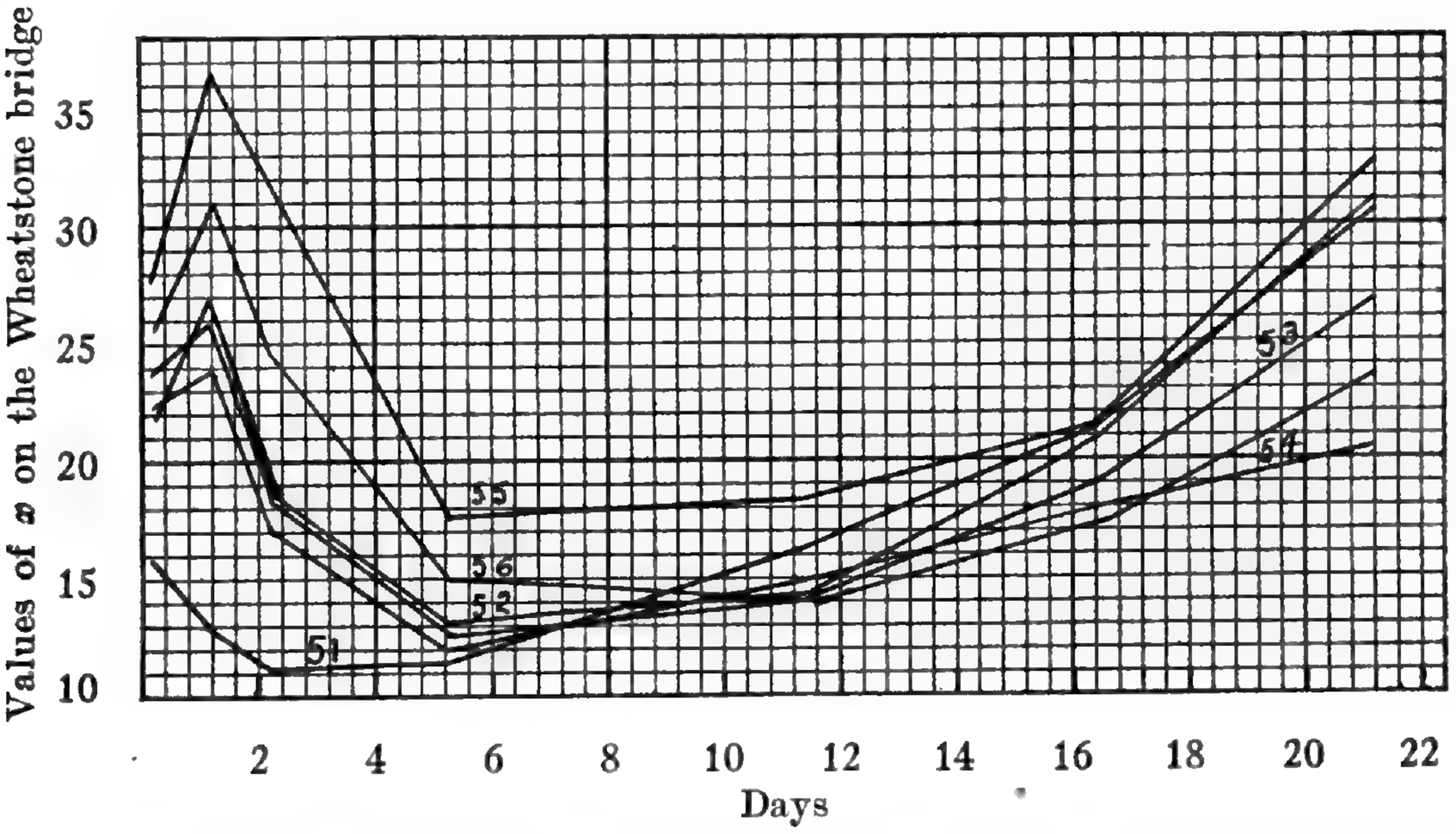

Fig. 6. Conductivity curves of cultures (series 11) in distilled water subsequent to treatment, as follows: No. 51, ether vapor, 30 minutes, roots in tumbler; No. 52, control—under bell jar 30 minutes, roots in tumbler; No. 53, ether vapor, 1 hour, roots in tumbler; No. 54, control—under bell jar 1 hour, roots in tumbler; No. 55, ether vapor, 2 hours, roots in tumbler; No. 56, control—under bell jar 2 hours, roots in tumbler. The plants were 25 days old at the time of treatment. In culture 55, 60cc. of the initial 100cc. of ether remained at the end of the 2 hours. The following periods represent the time elapsing in the various cultures between the removal of the cultures from the bell jar and the taking of the first reading (to which period should be added the duration of treatment, for the roots were in the distilled water during that time also): No. 51, 1 hour and 24 minutes; No. 52, 1 hour and 46 minutes; No. 53, 1 hour and 51 minutes; No. 54, 2 hours and 6 minutes; No. 55, 1 hour and 39 minutes; No. 56, 1 hour and 50 minutes.

one of the daily samples analyzed by the gas company (the officials of which kindly supplied the writer with the data and informed him that they may be considered an approximately fair average) showed the following constituents:

CO_2	3.0%
O_2	.5%
Illuminants (unsaturated hydrocarbons, e. g., ethylene and acetylene)	7.0%
CO	16.1%
CH_4	25.6%
H_2	42.8%
N_2	5.0%

Crocker and Knight ('08), in their work on the question of injury by illuminating gas and its constituents, concluded that "there is much evidence that indicates that the toxic limits of illuminating gas upon these flowers [carnations] is determined by the ethylene it contains." They used a small greenhouse of 1.69 cubic meters' capacity in which they placed potted plants for varying intervals, specified amounts of gas being introduced. The buds were easily injured but the vegetation was apparently not affected even after an exposure of about 72 hours, during which 10 liters of gas had been introduced, 2 or 4 liters at a time. The method was therefore somewhat different from the one employed by the author, in which the plants were placed in an atmosphere saturated with illuminating gas, but for a much shorter period. The underlying cause of the effect in both cases, however, is probably the same.

The etherization of plants as a practical process has been in operation for many decades, especially as a means of hastening the activities of plants, particularly of bringing them into bloom earlier. Some experimental work has also been done, as we have seen, on the effect of such treatment (though in most cases only when the anesthetics were in solution) upon the exosmosis of non-electrolytes, as determined by various methods, from plant or animal cells. It is interesting, therefore, to observe the exosmotic phenomena of electrolytes when the plants are anesthetized under various conditions.

To determine whether the amount of substance excreted corresponded to the conductivity readings, the water in the tumblers was evaporated and the residue weighed. The following are the results:

Total wt. of substance from illuminating gas-treated cultures (Nos. 33, 35, 37, 39, 41, and 43)	0.1514 grams
Total wt. of substance from ether-treated cultures (Nos. 45, 47, 49, 51, 53, and 55)	0.0674 grams
Total wt. of substance from the 12 controls	0.1077 grams
Total wt. of substance from 6 controls, therefore	0.0538 grams

We may obtain a rough basis for estimating this residue in terms of NaCl by comparing the figures just given with the data on a previous page which gave the corresponding specific conductivity values for some values of x on the Wheat-

stone bridge and also for various concentrations of NaCl. Thus 0.15 gram residue was obtained from 1500 cc. of the media from illuminating gas-treated cultures. This is equivalent to 0.10 gram in 1 liter, which in terms of NaCl would be

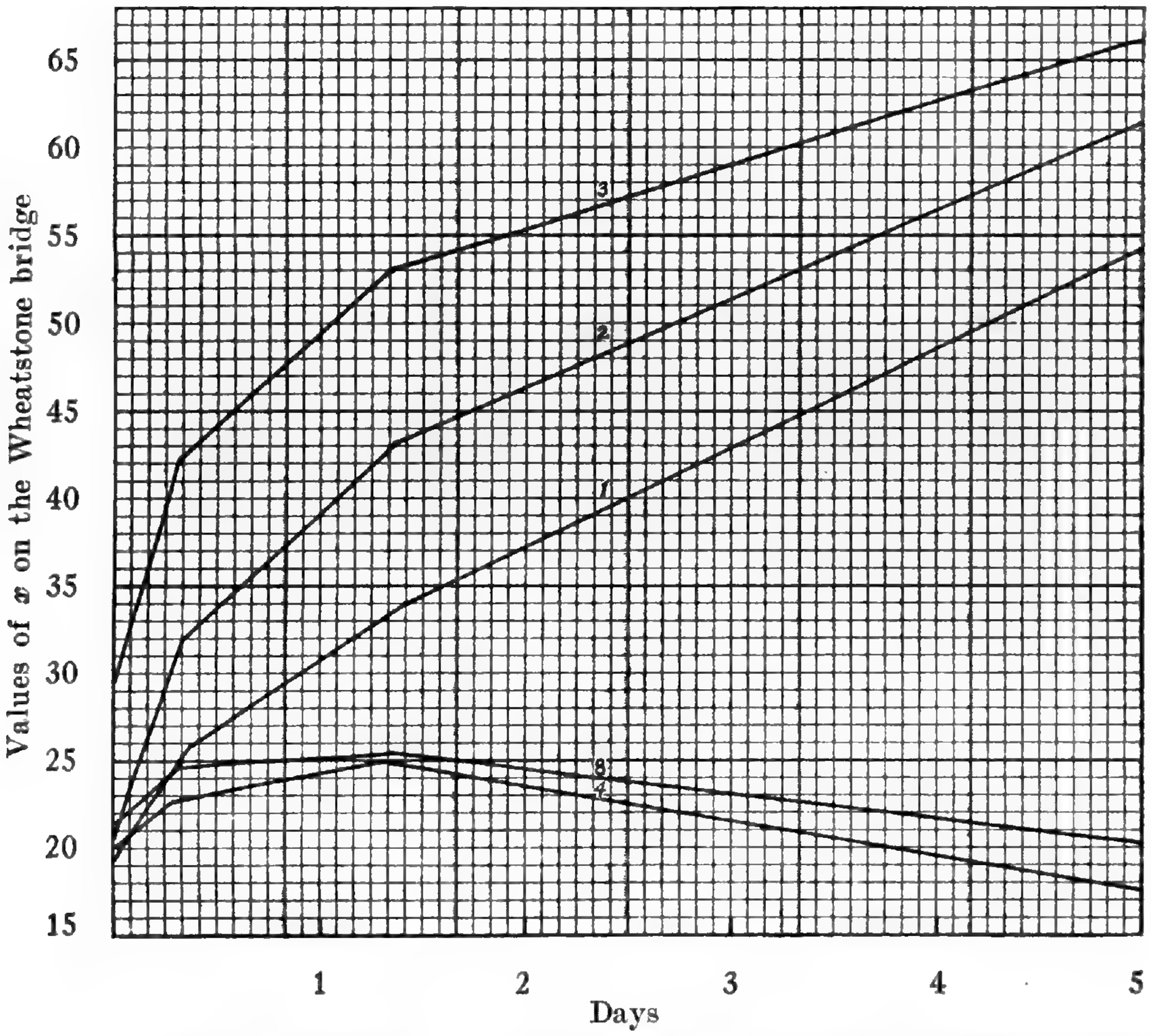

Fig. 7. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 1, temperature of —6 to —2°C., 1 hour, roots in tumbler; No. 2, temperature of —6 to —2°C., 2 hours, roots in tumbler; No. 3, temperature of —6 to —2°C., 3 hours, roots in tumbler; No. 4, control—room temperature, roots in tumbler; No. 8, control—room temperature, roots in tumbler. The plants were 23 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for the following respective periods (cultures 1–3 were being treated during part of that time): No. 1, 1 hour and 47 minutes; No. 2, 2 hours and 29 minutes; No. 3, 3 hours and 45 minutes; No. 4, 3 hours and 6 minutes; No. 8, 2 hours and 2 minutes.

approximately N/500. The specific conductivity of N/500 NaCl is about 25×10^{-5}, the x value of which on the Wheatstone bridge is 85. The average final reading of the 6 cultures treated with illuminating gas is 79.5. Hence the residue in terms of NaCl would be in the neighborhood of N/500.

VI. Effects of High and Low Temperatures

After the preliminary experiments noted above on the effect of heat had been carried out it was desired to study the question further and determine the resulting exosmosis curves at the extreme temperatures, high and low. The preliminary experiments had involved temperatures requiring a considerable time interval to produce positive results. The data now to be presented concern temperatures sufficient in themselves to effect decided injury in a very short period. By varying the time factor, therefore, results could readily be obtained on both sides of the point of injury.

For the experiment, the results of which are plotted in fig. 7, cultures were set out of doors for the time indicated, directly exposed to the winter temperature. The tops showed some signs of freezing after a few moments, but the effects did not become noticeably worse until the cultures were brought inside, when all the plants in each culture immediately drooped over the wire supports and became entirely limp, and soon died. The tops did not yellow, but retained the green color after death. Except for the root tips of the plants in No. 3, which were slightly brown at the end of 5 days, all the roots of the treated plants remained turgid, white, normal, and in healthy condition. This is interesting in view of the fact that while no ice was formed in No. 1, there was a slight fringe of it between the water and the tumbler in No. 2, and a hollow cylinder of ice one-fourth inch thick formed next to the tumbler wall in No. 3. In the last-mentioned culture there was also a film of ice over the surface of the water and the roots were frozen to the ice mass so that on lifting the plants from the tumbler the mass of ice adhered to the roots. The first readings were taken only after the ice had melted. The temperature at first was —6°C. but by the end of the first hour it had risen to —2°C., where it remained practically constant for the balance of the interval.

At a temperature of —6.5°C. it is seen by reference to fig. 8 that while for exposures of the plants alone (the roots being out of the water) of 2 and 3 minutes, marked exosmosis imme-

diately results, exposures of 1 minute or ½ minute produce no results. Culture 13 has rather high exosmosis for a control,

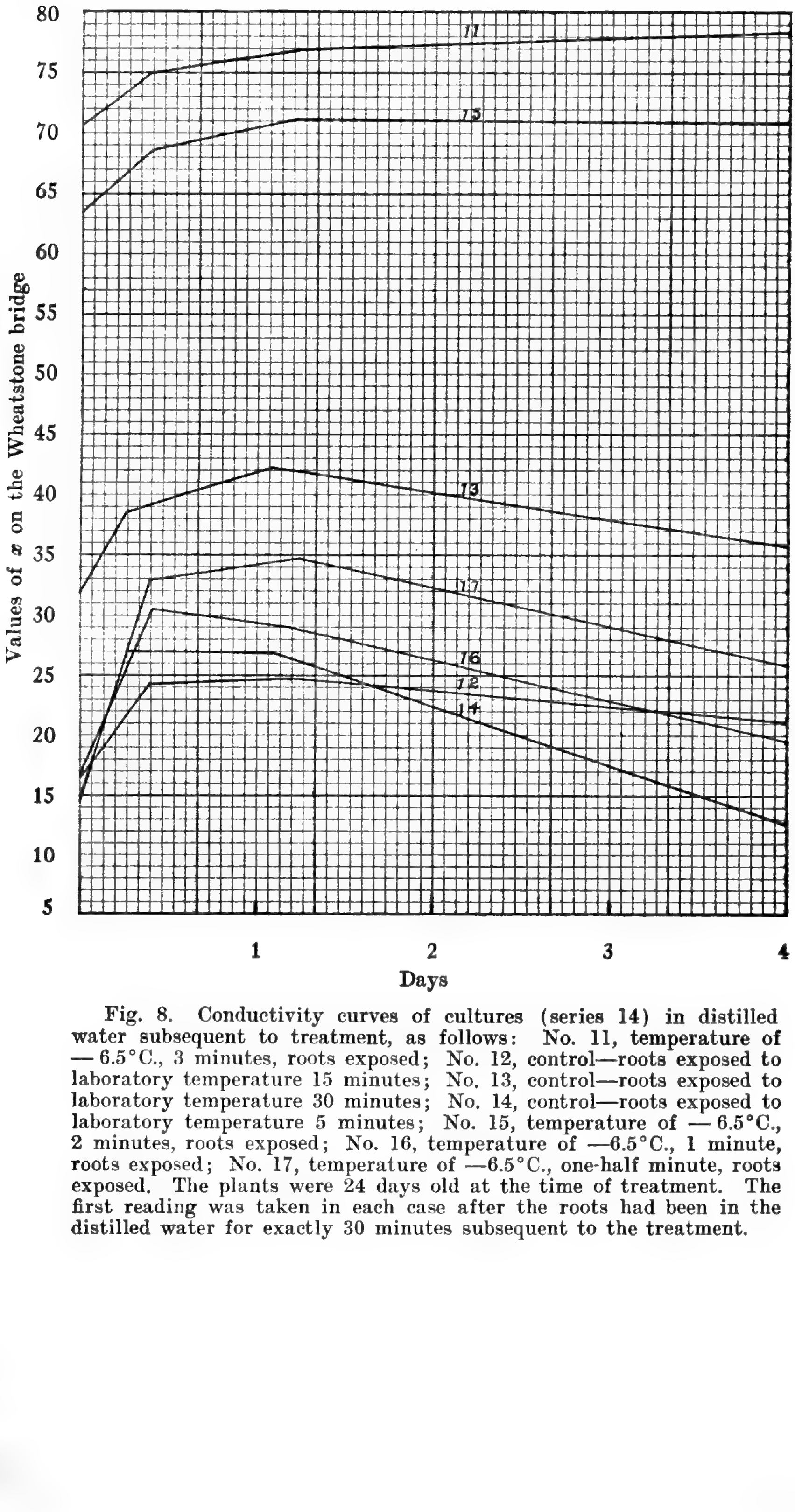

Fig. 8. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 11, temperature of — 6.5°C., 3 minutes, roots exposed; No. 12, control—roots exposed to laboratory temperature 15 minutes; No. 13, control—roots exposed to laboratory temperature 30 minutes; No. 14, control—roots exposed to laboratory temperature 5 minutes; No. 15, temperature of — 6.5°C., 2 minutes, roots exposed; No. 16, temperature of —6.5°C., 1 minute, roots exposed; No. 17, temperature of —6.5°C., one-half minute, roots exposed. The plants were 24 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for exactly 30 minutes subsequent to the treatment.

but this is readily accounted for by the exposure of its roots to the atmosphere of the laboratory for 30 minutes, a condition noted in other cases above.

Cultures 9 and 10 of this series, the results from which are not represented because both tops and roots were killed outright, the resulting exosmosis therefore being immediate and high (x being about 88.0 cm.), were exposed for 15 and 33 minutes respectively to a temperature of —6.5°C., the roots being out of the medium. In a very short time, on returning them to the laboratory, the tops wilted and drooped over the supporting wires and the roots became very flaccid. In the case of No. 11, however, an interesting gradation or intermediate condition was observed between it and Nos. 9 and 10 on one hand and between it and the controls on the other. While the tops in No. 11 wilted and drooped somewhat soon after being returned to the higher temperature of the laboratory, they did not become entirely limp and the roots were only slightly less turgid than those of the controls. Even after 4 days the tops of No. 11 were not drooping much, though the tips of the branches and the upper leaves were dead; the lower part of the stems and the lower leaves remained green and normal. The lateral roots and the older part of the main roots remained nearly normal, but the tips of the latter were flaccid and shrunken for about 2 inches. Culture 15 showed a very slight flaccidity in the tops and roots soon after the treatment, and after 4 days some of the younger leaves and the tips of the older leaves were blackened, curled, and dried somewhat, but the great part of the tops remained normal in appearance; the roots were slightly flaccid at the tips, but were in general practically normal. Cultures 12, 13, 14, 16 and 17 were normal in respect to both roots and tops.

The interval between 15 and 30 minutes is shown in fig. 9 to be the critical period for the pea plants exposed in a tumbler to a temperature of from —2°C. to —2.5°C., for an exposure of 30 minutes caused considerable exosmosis, while one of 15 minutes gave a curve approximately that for normal plants.

To contrast the effects of low and high temperatures, Nos.

25–28 inclusive are plotted in the same figure with Nos. 18 and 23. With plants enveloped in a steam bath the injury, as expected, is very speedy and effective. Even one-half minute —when the roots are exposed—causes immediate and marked

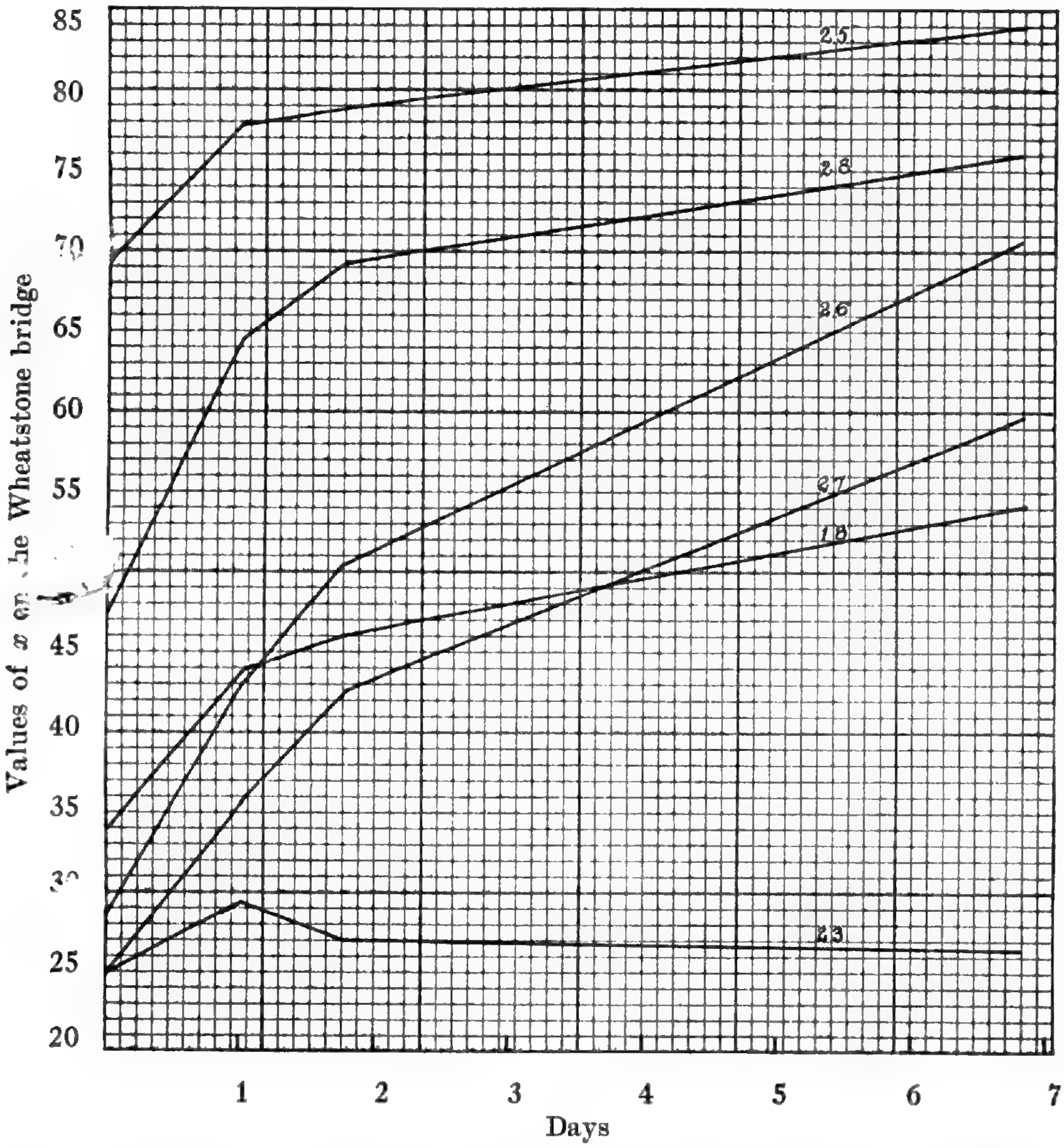

Fig. 9. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 18, temperature of —2.5°C., 30 minutes, roots in tumbler; No. 23, temperature of —2.0°C., 15 minutes, roots in tumbler; No. 25, steam, one-half minute, roots exposed; No. 26, steam, 2 minutes, roots in tumbler; No. 27, steam, 1 minute, roots in tumbler; No. 28, steam, 10 minutes, roots in tumbler. The plants were 29 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for the following respective periods (the cultures whose roots were in tumblers during the treatment were likewise in the distilled water): No. 18, 4 hours and 49 minutes; No. 23, 4 hours and 41 minutes; No. 25, 4 hours and 43 minutes; No. 26, 4 hours and 29 minutes; No. 27, 4 hours and 31 minutes; No. 28, 4 hours and 12 minutes.

exosmosis which is greater than that caused by a 10-minute exposure when the roots are in distilled water meanwhile. The condition of the plants immediately after the treatment and again after 7 days is given in table III. Here again is illus-

TABLE III

CONDITION OF PLANTS AFTER EXPOSURE TO VARIOUS TEMPERATURES

Culture no.	Condition of tops	Condition of roots
	Condition of plants immediately after the treatment:	
18	Considerably flaccid and drooping	Entirely normal
23	Very slightly drooping, nearly normal	Entirely normal
25	Drooping considerably	Normal
26 and 27	Drooping, green and damp	Normal
28	Drooping, green and damp	Apparently practically normal
	Condition of plants 7 days after the treatment:	
18	About half dead and half alive; 3 live stems with green, normal leaves	Entirely normal
23	Almost normal; tips of a few stems killed and some slightly injured, but some stems normal throughout; a few blackened leaves, but for the most part stems and leaves green and normal	Entirely normal
25	Dead	Only very slightly flaccid and nearly normal in appearance
26 and 27	Dead	Practically normal in appearance
28	Dead	Almost normal

trated, therefore, the case where there is considerable exosmosis without very marked visible effects resulting to the root tissues.

The effects of moist heat, as graphically represented in fig. 9, having been considered, we may now turn our attention to fig. 10, where the results are plotted of an exposure of plants to dry heat for short intervals, both with the roots directly exposed and with the roots remaining in the tumbler of water during the treatment.

It is seen that definite and positive exosmosis is obtained after a 4-minute exposure of the unprotected roots. The decline of the curve of No. 29, roots exposed for 2 minutes, is probably best accounted for by assuming greater hardihood of the plants in that culture, or that some condition effected an increase in transpiration. A 1-minute exposure (No. 30) pro-

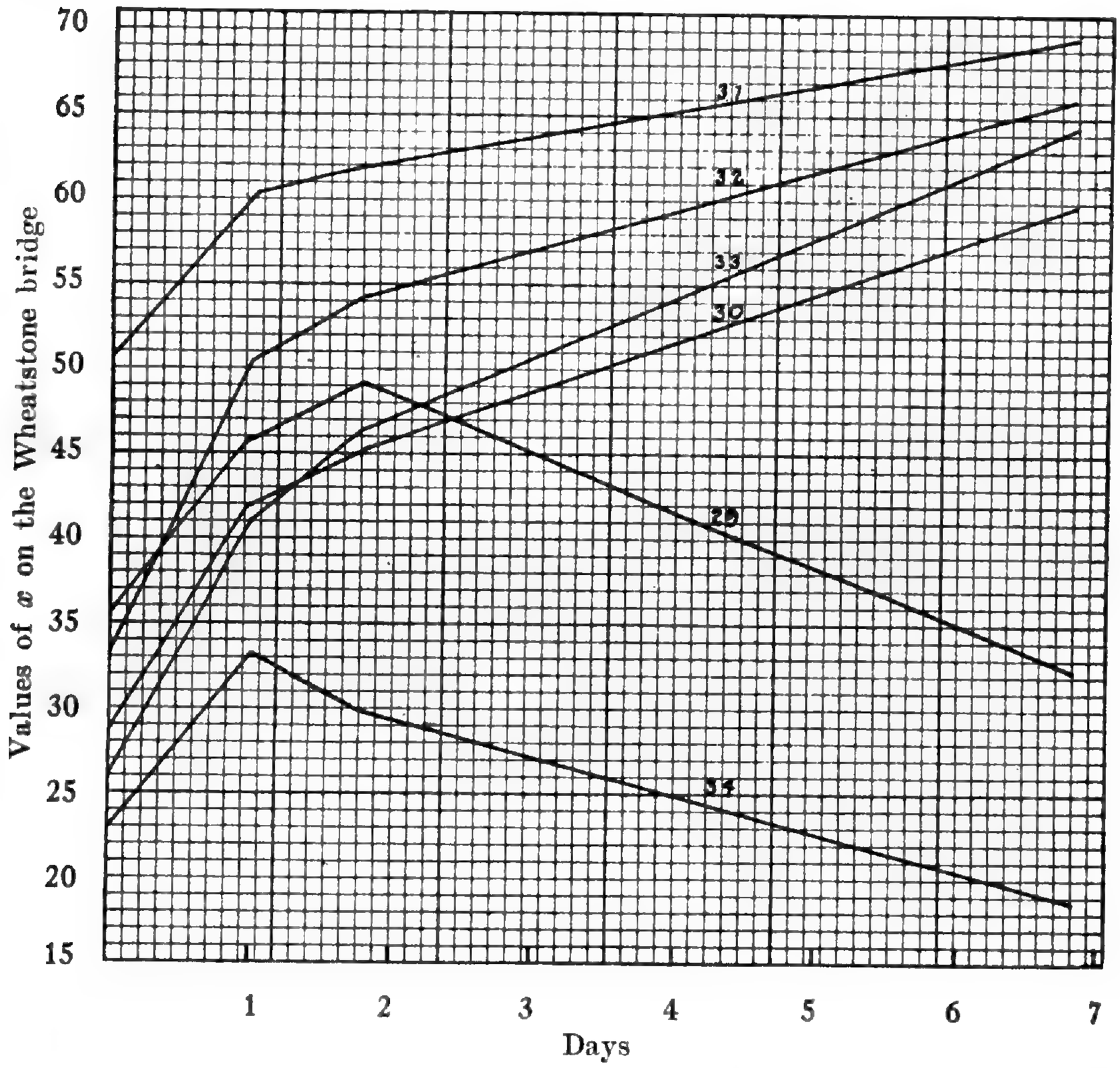

Fig. 10. Conductivity curves of cultures (series 14) in distilled water subsequent to treatment, as follows: No. 29, temperature of 92°C., 2 minutes, roots exposed; No. 30, temperature of 92°C., 1 minute, roots exposed; No. 31, temperature of 92°C., 4 minutes, roots exposed; No. 32, temperature of 92°C., 2 minutes, roots in tumbler; No. 33, temperature of 92°C., 4 minutes, roots in tumbler; No. 34, control—roots in tumbler at laboratory temperature. The plants were 29 days old at the time of treatment. The first reading was taken in each case after the roots had been in the distilled water for the following respective periods (the cultures whose roots were in tumblers during the treatment were likewise in the distilled water during that time): No. 29, 2 hours and 47 minutes; No. 30, 2 hours and 48 minutes; No. 31, 2 hours and 44 minutes; No. 32, 2 hours and 45 minutes; No. 33, 2 hours and 46 minutes; No. 34, 2 hours and 46 minutes.

duced less exosmosis at the beginning than was the case in No. 29, but finally caused more. The same irregularity is also noticed in Nos. 32 and 33. These irregularities near the boundary line of endurance have been discussed above. The tops of Nos. 29–33 were killed by the treatment, but the roots of all remained practically normal in appearance except in No.

31, where the tips were slightly shrunken at first but became almost normal in the water after 7 days.

In the temperature experiments we have thus used the extremes of temperature and have reduced the interval of exposure in order to approach the point at which the effect is just evident.

VII. Effects of Anesthetics in Solution

Having seen some of the effects of anesthetic vapors, we may turn our attention next to the results obtained with anesthetics in solution. In the investigations of others pertaining to the effect of anesthetics, already cited, the result has been almost universally noted that small amounts of anesthetics decrease the exosmosis of coloring matters, etc., while toxic amounts increase it. In most cases this exosmosis was explained on the basis of an alteration in the plasma membrane, small amounts of the anesthetics presumably reducing the permeability and large amounts increasing it. But a point worthy of note is that wherever such effects have been determined the substance under observation was either a colored compound or one of complex organic nature.

Thus Czapek ('11) used the myelin-formation of a tannoid substance, anthocyan, as a basis of observation. From the standpoint of a physical phenomenon, i. e., the lowering of surface tension, his experiments beautifully illustrated the principle under consideration. But from the standpoint of exosmosis in the broader sense we must include electrolytes (salts, bases, and acids) as well as tannin compounds in any discussion dealing with agents affecting exosmosis, and while the critical concentrations which he determined are undoubtedly characteristic of the plants and the compounds studied, the results given herewith show that they are not the limiting concentrations which effect the exosmosis of electrolytes from the roots of certain plants. The limiting concentrations which he found are given in table IV.

Czapek believed the permeability of the plasma membrane was altered under the influence of alcohols, ethers, etc., so that abnormal exosmosis occurred. Whatever may be the expla-

TABLE IV

CRITICAL CONCENTRATIONS (THOSE JUST SUFFICIENT TO CAUSE EXOSMOSIS) OF SOME ORGANIC COMPOUNDS AS DETERMINED BY CZAPEK FOR CERTAIN PLANTS

Agent	Plant	Concentration of agent	Surface tension*
Methyl alcohol	*Echeveria*	18% aqueous solution (by volume)	.71
Ethyl alcohol	*Echeveria* and *Saxifraga*	10–13% aqueous solution (by volume)	.65–.70
Ethyl ether	*Echeveria* and *Viola*	¼–½ saturated aqueous solution acting for 24 hrs	.61–.71
Chloroform	*Echeveria*	Saturated aqueous solution†	.98
Chloral hydrate		3.09% aqueous solution	.93
Ethyl acetate	Saxifraga hairs and variegated leaves of *Oplismenus imbecillus*	3% aqueous solution acting for 12 hrs	.69–.73
Ethyl acetate	Red beets	2% aqueous solution acting for 12 hrs	

* In terms of water as unity. † After 24 hours the cells had lost all tannin.

nation for the phenomena observed, it will be seen by comparing the results in the following experiments with the data just given that the limiting values found for the exosmosis of electrolytes do not at all correspond to the values found by Czapek for the exosmosis of the tannoid substance.

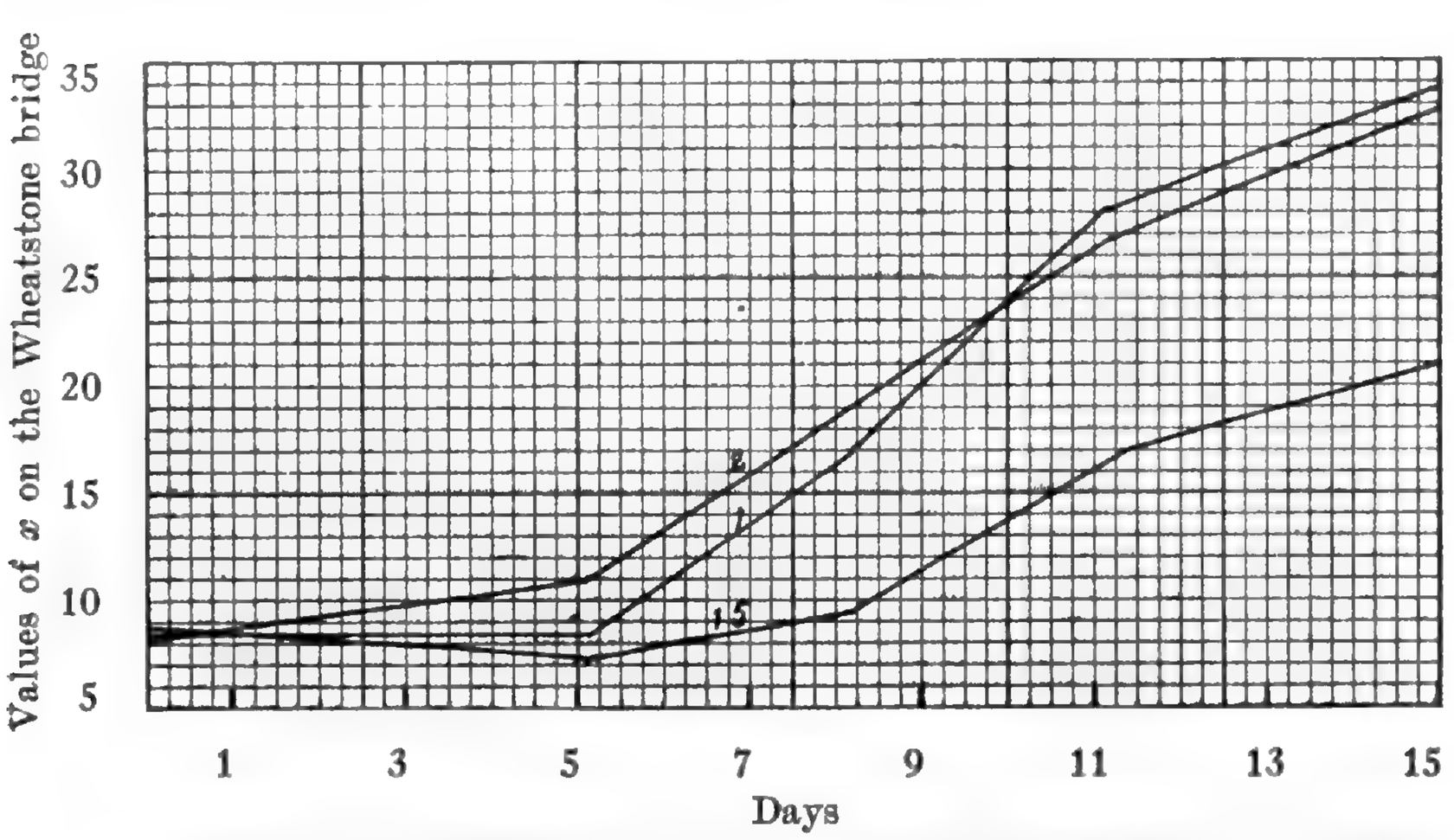

Fig. 11. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 1, ether vapor, 15 minutes, roots exposed; No. 2, 1 per cent ether in water, 15 minutes; No. 15, control—roots exposed under bell jar 15 minutes. The plants were 31 days old when treated. In culture 1, 11cc. of the initial 15cc. of ether remained after the 15-minute exposure. In Nos. 1 and 2, the first reading was taken exactly 30 minutes, and in No. 15, 48 minutes, after the roots were placed in the distilled water.

In fig. 11 are shown the results with ether in distilled water and, for comparison, also with ether vapor for the same period. The curves for the ether-treated cultures are closely parallel for the entire period of observation of 15 days, and both are

TABLE V

EFFECTS OF VARIOUS ANESTHETICS ON THE EXOSMOSIS FROM THE ROOTS OF PLANTS

(See curves in fig. 12)

Anesthetic	Time of exposure	Culture no.	Resulting exosmosis
Vapor Treatment, Roots Exposed			
Ether	30 minutes	3	About the same in Nos. 3 and 5
Illuminating gas	15 minutes	5	
Illuminating gas	30 minutes	7	Higher
Chloroform	30 minutes	9	Highest
Treatment with Anesthetics Dissolved in Water			
Ether, 4%	30 minutes	4	High
Ether, 4%	Throughout experiment	11	Highest
Ether, 10%	30 minutes	12	Higher
Illuminating gas-saturated sol'n.	15 minutes	6	Medium low
Illuminating gas-saturated sol'n.	30 minutes	8	Like control
Illuminating gas-saturated sol'n.	Throughout experiment	13	Medium low
Illuminating gas-saturated sol'n. frequently re-saturated	30 minutes	14	Slightly above control
Chloroform, 4%	30 minutes	10	Very high
Controls			
Roots exposed to the air under a bell jar	30 minutes	16	High for control
Roots exposed to the air under a bell jar	30 minutes	17	High for control
Roots not exposed, but in water from first		18	Normal for control

above that of the control. The excretion was nil during the first half hour and at the end of 5 days it was scarcely more, though it may have risen and fallen in the meantime, as no readings were taken in the interim. After 5 days a greater rise in the conductivity curve occurred with the ether-treated cultures than with the control; no apparent effects, however, were produced on either the tops or roots.

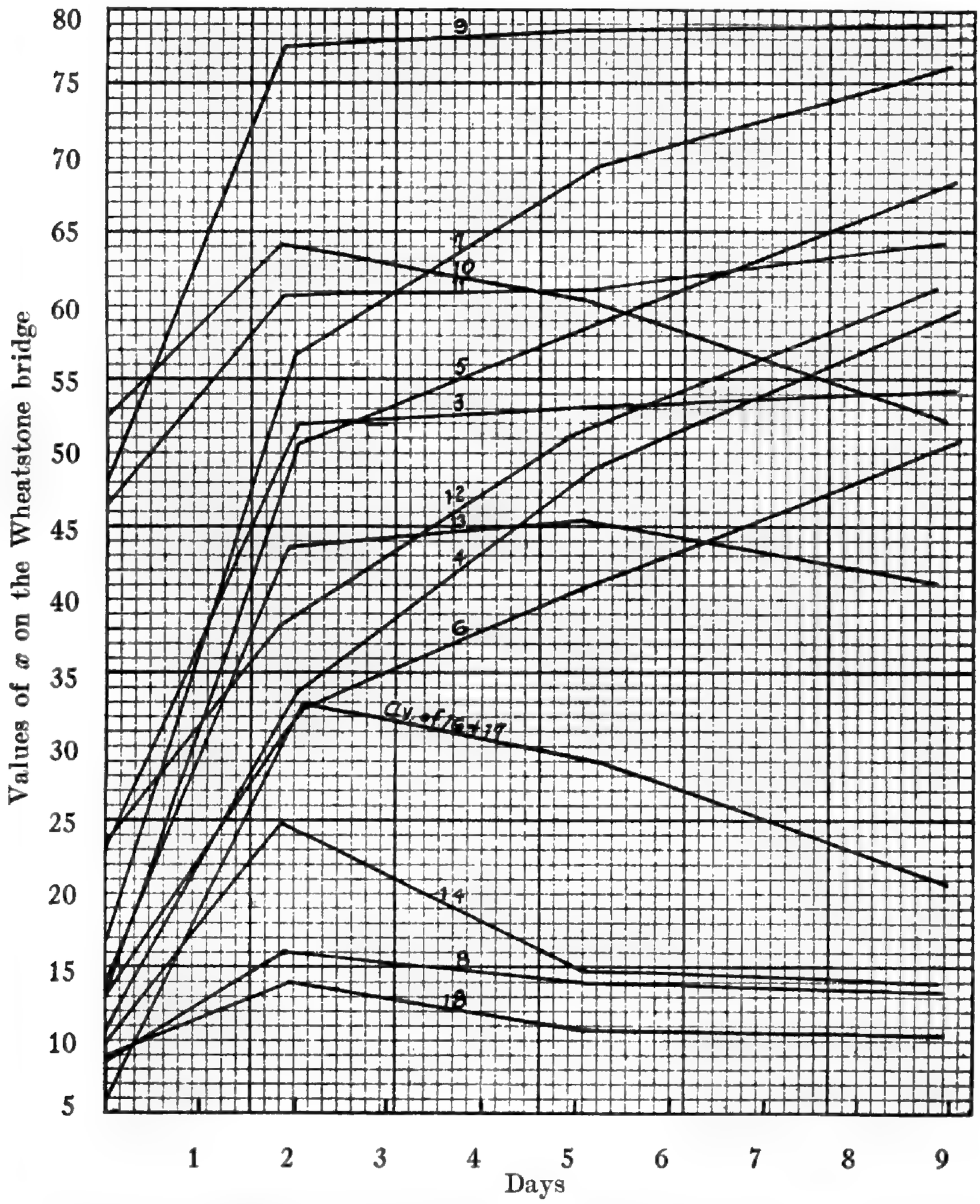

Fig. 12. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 3, ether vapor, 30 minutes, roots exposed; No. 4, 4 per cent ether in water, 30 minutes; No. 5, illuminating gas, 15 minutes, roots exposed; No. 6, distilled water saturated with illuminating gas, 15 minutes; No. 7, illuminating gas, 30 minutes, roots exposed; No. 8, distilled water saturated with illuminating gas, 30 minutes; No. 9, chloroform vapor, 30 minutes, roots exposed; No. 10, 4 per cent chloroform in water, 30 minutes; No. 11, 4 per cent ether in water, to the end of the experiment; No. 12, 10 per cent ether in water, 30 minutes; No. 13, distilled water saturated with illuminating gas, to end of experiment; No. 14, distilled water saturated with illuminating gas, 30 minutes (frequently saturated); No. 16, control—roots exposed 30 minutes under bell jar; No. 17, control—roots exposed 30 minutes under bell jar; No. 18, control—roots placed directly into distilled water. The percentages given above refer to volume-per cent. The plants were 37 days old when treated. The first reading was made after the roots had been in distilled water 30 minutes (No. 10, 36 minutes). In all cases treatment preceded placing of the roots in distilled water (conductivity of which was determined except in the cases of Nos. 11, 13, and 18). In culture 3, 17cc. of the initial 25cc. of ether remained at the end of the 30-minute exposure; in culture 9, 23.5cc. of the initial 25cc. of chloroform remained.

To show the comparative effects on the exosmosis from the roots of plants treated with ether, chloroform, and illuminating gas—both when applied as vapor and when introduced into the water—the conductivity curves of fig. 12 were plotted. The results, somewhat classified, are also given in table v. It will be seen that the quantity of anesthetics used and the duration of treatment varied in individual cases.

The indications are, therefore, that for an equal exposure the vapors range in order of effectiveness as follows: ether, least; illuminating gas, more; and chloroform, most. The difference in effectiveness between the ether and the chloroform is especially interesting, more so when we note that 8 cc. of ether were used and only 1½ cc. of chloroform. This would seem to be in harmony with the findings of Graham ('14); he was able to produce liver necrosis by some aliphatic halogen substituted compounds, but not by ether or chloral hydrate.

As regards the fact that No. 11 (4 per cent ether, remaining in the water) has a higher curve than No. 12 (10 per cent ether for 30 minutes) and especially at the beginning, it should be stated that in the case of Nos. 4, 6, 8, 10, 12, and 14, the treatment was given while the roots were in distilled water plus the anesthetics. Following the treatment the roots, after rinsing, were placed in distilled water, and at the end of one-half hour the first reading was taken. In the case of Nos. 11 and 13 the water containing the anesthetic was not replaced by fresh water and the first reading was taken one-half hour after the treatment began. Since the exosmosis during the first half hour is unusually rapid as a result of anesthetic treatment, it will be seen that in replacing the medium at the end of that period, the excreted material was thus discarded for that interval. Hence, such curves represent a secondary exosmosis. The curve of No. 11, therefore, is for total exosmosis, while that of No. 12 is for partial exosmosis.

The condition of the cultures which furnished the results plotted in fig. 11 is given for various periods in table vi.

In fig. 13 the secondary exosmosis after the first half hour is graphically represented for some organic compounds in considerable concentration. The purpose was, of course, to use a

concentration sufficiently effective to give results in a short interval of time. After the treatment the roots were rinsed and placed in distilled water. It is interesting to note that the alcohols used were only slowly effective at first, but that

TABLE VI

CONDITION OF PLANTS AFTER TREATMENT WITH ANESTHETICS

Culture no.	Condition of tops	Condition of roots
	Condition of plants 2 days after treatment:	
3 and 4	Slightly subnormal, but almost normal	Somewhat flaccid
5	Practically same as in Nos. 3 and 4	Practically normal
6	Practically same as in Nos. 3 and 4	Practically normal, but somewhat flaccid
7	Practically all dead	Somewhat flaccid
8	Almost normal	Slightly flaccid
9, 10, 11, and 12	Normal	Considerably flaccid
13	Normal	Practically normal
14	Normal	Slightly flaccid
16, 17, and 18	Normal	Normal
	Condition of plants 9 days after treatment:	
3	Much dried and yellowed	Practically normal
4	Slightly worse than in No. 3	Considerably flaccid
5	Same as in No. 4	Less flaccid than in No. 4
6	Mostly dried up	Practically normal
7	All dried up	Slightly flaccid
8	Practically normal	Practically normal
9	Practically normal	Considerably flaccid
10	Practically normal	Somewhat flaccid
11 and 12	Almost normal	Somewhat flaccid
13 and 14	Normal	Practically normal
16	Slightly subnormal	Practically normal
17 and 18	Normal	Normal

after 8 days the conductivity readings for those cultures were as high as those of the other cultures. Benzol and toluene produced almost identical effects. The effect produced by chloral hydrate remained constant after 1 day. Ethyl acetate and benzaldehyde were especially effective. The condition of the plants at the end of 8 days is given in table VII.

In fig. 14 are shown the effects of smaller amounts of the same substances, the curves of which are exhibited in fig. 13. Here, however, concentrations only one-fourth as great as those previously employed were used, but the chemicals were allowed to remain in the water during the entire period (or until evaporated, as may have been the case with some).

While the alcohols gave a greater effect than the control, they gave no greater exosmosis than one of the controls in the

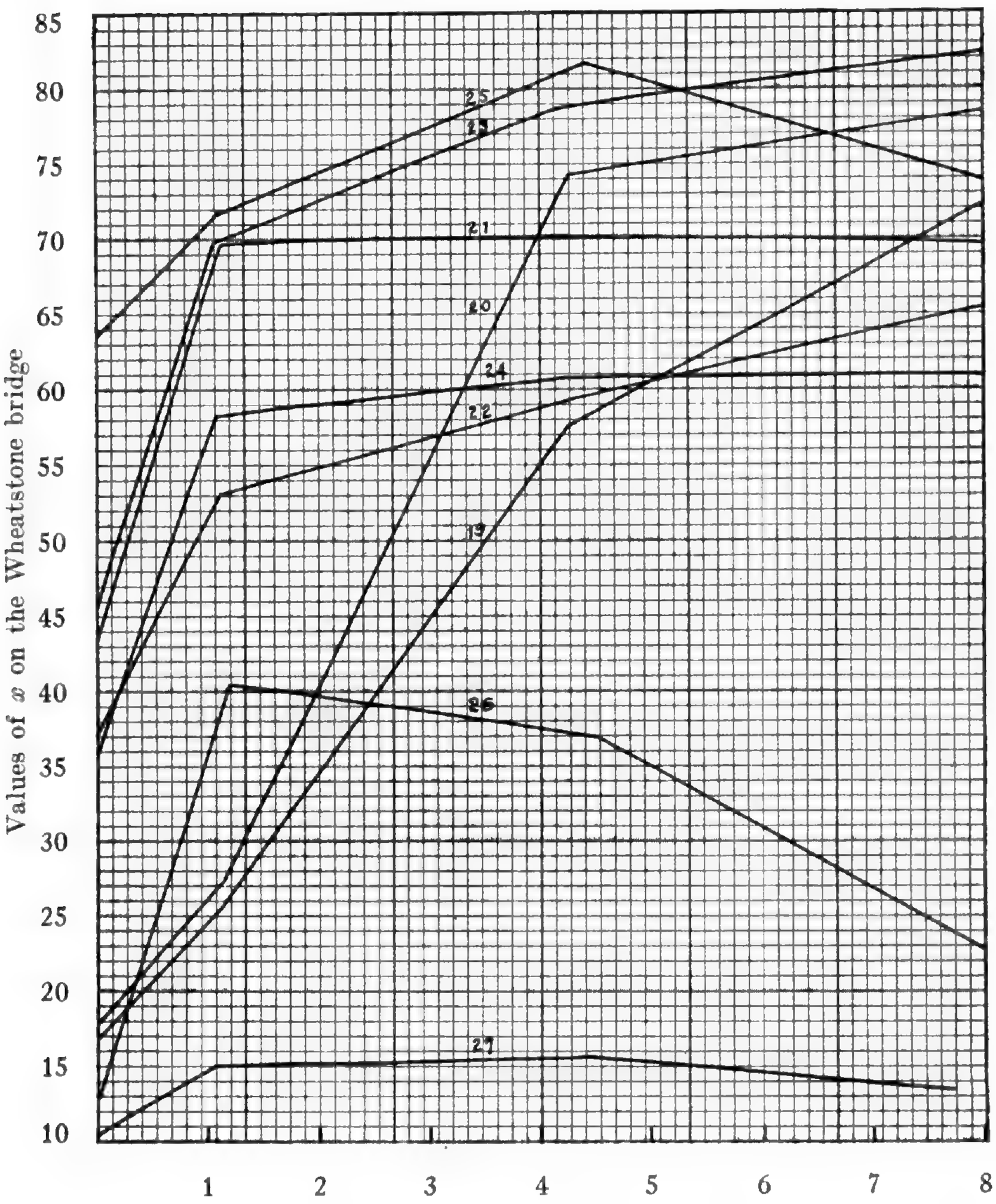

Fig. 13. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 19, 4 per cent ethyl alcohol in water, 30 minutes; No. 20, 4 per cent methyl alcohol in water, 30 minutes; No. 21, 4 per cent chloral hydrate in water, 30 minutes; No. 22, 4 per cent benzol in water, 30 minutes; No. 23, 4 per cent ethyl acetate in water, 30 minutes; No. 24, 4 per cent toluene in water, 30 minutes; No. 25, 4 per cent benzaldehyde in water, 30 minutes; No. 26, control—placed directly into distilled water; No. 27, control—placed directly into distilled water. The plants were 38 days old at the time of treatment. The first reading was taken in all cases after the roots had been in distilled water exactly 30 minutes. In the case of the treated plants the roots were in distilled water containing the anesthetic for the specified time, after which they were transferred to the distilled water, the conductivity of which was subsequently determined.

previous figure. The other substances, however, even in the small concentration employed, produced a marked rise in the conductivity of the medium during the first day, after which it remained practically constant. The benzaldehyde and the

TABLE VII

CONDITION OF PLANTS EIGHT DAYS SUBSEQUENT TO TREATMENT WITH EFFECTIVE CONCENTRATIONS OF ANESTHETICS FOR A SHORT PERIOD

Culture no.	Condition of tops	Condition of roots
19	Normal and in good condition	Considerably flaccid
20	Practically normal	More flaccid than those of No. 19
21	Somewhat subnormal	Somewhat flaccid
22	Some stems considerably affected, others almost normal	Considerably flaccid
23	Practically all dead	Very flaccid
24	About the same as in No. 22	Considerably flaccid
25	Considerably subnormal	Very flaccid
26	Normal; many green, vigorous, turgid leaves	Practically normal
27	Practically normal	Normal

ethyl acetate, which themselves give a high conductivity in aqueous solution, should be considered apart from the other substances, which give no such increase. The two substances mentioned are given here merely for the purpose of comparison with the others employed. A 1 per cent solution of ethyl acetate had a conductivity of 65.2 on the Wheatstone bridge, while that of a similar solution of benzaldehyde was 88.6. These corrections should therefore be applied to the curve values in order to obtain the true value of the exosmosis from the roots in those cultures. The condition of the plants after 8 days is given in table 8.

VIII. Effects of Substances Used Singly and Combined in Pairs

It is not the writer's purpose here to go into the historical aspect of the increasingly voluminous work on toxic agents, antagonistic action, and balanced solutions, and the numerous related subjects. But since those subjects have assumed such great importance in the realm of physiology it was thought desirable to consider the effect of certain toxic and unbalanced

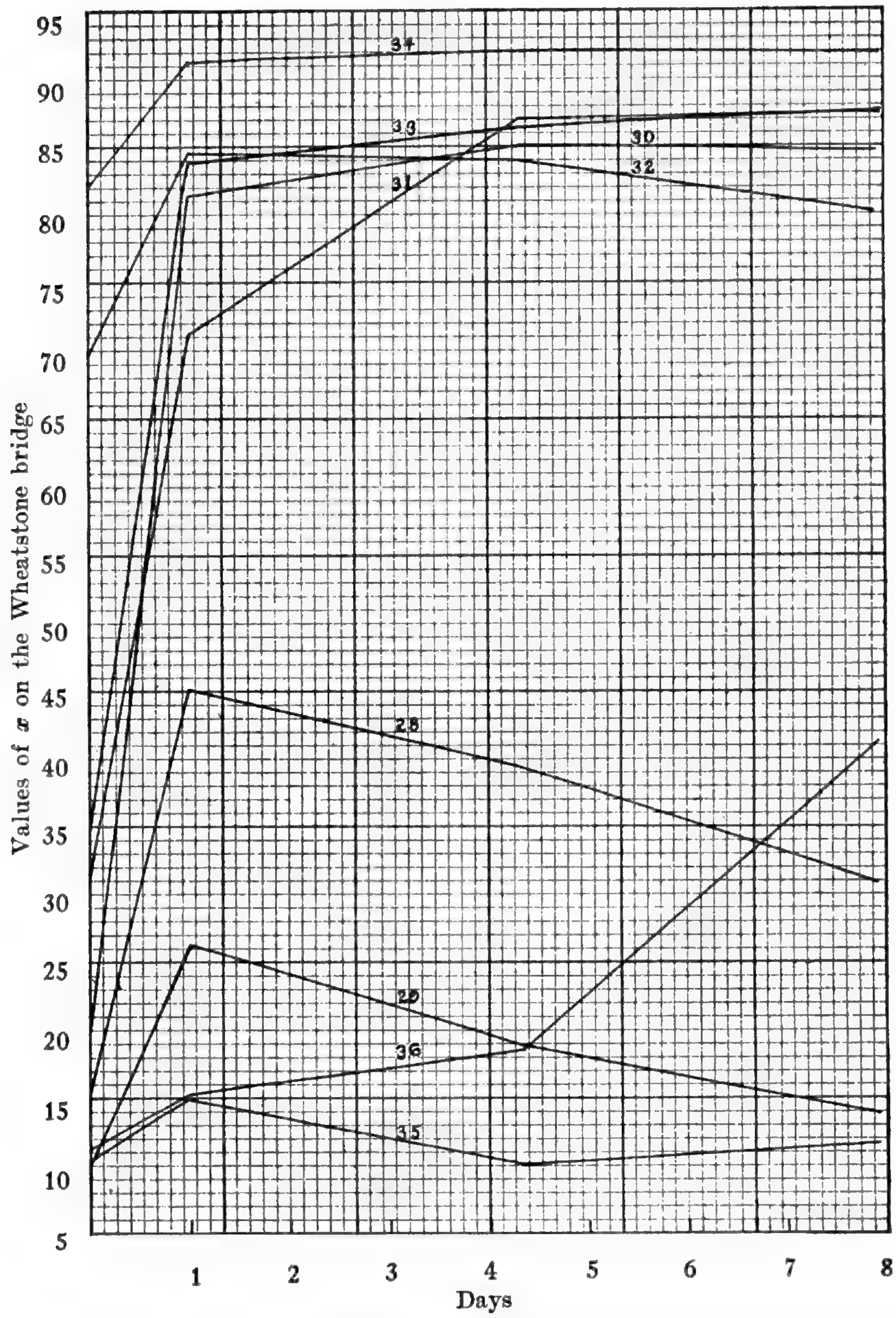

Fig. 14. Conductivity curves of cultures (series 15) in distilled water subsequent to treatment, as follows: No. 28, 1 per cent ethyl alcohol in water, to end of experiment; No. 29, 1 per cent methyl alcohol in water, to end of experiment; No. 30, 1 per cent chloral hydrate in water, to end of experiment; No. 31, 1 per cent benzol in water, to end of experiment; No. 32, 1 per cent ethyl acetate in water, to end of experiment; No. 33, 1 per cent toluene in water, to end of experiment; No. 34, 1 per cent benzaldehyde in water, to end of experiment; No. 35, control—placed directly into distilled water; No. 36, 1 per cent methyl alcohol in water, to end of experiment. The plants were 38 days old at the time of treatment. The first reading was taken in all cases after the roots had been in the distilled water containing the anesthetic exactly 30 minutes. The control, however, was exposed to the distilled water only, the first reading being taken after 30 minutes.

solutions on the exosmosis from plant roots in order to obtain a basis of comparison with the other agents used.

In this connection it might be well to consider more in detail the work of Lillie already referred to in the historical

TABLE VIII

CONDITION OF PLANTS EIGHT DAYS SUBSEQUENT TO TREATMENT WITH LOW CONCENTRATIONS OF ANESTHETICS FOR THE ENTIRE PERIOD

Culture no.	Condition of tops	Condition of roots
28	Somewhat subnormal	Slightly flaccid
29	Almost normal	Considerably flaccid; tips less flaccid than in No. 28 but upper part more so
30	Dead	Considerably flaccid
31	Almost dead	Very flaccid
32–34	Practically dead	Very flaccid
35	Practically normal	Practically normal
36	Practically normal	Somewhat flaccid

review. His work on *Arenicola* and the eggs of *Arbacia* pertains largely to the exosmosis of the pigment and the manner in which they were affected by isotonic salt solutions alone and in the presence of various anesthetics. From the effect observed, he concluded that the salts have a permeability-increasing effect on the plasma membrane which is counteracted by the anesthetics. But in dealing with the question of permeability it would seem that we must take into consideration the effect on the exosmosis, not only of any contained pigment, but of electrolytes as well.

It would have been exceedingly interesting, and would have furnished a means of strengthening or shattering his hypothesis, as the case might be, had Lillie also measured the electrical conductivity of the medium in which the Arenicola larvae and the Arbacia eggs were placed and thus determined whether the electrolytes contained in these organisms behaved as did the pigment. It would seem that the work of Loeb ('03), Peters ('04), and others might be considered as suggesting possibilities for electrolytic determinations along this line with marine organisms. Without such facts at hand any general conclusions in regard to permeability effects based on the coloring matter only must be considered imperfect. What

the reaction may be between the anesthetics and the larval pigment is another question which Lillie does not touch upon. In a recent article Miss Wheldale ('14), in discussing the natural and artificial extracts of plants, states that whereas artificial anthocyanin is soluble in ether the natural anthocyanins are not. May we not have a similar effect in the pigments concerned? Small amounts of the anesthetics may render those pigments insoluble and in that manner prevent their exosmosis rather than by bringing about any considerable alteration of the membrane; larger amounts of the anesthetics would act chemically on the membrane to a point of disintegration sufficient for the physical escape of the pigment.

It will be seen from the following experiments that in the case of roots of *Pisum sativum* certain salts caused a marked exosmosis of electrolytes. In the presence of anesthetics this exosmosis was not decreased or prevented, as Lillie found in the case of the pigments referred to, but was even increased. Hence these results do not indicate any permeability-decreasing action on the part of the anesthetics and are therefore in harmony with the findings of Dixon and Atkins ('13) and others. Another interesting condition is seen in the exosmosis resulting from single and combined salts acting for different periods of time. It was expected that such results would correspond with those obtained on plant-growth studies of antagonistic action between various nutrient and non-nutrient salts. That equally as high, or in some cases higher, exosmosis values were obtained from combined salts as from single salts is an unexpected and interesting result.

As previously indicated, the method used was to place the plants in the various solutions for the period specified and then transfer them, after careful rinsing of the roots, to distilled water in which the conductivity readings were to be taken. It was ascertained that the rinsing was effective in removing electrolytes from the roots. Figures 15 and 16 show the results for the briefer treatments with certain salts, and it is there seen that for a period of treatment less than 17 hours the N/20 $MgCl_2$ has no effect. While in the case of the culture treated for one-half hour with the $MgCl_2$, the conductivity

reading was higher at the end of four days than in the other cultures (2–5) of that group, and continued higher throughout, this fact loses its significance, as far as comparative effects are concerned, when the curve resulting from a 4-hour

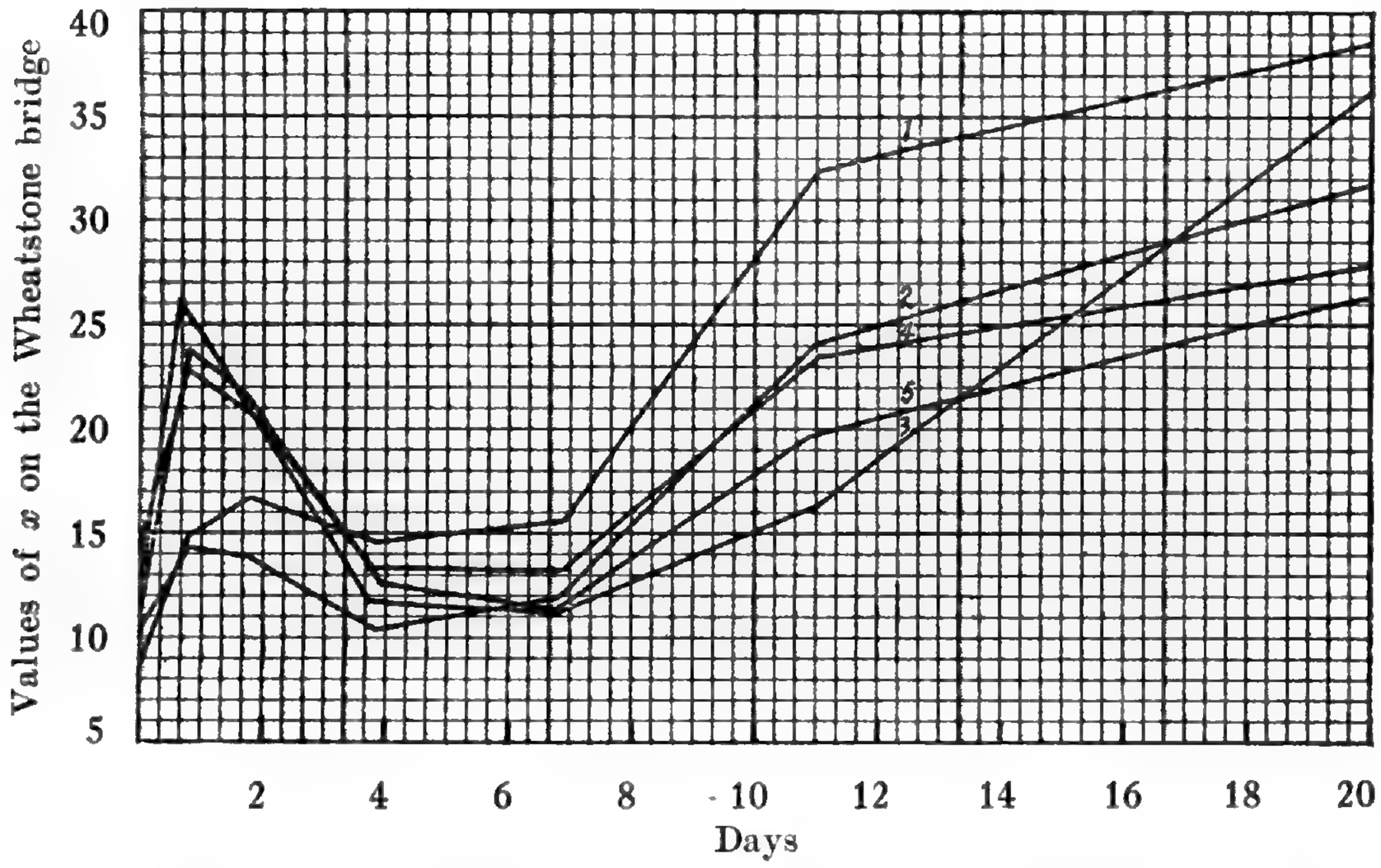

Fig. 15. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 1, N/20 $MgCl_2$, 30 minutes; No. 2, N/20 $CaCl_2$, 30 minutes; No. 3, N/20 $MgCl_2$ plus N/20 $CaCl_2$, 30 minutes; No. 4, control—placed directly into distilled water; No. 5, N/20 $MgCl_2$, 4 hours. The cultures were 17 days old at the time of treatment. The first reading was taken in all cases after the roots had been in the distilled water exactly 30 minutes.

treatment with $MgCl_2$ is considered, and should no doubt be interpreted as an individual variation irrespective of treatment. In the case of No. 6, however, the curve for which represents the results of a 17-hour treatment with N/20 $MgCl_2$, we no doubt have a real effect clearly distinguished from the controls.

At the end of 20 days in distilled water following the treatment the tops of Nos. 1–10 were all in about the same condition, those of the treated plants showing no injury. Likewise the roots of Nos. 1–5 and 8–10 were practically normal, with no, or only very slight, flaccidity; those of No. 6, however, were brownish in color and somewhat flaccid, while those of

No. 7 were brownish only in spots, but were of about the same flaccidity as those of No. 6.

Having found that a treatment of 17 hours under the conditions indicated above was not sufficient to yield the most

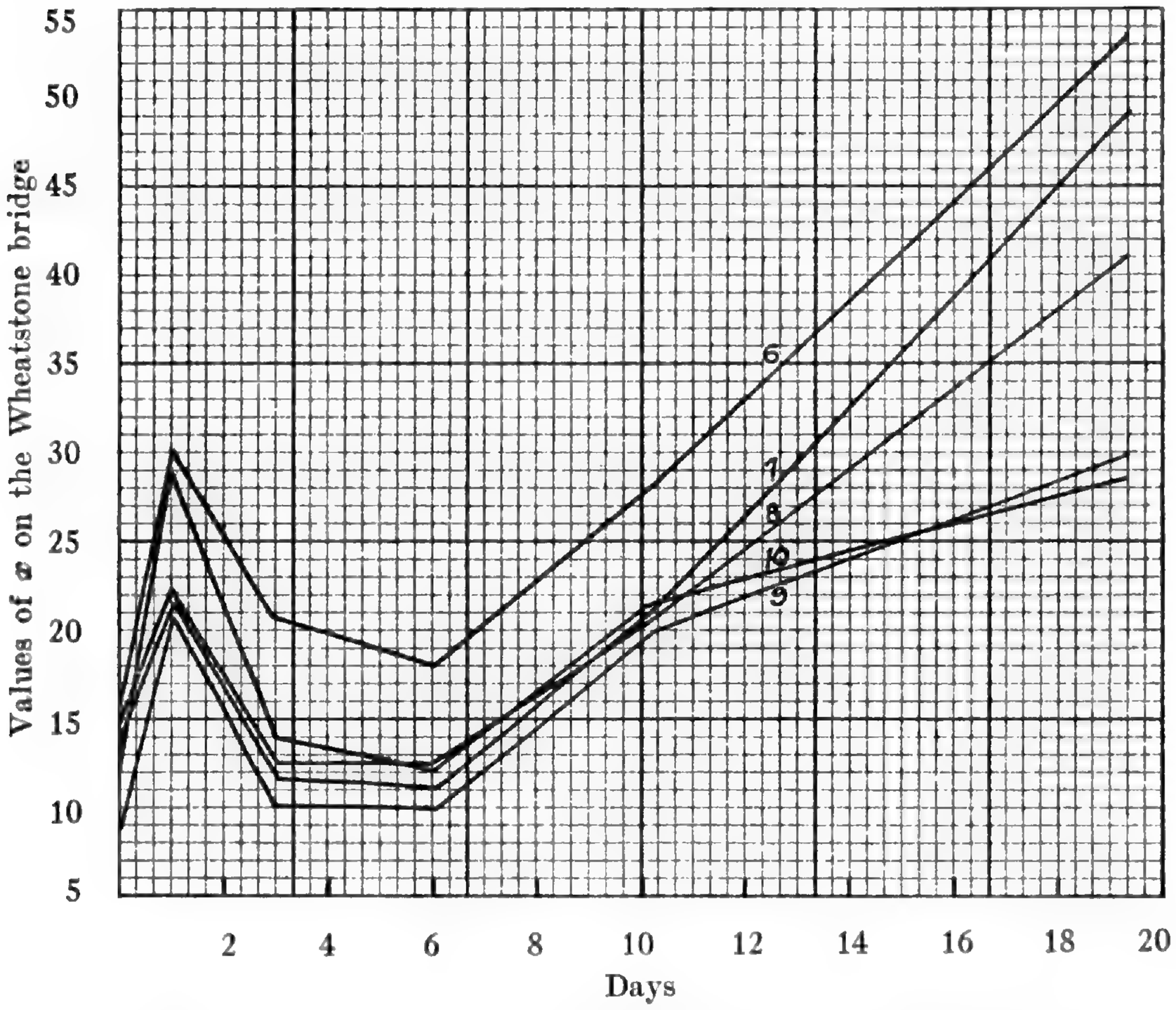

Fig. 16. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 6, N/20 $MgCl_2$, 17 hours; No. 7, N/20 $CaCl_2$, 17 hours; No. 8, N/20 $MgCl_2$ plus N/20 $CaCl_2$, 17 hours; No. 9, control—distilled water, renewed after 17 hours; No. 10, control—distilled water, not renewed. The cultures were 17 days old at the time of treatment. The first readings were taken in all cases after the roots had been in the distilled water exactly 30 minutes. No. 10 remained in the full nutrient solution until the treated cultures were transferred (after the 17-hour period) from the respective solutions to distilled water.

positive results, it was decided to try stronger concentrations and longer periods. Figure 17 shows the conductivity curves after a period of treatment extending 75 hours. Some interesting results were obtained. N/10 $MgCl_2$ gave the highest readings, closely followed by N/10 $MgCl_2$ plus N/10 $CaCl_2$; the N/20 $MgCl_2$ plus N/20 $CaCl_2$ curve is very similar to that

obtained from N/10 $MgCl_2$ plus N/20 $CaCl_2$, while the N/10 $MgCl_2$ plus N/100 $CaCl_2$ causes a rise higher than that in the two curves just mentioned after the fifth day. It was unexpected that N/20 $CaCl_2$ should exceed N/20 $MgCl_2$ in its

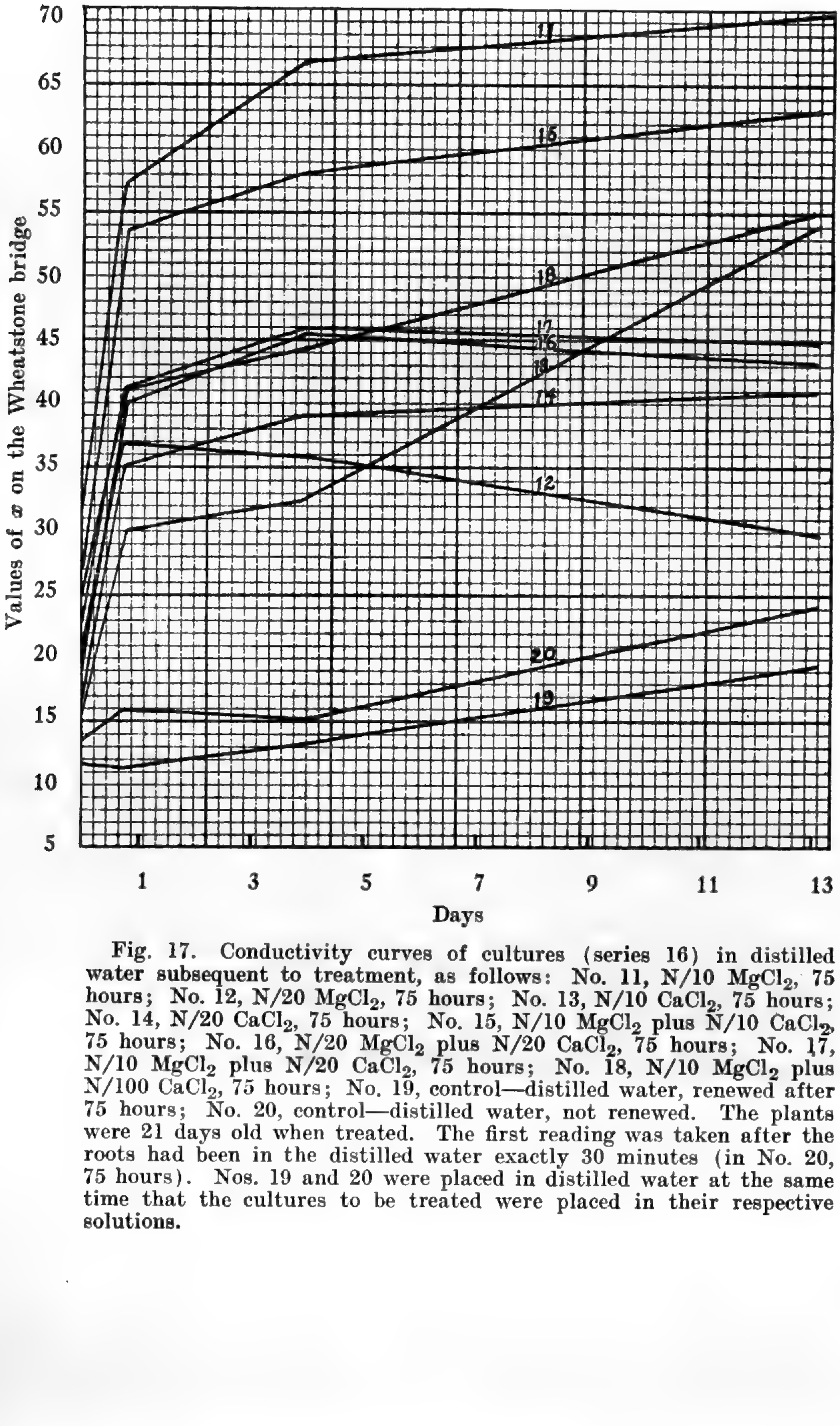

Fig. 17. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 11, N/10 $MgCl_2$, 75 hours; No. 12, N/20 $MgCl_2$, 75 hours; No. 13, N/10 $CaCl_2$, 75 hours; No. 14, N/20 $CaCl_2$, 75 hours; No. 15, N/10 $MgCl_2$ plus N/10 $CaCl_2$, 75 hours; No. 16, N/20 $MgCl_2$ plus N/20 $CaCl_2$, 75 hours; No. 17, N/10 $MgCl_2$ plus N/20 $CaCl_2$, 75 hours; No. 18, N/10 $MgCl_2$ plus N/100 $CaCl_2$, 75 hours; No. 19, control—distilled water, renewed after 75 hours; No. 20, control—distilled water, not renewed. The plants were 21 days old when treated. The first reading was taken after the roots had been in the distilled water exactly 30 minutes (in No. 20, 75 hours). Nos. 19 and 20 were placed in distilled water at the same time that the cultures to be treated were placed in their respective solutions.

effect on exosmosis and that the conductivity curve resulting from treatment with N/10 $CaCl_2$ should rise so high at the end.

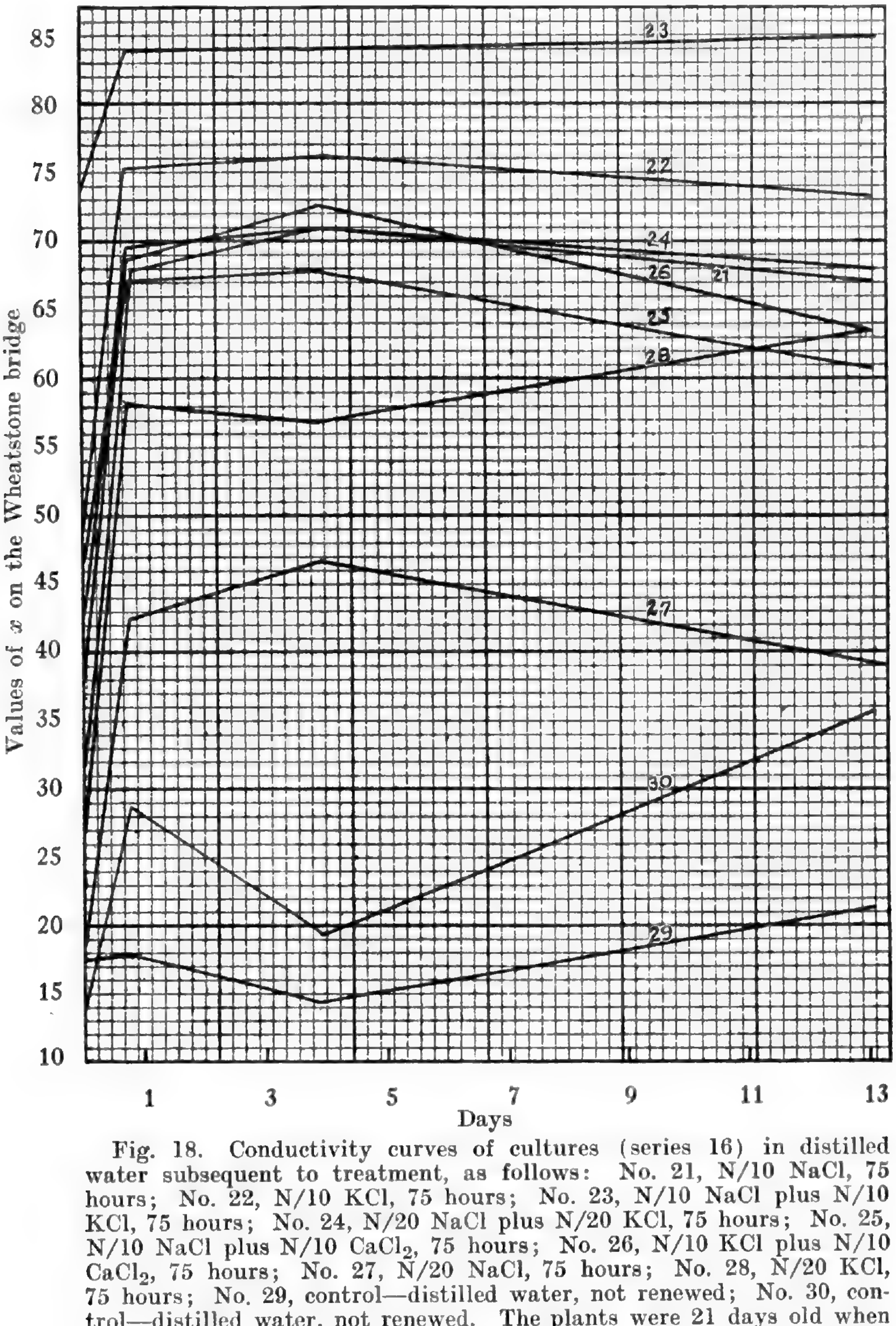

Fig. 18. Conductivity curves of cultures (series 16) in distilled water subsequent to treatment, as follows: No. 21, N/10 NaCl, 75 hours; No. 22, N/10 KCl, 75 hours; No. 23, N/10 NaCl plus N/10 KCl, 75 hours; No. 24, N/20 NaCl plus N/20 KCl, 75 hours; No. 25, N/10 NaCl plus N/10 $CaCl_2$, 75 hours; No. 26, N/10 KCl plus N/10 $CaCl_2$, 75 hours; No. 27, N/20 NaCl, 75 hours; No. 28, N/20 KCl, 75 hours; No. 29, control—distilled water, not renewed; No. 30, control—distilled water, not renewed. The plants were 21 days old when treated. The first reading was taken after the roots had been in the distilled water 30 minutes (in No. 29, 75 hours). Culture 30 was placed in distilled water at the end of the 75-hour period, having been in full nutrient solution up to that time.

At the end of 13 days in distilled water following the treatment, the tops of Nos. 11–20 were of the same appearance throughout, i. e., normal. The roots were also practically normal in the case of Nos. 12–20, except for a brownish color on those of Nos. 12, 13, 15, and 16–18, being especially evident in the case of No. 15. In addition to being brown, however, the roots of No. 11 were considerably flaccid.

Figure 18 shows similar relations for NaCl, KCl, and $CaCl_2$. It is seen that KCl is more effective than NaCl in causing exosmosis. Far from ameliorating the exosmotic condition, the treatment with combined NaCl and KCl likewise yields high conductivity readings of the medium, the N/10 concentration of each combined giving the highest. It can not be argued that this effect is due solely to the osmotic pressures of the solutions of the agents in question, for if that were the case we should expect more comparable results on the basis of the osmotic effects of the various solutions at the concentrations used. There is a reduction in the effect when the NaCl and KCl used singly are reduced to concentrations of N/20.

The condition of the plants 16 days after first applying the treatment, or 13 days after being in distilled water, is shown in table IX, from which it is evident that there was great exosmosis with but little or no visible effect accompanying it.

TABLE IX

CONDITION OF PLANTS TREATED WITH VARIOUS SALTS FOR DIFFERENT PERIODS OF TIME

Culture no.	Condition of tops	Condition of roots
21 and 22	Normal	Slightly brown and very slightly flaccid
23	Dead—badly wilted at end of treatment	Very limp and flaccid and brownish
24–28	Normal	Very slightly brownish but practically normal
29 and 30	Normal	Practically normal

That osmotic effects play practically no part in the phenomenon under consideration is indicated from the results of Loeb ('03) on *Gammarus* and those of True ('14) on Lupinus seedlings. The writer also performed experimental work to

determine this point. Solutions of pure saccharose of varying concentrations were used and the effects produced by the same during a period of 24 hours as compared with pure distilled water, measured by the determined conductivity of the medium both during the 24 hours and after (when the plants which had been in the sugar solutions were also placed in distilled water). These results are given in table x. As there seen, no differences were obtained from the different concentrations.

TABLE X

EXOSMOSIS FROM THE ROOTS OF PLANTS IN SUGAR SOLUTIONS AND DISTILLED WATER *

Time of readings	Culture 1 1.28% saccharose sol'n. 24 hours followed by dist. H_2O	Culture 2 2.56% saccharose sol'n. 24 hours followed by dist. H_2O	Culture 3 5.13% saccharose sol'n. 24 hours followed by dist. H_2O	Culture 4 control dist. H_2O throughout changed every day conductivity readings
Conductivity readings of the sugar solutions:				
Before roots placed in the solution	9.4	10.6	10.9	10.9
After 10 hrs	28.0	19.7	30.8	32.9
After 24 hrs	28.9	18.3	29.0	32.9
Increase over original sol'n. during 24 hrs	19.5	7.7	18.1	22.0
Conductivity readings of the distilled water:				
After ½ hr	9.4	8.6	8.8	8.3
After 23 hrs	10.5	11.5	11.0	10.4
After 48 hrs	10.9	11.3	10.2	10.0
Increase over dist. H_2O the first half hour †	3.4	2.6	2.8	2.3
Increase over dist. H_2O during 48 hours †	4.9	5.3	4.2	4.0

* All readings represent values of x on the Wheatstone bridge, the resistance in the box being 9,110 ohms.

† The average reading of the distilled water before placing roots in it was approximately 6.0.

In table XI are shown the effects produced by salts alone as well as by salts plus anesthetics in weak concentrations. It was desired to use approximately the same concentrations of anesthetics as indicated by the work of Lillie ('12), Osterhout ('13), and others. The conductivity of the water containing the anesthetics was not determined after the 53-hour treatment and hence the resulting exosmosis during that interval was not ascertained. But from other experiments on

the effect of anesthetics in solution we have seen that the exosmosis is rapid and considerable during the first day or so and then remains stationary, i. e., the curve becomes hori-

TABLE XI

EFFECTS OF SALT SOLUTIONS USED SINGLY AND COMBINED WITH ANESTHETICS UPON THE EXOSMOSIS FROM THE ROOTS OF PLANTS (PLANTS 40 DAYS OLD WHEN TREATED)

Culture no.	Treatment	Conductivity*				
		Readings		Increase over dist. H_2O**		
		After ½ hr.	After 42 hrs.	1st ½ hr.	Next 41½ hrs.	Total in 42 hrs.
31	N/10 $MgCl_2$, 53 hrs.....	35.4	57.1	29.4	21.7	51.1
32	N/10 NaCl, 53 hrs.....	34.4	60.9	28.4	26.5	54.9
33	N/10 KCl, 53 hrs.....	40.8	63.0	34.8	22.2	57.0
34	0.7% ether in H_2O, 53 hrs.....	10.0	11.6	4.0	1.6	5.6
35	0.7% $CHCl_3$ in H_2O, 53 hrs.....	12.1	36.3	6.1	24.2	30.3
36	0.7% benzol in H_2O, 53 hrs.....	11.3	17.7	5.3	6.4	11.7
37	N/10 $MgCl_2$ and 0.7% ether, 53 hrs.....	41.2	64.7	35.2	23.5	58.7
38	N/10 $MgCl_2$ and 0.7% $CHCl_3$, 53 hrs.....	45.5	57.2	39.5	11.7	51.2
39	N/10 $MgCl_2$ and 0.7% benzol, 53 hrs.....	44.0	49.4	38.0	5.4	43.4
40	N/10 NaCl and 0.7% ether, 53 hrs.....	37.4	59.5	31.4	22.1	53.5
41	N/10 NaCl and 0.7% $CHCl_3$, 53 hrs.....	47.5	62.4	41.5	14.9	56.4
42	N/10 NaCl and 0.7% benzol, 53 hrs.....	49.5	56.0	43.5	6.5	50.0
43	N/10 KCl and 0.7% ether, 53 hrs.....	50.2	76.0	44.2	25.8	70.0
44	N/10 KCl and 0.7% $CHCl_3$, 53 hrs.....	51.7	65.4	45.7	13.7	59.4
45	N/10 KCl and 0.7% benzol, 53 hrs.....	49.2	55.8	43.2	6.6	49.8
46 and 47	Control (dist. H_2O renewed after 53 hrs.)...	10.9	11.9	4.9	1.0	5.9
48	Control (dist. H_2O not renewed).....	15.2†	15.5‡	9.2§	.3	9.5‖
49 and 50	Control (full nutr. until Nos. 31–45 were placed in dist. H_2O).....	12.5	39.0	6.5	26.5	33.0

* All readings represent values of x on the Wheatstone bridge with a resistance in the box of 9,110 ohms.

** The average reading of the distilled water before placing roots in it was approximately 6.0.

† After 53 hours. ‡ After 95 hours. § In 53 hours. ‖ In 95 hours.

zontal. We can therefore safely infer that such was the case here, except possibly in the ether-treated cultures in which the roots and tops showed no effect whatever from the treat-

ment. We can thus account for the fact that the increase in the conductivity of the medium in Nos. 34, 35, and 36, was so slight and so similar to that given by the controls. It will be seen that the anesthetics did not antagonize the salts so far as exosmosis of electrolytes is concerned. The condition of the plants after the 53-hour treatment is shown in table XII.

TABLE XII

CONDITION OF PLANTS FIFTY-THREE HOURS AFTER TREATMENT WITH SOLUTIONS OF SALTS AND ANESTHETICS

Culture no.	Condition of tops	Condition of roots
31	Normal	Yellowish brown, somewhat flaccid
32	Practically normal	Slightly yellow, practically normal
33	Subnormal, drying considerably	Slightly yellow, practically normal
34	Normal	Practically normal
35	Normal	White, but considerably flaccid
36	Almost normal	Very flaccid
37	Practically normal	Yellowish and considerably flaccid
38	Almost normal	Somewhat flaccid
39	Drying considerably	Very flaccid
40	Normal	Almost normal
41	Drying somewhat	Considerably flaccid
42	Drying considerably	Very flaccid
43	Practically normal	Practically normal
44	Drying considerably	Considerably flaccid
45	Drying badly	Very flaccid
46–50	Normal	Practically normal

The concentration of the anesthetics used in the above experiments was near the boundary which would just produce exosmosis. To eliminate such action entirely when these substances were used alone, therefore, the concentrations used were reduced to a point below that at which they cause exosmosis to any appreciable extent, if at all. The results of that series are given in table XIII, where we see again no indications that there is any decreasing effect by the anesthetics on the exomosis induced by salts. On the contrary, the combined salt and anesthetic cause a greater exosmosis than the salt alone.

As measured by the resulting growth of roots, Hibbard ('13) found an antagonistic action between $CuSO_4$ and chloral hydrate. To determine if such action would also hold true in

the case of exosmosis, an experiment was set up, the results of which are given in table XIV. As there seen, there was no decrease in the exosmosis caused by either substance when the two were combined.

TABLE XIII

EFFECTS OF SALT SOLUTIONS USED SINGLY AND COMBINED WITH ANESTHETICS ON THE EXOSMOSIS FROM THE ROOTS OF TREATED PLANTS*

Culture no.	Treatment	Conductivity				
		Readings		Increase over dist. H_2O‖		
		After ½ hr.	After 41 hrs.	1st ½ hr.	Next 40½ hrs.	Total in 41 hrs.
1	1/8 saturated $CHCl_3$ in H_2O, 44 hrs	8.5†	11.0	2.5‡	2.5	5.0
2	M/200 chloral hydrate, 44 hrs	13.4†	18.9	7.4‡	5.5	12.9
3	N/10 NaCl, 44 hrs	38.4†	59.3	32.4‡	20.9	53.3
4	N/10 KCl, 46 hrs	53.6	76.2	47.6	22.6	70.2
5	1/8 saturated $CHCl_3$ in H_2O & N/10 NaCl, 44 hrs	46.2	61.6	40.2	15.4	55.6
6	1/8 saturated $CHCl_3$ & N/10 KCl, 46 hrs	47.2	76.5	41.2	29.3	70.5
7	M/200 chloral hydrate & N/10 NaCl, 46 hrs	49.1	79.3	43.1	30.2	73.3
8	M/200 chloral hydrate & N/10 KCl, 46 hrs	60.5	84.2	54.5	23.7	78.2
9	N/10 NaCl & N/10 KCl 46 hrs	70.7	82.7	64.7	12.0	76.7
10	N/20 NaCl & N/20 KCl, 46 hrs	41.8	71.7	35.8	29.9	65.7
11	Control (dist. H_2O renewed every 2 days)	11.4	10.8	5.4	−.6	4.8
12	Control (dist. H_2O not renewed)	16.7	25.0	10.7	8.3	19.0

* All readings represent values of x on the Wheatstone bridge with a resistance in the box of 9,110 ohms.

† Reading taken after 50 minutes. ‡ Increase in first 50 minutes.

‖ The average reading of the distilled water before placing roots in it was approximately 6.0.

Merely to get a basis of comparison between the effects produced by the various agents above mentioned and acid and alkali in certain concentrations, plants were placed in solutions of KOH and H_2SO_4 of approximately the limiting concentrations for root growth, as found by Kahlenberg and True ('96). Instead of excretion being greater than absorption the reverse was found to be true during the period the plants remained in the solutions. The plants, to all external appearances, were not affected adversely in the least, and when later

placed in distilled water gave practically no greater exosmosis than the control. With stronger concentrations a marked effect would undoubtedly be produced. The results obtained are given in table xv. Another point worthy of note in this

TABLE XIV

EFFECTS OF COPPER SULPHATE AND CHLORAL HYDRATE USED SINGLY AND COMBINED UPON THE EXOSMOSIS FROM THE ROOTS OF PLANTS

Cult. no.	Treatment	Specific conductivity of the sol'ns.*			Values of x,† or bridge readings of the Distilled Water				
		Before roots in the sol'n.	After 27 hrs. in the sol'n.	Increase in 27 hrs.	After ¼ hr. in the H_2O	After 63 hrs. in the H_2O	Increase the 1st ¼ hr. ‡‡	Increase the next 62¼ hrs.	Total increase in 63 hrs. ‡‡
1	M/10,000 $CuSO_4$, 28 hrs.....	2.92	16.68	13.76	19.7	55.4	13.7	35.7	49.4
2	M/100 $CuSO_4$, 27 hrs.....	142.40	151.10	8.70	22.0	22.4	16.0	.4	16.4
3	M/8,000 chloral hydrate, remaining to end of exp.....	.35	1.16	.81	20.6‡	13.1**	14.6℁	−7.5	7.1**
4	M/100 chloral hydrate, 26 hrs...	.37	3.04	2.67	14.8	16.8	8.8	2.0	10.8
5	M/10,000 $CuSO_4$ and M/8,000 chloral hydrate, 26 hrs.....	2.82	19.77	16.95	15.0	53.3	9.0	38.3	47.3
6	M/100 $CuSO_4$ and M/100 chloral hydrate, 26 hrs.	82.69	95.25	12.56	17.2	20.2	11.2	3.0	14.2
7	Control (dist. H_2O, changed every 4 days).....	.32	.79	.47	15.0‖	12.9††	9.0℁	−2.1	6.9††
8	Control (dist. H_2O, not changed)...	.....	.....	.....	14.8	10.7	8.8	−4.1	4.7

* The values given are to be multiplied by 10^{-6} to obtain specific conductivity values.

† Resistance in box 9,110 ohms.

‡ After 26 hours in the solution.

℁ The first 26 hours.

‖ After 26 hours in distilled H_2O.

‡‡ The average reading of the distilled water before placing roots in it was approximately 6.0.

** After 89 hours in the solution.

†† After 89 hours in the water.

connection and seen in table xv is the additional verification of the fact that the rinsing method used throughout this investigation was effective and that no electrolytes were carried

over on the roots from the full nutrient solutions, salt solutions, and other media to the distilled water, at least not in sufficient quantity to affect the validity of the results in any way. Although the conductivity of the acid and alkaline media was very high, it is seen by reference to table xv that after rinsing the roots in the usual manner and transferring the cultures to distilled water the readings were very low, thus showing that practically no electrolytes were carried over on the roots.

TABLE XV

CONDUCTIVITY READINGS OF THE CULTURE MEDIA OF PLANTS IN KOH, H_2SO_4, AND LATER IN DISTILLED WATER

Cult. no.	Treatment	Specific conductivity* of the sol'ns.				Values of x,† or bridge readings of the distilled water				
		Before roots in the sol'n.	After 22 hrs. in the sol'n.	After 47 hrs. in the sol'n.	Increase in 47 hrs.	After ½ hr. in the H_2O	After 50 hrs. in the H_2O	Increase the 1st ½ hr.††	Increase the next 49½ hrs.	Total increase in the 50 hrs.††
1	N/12,800 H_2SO_4, 47 hrs.....	2.39	1.50	1.03	−1.36	10.8	10.5	4.8	−.3	4.5
2	N/6,400 H_2SO_4, 47 hrs.....	5.62	2.53	1.17	−4.45	8.7	9.6	2.7	.9	3.6
3	N/400 KOH, 47 hrs.....	42.02	20.09	16.39	−25.63	11.5	8.7	5.5	−2.8	2.7
4	N/200 KOH, 47 hrs.....	58.50	27.98	24.16	−34.34	11.2	10.5	5.2	−.7	4.5
5	Control (dist. H_2O, not changed)...	.98	2.56	1.32	.34	22.8‡	17.8**	16.8‡	−5.0	11.8**

* The values given are to be multiplied by 10^{-5}.
† The resistance in the box was 9,110 ohms.
‡ After being in distilled water 47 hours.
†† The average reading of the distilled water before placing roots in it was approximately 6.0.
** After 97 hours.

IX. General Discussion

In the foregoing experiments we have been able to note the exosmosis of electrolytes following different treatments. As compared with the controls we have seen marked excretions in some cases and slight or no exosmosis in excess of that in the controls in others. In the normal untreated cultures, or controls, we have seen that there is almost universally a slight exosmosis from the roots into the distilled water for about 24

hours or so, and then in most cases there is a decline in the conductivity curve to a point approaching the original position, after which there may or may not be a gradual incline, depending, probably, on various factors.

It might be well briefly to consider some theoretical aspects of the subject, especially in regard to the causal agencies effecting the increased exosmosis of the treated cultures. The mere transfer of a culture from a full nutrient solution to distilled water is not in itself sufficient to account for the effects produced, as we have seen that osmotic effects play little or no rôle in this connection, a conclusion in harmony with the findings of Loeb ('03) and of True ('14). To what then is the exosmosis due? Can it all be laid at the door of cell cytolysis? What influence has an alteration of the plasma membrane?

In any case, we are dealing with the effect of physical and chemical factors upon the plant cell. For our purpose here it is not considered necessary to enter upon a discussion of the various ideas regarding the details of the structure of the cell and its limiting membrane, or the work and theories of the different investigators on both the animal and plant side concerning the permeability of the plasma membrane. Yet in passing, it may be well to mention Overton's theory regarding the lipoid nature of the plasma membrane, Nathansohn's idea of a mosaic structure of the same, Czapek's experiments indicating the presence of neutral fats in the membrane, Lepeschkin's view that the plasma membrane is a continuous film (some of the work of the last two investigators being summarized by Blackman, '12), and Kite's work on the structure of protoplasm, and also make note of the recent work of Cranner ('14) on the lipoid content of the cell wall.

The effect of the two physical factors, heat and cold, may undoubtedly be considered as resulting in a complete or incipient disorganization of the cell, depending upon the duration of exposure, and a consequent escape of some of the contents into the surrounding medium.

In the case of the various chemical factors or agents used the matter is probably not so simple or so easily disposed of. However, a conception that would fulfill the requirements

theoretically and also accord with the experimental results would seem to be based on the specificity of chemical reaction. The cell, with its complex aggregation of chemical substances, may be considered as interacting with the substance employed, be it anesthetic, toxic agent, salt solution, or other chemical. It may be assumed that each substance has a greater affinity (if we may use that tabooed chemical term) for a particular component of the cell than for other constituents and hence reacts accordingly. This was exemplified by the striking comparison between the effect produced by anesthetics in certain concentrations and that produced by the KCl or NaCl solution. The exosmosis, it is true, was considerable in both cases, but the resulting appearance of the roots was markedly different, the anesthetics causing indications of flaccidity, while the roots exhibiting quite as much exosmosis in the salt solutions, remained practically normal. If we assume that the anesthetic acted upon the colloidal matrix or gel portion of the cell and thus more or less destroyed its organization, while the salts reacted with the substances in the sol condition and left the matrix more or less intact, we would seem to have a basis for explaining the differences observed.

Anesthesia has been considered by Lillie, Osterhout, and others to be essentially a reversible process, provided that the concentration of the anesthetic was not sufficient to be toxic. The experimental work reported herewith, however, on the excretion of electrolytes induced by various anesthetics does not seem to substantiate that view. If the concentration of the anesthetics employed was below a certain point there was no observable effect whatsoever. By increasing the concentration the critical point was attained when excretion began, and as the concentration of the anesthetic was further increased, or as the period of application was lengthened, excretion likewise increased. The excretion process induced by anesthetics therefore conformed in every way to an irreversible chemical reaction. In Osterhout's conductivity measurements of tissue, secondary agglutinization phenomena may possibly have entered in to give the observed effects, and thus have masked the real chemical reaction. Recovery of organ-

isms after anesthetic treatment has also been considered by some as evidence indicating the reversibility of the anesthetic action. If such be viewed from the standpoint of chemical reactions, however, the mere fact of recovery of the organism to a normal condition following the application of anesthetics would not seem to be sufficient justification for concluding that the chemical reaction which initiated the effect is a reversible one, especially when one considers the manifold activities of the cell and the wonderful recuperative powers possessed by organisms, these no doubt involving numerous reactions. Hence the writer is inclined to the belief that an irreversible chemical reaction was at the basis of the phenomena observed as a result of the treatment of the plant with anesthetics and the consequent exosmosis of substances contained in the cell, and that any alteration of the plasma membrane resulting in changed permeability finds its best explanation on the basis of actual chemical reactions.

It is further believed that the results obtained by antagonistic pairs of salts and by single salts are also to be explained, as far as resulting exosmosis is concerned, in the specificity of the action of each. The method employed herein gives a delicate register of such action and is considered to be especially desirable because in it growth phenomena, with their resulting complex nutritive relations, may be left out of consideration. That the high conductivity readings in the case of the salts and certain other electrolytes was not due to insufficiency of the washing before the roots were placed in the distilled water was abundantly proved in various ways.

In regard to the method of experimentation employed in the work here reported, mention may well be made of its adaptability for delicate determinations pertaining to the relative toxicity of different substances. In the past such determinations have been made by means of growth measurements. It would seem that in this method we have, in some respects, a more rapid and satisfactory procedure for such work.

X. SUMMARY AND CONCLUSIONS

A brief historical review is given of the subject of excretion

from plant roots, exosmosis from living cells, and of excretion from leaves and other tissues.

The methods of experimentation are described.

A theoretical discussion is given of the various aspects of the subject.

The following are some of the experimental results obtained:

(a) Pea seedlings grew better in distilled water in which exosmosis from the previously treated plants of the first crop had occurred than in fresh distilled water, or in distilled water in which untreated plants had been grown.

(b) Peas and horse beans did not do as well in distilled water in which pea seedlings had already grown for 21 days as in fresh distilled water.

(c) Abundant exosmosis may occur from treated plants, even though the roots remain entirely normal in appearance. When the tops were badly affected and the roots remained normal, abundant exosmosis also occurred and the indications pointed in some cases to a downward flow of substances into the roots and out into the aqueous medium. No conclusive proof of this was obtained, however.

(d) Anesthetic vapors cause marked exosmosis upon considerable exposure of the plants to them, but there is none if the exposure be short. The interval required to initiate exosmosis was accurately determined. The order of effectiveness of the vapors tried is, ether, least; illuminating gas, more; and chloroform, most.

(e) The time limits for the exposure of plants to extremes of temperature in relation to exosmosis were determined. Comparison was also made between the effect of dry and moist heat.

(f) The exosmosis curves for various organic compounds were found. In general, at the concentrations used, marked excretion was produced.

(g) The effects of single salts, salts in pairs, and salts plus anesthetics in solution were ascertained as regards the exosmosis produced upon the plants in such solutions. Antagonistic relations in the sense of one substance decreasing the

exosmotic effect produced by another substance were found not to hold in the cases tried and under the conditions of the experiment.

It is with pleasure that the writer acknowledges his indebtedness to Dr. B. M. Duggar for numerous helpful suggestions in the prosecution of this work, and to Mrs. Amy Lyman Merrill for valuable assistance in the calculations involved and in the plotting of the curves; also to Dr. J. R. Schramm, who kindly aided in the tedious work of preparing the manuscript for the printer.

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MONOGRAPH OF THE NORTH AND CENTRAL AMERICAN SPECIES OF THE GENUS SENECIO—PART II[1]

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Introduction

The study upon which this monograph is based was begun nearly twenty years ago, at which time the author was an Assistant at the Gray Herbarium of Harvard University. Nearly every collection of any considerable size which came to the Herbarium, particularly from western United States, Mexico, and Central America, contained specimens of *Senecio*, many of which were either undetermined or referred doubtfully to some obscure or little known species. The identification of such material was often a laborious task, since all species recorded from a given region had to be listed and then specific identity established by a process of elimination. The available publications for such work were De Candolle's 'Prodromus,' Gray's 'Synoptical Flora,' and Hemsley's splendid contribution to the systematic literature of the botany of Mexico and Central America in the 'Biologia Centrali-Americana'; but the results obtained were often very unsatisfactory, because of the large number of new species published in scattered papers during the two decades following the appearance of the 'Synoptical Flora' and the 'Biologia.'

It was felt, therefore, that a revision of the genus, in the light of recent and more complete collections, which have accumulated from the numerous botanical explorations in different parts of North America, would be helpful to those concerned with this difficult group of plants and especially in the organization of material in different herbaria. A critical study of *Senecio* with the view of publishing eventually a

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monograph was suggested to me by Dr. B. L. Robinson, Curator of the Gray Herbarium, who very kindly offered to place at my disposal the entire representation of this genus in the Gray Herbarium, and who, moreover, willingly granted me the exceptional privilege of taking abroad the North American specimens, including all the types, for comparison and study in European herbaria. Accordingly nearly 2,000 mounted specimens were taken to Berlin; and through the courtesy of the authorities of the Royal Botanical Gardens and Museums of Berlin every facility in that institution, which is remarkably rich in Central and South American plants, was accorded me and work on the task was begun under the direction of Professor A. Engler.

It was necessary first of all to acquire a detailed knowledge of the general morphology of the genus *Senecio* as a whole, and also of the closely allied genera. The results of these investigations are briefly recorded in the first part of this monograph, namely 'Monographie der nord- und central-amerikanischen Arten der Gattung Senecio, I. Teil' which is frequently referred to in the following text. This preliminary work and the rich collections of the Gray and Berlin Herbaria form, therefore, the basis for the present systematic part of the monograph.

After completing my studies in Berlin I went to London, taking the Gray Herbarium specimens with me, and there spent several weeks, particularly in the examination of authentic and type specimens at the Kew Herbarium and in the Linnean Herbarium. The opportunity at Berlin, Kew, and Paris to actually compare side by side and in detail, recent specimens, or series of specimens, with many of the older types, some of which are more or less incomplete, has been of very great advantage, and, in fact, has made it possible to establish beyond doubt the identity of many of our American species.

In addition to those herbaria mentioned it also has been my good fortune to study this group of plants in several American institutions, notably the Herbarium of the Geological Survey of Canada, the United States National Her-

barium, the New York Botanical Garden Herbarium (including the Torrey Herbarium), the Herbarium of the Field Museum of Natural History, the Herbarium of the Philadelphia Academy of Natural Sciences, the Missouri Botanical Garden Herbarium, and a number of private collections. To the directors and curators of all these, as well as the owners of the private herbaria, and correspondents who have facilitated my work, I wish to express personal thanks; but I desire especially to extend most grateful acknowledgments to Dr. Benjamin Lincoln Robinson, Asa Gray Professor of Systematic Botany at Harvard University, and Geheimrath Professor Dr. Adolph Engler, Director of the Royal Botanical Gardens and Museum of Berlin, without whose coöperative interest and extreme liberality in the use of valuable scientific material under their charge, this work would have been impossible. I am also grateful to Mr. W. Botting Hemsley, of the Kew Herbarium, through whose courtesy I secured type material of certain rare Mexican species and a number of excellent drawings, some of which are herein reproduced.

I have cited exsiccatae rather freely, particularly such as occur in American herbaria, but by no means all that have been examined, and I have given even at the expense of much repetition detailed citation of specimens in different herbaria, hoping that this would be helpful in the interpretation of species and to future students of the genus. The few plates which it is possible to include are chosen to illustrate more especially the different sections as here defined.

SENECIO [TOURN.] LINN.

Senecio [Tourn. Inst. 456. *pl. 260.* 1700] L. Sp. Pl. **2**: 866. 1753; Gen. Pl., ed. 5, 373, n. 857. 1754; Hill, Hort. Kew. 25. 1768, and ed. 2, 1769; Juss. Gen. Pl. 181. 1789; Less. Syn. 391. 1832; DC. Prodr. **6**: 340. 1837; Endl. Gen. 458, n. 2811. 1838; Hook. Fl. Bor. Am. **1**: 331. 1840, in part; Torr. & Gray, Fl. N. Am. **2**: 436. 1843; Benth. & Hook. f. Gen. Pl. **2**: 446. 1873, in part; Pfeiffer, Nom. Bot. 2^2: 1136. 1874; Hemsl. Biol. Cent.-Am. Bot. **2**: 235. 1881, excl. *Cacalia;* Gray, Syn. Fl. N. Am. 1^2: 383. 1884, and ed. 2, 1888; Hoffmann in Engl. & Prantl,

Nat. Pflanzenf. IV. Abt. 5, 296. 1892, excl. *Emilia;* Greenm. Monogr. Senecio, I. Teil, 1901, and in Engl. Bot. Jahrb. **32**: 1–33. 1902; Dalla Torre & Harms, Gen. Siph. 563. 1900–1907, mainly.

Jacobaea Thunb. Fl. Cap. Prodr. Praef. 1794.

Obaejaca Cass. Dict. Sci. Nat. **35**: 270. 1825.

Roldana LaLlave & Lex. Nov. Veg., fasc. 2, 13. 1825.

Rugelia Schuttlew. in Chapm. Fl. Southern U. S. 246. 1860.

Cacalia, Cineraria, and *Gynoxis,* in part, of authors.

Heads heterogamous and radiate, or discoid. Involucre cylindrical campanulate, occasionally flask-shaped, usually subtended by calyculate bracteoles; bracts of the involucre uniseriate, or by overlapping subbiseriate, variable in number but tending to approach a definite series of numbers, namely 5–8–13–21. Ray-flowers when present disposed in a single row, fertile; rays sometimes more or less reduced. Disk-flowers perfect; corollas slenderly tubular to abruptly ampliated above into a campanulate 5-toothed limb, teeth mostly short. Anthers obtuse or slightly sagittate at the base. Style-branches subterete, recurved-spreading, truncate, rounded-obtuse, occasionally terminated by a small penicillate tuft of hairs, or (in the subgenus *Pseudogynoxis*) terminated by a triangular acute or acuminate appendage. Achenes subterete, usually ribbed, glabrous, or more or less hirtellous especially on the ribs. Pappus of numerous usually white setae.—Annual, biennial, or perennial herbs, shrubs, climbers, or even arboreous plants, with alternate or radical, very variable, pinnately or palmately veined, entire or variously divided leaves.

Synopsis of the Subgenera and Sections

Subgenus I. Eusenecio Hoffm. Style-branches truncate, rounded-obtuse or occasionally terminated by a penicillate tuft of hairs.

A. Stems erect or ascending, not climbing.
  a. Stems not abruptly terminated by a foreshortening of the main axis; oil-tubes not richly developed in the peripheral portion of the stem.
    a. Leaves pinnately veined; lateral nerves not numerous or conspicuous.
      I. Annual herbs ..... § 1. *Annui*

II. Biennial or perennial herbs (rarely annual).
1. Stems herbaceous.
* Heads usually radiate; flowers yellow, except in *S. Greenei* and *S. crocatus*.
† Stem leafy to the inflorescence; leaves laciniately pinnatifid to triternately divided.
0. Native species .....§ 2. *Eremophili*
00. Introduced species ...§ 3. *Jacobaeae*
†† Stem not uniformly leafy to the inflorescence; leaves pinnate or the lower simple and undivided.
0. Leaves pinnate or pinnatisect, rarely undivided .....§ 4. *Sanguisorboidei*
00. Lower leaves rotundovate, simple and undivided .....§ 5. *Bolanderiani*
††† Stem not uniformly leafy to the inflorescence; leaves simple and entire to lyrate-pinnatifid; plants either quite glabrous from the start or more or less permanently tomentose; pubescence never of long jointed hairs.
0. Plants glabrous or early glabrate; leaves upwardly reduced on the stem..§ 6. *Aurei*
00. Plants at first tomentose, later glabrate; leaves more uniform throughout and mostly pinnately divided .....§ 7. *Lobati*
000. Plants permanently tomentose or more or less glabrate; stem-leaves upwardly reduced .....§ 8. *Tomentosi*
†††† Stem leafy to the inflorescence (except in § 9); pubescence usually of long jointed hairs.
0. Stem-leaves not amplexicaul.
δ. Leaves not digitately divided ..§ 9. *Columbiani*
δδ. Leaves digitately divided .....§ 10. *Digitati*
00. Stem-leaves amplexicaul.
δ. Involucre ecalyculate .....§ 11. *Cineraroidei*
δδ. Involucre calyculate .....§ 12. *Amplectentes*

** Heads discoid; flowers whitish or purplish.
† Heads 2 cm. or more high; corollas deeply 5-lobed.....§ 13. *Rugeliae*
†† Heads 1 cm. high; corollas shortly 5-toothed .....§ 14. *Mulgedifolii*
2. Stems ligneous at the base.
* Involucre barely calyculate; plants densely white-tomentose throughout .....§ 15. *Incani*
** Involucre calyculate; plants glabrous or pubescent.....§ 16. *Suffruticosi*
3. Shrubs or tree-like plants.....§ 17. *Fruticosi*
β. Leaves palmately veined.....§ 18. *Palmatinerves*
γ. Leaves pinnately veined; lateral nerves parallel-arcuate, numerous and conspicuous..§ 19. *Multinervii*
b. Stems abruptly terminated by a fore-shortening of the main axis and bearing at the top two to several, more or less pedunculate axillary compound corymbose cymes; oil-tubes richly developed in the peripheral portion of the stem..§ 20. *Terminales*
B. Stems climbing .....§ 21. *Streptothamni*

Subgenus II. Pseudogynoxis Greenm. Style-branches terminated by triangular acute or acuminate dorsally hispidulous appendages.....§ 22. *Convolvuloidei*

Subgenus I. Eusenecio Hoffm.

Subgenus I. Eusenecio Hoffm. in Engl. & Prantl, Nat. Pflanzenf. IV. Abt. 5. 297. 1892; Greenm. Monogr. Senecio, I. Teil, 21, 30. 1901, and in Engl. Bot. Jahrb. **32** : 17, 26. 1902.

Annuals, biennials or perennials; stems erect, scandent or climbing; leaves pinnately or palmately veined; heads radiate or discoid; style-branches truncate or rounded-obtuse, not infrequently bearing a penicillate tuft of hairs at the extreme tip. Sect. 1–21.

Sect. 1. Annui Hoffm.

§ 1. Annui Hoffm. in Engl. & Prantl, Nat. Pflanzenf. IV. Abt. 5, 297. 1892; Greenm. Monogr. Senecio, I. Teil, 21, 23. 1901, and in Engl. Bot. Jahrb. **32** : 17, 19. 1902. *Obaejacae* DC. Prodr. **6** : 341. 1837.

Annual herbs; heads radiate or discoid; involucre narrowly campanulate or subcylindric, usually calyculate; achenes pubescent or glabrous. Sp. 1–7.

Key to the Species

A. Heads radiate or discoid; rays when present minute, barely surpassing the involucre.
  a. Plants viscid-pubescent ..... 1. *S. viscosus*
  b. Plants glabrous or pubescent, not viscid.
    a. Leaves coarsely dentate, auriculate-clasping by a broad base ..... 2. *S. mohavensis*
    β. Leaves chiefly pinnatifid, not greatly expanded at the base.
      I. Bracteoles black-tipped, heads discoid ..... 3. *S. vulgaris*
      II. Bracteoles not black-tipped; heads minutely radiate.
        1. Plants slightly pubescent ..... 4. *S. sylvaticus*
        2. Plants glabrous ..... 5. *S. aphanactis*

B. Heads radiate; rays conspicuous, much surpassing the involucre.
  a. Plants glabrous or pubescent, not arachnoid-tomentose.
    a. Leaves thin ..... 6. *S. californicus*
    β. Leaves thickish, succulent ..... 6*a*. var. *ammophilus*
  b. Plants arachnoid-tomentose ..... 7. *S. ampullaceus*

1. Senecio viscosus L. Sp. Pl. **2** : 868. 1753, and ed. 2, 1217. 1763; Sow. Eng. Bot. *pl. 32*. 1790; Willd. Sp. Pl. **3** : 1984. 1800; Oeder, Fl. Dan. *pl. 1230*. 1799; Schkuhr, Handb. *pl. 267*. 1808; DC. Prodr. **6** : 342. 1837; Gray, Syn. Fl. N. Am. **1**^{2} : 394. 1884; Greenm. Monogr. Senecio, I. Teil, 23. 1901, in Engl. Bot. Jahrb. **32** : 19. 1902, and in Gray, Manual, ed. 7, 853. 1907; Britton, Manual, ed. 2, 1029. 1905; Britton & Brown, Ill. Fl., ed. 2, **3** : 540. 1913.

Obaejaca viscosa Cass. Dict. Sci. Nat. **35** : 270. 1825.

A strong-scented annual, viscid-pubescent throughout; stem erect, 2 to 4 dm. high, usually branched from the base; leaves sessile, half-clasping, 3 to 6 cm. long, two-thirds as broad, once or twice pinnatifid with angulate-sinuate lobes and rounded sinuses; heads radiate (rarely discoid); rays inconspicuous; achenes glabrous.

Distribution: eastern North America from Nova Scotia to Pennsylvania, near the coast.

Specimens examined:

Nova Scotia: Pictou, 1 Nov., 1874, *Fowler* (Field Mus. Herb.); Pictou Landing, 21 July, 1883, *Macoun 14883* (Geol. Surv. Canada Herb.); Kentville, 22 Aug., 1902, *Fernald* (Gray Herb. and Geol. Surv. Canada Herb.).

New Brunswick: Shediac, 11 Sept., 1874, *Fowler* (Geol.

Surv. Canada Herb. *14882* and Kew Herb. *872,* in part); Painsec Junction, 8 Aug., 1901, *Churchill* (Gray Herb.).

Massachusetts: along Boston and Albany Railroad, Sept., 1879, *Boott* (Gray Herb.); streets of Cambridge, 1 Sept., 1897, *Robinson* (Gray Herb.).

Rhode Island: wharves at Providence, 4 Sept., 1874, *Congdon* (Gray Herb.); streets of Providence, coll. of 1876, *Bailey* (Gray Herb. and Field Mus. Herb.); East Providence, 20 July, 1890, *Collins* (Mo. Bot. Gard. Herb.).

Pennsylvania: on ballast, Girard Point, July, 1877, *Martindale* (Gray Herb.) and Aug., 1877, *Rothrock* (Field Mus. Herb.). Introduced from Europe.

2. S. mohavensis Gray, Syn. Fl. N. Am. 1^2: 446. 1884, and ed. 2, 454. 1886; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902. Plate 17.

Glabrous throughout; stems erect or nearly so, 1.5 to 4 dm. high, freely branching; leaves membranous, ovate to oblong-ovate, 2 to 6 cm. long, 1 to 4 cm. broad, apiculate-acute, irregularly toothed, or somewhat laciniate-dentate, the lowermost narrowed into a petiolate base, those of the stem sessile and amplexicaul; inflorescence a terminal corymbose cyme; heads 1 cm. high on slender peduncles, discoid or with much reduced ligulate flowers; involucre calyculate with few short inconspicuous bracteoles, 18–20-flowered; bracts of the involucre about 13, linear, acute, slightly shorter than the flowers of the disk; achenes canescent pubescent.

Distribution: southern California, Arizona, and northern Mexico.

Specimens examined:

California: Pleasant Cañon, Panamint Mountains, alt. 900 m., 10 May, 1906, *Hall & Chandler 6910* (Mo. Bot. Gard. Herb. and Field Mus. Herb.); Hall Cañon, Panamint Mountains, 18 April, 1891, *Coville & Funston 697* (U. S. Nat. Herb.); Panamint Valley, alt. 450 m., 5 May, 1897, *Jones* (Mo. Bot. Gard. Herb.); Mohave region, April–May, 1884, *Lemmon 3129* (Gray Herb.), TYPE; Colorado Desert, April, 1889, *C. R. Orcutt* (U. S. Nat. Herb. and Gray Herb.).

Arizona: Tempe, 21 April, 1892, *Ganong & Blaschka* (Gray Herb.).

Sonora: near the U. S. boundary line, 28 March, 1884, *Pringle* (Gray Herb. and U. S. Nat. Herb.).

3. S. vulgaris L. Sp. Pl. **2**: 867. 1753, ed. 2, 1216. 1763; Fl. Dan. *pl. 513.* 1770; Willd. Sp. Pl. **3**: 1979. 1800; Sow. Eng. Bot. *pl. 747.* 1800; Pursh, Fl. **2**: 528. 1814; DC. Prodr. **6**: 341. 1837; Reichb. Ic. Fl. Germ. & Helv. **16**: 35. *pl. 68* (CMLIX), *fig. I, 1–9.* 1854; Gray, Syn. Fl. N. Am. 1^2: 394. 1886; Greenm. Monogr. Senecio, I. Teil, 23. 1901, in Engl. Bot. Jahrb. **32**: 19. 1902, and in Gray, Manual, ed. 7, 853. 1907; Britton, Manual, ed. 2, 1029. 1905; Britton & Brown, Ill. Fl., ed. 2, **3**: 539. 1913.

Annual, 1 to 4 dm. high, glabrous or subfloccose pubescent especially in the axils of the upper leaves and in the inflorescence; leaves 2 to 8 cm. long, 0.5 to 2.5 cm. broad, more or less lyrately pinnatifid and angulate-toothed, lower leaves narrowed into a margined petiole, the upper sessile and semi-amplexicaul; heads discoid; the rather numerous small calyculate bracteoles as well as the bracts of the involucre usually black-tipped; achenes hirtellous-puberulent along the angles or ribs.

Distribution: Labrador, Newfoundland to North Carolina, west to Alaska, California, and New Mexico. Europe, Asia, and Africa.

Specimens examined:

Labrador: Hopedale, 4–6 Aug., 1897, *Sornborger 162* (Gray Herb.).

Newfoundland: rocky hills, St. John's, 1 Aug., 1894, *Robinson & Schrenk* (Gray Herb., U. S. Nat. Herb., Geol. Surv. Canada Herb., and Mo. Bot. Gard. Herb.); Funk Island, 23 July, 1887, *Palmer* (U. S. Nat. Herb.); rich soil, field near shore, Channel, 27 July–1 Aug., 1901, *Howe & Lang 802* (Gray Herb.); Barred Island, 13 Aug., 1903, *Sornborger* (Gray Herb.).

Nova Scotia: dry soil, roadsides, North Sydney, Cape Breton, 21–25 July, 1901, *Howe & Lang 639* (Gray Herb.);

Boylston, July, 1890, *Hamilton 22848* (Geol. Surv. Canada Herb.); Baddeck, Cape Breton Island, 25 July, 1898, *Macoun 19721* (Geol. Surv. Canada Herb.).

New Brunswick: along railroad, Conners, 22 July, 1908, *Mackenzie 3646* (Mo. Bot. Gard. Herb.); Shediac, 11 Sept., 1874, *Fowler 872* in part. (Kew Herb.).

Quebec: shore of St. Lawrence, Gaspé, Matane Co., *Forbes* (Gray Herb.); Gaspé Basin, 24 July, 1882, *Macoun 14889* (Geol. Surv. Canada Herb.).

Ontario: Ottawa, 20 July, 1891, *Scott 14885* (Geol. Surv. Canada Herb.); Belleville, 10 Aug., 1877, *Macoun 14890* (Geol. Surv. Canada Herb.); northeast of Sarnia, Lambton Co., *Wheatley* (Mo. Bot. Gard. Herb.); Wingham, Aug., 1890, *Morton 14886* (Geol. Surv. Canada Herb.); Kingston, Sept., 1896, *Fowler* (Field Mus. Herb.); Sarnia, 18 June, 1901, *Macoun 26677* (Geol. Surv. Canada Herb.).

Saskatchewan: between Cumberland House and Hudson Bay, *Richardson 14887* (Geol. Surv. Canada Herb.); Prince Albert, 13 July, 1896, *Macoun 12174* (Geol. Surv. Canada Herb.).

Alberta: waste ground, Prince's Island, near Calgary, 21 Aug., 1913, *Moodie 31* (Field Mus. Herb.).

British Columbia: Burrard Inlet, 22 July, 1889, *Macoun* (Gray Herb. and Geol. Surv. Canada Herb.); vicinity of Victoria, 9 April, 1908, *Macoun 78949* (Field Mus. Herb.); along railway embankment, Sicamous, 20 July, 1904, *Macoun 62191* (Geol. Surv. Canada Herb.); Cedar Hill, Vancouver Island, 21 May, 1887, *Macoun 14884* (Geol. Surv. Canada Herb.); near Victoria, 23 May, 1893, collector not indicated, *550* (Geol. Surv. Canada Herb.); Victoria, 10 June, 1875, *Dawson 14888* (Geol. Surv. Canada Herb.).

Alaska: vicinity of Sitka, July, 1891, *Wright 1538* (Mo. Bot. Gard. Herb.); Sitka, July, 1881, *McLean* (U. S. Nat. Herb.); Skagway, 29 July, 1907, *Cowles 889* (Field Mus. Herb. and Mo. Bot. Gard. Herb.).

Maine: Baker's Island, 19 July, 1883, *Redfield* (Mo. Bot. Gard. Herb.).

Vermont: waste ground, Rutland, 1 Sept., 1899, *Eggleston 1383* (Gray Herb.).

Massachusetts: Ipswich, *Oakes* (Gray Herb. and U. S. Nat. Herb.); Nahant, 6 July, 1878, *Kellermann* (Mo. Bot. Gard. Herb.); Revere Beach, 9 July, 1898, *Greenman 515* (Gray Herb.); Cambridge, *Chickering* (U. S. Nat. Herb.); roadsides, West Cambridge, 29 Sept., 1894, local collection (Gray Herb.); Swampscott, 21 June, 1897, *Weatherby* (Gray Herb.); Ipswich, July, 1874, *Morong* (Field Mus. Herb.).

Rhode Island: waste places, Providence, Sept., 1844, *Thurber* (Gray Herb.); Providence, 2 July, 1892, *Collins & Bailey* (U. S. Nat. Herb.); Cat Swamp, Providence, 23 June, 1895, *Collins* (U. S. Nat. Herb.); Providence, 16 Aug., 1873, *Congdon* (Field Mus. Herb.); Providence, July, 1878, *Bailey* (Mo. Bot. Gard. Herb.).

New York: Syracuse, June, 1887, *Overacker* (Mo. Bot. Gard. Herb.); Troy, collector and date not indicated (Gray Herb.); Ithaca, 12 Oct., 1892, *H. von Schrenk* (Mo. Bot. Gard. Herb.); near Fiske mansion, Ithaca, 21 May, 1884 (U. S. Nat. Herb.); Hunter's Point, Long Island, Sept., 1879, *J. Schrenk* (U. S. Nat. Herb.); Elmira City, 28 Aug., 1898, *Lucy* (Field Mus. Herb.); Troy, June, 1873, *Jesup* (Field Mus. Herb.).

Pennsylvania: Girard Point, Philadelphia, Aug., 1877, *Rothrock* (Field Mus. Herb.).

New Jersey: Camden, July, 1876, *Martindale* (U. S. Nat. Herb.); Kaighn's Point, Camden, 16 July, 1865, *Parker* (Mo. Bot. Gard. Herb.).

Maryland: vicinity of Oakland, 5 Sept., 1910, *Steele* (U. S. Nat. Herb.).

District of Columbia: waste ground, Washington, 14 Sept., 1891, *Blanchard* (Mo. Bot. Gard. Herb.); above Uniontown, 27 May, 1883, *Ward* (U. S. Nat. Herb.).

North Carolina: cultivated grounds, Biltmore, 4 May, 1897, *Biltmore Herb. 883*^{b} (Gray Herb., Mo. Bot. Gard. Herb., and Field Mus. Herb.).

Ohio: Oberlin, June, 1892 and 1895, *Ricksecker* (U. S. Nat. Herb.).

Michigan: waste ground, Keweenaw Co., July, 1887, *Farwell* (Gray Herb.).

Wisconsin: St. Croix Co., coll. of 1888, *Matthews* (U. S. Nat. Herb.); Preble, 20 May, 1883, *Schuette* (Field Mus. Herb.); Green Bay, 11 July, 1897 and 29 Sept., 1901, *Schuette* (Field Mus. Herb.).

Nebraska: Valley Co., July, 1886, *Webber* (Field Mus. Herb.).

Montana: Willow Creek, 14 June, 1883 *Scribner 123*[c] (Gray Herb.); Columbia Falls, 21 June, 1894, *Williams 965* (Gray Herb. and U. S. Nat. Herb.).

Wyoming: Sundance, 4 July, 1896, *Nelson 2201* (Mo. Bot. Gard. Herb.).

Colorado: valley near Empire, Sept., 1892, *Patterson* (Gray Herb.); along railroad at Georgetown, Aug.–Sept., 1892, *Patterson* (Field Mus. Herb.).

New Mexico: Sante Fe, 14 Sept., 1895, *Mulford 1301* (Mo. Bot. Gard. Herb.); 4 May, 1897, *A. A. & E. G. Heller 3657* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.).

Idaho: frequent in moist places, Julietta, Latah Co., 8 June, 1892, *Sandberg, McDougal & Heller 343* (Gray Herb., Field Mus. Herb., and U. S. Nat. Herb.); waste ground in the Palouse Country and about Lake Coeur d'Alene, June–July, 1892, *Aiton* (Field Mus. Herb. and Mo. Bot. Gard. Herb.).

Washington: on mountains near the lower Cascades, 29 May, 1886, *Suksdorf* (Gray Herb.); Seattle, 6 March, 1889, *Smith* (Mo. Bot. Gard. Herb.); in fields, Pullman, 2 June, 1894, *Piper* (Mo. Bot. Gard. Herb.); Hoquiam, 5 June, 1897, *Lamb 1146* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); San Juan Island, July, 1914, *Reynolds* (Field Mus. Herb.); Index, Snohomish Co., July, 1898, *Savage, Cameron & Lenocker* (Field Mus. Herb.); Granddalles, 3 Sept., 1904, *Westgate 3997* (U. S. Nat. Herb.); Klickitat Co., June, 1878, *Suksdorf* (Gray Herb.).

Oregon: cultivated fields, Sauvie Island, June, 1880, *Howell* (Gray Herb.); Portland, 1 June, 1884, *Henderson 555* (Mo. Bot. Gard. Herb.); Portland, Feb., 1900, *Lunell*, and without date *Sargent* (Gray Herb.); Bonneville, 6 Aug., 1895,

Canby (U. S. Nat Herb.); Catching Inlet, 10 May, 1911, *Smith 3700* (Field Mus. Herb.); Charleston Bay, 6 May, 1911, *Smith 3668* (Field Mus. Herb.); North Slough, 1 March, 1911, *Smith 3487;* Coos Co., 2 March, 1911, *Smith 3494* (Field Mus. Herb.); Portland, March, 1889, *Drake & Dickson* (Field Mus. Herb.); without definite locality, coll. of 1868–69, *Kellogg & Harford 536* (U. S. Nat. Herb.).

California: Oakland, March, 1864, *Bolander 2777* (Gray Herb. and Mo. Bot. Gard. Herb.) and May, 1865, *Bolander 434* (Gray Herb.); without definite locality, coll. of 1880, *Norton* (Mo. Bot. Gard. Herb.); near Mendocino, May, 1898, *Brown 758* (Mo. Bot. Gard. Herb.); Mendocino Co., June, 1898, *Brown 458* (Field Mus. Herb.); Stanford University, 2 March, 1902, *Baker 311* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Russian River, near Trenton, 16 March, 1902, *Heller & Brown 5072* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Big River, Mendocino Co., July, 1903, *McMurphy 374* (U. S. Nat. Herb.); near Saratoga, Santa Clara Co., 25 Feb., 1906, *Pendleton 288* (U. S. Nat. Herb.).

4. S. sylvaticus L. Sp. Pl. **2**: 868. 1753, and ed. 2, 1217. 1763; Sow. Eng. Bot. *pl. 748.* 1800; Willd. Sp. Pl. **3**: 1985. 1800; Fl. Dan. *pl. 869.* 1782; DC. Prodr. **6**: 342. 1837; Gray, Syn. Fl. N. Am. **1**^{2}: 394. 1884; Greenm. Monogr. Senecio, I. Teil, 23. 1901, in Engl. Bot. Jahrb. **32**: 19. 1902, and in Gray, Manual, ed. 7, 853. 1907; Britton, Manual, ed. 2, 1029. 1905; Britton & Brown, Ill. Fl., ed. 2, **3**: 539. 1913.

Obaejaca sylvatica Cass. Dict. Sci. Nat. **35**: 271. 1825.

Stem erect, simple or branched, 1 to 4 dm. or more high, usually somewhat pubescent; leaves more or less pinnatifid with unequal lobes, 2 to 15 cm. long, 1 to 8 cm. broad; the lower leaves petioled, the upper sessile, clasping and auriculate-sagittate; inflorescence naked or nearly so; heads cylindrical, sparingly calyculate, radiate; ligules barely surpassing the involucre, not infrequently much reduced; achenes canescent-pubescent.

Distribution: Newfoundland to Maine, Ohio, and on Pacific coast.

Specimens examined:

Newfoundland: railway ballast, Whitbourne, 17 Aug., 1894, *Robinson & Schrenk* (Gray Herb., U. S. Nat. Herb., Mo. Bot. Gard. Herb., and Geol. Surv. Canada Herb.).

Prince Edward Island: sand dunes, Tracadie Beach, 25 July, 1901, *Churchill* (Gray Herb. and Mo. Bot. Gard. Herb.); waste places, Brackley Point, 28 Aug., 1888; *Macoun 14874* (Geol. Surv. Canada Herb.).

Nova Scotia: clearings and open woods, Sydney, Cape Breton Island, 17 Aug., 1902, *Fernald* (Gray Herb.); Boylston, Aug., 1890, *Hamilton 22847* (Geol. Surv. Canada Herb.); Truro, without date, *Maccullock* (Gray Herb.); Elizabethtown, Cape Breton Island, 2 Aug., 1898, *Macoun 19719* (Gray Herb. and Geol. Surv. Canada Herb.); Baddeck Bay, Cape Breton Island, 11 Aug., 1898, *Macoun 19720* (Gray Herb. and Geol. Surv. Canada Herb.); sea cliffs, Black Hole, near Baxter's Harbor, 24 Aug., 1902, *Fernald* (Gray Herb.); on pebbly beach, Purcell's Cove, Halifax Harbor, 2–6 Sept., 1901, *Howe & Lang 1512* (Gray Herb.); open woods, Starrs Point, Kings Co., 23 Aug., 1902, *Fernald* (Gray Herb.); McNiels Harbor, Cape Breton Island, 4 Aug., 1898, sheet *19722* (Geol. Surv. Canada Herb.).

New Brunswick: Grand Manan, 26 July, 1891, *Churchill* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Falls of the St. John River, St. John, 22 July, 1902, *Williams & Fernald* (Gray Herb.).

Quebec: beach of Gaspé Bay, Gaspé Co., 24–27 Aug., 1904, *Collins, Fernald & Pease* (Gray Herb.).

British Columbia: Vancouver Island, 6 Aug., 1909, *Macoun 78950* and *78951* (Field Mus. Herb.).

Maine: island in Penobscot Bay, Aug., 1896, *F. L. & L. H. Harvey 554c* (U. S. Nat. Herb.).

Ohio: near Painsville, coll. of 1892, *Hacker 123* (Gray Herb.).

Washington: Seattle, Aug., 1909, *Piper* (U. S. Nat. Herb.); on old burn near farms, Port Crescent, Aug., 1911, *Webster 19* (U. S. Nat. Herb.); old camps, Granite Falls, Snohomish Co., 31 Oct., 1911, *Smith 4226* (Field Mus. Herb.); Iron Mountain,

Granite Falls, alt. 300 m., 28 Oct., 1911, *Smith 4224* (Field Mus. Herb.).

Oregon: region of Coos Bay, 10 Sept., 1911, *House 4848* (U. S. Nat. Herb.).

California: Vance's Camp, Humboldt Co., 5 June, 1911, *Smith 3778* (Field Mus. Herb.); vicinity of Eureka, 20 June, 1907, *J. P. Tracy 2571* (Univ. Calif. Herb. and Mo. Bot. Gard. Herb.).

5. S. aphanactis Greene, Pittonia, **1**: 220. 1888, and Fl. Franciscana 464. 1897; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

S. sylvaticus Gray, Bot. Calif. **1**: 410. 1876, not L.; Jepson, Fl. West. Mid. Calif. 512. 1901.

A slender annual, 1 to 3 dm. high, glabrous or somewhat tomentulose especially in the inflorescence; stem simple or branched; leaves linear to lanceolate, 1 to 4 cm. long, 1 to 12 mm. broad, entire to coarsely dentate or even pinnately lobed, glabrous or nearly so; the lower leaves narrowed into a petiolate base, the upper sessile; inflorescence terminal, few to several-headed; heads somewhat flask-shaped, 6 to 7 mm. high, radiate; involucre sparingly bracteolate, glabrous to tomentulose at the base; rays small, scarcely exceeding the involucre; achenes appressed-canescent.

Distribution: central California, northern Mexico and adjacent islands.

Specimens examined:

California: Mare Island, 30 March, 1874, *Greene* (Gray Herb. and Field Mus. Herb.), CO-TYPE; San Luis Obispo, *Brewer 463* (Gray Herb. and Mo. Bot. Gard. Herb.); San Luis Obispo, coll. of 1886, *Summis* (U. S. Nat. Herb.); Avalon, Santa Catalina Island, March, 1901, *Trask* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); edges of cañons and alkaline flats, San Diego, *Brandegee 3414* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); San Diego, Geological Survey of California 1860–61, *Cooper* (Gray Herb.); North American Pacific coast flora, *Parry 170* (Gray Herb.); San Diego, 5 Feb., 1884, *Orcutt* (Field Mus. Herb.).

Lower California: Cedros Island, April, 1897, *Brandegee* (Gray Herb. and U. S. Nat. Herb.); San Quentin Bay, *Palmer 606* (Kew Herb.).

6. S. californicus DC. Prodr. **6**: 426. 1837; Torr. & Gray, Fl. N. Am. **2**: 437. 1843; Gray, Bot. Calif. **1**: 410. 1876, Syn. Fl. N. Am. **1**^{2}: 393. 1884, and ed. 2, 454. 1886; Greene, Fl. Franciscana, 465. 1897; Greenm. Monogr. Senecio, I. Teil, 23. 1901 and in Engl. Bot. Jahrb. **32**: 19. 1902; Abrams, Fl. Los Angeles and vicinity 439. 1904.

S. californicus var. *laxior* DC. Prodr. **6**: 426. 1837; Torr. & Gray, Fl. N. Am. **2**: 437. 1843.

S. coronopus Nutt. Trans. Am. Phil. Soc. **7**: 413. 1841; Torr. & Gray, Fl. N. Am. **2**: 437. 1843.

An herbaceous glabrous annual; stem erect simple or branched, 1 to 5 dm. high; leaves oblong-spatulate to lanceolate, entire to subpinnatifid, 2.5 to 7 cm. long, .2 to 2 cm. broad, often reddish; the lower leaves often narrowed to a subpetiolate base, the upper sessile and auriculate-clasping at the base; heads radiate, few to several in a loose cyme; bracts of the involucre about 21, often brownish or black-tipped, much exceeded by the yellow conspicuous rays; achenes canescent-pubescent.

Distribution: central California, vicinity of Monterey, south to northern Mexico.

Specimens examined:

California: sand hills, back of Seaside, Monterey Co., 3 April, 1903, *Heller 6509* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Gigling Station, east of Del Monte, in sand, 11 May, 1903, *Heller 6710* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Bardins, Monterey Co., April, 1903, *Elmer 4893* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Del Monte, April, 1902, *Elmer 3576* (Mo. Bot. Gard. Herb.); Arroja Grande, San Luis Obispo Co., 21 Feb., 1886, *Summers* (Gray Herb.); Cuyama, near the boundary between Santa Barbara and San Luis Obispo Counties, 6 May, 1896, *Eastwood* (Gray Herb.); hillsides, Los Angeles Co., 19 March, 1888, *Hasse* (U. S. Nat. Herb.); Los Angeles, May,

1888, *Hasse* (Field Mus. Herb.); copses and grassy slopes, Los Angeles Co., May, 1890, *Hasse* (U. S. Nat. Herb.); Santa Monica, coll. of 1885, *A. Gray* (Gray Herb.); hillsides, Los Angeles Co., Aug., 1890 and June, 1891, *Hasse* (Mo. Bot. Gard. Herb.); "Pueblo los Angeles," *Gambell* (Gray Herb.); without definite locality, *Coulter 335* (Gray Herb.), and coll. of Nov., 1846, *Fremont* (Gray Herb.); Los Angeles, 5 April, 1890, *Fritchey* (Mo. Bot. Gard. Herb.); San Bernardino, *S. B. & W. F. Parish 198* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); San Bernardino, coll. of 1880, *Vasey 330* (Field Mus. Herb., U. S. Nat. Herb., and Gray Herb.); near San Bernardino, May, 1893, *Parish* (Mo. Bot. Gard. Herb.); mesas, San Bernardino Co., May, 1888, *Parish* (Mo. Bot. Gard. Herb.) and April, 1896, *Parish* (Field Mus. Herb.); San Bernardino Co., coll. of 1876, *Parry & Lemmon 206* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Arrow Head Springs, 15 May, 1891, *Fritchey 18* (Mo. Bot. Gard. Herb.); San Bernardino, *Parish 7* (Gray Herb.); "Cocomurgo," in sandy places, March, 1854, *Bigelow* (Gray Herb.); San Bernardino Co., Feb.–April, 1882, *Parish 233* (Gray Herb.); without definite locality, coll. of 1833, *Douglas 46* (Gray Herb.), CO-TYPE of var. *laxior;* vicinity of Riverside, alt. 600 m., March, 1903, *Hall 3721* (Gray Herb. and Field Mus. Herb.); San Diego, April, 1873, *Bolander & Kellock* (Gray Herb.); San Luis Rey, *Parry* (Gray Herb.); vicinity of Riverside, 26 March, 1907, *Reed 1252* (Field Mus. Herb.); vicinity of San Bernardino, 13 April, 1903, *Parish 5188* (Field Mus. Herb.); without definite locality, *Nuttall* (Gray Herb.); San Diego, April, 1905, *Brandegee* (U. S. Nat. Herb.) and April, 1902, *Brandegee 1647* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); San Diego, April, 1882, *Jones* (U. S. Nat. Herb.); hills, San Diego, 25 April, 1882, *Pringle* (U. S. Nat. Herb. and Field Mus. Herb.); San Diego, 4 May, 1882, *Orcutt 328* (Mo. Bot. Gard. Herb.); Potrero, 6 April, 1889, *Orcutt* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Moro hills, near Fallbrook, 28 April, 1903, *Abrams 3332* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Fallbrook, 27 March, 1882, *Jones 3118* (U. S. Nat. Herb.); San Diego, *Cleveland* (Field

Mus. Herb. and Mo. Bot. Gard. Herb.); San Diego, coll. of June, 1906, *K. Brandegee* (U. S. Nat. Herb.), and coll. of 1875, *Palmer 200* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); side hill, Del Mar, Oct., 1894 and 22 March, 1895, *Angier 14* and *97* (Mo. Bot. Gard. Herb.); Mesa, April, 1895, *Angier* (Field Mus. Herb.); La Jolla, San Diego Co., 17 Feb., 1895, *Snyder* (Field Mus. Herb.); Las Paderes Ranch, San Diego Co., 26 Feb., 1888, *Deane* (Field Mus. Herb.).

Lower California:

Todos Santos Bay, July, 1883, *Orcutt 708* (Gray Herb.); All Saints Bay, May, 1882, *Fish* (Gray Herb.); Punta Bauda, 25 Jan., 1883, *Orcutt 708* (Mo. Bot. Gard. Herb.); Nachoguero Valley, *Schoenfeldt 3401* (U. S. Nat. Herb.).

Var. **ammophilus** (Greene) Greenm. comb. nov.

Senecio ammophilus Greene, Bull. Cal. Acad. **1**: 193. 1886.

Leaves thickish, somewhat succulent, 2 to 4 cm. long, .2 to 1.5 cm. broad, the lower oblanceolate subentire, those of the stem auriculate-clasping, pinnately lobed into oblong or linear obtuse lobes.

Lower California: Cape San Quentin, 10 May, 1885, *Greene* (Gray Herb.), CO-TYPE.

The thick leaves of this variety give the plant a somewhat different appearance from typical forms of the species; but an examination of a large suite of specimens shows numerous transitional forms such as those secured by *Fritchey, Pringle, Bigelow, Palmer 200, Orcutt 708,* and *K. Brandegee.*

7. S. ampullaceus Hook. Bot. Mag. *pl. 3487.* 1836; DC. Prodr. **6**: 428. 1836; Torr. & Gray, Fl. N. Am. **2**: 440. 1843; Engelm. & Gray, Boston Jour. Nat. Hist. **5**: 250. 1845 (Pl. Lindh. **1**: 42. 1845); Gray Syn. Fl. N. Am. **1**^{2}: 393. 1884, and ed. 2, 1886; Coulter, Contr. U. S. Nat. Herb. **2**: 241. 1892; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

S. ampullaceus var. *glaberrimus* Engelm. & Gray, Boston Jour. Nat. Hist. **5**: 250. 1845 (Pl. Lindh. **1**: 42. 1845).

S. ampullaceus var. *floccosus* Engelm. & Gray, Boston Jour. Nat. Hist. **5**: 250. 1845 (Pl. Lindh. **1**: 42. 1845).

Annual, or occasionally becoming biennial, more or less floccose-tomentose throughout, somewhat glabrate; leaves oblong-obovate, acute to lanceolate and acuminate, 5 to 18 cm. long, 1 to 7 cm. broad, entire to coarsely and irregularly dentate; the lower leaves narrowed below into a winged petiole, those of the stem sessile, semiamplexicaul, gradually smaller towards the few to many headed cymose inflorescence; heads 10 to 12 mm. high, radiate, including the rays 1.5 to 3 cm. in diameter; involucre setaceous-calyculate; bracts of the involucre glabrous; achenes pubescent.

Distribution: eastern Texas.

Specimens examined:

Texas: San Felipe, Austin Co., *Drummond* (Kew Herb. and Gray Herb.), TYPE; Corsicana, *Reverchon* (Mo. Bot. Gard. Herb.); near Richland Station, 13 March, 1880, *Joor* (Mo. Bot. Gard. Herb.); Dawson, 16 April, 1903, *Reverchon 3965* and *5965* (Mo. Bot. Gard. Herb.); Llano, May, 1885, *Reverchon 1545* (U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); banks of Pecan Bayou, April, 1882, *Reverchon 81* (Gray Herb. and Mo. Bot. Gard. Herb.); sandy soils, Lampasas Co., May, 1884, *Reverchon 1321* (Mo. Bot. Gard. Herb.); Crabapple, Gillespie Co., *Jermy* (Mo. Bot. Gard. Herb.); Hockley, Harris Co., coll. of 1890, *Thurrow* (Field Mus. Herb.); banks of Colorado River, 4 April, 1914, *Young* (Mo. Bot. Gard. Herb. and Univ. of Texas Herb.); on dry ground, Hempstead, 24 April, 1872, *Hall 369* (Gray Herb., U. S. Nat. Herb., and Mo. Bot. Gard Herb.); without locality, coll. of 1848, *Wright* (Gray Herb.); Industry, Austin Co., coll. of 1890, *Wurzlow* (Field Mus. Herb.); banks of railroad near Rosenberg, Fort Bend Co., 13 April, 1900, *Eggert* (Mo. Bot. Gard. Herb.); common on prairies, Columbia, 10 April, 1899, *Bush 95* (Gray Herb. and Mo. Bot. Gard. Herb.); Columbia, 23 April, 1900, *Bush 122* (Mo. Bot. Gard. Herb.); Columbia, 25 March, 1900, *Canby, Sargent & Trelease 153* (U. S. Nat. Herb.); on moist prairie between the Brazos and the Colorado Rivers, April, 1844, *Lindheimer 268, 269* (Mo. Bot. Gard. Herb.), CO-TYPES of var. *glaberrimus* and *floccosus*.

SECT. 2. EREMOPHILI Greenm.

§ 2. EREMOPHILI Greenm. Monogr. Senecio, I. Teil, 21, 23. 1901, and in Engl. Bot. Jahrb. **32** : 17, 19. 1902.

Annual or biennial herbs, not infrequently becoming perennial by the development of a ligneous base; stems leafy; leaves laciniately pinnatifid; inflorescence a terminal corymbose or paniculate cyme; heads radiate, rays conspicuous; achenes glabrous or pubescent. Sp. 8–13.

KEY TO THE SPECIES

A. Plants glabrous; achenes smooth or slightly hirtellous.
  a. Heads 7 to 10 mm. high; involucral bracts 5 to 7 mm. long, usually conspicuously black-tipped.
    α. Involucre 3 to 5 mm. in diameter, 20–35-flowered ..... 8. *S. MacDougalii*
    β. Involucre 5 to 6 mm. in diameter, 35–50-flowered ..... 9. *S. ambrosioides*
  b. Heads 10 to 12 mm. high; involucral bracts 7 to 10 mm. long, not conspicuously black-tipped.
    α. Northern species (Canada and the U. S.) ..... 10. *S. eremophilus*
    β. Southern species (Mexico) ..... 11. *S. Townsendii*

B. Plants more or less tomentose; achenes canescent-pubescent.
  a. Leaves at first tomentulose, later glabrate ..... 12. *S. chihuahuensis*
  b. Leaves permanently tomentulose ..... 13. *S. durangensis*

8. **S. MacDougalii** Heller, Bull. Torr. Bot. Club **26** : 592. 1899; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902, in part; Rydb. in Fl. Colo. 397. 1906, in part; Wooton & Standley, Contr. U. S. Nat. Herb. **19** : 745. 1915.

S. eremophilus Gray, Syn. Fl. N. Am. **1**^{2} : 392. 1884, and ed. 2, 1886, in part, not Richards.

S. eremophilus var. *attenuatus* Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

Glabrous throughout or slightly puberulent above; stem simple or branched, 5 to 8 dm. high, leafy to the inflorescence; leaves more or less laciniately pinnatifid, 3 to 10 cm. long, 1.5 to 5 cm. broad, segments linear to lanceolate, entire to coarsely and unequally dentate; inflorescence terminating the stem and branches in corymbose cymes; heads 7 to 10 mm. high, radiate; involucre narrowly campanulate, calyculate, 3 to 5 mm. in diameter; bracts of the involucre usually 13 (8–13), linear-

lanceolate, 4 to 5 mm. long, commonly black-tipped; ray-flowers 5 to 8, light yellow; disk-flowers 14 to 30; achenes glabrous or slightly puberulent.

Distribution: New Mexico and Arizona.

Specimens examined:

New Mexico: Santa Fe Cañon, Aug., 1880, *Snow* (Mo. Bot. Gard. Herb.); Santa Fe Creek, 9 Sept., 1881, *Engelmann* (Mo. Bot. Gard. Herb.); Santa Fe, 14 Aug., 1895, *Mulford 1292* (Mo. Bot. Gard. Herb.); near Pecos, alt. 2040 m., 25 Aug., 1908, *Standley 5311* (Mo. Bot. Gard. Herb.); Pecos River National Forest, alt. 2560 m., 10 Aug., 1908, *Standley 4873* (U. S. Nat. Herb.); White Mountains, alt. 2130 m., 6 Aug., 1897, *Wooton 290* (Gray Herb. and Mo. Bot. Gard. Herb.); White Mountains, alt. 2255 m., 25 Aug., 1907, *Wooton & Standley 3672* (U. S. Nat. Herb.); head of Bear Creek, coll. of 1903, *Plummer* (U. S. Nat. Herb.); Gilmore's Ranch, White Mountains, alt. 2280 m., 23 Sept., 1906, *Standley* (Mo. Bot. Gard. Herb.); G. O. S. Ranch, Grant Co., 27 Aug.–12 Sept., 1911, *Holzinger* (U. S. Nat. Herb.).

Arizona: Walnut Cañon, alt. 2130 m., *MacDougal 342* (Gray Herb. and Field Mus. Herb.), CO-TYPE; near Flagstaff, May–Oct., 1900, *Purpus* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Mt. Agassiz, alt. 3050 m., 10 Sept., 1909, *Pearson 315* (U. S. Nat. Herb.); Humphrey Peak, July, 1883, *Rusby 337* (Gray Herb. and Field Mus. Herb.); Barfoot Park, Chiricahua Mountains, 24 Oct., 1906, *Blumer 1484* (U. S. Nat. Herb. and Field Mus. Herb.); Huachuca Mountains, Sept., 1882, *Lemmon 2785* (Gray Herb., U. S. Nat. Herb., and Field Mus. Herb.); Huachuca Mountains, 17 Oct., 1903, *Mearns 2581* (U. S. Nat. Herb.).

9. **S. ambrosioides** Rydb. Bull. Torr. Bot. Club **37**: 467. 1910; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 745. 1915.

S. eremophilus Gray, Pl. Fendl. 108. 1849, as to plant of Fendler; Pac. Rail. Rept. **4**: 111. 1856, as to plant of Bigelow; Syn. Fl. N. Am. **1**^{2}: 392. 1884, and ed. 2. 1886, in part, not

Richards.; Nelson, in Coulter & Nelson, Manual Cent. Rocky Mountains, 583. 1909, in part, not Richards.

S. MacDougalii Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902, in part, not Heller; Rydb. Fl. Colo. 397. 1906, in part, not Heller.

Herbaceous perennial, glabrous or essentially so throughout; stems one to several from a ligneous base, 3 to 5 dm. high; leaves oblanceolate to ovate-lanceolate in general outline, 3 to 13 cm. long, 1 to 5 cm. wide, more or less laciniately pinnatifid into linear to lanceolate, entire to coarsely and unequally dentate divisions; inflorescence a terminal corymbose cyme; heads usually numerous, 7 to 10 mm. high, radiate; involucre subcampanulate, 5 to 7 mm. in diameter, calyculate; bracts of the involucre usually 13, linear-lanceolate, 5 to 7 mm. long, commonly black-tipped; ray-flowers 5 to 8; disk-flowers 30 to 45; achenes hirtellous-puberulent.

Distribution: Wyoming to New Mexico, Idaho, and Arizona.

Specimens examined:

Wyoming: gravelly banks, Centennial Mountain, Albany Co., 2 Aug., 1902, *Nelson 8773* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); moist ground in open woods, Centennial, 27 July, 1900, *Nelson 7717* (Gray Herb. and Mo. Bot. Gard. Herb.); Bridger Peak, Carbon Co., 22 Aug., 1903, *Goodding 1942* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.).

Colorado: Chamber's Lake, alt. 2895 m., 13 Sept., 1896, *Baker* (Mo. Bot. Gard. Herb.); cañon west of Palmer Lake, alt. 2435 m., 12 Aug., 1896, *Crandall* (Mo. Bot. Gard. Herb.); Steamboat Springs, 20 July, 1903, *Goodding 1617* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Boulder, coll. of 1908, *Pace* (Mo. Bot. Gard. Herb.); Denver, 8 Sept., 1905, *Moffat* (Mo. Bot. Gard. Herb.); Georgetown, 19 Aug., 1895, *Shear 4720* (U. S. Nat. Herb.), coll. of 19 July, 1886, *Trelease,* and coll. of 26 July, 1886, *Letterman* (Mo. Bot. Gard. Herb.); Rocky Mountains, Powell's Colorado Exploring Expedition 1868, *Vasey 337* (Gray Herb.); Golden City, 18 Aug., 1870, *Greene 230* (Gray Herb.); Silver Plume, 21 Aug., 1895, *Shear 4999* (U. S. Nat. Herb.); Manitou, Aug., 1881, *Fritchey 14,* in part, and coll. of 16 Aug., 1884, *Letterman* (Mo. Bot. Gard. Herb.);

Ruxton Park, alt. 2700 m., 21 Aug., 1901, *F. E. & E. S. Clements 152* (Gray Herb., U. S. Nat. Herb., and Mo. Bot. Gard. Herb.); Breckenridge, coll. of 1887, *Bereman* (Mo. Bot. Gard. Herb.); Breckenridge, coll. of 1892, *Wislizenus 1063* (Mo. Bot. Gard. Herb.); Oro City, 23 July, 1873, Hayden's U. S. Geol. Survey, *Coulter*, in part (U. S. Nat. Herb.); Green Mountain Falls, alt. 2560 m., 2 Aug., 1892, *Sheldon 485* (U. S. Nat. Herb.); Hotchkiss, alt. 1585 m., 30 June, 1892, *Cowen 287* (U. S. Nat. Herb.); Oak Creek, Fremont Co., Aug., 1873, *Brandegee 716* (Mo. Bot. Gard. Herb.); Gunnison, 25 July, 1901, alt. 2300 m., *Baker 596* (Gray Herb. and Mo. Bot. Gard. Herb.); vicinity of Mount Carbon, Gunnison Co., alt. 2730–2800 m., 4 July and 10 Aug., 1910, *Eggleston 5835* and *6159* (U. S. Nat. Herb.); Pandora, 10 Aug., 1901, *Baker 748* (Gray Herb. and Mo. Bot. Gard. Herb.); Taylor River, 15 Aug., 1873, Hayden's U. S. Geol. Survey, *Coulter* (U. S. Nat. Herb.); Telluride, alt. 2740–3600 m., Aug., 1894, *Tweedy 354* (U. S. Nat. Herb.); Ute Pass, 2 July, 1896, *Shear 3695* (U. S. Nat. Herb.); near Pagosa Peak, alt. 3050 m., 8 Aug., 1899, *Baker 706* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Saguache Creek, Sept., 1873, Wheeler Expedition, *Wolf 1086* (U. S. Nat. Herb.); Parrott City, alt. 2740 m., *Baker, Earle & Tracy 475* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); northeast corner of North Park, 3 Aug., 1874, *Barber* (U. S. Nat. Herb.); Twin Lakes, Wheeler Expedition, 1873, *Wolf & Rothrock 562* (Gray Herb., and Field Mus. Herb.); Rocky Mountains, coll. of 1862, *Hall & Harbour 327* (Gray Herb. and Field Mus. Herb.), also coll. of 1861–62, *Parry 26* (Gray Herb. and Mo. Bot. Gard. Herb.); mouth of Bear Creek Cañon, 23 Aug., 1915, *Drushel & Dougan* (Drushel Herb.); upper Clear Creek Valley, alt. 3050 m., 10 Aug., 1874, *Engelmann* (Mo. Bot. Gard. Herb.); Leadville, 8 July, 1886, *Trelease* (Mo. Bot. Gard. Herb.); Tolland, alt. 2895 m., 29 July, 1913, *Overholts* (Mo. Bot. Gard. Herb.); near Breckenridge, alt. 2950 m., Aug., 1901, *Mackenzie 208* (Mo. Bot. Gard. Herb.); Penn's Gulch, near Sunset, 30 July, 1886, *Letterman* (Mo. Bot. Gard. Herb.).

New Mexico: pine forest, Jicarilla Apache Reservation,

near Dulce, alt. 2150–2470 m., 20 Aug., 1911, *Standley 8183* (U. S. Nat. Herb.); Chama, 8 Sept., 1899, *Baker* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Santa Fe Cañon, 3 Oct., 2380–2850 m., 8 July, 1911, *Standley 6564* (U. S. Nat. Herb.); Navajo Indian Reservation in the Tunitcha Mountains, 8 Aug., 1911, *Standley 7591* (U. S. Nat. Herb.); mountains near Las Vegas, July, 1881, *Vasey* (U. S. Nat. Herb.); Santa Fe Cañon, 7 July, 1897, alt. 2440 m., *A. A. & E. G. Heller 3819* (Gray Herb. and Mo. Bot. Gard. Herb.); Sante Fe Cañon, 3 Oct., 1913, *Rose, Fitch & Parkhurst 17714* (U. S. Nat. Herb.); Canoncinto, Santa Fe Co., coll. of 1879, *Brandegee 12078* (Mo. Bot. Gard. Herb.); creek bottom, Santa Fe, 20 Oct., 1846, *Fendler 475* (Gray Herb. and Mo. Bot. Gard. Herb.); Balsam Park, Sandia Mountains, alt. 2500 m., Aug.–Sept., 1914, *Ellis 281* (Mo. Bot. Gard. Herb.); Pecos River Indian Reservation, 6 Aug., 1898, *Coghill 144* (Mo. Bot. Gard. Herb.); Mineral Creek, Sierra Co., alt. 2130 m., 26 Sept., 1904, *Metcalfe 1415* (U. S. Nat. Herb.); Santa Antonita, Whipple's Exploration 1853–54, *Bigelow* (U. S. Nat. Herb. and Gray Herb.); Organ Mountains, alt. 2130 m., 23 Sept., 1906, *Wooton & Standley* (U. S. Nat. Herb.).

Utah: Big Cottonwood Cañon, Salt Lake Co., alt. 2774 m., 10 Aug., 1905, *Garrett 1591* (U. S. Nat. Herb.); Tate Mine, Marysvale, alt. 2740 m., 22 Aug., 1894, *Jones 5858* (Mo. Bot. Gard. Herb.); Bromide Pass, Henry Mountains, alt. 3050 m., 27 July, 1894, *Jones 5695ad* (U. S. Nat. Herb.); slope of Aquarius Plateau, alt. 2750 m., 2 Aug., 1875, *Ward 499* (U. S. Nat. Herb.).

Arizona: Navajo Indian Reservation, about the north end of the Carrizo Mountains, 29 July, 1911, *Standley 7376* (U. S. Nat. Herb.).

Among the specimens here cited, a few, particularly Parry's 26, Overholts', Mackenzie's 208, and Engelmann's plant from Upper Clear Creek Valley, might be almost equally well referred to the preceding species, *S. MacDougalii,* to which *S. ambrosioides* is very closely related; but in general the latter may be distinguished by the slightly larger and more numer-

ously flowered heads and usually, but not always, less pinnatisect leaves.

10. S. eremophilus Richards. in App. Frankl. 1st Journ. 31. 1823; Hook. Fl. Bor. Am. **1**: 334. 1840; Torr. & Gray, Fl. N. Am. **2**: 444. 1843; Eaton, Bot. King Exp. 191. 1871, in part; Gray, Syn. Fl. N. Am. **1**^{2}: 392. 1884, and ed. 2, 1886; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Nelson in Coulter & Nelson, Manual Cent. Rocky Mountains 583. 1909, in part.

S. pembrinensis Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbaceous perennial, glabrous or slightly puberulent in the inflorescence; stems erect, 3 to 8 dm. high, striate; leaves more or less laciniately pinnatifid with linear, lanceolate or oblong, entire or coarsely and unequally dentate divisions; the lower leaves petiolate, the upper subsessile; inflorescence terminating the stem in a somewhat leafy corymbose or paniculate cyme; heads rather large, 10 to 12 mm. high, radiate; involucre campanulate conspicuously calyculate; bracts of the involucre usually 13, linear-lanceolate, acute, 7 to 9 mm. long, glabrous, minutely brownish- or black-tipped; ray-flowers 8 to 10; disk-flowers 40 to 60; achenes ribbed, glabrous, or slightly hirtellous-puberulent.

Distribution: northwestern Canada to Nebraska, Colorado, and Utah.

Specimens examined:

Saskatchewan: Lipton, 11 Aug., 1911, *Clokey 1844* (Mo. Bot. Gard. Herb.); Qu'Appelle River, Assiniboia, Aug., 1883, *Macoun 14839* (Geol. Surv. Canada Herb. and U. S. Nat. Herb.); near Prince Albert, 10 July, 1896, *Macoun 12171* (Geol. Surv. Canada Herb.); in damp thickets north of Saskatchewan River, 22 Aug., 1872, *Macoun 14841* (Geol. Surv. Canada Herb.); Saskatchewan Plains, *Macoun 868* (Kew Herb.).

Alberta: "on gravelly banks of Cedar Lake, Lat. 54°," *Richardson* (Kew Herb.), TYPE; Pembina, coll. of 1873, *Coues* (Gray Herb.); on damp banks, Bow River at Morley, 6 Sept.,

1879, *Macoun 14840* (Geol. Surv. Canada Herb.); Dunvegan, Peace River, 17 Aug., 1879, *Dawson 26686* (Geol. Surv. Canada Herb.); Athabasca Plains, 14 Sept., 1872, *Macoun 1040* (Gray Herb. and Kew Herb.).

South Dakota: Sylvan Lake, 27 Aug., 1897, *Griffiths* (Mo. Bot. Gard. Herb.).

Nebraska: mountain range, south of White Clay Creek, 23 Aug., 1859, Lieut. F. T. Bryan's Expedition, 1856, *H. Engelmann* (Mo. Bot. Gard. Herb.).

Wyoming: on the summits of Big Horn Mountains, Aug., 1859, Reynolds' Expedition to the headwaters of the Missouri and Yellowstone Rivers, *Hayden* (Mo. Bot. Gard. Herb.); Laramie Mountains, *Hayden* (Gray Herb. and Mo. Bot. Gard. Herb.); Laramie Mountains, 17 Aug., 1899, *Schuehut* (U. S. Nat. Herb.).

Colorado: Cascade Cañon, July, 1880, *Eurney* (Mo. Bot. Gard. Herb.); Rocky Mountains, *Hall & Harbour 327*, in part (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Pike's Peak, alt. 3050 m., 25 Aug., 1915, *Drushel & Dougan* (Drushel Herb.); Manitou, Aug., 1881, *Fritchey 14* in part (Mo. Bot. Gard. Herb.), form.

var. **Kingii** (Rydb.) Greenm. comb. nov.

Senecio Kingii Rydb. Bull. Torr. Bot. Club **37**: 468. 1910.

S. eremophilus Eaton, Bot. King Exp. 191. 1871, as to plant of Watson.

S. Watsoni Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

Leaves oblanceolate to oblong-lanceolate, coarsely dentate to pinnatisect with relatively broad divisions; but through several specimens connecting directly with the above species.

Specimen examined:

Utah: Cottonwood Cañon, alt. 2590 m., Aug., 1869, *Watson 676* (Columbia Univ. Herb. and Gray Herb.), TYPE.

11. S. Townsendii Greenm.[1]

Herbaceous perennial, glabrous throughout; stem 6 to 10 dm. high, striate, often purplish; leaves coarsely, unequally

[1] **Senecio Townsendii** Greenm. sp. nov., herbaceus perennis ubique glabrus; caule 6–10 dm. alto, striato saepe purpurascenti; foliis inaequaliter et remote

and remotely dentate to laciniately pinnatifid, oblanceolate to oblong-lanceolate in general outline, 3 to 10 cm. long, 1 to 4 cm. broad, divisions linear and entire to dentate, acute or obtuse; lower leaves petiolate, the upper sessile; inflorescence a loose several to many-headed corymbose cyme; heads 10 to 13 mm. high, radiate; involucre narrowly campanulate, calyculate, glabrous; bracts of the involucre commonly 13, linear-lanceolate, 8 to 10 mm. long, terminated by a small black or brownish penicillate tip; flowers pale yellow; ray-flowers 5 to 8, occasionally much reduced; disk-flowers 35 to 50; achenes glabrous.

Distribution: northern Mexico.

Chihuahua: near Colonia San Garcia in the Sierra Madre, alt. 2285 m., 9 Sept., 1899, *Townsend & Barber 317* (Mo. Bot. Gard. Herb., Gray Herb., and U. S. Nat. Herb.), TYPE; Mound Valley, Sierra Madre Mountains, alt. 2130 m., 18 Sept., 1903, *Jones* (U. S. Nat. Herb.).

The Townsend and Barber specimens have been distributed as "*Senecio Chihuahuanus* Wats." and the Jones plant was distributed as "*Senecio eremophilus*" under which names they may be looked for in herbaria.

12. S. chihuahuensis Watson, Proc. Am. Acad. **23**: 280. 1888; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbacous perennial; stem erect, 4 to 5 dm. high from a rather slender rootstock, striate-angulate, somewhat purplish; early leaves oblanceolate, 3 to 5 cm. long, 1 cm. broad, laciniately dentate, arachnoid-tomentulose on both surfaces; later stem-leaves short-petiolate, or subsessile, oblong-ovate in general outline, about 8 cm. long, one-half to two-thirds as

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grosse-dentatis vel laciniato-pinnatis, oblanceolatis vel oblongo-lanceolatis in circumscriptione, 3–10 cm. longis, 1–4 cm. latis; laciniis linearibus et integris vel dentatis acutis vel obtusis; foliis inferioribus petiolatis, superioribus sessilibus; inflorescentibus laxe corymboso-cymosis multicapitatis; capitulis 10–13 mm. altis, radiatis; involucris anguste campanulatis calyculatis glabris; bracteis involucri 13 lineari-lanceolatis 8–10 mm. longis minute atro- vel fulvo-penicillatis; floribus pallide aurantiabus; floribus femineis 5–8 nonnunquam multo reductis; floribus disci 35–50; achaeniis striatis glabris.—Near Colonia San Garcia in the Sierra Madre, State of Chihuahua, Mexico, alt. 2285 m., 9 Sept., 1899, *Townsend & Barber 317* (Mo. Bot. Gard. Herb., Gray Herb., and U. S. Nat. Herb.), TYPE; Mound Valley, Sierra Madre Mountains, alt. 2135 m., 18 Sept., 1903, *Jones* (U. S. Nat. Herb.).

broad, subbipinnate, at first tomentulose, later becoming glabrous or essentially so, divisions narrow, unequal, cartilaginous-apiculate; inflorescence a terminal corymbose cyme; heads 10 to 12 mm. high, radiate; involucre cylindric-campanulate, calyculate with short linear subulate bracteoles; bracts of the involucre 7 to 9 mm. long, brownish- or black-tipped, shorter than the numerous flowers of the disk; ray-flowers about 8; achenes canescent-pubescent.

Distribution: northern Mexico.

Specimens examined:

Chihuahua: ledges of the Sierra Madre, alt. 2955 m., 7 Oct., 1887, *Pringle 1318* (Gray Herb., Kew Herb., and Mo. Bot. Gard. Herb.), TYPE.

13. S. durangensis Greenm. Field Col. Mus. Bot. Ser. **2**: 275. 1907. Plate 18.

S. ctenophyllus Greenm. Proc. Am. Acad. **43**: 20. 1907, not Phil.

An herbaceous annual, or becoming perennial by the development of a ligneous base; stem simple or branched, erect, 3 to 4 dm. high, arachnoid-tomentose; leaves lanceolate, 2 to 9 cm. long, 1 to 2.5 cm. wide, more or less pinnately divided, permanently arachnoid-tomentulose on both surfaces, lower leaves petiolate, upper sessile; inflorescence a terminal tomentulose corymbose cyme; heads numerous, 8 to 10 mm. high, radiate, calyculate; involucre campanulate, glabrous or nearly so; bracts of the involucre 13, linear-lanceolate, 5 to 6 mm. long, minutely black-tipped, penicillate; ray-flowers 5 to 8, ligules pale yellow; disk-flowers 20 to 30; achenes canous-hirtellous.

Distribution: northern Mexico.

Specimen examined:

Durango: barranca, below Sandia Station, alt. 2135 m., 15 Oct., 1905, *Pringle 10105* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.), TYPE.

SECT. 3. JACOBAEAE DC.

§ 3. JACOBAEAE DC. Prodr. **6**: 348. 1837; Hoffm. in Engl. & Prantl, Nat. Pflanzenf. IV, Abt. 5, 297. 1892; Greenm.

Monogr. Senecio, I. Teil, 21, 23. 1901, and in Engl. Bot. Jahrb. **32** : 17, 19. 1902.

Biennial or perennial herbs with lyrate or 2–3-pinnatisect leaves and radiate heads. Sp. 14–16.

Key to the Species

A.	Stem and leaves glabrous or nearly so; involucral bracts narrow, about 1 mm. broad; bracteoles usually black-tipped	*14. S. rupestris*
B.	Stems and leaves more or less permanently floccose-tomentulose; involucral bracts 1.5 to 2 mm. broad; bracteoles not black-tipped.	
a.	Upper stem-leaves once pinnate	*15. S. erucifolius*
b.	Upper stem-leaves 2–3-pinnatisect	*16. S. Jacobaea*

14. S. rupestris Waldst. & Kit. Descr. et Ic. Pl. Rar. Hung. **2** : 136. *pl. 128.* 1805; Reichb. Ic. Crit. **4** : 28. *pl. 334. fig. 514.* 1826; Strobl, Fl. Admont. **1** : 57. 1881, and in Flora **65** : 478, 479. 1882; von Hayek, Fl. Stierm. **2** : 564. 1913.

S. laciniatus Bert. in Desv. Jour. Bot. **2** : 76. 1813; Amoen. Ital. 102, 408. 1819.

Senecio nebrodensis var. *glabratus* DC. Prodr. **6** : 350. 1837.

Annual or biennial, sometimes becoming perennial, glabrous throughout or slightly pubescent; stem erect, 3 to 6 dm. high, simple or branched, striate; leaves lanceolate to obovate-lanceolate in general outline, 3 to 10 cm. long, 1 to 4 cm. broad, laciniately lobed or subpinnatiscent, thin in texture, the lobes again sharply dentate; the lower leaves narrowed into a subpetiolate base, the upper sessile and semiamplexicaul; inflorescence a terminal corymbose cyme; heads 8 to 10 mm. high, radiate; involucre calyculate with black-tipped bracteoles; bracts of the involucre about 21, linear-lanceolate, acute, 6 to 7 mm. long; ray-flowers about 13; disk-flowers numerous; achenes glabrous or slightly hirtellous.

Distribution: on ballast near Philadelphia. Introduced from Europe.

Specimen examined:

Pennsylvania: on ballast, Philadelphia, July, 1880, *Martindale* (Gray Herb.).

15. S. erucifolius L. Fl. Suecica, ed. 2, 291. 1755; Huds. Fl. Ang. 366. 1798; DC. Prodr. **6** : 351. 1837; Reichb. Ic. Fl.

Germ. & Helv. **16**: 38. *pl. 75* (CMLXVI). *fig. 1.* 1854; Cosson & Saint-Pierre, Fl. Paris, ed. 10, 518. 1861. Beck von Mannagetta, Fl. Nieder-Oesterr. 1221. 1893.

An herbaceous biennial or perennial, more or less floccose-tomentulose throughout and on the stem and lower leaf-surface often intermixed with hirsute hairs; stems erect, 3 to 10 dm. high, simple or branched; leaves lyrately pinnatifid to pinnatisect, 2 to 10 cm. long, 1 to 6 cm. broad, the lobes subentire, blunt, and submucronate to sharply dentate; lowermost leaves narrowed into a subpetiolate base, the upper sessile and semiamplexicaul; inflorescence a terminal few- to many-headed corymbose cyme; heads about 1 cm. high, radiate; involucre campanulate, calyculate; bracts of the involucre usually 13, lanceolate-oblong, 4 to 5 mm. long, glabrous or slightly floccose-tomentulose, with rather broad scarious margins; ray-flowers about 13; disk-flowers numerous, 50 to 60; achenes hirtellous.

Distribution: on ballast near Philadelphia. Introduced from Europe.

Specimens examined:

Pennsylvania: on ballast, Philadelphia, 30 Aug., 1879, *Parker* (Gray Herb.).

New Jersey: on ballast, Kaighn's Point, *Burk* (Field Mus. Herb.).

16. S. Jacobaea L. Sp. Pl. **2**: 870. 1753; Willd. Sp. Pl. **3**: 1997. 1800; DC. Prodr. **6**: 350. 1837; Sm. & Sow. Eng. Bot. **16**: *pl. 1130.* 1803; Schkuhr, Handb. *pl. 267.* 1808; Reichb. Ic. Fl. Germ. & Helv. **16**: 38. *pl. 73* (CMLXIV). *figs. II. 3, 4.* 1854; Gray, Syn. Fl. N. Am. **1**^{2}: 383. 1884, and ed. 2, 1886; Britton, Manual, ed. 2, 1029. 1905; Gray, Manual, ed. 7, 853. 1907; Britton & Brown, Ill. Fl., ed. 2, **3**: 542. 1913.

Jacobaea vulgaris Vahl in Fl. Dan. **6**: *pl. 944.* 1787; Gaertn. Fruct. **2**: 445. *pl. 170. fig. 1.* 1791. An erect, biennial or perennial herb, 3 dm. or more high, at first usually arachnoid-tomentulose, more or less glabrate; basal leaves petiolate, somewhat lyrate; stem leaves sessile, semiamplexicaul, ovate-oblong in general outline, 3 to 15 cm. long, 1.5 to 7 cm.

broad, 2–3-pinnatisect; inflorescence a terminal corymbose cyme; heads numerous, radiate; achenes pubescent.

Distribution: Newfoundland to New Jersey, occurring along roadsides, in pastures, and on ballast. Introduced from Europe.

Specimens examined:

Newfoundland: roadsides, St. John's, 7–19 Aug., *Robinson & Schrenk* (Gray Herb., U. S. Nat. Herb., Geol. Surv. Canada Herb., and Mo. Bot. Gard. Herb.).

Nova Scotia: L'Ardoire, Cape Breton Island, Aug., 1892, *Faxon* (Gray Herb.); Sydney and Mira Bay, Cape Breton Island, 17 Aug., 1898, *Macoun 19723* (Geol. Surv. Canada Herb.); eastern Nova Scotia, 16 Aug., 1890, *Chickering* (U. S. Nat. Herb.); Boylston, *Hamilton 22844* (Geol. Surv. Canada Herb.); Pictou, 1 Nov., 1874, *Fowler* (Field Mus. Herb.); Pictou Landing, 24 July, 1883, *Macoun 14859* (Geol. Surv. Canada Herb.); pasture, Windsor Junction, 11 July, 1901, *Howe & Lang 427* (Gray Herb.); pasture, near Pictou, 12–18 July, 1901, *Howe & Lang 540* (Gray Herb.).

Prince Edward Island: Tignish, 26 July, 1888, *Macoun, 14858* (Geol. Surv. Canada Herb.); Tracadie Beach, 27 July, 1901, *Churchill* (Gray Herb. and Mo. Bot. Gard. Herb.).

New Brunswick: Miramichi, *Fowler* (Gray Herb. and U. S. Nat. Herb.); near railroad station, Anagance, 19 July, 1901, *Churchill* (Gray Herb. and Mo. Bot. Gard. Herb.).

Quebec: on ballast-filling about fish houses, York, Gaspé Co., 25 Aug., 1904, *Collins, Fernald & Pease* (Gray Herb.).

Ontario: Burlington, 23 Aug., 1883, *Burgess 14857* (Geol. Surv. Canada Herb.).

Pennsylvania: on ballast, July, 1876, *Martindale* (Mo. Bot. Gard. Herb.).

New Jersey: on ballast, Camden, coll. of 1878, *Martindale* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); on ballast, Kaighn's Point, *Burk* (Field Mus. Herb.).

Sect. 4. Sanguisorboidei Greenm.

§ 4. Sanguisorboidei Greenm. Monogr. Senecio, I. Teil, 22,

23, 1901, and in Engl. Bot. Jahrb. **32**: 18, 19. 1902. *Lobati* Rydb. Bull. Torr. Bot. Club **27**: 169. 1900, in part.

Annuals, biennials, or perennials, often forming merely a rosette of leaves during the first year; stems erect, 1.5 to 10 dm. high from a distinctly annual root or from a rather stout rootstock; leaves once, twice, or thrice pinnately divided; heads numerous; achenes glabrous or pubescent. Sp. 17–29.

Key to the Species

A. Annuals or biennials.
  a. Bracts of the involucre usually 13, linear-lanceolate, 1 to 2.5 mm. broad ..... *17. S. sanguisorboides*
  b. Bracts of the involucre usually 21, linear or linear-lanceolate, 0.5 to 1.5 mm. broad.
    α. Lateral leaf-segments not abruptly contracted into a narrow base.
      I. Plants of southeastern United States. *18. S. glabellus*
      II. Plants of southwestern Texas and northern Mexico ..... *19. S. Greggii*
    β. Lateral leaf-segments abruptly contracted into a narrow base ..... *20. S. imparipinnatus*

B. Perennials; upright stem from a horizontal, ascending or suberect rootstock.
  a. Leaves 2–3-pinnatisect; segments narrow .... *21. S. Millefolium*
  b. Leaves once pinnate; segments narrowly obovate to subreniform.
    α. Heads numerous, small, 5 to 10 mm. high.
      I. Involucral bracts usually 21.
        1. Leaves glabrous; achenes hirtellous. *22. S. tampicanus*
        2. Leaves pubescent beneath; achenes glabrous ..... *23. S. hypotrichus*
      II. Involucral bracts usually 13.
        1. Lateral leaf-divisions longer than broad.
          * Midrib glabrous ..... *24. S. Sanguisorbae*
          ** Midrib floccose-tomentulose .... *25. S. pinnatisectus*
        2. Lateral leaf-divisions as broad as long ..... *26. S. coahuilensis*
    β. Heads fewer and larger, 10 to 14 mm. high.
      I. Leaves pinnately divided nearly to the midrib.
        1. Leaf-divisions few, cuneate to reniform ..... *27. S. leonensis*
        2. Leaf-divisions many, cuneate to linear ..... *28. S. montereyana*
      II. Leaves pinnately divided slightly more than half-way from margin to midrib ..... *29. S. zimapanicus*

17. S. sanguisorboides Rydb. Bull. Torr. Bot. Club **27**: 170. 1900; Wooton & Standley, Contr. U. S. Nat. Herb. **19**: 745. 1915.

Annual or biennial, glabrous or slightly white tomentulose in the axils of the leaves; stem 1.5 to 5 dm. high, striate; leaves usually pinnately divided into cuneate to reniform dentate or crenate-dentate divisions, the terminal division ovate-reniform, 1 to 5 cm. broad; basal and lower stem-leaves petiolate and occasionally undivided; upper stem-leaves sessile and amplexicaul; inflorescence a terminal few to several-headed corymbose cyme; heads radiate; involucre campanulate, barely calyculate; bracts of the involucre usually 13 (rarely 16), lanceolate, 6 to 6.5 mm. long, glabrous; ray-flowers 8 to 10; disk-flowers 30 to 50; achenes ribbed, glabrous.

Distribution: mountains of New Mexico.

Specimens examined:

New Mexico: Willow Gulch, Colfax Co., alt. 3050 m., Aug., 1896, *St. John 115* (Gray Herb.); Santa Fe Cañon, 7 July, 1897, alt. 2440 m., *A. A. & E. G. Heller 3820* (Mo. Bot. Gard. Herb.), CO-TYPE; Santa Fe Creek, 22 June, 1847, *Fendler 438* (Mo. Bot. Gard. Herb.); White Mountains, Lincoln Co., alt. 3048 m., 16 Aug., 1897, *Wooton 494* (Mo. Bot. Gard. Herb.); mouth of Pouchuelo Creek, Pecos River National Forest, alt. 2590 m., 30 June, 1908, *Standley 4093* (Mo. Bot. Gard. Herb.); mouth of Mora River, Pecos River National Forest, alt. 2470 m., 7 July, 1908, *Standley 4250* (Mo. Bot. Gard. Herb.); Pecos River Indian Reservation, 17 July, 1898, *Coghill 71* (Mo. Bot. Gard. Herb.).

18. S. glabellus Poir, Dict. **7**: 102. 1806; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Gray, Manual, 853, ed. 7, 1907; Britton & Brown, Ill. Fl. **3**: 540, ed. 2, 1913.

S. lyratus Michx. Fl. Bor. Am. **2**: 120. 1803, not L.

S. lobatus Pers. Syn. **2**: 436. 1807; Nutt. Gen. **2**: 165. 1818; Elliot, Sk. **2**: 332. 1824; Torr. & Gray, Fl. N. Am. **2**: 437. 1843; Gray, Syn. Fl. N. Am. **1**^{2}: 394. 1884, and ed. 2, 1886, mainly; Chapman, Fl. Southern U. S. 266, ed. 3, 1897; Britton & Brown, Ill. Fl. **3**: 481, ed. 1, 1898; Small, Fl. Southeastern U. S.. 1303. 1903, and ed. 2, 1913; Mohr, Contr. U. S. Nat. Herb. **6**: 815. 1901.

S. carolinianus Spreng. Syst. **3** : 559. 1826.

S. densiflorus Martens, Bull. Acad. Roy. Soc. Brux. **8** : 66. 1841.

S. Schweinitzianus Nutt. Trans. Am. Phil. Soc. **7** : 413. 1841.

Annual or biennial, glabrous or slightly tomentulose in the axils of the leaves; stems erect 1 to 10 dm. high, striate; radical leaves petiolate, lyrate, occasionally undivided; those of the stem petiolate or sessile and semiamplexicaul, pinnately divided into rather remote, narrowly cuneate to subreniform unequal divisions; inflorescence a terminal corymbose cyme; heads 6 to 8 mm. high, radiate; ray-flowers 8 to 12; disk-flowers about 50; achenes usually hirtellous-puberulent.

Distribution: North Carolina west to Illinois, Missouri, and South Dakota, south to Florida and eastern Texas. Common on river bottoms and flood-plains.

Specimens examined:

North Carolina: near Wilmington, April, 1888, *McCarthy* (U. S. Nat. Herb.); without locality, *Curtis* (Gray Herb.).

South Carolina: Goose Creek, 19 May, 1885, *A. C. & F. W. Maier* (Gray Herb.); swamps, Summerville, April, 1890, *Taylor* (Field Mus. Herb.).

Georgia: Macon, coll. of 1875, *Curtiss* (U. S. Nat. Herb.); central Georgia, coll. of 1846, *Porter* (Gray Herb.); Butler Island, McIntosh Co., 27 May, 1909, *Smith 2185* (Field Mus. Herb.).

Florida: without locality, *Chapman* (Gray Herb., U. S. Nat. Herb., and Kew Herb.); Fort Orange, 10 April, 1895, *Straub 103* (Gray Herb.); near Chattahooche, *Curtis 1565* (Gray Herb., U. S. Nat. Herb., Kew Herb., and Field Mus. Herb.); River Junction, 19 April, 1898, *Curtis 6370* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); Sand Point, 8 April, 1874, *Palmer 301* (Gray Herb., U. S. Nat. Herb., and Mo. Bot. Gard. Herb.); near St. Marks, coll. of 1843, *Rugel* (Mo. Bot. Gard. Herb., and Kew Herb.); Losman's Key, May, 1891, *Simpson 154* (U. S. Nat. Herb. and Field Mus. Herb.); New

Smyrna, *Burgess 563* (Field Mus. Herb.); Gulf Hammock, April, 1876, *Garber* (Field Mus. Herb.).

Illinois: in a damp meadow near Peoria, coll. of 1903, *McDonald* (Field Mus. Herb.); river bottom opposite Decatur, April, 1864, *Stewart* (Field Mus. Herb.); Eldred, Green Co., 9 May, 1891, *Andrews* (Mo. Bot. Gard. Herb.); opposite St. Louis, July, 1839, and May, 1845, *Engelmann* (Mo. Bot. Gard. Herb. and Kew Herb.); Mississippi Valley, St. Clair Co., colls. of 1874, 1875, and 1879, *Eggert* (Mo. Bot. Gard. Herb.); near Falling Spring, 1 June, 1890, *Glatfelter* (Mo. Bot. Gard. Herb.); East St. Louis, 11 June, 1890, *Hitchcock* (Mo. Bot. Gard. Herb.).

Kentucky: Muhlenberg, 5 June, 1901, *Price* (Mo. Bot. Gard. Herb.); without locality, *Short* (Kew Herb.).

Tennessee: in swamps, Rutherford Co., July, 1892, *Bain* (U. S. Nat. Herb.).

Alabama: Tuscaloosa, April, 1892, *Ward* (U. S. Nat. Herb.); Greensboro, coll. of 1857, *Watson* (Gray Herb.); Auburn, Lee Co., 9 April, 1898, *Earle & Baker* (Field Mus. Herb.).

Mississippi: damp fields, North Carrollton, 21 April, 1899, *Clute 24* (Field Mus. Herb.); without locality, coll. of 1843, *Holton* (Kew Herb.).

South Dakota: Fort Pierre, July, 1853, *Hayden* (Mo. Bot. Gard. Herb.).

Missouri: Courtney, 15 May, 1896, *Bush 701* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); vicinity of St. Louis, coll. of about 1840, *Duerinck* (Mo. Bot. Gard. Herb.); Creve Coeur Lake, 8 May, 1859, *Glatfelter* (Mo. Bot. Gard. Herb.); near St. Louis, *Hus 4007* (Mo. Bot. Gard. Herb.); St. Louis Co., 24 May, 1896, *Shannon 250* (Mo. Bot. Gard. Herb.); St. Louis Co., 20 May, 1879, *Eggert* (Mo. Bot. Gard. Herb.); Jefferson Barracks, 6 May, 1890, *Hitchcock* (Mo. Bot. Gard. Herb.); Jefferson Co., 5 May, 1896, *Eggert* (Mo. Bot. Gard. Herb.); Kimmswick, 20 May, 1860, *Engelmann* (Mo. Bot. Gard. Herb.); Kimmswick, 23 May, 1885, *Wislizenus* (Mo. Bot. Gard. Herb.); Sulphur Springs, 14 Aug., 1910, *Sherff 1062* (Field Mus. Herb.); Osage, 13 May, 1901, *Norton* (Mo. Bot. Gard. Herb.);

Batesville, Butler Co., 21 May, 1908, *Smith 534* (Field Mus. Herb.); St. Louis, coll. of 1832, *Drummond* (Kew Herb.); St. Louis, *Riehl 382* (Kew Herb.).

Arkansas: Fulton, 17 April, 1905, *Bush 2354* (Mo. Bot. Gard. Herb.); Fulton, 24 April, 1914, *Palmer 5381* (Mo. Bot. Gard. Herb.); Arkansas Post, 20 March, 1909, *Kellogg* (Mo. Bot. Gard. Herb.); Little Rock, 22 April, 1909, *McNair* (U. S. Nat. Herb.); Little Rock, June, 1886, *Hasse* (Field Mus. Herb.).

Louisiana: without locality, *Hale* (Gray Herb. and Kew Herb.); Gretna, 28 April, 1899, *Ball 315* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); between New Orleans and Balize, May, 1829, *Berlandier 556, 1946* (Gray Herb. and Mo. Bot. Gard. Herb.); Balize, April, 1839, *Lindheimer* (Mo. Bot. Gard. Herb.); Baton Rouge, 22 Jan., 1874, *Joor* (Mo. Bot. Gard. Herb.); Holly Ridge, West Carroll Parish, July, 1910, *Mosely* (Field Mus. Herb.); swampy woods, Natchitoches, 16 April, 1915, *Palmer 7253* (Mo. Bot. Gard. Herb.); New Orleans, *Drummond 176, 626* (Kew Herb.); New Orleans, coll. of 26 March, 1847, *Bromfield* (Kew Herb.).

Texas: low ground, San Augustine, 31 March, 1915, *Palmer 7114* (Mo. Bot. Gard. Herb.).

Forma **robustior**, forma nova.

Stout herb; upper stem-leaves 1.5 to 2 dm. long, 8 to 10 cm. wide; the large lateral obovate leaf-lobes alternating with smaller wedge-shaped divisions of the leaf.

Georgia: ditch banks, near Savannah, 21 March, 1882, *J. D. Smith* (Gray Herb.), TYPE. This plant appears to be a giant form with rather marked foliage.

19. S. Greggii Rydb. Bull. Torr. Bot. Club **27**: 170. 1900.

S. tampicanus Gray, Pl. Fendl. 109. 1849 (in Mem. Am. Acad. N. S. **4**), not DC.

S. lobatus Gray, Pl. Wright., part 2, 99. 1853 (in Smithson. Contr. **5**), not Pers.

Annual or biennial, glabrous or with a slight tomentum in the leaf-axils and on the upper side of the leaf along the mid-

rib; stems one to several from a common base, 1.5 to 4 dm. high, striate; leaves lyrate to pinnately divided into cuneate to subrotund divisions; inflorescence a terminal corymbose cyme; heads 5 to 8 mm. high, radiate; involucre campanulate, slightly calyculate; bracts of the involucre about 21, linear-lanceolate, 3 to 5 mm. long, glabrous; ray-flowers 8 to 12; disk-flowers 45 to 60; achenes hispidulous.

Distribution: southern New Mexico, western Texas, and northern Mexico.

Specimens examined:

New Mexico: banks of the Rio Grande near El Paso, *Wright 1413* (Gray Herb.).

Texas: valley of the Rio Grande, below Doñana, Mexican Boundary Survey, *Parry 659* (U. S. Nat. Herb.); El Paso, May, 1881, *Vasey* (U. S. Nat. Herb.); southeastern Texas, Sept., 1879 to Oct., 1880, *Palmer 754* (Gray Herb.).

Chihuahua: valley of Rio Parral, near Santa Rosalia, 21 April, 1847, *Gregg 11,* (Gray Herb.) CO-TYPE; valley near Ortiz, 11 April, 1887, *Pringle* (Field Mus. Herb.).

20. **S. imparipinnatus** Klatt, Natur. Gesell. Halle **15**: 333. 1881; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

S. lobatus Gray, Syn. Fl. N. Am. 1^2: 394. 1884, and ed. 2. 1886, in part, not Pers.; Coulter, Contr. U. S. Nat. Herb. **2**: 241. 1892, in part, not Pers.

Annual or biennial, glabrous or slightly floccose-tomentulose in the axils of the leaves; stems slender, 1.5 to 4 dm. high, simple or branched from the base; leaves 2 to 10 cm. long, 1 to 3 cm. broad, lyrate to pinnately divided or the lowermost occasionally undivided; the upper stem-leaves remote, sessile, and pinnately divided into small linear and entire to abruptly cuneate and unequally toothed lateral divisions; inflorescence a terminal few-headed corymbose cyme; heads 6 to 8 mm. high, radiate; involucre campanulate, glabrous, minutely calyculate; bracts of the involucre usually 21, linear-lanceolate, 3 to 5 mm. long, acute; ray-flowers 8 to 12; disk-flowers commonly 50 to 60; achenes hirtellous-puberulent.

Distribution: western Louisiana, Oklahoma, and Texas.

Specimens examined:

Louisiana: without locality, *Leavenworth* (Gray Herb. and Kew Herb.).

Oklahoma: Rock Creek, coll. of 1884, *Tufts* (U. S. Nat. Herb.); between Fort Cobb and Fort Arbuckle, coll. of 1868, *Palmer 462* (U. S. Nat. Herb.); near Indianola, *Pope* (Gray Herb.); Muskogee, May, 1894, *Schenck* (Field Mus. Herb.); near Paul's Valley, Garvin County, 19 April, 1913, *Stevens 108* (Mo. Bot. Gard. Herb.).

Texas: Dallas, 16 April, 1901, *Reverchon 558* (Mo. Bot. Gard. Herb.); in waste ground, Tarrant Co., 5 May, 1912, *Ruth 367* (Mo. Bot. Gard. Herb.); Waco, *Pace 122* (Mo. Bot. Gard. Herb.); Navarro Co., 22 May, 1880, *Joor* (Mo. Bot. Gard. Herb.); wet ground, Houston, May, 1872, *Hall 368* (U. S. Nat. Herb. and Field Mus. Herb.); Harrisburg, 24 April, 1899, *Eggert* (Mo. Bot. Gard. Herb.); Harris Co., 13 and 22 May, 1876, *Joor* (Mo. Bot. Gard. Herb.); vicinity of Huntsville, 6–12 May, 1910, *Dixon 516* (Field Mus. Herb.); Columbia, 6 April, 1899, *Bush 56* (Mo. Bot. Gard. Herb.); Columbia, 31 March, 1902, *Bush 1263* (Mo. Bot. Gard. Herb.); along Corpus Christi Bay, 21 March, 1894, *Heller 1476* (Gray Herb., U. S. Nat. Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Corpus Christi, 7 April, 1905, *Tracy 8927* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); low prairies near Rosenberg, 5 April, 1900, *Eggert* (Mo. Bot. Gard. Herb.); Richmond, 15 March, 1914, *Palmer 4954* (Mo. Bot. Gard. Herb.); Hungerford, 4 March, 1914, *Palmer 4844* (Mo. Bot. Gard. Herb.); Austin, March, 1870, *Bodin 52* (U. S. Nat. Herb.); "Bejar a la villa de Austin," *Berlandier 1741, 421* (Gray Herb.), CO-TYPE; near Belknap, 20 April, 1858, *Sutton Hays 515* (Field Mus. Herb.); Brazos, coll. of 1889, *Nealley 91, 280* (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Brazos, April, 1859, *Lindheimer* (Mo. Bot. Gard. Herb.); bottom land between Laredo and Palafox, *Schott* (Field Mus. Herb.).

21. S. Millefolium Torr. & Gray, Fl. N. Am. **2**: 444. 1843; Gray, Syn. Fl. N. Am. 1^2: 392. 1884, and ed. 2, 1886; Chap-

man, Fl. Southern U. S., ed. 3, 266. 1897; Small, Fl. Southeastern U. S. 1305. 1903, and ed. 2, 1913.

An herbaceous perennial, glabrous or with a white floccose-tomentum at the base of the stem and in the axils of the leaves; stems 3 to 7 dm. high, striate; leaves bi–tri-pinnately dissected into linear segments; basal and lower stem-leaves petiolate, 1 to 2.5 dm. long, 1.5 to 6 cm. wide, the upper ones sessile; inflorescence terminating the stem in a corymbose cyme; heads 8 to 10 mm. high, radiate; involucre campanulate, sparingly calyculate, glabrous; bracts of the involucre 4 to 6 mm. long; ray-flowers 8 to 12; disk-flowers numerous, usually 50 to 60; achenes hirtellous-puberulent.

Distribution: mountains of North Carolina and South Carolina.

Specimens examined:

North Carolina: slope of Caesar's Head, 3 Sept., 1876, *Engelmann* (Mo. Bot. Gard. Herb.); without locality, coll. of 1888, *Boynton* (U. S. Nat. Herb.); dry, rocky places on White Oak Mountains, Polk Co., alt. 850 m., 4 May, 1897, *Biltmore Herb. 1301*[b] (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.); Skyuka Mountains, Polk Co., 25 May, 1899, *Churchill* (Gray Herb.).

South Carolina: Table Rock, coll. of 1842, *Buckley* (Gray Herb. and Mo. Bot. Gard. Herb.); "Carolina," *Fraser* (Gray Herb.), part of TYPE; Caesar's Head, Aug., 1876, *Canby* (U. S. Nat. Herb.).

22. S. tampicanus DC. Prodr. **6**: 427. 1837; Hemsl. Biol. Cent.-Am. Bot. **2**: 248. 1881, excl. plant of Wright.

S. Ervendbergii Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Field Col. Mus. Bot. Ser. **2**: 275. 1907.

Glabrous throughout; stem 4 dm. or more high, terete, striate, leafy; leaves thin, pinnately divided into cuneate to obovate, unequally dentate divisions; lower leaves petiolate, 1 to 3 dm. long, the upper ones sessile and amplexicaul by a large stipular-like base; inflorescence a terminal compound corymbose many-headed cyme; heads small, 5 to 7 mm. high,

radiate; involucre campanulate, glabrous, minutely calyculate; bracts of the involucre 21, linear-lanceolate, 3 to 4 mm. long; ray-flowers about 13; disk-flowers numerous, 70 to 90; achenes hirtellous along the ribs.

Distribution: eastern Mexico.

Specimens examined:

Tamaulipas: Tampico, coll. of 1827, *Berlandier 186* (Berlin Herb., tracing and fragments in Gray Herb.), CO-TYPE.

Vera Cruz: Wartemberg, near Tantoyuca, coll. of 1858, *Ervendberg 90* (Gray Herb.); without locality, *Liebmann 172* (Copenhagen Herb., tracing and fragments in Gray Herb.).

Puebla: near Metaltoyuca, alt. 240 m., 27 Feb., 1898, *Goldman 74* (U. S. Nat. Herb. and Gray Herb.).

San Luis Potosi: without definite locality, *Parry & Palmer 533* (Gray Herb.).

23. S. hypotrichus Greenm.[1]

S. Sanguisorbae Hemsl. Biol. Cent.-Am. Bot. **2**: 246. 1881, in part, not DC.

An herbaceous perennial; stem 7 dm. high, erect, striate, glabrous, somewhat purplish, branched above; leaves pinnately divided into cuneate to rhomboic-ovate dentate unequal divisions, glabrous above, crisp-hirsute beneath; lower leaves including the petiole 2 to 3 dm. long, 4 to 9 cm. broad, the upper stem-leaves sessile, semiamplexicaul and gradually reduced towards the terminal corymbose cyme; heads 8 to 10 mm. high, radiate; involucre campanulate, sparingly calyculate; bracts of the involucre usually 21, linear-lanceolate,

[1] **Senecio hypotrichus** Greenm. sp. nov. herbaceus perennis; caule erecto circiter 7 dm. alto tereti striato stramineo vel plus minusve purpurascenti glabro, superne ramoso; foliis pinnatifidis, inferioribus petiolatis usque ad 3 dm. longis, 4 to 9 cm. latis, superioribus sessilibus et semiamplexicaulibus gradatim reductis, laciniis anguste cuneatis vel obovatis vel rhombo-ovatis subcrenato-dentatis supra glabris subtus crispo-hirsutis; inflorescentiis terminalibus corymboso-cymosis; capitulis 8–10 mm. altis radiatis; involucri squamis plerumque 21 lineari-lanceolatis 5–6 mm. longis glabris; flosculis liguliferis saepius 13, ligulis oblongis, 6–7 mm. longis, 2.5 mm. latis, 4–5-nerviis; floribus disci 60–70; achaeniis glabris. —Region of San Luis Potosi, Mexico, alt. 1830–2440 m., coll. of 1878, *Parry & Palmer 533* (U. S. Nat. Herb.), TYPE. The Gray Herbarium specimen of Parry and Palmer's No. 533 differs from the United States National Herbarium specimen above cited in having glabrous leaves, smaller and more numerously flowered heads and hirtellous achenes; it has been referred to *S. tampicanus* DC.

5 to 6 mm. long, glabrous; ray-flowers 13, rays oblong, 6 to 7 mm. long, 2.5 mm. broad, 4–5-nerved; disk-flowers 60 to 70; achenes glabrous.

Distribution: central Mexico.

San Luis Potosi: "region of San Luis Potosi," alt. 1830–2440 m., coll. of 1878, *Parry & Palmer 533* (U. S. Nat. Herb.), TYPE.

24. S. Sanguisorbae DC. Prodr. **6**: 427. 1837; Hemsl. Biol. Cent.-Am. Bot. **2**: 246, 1881, in part; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbaceous perennial; stem erect, 3 to 10 dm. high, striate, glabrous, simple or branched; leaves pinnately divided, the radical and lower stem-leaves petiolate including the petiole 1 to 4 dm. long, 3 to 13 cm. broad, glabrous on both surfaces or slightly subarachnoid beneath, the upper stem-leaves sessile and more or less amplexicaul; lateral leaf-segments oblong-cuneate to oblong-ovate, 1 to 7 cm. long, .3 to 5.5 cm. broad, rather coarsely dentate, the terminal segment usually broadly obovate; inflorescence a terminal many-headed corymbose cyme; heads 6 to 8 mm. high, radiate; involucre narrowly campanulate, sparingly calyculate; bracts of the involucre 8 to 13, linear-lanceolate 4.5 to 6 mm. long, glabrous; ray-flowers 5 to 8; disk-flowers 15 to 25; achenes glabrous.

Distribution: southern Mexico.

Specimens examined:

Hidalgo: by brooks, Sierra de Pachuca, alt. 3050 m., Aug., 1902, *Pringle 9959* (Gray Herb. and Mo. Bot. Gard. Herb.); Sierra de Pachuca, 1 Sept., 1903, *Rose & Painter 6739* (Gray Herb.).

Mexico: Toluca, coll. of 1854, *Schaffner* (Gray Herb. and Berlin Herb.); Valley of Mexico, Sante Fe, *Bourgeau 832* (Gray Herb., U. S. Nat. Herb., Berlin Herb., and Kew Herb.); without locality, *Gregg 691* (Mo. Bot. Gard. Herb.); Cima, 24 Aug., 1910, *Orcutt 3767* (Mo. Bot. Gard. Herb.); in moist soil along brooks, Mt. Ixtaccihuatl, alt. 3050–3350 m., Nov., 1905, *Purpus 1514* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb.); in moist soil, Mt. Popocatepetl, Sept., 1908, *Purpus*

3044 (Field Mus. Herb. and Mo. Bot. Gard. Herb.); Mt. Popocatepetl, 7 and 8 Aug., 1901, *Rose & Hay 6069* (U. S. Nat. Herb.); without locality, *Uhde 582, 602, 603, 609, 624* (Berlin Herb.); without locality, coll. of 1848–49, *Gregg 673* (Gray Herb.).

Michoacan: Angangueo, *Hartweg 313* (Berlin Herb.); cool summits of mountains near Patzcuaro, 2 Aug., 1892, *Pringle 4129* (Gray Herb., U. S. Nat. Herb. and Mo. Bot. Gard. Herb.).

25. S. pinnatisectus DC. Prodr. **6**: 427. 1837; Hemsl. Biol. Cent.-Am. Bot. **2**: 245. 1881; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

Cineraria pinnata La Llav. & Lex. Nov. Veg. Descr. fasc. 1, 26. 1824.

An herbaceous perennial; stem erect, 4 dm. or more high, striate, glabrous or slightly tomentulose; leaves pinnately divided, the lower petiolate, including the petiole 1 to 3 dm. long, 3 to 8 cm. broad, the upper sessile and amplexicaul, at first white floccose-tomentulose, later glabrate except for the persistent tomentum along both sides of the rhachis; lateral divisions of the leaf narrowly oblong, sharply serrate-dentate, terminal division obovate-cuneate; inflorescence a terminal compound compact corymbose cyme; heads numerous, 6 to 7 mm. high, radiate; involucre calyculate, glabrous; bracts of the involucre usually 13; ray-flowers commonly 6 to 8; disk-flowers 15 to 20; achenes glabrous.

Distribution: southern Mexico.

Specimens examined:

Hildalgo: Real del Monte, *Ehrenberg 386* (Berlin Herb. and Gray Herb.), also *386*[a], *386*[b] (Berlin Herb.); Real del Monte, coll. of 1830, *Graham* (Gray Herb. and Kew Herb.).

Michoacan (?): Angangueo, *Chrismar* (Berlin Herb.); "Cuesta de las papao Angangueo," *Schiede* (Berlin Herb.).

Mexico, without definite locality: *Bates, Mackenzie,* and also *Parkinson* (Kew Herb.).

This species is closely related to the preceding, but differs in the narrower lateral leaf-segments, slightly smaller heads,

and persistent floccose tomentum along the rhachis or midrib.

26. S. coahuilensis Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902; Field Col. Mus. Bot. Ser. **2** : 275. 1907. Plate 19, fig. 2.

An herbaceous perennial, glabrous or essentially so throughout; stem erect, 3 to 8 dm. high, branched, striate; leaves pinnately divided into obovate to subreniform cuneate-dentate divisions, thickish and firm in texture, glabrous on both surfaces or slightly pubescent on the veins beneath; lower leaves including the petiole 1 to 3 dm. long, 2 to 5 cm. broad, the upper stem-leaves sessile and amplexicaul; inflorescence terminating the stem and branches in a compound corymbose cyme; heads 7 to 10 mm. high, radiate; involucre campanulate, calyculate with a few small bracteoles, glabrous; bracts of the involucre 13 to 18, linear-lanceolate, 4 to 6 mm. long, thickish; ray-flowers 8 to 10, rays oblong, 3 to 5 mm. long, 4-nerved; disk-flowers 35 to 45; achenes ribbed, glabrous.

Distribution: northern Mexico.

Coahuila: Lerios, Feb. to Oct., 1880, *Palmer 755* (Gray Herb., Kew Herb., and U. S. Nat. Herb.), TYPE; without locality, coll. of 1848-49, *Gregg 403* (Gray Herb. and Mo. Bot. Gard. Herb.).

27. S. leonensis Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902; Field Col. Mus. Bot. Ser. **2** : 276. 1907. Plate 19, fig. 1.

An herbaceous perennial, more or less lanate-tomentose throughout, somewhat glabrate in age; stem 2 to 3 dm. high, leafy at the base, essentially naked above; leaves petiolate, pinnately divided, including the petiole 8 to 12 cm. long, about 3 cm. broad, at first lanate-tomentulose on both surfaces, later glabrate; divisions of the leaf rather coarsely, somewhat unequally and sharply dentate, the terminal segment subreniform, the lateral ones (3 to 6 on either side) obovate-cuneate; heads few, about 1 cm. high, radiate; involucre campanulate, slightly calyculate and, as well as the bracteate peduncle, tomentulose; bracts of the involucre about 13; disk-flowers numerous, 50 to 60; achenes pubescent.

Distribution: northern Mexico.

Specimen examined:

Nuevo Leon: Sierra Madre, near Monterey, 1 June, 1889, *Pringle 2894* (Gray Herb.), TYPE.

28. S. montereyana Wats. Proc. Am. Acad. **25**: 155. 1890; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbaceous perennial, more or less white-tomentose throughout; stems one to several, 2.5 to 4 dm. high, from a rather stout ascending rootstock; leaves mostly radical, including the petiole 1 to 2 dm. long, 1.5 to 3 cm. broad, pinnately divided into narrow, oblong, cuneate to sublinear, entire or few-toothed divisions, at first white-floccose-tomentose on both surfaces, somewhat glabrate above; heads few, 10 to 12 mm. high, radiate, on long naked peduncles; involucre campanulate, calyculate with minute bracteoles, tomentose; bracts of the involucre slightly shorter than the numerous flowers of the disk; ray-flowers about 12; achenes hirtellous-pubescent.

Distribution: northern Mexico.

Specimens examined:

Nuevo Leon: dry shaded ledges of the Sierra Madre, near Monterey, 27 June, 1888, *Pringle 1922* (Gray Herb., U. S. Nat. Herb., Kew Herb., and Mo. Bot. Gard. Herb.), TYPE.

29. S. zimapanicus Hemsl. Biol. Cent.-Am. Bot. **2**: 248. 1881; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

An herbaceous perennial; stems 3 to 4.5 dm. high, simple, leafy below, nearly naked above, striate, more or less pubescent with flaccid-hirsute, jointed, and somewhat matted hairs; leaves mostly basal, sessile or essentially so, 3 to 18 cm. long, 1 to 3 cm. broad, pinnately lobed or divided into oblong-ovate dentate divisions, flaccid-hirsute or subarachnoid-pubescent on both surfaces, more densely so beneath; inflorescence a terminal corymbose few-headed cyme; heads large, 10 to 14 mm. high, conspicuously calyculate, radiate; bracts of the involucre commonly 21 (15–21) linear-lanceolate, 7 to 9 mm. long, thickish, glabrous except at the penicillate tip; ray-

flowers 12 to 15, rays oblong, 10 to 12 mm. long; disk-flowers numerous; achenes about 3 mm. long, ribbed, slightly pubescent on the ribs.

Distribution: eastern Mexico.

Specimens examined:

Hildago: Zimapan, *Coulter 423* (Kew Herb.), TYPE.

Tamaulipas: near Miquihuana, alt. 2140 to 2740 m., 10 June, 1898, *Nelson 4492* (Gray Herb. and U. S. Nat. Herb.).

SECT. 5. BOLANDERIANI Greenm.

§ 5. BOLANDERIANI Greenm. Monogr. Senecio, I. Teil, 22, 23. 1901, and in Engl. Bot. Jahrb. 32 : 18, 19. 1902.

Slender, herbaceous perennials; stems erect or nearly so, 1 to 5 dm. high, from a slender more or less horizontal rootstock; leaves undivided and orbicular-ovate to pinnatifid; heads of medium size, about 1 cm. high, radiate; achenes glabrous. Sp. 30–32.

A. Stems 1.5 to 5 dm. high, leafy to the inflorescence.
  a. Leaves usually pubescent beneath; bracts of the involucre 6 to 9 mm. long, more or less hairy.. *30. S. Bolanderi*
  b. Leaves glabrous on both surfaces; bracts of the involucre 5 to 6.5 mm. long, glabrous ..... *31. S. Harfordii*
B. Stems 1 to 2 dm. high, leafy only at the base..... *32. S. Flettii*

30. S. Bolanderi Gray, Proc. Am. Acad. **7** : 362. 1868; Bot. Calif. **1** : 411. 1876, in part; Syn. Fl. N. Am. **1**^{2} : 392. 1884, and ed. 2, 1886, in part; Howell, Fl. N. W. Am. **1** : 379. 1900, in part; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32** : 19. 1902.

A slender herbaceous perennial; stems ascending or erect, from a creeping rootstock, 1.5 to 5 dm. high, striate, often somewhat purplish; radical and lower stem-leaves undivided and crenately lobed-dentate to pinnately divided into oblong, obovate to subrotund, crenate to sharply dentate divisions, glabrous above, usually pubescent beneath, including the petiole .5 to 1.5 dm. long, 1 to 3 cm. broad; the upper stem-leaves sessile; inflorescence terminating the stem in a few-headed subcorymbose cyme; heads 10 to 12 mm. high, radiate; involucre campanulate, calyculate, usually tawny pubescent; bracts of the involucre about 13, linear-lanceolate, 6 to 9 mm.

long; ray-flowers 5 to 8; disk-flowers rather numerous, 25 to 45; achenes glabrous.

Distribution: California and Oregon, near the coast.

Specimens examined:

California: on sand-stone bluffs at the mouth of the river below Mendocino City, May, 1866, *Bolander 4816* (Gray Herb., Field Mus. Herb., and Mo. Bot. Gard. Herb.), TYPE; Humboldt, coll. of 1868–69, *Kellogg & Harford 539* (U. S. Nat. Herb. and Mo. Bot. Gard. Herb); Humboldt, coll. of 1866, *Kellogg 539* (Gray Herb.); Redwoods, Eel River, coll. of 1878, *Rattan 33* (Gray Herb.); near Crescent City, Del Monte Co., June, 1892, *Burt-Davy & Blasdale 1072* (Field Mus. Herb.).

Oregon: Coast Mountains, Lat. 42°, June, 1884, *Howell 162* (Gray Herb.); Newport, June, 1892, *Mulford* (Mo. Bot. Gard. Herb.).

31. S. Harfordii Greenm. Contr. U. S. Nat. Herb. **11**: 597. 1906.

S. Bolanderi var. *oregonensis* Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902.

A slender herbaceous perennial, glabrous throughout; stem erect or ascending from a creeping rootstock, 2 to 5 dm. high, usually leafy; leaves mostly pinnately divided into cuneate to subrotund crenate to laciniate-dentate divisions; the radical and lower stem-leaves petiolate, including the petiole 4 to 14 cm. long, 1 to 5 cm. broad, occasionally undivided, subrotund and crenately lobed and the lobes again crenate-dentate, thin in texture, pale green in the dried state; the upper stem-leaves sessile; inflorescence a few-headed corymbose cyme; heads 8 to 10 mm. high, radiate, including the conspicuous yellow rays 1.5 to 2 cm. in diameter; bracts of the involucre usually 13, narrowly lanceolate, 5 to 6 cm. long, acuminate, acute, glabrous; ray-flowers usually 5 (–8); disk-flowers 15 to 25; mature achenes 2.5 to 3.5 mm. long, glabrous.

Distribution: mountains of Washington and Oregon.

Specimens examined:

Washington: on mountains near the Lower Cascades, Skamania Co., 29 May, 1886, *Suksdorf* (Gray Herb.); in

woods, Lower Cascades, 29 May, 1887, *Suksdorf 872* (Mo. Bot. Gard. Herb.); summit of Mt. Adams, 4 Aug., 1899, *Flett 1087* (Piper Herb.).

Oregon: Rooster Rock, June, 1877, *Howell* (Gray Herb.); Cascade Mountains, 31 May, 1868–69, *"Kellogg & Harford,"* namely *Harford & Dunn 540* (Gray Herb.), TYPE; near Bonneville, Multnomah Co., 11 July, 1885, *Suksdorf 572* (Gray Herb.); Multnomah Falls, 25 June, 1904, *Piper 6212* (Gray Herb.); Bonneville, 24 June, 1905, *Palmer* (U. S. Nat. Herb.).

32. S. Flettii Wiegand, Bull. Torr. Bot. Club **26**: 137, *pl. 355.* 1899; Greenm. Monogr. Senecio, I. Teil, 23. 1901, and in Engl. Bot. Jahrb. **32**: 19. 1902; Piper, Contr. U. S. Nat. Herb. **11**: 597. 1906.

An herbaceous perennial, 1 to 2 dm. high, glabrous throughout; leaves mostly basal, petiolate, including the petiole 4 to 12 cm. long, 1.5 to 2 cm. broad, undivided, ovate-orbicular and crenate-dentate to pinnately parted, upper stem-leaves few, 1 to 3, incisely pinnate to linear and bractiform; inflorescence terminating the stem in a few-headed corymbose cyme; heads about 1 cm. high, radiate; involucre narrowly campanulate, sparingly calyculate; bracts of the involucre 8 to 13, linear-lanceolate, 5 to 6 mm. long, thickish, glabrous; ray-flowers commonly 5; disk-flowers about 20; achenes glabrous.

Distribution: Washington.

Specimens examined:

Washington: loose rocks, Olympic Mountains, alt. 1830 m., 27 Aug., 1898, *Flett 801* (Piper Herb.), CO-TYPE; Olympic Mountains, Clallam Co., Aug., 1900, *Elmer 2620* (Mo. Bot. Gard. Herb.); Angeles, Clallam Co., 29 June, 1908, *Flett 3351* (U. S. Nat. Herb.); in volcanic sands, Olympic Mountains, alt. 1525 m., Sept., 1890, *Piper 929* (Gray Herb., Mo. Bot. Gard. Herb., and U. S. Nat. Herb.); crevices of volcanic rock, Olympic Mountains, alt. 2135 m., Aug., 1895, *Piper 2196* (U. S. Nat. Herb., Gray Herb., and Piper Herb.); Yakima Region, coll. of 1882, *Brandegee 176* (Mo. Bot. Gard. Herb.).

(To be continued.)

EXPLANATION OF PLATE

PLATE 17

Senecio mohavensis Gray
California

From the type specimen, Lemmon No. 3129, in the Gray Herbarium of Harvard University.

GREENMAN—MONOGRAPH OF SENECIO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 18

Senecio durangensis Greenm.
Mexico

From the type specimen, Pringle No. 10105, in the Gray Herbarium of Harvard University.

GREENMAN—MONOGRAPH OF SENECIO

COCKAYNE, BOSTON

EXPLANATION OF PLATE

PLATE 19

Fig. 1. *Senecio leonensis* Greenm.
Mexico

From the type specimen, Pringle No. 2894, in the Gray Herbarium of Harvard University.

Fig. 2. *Senecio coahuilensis* Greenm.
Mexico

From the type specimen, Palmer No. 755, in the Gray Herbarium of Harvard University.

GREENMAN—MONOGRAPH OF SENECIO

COCKAYNE, BOSTON

Explanation of Plate

PLATE 20

Fig. 1. *Senecio Burkei* Greenm.
Canada

From Macoun's No. 69359 in the Gray Herbarium of Harvard University.

Fig. 2. *Senecio saxosus* Klatt
United States

From Baker's No. 770 in the Herbarium of the Missouri Botanical Garden.

GREENMAN—MONOGRAPH OF SENECIO

COCKAYNE, BOSTON

THE THELEPHORACEAE OF NORTH AMERICA. IV[1]

EXOBASIDIUM

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EXOBASIDIUM

Exobasidium Woronin, Naturforsch. Ges. Freiburg Verhandl. **4**: 397–416. *pl. 1–3*. 1867.—Saccardo, Syll. Fung. **6**: 664. 1888.—Hennings, in Engl. & Prantl, Nat. Pflanzenfam. (**I**.1**) : 103. 1897.

The type species of the genus is *Exobasidium Vaccinii* Fuck. ex Wor.

Fungi parasitic in leaves, shoots, and flowers, which they deform more or less, producing on the surface of these organs an effused hymenium, rarely composed of basidia alone and more usually felt-like and composed chiefly of interwoven hyphae bearing basidia and conidiophores; basidia simple; spores white, simple or septate.

Exobasidium resembles so closely in the thinness of its fructifications such species of *Corticium* and *Peniophora* as *Corticium byssinum, Peniophora asperipilata, P. pilosa,* and *P. subalutacea* that I follow Saccardo and include it with the above genera in the *Thelephoraceae.* Hennings in Engler & Prantl's 'Die Natürlichen Pflanzenfamilien,' has raised *Exobasidium* to ordinal rank but this is not justified by the structure of the many fructifications of *Exobasidium* which I have sectioned; the illustrations in text-books of the structure in section of the fructification are decidedly diagrammatic and simplified.

In his work already cited, Woronin gives a detailed account of the morphology and life history of *Exobasidium Vaccinii* and illustrates this account with three double plates. The interest in this fungus which Woronin's work aroused has

[1] Issued October 8, 1915.

NOTE.—Explanation in regard to the citation of specimens studied is given in Part I, Ann. Mo. Bot. Gard. **1**: 202, footnote.

resulted in the publication of other species by various authors, whose descriptions contrast sharply with that of Woronin in giving little weight to the morphological characters of the fungus under consideration, but extended description of the form and color of the gall of a particular collection, with passing reference to the occurrence of the fungus upon a hitherto unpublished host. In case of the galls, the descriptions usually fail to state what other forms besides the one mentioned the galls may have on other organs of the new host and likewise omit mention of the different forms they may have at other times in the year than the particular time at which the type collection was made. Woronin's description of *E. Vaccinii* was based upon field observations extended through two seasons, during which more than a thousand specimens were collected. He gives one double page colored plate to show the various types of galls produced by the different organs of *Vaccinium vitis-idaea.*

Plate 21 is a photographic reproduction, reduced one-fifth, of Woronin's colored plate; it shows the forms of galls as determined by the particular organ of the host, *Vaccinium vitis-idaea,* which makes hypertrophic response to local stimulation by the parasitic fungus. A local change of color from green to some shade of red is common in plant portions infested with *Exobasidium.* In the photographic reproduction of Woronin's plate the reddened areas of the original appear light colored. In fig. 1, the left side of the uppermost leaf was attacked by the fungus, producing what I term a leaf spot gall. The affected region of the leaf is reddened on the upper side and bears the fructification which may be felty or scurfy on the under side; this leaf is not distorted much in form and thickness.

Figures 2–9 present leaf galls, reddened on the upper side of the leaf and distorted and thickened by hypertrophic growth so as to become more or less concave with respect to the upper surface. I designate this form of gall as leaf concavity.

Figures 10–17 illustrate shoot galls, in the production of which, stems of the current season's growth have been greatly

enlarged and have turned pale and slightly pink under the stimulus of the infecting fungus. In figs. 10–15 the lateral axillary buds along the infected stem have abnormally enlarged by the stimulation of the fungus and have developed in several instances short, delicate, wax-like or coralloid branchlets of carmine color. Such branchlet shoot galls are beautiful objects in their vegetative condition; they constitute a noteworthy type of gall which is quite different in appearance from the more common leaf galls, produced in response to local infection of leaves. Nevertheless, the common cause of these different gall forms is well brought out by Woronin's illustrations, especially by figs. 11, 12, 13, and 15. Upon shoot galls similar to the above, there have been published *Exobasidium Andromedae* Karst. non Peck for the shoot galls of *Andromeda polifolia, E. cassiopes Peck* for the shoot gall of *Cassiope Mertensiana,* and *E. Oxycocci* Rostrup for that of *Oxycoccus palustris.*

Figures 16–18 show the flower type of gall of *Vaccinium vitis-idaea,* that is, the abnormal growth form made by individual flowers in response to the stimulation of their tissues by the fungus. That both the flower gall and the leaf gall have a common cause has been brought out well by the selection of the specimens used for figs. 16 and 17. In fig. 18 there is presented local infection of a single flower. This is important because isolated flower galls upon a new host have in some cases been regarded as *prima facie* evidence that they have been caused by a new species of *Exobasidium.*

Other host plants produce some types of galls, when infected with *Exobasidium,* which were not figured by Woronin for *Vaccinium vitis-idaea* but which are more or less common. Such gall types are:

(a) Leaf type in which scattered whole leaves of the host are infected. These leaves redden more or less on the upper side and bear on the whole under side the scurfy or felty fructification but are not notably thickened or deformed. This gall differs from the leaf spot gall of Woronin's fig. 1 merely in having the whole of the leaf infected.

(b) Shoot gall with all the leaves toward the tip of the

shoot infected but not deformed. These leaves may be almost normally green on the upper side or they may be more or less reddened, sometimes to carmine red; on the under side they become clothed with the felty fructification of the fungus but the leaves are not deformed. This is merely a more general infection than the leaf type *a,* described above, and is often associated with it on the same plant as well as with the leaf spot and leaf concavity forms.

(c) Bag gall of *Andromeda ligustrina.* This is the extreme in gall production. This gall finally becomes a hollow bag which attains a maximum size of 10–15 cm. in length by 5–10 cm. in diameter. These bag galls are either terminal or lateral on leafy shoots of the current season's growth. When lateral, such a gall has the morphological position of a leaf.

(d) Bud gall of *Symplocos tinctoria.* The expanding leaf buds are deformed into a subglobose mass which may be 3–3½ cm. in diameter. In this gall, the undeveloped stem of the bud is greatly enlarged and the individual leaves of the bud are greatly thickened and deformed.

In North America, we have a large number of species of *Ericaceae* which produce galls when infected by *Exobasidium.* The specimens which have accumulated under *Exobasidium* in herbaria show that none of the gall forms which I have designated under distinctive names in the preceding paragraph are isolated forms. Favorable hosts show a connection and gradation between the various gall forms as intimate as that presented by Woronin for *Vaccinium vitis-idaea.* However, the terms which I employ are useful for contrasting and comparing the data presented by the specimens which I have studied. These data are later given in tabular form.

The microscopic examination of an Exobasidium gall shows that it is composed principally of the tissues of the host plant. Hyphae of the fungus ramify about between the cells of the host and, in the galls in which deformation has taken place, the presence of the fungous hyphae has caused the host both to multiply and enlarge its cells in the infected region. The gall is, therefore, a direct product of the host plant, which

is stimulated to growth by the presence of the parasitic vegetative hyphae, by absorption of organic products from the host, and, undoubtedly, by excreta from the hyphae. We may see from Woronin's figures that the various organs of a given host produce different galls when infected by the same fungus; from which we may conclude that the several organs of the host make different growth responses to the same stimulating cause. We have in the host itself, in its several organs, and also in the age of tissues of these organs, as I shall point out later, factors not only able to produce, but actually producing, diversity in gall form even though but a single species of *Exobasidium* is the parasitic stimulant. Of what value, then, is the form of the gall as a taxonomic character for species of *Exobasidium?*

The different organs of the host differ in the resistance which they offer to infection by *Exobasidium.* Woronin notes in his work cited that out of more than a thousand specimens of *Exobasidium Vaccinii,* only twelve showed flower galls. Hence the flowers of *Vaccinium vitis-idaea* are much less subject to infection than the leaves. In only the one case, which he illustrates by fig. 18, did he observe local infection of a flower. In figs. 16 and 17, the infected flowers are borne on infected shoots and may have become infected through these shoots. We may therefore conclude that in a given host a high resistance of certain organs to infection by *Exobasidium* restricts the galls for that host to fewer organs and to a smaller number of forms than in some other host with a lesser resistance.

That the age of the organs, or their cells, of a host is an important factor in the determination of gall form is apparent if one observes throughout a season the succession of galls produced by a favorable host. In this connection Richards[1] has stated, "and also on Gaylussacia resinosa in the earliest formed distortions, whole shoots are transformed. Later in the season the Exobasidium forms only slight local distortions on the leaves, and still later one finds forms which do not distort the tissues of the host plant at all, but simply form a

[1]Bot. Gaz. 21 : 107. 1896.

scurf on the lower side of the leaves. The same succession is found in the forms on Andromeda down to the last mentioned.'' Richards determined by culture experiments that the remarkable bag galls of *Andromeda ligustrina* are merely early (June in Massachusetts) productions under the same specific fungous stimulus which later in the season induces leaf concavities on this host. The account of his experiments[1] may be summarized as follows: During July, Exobasidium spores were removed with suitable precautions from fresh mature bag galls of *Andromeda ligustrina* and were immediately transferred to buds and young leaves of experimental plants of the same species, which were isolated in a moist chamber. In about ten days faint discolorations of the leaves were noticed, at first yellowish and then pink. About five days later, the spots which had considerably enlarged, began to show unmistakable signs of thickening, forming the peculiar concavities in the leaves seen in other Exobasidia. In external form, and also in the matter of basidia and spores, this distortion resembled precisely the leaf form on *Andromeda ligustrina,* and indicates that the *Exobasidium* which produces the bag galls of the young buds is identical with the fungus which produces the leaf form found later in the season.

The foregoing presentation of the Exobasidium gall as a growth response of the host under stimulation by the fungus shows that very different forms of galls and differences in regard to abundance of each form on a host may result—

(a) From the different organs making the response.

(b) From differences in resistance of the several organs, which, in many cases, may undoubtedly be so great as to give complete immunity for certain organs.

(c) From the age of the organ attacked.

Since the host produces a great variety of gall forms as growth responses to attack by a single species of *Exobasidium,* how are we to decide whether a given gall form is ever sufficiently distinct to entitle its causative organism to separate specific rank? Gall forms are host products to so large an

[1] *loc. cit.,* p. 105.

extent that they can have little, if any, value for discriminating between species of *Exobasidium*. Into the formation of such galls so many other factors besides the Exobasidium hyphae enter that it is impossible to consider galls as homologous with the fructification of an ascomycete or that of a toadstool, and they should not be used therefore in the way these true fungous fructifications are used for affording in their form specific characters. As a matter of fact, the layer of basidia and conidia-bearing hyphae at the outside of the gall comprise the whole fructification of the parasitic fungus; this layer alone is morphologous with a toadstool. The mere form of the foreign substratum covered by the resupinate fructification of *Exobasidium* should have no greater taxonomic weight than it has in the closely related genus *Corticium*.

We should now consider the distribution of *Exobasidium Vaccinii* as a parasite upon various genera and species of the *Ericaceae*. Woronin limited his investigation of *E. Vaccinii* to what he observed on *Vaccinium vitis-idaea* and left the matter there for other investigators to go on with, if they were so disposed. As the collections which are made on this host nearly always show the fungus occurring in leaf spot galls and leaf concavity galls, and since these forms of galls are the only ones on this host common enough for distribution in published exsiccati, the species *Exobasidium Vaccinii* seems to have become altogether too closely associated with, and limited in mycological practice to, merely the very commonest gall forms which are produced under stimulation by *E. Vaccinii*. For example, Shear[1] states, "The typical form of *Exobasidium Vaccinii* occurs on *Vaccinium vitis-idaea*, producing hypertrophied spots on the leaves. No record has been found of the occurrence of hypertrophied shoots on this host similar to those found on cranberry plants. Rostrup[51] seems to have been the first to describe this form. In 1883 he reported it as occurring on *Oxycoccus palustris* in Denmark."

[1] Cranberry Diseases. U. S. Dept. Agr., Bur. Pl. Ind., Bul. 110: 36. 1907.

Without doubt, this misapprehension of the galls produced by *Vaccinium vitis-idaea* is due to the scarcity of copies of Woronin's original account of *Exobasidium Vaccinii,* for Woronin is at great pains to show that to *E. Vaccinii* are due both shoot galls and flower galls.

That the erroneous tendency of limiting to *E. Vaccinii* the production of only the commonest leaf galls is potent, is apparent from inspection of the table towards the close of this paper where under the heading, "Exobasidium Vaccinii (Fuck.) Wor. The following have been referred here invariably" there are grouped all Exobasidium galls produced by *Vaccinium vitis-idaea, V. vacillans, V. árboreum, V. pennsylvanicum, V. stamineum, Gaylussacia frondosa, G. resinosa, Arctostaphylos uva-ursi, A. nevadensis, Arbutus Menziesii, Rhododendron canadense, R. maximum,* and *Lyonia jamaicensis.*

Our *Gaylussacia frondosa* and *G. resinosa* of this list merit some detailed consideration for they compare very favorably with *Vaccinium vitis-idaea* as hosts for *Exobasidium Vaccinii.* The galls of these two species of *Gaylussacia* include during the season two shoot forms, leaf concavity type, leaf spot type, and the flower type. The flower type of gall is probably very rare; I have seen a dried herbarium specimen of it collected by Dr. Farlow, at Brewster, Massachusetts, and two others, preserved in alcohol in Seymour Herbarium, one of which was collected by A. B. Seymour, at Woods Hole, Massachusetts, and the other by Mrs. Pier, at Biddeford, Maine. These flower galls have a diameter of 10–12 mm.; all the floral organs are enlarged as in case of the flower galls illustrated by Woronin. Bartholomew collected and distributed in his 'Fungi Columbiani,' 3429, the shoot gall of the wax-like or coralloid type such as is produced by *Vaccinium vitis-idaea. Gaylussacia resinosa* very frequently produces as its earliest galls the other form of shoot gall with all the leaves felty on the whole under surface, more or less reddened above, and not deformed. Such a shoot gall is produced by *Vaccinium Myrtillus* in Europe; it has usually been regarded by European mycologists as due to *Exobasidium Vaccinii.* Its regular

occurrence in North America in a series of *E. Vaccinii* forms confirms the correctness of the reference.

As we take up the consideration of North American species of *Exobasidium* which have been published since 1867, we find that in nearly all cases peculiarities of galls have furnished the distinctive portion of the description. These odd or striking forms of galls have been discovered upon new hosts, as was to be expected, for a new host species would without doubt have composition and properties at least slightly different from those of *Vaccinium vitis-idaea*—so different that the growth response, i. e., the gall of this new host, might differ somewhat, perhaps differ notably, from that of *V. vitis-idaea,* even though the stimulus should be given by the same fungus. Two of the specific names to be considered are based entirely upon the occurrence of *Exobasidium* on a new host, and the other eight are founded upon more or less noteworthy galls. Reference to the second division of my table shows that gall form rather than host has caused the publication of specific names in *Exobasidium.*

Exobasidium Peckii, for example, was published as the cause of flower galls produced by *Andromeda Mariana.* Its flower galls are produced so frequently that they attracted attention; leaf concavity galls are common here also. The morphological characters of the fungous cause of these galls agree closely with those of *Exobasidium Vaccinii,* and the galls themselves are of types that *Vaccinium vitis-idaea* produces under stimulation by *Exobasidium Vaccinii.* No evidence of any nature has been offered tending to show that *E. Peckii* is not *E. Vaccinii* in all respects. The frequent production of flower galls by *Andromeda Mariana* can be simply accounted for as due to the susceptibility of the young flower to infection by the fungus, that is, to a special property of this host. I regard *Exobasidium Peckii* as a synonym of *E. Vaccinii.*

In connection with the discussion of *E. Peckii,* attention should be called to occasional flower galls produced by *Lyonia* (*Andromeda*) *ferruginea.* I have seen only four specimens of these galls, two from Georgia and two from Florida. All

resemble monstrous flowers—up to 5 cm. long in the dried state—with all floral organs enlarged proportionally, as in the flower galls of *Andromeda Mariana, Gaylussacia resinosa,* and *Vaccinium vitis-idaea.* Only flower galls are as yet known to me for *Lyonia ferruginea,* but as the morphological characters of the fungus found on the galls are those of *Exobasidium Vaccinii,* I regard these galls as similar to those of *Andromeda Mariana* but much larger and due to *Exobasidium Vaccinii.* The large size of these Lyonia galls is the expression of the growth response of the flower tissue of this host. It will be interesting if further collections of this host show that only the flowers are susceptible to infection by *Exobasidium.*

Exobasidium Oxycocci was proposed as a name for the fungus causing the shoot galls of wax-like or coralloid habit which are produced by *Oxycoccus palustris.* Similar galls are produced in the United States by *Vaccinium macrocarpon* and *V. intermedium.* Shoot galls of *V. macrocarpon* are illustrated in color by Shear[1] and also the leaf spot and leaf concavity galls which this host produces. The morphological characters of the fungus producing the shoot galls on the cranberry species of *Vaccinium* are the same as those of *Exobasidium Vaccinii;* the galls produced by cranberry plants are such as *E. Vaccinii* produces. As there is no evidence of any kind that *E. Vaccinii,* common throughout the same region, does not cause the cranberry galls, the name *E. Oxycocci* seems quite unnecessary.

Exobasidium Cassiopes and *E. Karstenii* have been published as causes of the shoot galls produced by *Cassiope Mertensiana* and *Andromeda polifolia* respectively. These shoot galls are of the wax-like or coralloid type such as *Vaccinium vitis-idaea* produces under stimulation by *Exobasidium Vaccinii.* As the morphological characters of the so-called *E. Cassiopes* and *E. Karstenii* are those of *E. Vaccinii,* and as no evidence has ever been presented that *E. Vaccinii* does not cause the galls referred to, *E. Cassiopes* and *E. Karstenii* should also be regarded as synonyms of *E. Vaccinii.*

[1] *loc. cit., pl. 8.*

Exobasidium Andromedae Peck is based on the bag gall produced by *Andromeda ligustrina.* This gall described in detail on a preceding page, is so very large and remarkable in structure that it did seem that here, if anywhere, must be the anomaly for higher fungi of a fungous cause, specifically different from *Exobasidium Vaccinii,* yet having the same morphological characters. From this point of view, Richards' experiment,[1] already described, of growing on the leaves of *Andromeda ligustrina* a July crop of leaf concavity galls from spores produced by a bag gall which had matured at the beginning of July, was very illuminating. It showed that such a bag gall is noteworthy only because it shows peculiar properties inherent early in the season in shoots and leaves of *Andromeda ligustrina,* that this bag gall belongs in the series with, and is caused by, the same fungus as the leaf concavity galls such as *Exobasidium Vaccinii* produces.

Richards made other experiments tending to show that *E. Vaccinii* produces the bag galls on *Andromeda ligustrina.* He demonstrated that the latter species is not immune to undoubted *Exobasidium Vaccinii,* that it is as susceptible to such spores as to those produced by its own bag galls. In July, spores of *E. Vaccinii* gathered from leaf concavity galls of *Gaylussacia resinosa* were transferred to buds and young leaves of *Andromeda ligustrina.* After about the same lapse of time as when spores from the bag galls were used, there appeared on the Andromeda leaves infected with *Exobasidium Vaccinii* distortions very similar to those produced by spores from the bag galls. As the large bag gall was the only occasion for the name *E. Andromedae* Peck, I agree with Richards that this name is a synomym of *E. Vaccinii.*

In confirmation from the herbarium side of the correctness of the above conclusion, I have a specimen collected in Idaho by Professor Piper, 772, on *Menziesia glabella,* which has a small terminal bag gall such as is produced by *Andromeda ligustrina,* and also a leaf concavity gall.

In the light of what we now know about bag galls the names *Exobasidium Azaleae, E. discoideum,* and *E. Rhododendri*

[1] *loc. cit.*

appear superfluous, for their galls pass through the concavity stage and the morphological characters of the fungi concerned differ in no respect from those of *E. Vaccinii.*

Exobasidium Cassandrae was based on a leaf concavity of *Cassandra calyculata.* The new host was the sole basis for this new name and its author closed his description with the comment, "perhaps this is only a form of E. Vaccinii." Since we now regard *E. Vaccinii* as able to infect many species of the *Ericaceae,* the host alone in this case (with the morphological characters of the fungus agreeing with those of *E. Vaccinii*) does not afford sufficient justification for regarding *E. Cassandrae* as distinct from *E. Vaccinii.*

Exobasidium Arctostaphyli was founded on a leaf spot on *Arctostaphylos pungens.* As in the case of *Exobasidium Cassandrae,* there is no evidence whatever that the fungus concerned is not *E. Vaccinii,* the characters of the fungus and its work being quite those of the latter species.

The usual errors in connection with the preceding series of synonyms which are grouped together in the second division of my table are due, it seems to me, to attaching to a strange gall form—a host product—the same weight which one would give to a toadstool, and to ignoring the true fructifications of the *Exobasidium* concerned. In the taxonomy of the *Hymenomycetes,* species are based upon differences in morphological characters. It is so remarkable an innovation in our taxonomic usage in this group of plants to propose a new species which has precisely the same morphological characters as a well-known and established one that it makes it incumbent upon, and an unusual opportunity for, an author so establishing a species to show conclusively the truth of the paradox that actually good and distinct species of *Hymenomycetes* have the same morphological characters. In all the cases which have been considered, no evidence tending toward such proof has been offered. In the above, I but express the views of many of the best mycologists, who have consistently regarded the above-mentioned Exobasidium names as synonyms of *E. Vaccinii.*

Winter[1] wrote of *Exobasidium Vaccinii* in Europe where there is a similar confusion as to species, "der Pilz erzeugt ausnahmslos Formänderungen der verschiedensten Art an den von ihm bewohnten Pflanzentheilen . . . . . Ich finde zwischen den einzelnen verschiedene Nährpflanzen bewohnenden Formen keine wesentlichen Unterschiede."

The specimens which I have studied show that we have in North America perhaps three species of *Exobasidium,* two of which are rare and are present in herbaria in so few specimens that present conclusions concerning them are somewhat tentative. These species are as follows:

1. *E. Vaccinii* (Fuck.) Wor.

This species is common and wide-spread and is parasitic on many ericaceous host plants. There is as yet no evidence of which I am aware tending to show that so-called physiological races or forms with parasitism limited to a particular host exist in this species. This fungus attacks leaves developing leafy shoots, and flowers of susceptible plants, making its most successful infections when these organs are very young. The vegetative hyphae live in the infected organs between the cells, which are stimulated by the presence and activities of the parasitic hyphae to make a more or less marked hypertrophic growth response, termed a gall. The galls are of varied and sometimes strange form according to the host, the organ, and its age. The distribution of the galls upon the host is dependent upon the susceptibility of its various organs to infection.

In fruiting, the hyphae push through the epidermis to the surface and produce there a resupinate fructification which is amphigenous in the case of galls from tissues so young that they form galls of wax-like or coralloid structure, and hypophyllous on the more common leaf galls. The fructification is variable in thickness, consisting sometimes of scattered clusters of basidia but usually with hyphae present in variable quantity between the basidia so that the fructification may attain a maximum thickness of 60–70 μ, as in the case of col-

[1] In Rabenhorst, Krypt. Flora 1[1]: 322. 1884.

lections on *Vaccinium vitis-idaea.* As shown by Richards,[1] these hyphae bear simple, acicular, conidia about 6–9×1–1½ μ. Conidia are nearly always present in the preparations but have been entered only occasionally in my table. The basidia are generally 4-spored. The basidiospores from herbarium specimens are colorless, simple or with some uniseptate, 10–20×2½–5 μ, but are usually about 12–18×3–3½ μ. They are sometimes a little shorter, or a little longer, or a little thinner, or a little thicker, but are so variable within the extremes stated for different collections on the same host within the same regions or distant regions—as will be seen by reference to my table—that a moderate latitude in spore dimensions seems evident.

2. *E. Vaccinii uliginosi* Boud.

The European specimen of this species distributed from Norway in Briosi and Cavara, 'Funghi Paras.,' 261, has a resupinate, hypophyllous felty fructification, 30–45 μ thick, which is composed almost wholly of large basidia, standing close together and presenting in sections the appearance of a distinct palisade layer. This fructification begins below the epidermis and tears the cells of the latter loose and apart from each other and carries them outward between the basidia. The hymenium is abundantly fruited with basidiospores, borne two to a basidium. The spores are simple, colorless, even, curved towards the base, 18–20×6–7 μ. No conidial hyphae could be found between the basidia in this specimen.

The specimen distributed in Eriksson, 'Fungi Par. Scand.,' 286a, has similar spores 16–20×8 μ. This specimen is in poorer condition and does not show basidia clearly. In some places the fructification is composed of very fine, short-celled hyphae, which are not bearing conidia. Both the above specimens are shoot galls with leaves felty below and reddened above.

Professor Piper, 443, collected on *Vaccinium membranaceum,* at Mt. Ranier, Washington, in August, a shoot gall similar to the European specimens and having a well fruited

[1] *loc. cit.*

Exobasidium with 2-spored basidia and spores 16–20×8 μ. The fungus agrees in all respects with the specimen in Briosi and Cavara, 261. Several other collections on *Vaccinium membranaceum* of buff colored leaf concavity and leaf spot galls appear to bear *Exobasidium Vaccinii*. The very thick spores, borne two to a basidium, distinguish *E. Vaccinii uliginosi* from *E. Vaccinii*.

3. *E. Symploci* Ell. & Mart.

This fungus attacks the developing leaf buds of *Symplocos tinctoria* and deforms them into a lobed mass. In fruiting, the hyphae protrude on the surface of the mass and bear acicular, simple, colorless, slightly curved conidia, ranging from about 7×1 μ upward. The largest spores are 24×2 μ, acicular, curved, and of the same form as those of intermediate size and so on down to attached conidia. I have not found any of the largest spores attached, nor have I found basidia. In the original description the reference to spore characters is "conidia hyaline, cylindric, nearly straight, 15–21×2 μ."

I conclude that basidia have yet to be demonstrated for this fungus.

As I have had an opportunity to examine a large number of Exobasidium specimens, collected in widely separated localities, on many hosts and at various times in the growing season, it has seemed that a concise summary of the data obtained in regard to each specimen might prove useful for comparison purposes to others who study our specimens of this genus in the future. Pains have been taken to give the hosts accurately. I am indebted to Dr. J. M. Greenman for aid in host determinations in several cases.

In the matter of spores the stated dimensions are those of the preparations which were studied. No effort was made to study preparation after preparation from the same collection in order to find spores possibly larger or smaller than those of the first preparation which showed the spores well. The dimensions stated are those obtained by treating all specimens in exactly the same way and give such results as herbarium specimens afford.

TABLE I

COMPARATIVE TABLE OF DATA CONCERNING SPECIMENS OF EXOBASIDIUM EXAMINED

Host	Spore measure	Gall	Date	Locality	Coll. or herb.
EXOBASIDIUM VACCINII (FUCK.) WOR. THE FOLLOWING HAVE BEEN REFERRED HERE INVARIABLY					
Vaccinium vitis-idaea	14–16.8×2.8 μ (Wor.)	Leaf spot, leaf concavity—scurfy or felty below and reddish above—shoot gall, flower gall.	May to Sept.	Russia	Woronin's article
	12–15×3–3½ μ	Leaf spot, leaf concavity—scurfy or felty below and reddish above.	July	Germany	Krieger, Fung. Sax., 62
	12–15×3 μ	Leaf concavity, felty below, red above.	Aug.	Sweden	Romell
	12–15×3–3½ μ	Same as preceding.	Aug.	Sweden	Burt
V. vacillans	12–14×3 μ	Many leaves, felty under, reddish above.	June	Mass.	Sey. & Earle, Ec. Fung., 137a
	12×2½–3 μ	Leaf spot, scurfy below, reddish above.	July	Mass.	Sey. & Earle, Ec. Fung., 137b
	12–15×3 μ	Leaf spot, felty below, red above.	July	Mass.	Sey. & Earle, Ec. Fung., 137c
	12–15×3–3½ μ	Many leaves, felty under, reddish above.	June	Md.	Barth., Fung. Col., 3324
	15×3 μ	Same as preceding.	May	D. C.	Barth., Fung. Col., 1728
	12–18×3–4 μ	Same as preceding.	May	Md.	Barth., Fung. Col., 3231
	Conidia 6–9×1 μ	Same as preceding.	May	Mo.	Mo. B. G. Hb., 4949
V. arboreum	15×3–3½ μ	Leaf spot, scurfy below, reddish above.	April	Ala.	Ala. Biol. Surv.
	12–15×3 μ	Same as preceding.	April	Ala.	Mo. B. G. Hb., 4975
V. pennsylvanicum	12–13×3 μ	Leaf spot, scurfy below, reddish above.	.....	Wis.	Mo. B. G. Hb., 4985
	11–13×3 μ	Leaf spot, felty below, reddish above.	Aug.	Wis.	Mo. B. G. Hb., 44414
	Immature	Leaf spot, scurfy below, reddish above.	.....	N. Bruns.	Mo. B. G. Hb., 44415
	11–13×3 μ	Same as preceding.	.....	Minn.	Mo. B. G. Hb., 44416
V. stamineum	12–15×3 μ	Leaf spot, scurfy below, dark red above.	April	Ala.	Ala. Biol. Surv.
	12–15×3–4½ μ	Same as preceding.	April	Ala.	Mo. B. G. Hb., 4976
	12×3 μ	Same as preceding.	May	Ala.	Mo. B. G. Hb., 4971
	12–15×3–3½ μ	Leaf spot, scurfy below, buff and red above.	June	N. Y.	Mo. B. G. Hb., 4991

V. membranaceum	12–14×3–3½ μ	Leaf concavity, scurfy, yellowish buff.	Sept.	Wash.	Suksdorf, 448
	13–15×3 μ	Same as preceding.	Aug.	Wy.	Mo. B. G. Hb., 44413
	15–19×4–5 μ	Barely a concavity, scurfy, yellowish buff and spots red margined.	Aug.	Wash.	Suksdorf, 504
	12–18×4–5 μ	Same as noted for preceding.	Sept.	Wash.	Suksdorf, 504
	Too immature.	Leaf spot, scurfy below, yellowish.	July	Idaho	Mo. B. G. Hb., 4989
Gaylussacia frondosa	12–15×3–3½ μ	Shoot gall—all later leaves of shoot with whole of each felty below, reddish above.	June	Mass.	Bartholomew, Fung. Col., 3323
	Sterile	Leaf spot, leaf concavity, reddish above.	June	N. Y.	Mo. B. G. Hb., 4953
	12–14×3 μ	Leaf spot, leaf concavity, reddish above.	July	N. Y.	Mo. B. G. Hb., 4957
	Sterile	Leaf concavity, scurfy below, red above.	May	Fla.	Mo. B. G. Hb., 44404
	14×3 μ	Leaf spot, scurfy below, buff colored.	Sept.	Mich.	Waite, 118
	Sterile	Leaf spot, scurfy below, buff or red above.	Sept.	Mass.	Mo. B. G. Hb., 4948
G. resinosa	Immature	Whole leaves, scurfy below, reddish above.	May	Va.	Barth., Fung. Col., 3232
	Conidia 6–9×1–1½ μ	Shoot gall—whole leaves felty below, green or slightly reddened above.	May	Md.	Barth., Fung. Col., 3523
	15×3–3½ μ	Leaf concavity, felty below, red above.	May	Md.	Barth., Fung. Col., 3430
	Conidia	Leaf concavity, shoot gall of the V. vitis-idaea coralloid type.	May	Md.	Barth., Fung. Col., 3429
	Immature	Shoot gall of coralloid type, flower gall.	June	Mass.	Seymour Herb., T54
	Sterile	Leaf concavity, felty below, red above.	July	Mass.	Sey. & Earle, Ec. Fung., 488
	Conidia 6–10×1–1½ μ	Leaf concavity, shoot gall with whole leaves felty under, reddened above.	July	N. Y.	Mo. B. G. Hb., 4781
	Conidia 6–9×1 μ	Shoot gall with whole leaves felty under, reddened above.	.....	Wis.	Mo. B. G. Hb., 4961

TABLE I (Continued)

Host	Spore measure	Gall	Date	Locality	Coll. or herb.
G. resinosa —continued	10–12×2½–3 μ Conidia 6–9×1–1½μ	Shoot gall of coralloid type, leaf concavity, flower gall.	July	Maine	Seymour Herb., T55
	Conidia 6–8×1 μ	Shoot gall with whole leaves felty below.	.....	.....	Mo. B. G. Hb., 4946
Arctostaphylos uva-ursi	Sterile	Shoot gall with all leaves felty below, reddened above.	July	Wash.	Piper, 434
	12–15×3 μ	Shoot gall of the V. vitis-idaea coralloid type.	Aug.	Col.	Barth, Fung. Col., 2729
A. manganita	12×3 μ	Whole leaves felty below, reddened above.	July	Cal.	Seymour Herb.
A. nevadensis	16×4½ μ	Shoot gall of coralloid type.	July	Wash.	Suksdorf, 840
	12–14×3 μ	Shoot gall with all leaves felty below, dark red above.	Aug.	Wash.	Piper, 428
Arbutus Menziesii	12–15×2–4 μ	Leaf concavity, felty below, red above.	.....	Cal.	Ell. & Ev., N. Am. F., 1586b
Lyonia jamaicensis	15×3½ μ	Leaf concavity to leaf bags, drying reddish brown.	March	Jamaica	Mo. B. G. Hb., 44403
Rhododendron albiflorum	Spores soon 3-septate 15–22×4–6 μ Basidia 4-spored	Leaf spots, scurfy below, buff colored.	Sept.	Wash.	Suksdorf, 841
	12–20×4–5 μ and as above	Leaf spots, scurfy below, buff colored.	Sept.	Wash.	Suksdorf, 449
R. canadense	Conidia	Leaf spot, scurfy below, reddish above.	Sept.	Newf.	Mo. B. G. Hb., 42608
		Same as preceding.	Aug.	Newf.	Mo. B. G. Hb., 4981
R. maximum	12–15×4 μ	Leaf concavity, red.	July	N. Car.	Mo. B. G. Hb., 4951

EXOBASIDIUM VACCINII (FUCK.) WOR. THE FOLLOWING SYNONYMS ARE BASED ON GALL FORMS AS STATED:					
Exobasidium Azaleae Peck, = E. discoideum Ell.					
Azalea nudiflora	15–16×3 μ	Terminal bags, lateral leaf bags.	May	Ala.	Ala. Biol. Surv.
	13–18×3–4½ μ	Leaf bag, scurfy leaf spots, reddish above.	May	Ala.	Mo. B. G. Hb., 4964
	Sterile	Leaf bag suspended by a point.	April	Ala.	Mo. B. G. Hb., 4963
	Sterile	Flowers modified into obconic galls.	June	Mass.	A. B. Seymour Herb.
A. cult. sp.	12–15×3–3½ μ	Flower and leaf bag galls.	June	Mass.	Sey. & Earle, Ec. Fung., 489
A. viscosa	13–18×3–3½ μ	Bag gall, suspended from leaf.	July	N. J.	E. & Ev., N. Am. F., 1718
	Sterile	Bag gall, suspended from leaf.	May	Miss.	Mo. B. G. Hb., 4970
	Conidia	Flower and leaf bag galls.	April	Miss.	Mo. B. G. Hb., 4960
	Sterile	Bag gall, suspended from leaf.	Aug.	Mass.	Mo. B. G. Hb., 44405
	18×3½ μ	Leaf spots, scurfy below, reddened above.	Sept.	Mass.	Mo. B. G. Hb., 44410
Exobasidium Rhododendri Cramer					
Rhododendron ferrugineum	12–15×3–3½ μ	Leaf concavity, bag gall suspended from leaf.	Sept.	Switz.	Rabenhorst, Fung. Eur., 1910
	13–15×3–4 μ	Bag gall, suspended from leaf.	Sept.	Germ.	Magnus, Mo. B. G. Hb.
	14×3 μ	Bag gall, suspended from leaf.	Aug.	Austria	Magnus, Mo. B. G. Hb.
	Sterile	Bag gall, suspended from leaf.	Aug.	Switz.	Kunze, Fung. Sel. Ex. 302
Exobasidium Peckii Halst.					
Andromeda Mariana	12–13×3 μ	Leaf concavity, reddened above; flower gall—flower organs all enlarged.	May	Fla.	A. B. Seymour Herb.
	11–15×3 μ	Same gall forms as the preceding.	May	Fla.	Mo. B. G. Hb., 4966
	12–18×3–4 μ	Same gall forms as the preceding.	June	N. Y.	Sey. & Earle, Ec. Fung., 487
	12–18×3–3½ μ	Leaf concavity, felty below, reddened above.	June	N. J.	Ell. & Ev., Fung. Col., 1210
	Conidia 6–9×1–1½ μ	Leaf concavity, reddened above.	June	Fla.	Mo. B. G. Hb., 4954
Lyonia ferruginea	16–18×4 μ	Flower gall, 2½×2½ cm.—all the organs present and proportionately enlarged.	May	Ga.	U. S. Dept. of Agr.

TABLE I (Continued)

Host	Spore measure	Gall	Date	Locality	Coll. or herb.
Lyonia ferruginea —continued	15×3½–4 μ	Same as above—3–5 cm. long, 1–2½ cm. thick.	June	Ga.	Mo. B. G. Hb., 4955
	12×3½ μ	Flower gall of same type as preceding.	April	Fla.	Mo. B. G. Hb., 4962
		Flower gall of same type as preceding.	.....	Fla.	Mo. B. G. Hb., 44409
Exobasidium Andromedae Peck					
Andromeda ligustrina	15–18×3–3½ μ	Bag gall, terminal on shoot.	June	Mass.	H. L. Jones
	15–18×3–3½ μ	Bag gall, terminal on shoot.	June	Mass.	Rush.
	Conidia	Bag gall, terminal on shoot.	June	Mass.	Duggar, Mo. B. G. Hb.
	17×3½ μ	Leaf bag, terminal bag.	June	N. Y.	Shear, N. Y. Fung., 117
	12–16×3 μ	Bag gall, terminal on shoot.	.....	N. J.	Ellis, N. Am. Fung., 107
	12–15×3½–4 μ	Bag gall in the place of a leaf.	April	Fla.	Mo. B. G. Hb., 44326
Menziesia glabella	10–13×2–2½ μ 10–18×1½–2½ μ	Bag gall, terminal on shoot. Leaf concavity of E. Vaccinii type.	Aug.	Idaho	Piper, 772
Exobasidium Cassandrae Peck					
Cassandra calyculata	12–15×3–4 μ	Leaf concavity, felty below, red above.	.....	N. Y.	Peck, Ellis N. Am. F. 722
	12–15×3–4½ μ	Leaf concavity, scurfy below, red above.	.....	N. Y.	Clinton
	15×3½ μ	Leaf concavity, felty below, red above.	Aug.	Canada	Ell. & Ev. N. Am. F., 2312a
	15×3–4½ μ 12×3 μ	Leaf concavity, felty below, red above. Whole leaf, felty below, red above.	July	Mich.	Trelease, Mo. B. G. Hb.
	Conidia	Shoot gall—all leaves felty under, reddish above.	.....	Newf.	Robinson & von Schrenk, Mo. B. G. Hb.
	14×3½ μ	Leaf spot, felty below, red above.	July	Russia	Fung. Rossiae Ex. 72
Exobasidium Arctostaphyli Harkn.					
Arctostaphylos pungens	12–17×3–5 μ	Leaf spot, scurfy below, red above.	.....	Cal.	Ell. & Ev., N. Am. F. 1586a
	12–18×4½ μ	Leaf spot, scurfy below, red above.	.....	Cal.	Harkness, Mo. B. G. Hb.

Exobasidium Cassiopes Peck					
Cassiope Mertensiana	12–13×3 μ	Shoot gall of the V. vitis-idaea coralloid type.	Aug.	Wash.	Suksdorf, 501
	12–13×3 μ	Shoot gall like the preceding.	Aug.	Wash.	Piper, 771
Exobasidium Oxycocci Rostrup					
Vaccinium macrocarpon	15×3–3½ μ Conidia 6–9×1–1½ μ	Shoot gall of the V. vitis-idaea coralloid type.	.....	Mass.	Minns in U. S. Dept. of Agr. Hb.
	12–15×3 μ	Shoot gall like the preceding.	Sept.	Mass.	Trelease, Mo. B. G. Hb.
	12×3 μ	Leaf spot, leaf concavity, scurfy, red above.	Aug.	Mass.	Ell. & Ev., N. Am. F. 2312b
V. intermedium	12–14×3 μ	Shoot gall of coralloid type.	June	Wash.	Piper, 39
Exobasidium Karstenii Sacc. & Trott. = E. Andromedae Karst. non Peck					
Andromeda polifolia	12×3 μ	Shoot gall, coralloid—all the leaves reddish livid.	July	Finland	Karsten
	12–15×3 μ	Shoot gall like the preceding	July	Finland	Thuem., Myc. Univ. 1110
	Sterile	Shoot gall like the preceding.	June	N. H.	Mo. B. G. Hb., 4778
Exobasidium Vaccinii myrtilli (Fuck.) Juel					
Vaccinium Myrtillus	13–15×3 μ	Shoot gall with all leaves felty below, reddened above.	June	Germany	Krieger, Fung. Sax. 665
	Conidia 6–9×1–1½ μ	Shoot gall like the preceding.	May	Germany	Thuem., Myc. Univ. 115
V. uliginosum	12–15×3–4½ μ	Leaf concavity; shoot gall like above.	July	Germany	Krieger, Fung. Sax., 768
	12–14×3 μ	Shoot gall with all leaves felty below, reddish above.	.....	Finland	Karsten
	10–12×3 μ	Shoot gall like the preceding.	.....	Sweden	Eriksson, Fung. Par., 286b
V. deliciosum	11–12×3 μ Conidia 6–8×1 μ	Shoot gall like the preceding.	Aug.	Wash.	Piper, 842
V. sp.	12–14×3–3½ μ	Shoot gall redder above than preceding.	Sept.	Wash.	Suksdorf, 447

TABLE I (Continued)

Host	Spore measure	Gall	Date	Locality	Coll. or Herb.
		EXOBASIDIUM VACCINII ULIGINOSI BOUD.			
Vaccinium uliginosum	18–20×6–7 μ Basidia 2-spored	Shoot gall with all leaves felty below, red above.	Aug.	Norway	Briosi & Cavara, Fung. Par., 261
V. Myrtillus	15–17×7–8 μ	Shoot gall like the preceding.	.....	Norway	Eriksson, Fung. Par., 286a
V. membranaceum	16–20×8 μ Basidia 2-spored	Shoot gall like the preceding.	Aug.	Wash.	Piper, 443
		EXOBASIDIUM SYMPLOCI ELLIS & MART.			
Symplocos tinctoria	7–14×1½–2 μ, perhaps all are conidia	Leaf bud gall, mass 3×2 cm.	March	Fla.	Ell. & Ev., N. Am. F., 1696
	As above	Same as preceding.	March	Fla.	Mo. B. G. Hb., 4968
	8–24×1½–2 μ, perhaps all are conidia	Same as preceding.	April	Ala.	Mo. B. G. Hb., 4969
	Immature	Same as preceding.	April	Ind.	Rhodes, Mo. B. G. Hb.

Systematic Summary

1. Exobasidium Vaccinii Fuck. ex. Wor. Naturforsch. Ges. Freiburg Verhandl. **4**: 397–416. *pl. 1–3.* 1867. Plate 21.

Fusidium Vaccinii Fuck. Bot. Zeit. **19**: 251. 1861.—*Exobasidium Andromedae* Peck, Buffalo Soc. Nat. Hist. Bul. **1**: 63. 1873; N. Y. State Mus. Rept. **26**: 73. 1874.—*E. Azaleae* Peck, Buffalo Soc. Nat. Hist. Bul. **1**: 63. 1873; N. Y. State Mus. Bul. **26**: 72. 1874.—*E. discoideum* Ellis, Torr. Bot. Club Bul. **5**: 46. 1874.—*E. Rhododendri* Cramer in Rabenh. Fung. Eur. 1910. 1875.—*E. Andromedae* Karst. in De Thuemen, Myc. Univ. 1110. 1878; Finland Natur och Folk Bidrag **37**: 153. 1882.—*E. Karstenii* Sacc. & Trott. in Sacc. Syll. Fung. **21**: 420. 1912.—*E. Cassandrae* Peck, N. Y. State Mus. Bul. **29**: 46. 1874.—*E. Arctostaphyli* Harkn. Calif. Acad. Sci. Bul. **1**: 30. 1884.—*E. Myrtilli* (Thuem.) Karst. Finlands Natur och Folk Bidrag **37**: 152. 1882.—*E. Vaccinii Myrtilli* (Fuck.) Juel, Svensk. Bot. Tids. **6**: 364. 1912.—*E. Oxycocci* Rostr. Bot. Tidsskr. **14**: 243. 1885.—*E. Cassiopes* Peck, N. Y. State Mus. Rept. **45**: 24. 1893.—*E. Peckii* Halst. Torr. Bot. Club Bul. **20**: 437. 1893.

Illustrations: Woronin. *loc. cit.*—Richards, Bot. Gaz. **21**: *pl. 6. f. 1–20.*—Petri, Ann. Myc. **5**: 342–346.—Brefeld, Untersuch. Myk. **8**: *pl. 1. f. 17–22.*—Duggar, Fung. Dis. *f. 215, 216.*—Shear, U. S. Dept. Agr., Bur. Pl. Ind. Bul. 110: *pl. 7. f. A–D.*—Juel, Svensk. Bot. Tids. **6**: 353–372. *f. A–C.*—Engl. & Prantl, Nat. Pflanzenfam. (**I.** 1**): 104. *f. 65.*—Other illustrations in many text-books. References to other illustrations in Sacc. Syll. Fung. **19**: 694.

Fructifications hypophyllous or amphigenous, resupinate, effused, scurfy or felty and compact, grayish, consisting of somewhat scattered clusters of basidia or of basidia and fine, suberect, more or less interwoven and branched hyphae which bear conidia and give to the fructification a maximum thickness ranging up to 60–70 μ; basidia with 4 sterigmata usually; basidiospores colorless, simple or with some 1-septate, 10–20$\times$2$\frac{1}{2}$–5 μ, but usually about 12–18$\times$3–3$\frac{1}{2}$ μ, becoming 3-septate in germinating; conidia simple, 6–9$\times$1–1$\frac{1}{2}$ μ.

Parasitic in leaves, young shoots, and flowers of various ericaceous hosts, and stimulating the infected parts to the production of leaf, shoot, or flower galls which bear the fructifications on their surface. Leaf galls are usually somewhat reddish on the upper side and bear the fructification on the lower side.

From Newfoundland to Florida and westward to California and Washington, also in Jamaica.

I have referred here, with some doubt, the *Exobasidium* causing yellow-buff leaf spot galls on *Rhododendron albiflorum,* collected on mountains in Washington by W. N. Suksdorf. The basidia are 20–30×6 μ, with 4 prominent sterigmata; the basidiospores are mostly 18–21×4½–6 μ, and are nearly all 3-septate. Some of these spores are germinating, hence the septation of the spores may possibly be due to their over maturity when collected, combined with weather conditions at that time favorable to germination. Other collections which show the full series of gall forms on this host are desirable and should give the needed information in regard to septation of the spores.

Specimens examined:

Exsiccati: Ellis, N. Am. Fung., 107, 722; Ell. & Ev., N. Am. Fung., 1586a, 1586b, 1718, 2312a, 2312b; Ell. & Ev., Fung. Col., 220, 1210; Bartholomew, Fung. Col., 1728, 2729, 3231, 3232, 3323, 3324, 3429, 3430, 3523; Seymour & Earle, Econ. Fung., 137a, 137b, 137c, 487, 488, 489; Shear, N. Y. Fung., 117; De Thuemen, Myc. Univ., 115, 210, 1110, 1808; Eriksson, Fung. Par., 286b; Jaczewski, Komarov & Tranzschel, Fung. Rossiae Ex., 72; Kunze, Fung. Sel. Ex., 302; Krieger, Fung. Sax., 62, 665, 768; Rabenhorst, Fung. Eur., 1910; Romell, Fung. Scand., 38.

Austria: On *Rhododendron ferrugineum,* Tyrol, *P. Magnus* (in Mo. Bot. Gard. Herb., 4988).

Germany: On *Vaccinium vitis-idaea,* Königstein, *Krieger,* Krieger, Fung. Sax., 62; Bavaria, *De Thuemen,* Myc. Univ., 910; on *Rhododendron ferrugineum, P. Magnus;* on *Vaccinium Myrtillus,* Leipzig, *G. Winter,* De Thuemen, Myc.

Univ., 115; Königstein, *Krieger,* Fung. Sax., 665; on *V. uliginosum,* Altenberg, *Krieger,* Fung. Sax., 768.

Russia: On *Cassandra calyculata,* Novgorod, Jaczewski, Fung. Rossiae Ex., 72.

Finland: On *Vaccinium uliginosum,* Mustiala, *P. A. Karsten;* on *Andromeda polifolia,* Mustiala, *P. A. Karsten;* and also in De Thuemen, Myc. Univ., 1110.

Sweden: On *Vaccinium vitis-idaea,* Femsjö, *L. Romell;* Upsala, *E. A. Burt;* on *Andromeda polifolia, L. Romell,* Romell, Fung. Scand., 38; on *Vaccinium uliginosum,* Eriksson, Fung. Par. Scand, 286b.

Switzerland: On *Rhododendron ferrugineum,* Luzern, *G. Winter* in Kunze, Fung. Sel. Ex., 302; same host, Maderaner Thal, *Cramer,* Rabenhorst, Fung. Eur., 1910.

Canada: on *Cassandra calyculata,* London, *J. Dearness,* Ell. & Ev., N. Am. Fung., 2312a.

Newfoundland: on *Cassandra calyculata,* Pennie's River, *B. L. Robinson & H. von Schrenk* (in Mo. Bot. Gard. Herb., 4779); on *Rhododendron canadense,* Bluff Head, *A. C. Waghorne, 940* (in Mo. Bot. Gard. Herb., 42608); Virginia Water, *B. L. Robinson & H. von Schrenk* (in Mo. Bot. Gard. Herb., 4981).

New Brunswick: on *Vaccinium pennsylvanicum, Hays, 16* (in Mo. Bot. Gard. Herb., 44415).

Maine: on *Gaylussacia baccata,* Biddeford, *Mrs. A. M. Pier* (in Seymour Herb., T55).

New Hampshire: on *Andromeda polifolia,* Shelburne, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 4778).

Massachusetts: on *Vaccinium vacillans,* Arlington, Magnolia, and Medford, *A. B. Seymour,* Sey. & Earle, Econ. Fung., 137a, 137b, 137c respectively; Plymouth, *E. Bartholomew,* Fung. Col., 3324; Weston, *A. B. Seymour, T56* (in Seymour Herb.); Rafes Chasm, *A. B. Seymour, T58* (in Seymour Herb.); Middlesex Falls, *J. G. Jack* (in Seymour Herb.); on *V. macrocarpon,* Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 4982); Chatham, *Miss Minns,* and also (in U. S. Dept. Agr. Herb.); Harwich, *B.D.Halsted,* Ell.& Ev.,N.Am. Fung., 2312b; Waverly, *A. B. Seymour, T60* (in Seymour

Herb.); on *V. pennsylvanicum,* Rafes Chasm, *A. B. Seymour T59* (in Seymour Herb.); on *Gaylussacia frondosa,* Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 4948); Plymouth, *E. Bartholomew,* Fung. Col., 3323; on *G. resinosa,* Manchester, *W. C. Sturgis,* Sey. & Earle, Econ. Fung., 488; Falmouth, *A. B. Seymour, T53* (in Seymour Herb.); Woods Hole, *A. B. Seymour, T54* (in Seymour Herb.); Dartmouth, *W. G. Farlow* (in Seymour Herb.); Brewster, *W. G. Farlow* (in Seymour Herb.); on *Andromeda ligustrina,* Cambridge, *Mr. Rush;* Dedham, *H. L. Jones,* and also *B. M. Duggar* (in Mo. Bot. Gard. Herb., 44411); Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 44410); Hampden, *A. B. Seymour, T51* (in Seymour Herb.); Granville, *A. B. Seymour* (in Seymour Herb.); on *Rhododendron cult. sp.,* Brookline, *A. B. Seymour,* Sey. & Earle, Econ. Fung., 489; on *R. nudiflorum,* Granville, *A. B. Seymour* (in Seymour Herb.); on *R. viscosum,* Woods Hole, *W. Trelease* (in Mo. Bot. Gard. Herb., 44405, 44408).

New York: on *Vaccinium stamineum,* Ithaca, *W. Trelease* (in Mo. Bot. Gard. Herb., 4991); on *Gaylussacia frondosa,* Eastport, *J. Schrenk* (in Mo. Bot. Gard. Herb., 4953); Eastport, *H. von Schrenk* (in Mo. Bot. Gard. Herb. 4957); on *G. resinosa,* Deer Park, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 4781); on *Andromeda ligustrina,* Alcove, *C. L. Shear,* N. Y. Fung., 117; on *A. Mariana,* Westbury, *F. C. Stewart,* Sey. & Earle, Econ. Fung., 487; on *Cassandra calyculata,* Adirondack Mts., *C. H. Peck,* Ellis, N. Am. Fung., 722; Buffalo, *G. W. Clinton.*

New Jersey: on *Andromeda ligustrina, Ellis,* N. Am. Fung., 107; on *A. Mariana,* Newfield, *Ellis,* Ell. & Ev., Fung. Col., 1210; on *Rhododendron viscosum,* Newfield, *Ellis,* Ell. & Ev., N. Am. Fung., 1718; and (in Mo. Bot. Gard. Herb., 4959).

Maryland: on *Vaccinium vacillans,* Rosecraft, *Bartholomew,* Fung. Col., 3231; on *Gaylussacia resinosa,* Lanham, *E. Bartholomew,* Fung. Col., 3429, 3430; *Bartholomew & Swingle,* Fung. Col., 3523.

District of Columbia: on *Vaccinium vacillans,* Takoma Park, *C. L. Shear,* Fung. Col., 1728.

Virginia: on *Gaylussacia resinosa,* Vienna, *E. Bartholomew,* Fung. Col., 3232.

North Carolina: on *Rhododendron maximum, H. von Schrenk* (in Mo. Bot. Gard. Herb., 4951); on *R. nudiflorum, H. von Schrenk* (in Mo. Bot. Gard. Herb., 4950).

Georgia: on *Lyonia ferruginea,* Brunswick, comm. by U. S. Dept. Agr. Herb.; *W. Trelease* (in Mo. Bot. Gard. Herb., 4955).

Florida: on *Gaylussacia frondosa,* Dunedin, *S. M. Tracy, 6649* (in Mo. Bot. Gard. Herb., 44404); on *Andromeda ligustrina,* St. Leo, *Rev. Jerome* (in Mo. Bot. Gard. Herb., 44326); on *A. Mariana,* White Springs, *H. H. Hume, 88* (in Mo. Bot. Gard. Herb., 4966), and also (in Seymour Herb.); *Chapman* (in Mo. Bot. Gard. Herb., 4954); on *Lyonia ferruginea, Chapman* (in Mo. Bot. Gard. Herb., 44409).

Alabama: on *Vaccinium arboreum,* Auburn, *Ala. Biol. Surv.,* and also (in Mo. Bot. Gard Herb., 4975); on *V. stamineum,* Auburn, *Ala. Biol. Surv.,* and also (in Mo. Bot. Gard. Herb., 4976); Auburn, *F. S. Earle & L. M. Underwood* (in Mo. Bot. Gard. Herb., 4971); on *Rhododendron nudiflorum,* Auburn, *Ala. Biol. Surv.,* and also (in Mo. Bot. Gard. Herb., 4964, 4963).

Mississippi: on *Rhododendron viscosum,* Ocean Springs, *F. S. Earle* (in Mo. Bot. Gard. Herb., 4970); and *S. M. Tracy* (in Mo. Bot. Gard. Herb., 4960).

Michigan: on *Galylussacia frondosa,* Lansing, *M. B. Waite, 118* (in U. S. Dept. Agr. Herb.); on *G. resinosa,* Agricultural College, *G. H. Hicks* (in Seymour Herb.); on *Cassandra calyculata,* Republic, *W. Trelease* (in Mo. Bot. Gard. Herb., 4983); Agricultural College, *G. H. Hicks* (in Seymour Herb.).

Minnesota: on *Vaccinium pennsylvanicum,* Hokal, *L. H. Pammel* (in Mo. Bot. Gard. Herb., 44416).

Wisconsin: on *V. pennsylvanicum,* La Crosse, *L. H. Pammel* (in Mo. Bot. Gard. Herb., 44414); Kirtland, (in Mo. Bot.

Gard. Herb., 4985); on *Gaylussacia resinosa,* Kirkland (in Mo. Bot. Gard. Herb., 4961).

Missouri: on *Vaccinium vacillans,* Crystal City, (in Mo. Bot. Gard. Herb., 4949).

Wyoming: on *V. membranaceum,* Teton Mts., *A. Nelson, E. Nelson, 6525* (in Mo. Bot. Gard. Herb., 44413).

Idaho: on *V. membranaceum,* Forest, Nez Perces Co., *A. A. & E. G. Heller, 3465* (in Mo. Bot. Gard. Herb., 4989); on *Menziesia glabella,* Bitter Root Mt., *C. V. Piper, 772.*

Colorado: on *Arctostaphylous uva ursi,* Glacier Lake, *Bartholomew & Bethel,* Fung. Col., 2729.

Washington: on *Vaccinium deliciosum,* Mt. Rainier, *C. V. Piper, 842;* on *V. membranaceum,* Mt. Paddo, *W. N. Suksdorf, 448;* Chiquash Mts., *W. N. Suksdorf, 504;* on *Vaccinium sp.,* probably *V. membranaceum,* Mt. Paddo, *W. N. Suksdorf, 447;* on *V. intermedium,* Seattle, *C. V. Piper, 39;* on *Arctostaphylos uva ursi,* Orchard Point, *C. V. Piper, 434;* on *A. nevadensis,* Mt. Paddo, *W. N. Suksdorf, 840;* Longwire Springs, *C. V. Piper, 428;* on *Cassiope Mertensiana,* Chiquash Mts., Skamania Co., *W. N. Suksdorf, 501;* Olympic Mts., *C. V. Piper, 771;* on *Rhododendron albiflorum,* Chiquash Mts., Skamania Co., *W. N. Suksdorf, 841;* Mt. Paddo, *W. N. Suksdorf, 449.*

California: on *Arctostaphylos pungens, H. W. Harkness* (in Mo. Bot. Gard. Herb., 4972); and also Ell. & Ev., N. Am. Fung., 1586a; on *A. manganita,* Sisson's, Siskiyou Co., *W. C. Blasdale* (in Seymour Herb.); on *Arbutus Menziesii, H. W. Harkness,* Ell. & Ev., N. Am. Fung., 1586b.

Jamaica: on *Lyonia jamaicensis,* Cinchona, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 44403).

2. **E. Vaccinii uliginosi** Boud. Soc. Bot. Fr. Bul. **41**: CCXLIV. 1894.

Illustrations: Juel, Svensk. Bot. Tids. **6**: 353–372. *pl. 7. f. 5. text. f. D.*

Fructification hypophyllous, resupinate on the whole lower surface of the leaves, felty, 30–45 μ thick, composed of large basidia arranged side by side in a compact hymenium; basidia

with 2 sterigmata; spores colorless, even, curved towards the base, 16–20 × 7–8 μ.

Parasitic on *Vaccinium membranaceum,* which produces shoot galls with all the later leaves of the gall red on the upper side, felty below, and but slightly, if at all, deformed.

Mt. Rainier, Washington. August.

In the original description of this species, the spore dimensions are stated as 25–32 × 8–12 μ. The European specimens in the exsiccati cited below, which European authors refer here, have spores of the dimensions of the American collection. Shoot galls of the type stated are the only form known to be caused by this species, but other forms may yet be found.

Specimens examined:

Exsiccati: Briosi & Cavara, Fung. Par., 261; Eriksson, Fung. Par. Scand., 286a under the name *Exobasidium Vaccinii.*

Norway: on *Vaccinium Myrtillus,* Eriksson, Fung. Par. Scand., 286a; on *V. uliginosum, G. von. Lagerheim,* Briosi & Cavara, Fung. Par., 261.

Washington: on *Vaccinium membranaceum,* Mt. Rainier, *C. V. Piper, 443.*

3. **E. Symploci** Ell. & Mart. Am. Nat. **18**: 1147. 1884.

Fructification amphigenous, resupinate, effused, consisting of lax, slender, colorless hyphae which bear solitary conidia at the tips of very short, lateral, ascending branches; conidia colorless, even slightly curved, acicular, 7–24×1–2 μ; basidia and basidiospores unknown.

Parasitic on *Symplocos tinctoria* which produces bud galls 3–3½ cm. in diameter, lemon yellow, subglobose and sublobate.

Florida, Alabama, and Indiana. March and April.

In the original description it is stated that the galls are distorted flower buds. In a specimen collected in Indiana, the gall is a partially developed leaf bud.

Specimens examined:

Exsiccati: Ell. & Ev., N. Am. Fung., 1696.

Florida: on *Symplocos tinctoria,* Green Cove Springs, *G. Martin* (in Mo. Bot. Gard. Herb., 4968); and in Ell. & Ev., N. Am. Fung., 1696.

Alabama: on *Symplocos tinctoria,* Auburn, *Ala. Biol. Surv.* (in. Mo. Bot. Gard. Herb., 4969).
Indiana: on *Symplocos tinctoria,* Robertsdale, *A. M. Rhodes* (in Mo. Bot. Gard. Herb., 741178).

SPECIES IMPERFECTLY KNOWN

E. decolorans Harkness, Cal. Acad. Sci. Bul. **1**: 31. 1884.

"Receptaculum effused, producing conspicuous yellowish-white, orbicular spots, 1–2 cm. in diameter, not at all distorting the leaf; spores appearing upon the under surface, hyaline, straight, μ 7–8 × 4–5.

"On living leaves of Rhododendron occidentale. Tamalpais [Cal.]. Autumn. 2887."

The above is the original description. I have seen no specimens referable here nor on the host stated.

EXCLUDED SPECIES

E. mycetophilum Peck ex Burt, Torr. Bot. Club Bul. **28**: 285–287. *pl. 23.* 1901.

Tremella mycetophila Peck, N. Y. State Mus., Bul. **28**: 53. *pl. 1. f. 4.* 1879.

This curious structure on *Collybia dryophila,* I no longer regard as parasitic but, rather, as a teratological production of *C. dryophila,* induced by protracted wet weather during development of the fructification.

(To be continued.)

Explanation of Plate

PLATE 21.

This plate is a photographic reproduction, ×⅘, of Plate 1 by Woronin[1] of the various galls produced by *Vaccinium vitis-idaea* when parasitized by *Exobasidium Vaccinii*. The original plate is colored and with all figures natural size; red colors of the original have photographed light colored.

Fig. 1. Leaf spot gall, on left side of uppermost leaf; the leaf is reddish on the upper side in the infested area, not deformed, and was felty or scurfy on the lower side.

Figs. 2–9. Leaf concavity galls. More or less deformation of the infected region is present here.

Figs. 10–15. Shoot galls of the wax-like or coralloid type. Extended portions of leafy shoots are infected. Figure 11 shows whole branchlets completely hypertrophied.

Figs. 16–17. Flower galls borne on, and a part of, shoot galls.

Fig. 18. Flower gall. Local infection of a single flower, noted as the only such instance observed.

[1] *loc. cit.*

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TOXICITY OF GALACTOSE FOR CERTAIN OF THE HIGHER PLANTS[1]

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In the course of investigations upon the effect of sugars on the growth of certain higher plants, the sugar galactose was employed. In experiments with vetch (*Vicia villosa*) the plants grown in the presence of 2 per cent galactose showed very marked injury, the injury being especially manifest by a killing of the roots and accompanied by a reduction in the growth of tops. The results secured were the more surprising in view of the fact that lactose sugar employed coincidently influenced beneficially the growth of the same plant. Certain experiments were therefore made to determine whether or not the effect of the galactose was consistent.

Method of experimentation.—The plants were grown under sterile conditions on agar media containing Pfeffer's nutrient solution[2] of one-half its normal strength. This solution is neutral in its reaction. The solution contained varying amounts of galactose sugar, the source of which is indicated in each case.

[1] The writer acknowledges gladly his indebtedness to the officers of the Missouri Botanical Garden for facilities and courtesies extended to him during his stay in St. Louis.

[2]

$CaNO_3$	2	grams
KNO_3	0.5	grams
KCl	0.25	grams
K_2HPO_4	0.50	grams
$MgSO_4$	0.50	grams
Fe_2Cl_3	4	milligrams
Dist. water	6	liters

The seed employed were sterilized by means of a method devised in the Laboratory of Plant Physiology of Cornell University by Dr. J. K. Wilson.[1] In brief it is as follows: 10 grams of chloride of lime are shaken up with 150 cc. tap water and after standing for ten minutes the supernatant liquid is filtered. The filtrate is used as the sterilizing agent. The seeds are placed in a test-tube covered with about five times their volume of the filtrate and the tube then tightly stoppered. The seeds are treated for from 4 to 24 hours, depending upon the character of the seed. In the experiments here mentioned the vetch seeds were exposed to this treatment for 12 hours and the peas for 4 hours. The seeds are directly transferred to the culture vessels from the chloride of lime solution, care being observed to drain off all of the chloride of lime solution. In transferring the seed the usual bacteriological precautions are observed.

Experiment with vetch (*Vicia villosa*).—The plants were grown in large glass cylinders 60 cm. high and 10 cm. in diameter, having a volume of approximately 4 liters. In each of the cylinders were placed 250 cc. of the nutrient solution plus 1 per cent washed agar and galactose sugar. The cylinders were then fitted with cotton plugs and sterilized for one hour in an autoclave at a pressure of 15 pounds. The cultures were made in triplicate and the galactose was tested at 2 per cent and at 0.2 per cent concentration. After a growth period of 30 days the cultures showed the injurious action of the galactose, in each case the roots being markedly injured. The primary root tip coming in contact with the agar medium was killed and the lateral root produced met with the same injury, so that ultimately a multi-branched root system was produced after the manner of the pea roots shown in pl. 22 fig. 5. Whatever portions of the roots remained in contact with the agar medium were ultimately killed. It should be mentioned in this connection that the vetch grown in the presence of glucose, saccharose, lactose or maltose at concentrations of 2 per cent was greatly benefited. These sugars are absorbed and assimilated.

[1] Am. Jour. Bot. **2:** 420–427. 1915.

Experiment with Canada field pea (*Pisum sativum*).—In the first experiment with the pea the large cylinders were again employed and to each were added 200 cc. of the nutrient solution plus 1 per cent agar and the sugar whose effect was to be tested. Cultures were made with raffinose, saccharose, lactose, glucose, and galactose ("Merck's Highest Purity"), the concentration of the sugar employed in each case being 2 per cent. The cylinders were fitted with cotton plugs as in the previous experiment and then sterilized for a period of one hour. In each cylinder were sown four peas which had

TABLE I

DATA ON CANADA FIELD PEA

(Duration 25 days. Taken February 13)

Culture	No. of plants	Height of plants cm.	Total green wt. grams	Dry wt. coty-ledons grams	Dry wt. roots grams	Dry wt. tops grams	Total dry wt. grams	Av. dry wt. grams	Gain per plant grams
Glucose	3	44 40 38	6.250	.155	.170	.364	.689	.229	+.085
Lactose	4	40 40 33 33	6.700	.169	.105	.355	.629	.157	+.007
*Raffinose	4	32 33 24 33	6.500	.192	.130	.328	.650	.162	+.012
Saccharose	4	39 35 36 35	7.600	.160	.144	.430	.734	.183	+.036
Check	3	32 23 34	4.450	.150	.075	.190	.415	.138	—.012
Maltose	4	33 40 34 28	6.600	.222	.142	.386	.750	.187	+.034
Galactose	Plants small and roots injured. (See pl. 22, figs. 1a and 5.)								

* Reducing sugar formed in medium probably as a result of secretion of invertase and raffinase from roots. Acidity of entire medium at time of examination equivalent to 0.7 cc. N/10 KOH.

been sterilized by the method described. The plants were grown for a period of twenty-five days and then data taken on the various cultures. The various cultures are shown in pl. 22 fig. 1. The galactose plants are separately shown in pl. 22 fig. 5 and the detailed data are given in table I.

An examination of the table reveals the fact that every sugar acted beneficially except galactose. If the plants had been examined a month later (as was the case with other cultures), much greater differences would have been secured between the check cultures and the sugar-containing cultures. Lactose is undoubtedly utilized by Canada field pea as well as by vetch and probably before assimilation is converted into glucose and galactose. Raffinose, which is also utilized, yields on hydrolysis first levulose and melibiose, and the latter is further transformed to galactose and dextrose. In the light of the foregoing, it would appear from the results secured with lactose and raffinose that levulose and glucose must exert some protective action against the injurious action of galactose.

Influence of concentration of galactose.—In all of the previous experiments the galactose sugar was employed at only two concentrations, namely, 0.2 per cent and 2 per cent. In the following experiment a series of cultures was made containing galactose at the following concentrations: 0.125 per cent, 0.25 per cent, 0.50 per cent, 1.0 per cent, 2.0 per cent, and control cultures lacking galactose. The plants were grown in large test-tubes 30 cm. × 4 cm., containing 50 cc. of the nutrient medium plus 1 per cent agar. The galactose sugar employed in this experiment was provided by Dr. C. S. Hudson[1], Chief of the Carbohydrate Laboratory, U. S. Bureau of Chemistry. The galactose sugar provided had been recrystallized and was stated by Dr. Hudson to be of a very high degree of purity and probably purer than any which could be secured upon the market. The tubes were plugged with cotton and sterilized in an autoclave at 15 pounds pressure for a period of 20 minutes. One pea was sown in each tube and the cul-

[1] The writer gratefully acknowledges his indebtedness to Dr. Hudson for the galactose furnished.

tures made in triplicate. The seeds germinated in four days and even by this time in the higher concentrations of galactose, browning of the cotyledons was becoming evident. This browning of the cotyledons intensified with time and at the end of 20 days the peas in the 1 per cent and 2 per cent galactose cultures showed marked discoloration, and death of roots soon occurred. The height of tops was also markedly affected in the presence of galactose of a concentration of 1 per cent or over. (See pl. 22 fig. 4.) The above experiments were repeated with wheat and corn and the results secured were similar.

Antagonistic action of glucose toward toxicity of galactose.—It was noted previously that raffinose and lactose are utilized by Canada field pea, and this has been verified by other experiments. The use of lactose by vetch has also been decidedly shown by experiments not yet reported. Since both lactose and raffinose are assimilated by pea and vetch, and since it is highly probable, as previously suggested, that these sugars are hydrolyzed before assimilation, it is possible that the glucose and levulose exercise a protective action against the galactose.

An experiment was made to test the hypothesis with respect to glucose. Test-tube cultures were prepared as in the previous experiment, but in this case were made in quadruplicate. One series contained 1 per cent glucose plus 1 per cent galactose and the second series contained 1 per cent galactose alone. The plants were grown for 25 days in the greenhouse and the general results are clearly evident in pl. 22 figs. 2 and 3. In the case of the 1 per cent galactose culture the primary roots were killed, but with the 1 per cent glucose added, the primary root tip was killed and the epidermis and part of the cortex, but the inner part of the root was not apparently injured, for secondary roots developed which seemed to be more resistant to the toxic action of the galactose, for these root tips suffered no injury and not even a browning of the root was secured as was the case with the primary root (pl. 22 fig. 3). The experiment was repeated a second time and the results secured are concordant with the first.

Discussion.—So far as the writer has been able to discover, no previous mention has been made of the toxic nature of galactose for plants. Molliard[1], however, intimates that galactose is toxic for radish, for unlike other sugars, the galactose permitted no development beyond a 5 per cent concentration and with 2 per cent galactose the plants are very small. He concludes that galactose is not utilized by radish.

That galactose is injurious to the green plants employed is definitely shown. It does not appear to be toxic to fungi since *Aspergillus niger,* several species of *Penicillium,* a species of *Fusarium,* and a species of *Mucor* were all found growing in cultures which became contaminated. It is definitely known also that certain yeasts are able to ferment galactose. The character of the injury effected by the galactose in the above experiment and the method of action have not yet been determined. Incidental observations indicate that the galactose on penetrating kills the cells in its path. In the case of peas grown on 1 per cent galactose the peripheral layers of the cotyledon showed the original starch reserve undigested. In the presence of glucose it was only the epidermis and part of the cortex which suffered injury. It would appear that the outer layers of cells were injured before sufficient glucose had accumulated to render them resistant to the toxic action of galactose, or perhaps the penetrability of the inner cells for galactose was altered by the presence of glucose. In what manner the glucose antidotes the toxicity of galactose cannot yet be stated. It may be possible that it is the oxidation products of galactose that are the injurious agents and that the glucose prevents the formation, or modifies the character, of the oxidation products and that the toxicity is thereby overcome. Investigation into other phases is in progress.

[1] Molliard, Marin. Action morphogénique de quelques substances organiques sur les végétaux supérieurs. Rev. Gén. de Bot. **19**: p. 331. 1907.

Explanation of Plate

PLATE 22

Fig. 1. *a*, galactose 2 per cent; *b*, lactose 2 per cent; *c*, check—no sugar; *d*, raffinose 2 per cent; *e*, saccharose 2 per cent; *f*, glucose 2 per cent. (Cotton plugs were removed at the time of photographing.)

Fig. 2. The two outside tubes contain 1 per cent galactose while the two middle ones contain 1 per cent galactose plus 1 per cent glucose.

Fig. 3. The small plant was grown on 1 per cent galactose; the larger one on 1 per cent galactose plus 1 per cent glucose.

Fig. 4. *a* and *b*, 2 per cent galactose; *c*, 1 per cent galactose; *d*, 0.500 per cent galactose; *e*, 0.250 per cent galactose; *f*, 0.125 per cent galactose; *g*, check—no galactose.

Fig. 5. Peas (shown in fig. 1*a*), showing character of root growth when tips alone come in contact with 2 per cent galactose-containing medium.

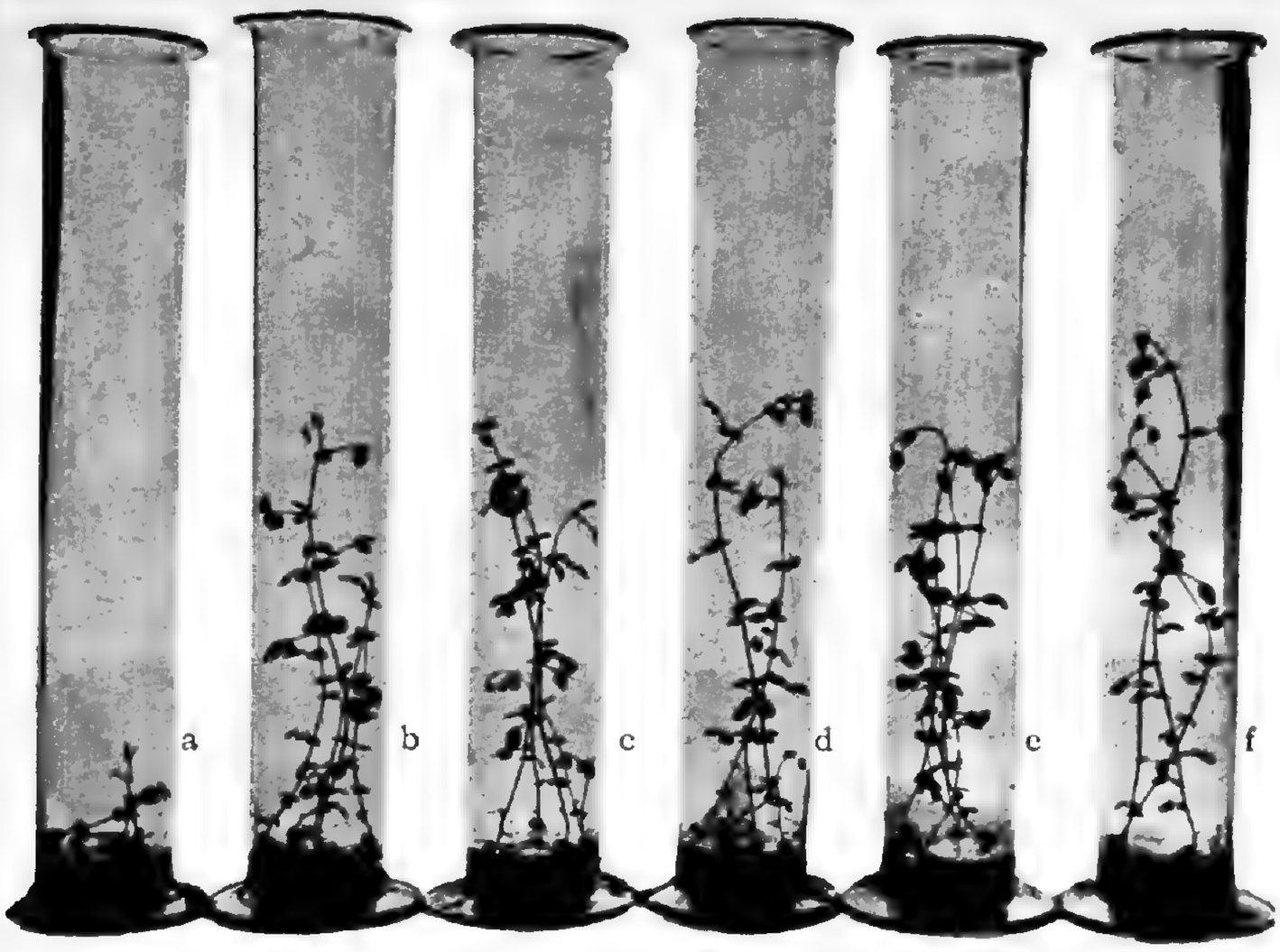

Fig. 1

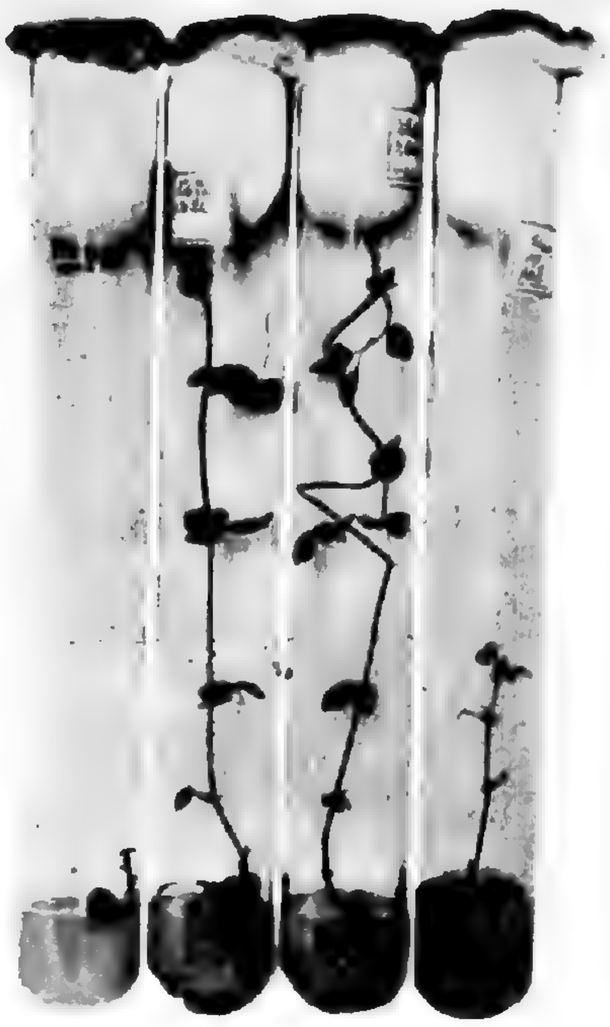

Fig. 2

Fig. 3

Fig. 4

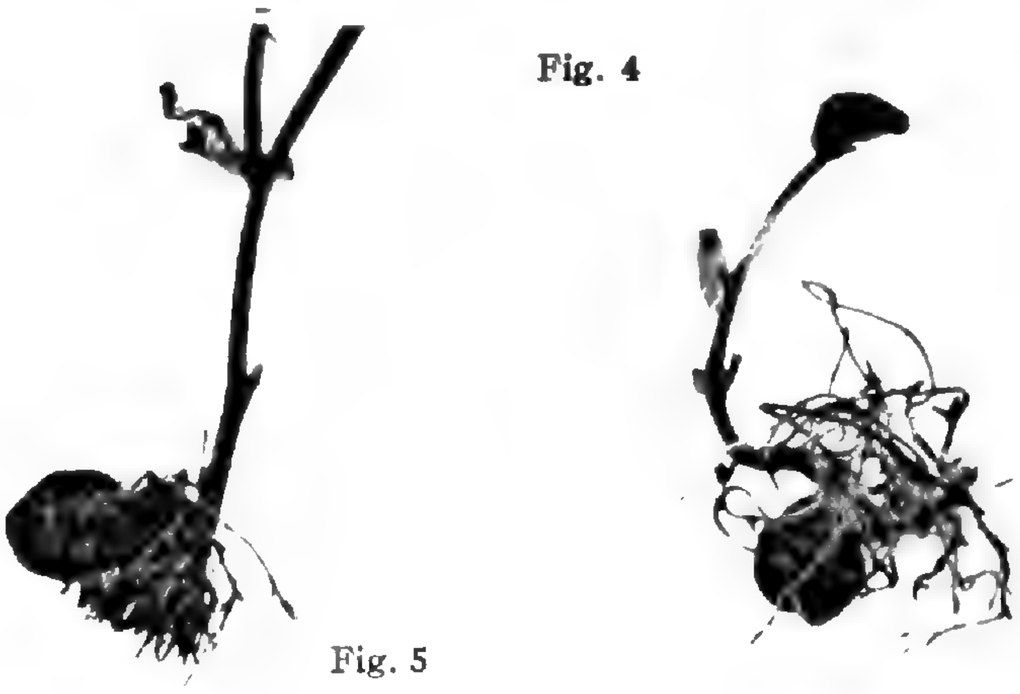

Fig. 5

KNUDSON—TOXICITY OF GALACTOSE

COCKAYNE, BOSTON

COMPARATIVE STUDIES IN THE POLYPORACEAE

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The subclass *Basidiomycetes* of the class *Fungi* contains a natural group of plants sharply separated from related groups in that the hymenium (basidia, paraphyses, etc.) forms the lining of hollow tubes on the ventral surface of the fruit body. This group of plants constitutes the tribe *Polyporeae.* It is divided into two families, the *Boletaceae* and the *Polyporaceae.* The *Boletaceae* are separated from the *Polyporaceae* in that they are fleshy and soon decay and the tubes are easily separated from the pileus, while the *Polyporaceae* vary in texture from coriaceous to hard and woody, and the tubes are inseparable from the pileus. These characters are susceptible of some variation, as there are a very few fleshy species in the latter family, and in two or three cases the hymenium is waxy and the tubes separable. In this article we are concerned only with the *Polyporaceae.*

Historical

Accurate knowledge of the classification of the *Polyporeae* dates back only to the last few years of the eighteenth or the beginning of the nineteenth century. The first attempt worthy of consideration was that of Persoon in 1801, although we still have occasion to refer to articles by earlier writers, especially Bulliard (Herbier de la France, 1780–1793), Schaeffer (Fung. Bav. 1780), and Sowerby (Eng. Fung. 1797–1809). These three, while contributing considerable in the way of illustrations of the species known at that time, knew very little about the correct classification of the species they illustrated. The binomial method of naming species had come into general use following its introduction by Linnaeus (Species Plantarum) in 1753, and many new species were described in the succeeding years, but the descriptions were inadequate and

the type specimens not preserved, so that it is impossible to tell to what plants the descriptions refer.

By the beginning of the nineteenth century those interested in this line of study had begun to feel the need of permanent herbaria containing specimens of all the species described. The appreciation of this need augmented the demand for a more systematic and a more natural arrangement of the genera and species of fungi.

It thus came about that while Linnaeus in 1753 had listed but one genus, *Boletus,* and 12 species of pore fungi (*Boletaceae* and *Polyporaceae*), the number of genera had increased to 3 and the number of species to 93 when Persoon published his 'Synopsis Fungorum,' in 1801. This was followed by the work of Albertini and Schweinitz (Conspectus Fungorum) in 1805, which was modeled after the work of Persoon and contributes nothing to the systematic arrangement of the *Polyporeae.* It must not be supposed, however, that there was any extraordinary change from the incomplete descriptions of the earlier writers to a more or less perfect standard of description that should include all the facts necessary for the identification of the species. The descriptions in Persoon's 'Synopsis' were still far from what could be desired, and it is only where these are supplemented by herbarium specimens or by accurate illustrations or by both that the species can be identified beyond all doubt. But the fact remains that the beginning of the nineteenth century witnessed a growing inclination on the part of mycological systematists toward a form of record for the species that would be more concrete in its conception and thus give an added impetus to the study of the fungi.

Among the vast array of mycologists produced in the nineteenth century by far the most prominent was Elias Fries. His first work of importance was the 'Systema Mycologicum,' published in 1821–1832, in which the known fungi were marshalled in order. To the genera of the *Polyporeae* listed by Persoon he added the genus *Polyporus* (first proposed by Micheli in the eighteenth century) and thus made the first attempt to separate the *Boletaceae* from the *Polyporaceae.*

The genera treated by him contained 164 species in all, of which probably two-thirds were in the single genus *Polyporus*. This genus was divided into 3 sections, *Favolus, Microporus,* and *Polystictus,* the first named being later raised to generic rank. The section *Microporus* contained by far the largest number of species. It was divided into 5 subgenera: *Mesopus, Pleuropus, Merisma, Apus,* and *Resupinatus*. This arrangement was continued in his 'Epicrisis Systema Mycologicum,' published in 1836–38. In the meanwhile the genera *Trametes, Cyclomyces, Hexagona, Favolus, Laschia,* and *Porothelium* had been carved from the old genus *Polyporus,* and the number of species described had increased to 361 (entirely exclusive of the genus *Boletus*). Of these, 280 were included in the genus *Polyporus*. The same disposition of the pore fungi was followed by Fries in his last publication, 'Hymenomycetes Europaei,' in 1874, and, indeed, that system has either been followed in its entirety since or has served as a foundation for all other systems of classification that have been proposed from time to time by others.

Correlated with the increase in the number of described species there is manifest a tendency on the part of some later writers toward a change in the conception of what should constitute a genus. There has been a tendency away from the old idea of large genera containing a heterogeneous collection of species, and toward the breaking up of genera into smaller units consisting of closely related individuals. This tendency finds its best expression in the work of Karsten, Quelet, and Murrill, each of whom has published papers dealing with the classification of the *Polyporaceae*.

IMPORTANT MICROSCOPIC CHARACTERS USED BY EARLIER WORKERS

Having glanced at the beginnings of the various classifications that have been proposed, we may now turn our attention to an analysis of the characters used in separating genera and species. For the most part the generic characters were macroscopic ones, such as presence or absence of a stipe, consistency of the sporophore, nature of the hymenium, etc.,—characters that arrested the attention of the collector without

recourse to the microscope, for the microscope was unknown when the foundations of this study were laid. In the separation of species other macroscopic characters of minor importance were used. Color, pubescence, habitat, form, size, etc., were characters that were largely drawn upon in fixing the limits of species.

It was unfortunate, however, that though the characters named are the most conspicuous ones, yet they are more subject to modification and variation than are certain internal characters that require the use of the microscope for their detection. Perhaps the desideratum in systematic botany would be a classification in which genera are well defined and sharply separated from each other by gross morphological characters, and in which the microscope would be necessary only in determining specific characters. Perhaps this demand is more nearly filled in the family *Agaricaceae* than in any other group of the fungi. There the genera are divided into sections on the color of the spores, and the genera in these sections are more or less well differentiated on gross morphological characters.

In those groups of the fungi that have been most carefully studied, e. g., the *Myxomycetes,* considerable attention has been paid to the minute anatomical structure of the plant. Spore markings that are scarcely visible, except with an oil-immersion lens, have been used as points of separation in closely related forms, and in certain of the *Discomycetes* the spore markings and the nature of the paraphyses have been largely drawn upon to furnish specific characters. Durand[1] has gone somewhat farther, and in his studies in the fleshy *Pezizineae* has taken into account the structure of the apothecium in fixing the limits of the families. Burt[2] has recently set new limits to some of the genera of the *Thelephoraceae,* in keeping with their inner anatomical structure. In the *Polyporaceae,* Miss Ames[3] has recently attempted to outline a scheme of classification of the genera based largely on the structure of the sporophores, but only a few forms

[1] Bul. Tor. Bot. Club **27**: 463–495. 1900.
[2] Ann. Mo. Bot. Gard. **1**: 195–196. 1914.
[3] Ann. Myc. **11**: 211–253. 1913.

were investigated and the results not as satisfactory as could be desired.

It is a significant fact, however, that no attempt has been made to classify the *Polyporaceae* on the basis of spore or other hymenial characters, although it is recognized that, outside of the algae, the organs concerned in reproduction are usually subject to less variation than are external morphological characters. That no such attempt has been made is due to two causes: first, the dislike on the part of students of the careful and painstaking observations that must often be made to determine those characters; and second, to the widespread belief that the pore fungi are spore-bearing only for a short interval of time during the year, and that they must be examined at the right moment or the spores will have disappeared. When it has been shown that the second objection is invalid and that hymenial characters are usually not hard to make out, the first objection will largely disappear.

In the course of the last year the writer has spent a considerable portion of his time in searching for these characters, not only in the *Polyporaceae* but in other related families as well. The methods employed are given on a following page, and suffice it to say here that probably 75 per cent of the collections examined contained spores, and a large percentage afforded other microscopic characters that played a considerable part in distinguishing one species from another. The characters that may be obtained by the use of the microscope are here enumerated and some indication given as to their possible value.

Discussion of Microscopic Characters Now Available for Use as Generic and Specific Characters

The characters that may be obtained by the methods outlined on a following page are as follows: spore characters, presence or absence of cystidia, setae and other sterile organs in the hymenium, basidial characters, hyphal characters, and the presence or absence of sterile structures in the subhymenial tissue.

Spore characters.—Spore characters are probably worthy of a great deal more consideration than they have yet received in the greater part of the mycological work that has been done up to the present time. As previously stated, in the *Agaricaceae* the primary divisions of the family are made on the basis of spore colors. This distinction was made as early as 1821 by Fries in his 'Systema Mycologicum.' The fact that this character was so early recognized was not because spores are more abundant or their colors more striking in the gill fungi, but because the period of spore production more closely coincides with the period of maximum development of the plants. Unfavorable conditions, i. e., drought, superabundance of moisture, cold, etc., result in the disorganization of the tissue in a fleshy fungus, and consequently the duration of the period of spore liberation is permanently shortened. In the coriaceous or woody forms these same conditions result only in a temporary suspension of the act of spore liberation and with the return of normal conditions the suspended function again becomes active. In this way the period during which spores are present in the hymenium of a pore fungus is greatly lengthened, and it is safe to assume that the number of mature spores present at a given time in the hymenium of one of the more durable pore fungi is less than the number of mature spores on an equal hymenial surface of a gill fungus. Contrary to the condition in the *Agaricaceae,* the introduction of spore colors as generic characteristics would mean an entire revision of all the genera, and it may well be doubted whether the advantage obtained from such a limitation of genera would compensate for the confusion that would be sure to arise. On this basis, however, the species could easily be grouped into sections under the genera, but even were that done the white-spored species so far outnumber those with colored spores that the adoption of the idea would delimit only a small group of species that perhaps could be better separated in other ways.

Very little exact evidence bearing on the variation in size in the spores of a given species is obtainable. The work of

Falck[1] showed that the mature spores of certain species of *Lenzites* were very constant in the length of their short axes, the variations being only a fraction of one micron, while the length of the long axis varied considerably, although in that case the variation rarely went beyond 3 μ in different spores from different fruit bodies. Cotton[2] investigated variations in the spores of *Stropharia semiglobata* and found that when the pileus was cut from the stem and a series of spore prints obtained from the former, the spores shed during the first hour measured 18×10 μ, while those shed during the twenty-third hour measured 15×9 μ, and those shed during the eighty-third hour measured only 12×7 μ. The diminution in size was ascribed to the artificial conditions, i. e., the pileus being severed from the stipe, under which the spores were produced. Experiments carried on with sporophores collected and placed in large test-tubes and supplied with water, showed that the spores shed the first day did not differ in size from those shed during the fifth or sixth day. The first experiment suggests the possibility that in plants growing in nature the size of the spores might be reduced if the fungus was growing on a substratum in which the required amount of food substances was not present. No comparative studies along this line have yet been reported and the question of the amount of variation in size of spores is still an open one. However, spore measurements have been very successfully used in separating species of fungi and no doubt the limit of their usefulness has not yet been reached in systematic mycology.

Inaccurate spore measurements may creep into the literature through a misdetermination of species quite as easily as species may be misdetermined because of inaccurate spore measurements. The former condition is especially liable to be pronounced in the literature of a fungous flora as little known as is that of this country, and where species are not determined on microscopic characters, but these same characters are entered in the literature when the species is re-

[1] Moeller's Hausschwamm-forschungen, Heft 3, pp. 79–96. 1909.
[2] Trans. Brit. Myc. Soc. **4**: 298–300. 1914.

corded. This latter procedure is entirely commendable, but it has been so much abused that the spore characters carried in the literature are far from being reliable in a large number of cases. However, allowances must be made for some variation in measurement by different individuals as no two persons will report exactly the same measurements for one species.

The shape of the spores is probably subject to somewhat less variation with age than is the size. Spores begin to take their characteristic shape while they are yet comparatively immature and from seeing such a spore one can judge of its mature form more accurately than of its mature size. Often the spores of two or more species are so similar in shape that it is perhaps best not to try to distinguish between them, although the distinction may be perfectly apparent to one who has before him the spores of all the species in question. The terms used to describe spore forms are not as rigidly defined as we could wish, and it does not add to the clearness of distinction between two species to describe the spores of one as "elongate-ellipsoid" and of the other as "narrowly fusoid" and expect the users of the manual to distinguish the species on that basis. There are many cases, however, where the form of the spores may be used to good advantage.

Spore markings are so universally absent in the *Polyporaceae* that the subject requires very little comment here. There are probably not more than a dozen species that are characterized in this way and they are so widely separated that the character is given an added value. In some groups of the fungi, especially among the *Ascomycetes*, not only the presence or absence of markings on the spore wall but also the nature of these markings is taken into account.

Cystidia.—Cystidia may be defined as more or less conspicuous sterile organs found either in the hymenium or in the subhymenial tissue of various basidiomycetous fungi. They are usually unicellular and they may be smooth or they may have a more or less incrusted surface, the incrusting substance probably always being calcium oxalate. The name "setae" has been given to these bodies when they are colored

(usually brown) and sharp-pointed, and that distinction is maintained in this paper, although there may be some doubt as to the advantage that accrues from its use. The presence or absence of setae has been made a generic character in some groups of the *Basidiomycetes*, and even in the *Polyporaceae* the genus *Mucronoporus* was founded by Ellis and Everhart on the presence of the setae in the hymenium. The genus probably has not received the acceptance that it has deserved at the hands of mycologists. It is difficult to say at times whether a given structure should be designated as a cystidium or not, but the writer is of the opinion that the term should be used in its broadest sense, except that it should not be applied to those structures usually referred to as paraphyses. These latter can usually be distinguished by the frequency of their occurrence as they usually alternate with the basidia, while cystidia or setae are scattered irregularly through the hymenium. In by far the largest number of cases the cystidia are very conspicuous on account of their size, coloration, incrustation, or other characters. In a few cases the presence or absence of setae is a variable character, in some specimens being abundant and in others very scarce. In such cases the writer has found it advisable to make longitudinal sections of the tubes, as the setae are sometimes more abundant in one part of the tubes than in another. A cross-section of the tubes of *Fomes igniarius* will sometimes fail to show a single seta, but in only one specimen has the writer failed to locate them in longitudinal sections from the hymenium of the same plant. They are also almost entirely lacking in some specimens of *Polyporus dryophilus*.

Basidia.—It is very seldom that the basidia offer characters that can be used in separating species. They are almost universally 4-spored in the *Polyporaceae* and in those few species where 2- and 3-spored basidia do occur there are always a goodly number of 4-spored ones present also. In a very few cases the basidia are conspicuous on account of their large size. This is true of *Trametes Peckii* where they are 8–10 μ broad, while usually they vary from 3 to 6 μ broad.

Hyphal characters.—The characters of the hyphae that make up the subhymenial tissue and the tissue of the trama of the pileus have never been used in the classification of the *Polyporaceae.* While the size of the hyphae may depend to a considerable degree on the food supply of the plant, yet in examining a large number of species the writer has found that some are characterized by hyphae two to three times as large as in most species. These cases have been thoroughly investigated as far as herbarium material would permit and as all specimens have showed the character about equally well, it has been taken as a means of identifying the species in which it has occurred. The writer knows of no factor or combination of factors that would be operative on a large number of individuals from widely separated localities and in the case of but a limited number of species. If it be dependent on nutrition, then the species possessing this character are so constantly associated with that kind of nutrition that the character is as constant a one as can be obtained. The same is true of the unbranched hyphae of the context of *Polyporus albellus.*

Incrustation of the hyphae has never been observed in the pileate *Polyporaceae,* though it is a well-marked character in the species of certain groups of resupinate fungi.

METHODS EMPLOYED

A few words may not be amiss here concerning the methods employed by the writer in obtaining these microscopic characters. In general the method is that already described in a previous number of this journal.[1]

Obtaining spore prints.—In the case of fresh specimens just brought into the laboratory from the field, spore prints are very easily obtained by placing the specimens on a glass slide in such a manner that the tubes are in a perpendicular position so that the spores do not lodge on the sides of the tubes when they are liberated from the basidia. The slide with the fungus in position should be either wrapped in waxed paper or left over night or for several hours in the collecting

[1] Burt, E. A. *loc. cit.*

basket or other receptacle in which a fairly high humidity will be maintained, so that the liberation of the spores will not be prematurely stopped by the drying-out of the tissues of the fungus. If the specimens are dry when brought into the laboratory they may be moistened thoroughly with water and then treated as described above. One unaccustomed to this procedure will be surprised to find how large a percentage of the collections so treated will produce a good spore print. Specimens collected on the warm days that frequently come in January and February have often been treated in the above manner with gratifying and surprising results. When desiccation takes place by exposure to the air the vitality of many species is not destroyed. Buller[1] was able to restore normal vitality to such plants by placing wet cotton-wool on their upper surfaces. He was even able to revive the fruit bodies of *Daedalea unicolor* after they had been exposed to ordinary air at room temperatures for eight years and three months, and of *Schizophyllum commune* after an exposure of six years and three months. In most species, e. g., *Polyporus versicolor, P. hirsutus,* and *Lenzites betulina* the vitality was retained for a period of but two to three years.

Sectional preparations.—In case one is working with material that has been in the herbarium for several years the above method will not answer. Neither does it furnish any evidence as to the other microscopic characters of the plants. One must then resort to sectional preparations. These are cut free-hand with a very sharp sectioning razor. Free-hand sections are quickly made and the results from them are usually better than from microtome sections. It is impossible for the spores to retain their position on the basidia when subjected to the different processes involved in preparing material for microtome sectioning. The first requisite in successful free-hand sectioning is material in good condition; the second is a very sharp razor (preferably flooded with alcohol); the third is some little skill and experience. The hymenium of the specimen is first moistened with alcohol, then with water,

[1] Researches on fungi, pp. 105–111. 1909; and in Trans. Brit. Myc. Soc. 4: 106–112. 1913.

and a piece about 2 mm. square on the hymenial surface is cut out with a scalpel. If material is abundant the process may be reversed and a larger piece than needed may be cut out with the scalpel, trimmed to the requisite size, immersed in 95 per cent alcohol for a few seconds and then transferred to water. In the writer's experience the latter method is the more preferable and has probably been the one most used. The material does not soften while in alcohol, but that reagent is used only to facilitate the absorption of water by the tissue. Any rigidity that may be imparted to the tissue by the alcohol is probably overcome when the material is transferred to water. In some cases when this transfer is made the tissue either becomes very soft or very friable so that no razor, however keen, will cut a clean section through it. It is here that the latter method obtains preference over the former, for after some experience one can judge of the probable effect the water will have and by shortening the period that the material remains in the water the tissue is in better condition for sectioning.

The most instructive preparations are often those containing both longitudinal and cross-sections of the tubes. Such sections are easily obtained in one mount by cutting out the piece of material somewhat longer in one direction than stated above—say about 2×4 mm. on the surface. Several longitudinal sections may be cut from this and the position of the remaining bit of tissue so changed that cross-sections may be obtained.

For sectioning, the tissue is placed in the proper position in a piece of pith and as the sections are cut they may either be transferred directly to the slide by means of a camel's-hair brush dipped in alcohol, or they may be allowed to accumulate in the alcohol on the razor and then flooded off into a watch-glass containing alcohol. By the last method one can pick out with more accuracy the thinner sections by observing them under the lens of a low-power dissecting microscope. The writer has found it to be sufficient in most cases to transfer the sections directly to the slide, disregarding the thicker sections that are cut, or brushing them off the edge of the

razor with an outward stroke of the finger. The sections are placed in a drop of 7 per cent KOH solution on the slide. This immediately expands the hyphae of the tissue to their normal size. The KOH solution is then drained off and a drop of stain added.

Staining and mounting.—I have tested a considerable number of the more common stains and so far I have failed to find one that gives universally good results if the sections are to be made into permanent mounts. For temporary mounts there is nothing superior to a 1 per cent water solution of eosin, but when sections so stained are mounted in glycerin the color soon completely disappears. The same strength solution of alcohol eosin (in 95 per cent alcohol) often gave a good permanent stain but quite as often it, too, faded out in the course of several weeks, and when used it gives a precipitate that must be washed off with water before the cover glass is applied. Why this stain should remain permanent in some cases and not in others is a question that has not been answered. It may be due to the KOH that remains on the slide and in the sections, but flooding the sections with water after draining off the KOH solution did not seem to have any beneficial effect. Different strengths of alcohol were used in preparing the stain, but with alcohols weaker than 95 per cent the stain disappeared even more quickly and the precipitation obtained was so great that such stains were of no value. From the facts observed it seems more reasonable to suppose that the difference may be in the tissue of the fungus rather than in the stain or the glycerin. A solution containing equal parts of a 1 per cent water solution and a 1 per cent alcoholic solution of eosin gave no better results.

Magdala red, Congo red, neutral red, acid fuchsin, methylen blue, and saffranin T were used, and of these, only the last one gave a permanent stain and it has been used in a large part of the work. It is a rapid stain, though probably not quite so rapid as alcoholic eosin, and it is well to leave the stain on the sections for about one minute. A 1 per cent alcoholic solution was used, the stain being dissolved in 95 per cent alcohol. When a drop of this stain is added and drained

off, the sections must not be allowed to become dry or an orange precipitate is obtained that necessitates the addition of alcohol to dissolve it. This also dissolves the stain from the tissues and the sections must be restained. This precipitate is not formed if a little water is added to the stain after it is made up. This stain imparts a uniform dull red color to the tissue but the color brightens when glycerin is drawn under the cover glass. Since it is not a differential stain its use is not advised where only temporary mounts are desired. It gives best results with very thin sections or with sections in which the hyphae are loosely arranged.

After the cover glass is applied the sections are ready to be examined under the microscope, but if the saffranin T stain is used, it is better to place a drop of glycerin at one side of the cover glass, at the same time drawing off some of the surplus water from the opposite side by means of filter paper. Several slides of each species are retained and mounted in 66 per cent glycerin. After a week or more all traces of the glycerin are removed from near the outer edge of the cover glass by means of a soft cloth dipped in 95 per cent alcohol. The slides are then ringed with some suitable cement—gold-size being most often used—labeled, and filed away in order. It will usually facilitate subsequent examination of the slides if the spore characters for each species are written on a slip of gummed paper and glued to one end of the slide.

It is sometimes quite impossible to find spores in the sections treated in the manner outlined above, since they are often easily removed from the sterigmata and washed away before the cover glass is applied. To overcome this difficulty the writer sometimes finds it advisable to distribute between two slides the sections obtained, one slide to be treated as outlined above, the other to be mounted for temporary observation only. This last one should be stained with a water solution of 1 per cent eosin, a drop of the solution being added to the drop of KOH containing the sections. Sometimes the staining is unnecessary, especially if one is dealing with species which have colored hyphae and colored spores. A

preparation made in this manner will often show spores when other methods of demonstrating them have failed.

Even with the most careful manipulation one will sometimes fail to find the spores, and, indeed, some species seem to be almost always sterile. In the case of *Fomes fomentarius* I cut sections of all the specimens available, and only when as a last resort, I sectioned a small and very unpromising specimen did I find the spores. I have been able to locate them in but one of the few specimens of *Polyporus graveolens* that were available for examination.

As stated above, the literature dealing with American *Polyporaceae* contains many inaccurate observations concerning spores. This is due mostly to a lack of care in making sure that a given body in the hymenium is really the spore of the fungus in question. The writer is of the opinion that spores should not be recorded for a collection unless they are obtained from a spore print or are seen attached to basidia. The spores found on basidia are usually somewhat immature, at least as regards size, but from their shape one can judge whether the spores found free-floating in the mount have any relation to the species under consideration. Where such free spores alone are present there is always the possibility that they belong to some other fungus and they should not be taken into consideration unless present in large numbers. One must also guard against the fact that the cut ends of hyphae may be in such a position as to appear globose in form and such may be mistaken for spores.

Examining the context hyphae.—In obtaining the characters of the hyphae of the context a bit of tissue is picked out with the forceps and mounted on a slide in a drop of KOH solution. In the case of some of the species of the genus *Fomes* where the context is hard and woody, it is usually better to boil a bit of the context in a KOH solution for a few minutes. In this way the tissue is softened and when teased apart on the slide with needles, a cover glass added, and pressure applied, the hyphae will generally separate out so that their characters may be obtained. In all cases the

hyphal measurements given are for the hyphae in the context of the plant and not for those in the subhymenial tissue.

STATEMENT OF PROBLEM

The writer presents in this paper the results obtained by carefully investigating some of the more common species of pore fungi, using the methods outlined on the preceding pages. There are certain groups of species in the *Polyporaceae* that are very much in need of just such treatment, and it is to these groups that the writer has turned his attention. The groups consist of closely related species that have been separated heretofore largely on external characters and in a great many cases the results have only led to confusion. The problem, as the writer saw it, was one involving a contribution toward a more exact characterization of these species and their separation, wherever possible or feasible, on some constant internal microscopic character. Some species are well enough marked by external characters so that such distinctions should be used only as supplementary characters, while in other cases the characters obtained by this study should displace those hitherto used.

The results obtained were not as gratifying as was expected when the work was undertaken. Only a small beginning has been made, for it is a laborious task involving the cutting and examination of many sections for each species in order to be sure that the characters shown by the first sections are constant for all collections of the same species. The work should be carried on although several years would be required for its completion. Permanent mounts of the sections have been made for each species and these are available for future reference. Criticisms and suggestions, both of methods employed and results obtained, are invited and will be given careful consideration.

ACKNOWLEDGMENTS

Acknowledgments and thanks are due to Dr. E. A. Burt of the Missouri Botanical Garden for aid, criticism, and advice in the preparation of the paper and for free access to

his valuable herbarium; to Dr. B. M. Duggar for his interest in the work and for aid in various ways; to the Missouri Botanical Garden for the use of the herbarium material and library facilities; to Mr. C. G. Lloyd of Cincinnati, Ohio, for aid in determining some of the species.

POLYPORUS ABIETINUS DICKS. EX FRIES AND P. PARGAMENUS FRIES

P. abietinus was first described by Dickson,[1] in 1793, and appears to be almost cosmopolitan in its distribution. In the United States it is found wherever coniferous forests abound, from Canada to the Gulf of Mexico, and from the Atlantic to the Pacific Ocean. It is never found on the wood of deciduous trees, and as will be pointed out later, this fact affords almost the only constant character by means of which it can be separated from its near relative, *P. pargamenus*.

P. pargamenus was described by Fries,[2] in 1838, from plants collected on pine wood in Arctic America by the Franklin Expedition. The plant has not been reported from the western coast of the United States, but has been found in practically every state east of the Mississippi River, ranging west as far as Wisconsin, Kansas, Arkansas, and Colorado. It is also found in Europe. Most of the collections in this country under the name *P. laceratus* Berk., *P. xalapensis* Berk., or *P. ilicincola* Berk. and Curt., belong to this species. An examination of *P. pseudopargamenus*, as distributed by de-Thuemen,[3] shows it to be identical with *P. pargamenus*. The writer has not seen authentic specimens of the other species named above, but they are given as synonyms by Murrill.

By some writers the two species have been confused, due to the fact that the type specimens of *P. pargamenus* were reported as growing on the wood of coniferous trees, while in the United States the plant that has gone under the name *P. pargamenus* is confined entirely to the wood of deciduous trees. This has led some authors to regard the original *P.*

[1] Pl. Crypt. Brit. 3: p. 21. 1793.
[2] Epicr. Syst. Myc. p. 480. 1838.
[3] Myc. Univ. 1102.

pargamenus as probably a synonym for *P. abietinus*. In that event, the species on the wood of deciduous trees would have to be given another name. This point can be settled only by a study of the type specimens of *P. pargamenus*, if they are still preserved. Nearly all the exsiccati material has been distributed under the name *P. pargamenus*, and the plant is so common and the name so well established that it is the writer's opinion it should not be changed without recourse to the types.

The two species under discussion are very closely related and they are connected by intermediate forms to such an extent that it is difficult to refer some collections to their proper species. However, the usual form of the fructification is distinct enough. *P. abietinus* is usually much smaller, is frequently effused-reflexed with a narrow and often laterally continuous pileus, rarely more than 2 cm. in length, and the tubes sometimes break up into lamellae-like plates—a condition I have never found in *P. pargamenus*. That species often grows much larger than *P. abietinus*, sometimes attaining a length of 6–7 cm., and is often fan-shaped or cuneate in outline and attached by a narrow, attenuate, sometimes stem-like base, so that the form and size of the fruiting body will usually separate it from *P. abietinus*. The color, zonation, and pubescence of the pileus is similar in both species, though the pubescence is often inclined to be strigose in the latter plant and more velvety in the former. Both species often have a violaceous or lavender tint to the hymenium or on the margin of the pileus.

The microscopic appearance of the hymenium of the two species does not furnish additional characters for their separation. The spores are similar in size and shape, being cylindric or sometimes allantoid, hyaline, smooth, and measuring 5–7 $\times$ 1.5–2.5 μ (not globose, 4.5–5.5 μ as stated by Murrill). Murrill states that no cystidia are present in the hymenium of *P. abietinus* and to the writer's knowledge their presence has never been recorded. I have examined several collections of both *P. abietinus* and *P. pargamenus* and I find that the plants vary as regards this character. I am of the opinion that cystidia are probably always present, but at times are so rare

or so inconspicuous that close observation is necessary to detect them and I have often examined whole sections without being able to locate them. A similar section taken elsewhere in the hymenium may show an abundance of them. The accompanying illustrations (figs. 1 and 2) show the different forms they may assume, but perhaps the most common form is as shown in *a* of fig. 1. They are often scarcely larger in size than the basidia, but are different in shape, usually with the appearance of slender pegs tapering to a rather blunt point. Rarely they are somewhat fusiform in shape and reach a length of 20 μ and a thickness of 6 μ. These sizes are unusual, however. They are colorless or almost so, sometimes scarcely extending beyond the basidia, but sometimes projecting enough that one can easily pick them out with the low power of the microscope. They are usually unincrusted, but sometimes their tips are somewhat capitate with small crystals (see fig. 2). They are then much more conspicuous, and in some collections this appears to be the predominating condition.

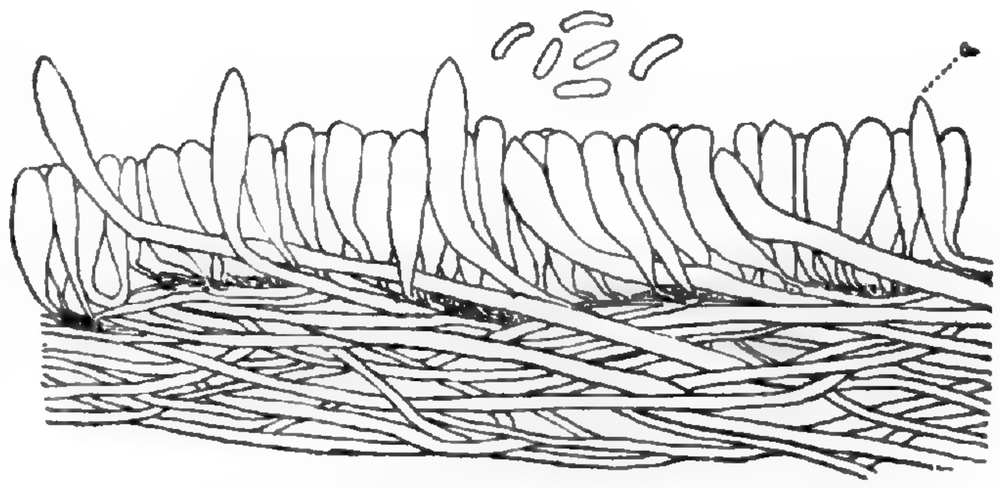


Fig. 1. Section of the hymenium of *P. abietinus* showing cystidia and spores.

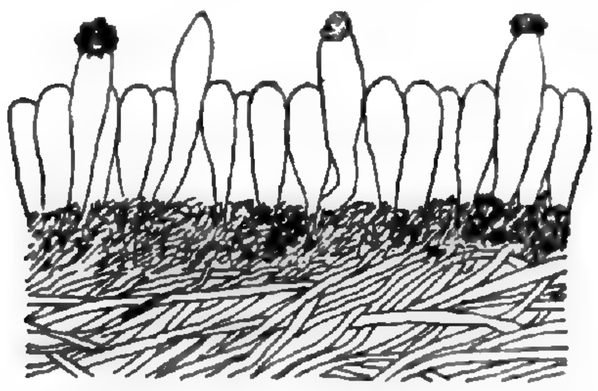


Fig. 2. Section of the hymenium of *P. abietinus* showing cystidia incrusted at the apex.

Before the writer had seen this more conspicuous type it was thought these sterile, inconspicuous structures might be basidia that had discharged their spores and had thus been rendered hyaline, as it is frequently found in other species that the mature spore-bearing basidia project somewhat beyond those that have not reached maturity. The shape of these bodies and the fact that they often assume a capitate apex, as do cystidia of many other species, make this view untenable. If more proof were needed it might be pointed out that these bodies are present in young specimens and in

the growing margins of mature specimens where it is evident that no mature basidia have yet been formed.

Neither can these structures be regarded as paraphyses that have become elongated and, therefore, more conspicuous. While there may be no ground for the belief that paraphyses can not assume such a form, yet there is no evidence to indicate that conspicuous sterile structures ever have arisen in such a manner. Moreover, the distribution of these structures under consideration makes impossible any such idea, as they are scattered promiscuously and do not alternate with the basidia.

These two species then are to be distinguished only by their habitat, and the size and shape of the pileus. In my own collecting experience the former character alone is enough to separate them, but when once the two plants are learned, the matter of form and size will usually be sufficient for the identification of the specimens, even if the habitat be unknown.

As stated above, the hymenium of *P. abietinus* may at times be lamellate. This statement is made only after a careful study of the facts in the case. They are as follows: There is a plant with apparently the same distribution as *P. abietinus,* in which the hymenium is entirely lamellate. No exactly intermediate conditions have ever been seen by the writer, though he has collected both forms in Colorado. In all other characters the two plants are precisely similar. The host is always the wood of coniferous trees; the pubescence and coloration of the pileus is the same; the spores and cystidia are similar; and the hymenium often has the violaceous tint characteristic of *P. abietinus.* *Irpex fuscoviolaceus* is in all probability only another form of the same plant, although I have never seen specimens of that species with the well-marked lamellate hymenium of this form. The illustration (pl. 23 fig. 1) is from specimens communicated by Prof. C. R. Orton, of State College, Pennsylvania. He writes that the rot produced by this fungus is almost identical with the one produced by *P. abietinus.* Patouillard[1] represents the cystidia of *Irpex*

[1] Hym. Eur. *pl. 3. f. 23.* 1887.

fuscoviolaceus as incrusted at the apex in the same manner as shown in the accompanying illustration of *P. abietinus.* I have also found this condition to be predominant in the lamellate form of our species.

The following comparative synopsis of the two species discussed in this section is appended here:

1. **Polyporus abietinus** Dicks. ex. Fries.

Plate 23, figs. 1, 2.

Pileus coriaceous, *sessile or effused-reflexed,* 0.5–5 × 0.5–5 × 0.1–0.2 cm., white, cinereous, or blackish with age, villous, zonate; context not more than 1 mm. thick; tubes not more than 3 mm. long, the mouths white, bay, or violaceous, averaging 2–3 to a mm. in poroid forms, *but sometimes entirely lamellate;* spores cylindric or allantoid, hyaline, 5–7 × 1.5–2.5 μ; cystidia present or inconspicuous, hyaline, rarely incrusted at the apex, 3–6 μ in diameter, projecting 5–15 μ; hyphae of context hyaline, 3–4 μ in diameter.

On wood of *coniferous* trees, especially of *Pinus.*

Illustrations: Dicks. Pl. Crypt. Brit. **3**: *pl. 9. f. 9.*—Fl. Dan. *pl. 1298, 2079. f. 2.*—Gill. Champ. Fr. *pl. 463.*—Swant. Brit. Fung. *pl. 33. f. 2–3.*

Specimens examined: Barth. Fung. Col. 3108.—Cooke, Brit. Fung. 512, 605.—Thuem. Myc. Univ. 6, 706.—Ell. N. Am. Fung. 8.—Ell. & Ev. Fung. Col. 303.—Krieg. Fung. Sax. 1205.—Rab.-Wint. Fung. Eur. 3235 (as *Irpex fuscoviolaceus*).—Rav. Fung. Am. 422; Fung. Car. I, 12.—Shear, N. Y. Fung. 307.—Mo. Bot. Gard. Herb. 4726, 4727, 4728 (Newfoundland), 3854, 4213 (New York), 4214 (Labrador), 4220 (Alabama), 4074 (Colorado).—Burt Herb. (collections from Vermont and Washington).—Overholts Herb. 2001 (Colorado), 2465 (Pennsylvania), 2472 (Maine).

2. **Polyporus pargamenus** Fries. Plate 23, fig. 9.

Pileus coriaceous, *sessile, often narrowed at the base,* 1–7 × 1–7 × 0.1–0.4 cm., whitish, cinereous, or brownish with age, villous or *velvety-pubescent,* zonate; context less than 1 mm. thick; tubes not more than 3 mm. long, the mouths white, bay, or violaceous, averaging 2–3 to a mm. in poroid

forms *but usually soon irpiciform;* spores cylindric or allantoid, hyaline, 5–6 × 1.5–2.5 μ; cystidia present or inconspicuous, hyaline, rarely incrusted at the apex, 4–5 μ in diameter, projecting 5–15 μ; hyphae of context hyaline, 4–5 μ in diameter.

On wood of *deciduous* trees.

Illustrations: Freeman, Pl. Dis. *f. 36.*—Hard, Mushrooms, *f. 345.*

Specimens examined[1]: Barth. Fung. Col. 2825, 2924 (as *Coriolus prolificans*).—Ell. N. Am. Fung. 312.—Ell. & Ev. Fung. Col. 302.—Rav. Fung. Am. 423, 108 (as *Irpex fusco-violaceus*).—Rav. Fung. Car. I, 13.—Rab.-Wint. Fung. Eur. 3331.—Shear, N. Y. Fung. 38.—Thuem. Myc. Univ. 1102 (as *P. pseudopargamenus*).—Mo. Bot. Gard. Herb. 4086 (Missouri), 4431 (Arkansas), 3855 (New York), 4443 (Indiana), 4439 (Kentucky), 4433 (Illinois), 4436 (Alabama), 4559 (Georgia), 4557 (Florida), 42875 (New Hampshire).—Burt Herb. (collections from Pennsylvania, Vermont, Kansas, and Massachusetts).—Overholts Herb. 476, 269, and others (Ohio), 1756 (Colorado).

Polyporus adustus Willd. ex Fries, P. fumosus Pers. ex Fries, P. fragrans Peck, and Related Species

Perhaps no species have been more confused in American mycology than these three, together with a few other closely related forms both of Europe and America. They all agree in the one character of having a hymenium that usually becomes more or less smoke-colored at maturity. In *P. adustus* and its closest relatives, *P. crispus* Fries and *P. Burtii* Peck, the hymenium is usually black or grayish black from the first, while in *P. fumosus* and *P. fragrans* it frequently becomes

[1] Ell. & Ev. Fung. Col. 804, distributed as *P. pargamenus*, is *P. hirsutus* (certainly not *P. pubescens* as stated by Lloyd, Letter No. 52, p. 20). Ell. & Ev. N. Am. Fung. 1934, distributed as *P. pargamenus*, is not this species. The appearance of the plant suggests a form of *Irpex tulipifera.* I have made a microscopic study of the hymenium of the specimen and I find it has the larger incrusted cystidia of that species and not the inconspicuous cystidia of *P. pargamenus.* Mycological literature contains several names for plants closely related to, if not identical with, *Irpex tulipifera* and until the limits of the species are better known the writer hesitates to refer the above specimen with certainty.

darker in mature plants but often remains white, sometimes assuming an ochraceous tint in herbarium specimens.

Of the above-named species, the first three have been referred to *P. adustus* by Murrill. *P. adustus* was described by Willdenow[1] in 1787. *P. crispus* was first described as a species by Persoon,[2] in 1799, and was later (1815) accepted by Fries[3] and so maintained by him in his 'Hymenomycetes Europaei.' *P. Burtii* was described from Vermont by Peck,[4] in 1897, and has not since been reported. *P. fumosus* was first described by Persoon,[5] in 1801, and *P. fragrans* by Peck,[6] in 1878. There are several other names for plants closely related to, if not identical with, these species but the writer has had no opportunity to study them. One of these, *P. subcinereus,* described by Berkeley, in 1839, is said to have been repudiated by its author and the plants referred to *P. adustus. P. Halesiae* Berk. & Curt.[7] is probably distinct, and *P. Lindheimeri* Berk. & Curt.[8] is not at all related to *P. adustus,* as stated by Murrill, but is a large-pored species with a brown context.

In working over the collections referred to *P. adustus* in the herbarium of the Missouri Botanical Garden, the herbarium of Dr. E. A. Burt, and the writer's herbarium, it became evident that we are here concerned with a species that has been used as a sort of dumping-ground for all plants with a black hymenium and a rather thin context, while plants of thicker context and lighter-colored hymenium have been referred to *P. fragrans* or to *P. fumosus,* according to whether a pleasant odor was or was not noticed in the plants. Such procedure has resulted in the bringing together of a heterogeneous mass of material under the name *P. adustus.* This material was very readily separated into three fairly distinct sections besides the collections that properly belonged under

[1] Fl. Berol. p. 392. 1787.
[2] Persoon, C. H. Obs. Myc. **2**: p. 8. 1799.
[3] Fries, E. Obs. Myc. **1**: p. 127. 1815.
[4] Bul. Tor. Bot. Club **24**: p. 146. 1897.
[5] Syn. Fung. p. 530. 1801.
[6] Rept. N. Y. State Mus. **30**: p. 45. 1878.
[7] Grev. **1**: p. 52. 1872.
[8] *Ibid.* p. 50. 1872.

P. fumosus. After considerable study the writer has decided that to *P. adustus* should be referred those collections with a thin, finely tomentose pileus, a thin, even margin, and minute black pores. The species does not grow densely imbricate as in *P. crispus* (see pl. 23 fig. 7) and does not have the crisped margin of that species. The illustration of *P. adustus* given by Patouillard[1] represents our plant very well. From *P. Burtii* it is to be distinguished by the smaller and more equal pores, the thinner, sterile margin of the pileus, and the firmer context. It is much more abundant than the other three species and frequently grows semi-resupinate.

According to Fries, *P. crispus* differs from *P. adustus* in having a thin, crisped, margin and large unequal pores. One lot of segregates from my *P. adustus* material possesses just those distinguishing characters, and I have, therefore, revived the Friesian name and applied it to my plants. They are certainly distinct from the specimens referred to *P. adustus* though connected by intergrading forms to some extent. The illustrations (pl. 23 figs. 7 and 8) show typical specimens of the two species.

I have seen no specimens other than the types that could be referred to *P. Burtii.* The type specimens differ from the above conception of *P. adustus* in having a somewhat thicker context, a thicker margin that is fertile below, and larger and more unequal pores. The hymenium is black, as in that species, and the surface of the pileus is finely tomentose. The flesh of the pileus is also very soft and almost floccose in texture. It has been held by some that the mouths of the tubes in *P. adustus* become larger and more irregular in mature plants, and if such a character stood alone in the differentiation of these forms it probably should not be considered a specific character. But it is the writer's opinion that in *P. adustus* they do not become much larger in old plants, and since *P. Burtii* differs also from that species in the other characters mentioned above, we must consider it a valid species, at least until other collections throw more light on the subject. From *P. crispus* it may be separated by the fact that the

[1] Tab. Anal. Fung. *f. 142.*

margin is not crisped, sterile, and thin, that the pubescence of the pileus is not nearly so prominent, and that the context is soft and floccose. The type specimens are not densely imbricate as in *P. crispus* but more nearly approach the condition found in *P. adustus*.

The microscopic characters of these three species are identical and do not afford additional means of separating them. The tramal tissue of the pores is decidedly brown in color, the hyphae are small, and a large percentage of them are cut transversely in a cross-section of the hymenium. The spores in all three species are oblong or oblong-ellipsoid, and measure 3.5–4.5 × 1.5–2.5 μ. There are no cystidia or other sterile bodies in the hymenium.

In endeavoring to find characters on which to separate the three above-named species (and especially *P. adustus*) from specimens heretofore referred to *P. fumosus* and *P. fragrans*, recourse was had to microscopic sections of the hymenium. It was at once apparent that when longitudinal sections were prepared, according to directions given on page 678 of this paper, the tramal tissue of the tubes of *P. adustus, P. crispus*, and *P. Burtii* were decidedly brown in color, while those of *P. fumosus* and *P. fragrans* were entirely hyaline, except for the eosin stain. This character has been tested out thoroughly and is believed to be a satisfactory and constant one on which to differentiate these two groups of species. By obscuring the labels on the slides containing the sections of the different species it was found possible to easily separate the sections of the species of the one group from those of the other group by this character, and then verify the separation by uncovering the labels. Since suitable sections can be readily prepared in a very few minutes, the task of deciding between the two groups is an easy one when they cannot be readily separated on the general appearance of the specimens. Some such method of procedure is especially desirable in separating *P. adustus* from *P. fumosus*, since thin or young specimens of the latter are easily confused with the former species. However, care must be taken not to confuse the dark color sometimes obtained in thick sections of *P. fumosus* with the truly

brown color of the hyphae in *P. adustus*. In the hyphae of the latter species the color is brown, whether the sections are thick or thin. This test will usually apply to cross-sections of the tubes as well as to longitudinal sections, except that when the hymenium of a growing specimen is bruised, dried, and then sectioned, the mouths of the tubes and the hyphae at the ends of the tubes often show a brownish discoloration that may be confusing. *P. crispus* and *P. Burtii* usually are easily distinguished without this test, but the results are even more marked in the case of those two species than in *P. adustus*.

When Peck first described *P. fragrans* he stated that it was closely related to *P. fumosus*, but differed in having unequal pores and an agreeable odor. In a later report he remarked that it should perhaps be considered a variety of that species. Microscopically the two plants are the same. There are no cystidia and the spores are oblong-ellipsoid, and measure 4.5–6 × 2–3 μ, thus being slightly larger than the spores of the three species discussed above. The spore characters given for both species in the 'North American Flora' are erroneous. From our present knowledge of the variability of odors in the fungi[1] we are not warranted in laying much stress on the fragrant odor ascribed to *P. fragrans*. Bresadola[2] discusses *P. fumosus* under the name *P. imberbis* and states that the plant at times has a subanise odor. I have never obtained such an odor from plants heretofore referred to that species, but frequently the plants do have an odor that I would not describe as pleasant. In the face of such evidence, it seems reasonable to conclude that the odor alone should not separate the two species in question. As to the size and regularity of the pores of the two species, I find collections of *P. fumosus* in which the younger specimens have minute pores and the older ones have large and irregular pores, and collections of *P. fragrans* with both large and small pores. I conclude,

[1] e. g., *Polyporus graveolens* Schw. I have collected this species several times and have had growing plants under observation for three seasons and at no time have I been able to obtain the slightest trace of an odor that would warrant the application of "sweet knot" to that species. Similar results have been reported by others. There is good authority, however, for stating that it is at times very fragrant.

[2] Fung. Trid. p. 29.

therefore, that we are here dealing with a character that varies with the age of the plants or even varies in different plants of approximately the same age. In other characters the two species are identical. Bearing in mind then the following points: (1) Peck's admission concerning his species, (2) the little reliance that is to be placed on odors in at least some of the fungi, (3) the evidence that *P. fumosus* is sometimes fragrant as it grows in Europe, and (4) the variability in the size of the pores in a single collection, we can only conclude that *P. fragrans* is at most only a form of *P. fumosus* and not worthy of a distinct name.

There are a few other names that need to be mentioned before dismissing this group of species. *P. salignus* Pers. ex Fries is generally held to be *P. fumosus,* and Fries' illustration[1] certainly agrees with the species as it grows in this country. *P. Holmiensis* Fries, as distributed by Romell,[2] is surely our plant and it is so regarded by Bresadola. *P. imberbis* Bull. ex Fries, as represented by Bresadola, is the same plant, but the name was not recognized by Fries in his 'Systema Mycologici' and so cannot be used for our plant.

The following key will aid in distinguishing the four species presented here:

Pileus rather thin; hymenium black or smoky black; tramal hyphae distinctly brown in section 1

Pileus thicker; hymenium pallid to somewhat smoky; tramal hyphae hyaline or nearly so in section ..... *4. P. fumosus*

1. Pileus finely tomentose; margin thin, even, sterile below; context firm when dry; pores minute; plants slightly, if at all, imbricate ..*1. P. adustus*

   Pileus adpressedly fibrillose on the margin, usually strigose toward the base; margin thin, crisped or wavy, sterile below; context firm when dry; pores larger and unequal; plants usually closely imbricate ..... *2. P. crispus*

   Pileus finely tomentose; margin acute but thicker than in the preceding species, even, fertile below; context soft and floccose; pores unequal; plants scarcely imbricate ..... *3. P. Burtii*

1. **Polyporus adustus** Willd. ex Fries. Plate 23, fig. 8.

Pilei *not much imbricate* though somewhat so at times, 1–6 × 3–8 × 0.1–0.6 cm., white to smoky white or pale tan, rarely with reddish blotches or zones, *finely tomentose to short villous-tomentose,* zonate or azonate; margin *thin, even,*

[1] Ic. Hym. **2:** *pl. 181.*

[2] Fung. Scand. 11.

often black in dried specimens, sterile below; context white or pallid, firm and corky when dry, 1–4 mm. thick, in large specimens separated from the hymenium by a narrow dark line; tubes less than 2 mm. long, the mouths *grayish black to black, scarcely visible to the naked eye, averaging about 6 to a mm.;* tramal tissue decidedly *brown in color under the microscope;* spores oblong or oblong-ellipsoid, rarely slightly curved, smooth, hyaline, 3.5–5 × 1.5–2.5 μ; cystidia none.

On dead wood of deciduous trees.

Illustrations: Pat. Tab. Anal. Fung. *f. 142.*—Rostk. in Sturm's Deutsch. Fl. **3**: fasc. 16. *pl. 38.*

Specimens examined: Cooke, Fung. Brit. 2.—Ell. N. Am. Fung. 6.—Ell. & Ev. Fung. Col. 206.—Krieg. Fung. Sax. 1319. —Rabenh. Herb. Myc. 412.—Rav. Fung. Am. 421.—Shear, N. Y. Fung. 32.—Mo. Bot. Gard. Herb. 4222 (Newfoundland), 4223 (New York), 3851 (Missouri).—Burt Herb. (collections from Vermont, Ohio, Massachusetts, and New York).—Overholts Herb. 284 (Ohio), 572 (Missouri), 2239 (New York), 1780 (Colorado), and others.

2. Polyporus crispus Pers. ex Fries. Plate 23, fig. 7.

Pilei *more or less densely imbricate and overlapping,* 2–7 × 1–5 × 0.1–0.4 cm., gray to avellaneous, sometimes cinnamon to clay-colored in herbarium specimens, *adpressedly fibrillose toward the margin, usually strigose toward the base,* zonate or azonate; *margin very thin, radiate-lineate, crisped or wavy,* often becoming black, sterile below; context white or pallid, often brownish in herbarium specimens, soft and fibrous to corky, 1–3 mm. thick, usually separated from the hymenium by a narrow dark line; tubes 1–3 mm. long, the mouths *grayish black to black, unequal, irregular, averaging 3–6 to a mm.;* tramal tissue decidedly brown in color under the microscope; spores oblong or oblong-ellipsoid, smooth, hyaline, 3.5–4.5 × 1.5–2.5 μ; cystidia none.

On dead wood of deciduous trees.

Illustrations: Fl. Dan. *pl. 1850.*

Specimens examined: Romell, Fung. Sax. 8 (as *P. adustus*).—Thuem. Myc. Univ. 604 (as *P. fumosus*).—Mo. Bot.

Gard. Herb. 42868, 42848 (Arkansas), 4180 (Missouri).—Overholts Herb. 386 (Indiana), 105 (Ohio).

3. Polyporus Burtii Peck. Plate 23, fig. 4.

Pilei not closely imbricate, 1–2.5 × 2–5 × 0.3–0.5 cm., gray or pinkish buff, *finely tomentose,* azonate; margin *acute but rather thick, deflexed, even, concolorous, fertile below;* context *soft and sub-floccose* in dried plants, 2–4 mm. thick; tubes 1–2 mm. long, *the mouths grayish black to smoky black,* unequal, irregular, *averaging 2–4 to a mm.;* tramal tissue decidedly brown in color under the microscope; spores oblong-ellipsoid, smooth, hyaline, 4–4.5 × 1.5–2 μ; cystidia none.

On stump of yellow birch. Known only from the type locality, Middlebury, Vermont.

Specimens examined: Burt Herb. (type collection).

4. Polyporus fumosus Pers. ex Fries. Plate 23, fig. 3.

Pilei simple or imbricate, 2–10 × 3–15 × *0.5–2 cm.,* white to ochraceous or smoky white, sometimes stained with reddish, *finely tomentose to glabrous, sometimes with a rather broad, marginal furrow;* context white or pallid, soft corky to woody when dry, *2.5–10 mm. thick,* usually zonate, always separated from the hymenium by a narrow dark line, *anise-scented or with a disagreeable odor;* tubes 1.5–4 mm. long, the mouths *white to grayish black, usually becoming black when bruised,* averaging 3–4 to a mm.; tramal tissue hyaline or nearly so under the microscope; spores oblong-ellipsoid, smooth, hyaline, 4.5–6 × 2–3 μ; cystidia none.

On dead wood of deciduous trees, especially elm.

Illustrations: Fries, Ic. Hym. *pl. 181* (as *P. salignus*).—Bres. Fung. Trid. *pl. 135* (as *P. imberbis*).—Massee, Brit. Fung. Fl. *f. 14–15.*—Rostk. in Sturm's Deutsch. Fl. **3**: fasc. 16. *pl. 42.*

Specimens examined: Ell. & Ev. N. Am. Fung. 2902.—Shear, N. Y. Fung. 31.—Thuem. Myc. Univ. 5.—Mo. Bot. Gard. Herb. 43648 (Missouri), 4277 (Kansas).—Overholts Herb. 455, 527 (Ohio), 436 (Canada), 370 (Indiana), and others.

THE WHITE SPECIES OF POLYPORUS — THOSE WATERY AND FLESHY-TOUGH WHEN FRESH AND WITH WHITE CONTEXT AND SPORES

This group of plants has probably been the source of more trouble and exasperation to those collecting them than any other group in the *Polyporaceae*. Collectors have sent them to various mycologists for determination, and quite often no two will agree on the name that should be applied to any one form.

The group of species with which we are here concerned has been divided into two genera by Murrill, namely, the genus *Tyromyces* and the genus *Spongipellis*. Since the characters that separate the latter from the former genus are not always well defined, it would seem better had they been united into one genus. The group includes those species found only during the summer and fall, growing on logs or on living trees, and further characterized by being white or whitish throughout, and having a more or less watery and soft fibrous context. Some of the species have characteristic odors that will usually aid in their identification. When dry the context of some of these is soft and friable, sometimes more solid, and sometimes differentiated into an upper soft portion and a lower firm portion. We cannot include here all of the species referred by Murrill to the two above-named genera, partly because there has been no opportunity to study all of them and partly because many of them are limited in their distribution and are only infrequently found by collectors. Those that are of common occurrence in the Ohio and the upper Mississippi River valleys have been studied and the results here presented. The series thus limited includes the following species: *P. albellus* Peck, *P. caesius* Schrad. ex Fries, *P. chioneus* Fries, *P. delectans* Peck, *P. fumidiceps* Atk., *P. galactinus* Berk., *P. lacteus* Fries, and *P. spumeus* Sow. ex Hornemann. These are not all closely related and most of them are not difficult to determine but they have been more or less confused in this country, and their distinguishing characters are here pointed out.

P. chioneus, P. albellus, and P. lacteus.—*P. chioneus* was described by Fries,[1] in 1815. In his 'Hymenomycetes Europaei,' published in 187[illegible] (p. 546), he described it somewhat more fully as follows: "Albus, pileo carnoso, molli, laevigato, azono, postice s[illegible]epe porrecto, margine inflexo; poris curtis, exiguis, rotundi[illegible], aequalibus, integerrimis. . . . . Ad truncos v. c. *Betulae*. . .[illegible]. . . unciam latus, odore acido." In 1878 Peck[2] described *P. al[illegible]ellus* from New York, also growing on birch. Peck eviden[illegible]ly was not acquainted with *P. chioneus,* but he regarded his species as probably more closely related to *P. parado[illegible]us* Fries and *P. betulinus* Bull. ex Fries. The only points o[illegible] difference in the descriptions of *P. albellus* and *P. chioneus* are: (a) in size, Peck's species being described as "two to f[illegible]our inches broad, one to one and a half thick," and (b) in pub[illegible]scence, the pileus being "smooth or sometimes slightly rough[illegible]ened by a slight strigose tomentum." Both descriptions [illegible]ention the soft context, white color, and "acid" odor. S[illegible]ccardo[3] has listed *P. albellus* as a synonym for *P. betulinus,* and while the general form and size of the two species is at times somewhat similar, it does not require close observatio[illegible]. to distinguish them. The same cannot be said of *P. albellu*[illegible] and *P. chioneus.* Murrill[4] has listed them as synonyms a[illegible]d the writer has expressed the same opinion in a recent pa[illegible]per.[5]

P. lacteus may well be br[illegible]ought into the discussion at this point. It was described in 1[illegible]321. The description and figure[6] call for a plant similar in [illegible]ize and habit to *P. chioneus* but differing from that species [illegible]nd from *P. albellus* in having a decidedly pubescent pileus a[illegible]d a lacerated and labyrinthiform hymenium. These characte[illegible]s should be sufficient to separate at once *P. lacteus* from the [illegible]other two species, and the writer can neither accept nor under[illegible]stand the determinations of those who would refer our commo[illegible] plant with a glabrous pileus and

[1] Obs. Myc. 1: p. 125. 1815.
[2] Rept. N. Y. State Mus. 30: p. 45. 1878.
[3] Syll. Fung. 6: p. 139. 1888.
[4] N. Am. Fl. 9: p. 35. 1908.
[5] Ann. Mo. Bot. Gard. 1: p. 97. 1914.
[6] Fries, E. Ic. Hym. 2: *pl. 182. f. 1.*

even hymenium to *P. lacteus*. Romell,[1] after a short description of *P. lacteus* as he understands it, says:

> "This species seems to be identical with one known in America as *Polyporus chioneus*. . . . . My specimens agree with the authentic specimens of *P. lacteus* at Kew. In Fries' herbarium neither *P. lacteus* nor *P. chioneus* is represented by authentic specimens as far as I know. There is, however, a collection referred to *P. chioneus* by Robert Fries, and this collection differs from my plant not only by the *glabrous surface of the pileus* but also by having the hyphae substantially *parallel and simple*. . . . . ." (Italics are the writer's.)

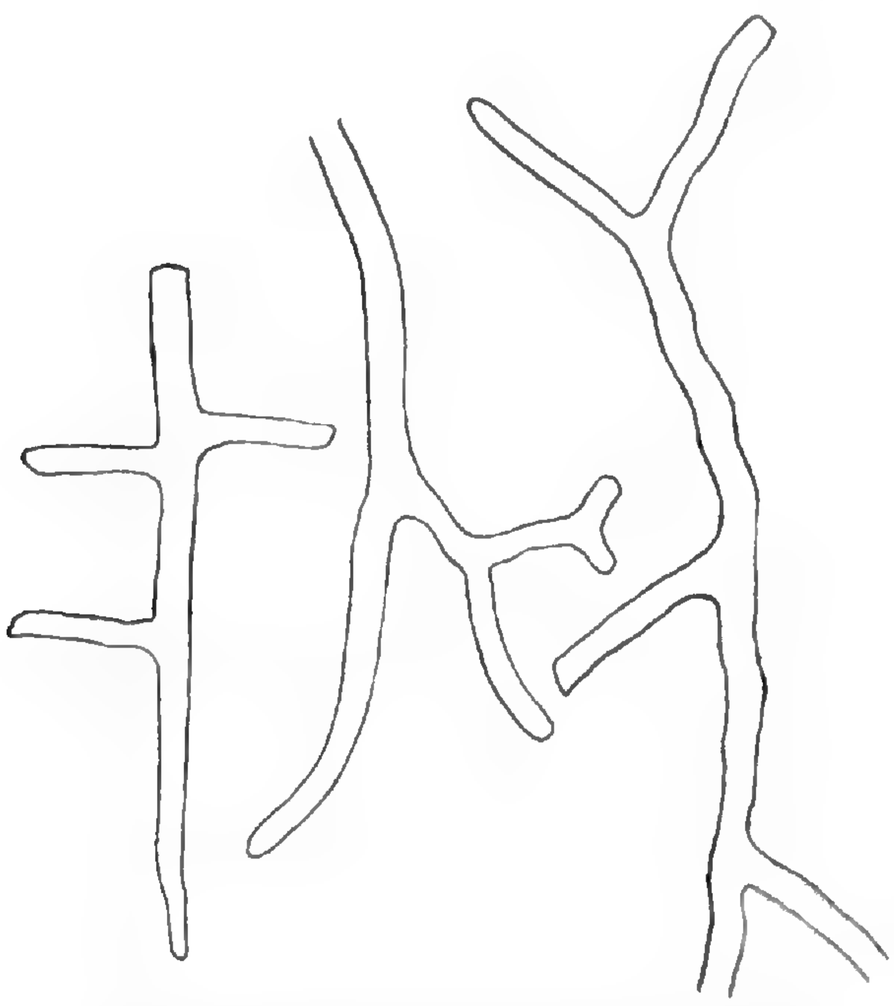


Fig. 3. Hyphae of *P. chioneus*.

It is unfortunate if, with the easy access to Fries' description, American mycologists of repute have sent specimens of a pubescent *Polyporus* to Europe under the name, *P. chioneus*. On the other hand, if the determination were that of an amateur it should not have been seriously considered by Mr. Romell. Whichever may have been the case, it is the writer's opinion that such determinations are the exceptional ones and not the rule, for the plant that is usually referred to *P. chioneus* (including *P. albellus*) is usually, if not always, entirely glabrous and has even tube mouths. In fact, it is the writer's opinion that *P. lacteus* and *P. chioneus* have been less confused in this country than in Europe. If there has been a tendency to confuse *P. lacteus* with anything it is with *P. galactinus*, as I have found several collections so misdetermined. The important point of the extract from Romell's paper is, however, that the collection to which reference is there made as having a glabrous pileus and simple hyphae in the context, in all probability represents the species that is interpreted in this paper as *P. albellus*.

Having fixed upon the distinguishing characters of *P.*

[1] Hym. Lapp. p. 15.

chioneus and accepting Fries' idea of *P. lacteus,* it becomes an easy matter to differentiate between *P. chioneus* and *P. albellus.* As stated above, and as will be seen in the accompanying illustration (fig. 4), the hyphae in the context of *P. albellus* are unbranched or at most very infrequently branched, while those of *P. chioneus* (fig. 3) are branched to a very great degree, and they vary considerably in size, some being narrow (5–6 μ) and others twice as thick. This is not the only distinguishing character, nor the one that was first hit upon by the writer, although it is probably the most reliable. The relative thinness of the pileus in proportion to its length is a distinguishing character of *P. chioneus.* In other words, the pileus is usually thin and spreading in *P. chioneus,* while in *P. albellus* it is thicker, convex or ungulate, and triangular in section. This is only a general statement of a character that varies considerably. An additional character is found in an examination of a cross-section of the hymenium, though the sections must be cut very thin to see it at its best. In sections of *P. albellus* the hyphae in the trama of the pores appear to run in all directions and give a peculiar, ever-changing appearance as they are viewed at changing foci. They are also all of one size. In *P. chioneus* the hyphae in the trama of the pores all run in one direction and practically all are cut transversely in a cross-section of the hymenium. The trama is seen to be made up of a background of a pseudocellular structure, with minute openings that indicate the cavities of the closely compacted hyphae. Interspersed over this background one sees cross-sections of hyphae two to three times larger, and standing out much more plainly than the sections of the compact hyphae in the background. It was at first thought these

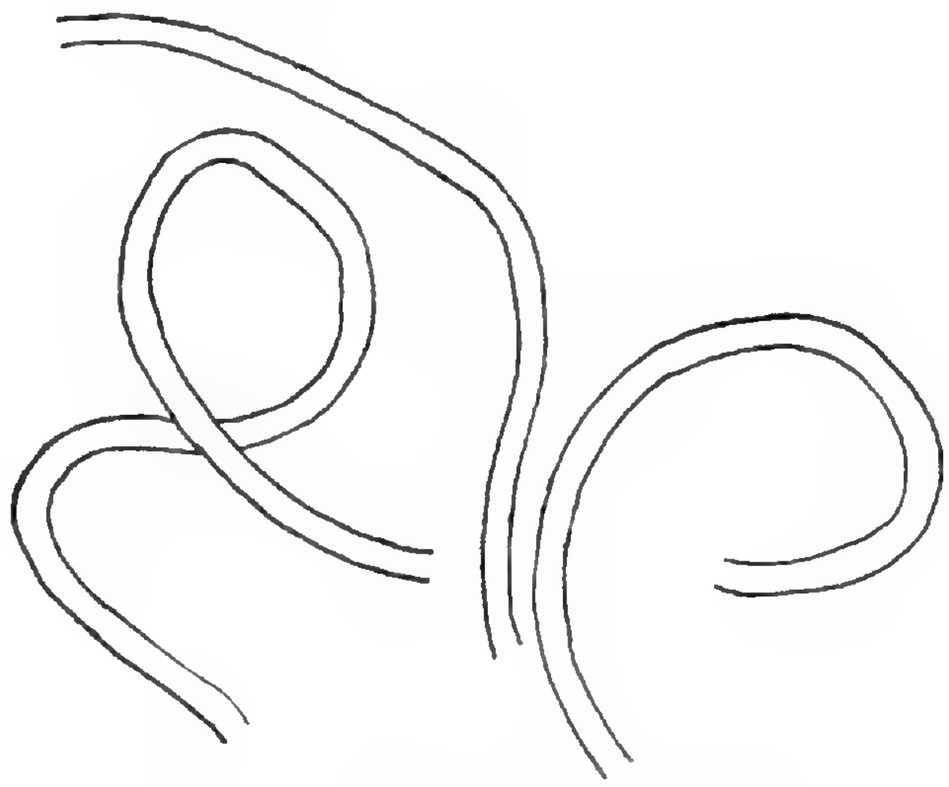


Fig. 4. Hyphae of *P. albellus.*

larger hyphae might belong to some other fungus living within the tissues of this species. This supposition is rendered improbable, however, by the fact that they are invariably present in all collections, and that while other fungi frequently attack all of these white species, their hyphae are invariably much smaller than those of the fungi attacked.

The evidence seems very clear, however, that these two species should be considered as distinct. When once differentiated they can usually be separated on the basis of their general habit, without recourse to the character of the branched or unbranched hyphae in the context, though that character can always be relied upon in establishing beyond a doubt the identity of the species. In other characters the two species are very similar. Both are glabrous or practically so; are covered with a thin grayish or yellowish pellicle that becomes more evident when the plants are dried; have a sweet acid odor when fresh, a soft and friable context when dry; and the spores are the same, being cylindric, often slightly curved, and measuring 3–4×0.7–1.5 μ. There are no cystidia.

There is considerable doubt in the writer's mind as to whether the true *P. lacteus* occurs in this country. There is a collection in the herbarium of the Missouri Botanical Garden and another in the writer's herbarium that should perhaps be referred to that species, but the hymenium has been disorganized by the growth upon it of another fungus, so that no spores are present. If future collections should show that the spores are similar to those of *P. chioneus,* the plants should in all probability be referred to *P. lacteus.* The pileus is somewhat strigose or fibrillose-pubescent, though the mouths of the tubes are not labyrinthiform. The pileus is too pubescent for either *P. chioneus* or *P. albellus* to which latter species the plants were once referred by Lloyd. It is possible that they represent *P. lacteus* as more recently defined by Lloyd.[1] I have seen no specimens so referred by him and his description of the plant as "a common white species" and again as "a frequent plant" throws some doubt on my opinion, for the plant is a rare one.

[1] Letter No. 49, p. 14.

According to the writer's notes on specimens of *P. lacteus* in the herbarium of the New York Botanical Garden, that species, as it appeared in the 'North American Flora,' is *P. albellus* as here defined, at least in part. Neither can the writer accept Romell's interpretation of *P. lacteus,* but if such a plant exists it must agree in the main with Fries' description and figure, and neither of the above interpretations do so agree. I do not know what Bresadola's latest ideas on the subject are, but at one time he regarded *P. lacteus* and *P. chioneus* as synonyms—a position just as untenable as that taken by Murrill and Romell.

According to the above interpretation of *P. chioneus* and *P. albellus,* the presentation of the two species in a recent paper[1] by the writer should be modified, and those collections that show simple hyphae in the context should be referred to *P. albellus* and those with branched hyphae should be referred to *P. chioneus.*

P. delectans and P. spumeus.—The first one of these species was described by Peck,[2] in 1884, from specimens collected in Ohio by Morgan. It is a large or medium-sized plant and was described as having a fleshy-fibrous context, a glabrous or floccose-tomentose pileus, and long tubes with large unequal mouths. By this last character and by the large size of the plant and the ellipsoid or subglobose spores it is easily distinguished from the species discussed above. In size of pores and length of tubes it is intermediate between the above species and *P. obtusus* Berk. A much more closely related species, however, is *P. spumeus.* The original notes of Sowerby on this species are very meager. The plant is described as "oozes from decaying elms in a very soft frothy mass, hardening in a day or two; and if it dries favorably, the pileus becomes hispid. The pores are small and nearly round; the tubes not long." In Sowerby's text[3] this species is followed by *P. betulinus.* Plates 211 and 212 are cited as representing the two species, respectively. Plate 211 shows a

[1] *loc. cit.* p. 97.
[2] Bul. Tor. Bot. Club 11: p. 26. 1884.
[3] Colored Figs. Eng. Fung. *pl. 211–212.* 1797–1803.

plant with a substipitate base, an incurved margin, and short tubes. One figure shows the plant from a front-underneath view, the other shows half of the plant with the cut surface outward and the hymenium upward. Plate 212 shows practically the same thing but with a little more detail, and it is a fair representation of *P. betulinus*. All later descriptions of *P. spumeus* are either based entirely on pl. 211, or else on plants that have no resemblance to the one that has since been referred to *P. spumeus*. Fries' description[1] says: "basi stipitiformi, margine incurvato."

This gives us but two alternatives from which to choose. Either Sowerby confused his illustrations of *P. spumeus* and *P. betulinus* and inserted two plates of the same species (*P. betulinus*), or else there existed at that time a plant closely related to *P. betulinus* but growing on elm and thought by Sowerby to be distinct. Since the mutual resemblance of Sowerby's two plates is so great, it is the writer's opinion that he had drawn two plates of *P. betulinus* and by mistake inserted both of them instead of one of that species and one of *P. spumeus*. This theory is borne out by the fact that he makes no mention of a stipe-like base nor an incurved margin to the plant. We may also conclude that Fries' description was drawn, in part at least, from pl. 211, for it is inconceivable that with access to Sowerby's figure he would have referred to that species a plant that departs so widely from the authentic illustration, unless he was also of the opinion that pl. 211 was a mistake.

This mistake (for so it seems we must regard it) has caused some little confusion in the literature. Fries' idea of *P. spumeus* was evidently gained, in part at least, from Sowerby's plate, for he refers as a synonym for *P. spumeus, Boletus suberosus* of Wahlenberg[2]. But Wahlenberg was aware of the existence of a *Boletus suberosus* of Linnaeus[3] and expressed the doubt that his species was the same as that one. *Boletus suberosus* of Linnaeus has always been regarded as

[1] Hym. Eur. p. 552. 1874.
[2] Fl. Upsal. p. 457. 1820.
[3] Sp. Plant. p. 1176. 1753.

a synonym for *P. betulinus.* In 1823 Hornemann[1] published a figure of *P. spumeus* entirely different from Sowerby's original figure, but in all probability a better representation of his original species. It was not, however, so accepted at the time. In the text accompanying the plates in 'Flora Danica,' Hornemann refers to Sowerby's original figure as a variety (var. *stipitatus*) of *P. spumeus.* This was evidently only a makeshift to dispose of a troublesome figure, and since the figure itself was evidently an error, Hornemann's disposition of it need have no weight. Subsequent writers did not concur in his opinion, however, and the confusion was only made worse, for now some regarded that there were two distinct plants passing under the name of *P. spumeus.* In Hooker's 'English Flora,'[2] in which the fungi were written up by Berkeley, both Hornemann's and Sowerby's illustrations are cited as representing *P. spumeus,* and Hornemann's figure is given priority in the order of citation. Again the plant is described as possessing an obsolete stipe and an incurved margin—characters either taken from Sowerby's illustration or copied from Fries. That Berkeley was in doubt as to the correctness of Sowerby's plate is evidenced by the statement: "According to Fries, the figure of Sowerby represents the species in an imperfect state. . . . . ." In 1874 Fries[3] accepted Sowerby's figure as representing *P. spumeus* and referred Hornemann's figure to *P. epileucus.* This reference was evidently followed by Saccardo. Berkeley[4] published an illustration of *P. spumeus* that corresponds well with Hornemann's figure and agrees with the plants since referred to that species. Thus there has arisen an interesting situation in which, according to the writer's interpretation, a well-known species is referred to an erroneous illustration that cannot possibly represent it, while the authentic illustration is referred to another species. Of course it is possible that Hornemann may have misinterpreted Sowerby's *P.*

[1] Fl. Dan. *pl. 1794.* 1823.
[2] Eng. Fl. 5[2]: p. 139. 1836.
[3] Hym. Eur. p. 552. 1874.
[4] Outl. Brit. Fung. *pl. 16. f. 4.* 1860.

spumeus, in which case the name should be written *P. spumeus* Hornemann, Fl. Dan. *pl. 1794.* 1823, since there is no doubt that Hornemann's figure represents *P. spumeus* as it is known in Europe to-day. But the writer prefers to accept Hornemann's plate as a correct interpretation of Sowerby's species (disregarding pl. 211) and write the name as *P. spumeus* Sow. ex Hornemann. If the writer's theory is correct, there never existed a plant, the name of which could be written as *P. spumeus* Sow. ex. Fries, Syst. Myc. **1**: 358. 1821,[1] since Fries never illustrated the plant, and his descriptions, several times repeated, were based, in part at least, on the erroneous pl. 211 of Sowerby.

In the American literature the plant was first described by the writer in a recent paper.[2] The relation of Sowerby's figure to the species was not then understood and the statement was there made that "the plants so referred do not agree with the figure given by Sowerby, nor with Fries' description." There are but few references to its occurrence in this country, although it is a fairly common species. Lloyd reports receiving it from several widely separated localities.

Whether others may agree with the writer or not, the evidence here presented should at least have the effect of doing away with the inconsistency of citing both Sowerby's illustration and that of Hornemann as representing the same species.

P. spumeus is not likely to be confused with any species except *P. delectans.* These two intergrade to some extent. The former species has a strigose-tomentose surface to the pileus while the latter is glabrous or only slightly tomentose. Heavy rains or a little handling of the plant may cause the pubescence on *P. spumeus* to become matted and appressed, but when specimens are found growing imbricated so that the lower pilei are protected by the ones above, the character is very marked. The tubes in both species are long and slender, but in *P. delectans* the mouths are larger and more sinuous, usually measuring 0.5–1 mm. in diameter, while those of *P. spumeus* are smaller, measuring about 3–4 to a mm., and col-

[1] cf. Ann. Mo. Bot. Gard. **1**: p. 99. 1914.
[2] *loc. cit.*

lapse when dry. This collapsing is due to the thinness of the dissepiments—a character easily made out in transverse sections of the hymenium. The illustration (pl. 24 fig. 14) shows the larger tubes of *P. delectans*. The spores of the two species are practically the same, varying from ellipsoid to ovoid or subglobose, and measuring 5–6×4–5 μ. They are frequently guttulate in both species. There are no cystidia in the hymenium.

P. galactinus.—This species is a fairly well-marked one and only its distinguishing features will be pointed out here. It was originally described by Berkeley from specimens collected in Ohio by Lea. It is eastern in its range in the United States, occurring from Maine to Missouri and probably no farther south than West Virginia. There are but three common plants in this section of *Polyporus* that possess characteristic odors when fresh and growing. *P. galactinus* is one of them. The odor is usually described as "acid," but to the writer it is a very pleasant and fragrant odor, but not persisting in the dried plants. Characters are not wanting to separate this species from the group just discussed in this section. The pileus is strigose-pubescent, as shown in the illustration (pl. 24 fig. 15), the tubes are very small, and the spores are minute, ellipsoid or subglobose, uninucleate, and measure 3–4 × 2–3 μ. From *P. delectans* and *P. spumeus* it may be separated by the minute pores and the smaller spores. From *P. fumidiceps* Atk. it differs in the decidedly pubescent pileus and larger size. From *P. caesius*, which it resembles in its hairy covering, it differs in its larger size and ellipsoid spores. There are no cystidia.

P. caesius.—This species has long been recognized as a well-marked one, characterized by the villous-strigose pubescence on the pileus, the bluish or grayish blue tint often present on the hymenium, and the minute, cylindric, curved spores. From *P. galactinus* it is separated by its small size and different spores; from *P. chioneus* and *P. albellus* by the pubescent pileus; from *P. lacteus* by the more strigose pileus and the unbranched hyphae of the context.

P. fumidiceps.—This species was described by Atkinson[1] in 1908, and has not since been reported. Since the writer finds it to be a rather common species in Missouri, and since a description has not appeared in the American literature, a few notes will be appended and the plant described on a following page.

In size and shape the species corresponds most closely to *P. chioneus*, but it is of a different color and the spores are ellipsoid to subglobose. From *P. galactinus* and *P. caesius* it is separated by the almost or quite glabrous pileus and from the latter also by the spores. The writer finds it most often on dead willow logs in willow thickets along river bottoms. The types were described from similar locations. Fresh plants have the same peculiar fragrant odor that is found in *P. galactinus.*

The following key will aid in the determination of the species here discussed:

Spores cylindric-oblong, often allantoid 1
Spores ellipsoid to globose 3
1. Pileus villous-strigose; hymenium often bluish or grayish blue..*5. P. caesius*
Pileus glabrous or very slightly pubescent 2
2. Hyphae of context simple or very slightly branched; pileus usually triangular in section; tubes usually 4–9 mm. long .....*2. P. albellus*
Hyphae of context much branched; pileus usually more applanate; tubes 1–3 mm. long .....*1. P. chioneus*
3. Spores 5–6 μ in longest direction; plants not fragrant when fresh 4
Spores 2–4 μ in longest direction; plants fragrant when fresh 5
4. Pileus strigose-tomentose or strigose-hispid, especially on the margin; tubes collapsing on drying, the mouths equal, small, averaging 3–4 to a mm. .....*3. P. spumeus*
Pileus glabrous or floccose-tomentose; tubes scarcely collapsing on drying, the mouths usually somewhat sinuous, averaging 1–2 to a mm. .....*4. P. delectans*
5. Pileus glabrous or nearly so .....*7. P. fumidiceps*
Pileus conspicuously pubescent, often strigose-tomentose at the base.... .....*6. P. galactinus*

1. Polyporus chioneus Fries. Plate 24, fig. 13, 16b

Pileus soft and watery when fresh, rigid when dry, 2–7 × 1–6 × *0.5–1.5* cm., white, often grayish or yellowish when dry, glabrous or nearly so, *covered with a thin continuous gray or yellowish pellicle that becomes more evident when the plants are dried;* context white, *usually with a fragrant*

[1] Ann. Myc. **6**: p. 61. 1908.

odor when fresh, soft and friable when dry, *2–7 mm. thick; tubes 1.5–3 mm. long,* the mouths white or yellowish, averaging 3–4 to a mm.; spores cylindric or allantoid, minute, hyaline, 3–4 × 0.7–1.5 μ; cystidia none; hyphae of context hyaline, much branched.

On dead wood of deciduous trees.

Specimens examined: Mo. Bot. Herb. 4311 (Missouri).—Burt Herb. (collections from Vermont and New York).—Overholts Herb. 2325, 2261, 2277, 2276 (New York), 2326 (Ohio).

2. Polyporus albellus Peck.

Plate 23, fig. 5, Plate 24, fig. 16a.

Pileus soft and watery when fresh, rigid when dry, *more or less triangular in section,* 1–8 × 1–7 × *1–4* cm., white or yellowish, glabrous or nearly so, *covered with a thin yellowish pellicle that is more evident in dried plants,* but often disappears in patches; context white, soft and friable when dry, *0.5–3 cm. thick;* tubes 4–9 mm. long, the mouths white or yellowish, averaging 3–4 to a mm.; spores cylindric or allantoid, minute, hyaline, 3–4 × 0.7–1.5 μ; cystidia none; hyphae of context hyaline, unbranched or nearly so.

On dead wood of deciduous trees.

Specimens examined: Mo. Bot. Gard. Herb. 43756 (Idaho).—Burt Herb. (collection from Pennsylvania).—Overholts Herb. 591 (Vermont), 408, 149, 207 (Ohio), 2243, 2270 (New York), 440 (Missouri).

3. Polyporus spumeus Sow. ex Hornemann.

Plate 24, figs. 10, 11, 14a.

Pileus soft and watery when fresh, rigid on drying, *5–20* × *6–20* × *2–6 cm.* (much thinner when dried), white or somewhat yellowish, *villous-strigose or matted strigose-tomentose;* context white, rigid on drying, 1–3 cm. thick; *tubes 0.5–1.5 cm. long,* collapsing when dried, the mouths white or yellowish, *averaging 2–4 to a mm.;* spores *ellipsoid to subglobose,* hyaline, smooth, often once guttulate, *5–6* × *4–5* μ; cystidia none.

Illustrations: Hornemann, in Fl. Dan. *pl. 1794.*—Berk. Outl. Brit. Fung. *pl. 16, f. 4.*

Specimens examined: Cooke, Fung. Brit. 511[1].—Thuem. Myc. Univ. 709[1].—Mo. Bot. Gard. Herb. 43719 (Missouri).—Overholts Herb. 101 (Ohio), 526, 625 (Missouri).

4. Polyporus delectans Peck. Plate 24, fig. 14b.

Pileus soft and watery when fresh, *3–15* × *5–20* × *1.5–5* cm., white, yellowish, or grayish, *glabrous to finely tomentose;* context white, often with a soft upper layer and a more firm lower layer, firm when dry, 0.5–2 cm. thick; tubes 0.5–1.5 cm. long, the mouths white or yellowish, *averaging 1–2 to a mm.; spores ellipsoid to subglobose,* often uninucleate, hyaline, smooth, *4–5* × *5–6* μ; cystidia none.

Growing from wounds of living trees and on old logs.

Illustrations: Jour. Cinc. Soc. Nat. Hist. **8**: *pl. 1.*

Specimens examined: Overholts Herb. 145, 519, 250, 415, 659, 93, 258, 255 (all from Ohio and Missouri).

5. Polyporus caesius Schrad. ex Fries.

Pileus more or less triangular in outline, rather soft and watery when fresh, 1–5 × 1–4 × 0.5–2 cm., white or grayish, *rarely bluish gray, villous-pubescent or strigose;* context white, 3–10 mm. thick; tubes 3–5 mm. long, white or *grayish blue, large, unequal, averaging 1–3 to a mm., the dissepiments thin, torn and lacerated; spores cylindric or allantoid,* smooth, hyaline, *3–4* × *0.7–1.5* μ; cystidia none.

On dead wood of deciduous trees.

Illustrations: Sow. Col. Fig. Eng. Fung. *pl. 226* (as *Boletus albidus*).—Gill. Champ. Fr. *pl. 458.*

Specimens examined: Krieg. Fung. Sax. 1913.—Mo. Bot. Gard. Herb. 43650 (Missouri).—Burt Herb. (collections from Canada and New York).—Overholts Herb. 627 (Missouri), 2271 (New York).

[1] These specimens or sections of specimens are not well preserved. They contain no spores, and while the general appearance, i. e., shape of pileus, size of pores, length of tubes in comparison with thickness of context, etc., are very much the same, the context appears to be more woody and zonate than in our specimens. Ellis N. Am. Fung. 1103 is referred to *P. spumeus* Fries. It is the same as distributed by Cooke, Fung. Brit. 603, under the name *P. spumosus* Fries. There is no such species listed by Saccardo. Lloyd (Letter No. 52, p. 25) refers the Ellis specimen to *Fomes geotropus* Cooke.

6. Polyporus galactinus Berk.

Plate 24, figs. 12, 15, 17.

Pileus more or less triangular in sections, sometimes gibbous behind, rather firm but watery, 3–8 × 5–10 × 1–3 cm., white or yellowish, *strigose-tomentose at the base, short tomentose on the margin;* context fibrous when fresh, hard and *sometimes resinous when dry,* white, 0.3–2 cm. thick, *strongly zonate, with a strong fragrant odor in fresh specimens;* tubes 5–10 mm. long, the mouths white or yellowish, *minute, averaging 4–6 to a mm.;* spores *ellipsoid,* smooth, hyaline, once guttulate, minute, *3–4 × 2–3 μ*; cystidia none.

On old logs in woods, especially in overflow river bottoms.

Specimens examined: Mo. Bot. Gard. Herb. 4092, 43636 (Missouri), 4138.—Overholts Herb. 42, 489, 382, 134, 252, 2178, 511, 611, 583 (mostly from Ohio and Missouri).

7. Polyporus fumidiceps Atkinson. Plate 23, fig. 6.

Pileus *thin,* soft and watery when fresh, 1–4 ×2–5 × *0.5–1* cm., vinaceous buff to avellaneous or wood-brown, *minutely pubescent or glabrous;* context white, watery, *with a strong fragrant odor, 2–5 mm. thick;* tubes 2–5 mm. long, sometimes olive-green within on drying, the mouths concolorous, *averaging 4–5 to a mm.;* spores *ellipsoid to subglobose,* smooth, hyaline, *2.5–3.5 × 1.5–2.5 μ*; cystidia none.

On dead wood of deciduous trees, especially willows, in woods and along overflow river bottoms.

Specimens examined: Mo. Bot. Gard. Herb. 43712 (Missouri).—Burt Herb. (part of type collection, from New York). —Overholts Herb. 552, 2305, 2318 (Missouri).

Polyporus lucidus Leyss. ex Fries, P. Tsugae Murr., P. Curtisii Berk., and Closely Related Species

These species form a rather natural group of plants possessing the common character of a laccate or varnished pileus. *P. lucidus* was described in 1780 by Leysser (as *Boletus*) from plants collected in England. The description calls for a plant with a lateral stipe and it is so figured by English mycolo-

gists. *P. Curtisii* was described by Berkeley, in 1849,[1] from plants collected in South Carolina by Curtis. *P. Tsugae* was more recently described by Murrill[2] from plants collected in New York City on decaying trunks and stumps of *Tsuga canadensis*. *Ganoderma sessile* was described at the same time and by the same author.

In Murrill's first treatment of this section[3] *Polyporus lucidus* was reported as a synonym for *P. pseudoboletus*, the latter name being used for the plant. The species was reported as occurring in most of the states east of the Mississippi River with the exception of the New England states. *P. Curtisii* was there listed as a synonym for *P. pseudoboletus* with the remark that specimens referred to *P. Curtisii* were only variations of the other species, due to age, rapidity of growth, and perhaps to differences in the host. The next species described was *Ganoderma sessile* and that was described as differing from *G. pseudoboletus* in being annual and sessile, with a very acute margin and a more rugose surface. It was reported as occurring in Indiana, New York, Ohio, Alabama, Louisiana, and Kentucky. In the 'North American Flora,'[4] six years later, the names *Ganoderma pseudoboletus* and *Polyporus lucidus* were both entirely omitted and *P. Curtisii* was restored as a specific name. No comment was made as to why this was done, nor as to what disposition was made of the numerous collections previously referred to *Ganoderma pseudoboletus*. The writer has seen material referred to *G. sessile* by Murrill, and the supposition is that all collections, except those belonging under *Polyporus Curtisii*, were referred to his new species *Ganoderma sessile*. This supposition is borne out by the fact that the description of that species is there so amended as to include stipitate forms also, while the species as originally described was limited to sessile forms. We must also conclude that *G. sessile* was regarded by its author as distinct from *Polyporus lucidus* of Europe, else that name or an older one would have

[1] Lond. Jour. Bot. and Kew Gard. Misc. **1**: p. 101. 1849.
[2] Bul. Tor. Bot. Club **29**: p. 601. 1902.
[3] *loc. cit.*
[4] N. Am. Fl. **9**: p. 120. 1908.

been used. Mr. Murrill remarks concerning *Ganoderma sessile*[1]: "Very similar in its stipitate forms to *Polyporus lucidus* of Europe." The American plants are usually referred to *P. lucidus* by European mycologists, and taking into account the general agreement with the European descriptions and illustrations, and the fact that Murrill has consistently failed to cite any distinguishing characters upon which the legitimacy of his species might be established, we must conclude that there is no such distinction to be made between the European and the American plants. The American plant is variable in respect to the presence or absence of a stipe, and that cannot enter into the discussion.

There is a tendency among mycologists[2] to disregard the *Ganoderma Tsugae* described by Murrill. To the writer this species appears to be a perfectly good one, although it cannot be differentiated on host character alone. A further discussion of this species is reserved for a following paragraph.

In 1908 Atkinson[3] described a species of *Ganoderma* which he called *G. subperforatum*. After an examination of the type specimens the writer referred[4] this species to *Polyporus lucidus*. This leaves us three species of this section of *Polyporus* that are found in the central states. There are no spore characters of sufficient importance or constancy that can be used in separating them. There is a color difference but it probably cannot always be relied upon. The pileus of *P. Tsugae* is shining and mahogany-colored or darker; that of *P. lucidus* is of a lighter red color; and that of *P. Curtisii* is yellowish, at least in mature plants. Moreover, *P. Curtisii* is southern in its distribution, not being found north of the Ohio River; *P. Tsugae* is not reported south of Virginia; and *P. lucidus* is not limited in its north and south distribution in the United States.

[1] Northern Polypores, p. 55. 1914.

[2] cf. Atkinson, Bot. Gaz. **46**: p. 335. 1908. *G. Tsugae* is here listed as a synonym for *G. pseudoboletus* (=*P. lucidus*). Later on the same page it is given varietal rank; also Lloyd (Letter No. 52, p. 27) cites it as a synonym for *Fomes lucidus*.

[3] Bot. Gaz. **46**: p. 337. 1908.

[4] *loc. cit.* p. 123.

A more constant difference that serves to separate *P. Tsugae* is the color of the context. In *P. lucidus* and *P. Curtisii* the context is never pure white, but is usually separated into an upper light-colored and a lower brown layer. This lower layer is more firm than the upper one and often contains horny fibers. In *P. Tsugae* the context is uniform in texture and almost pure white throughout, but often with a very slight tinge of brown next the tubes. Under the microscope this effect is magnified. There are no brown hyphae in the context of *P. Tsugae,* while in the other two species brown hyphae are very pronounced, especially in the layer of context next the tubes. A comparison of the size of the hyphae in the three species is interesting but does not always give conclusive evidence as to the identity of the species. The hyphae of *P. Curtisii* vary from 4 to 6 μ in diameter. Those of *P. lucidus* are more variable. In some cases they cannot be differentiated from those of *P. Curtisii* in point of size, but in some specimens they attain a diameter of 10 μ. Those of *P. Tsugae* often attain a diameter of 15 μ. The difference in the branching of the hyphae of these three species is very striking and is shown in figs. 5 and 6, all drawn to the same scale. Figure 5a represents the hyphae of *P. Curtisii,* which are not extremely branched but can by no means be said to be unbranched. Figure 5b shows the hyphae of *P. lucidus,* and the branching does not differ materially from that of *P. Curtisii.* In both species the large hyphae may extend more than across the field of the high-power microscope and not branch at all in that distance. This condition is never found in the hyphae of *P. Tsugae.* There the hyphae are extremely branched, as shown in fig. 6. The large hyaline

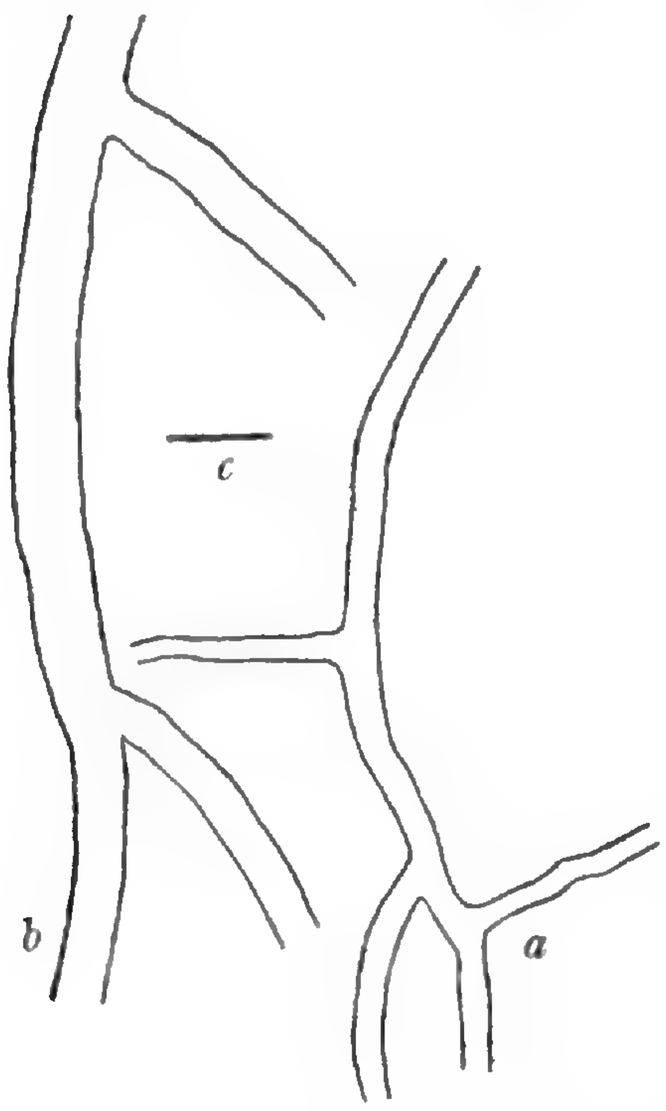


Fig. 5. *a,* hyphae of *P. Curtisii; b,* hyphae of *P. lucidus; c,* width of hyphae of *P. Tsugae.*

hyphae are not continuous for any distance but break up into numerous smaller branches that are often rapidly narrowed to fine thread-like hyphae. This condition must be seen to be best appreciated. It affords, however, another character on which the species can be separated from those closely allied.

The following brief diagnoses of these species is appended:

1. Polyporus Curtisii Berk.

Plants perhaps always stipitate; pileus reniform or flabelliform, 3–12 × 3–20 × 0.7–2 cm., covered with a thin crust that is *at least in part ochraceous in mature plants,* zonate; context *soft and nearly white above, brown and firmer next the tubes,* 0.5–1.5 cm. thick; tubes 0.3–1.2 cm. long, the mouths white to brownish, averaging 3–5 to a mm.; stipe lateral, with color and context as in the pileus; spores light brown, ovoid with a truncate base, apparently echinulate, 8.5–11.5 × 4.5–7 μ; cystidia none; hyphae of context hyaline or brown, *4–6 μ in diameter.*

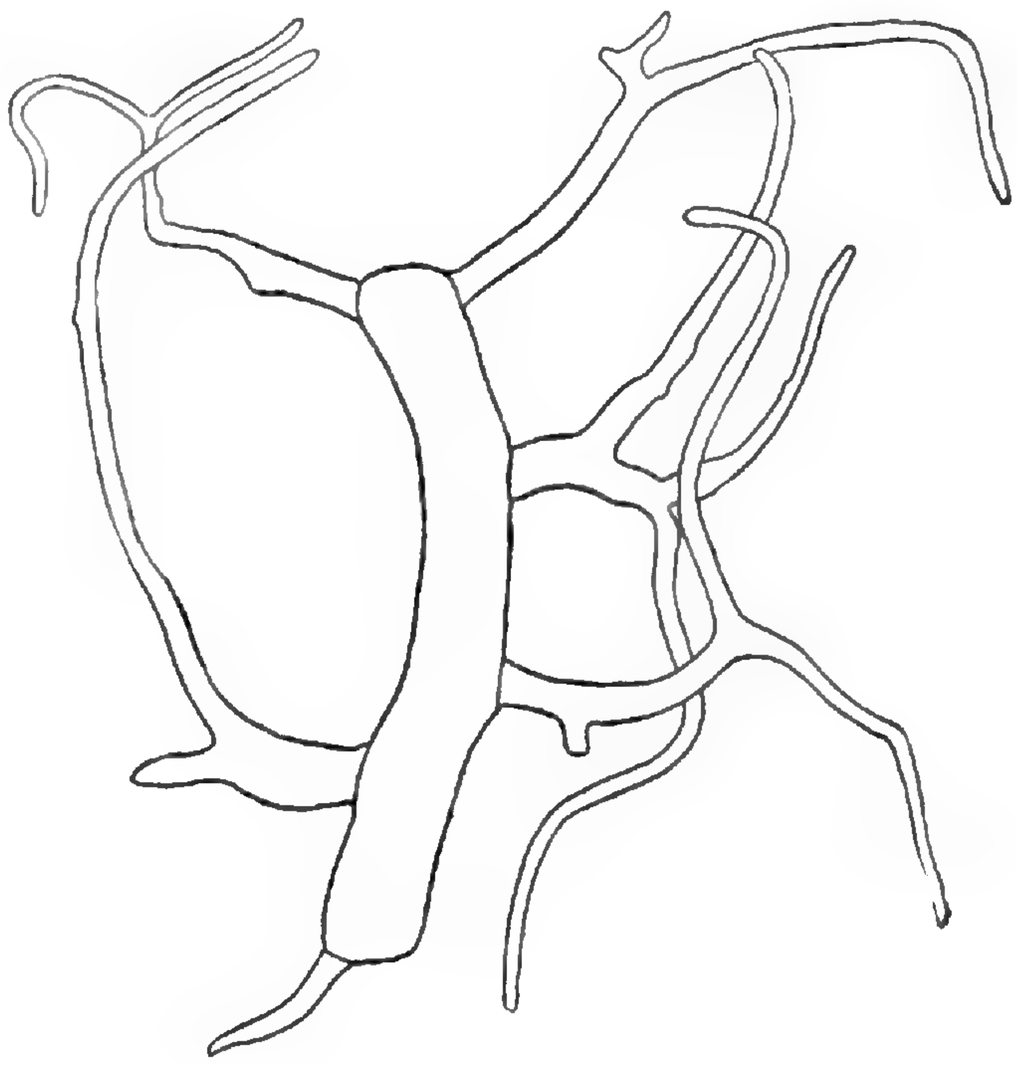


Fig. 6. Hyphae of *P. Tsugae.*

On and about trunks of *deciduous* trees.

Illustrations: Bot. Gaz. **46**: *f. 1–3.*

Specimens examined: Ell. N. Am. Fung. 802.—Rab.-Wint. Fung. Eur. 3430.—Mo. Bot. Gard. Herb. 1438 (Louisiana), 4746 (Alabama).—Overholts Herb. 305 (Florida), 962, 518 (Missouri), 2235 (New York). Also reported from most of the other states east of the Mississippi and south of the Ohio Rivers.

2. Polyporus lucidus Leyss. ex Fries.

Plants sessile or stipitate; pileus dimidiate or reniform, 3–12 × 3.5–20 × 0.5–2.5 cm., covered with a thin *reddish or*

chestnut crust, zonate; context white to light brown, *usually separated into an upper light-colored layer and a lower brown layer, never entirely white,* 0.2–1.5 cm. thick; tubes 0.3–1.5 cm. long, the mouths white to umber, averaging 3–5 to a mm.; stipe lateral or excentric when present, with color and context as in the pileus; spores light brown, ovoid with a truncate base, smooth or appearing echinulate, 9.5–11 × 5–6.5 μ; cystidia none; hyphae of context hyaline or brown, branched, *4–10 μ in diameter.*

On and about stumps and trunks of *deciduous* trees.

Illustrations: Bot. Gaz. **46**: *f. 5.*—Dufour, Atlas Champ. *pl. 49. f. 116.*—Gill. Champ. Fr. *pl. 457.*—Hard, Mushrooms, *f. 332.*—Krombh. Abbild. u. Beschr. *pl. 4. f. 22–24.*—Rostk. in Sturm's Deutsch. Fl. **3**: fasc. 5. *pl. 13.*

Specimens examined: Ell. N. Am. Fung. 5.—Ell. & Ev. Fung. Col. 202 (Delaware).—Krieg. Fung. Sax. 1116.—Rav. Fung. Am. 5.—Thuem. Myc. Univ. 104.—Mo. Bot. Gard. Herb. 43149, 4095, 4024, 4144 (Missouri), 43939 (Illinois).—Burt Herb. (collection from Vermont).—Overholts Herb. (collections from New York, Florida, Ohio, Illinois, and Missouri).

3. Polyporus Tsugae Murrill ex Overholts n. comb.

Plants stipitate; pileus flabelliform or reniform, 5–15 × 7–20 × 1–4 cm., with a *mahogany-colored or almost black, shining,* incrusted surface, sulcate; context *white or nearly so throughout,* 0.5–2 cm. thick; tubes 0.5–1 cm. long, the mouths white to brown, averaging 4–6 to a mm.; stipe present, with color and context as in the pileus; spores light brown, ovoid with a truncate base, apparently echinulate, 9–11 × 6–7 μ; cystidia none; *hyphae of context very irregular and much branched, up to 15 μ in diameter.*

On or about stumps and trunks of *hemlock and pine.*

Specimens examined: Burt Herb. (collection from Vermont).—Overholts Herb. 2338 (Vermont).

Fomes Ellisianus And. and F. fraxinophilus Peck

Fomes fraxinophilus was described by Peck from New York in 1882. It was first described as a *Polyporus* and later trans-

ferred to the genus *Fomes*. *F. Ellisianus* was described from Montana by Anderson in 1891, and redescribed as *Polyporus circumstans* by Morgan from South Dakota in 1895. The former species is abundant in the central and eastern United States, growing only on the trunks of ash trees. The latter species is found occasionally in the western United States, growing only on trunks of *Shepherdia*.

Lloyd has recently expressed the opinion that these two species are identical, except for host, and he has so treated them in his recent synopsis of the genus *Fomes*. The plants are much alike in their old stages but I cannot agree with him that *Fomes Ellisianus* is *"exactly the same plant"* as our eastern species on the ash. First, there is the distinction in host, but that of itself would not be important. Second, plants of *F. Ellisianus* that are fairly mature have a decidedly corrugated or radiate-rugose surface and a reddish tinge of color. I have seen no indication of either of these characters in *F. fraxinophilus* though I have been familiar with that species for a number of years and have observed it in all stages of growth. When the plants are several years old they become similar in appearance and it would be an easy matter to mistake the one for the other if the host were unknown. But the characters pointed out here are believed to be amply sufficient for retaining the two plants as distinct species.

The following brief descriptions are appended:

1. **Fomes Ellisianus** Anderson.

Pileus convex to ungulate, 3–10 × 3–8 × 1.5–4 cm., pallid to brown, *radiate-rugose and with a reddish tinge when young, black and usually somewhat rimose with age,* sulcate; context pallid to wood-colored, punky to corky, 0.5–2 cm. thick; tubes 2–6 mm. long each season,[1] *not distinctly stratified,* the mouths white or yellowish, *averaging 2–3 per mm.;* spores oblong-ellipsoid to broadly ellipsoid, 6–8 × 4–5 μ; cystidia none; hyphae hyaline, 3–5 μ.

On Shepherdia in the west-central states.

[1] The tubes in this plant are sometimes continuous to a length of 1.5 cm., but I do not believe that such lengths are attained in a single year's growth.

Illustrations: Bot. Gaz. **16**: *pl. 12.*—Jour. Cinc. Soc. Nat. Hist. **18**: *pl. 1. f. 4* (as *P. circumstans* Morg.).

Specimens examined: Anderson, Paras. Fung. Mont. 537 (as *P. fraxinophilus*).—Baker, Pl. N. N. Mex. 55.—Mo. Bot. Gard. Herb. 4272 (New Mexico).—Burt Herb. (collections from Montana and New Mexico). Also reported from North Dakota and Colorado.

2. Fomes fraxinophilus Peck.

Pileus convex to somewhat ungulate, 2–25 × 3.5–40 × 1.5–10 cm., *at first white,* soon grayish black or black, *not rugose, somewhat rimose* with age, sometimes sulcate; context woody, 0.5–1.5 cm. thick; tubes 2–4 mm. long each season, *indistinctly stratified,* the mouths white to brownish, *averaging 2–3 to a mm.;* spores ellipsoid to ovoid, 5–6 × 6–7 μ; cystidia none; hyphae 3–5 μ.

On living or dead ash trees.

Illustrations: U. S. Dept. Agr., Bur. Pl. Ind. Bul. 32: *pl. 2.*—Hard, Mushrooms, *f. 350.*

Specimens examined: Ell. & Ev. N. Am. Fung. 3302 (Kansas); Fung. Col. 909 (Kansas).—Mo. Bot. Gard. Herb. 4780, 1437, 4826 (Missouri).—Burt Herb. (collections from Kansas).—Overholts Herb. 46, 157, 159, 122, etc. (Ohio), 559, 624 (Missouri), 626 (Iowa). Also reported from Kentucky, Nebraska, Pennsylvania, Indiana, and New York.

Fomes igniarius Linn. ex Gillet and F. nigricans Fries

Much confusion has existed concerning the limits of these two species, and many different ideas are stated in the literature. Murrill has referred *Fomes nigricans* as a synonym for *F. igniarius.* Lloyd has kept them apart, though recognizing a close relationship between them. Others have concluded with Bresadola that we are here dealing with two species that can be easily separated on the presence or absence of setae in the hymenium. Romell has held that such is not the case, but that setae may be present or rare in either species, and has stated that they are usually most abundant near the bottom of the tubes. This would account for the fact that some

observers have stated that they have been unable to find setae in the hymenium of *F. nigricans*.

The original illustration of *F. nigricans* does not agree with any present-day conception of what the species really was. The manner in which the plates for Fries' 'Icones' were gotten together does not at all preclude the existence of grave errors regarding the identity of the species there illustrated. Hence the original illustration of *F. nigricans* has been discounted by careful European workers, they preferring to base the species rather on specimens authenticated by Fries himself. Of these, there appear to be specimens both at Upsala and at Kew.

The *F. nigricans* of my 'Ohio Polyporaceae' proves to be *F. Bakeri* Murrill. The specimens referred by me to *F. igniarius* are of two types. One of these has the pileus convex or ungulate, the surface sometimes becoming rimose, and setae not at all abundant. The second type is most commonly found on birch trees. The pileus is plane or slightly convex, sometimes shining black in color, and the surface often cracks in both directions but does not become roughly rimose. The setae are often more abundant. Of this second form, Lloyd recently wrote as follows concerning a collection sent to him by me: "It agrees with his (Fries') specimens (of *F. nigricans*) both at Upsala and at Kew. . . . . It is usually thinner than typical *F. igniarius* and the setae are more abundant than in the type form."

On the strength of this information I am now able to separate my collections of these forms into what I am convinced are the two species, *F. igniarius* and *F. nigricans*, respectively. I have examined all available material of the two species and have thoroughly confirmed Romell's observation on the presence of the setae. In but one collection was I unable to find setae and I do not doubt that further attempts would show their presence in that instance. It is advisable, however, as stated on a previous page of this article, to cut *longitudinal* sections of the hymenium, since by so doing one will be more likely to strike the setae if there is any variation in their abundance at particular places in the tubes.

The characters cited above do not appear to the writer to be sufficient to warrant the complete separation of the two species. They are sufficiently distinct, however, to enable one to refer to one form or the other all the specimens collected. It has been thought best to refer *F. nigricans* as a variety of *F. igniarius.*

The following diagnosis of the species and its variety is appended:

1. Fomes igniarius Linn. ex Fries.

Typical form: Pileus *convex or ungulate,* 3–10 × 5–20 × 2–10 cm., grayish black or black, *rarely roughly rimose with age,* not incrusted; context hard and woody, brown, 0.5–1 cm. thick; tubes 2–5 mm. long each season, the older layers conspicuously white-stuffed or incrusted, the mouths brown, averaging 4–5 per mm.; spores globose or subglobose, smooth, hyaline, 4–6 μ; setae present though sometimes rare, sharp-pointed, 16–25 × 6–8 μ; hyphae 3–4 μ.

Var. *nigricans* Fries: Pileus *plane to convex,* 3–10 × 3–15 × 2–7 cm., black, *sometimes shining black, the surface often cracked in both directions but never roughly rimose;* context and tubes as in the typical form, decidedly white incrusted; spores, setae, and hyphae as above, the setae often abundant.

On trunks of living deciduous trees.

Illustrations: Published illustrations passing under the name of this species and its variety are abundant, but typical representations of my plants so referred are scarce. The type form intergrades into the variety to such an extent that some illustrations are hard to refer. The typical form is represented by Hard, Mushrooms, *f. 349,* and in *pl. 25. f. 18.* of this paper. The variety is well represented by Lloyd, Myc. Notes 29: *f. 193;* Rostkovius in Sturm's Deutsch. Fl. **3**: fasc. 17. *pl. 51.*

Specimens examined[1]: Ell. & Ev. N. Am. Fung. 915 (Kentucky).—Krieg. Fung. Sax. 526.—Thuem. Myc. Univ. 105.—Mo. Bot. Gard. Herb. 4037* (New York), 4043* (New York),

[1] Collections assigned to var. *nigricans* are marked with an asterisk.

43627* (Vermont), 42958 (Florida).—Burt Herb. (collections from Vermont and Canada).—Overholts Herb. 378* (Indiana), 423 (Ohio), 2460* (Vermont), 2256 (New York), 450 (Missouri).

Fomes scutellatus Schw. ex Cooke and F. ohiensis Berk. ex Murrill

These two species are closely related and have on more than one occasion been treated as a single species. *Fomes scutellatus* was first collected by Schweinitz on dead *Syringa* in Pennsylvania. It has since been reported on a few other hosts, namely, alder, witch-hazel, and sweet-gum. *F. ohiensis* was originally described from Ohio by Berkeley and is a very common species in that state. It is especially abundant on dead limbs on the ground in woods in September and October. Quite frequently it grows on fence posts, pickets, and a variety of other structural timbers. Both species were formerly frequently referred to the genus *Trametes,* but it seems best to restrict that genus to annual forms only.

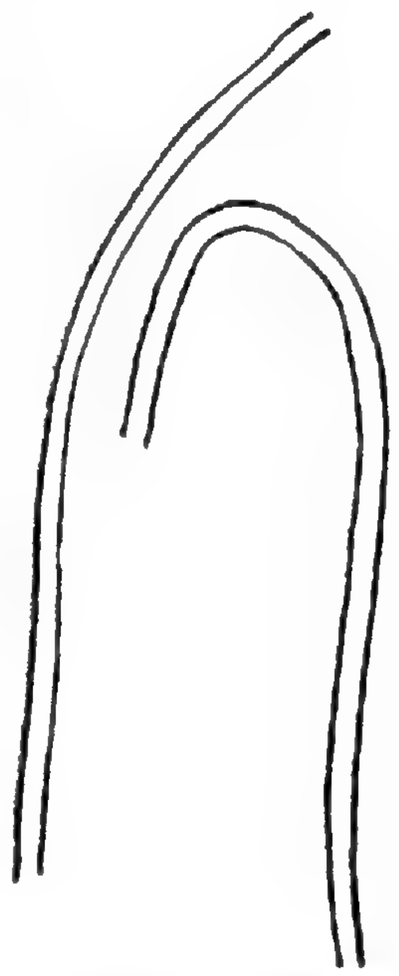


Fig. 7. Hyphae of *F. ohiensis.*

Besides the host distinction, other characters may be used to distinguish between the two species. In typical specimens of *F. scutellatus* the pileus is entirely black and attached dorsally to the under side of branches. *F. ohiensis* is rarely found so attached, and the whole plant is at first white, the upper or basal part of the pileus becoming blackish with age, as in many species of *Fomes,* but the margin remaining white, even in perennial forms. *F. scutellatus* is rarely ungulate in form, while old specimens of *F. ohiensis* become steep in front, much as in *F. fomentarius.*

The spores of *F. scutellatus* have never been recorded and Lloyd has recently stated[1] that he has failed to find them even in freshly collected material. Murrill records them as

[1] Syn. Fomes, p. 218. 1915.

"*smooth, hyaline,*" but that conclusion is reached only from inference. I find them to be cylindric, hyaline, smooth, 8–9 × 2.5–3.5 *μ*. They thus differ from those of *F. ohiensis,* which are ovoid with a truncate base, hyaline, smooth, 10–12 × 6–7 *μ*. It is apparent then that the spores of *F. ohiensis* are similar in shape to those found in all species recently segregated into the genus *Ganoderma,* while those of *F. scutellatus* point to an alliance of that species with the genus *Trametes,* they being typical trametoid spores.

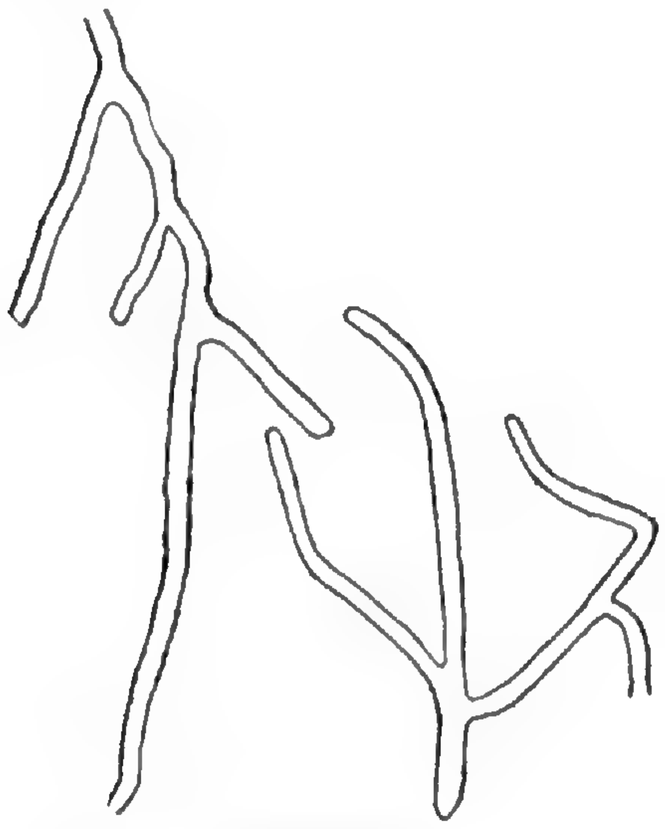


Fig. 8. Hyphae of *F. scutellatus.*

It is only in rare cases that the branching of the hyphae of the context can be used as a distinguishing character. The hyphae of *F. scutellatus* are much branched, while those of *F. ohiensis* are practically simple. These differences are shown in figs. 7 and 8.

It is thus apparent that these closely related species are separated by rather wide differences, and their determination need no longer be considered difficult.

The following descriptions are appended:

1. Fomes scutellatus Schw. ex Cooke.

Pileus *convex,* sometimes attached by the vertex and circular in outline, 0.5–1.5 × 0.5–2 × 0.1–0.5 cm., *entirely dark brown or black,* at least when mature, slightly sulcate; context corky, about 2 mm. thick; tubes 1–2 mm. long, the mouths white or pallid, averaging 4–5 per mm., thick-walled; spores *cylindric, 8–9 × 2.5–3.5 μ*; cystidia none; hyphae hyaline to light brown, *much branched,* 2–4 *μ*; basidia 6–9 *μ* broad.

Usually growing on alder and witch-hazel.

Specimens examined: Ell. & Ev. N. Am. Fung. 1597 (Pennsylvania); Fung. Col. 1010 (Vermont).—Mo. Bot. Gard. Herb. 4469 (New Jersey).—Burt Herb. (collections from New York and Vermont).—Overholts Herb. 337 (Ohio), 2394 (Florida). Also reported from Maine, Delaware, and Alabama.

2. Fomes ohiensis Berk. ex Murrill.

Pileus *convex to ungulate,* sometimes attached by the vertex and circular in outline, 0.5–2.5 × 0.5–3 × 0.2–1 cm., *pure white, then black at the base, the margin remaining white,* often zonate or sulcate; context corky or woody, 1–3 mm. thick; tubes 1–4 mm. long, the mouths white, averaging 3–5 per mm., thick-walled; spores[1] *ovoid with a truncate base, 10–12 × 6–7 μ*; cystidia none; hyphae hyaline, *unbranched,* 3–4 μ; basidia 8–11 μ broad.

On dead wood and on structural timbers.

Specimens examined: Ell. N. Am. Fung. 923 (as *Trametes*) (Ohio).—Burt Herb. (collection from South America, ex Herb. Romell).—Overholts Herb. 38, 39, 131, and others (Ohio), 479 (Missouri), 503 (Illinois). Also reported from Kansas, Michigan, and New York.

Trametes Pini Thor. ex Fries, T. Abietis Karst., and T. piceinus Peck.

Trametes Pini dates from the year 1803, when it was described by Thore,[2] and again in the following year, 1804, by Broteri.[3] The typical form of the perennial plant is rather large, has a more or less ungulate pileus, and in age becomes blackish and rimose. At times, however, the first year's growth is thin and applanate and thus differs markedly in form from the typical plant. This condition was observed by Peck and the name *Polyporus* (later changed to *Trametes*) *piceinus* was proposed by him for the form that he collected on *Picea* about 1889.[4] Karsten had already[5] described the same plant in Europe, in 1882, as *Fomes Abietis,* and the two names have been used interchangeably in this country for several years. In 1889 Karsten[6] referred to his species as

[1] According to Murrill (N. Am. Flora **9**: p. 96. 1908) the spores of the size and form given here are conidial, but they represent the only type of spore I have been able to find in the hymenium of this species.

[2] Chlor. Land. p. 487. 1803.

[3] Fl. Lusit **2**: p. 468. 1804.

[4] Rept. N. Y. State Mus. **42**: p. 121. 1889.

[5] Bidrag Finl. Nat. Folk. **37**: p. 242. 1882.

[6] Finl. Basidav, p. 336. 1889.

Trametes Pini var. *Abietis,* and that name has also appeared in the American literature. The writer has not seen Karsten's types and his opinion as to the synonymy of the species of Peck and Karsten is based entirely on the use of the names in this country and on the fact that *T. Pini* var. *Abietis,* as distributed by Romell,[1] is certainly to be referred to Peck's species. In the case of *Polyporus piceinus* and *Trametes Pini,* however, the evidence is not so clear, and there are yet mycologists who distinguish between the two species.

Peck has stated[2] that the pileus of *T. piceinus* is persistently tomentose, while that of *T. Pini* is not tomentose, and on this ground and also in view of the fact that the former is thin and applanate while the latter is thick and ungulate, the two have been kept apart to some extent, though Murrill, in 1908, declared them to be not specifically distinct. During the summer of 1913 and again in 1914 the writer had the privilege of collecting in the almost unexplored (mycologically) region of the Rocky Mountains in central Colorado. Here the forests are principally composed of the lodge-pole pine (*Pinus Murrayana*) and the Engelmann spruce (*Picea Engelmannii*), the former genus being the typical host of *T. Pini* and the latter the same for *T. piceinus.* No extensive field observations had been previously reported as to the intermingling of these supposed species of fungi, and the opportunity was taken to procure some notes on the subject. In that region the species is more abundant on the spruce than on the pine, probably because the best spruce forests follow the courses of the streams, while the pine often represents the only tree growth on the mountain sides and in the higher parts of the mountain parks where the soil often contains a higher percentage of sand. Such forests are not dense and quickly become dry, unless kept moist by daily rainfalls. Hence the statement that *T. Pini* is more often found on spruce in that locality is not surprising. In one instance in an area of no more than four square feet on a spruce snag the writer counted 18 sporophores, and of these about half were the *T. Pini* form and

[1] Fung. Scand. 7.
[2] Rept. N. Y. State Mus. **54**: p. 170. 1901.

the rest were good specimens of the thin form known as *T. piceinus*. There is no doubt in the writer's mind that all these sporophores came from a common mycelium. In 1914 a similar find was made, the substratum being an old spruce log. Portions of these two collections are preserved in the writer's herbarium. Attempts were later made to separate the specimens in these collections by means of microscopic characters, but it was found to be impossible. In view of these observations it is seen that the recently expressed opinion of Meinecke[1] that the variation in shape is due to the host, is not true for the fungus, as it sometimes occurs in Colorado.

In some localities it may be more convenient to consider the thin form as a variety of *T. Pini,* for it must be admitted that the two forms do not always grow in such close association as described above. Yet the evidence is clear that they cannot be regarded as distinct species.

The writer believes that it will add to the clearness of the general situation in the *Polyporaceae* to include in the genus *Fomes* all perennial plants of whatever structure. This not only simplifies the definition of the genus *Fomes,* but also gives a clearer idea of the genus *Trametes.* As it has been commonly understood, the genus *Trametes* is a very poorly defined one, and any attempt to make its limits clearer is a step in the right direction. The transfer of this species to *Fomes* has already been made by Lloyd[2]. The species is here described under that name.

1. **Fomes Pini** Thor. ex Lloyd.

Sporophores very variable, the variations grouping themselves as follows:

Typical form: Sporophore *perennial, often ungulate, 6–15* × *4–20* × *1–15* cm., at first tawny and with elevated zones of appressed tomentum, becoming blackish and glabrous, the surface cracking or becoming rough and irregular; context not more than 5 mm. thick, tawny or ochraceous tawny, woody; tubes 2–6 mm. long each season, the mouths ochraceous to

[1] Forest tree diseases common in California and Nevada, p. 43. 1914.
[2] Syn. Fomes, p. 275. 1915.

brown; spores globose or subglobose, hyaline, 4–5 μ broad; setae abundant, sharp-pointed, brown, extending 20–30 μ beyond the basidia; hyphae 3–5 μ.

Var. *Abietis* Karsten: Sporophores *usually annual, rather thin and applanate, 1–5 × 1–7 × 0.3–1* cm., tawny or russet-tawny toward the margin, the immediate margin sometimes brighter-colored, zonate with elevated ridges of tomentum, grayish black or brownish black toward the base; context colored as in the typical form, 1–3 mm. thick; tubes *usually in a single layer;* spores, setae, and hyphae, as in the typical form.

On wood of coniferous trees, both living and dead.

Illustrations: Boudier, Ic. Myc. *pl. 161.*—Delacroix, Atlas Path. Veget. *pl. 19. f. 10–12.*—Meinecke, For. Tree Dis. Calif. and Nev. *pl. 4–5.*—Rostk. in Sturm's Deutsch. Fl. **3**: fasc. 17. *pl. 50.*

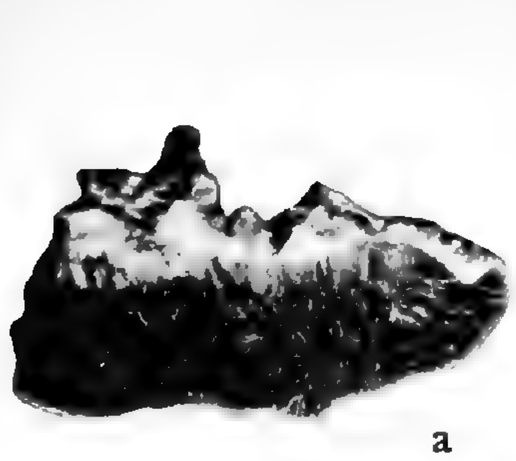
Specimens examined: Ell. N. Am. Fung. 602 (New Jersey).—Ell. & Ev. N. Am. Fung. 2507 (as *T. Abietis*) (Canada).—Linh. Fung. Hung. 348.—Rabenh. Crypt. Samm. Schule & Haus 8; Herb. Myc. 118.—Romell, Fung. Scand. 7 (as *T. Pini* var. *Abietis.*—Seym. & Earle, Econ. Fung. **11**: 549.—Mo. Bot. Gard. Herb. 42958 (Washington), 4609 (Newfoundland), 42970 (Maine), 42954 (Michigan), 42956 (Vermont), 4618 (Colorado), 43810 (Missouri), and others.—Overholts Herb. 154 (Ohio), 630, 2033, 642, and 2391 (Colorado), 2458 (Montana), and others.

Graduate Laboratory, Missouri Botanical Garden.

Explanation of Plate

PLATE 23

Fig. 1. Specimens of *P. abietinus* with lamellate hymenium.
Fig. 2. Surface view of typical sporophores of *P. abietinus.*
Fig. 3. Typical sporophores of *P. fumosus.*
Fig. 4. *P. Burtii.* Photograph of type specimens.
Fig. 5. Upper surface of *P. albellus.*
Fig. 6. *P. fumidiceps,* showing upper surface and section through a sporophore.
Fig. 7. *P. crispus,* showing the densely imbricate mode of growth and the pubescent pileus.
Fig. 8. *P. adustus.* View of surface of pileus and hymenium.
Fig. 9. Typical sporophores of *P. pargamenus.*



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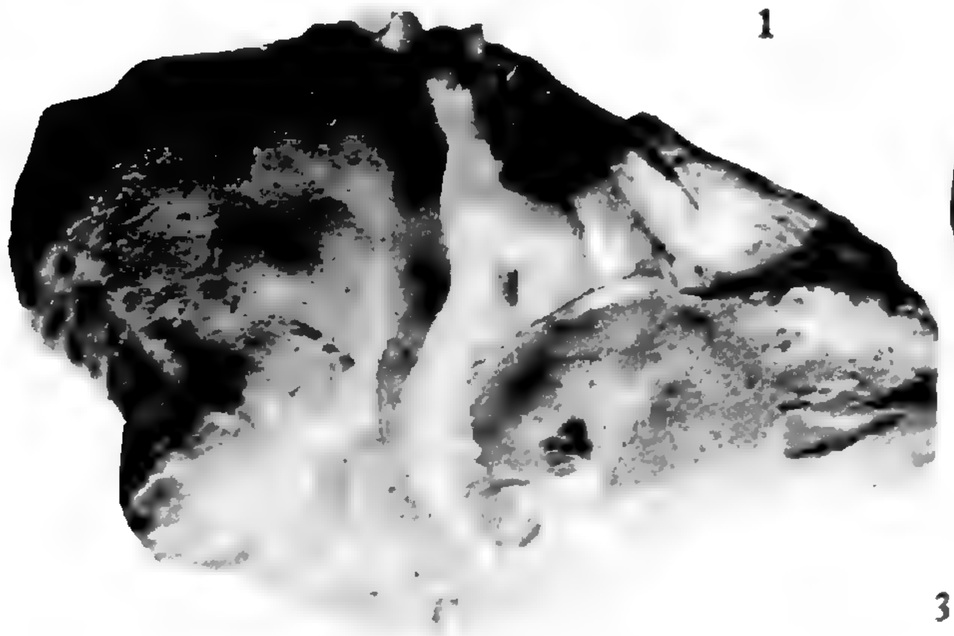

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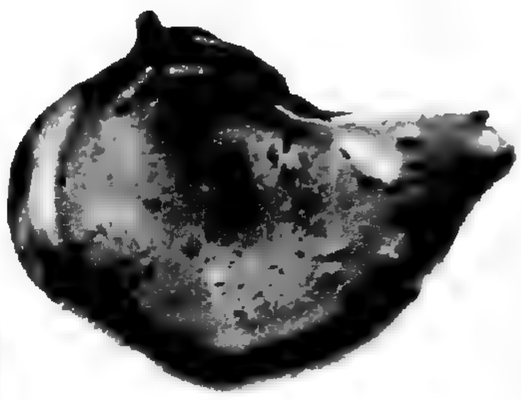

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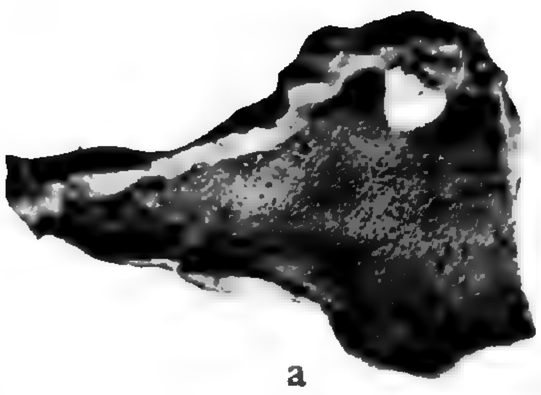

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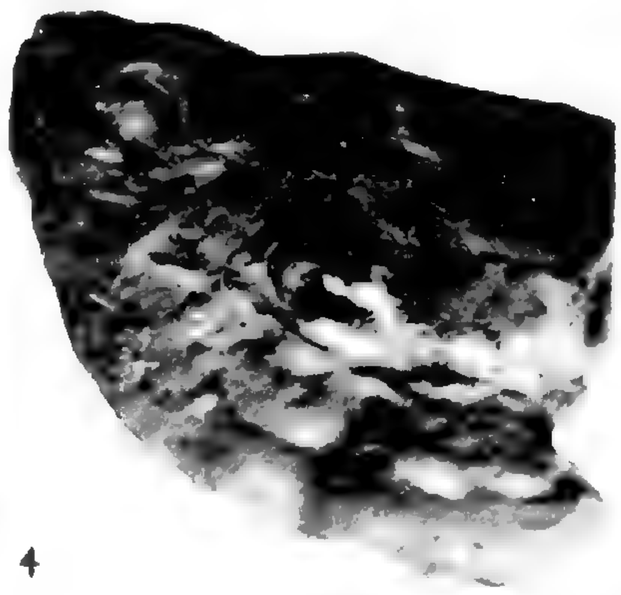

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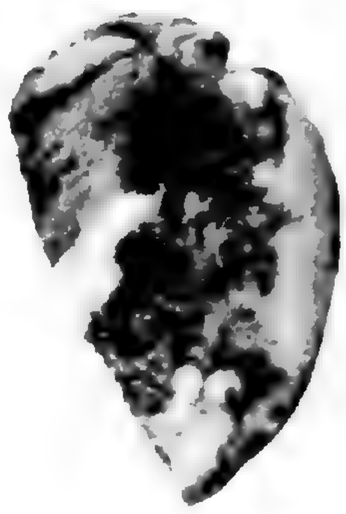

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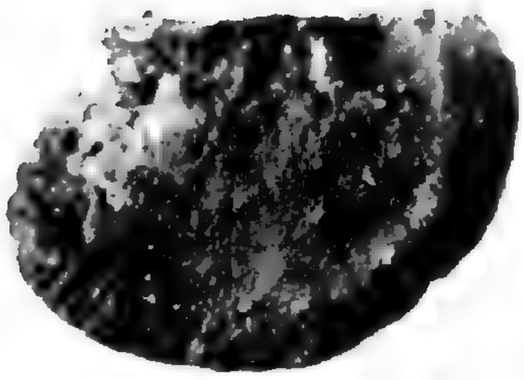

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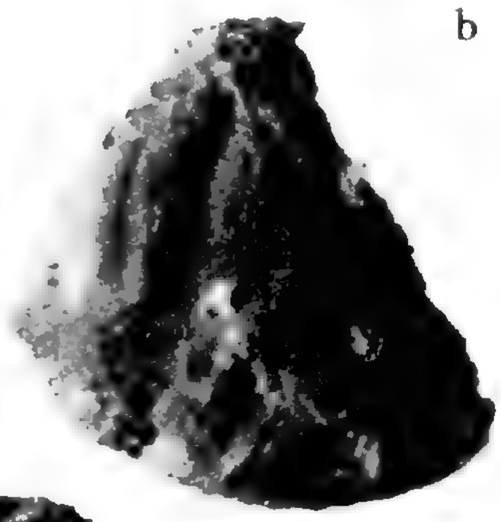

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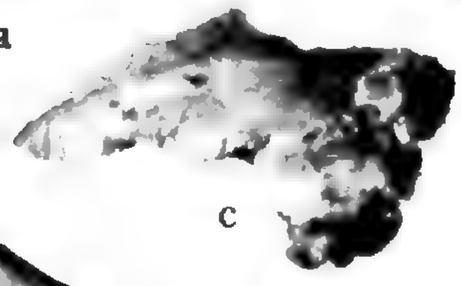

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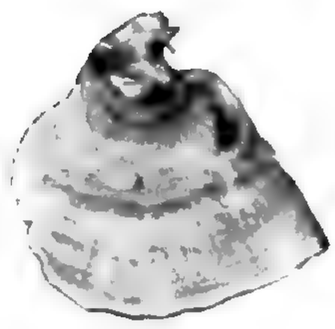

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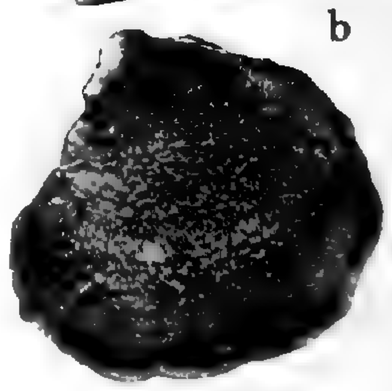

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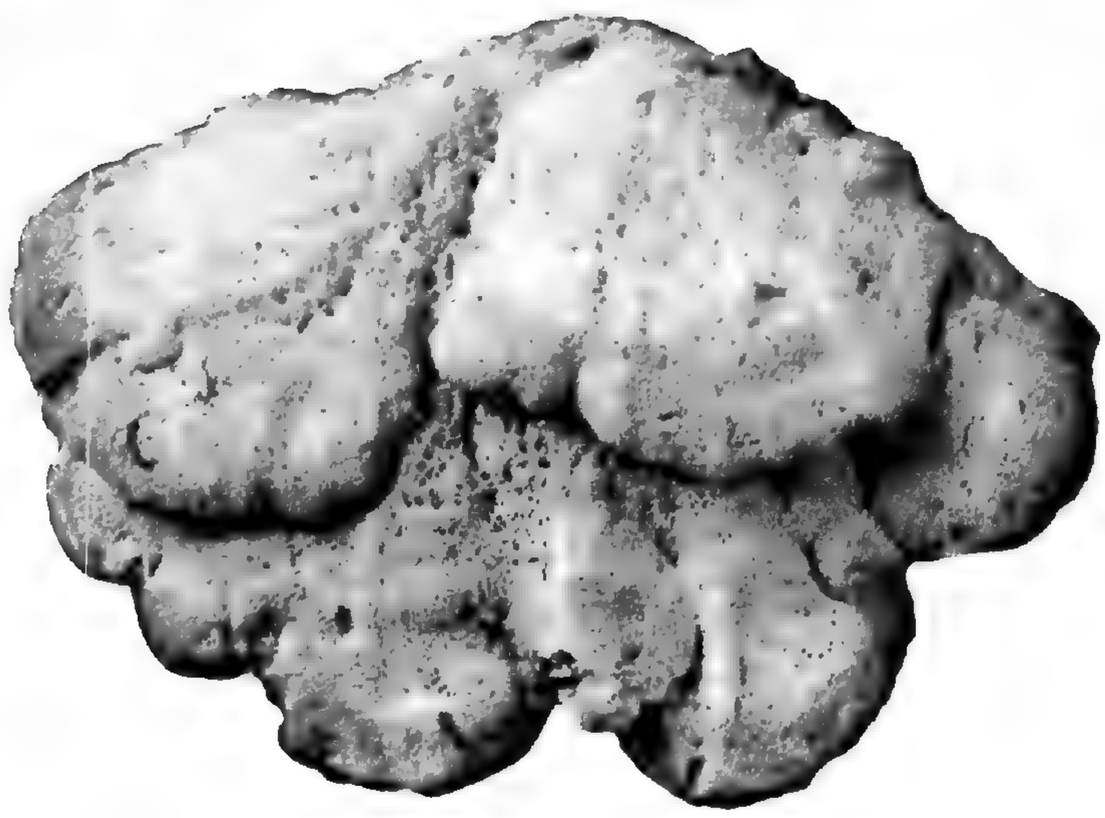
OVERHOLTS—POLYPORACEAE

COCKAYNE, BOSTON.

Explanation of Plate

PLATE 24

Fig. 10. View of hymenium of *P. spumeus*.
Fig. 11. The pores of *P. spumeus* somewhat enlarged.
Fig. 12. Section through a sporophore of *P. galactinus*. Note the prominent zonation of the context.
Fig. 13. Upper surface of *P. chioneus*.
Fig. 14. Comparison of the size of the tubes in (a) *P. spumeus* and (b) *P. delectans*.
Fig. 15. Upper surface of *P. galactinus*. Note the prominent pubescence.
Fig. 16. Sections showing the relative thickness of the pilei in (a) *P. albellus* and (b) *P. chioneus*.
Fig. 17. Hymenium of *P. galactinus*.



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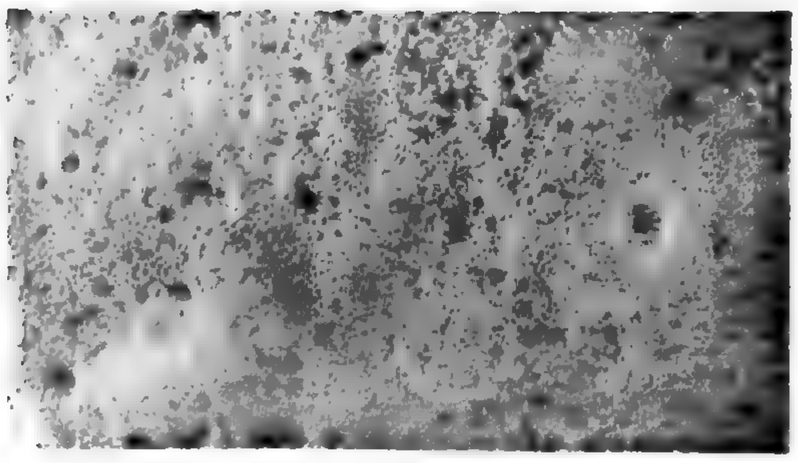

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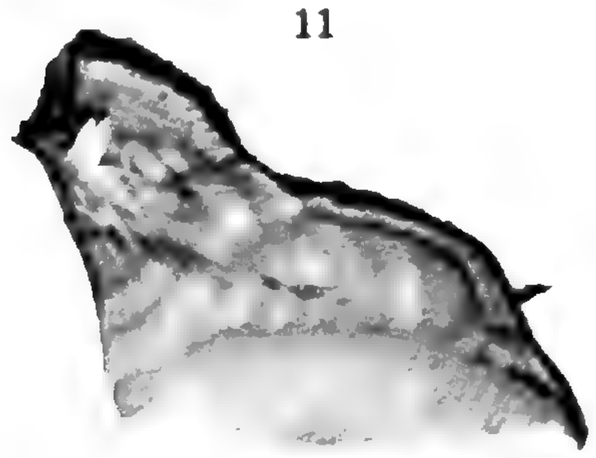

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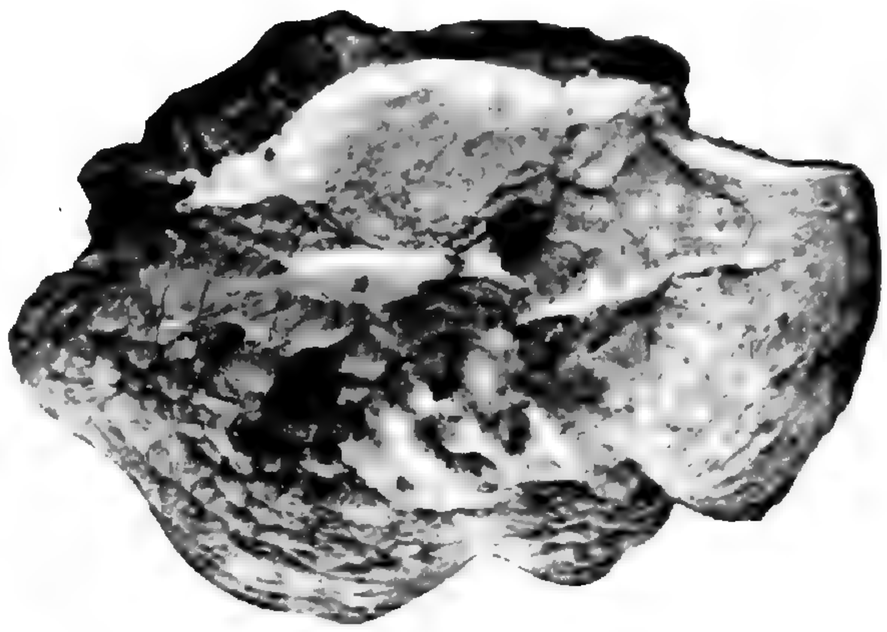

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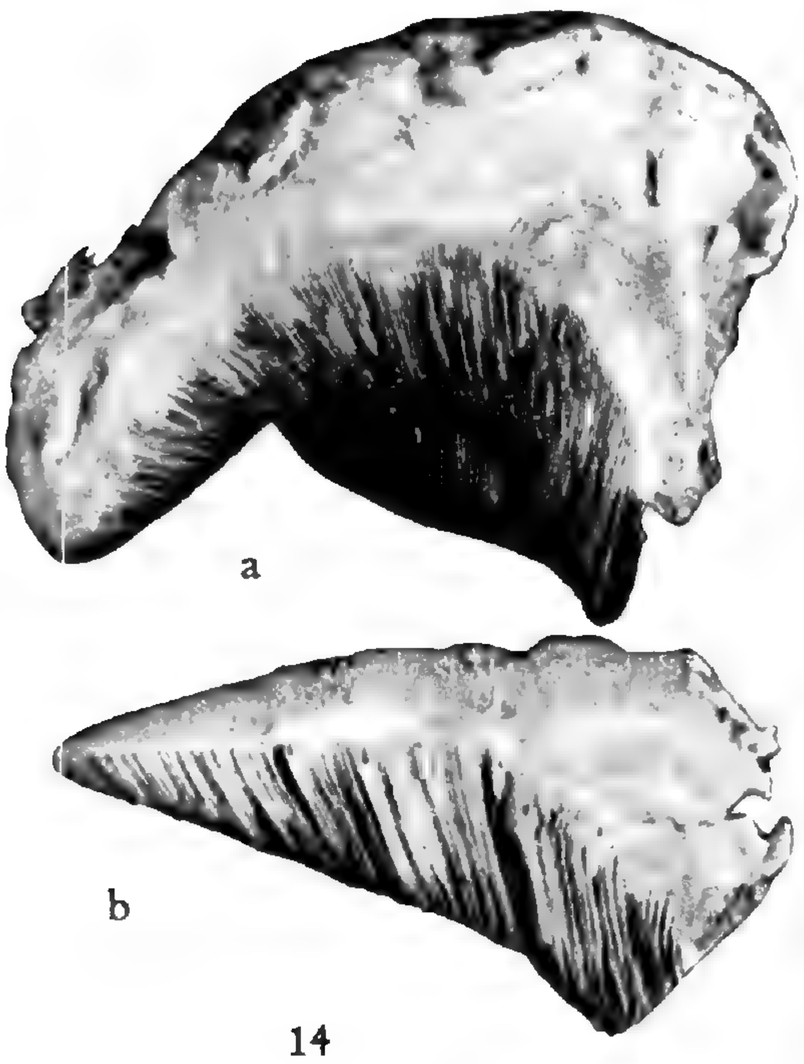

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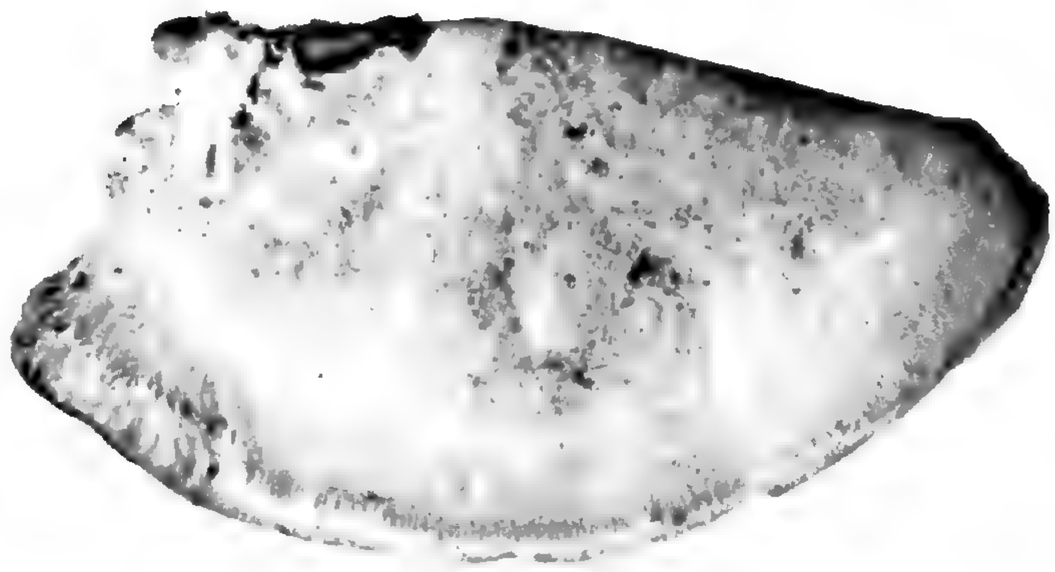

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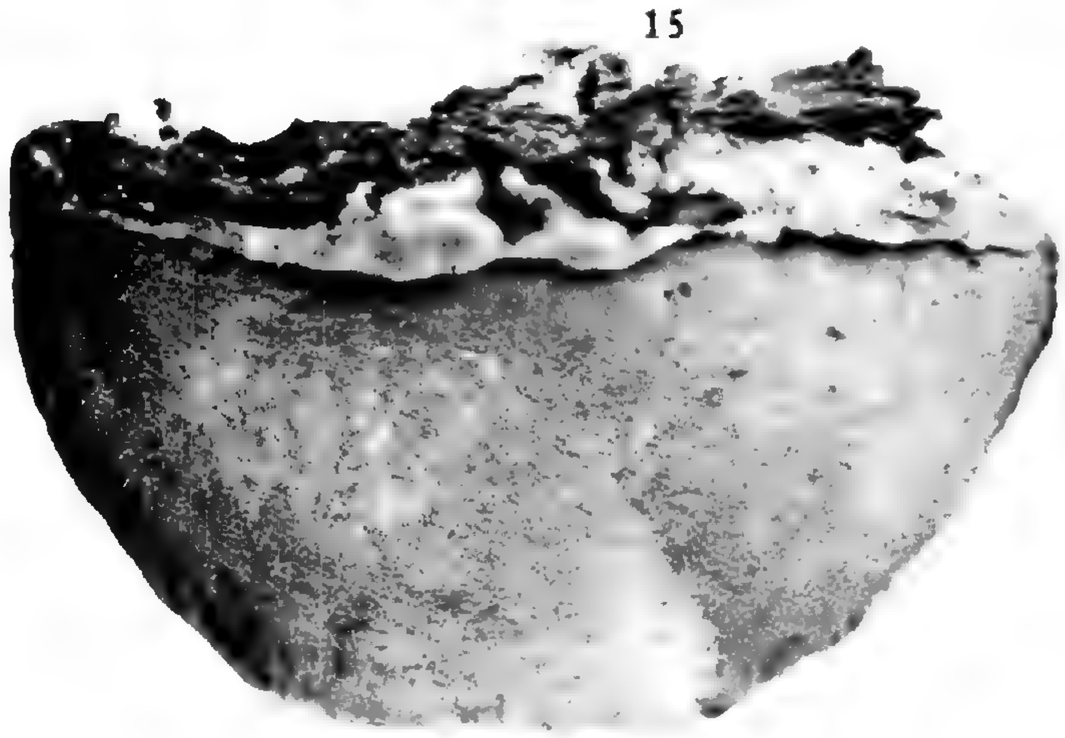


17

OVERHOLTS—POLYPORACEAE

COCKAYNE, BOSTON.

EXPLANATION OF PLATE

PLATE 25

Fig. 18. Sporophore of *F. igniarius* growing on beech trunk.

Fig. 19. View of upper surface and section through a sporophore of *F. fraxinophilus*.

Fig. 20. Section through a typical sporophore of *F. igniarius* var. *nigricans*. Note the strongly white incrusted layers of tubes and context.

Fig. 21. Surface view of the same specimen of *F. igniarius* var. *nigricans*.

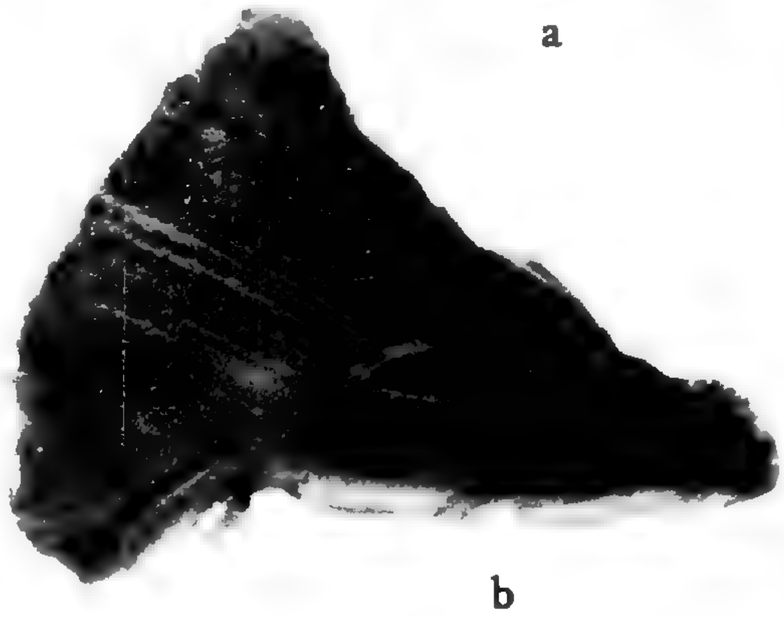
Fig. 22. Sporophores of *F. ohiensis*.

Fig. 23. *F. Ellisianus*, showing rugose upper surface and section of hymenium with long tubes.

Fig. 24. Sporophores of *F. scutellatus* on limbs of alder.

18

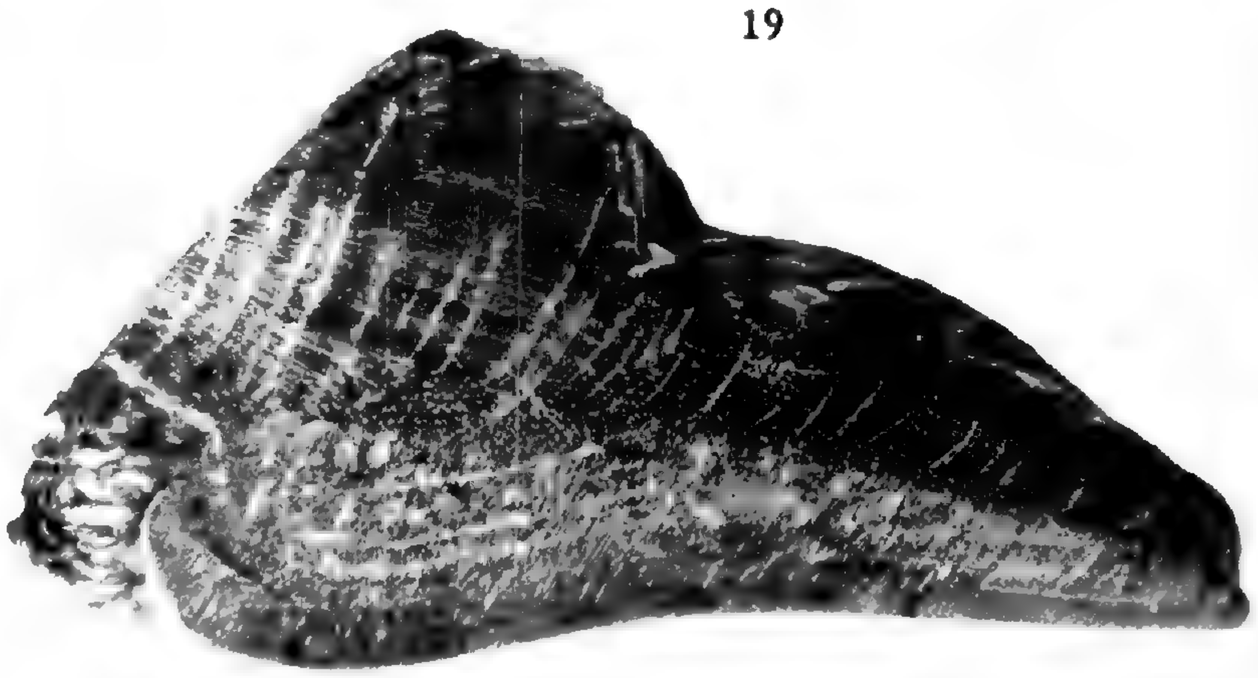
a



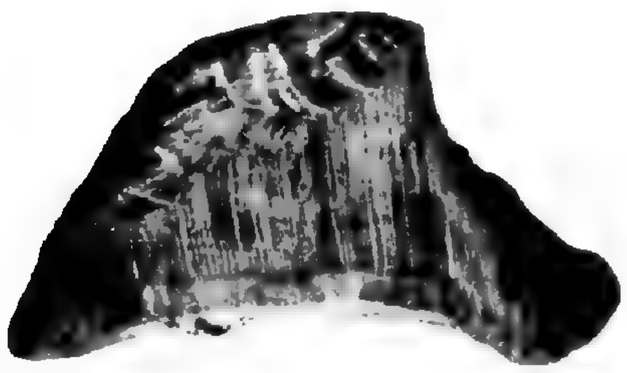
b

19

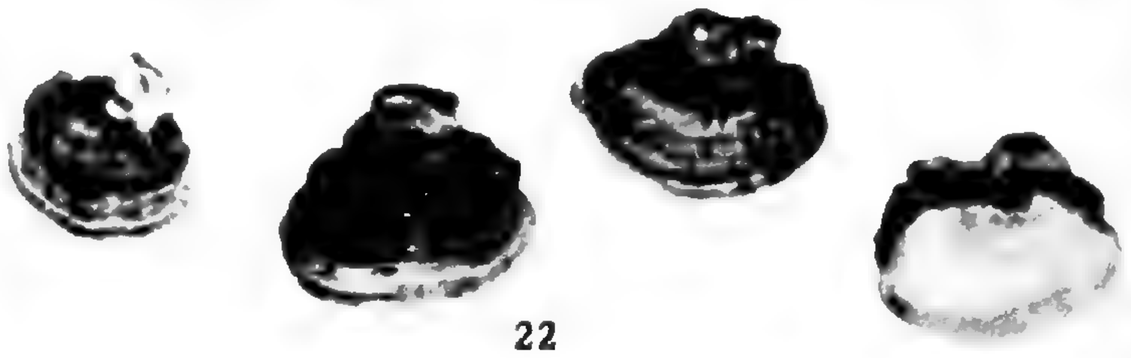
21



20



a



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a

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24

OVERHOLTS--POLYPORACEAE

COCKAYNE, BOSTON.

THE THELEPHORACEAE OF NORTH AMERICA V[1]

Tremellodendron, Eichleriella, and Sebacina

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The group of fungi comprising the present part probably attains its greatest development both in form and numbers in the western continent where it culminates in the erect *Tremellodendron,* apparently confined to North America. This continent has five of the seven species of *Eichleriella;* it has twenty-six species of *Sebacina* against fifteen for the Old World.

The better-known species of these genera were originally described in *Thelephora, Stereum,* and *Corticium,* with which they conform so closely in general habit of growth and consistency of the fructification that it is impossible to separate them from the latter except by microscopic examination of preparations which show the mature basidia to be longitudinally cruciately septate. Collectors invariably roughly grade their findings of *Sebacina* as *Corticium.* The recognition of longitudinally septate basidia is not always easy with the aid of the microscope; for example, the fungus originally described as *Stereum Leveillianum* B. & C. has been studied critically at several times by experts without their observing the true structure of the basidia.

I regret that the present account of our species and their range in North America does not include all the material at hand. The Missouri Botanical Garden herbarium contains several hundred undetermined specimens of possible Corticiums which have been received during the last two years.

NOTE.—Explanation in regard to the citation of specimens studied is given in Part I, Ann. Mo. Bot. Gard. 1 : 202. 1914, footnote. The technical color terms used in this work are those of Ridgway, Color Standards and Nomenclature. Washington, D. C., 1912.

[1] Issued December 20, 1915

I have looked through these collections very carefully to sort out, without examination now of everything by microscopic methods, just those specimens which ought to be studied at once for citation in this part, but some of the specimens most desirable for citation have undoubtedly been deferred for the present as probable Corticiums.

As it is really a nice microscopical task to recognize longitudinally septate basidia when they are not at their best, some notes, based on my experience, may be helpful. Species of *Tremellodendron* are the most easily recognized, for a little of the moistened and softened hymenium may be picked out with a scalpel, placed in a drop of water, stained with aqueous solution of eosin, 7 per cent potassium hydrate solution added, and then crushed down by pressure on the cover glass. In the detection of species of *Eichleriella* and *Sebacina,* thin vertical sections of the fructification are necessary. After the sections have been made turgid and clear by potassium hydrate solution, the latter should be drained off and the sections stained by merely a sufficient amount of solution of Gruebler's eosin soluble in alcohol, and mounted in water for temporary examination. It may be necessary to spread apart the tissues of the preparation somewhat by pressure upon the cover glass. If the preparation is to be preserved permanently in glycerin, a drop of dilute solution of sodium chloride should be run under the cover glass before the glycerin is added to insure a permanent stain by the Gruebler eosin.

Longitudinally cruciately septate basidia are simple and pyriform or subglobose when young, but so are the probasidia of *Septobasidium,* the possible storage organs of *Corticium polygonium,* and the basidia of some species of *Corticium.* The basidia of the latter are likely to form a layer at the surface of the fructification and are certainly simple if any can be detected bearing sterigmata and perhaps spores while still non-septate. In a fructification having longitudinally septate basidia, the hymenial surface is usually composed of paraphyses and of long, slender sterigmata arranged side by side; in this surface layer—but sometimes at a con-

siderable distance from the surface, as in *Thelephora Helvelloides* Schw.—is situated the layer of basidia. Only very rarely do the basidia of *Sebacina* or *Eichleriella* constitute the surface of the fructification.

If a fructification contains a palisade layer of deeply staining, pyriform bodies among or underneath the paraphyses and with no simple basidia in the surface layer, more or less prolonged examination of the pyriform bodies is likely to show longitudinal septa in some of them.

The three genera which comprise the present part of this monograph, are treated here by the writer, because their general habit and consistency conform so closely with *Thelephoraceae* having simple basidia, that they may be regarded as a connecting group, although belonging with the *Tremellaceae* by the structure of their basidia. Such of the species as were described in the past were described as *Thelephoraceae* or by authors with special knowledge of the *Thelephoraceae;* the taxonomic recognition of fungi of these genera seems likely to continue to fall in the future to students of the *Thelephoraceae,* for other mycologists will hardly care to glean for material of so few species among the many *Thelephoraceae* of similar aspect.

TREMELLODENDRON

Tremellodendron Atkinson, Jour. Myc. **8**: 106. 1902; Saccardo, Syll. Fung. **17**: 208. 1905.

The type species is *Merisma candidum* Schw.

Fructifications coriaceous, erect, pileate, branched or rarely simple; hymenium amphigenous or inferior; basidia longitudinally cruciately septate; spores white, even.

The species of *Tremellodendron* are indigenous to North America; none have been reported for other regions, so far as I am aware. The fructifications spring up on the ground in deep woods during wet weather in summer and early autumn, and have the general habit of *Thelephora vialis,* of branched Clavarias, or, very rarely, of simple clubs. In active vegetative condition the fructifications may be distinguished from species of *Clavaria* of similar habit by coriaceous and

tough consistency and by lack of brittleness. The longitudinally septate basidia afford a decisive character in all doubtful cases.

The specific distinctions between the more common species of this genus are based largely upon the form of mature and well-developed fructifications; very young, deformed, or fragmentary specimens can not be referred very confidently to their species.

Key to the Species

Fructifications branched when well developed. Simple forms may be present when very young or in the same colony with normal branched forms 1
Fructifications simple 4
1. Fructifications normally cespitose, more or less grown together 2
1. Fructifications solitary or scattered 3
2. With pileate divisions flattened, grown together at many points of contact, forming rosette-like masses 2–15 cm. in diameter ..*1. T. pallidum*
2. With the stems grown together into a main stem 2–10 mm. thick; pileate divisions cylindric, spreading, grown together at only few points of contact; the smaller divisions about 1½ mm. thick ..... *2. T. candidum*
2. Sometimes with both stems and pileate divisions grown together into compact bundles, usually merely closely cespitose and with the branches intricately intertangled; much slenderer than preceding species and with the habit of *Pterula* ..... *5. T. merismatoides*
3. Stem about 1½ mm. thick, palmately few-branched; branches once or twice similarly branched, cylindric or subcylindric, often channelled on the upper side; basidia 15×9 μ; spores 9–15×4½–6 μ, pointed at the base only ..... *3. T. Cladonia*
3. Stem about ½–1 mm. thick, sometimes with occasional, scattered, divergent branches from its side, dilated at the upper end, divided into a few, short, finger-shaped branches; basidia 20–24×12–14 μ; spores 14–16×6–7 μ, pointed at both ends, Known from Jamaica only ..... *4. T. tenue*
4. Fructification dark orange, probably with medullary tissue pale as in all the preceding species; basidia subglobose, 10–12 μ in diameter ..... *6. T. aurantium*
4. Fructification black with the exception of the hymenium; hymenium olive-ocher, amphigenous on the lower third of the fructification; basidia 11×7 μ. Known from Porto Rico only ..... *7. T. simplex*

1. **Tremellodendron pallidum** (Schw.) Burt, n. comb.

Plate 26, fig. 6.

Thelephora (*Merisma*) *pallida* Schw. Am. Phil. Soc. Trans. N. S. **4**: 166. 1834.—*T. Schweinitzii* Peck, N. Y. State Mus. Rept. **29**: 67. 1878; Saccardo, Syll. Fung. **6**: 534. 1888.—*Tremellodendron Schweinitzii* (Peck) Atk. Jour. Myc. **8**: 106. 1902.

Illustrations: Hard, Mushrooms *f. 381.*—Moffatt, Chicago Acad. Sci. Bul. 7: *pl. 22. f. 1.* 1909.

Type: in Herb. Schweinitz and a portion in Curtis Herb.

Fructification cespitose, erect, white or pallid, drying warm buff, stipitate by one to several or many stems which may be distinct below or arise from a common, swollen, basal mass; above, the stems branch into flattened, more or less furrowed, pileate divisions which grow together at surfaces of contact to form a somewhat cup-shaped or rosette-like mass; divisions in center of mass somewhat subulate at the apex, those at margin dilated and sometimes fimbriate, splitting when dry into sharp fibers or spicules; hymenium inferior, warm buff, best developed towards the base of the pileate divisions; basidia pyriform, longitudinally cruciately septate, 12–15 × 9 μ; spores from a spore collection, white, simple, 10–12 × 4½–5½ μ, and 9–12 × 4½ μ from an herbarium specimen.

Fructifications 2–10 cm. high, 2–15 cm. broad.

On the ground in deep woods. Canada to South Carolina and westward to Missouri. June to October. Common.

Full-grown and well-developed specimens are rosette-like and resemble *Thelephora vialis* when viewed from above but may have the pileate mass supported by many stems; small specimens with only a single stem do occur. The large specimens are apparently due to the concrescence of many small fructifications. In the large specimens the pileate divisions on the outside of the mass become broader and more flattened than those in the interior. The flattened form of the divisions of the pileus and their growing together at numerous points of contact are characters separating *Tremellodendron pallidum* from *T. candidum*. The small specimens, distributed as *T. pallidum* in published exsiccati, are often so immature and fragmentary that they cannot be distinguished from *T. candidum*.

Forms of *T. pallidum* which have the tips of pileate divisions split into sharp fibers or spicules are the *Thelephora cristata* and *T. serrata* of Schweinitz, 'Syn. N. Am. Fungi,' Nos. 621 and 623.

Specimens examined:

Exsiccati: Ravenel, Fungi Car. II, 29; Ellis, N. Am. Fungi, 510; Ell. & Ev., Fungi Col., 1208; Shear, N. Y. Fungi, 50.

Canada, Ontario: London, *J. Dearness,* and also in Ell. & Ev., Fungi Col., 1208; Belleville, *J. Macoun, 174, 230* (both in Can. Geol. Surv. Herb.).

Maine: N. Parsonfield, *R. G. Leavitt.*

Vermont: near Burlington, *L. R. Jones,* two collections; Middlebury, *E. A. Burt,* two collections.

Massachusetts: *Sprague, 773* (in Curtis Herb. under the name *Thelephora vialis*); Brookline, *S. Davis.*

Connecticut: East Hartford, *C. C. Hanmer;* and also No. 1567 (in Hanmer Herb.).

New York: Alcove, *C. L. Shear,* N. Y. Fungi, 50; Floodwood, *E. A. Burt;* Taughannock, *H. H. Whetzel,* Cornell Univ. Herb., 13600; Buffalo, *G. W. Clinton* (in U. S. Dept. Agr. Herb.); Tarrytown, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 42800).

New Jersey: Laning (in Mo. Bot. Gard. Herb., 701330, 701331, 701333); Newfield, *J. B. Ellis* (in Mo. Bot. Gard. Herb., 5162), and also N. Am. Fungi, 510.

Pennsylvania: Bethlehem, *Schweinitz,* type (in Herb. Schweinitz, and a portion in Curtis Herb. and also the Nos. 621 and 623 of Schweinitz, 'Syn. N. Am. Fungi,' under the names *Thelephora cristata* and *T. serrata,* respectively); Trexlertown, *W. Herbst* (in Lloyd Herb.); Kittanning, *D. R. Sumstine.*

Delaware: Newark, *H. S. Jackson, B10.*

District of Columbia: Washington, *O. F. Cook, 2,* comm. by P. L. Ricker.

Virginia: Great Falls, *C. L. Shear, 1044.*

North Carolina: Blowing Rock, *G. F. Atkinson,* Cornell Univ. Herb., 10666, 10667, 10669, 10664 (of which the first two numbers and part of the third are in Cornell Univ. Herb. and part of the third and the last in Mo. Bot. Gard. Herb.).

South Carolina: Ravenel, Fungi Car. II, 29.

Ohio: *C. G. Lloyd, 2346* (in Lloyd Herb.); Loveland, *D. L. James* (in U. S. Dept. Agr. Herb.).

West Virginia: Eglon, *C. G. Lloyd, 02601.*

Kentucky: *S. M. Price* (in Mo. Bot. Gard. Herb., 5141, 5144, 701332, 712372); Mammoth Cave, *C. G. Lloyd, 1071.*

Illinois: *H. C. Beardslee* (in Lloyd Herb., 2175); Newton's Ferry, *E. T. & S. A. Harper, 441;* Riverside, *E. T. & S. A. Harper, 696.*

Wisconsin: Blanchardville, Univ. of Wis. Herb., 52; Madison, *E. T. & S. A. Harper, 881; C. J. Humphrey, 948* (in Mo. Bot. Gard. Herb., 44783).

Iowa: *T. J. Fitzpatrick* (in Lloyd Herb.).

Missouri: St. Louis, *N. M. Glatfelter* (in Mo. Bot. Gard. Herb., 701335, 701370, 701371); Cliff Cave, *J. B. S. Norton* (in Mo. Bot. Gard. Herb., 5126); Columbia, *B. M. Duggar, 140;* Creve Coeur, *Miss E. M. Briggs* (in Mo. Bot. Gard. Herb., 44756).

2. T. candidum Schw. ex Atkinson, Jour. Myc. **8**: 106. 1902. Plate 26, fig. 3.

Merisma candidum Schweinitz, Naturforsch. Ges. Leipzig Schrift. **1**: 110. 1822.—*Thelephora candida* Fries, Elenchus Fung. 168. 1828; Schweinitz, Am. Phil. Soc. Trans. N. S. **4**: 166. 1834.

Type: in Herb. Schweinitz, Acad. Nat. Sci. Phila.

Fructifications cespitose, erect, coriaceous-soft, white, drying warm buff, stipitate; stem thick, palmately branched, with branches spreading, branching, cylindric or subcylindric; hymenium inferior on the main branches, often amphigenous on secondary branches; basidia longitudinally septate, 10–12 × 7½–9 μ; spores colorless, simple, even, 7½–10 × 4½–5½ μ.

Fructifications 2½–5 cm. high, 2–5 cm. broad; stem 2–10 mm. thick; smaller pileate branches about 1½ mm. thick.

On ground in open woods. Vermont to North Carolina and westward to Missouri. July to September. Infrequent.

The type of *T. candidum* has the dimensions given above for recent collections. In the original description Schweinitz noted that fructifications may attain a breadth of 15 cm.; at that time he had not given specific recognition to the large and common *T. pallidum* and it may be that the large specimens to which he referred were of the latter species. *T. candidum* is closely related to *T. pallidum* but contrasts with the latter in having consolidation between adjacent fructifications

confined to the main stems from the base upward to about the region of branching; from here the branches spread so that they grow together only rarely; furthermore, the branches are distinctly cylindric or subcylindric. The spores average a little shorter than those of related species.

Specimens examined:

Vermont: Lake Dunmore, *E. A. Burt;* Newfane, *C. D. Howe.*

Massachusetts: Woods Hole, *G. T. Moore.*

New York: Alcove, *C. L. Shear, 1218;* Fishers Island, *C. C. Hanmer, 192, 193, 194* (all in Hanmer Herb.).

North Carolina: *Schweinitz,* type (in Herb. Schweinitz); Blowing Rock, *G. F. Atkinson,* Cornell Univ. Herb., 10662, 10668 (in Mo. Bot. Gard. Herb., 44775, 44776) and (in Cornell Univ. Herb., 10663).

Ohio: Granville, *H. L. Jones.*

Missouri: near St. Louis, *N. M. Glatfelter* (in Mo. Bot. Gard. Herb., 701336).

3. T. Cladonia (Schw.) Burt, n. comb. Plate 26, figs. 1, 2.

Merisma Cladonia Schweinitz, Naturforsch. Ges. Leipzig Schrift. **1**: 110. 1822.—*Thelephora Cladonia* Fries, Elenchus Fung. 168. 1828; Epicr. 537. 1836–1838; Schweinitz, Am. Phil. Soc. Trans. N. S. **4**: 166. 1834; Saccardo, Syll. Fung. **6**: 535. 1888.—*Thelephora gracilis* Peck, Torr. Bot. Club Bul. **25**: 371. 1898.

Type: in Herb. Schweinitz.

Fructifications solitary or gregarious, erect, coriaceous-soft, pallid, drying warm buff, sometimes with the older portions pale olive-gray, stipitate; stem cylindric, palmately branched into a few—often three—cylindric branches, each or some of which occasionally branch again in similar manner; branches arranged in a plane from flattened end of stem or branch or in a circle about the cylindric end of the stem which is then sometimes perforate and the branches often channelled; hymenium amphigenous, or inferior when the branch is channelled; basidia longitudinally septate, pyriform, 15×9 μ; spores colorless, simple, even, curved, $9–15 \times 4\frac{1}{2}–6$ μ.

Fructifications 2½–5 cm. high, 7 mm.–2 cm. broad; stem about 1½ mm. thick.

On ground in woods. Canada to Mississippi and westward to Missouri. August and September.

The fructification of this species is smaller than that of *T. candidum* and has but few branches, which are often arranged in a circle about the end of the stem so as to appear somewhat proliferous on the margin of an imperfect cup as in some species of the lichen, *Cladonia*—hence the specific name—or with the branches standing up side by side from the compressed apex of the main stem. Both forms of branching have been found so associated in the same collection as to preclude the possibility of regarding this difference as a basis for two species. The branches are so frequently in threes that "trifaria" was contemplated as a name for the species by one author.

Specimens examined:

Canada: *J. Macoun, 78.*

Vermont: Smugglers Notch, *L. R. Jones;* Middlebury, *E. A. Burt;* Brattleboro, *C. C. Frost* (in Univ. Vermont Herb.).

Massachusetts: *Sprague, 871* (in Curtis Herb., 5762).

New York: Hague, *C. H. Peck, 7;* Ithaca, *G. F. Atkinson,* Cornell Univ. Herb., 7708.

Pennsylvania: Trexlertown, *W. Herbst* (in Lloyd Herb.).

District of Columbia: Takoma Park, *P. L. Ricker, 822* (in Ricker Herb.).

North Carolina: *Schweinitz,* type (Herb. Schweinitz and a portion in Curtis Herb.); Blowing Rock, *G. F. Atkinson* (in Cornell Univ. Herb., 10665, 10008. A part of the latter number is in Mo. Bot. Gard. Herb., 44774).

Georgia: Tallulah Falls, *A. B. Seymour,* Farlow Herb., O, P, Q, R, U, W (in Mo. Bot. Gard. Herb., 44619, 44623–44625, 44628, 44630).

Alabama: *F. S. Earle, 13,* type of *Thelephora gracilis* (in Coll. N. Y. State).

Mississippi: Biloxi, *Mrs. F. S. Earle, 32A.*

Ohio: Cincinnati, *A. P. Morgan* (in Lloyd Herb., 32); Loveland, *D. L. James.*

West Virginia: Eglon, *C. G. Lloyd, 02634.*
Missouri: Creve Coeur, *E. A. Burt* (in Mo. Bot. Gard. Herb., 44755).

4. T. tenue Burt, n. sp. Plate 26, fig. 7.

Type: in Burt Herb. and in N. Y. Bot. Gard. Herb.

Fructifications scattered, erect, very slender, coriaceous-soft, drying warm buff, stipitate; stem equal, flexuous, drying somewhat twisted and flattened, becoming fibrillose, sometimes giving off two or three scattered, divergent, small branches, dilated above and divided in a few palmately arranged, finger-shaped branches; hymenium inferior on the dilated portion and branches; basidia longitudinally septate, 20–24 × 12–14 μ; spores colorless, simple, even, curved, pointed at both ends, 14–16 × 6–7 μ.

Fructifications 2–3½ cm. high, 3 mm. broad; stem 1½–2½ cm. long, about ½–1 mm. thick.

On the ground in wet mountainous region, altitude 3000–5200 ft. Jamaica. December and January.

This species is characterized by its long and slender stem, few branches, and the largest basidia and spores of any species of the genus. The spores differ from those of the other species in being pointed at the apex.

Specimens examined:

Jamaica: Chester Vale, *W. A. & E. L. Murrill,* N. Y. Bot. Gard., Fungi of Jamaica, 400, type; Cinchona, *W. A. & E. L. Murrill,* N. Y. Bot. Gard., Fungi of Jamaica, 614.

5. T. merismatoides (Schw.) Burt, n. comb. Plate 26, fig. 4.

Clavaria merismatoides Schweinitz, Am. Phil. Soc. Trans. N. S. **4**: 182. 1834.—*Merisma Schweinitzii* Leveille, Ann. Sci. Nat. Bot. IV. **5**: 157. 1846.—*Lachnocladium merismatoides* (Schw.) Morgan, Cincinnati Soc. Nat. Hist. Jour. **10**: 193. 1888.—*Pterula merismatoides* (Schw.) Saccardo, Syll. Fung. **6**: 742. 1888.—*Thelephora merismatoides* Lloyd, Letter No. 26: 2. 1909. Nomen nudum.—*Tremellodendron merismatoides* Lloyd, Letter No. 40: 2. 1912. Nomen nudum.—*Thelephora pteruloides* Berk. & Curt., Hooker's Jour. Bot. **1**: 238. 1849; Grevillea **1**: 148. 1873.

Type: In Herb. Schweinitz, Acad. Nat. Sci. Phila.

Fructifications erect, cespitose or fasciculate, and sometimes with stems grown together, coriaceous, branched, pallid, drying with stems warm buff and branches tawny; branches few, rather straight, filiform, angular-terete; branchlets many, dilated and fimbriate at the apex, then splitting into spreading branchlets; hymenium glabrous, amphigenous; basidia longitudinally septate, pyriform, 12–15 × 8–9 μ; spores in preparations from herbarium specimens hyaline, even, simple, 8–10 × 4½–5 μ.

Cluster of fructifications 2–5 cm. high, 2–3 cm. broad. Individual from cluster has stem 5–10 mm. long, ½–1 mm. thick; branches about ¼–⅓ mm. thick.

On the ground in open woods. Massachusetts and New York to South Carolina and westward to Missouri. June to August.

This is a small species with the habit of a *Pterula* but with coriaceous structure and longitudinally septate basidia. The fructifications of a cluster may have their stems distant from one another by spaces equal to the diameter of the stems, but the branches interlock above; in other cases the fructifications are crowded closely together and united throughout their whole length. *T. merismatoides* may be distinguished from the preceding species by the smaller diameter of the stems and branches and from all the following species by its cespitose to fasciculate habit.

The collection from West Virginia, distributed as *Thelephora pteruloides* in Ell. & Ev., 'N. Am. Fungi,' 3415 and 'Fungi Col.,' 1117, has the hymenium composed of basidia standing side by side in a distinct palisade layer and the basidia not longitudinally septate in my opinion.

Specimens examined:

Massachusetts: near Boston, *Murray,* comm. by Sprague, 250 (in Curtis Herb. under the name *Thelephora pteruloides* B. & C.); Woods Hole, *G. T. Moore, 58.*

New York: Ithaca, *G. F. Atkinson, 37;* Fishers Island, *C. C. Hanmer, 1478* (in Hanmer Herb.).

New Jersey: Haddonfield, *T. J. Collins* comm. by C. G. Lloyd.

Pennsylvania: Bethlehem, *Schweinitz,* type (in Herb.

Schweinitz); York County, *N. M. Glatfelter* (in Mo. Bot. Gard. Herb., 44742); Kittanning, *D. G. Sumstine.*

South Carolina: *M. A. Curtis, 1745* (the type and cotype of *Thelephora pteruloides* in Kew Herb. and Curtis Herb. respectively).

Ohio: Cincinnati, *A. P. Morgan,* Lloyd Herb., 2589 (determined by Morgan as *Thelephora filamentosa*).

Wisconsin: Lake Geneva, *E. T. & S. A. Harper, 842.*

Missouri: Meramec Highlands, *N. M. Glatfelter* (in Mo. Bot. Gard. Herb., 44743).

6. T. aurantium Atkinson, Ann. Myc. **6**: 59. 1908.

Type: in Cornell Univ. Herb. but cannot be found at present.

"Plants simple, slender, 1–3 cm. long, 2–3 mm. stout, dark orange, tough. Basidia subglobose, 10–12 μ, longitudinally divided; sterigmata 4, long, slender, flexuous. Spores oboval-subelliptical, granular, then with an oil drop, 7–10 $\times$ 5–6 μ, white, hyaline.—C. U. herb., No. 10684, ground, woods, along small stream crossing Boone Road, Blowing Rock, Blue Ridge Mts., N. C. G. F. Atkinson, Aug. 19–Sept. 22, 1901."

—Original description.

T. aurantium differs from the preceding species of *Tremellodendron* by its simple fructifications. I have seen no specimens referable here. Professor Atkinson had intended to make a negative from his type so that I could include a figure of the species, but, upon going to the envelopes labelled *T. aurantium,* he found that they contained—by error of a helper—*T. merismatoides* instead. The specimens of *T. aurantium* have not been found.

7. T. simplex Burt, n. sp. Plate 26, fig. 5.

Type: in Mo. Bot. Gard. Herb. and in Farlow Herb.

Fructifications scattered, erect or suberect, drying hard, brittle, somewhat longitudinally wrinkled and sometimes compressed, black above, olive-ocher with the hymenium towards the base; hymenium amphigenous on the lower third of the fructification, olive-ocher, hyaline under the microscope, with surface consisting of colorless clavate paraphyses 5 μ thick,

and with basidia and spores at base of the paraphyses; basidia longitudinally septate; 11 × 7 μ; spores colorless, even, 7½–9 × 5–6 μ.

Fructifications about 2 cm. long, about 2 mm. thick.

In cane field. Porto Rico.

T. simplex is noteworthy by the column composed of longitudinally arranged, black hyphae, which extends the whole length of fructification and constitutes the whole, upper, sterile two-thirds of the fructification and is clothed by the ochraceous hymenium on the lower third. The specimens are broken off at the base, hence I cannot be sure that a stem was not originally present, but if present it would doubtless have been included in the packet. The general habit is that of a small *Geoglossum* or cylindric *Xylaria*.

Specimens examined:

Porto Rico: *J. R. Johnston,* comm. by W. G. Farlow, type (in Mo. Bot. Gard. Herb., 5119).

EICHLERIELLA

Eichleriella Bresadola, Ann. Myc. **1**:115. 1903.—*Hirneolina* as a section of *Sebacina* Patouillard, Essai Taxon. 24. 1900.—*Hirneolina* (Pat.) Saccardo, Syll. Fung. **17**: 208. 1905.

Fructifications coriaceous, waxy or membranaceous, subgelatinous, cup-shaped or plano-concave, rarely pendulous, hymenium typically superior, discoid, inferior in pendulous forms, even or somewhat rugulose; basidia globose-ovoid, cruciately divided, with 2–4 sterigmata; spores hyaline, cylindric, somewhat curved. It is a *Stereum* or *Cyphella* with tremellaceous hymenium.

The type species of the genus is *Eichleriella incarnata* Bres.

The original definition of *Eichleriella,* which is translated above, should be broadened to accurately describe our North American species, which are as coriaceous as *Stereum spadiceum.* All have the hymenium inferior. *Eichleriella gelatinosa* is our only species with subgelatinous hymenium.

But few species of this genus are known. Five species of *Eichleriella* have been recognized up to the present time in North America, three in Europe, and two in South America;

of our five, only one species, *Eichleriella Leveilliana,* ranges through the eastern United States; *E. spinulosa* occurs in both Europe and North America.

Key to the Species

Fructifications gray, small, ½–2 mm. long, ½–1 mm. broad, with habit of *Cyphella* ..... *1. E. Schrenkii*

Fructifications the color of raspberries and cream, and peltate at first, 1–5 cm. long, ½–1½ cm. broad ..... *2. E. Leveilliana*

Fructifications ochraceous buff, 200–300 μ thick; hymenium even; known from Cuba and Brazil ..... *3. E. alliciens*

Fructifications wood-brown, with whitish margin; hymenium dry, with tubercules like *Radulum* ..... *4. E. spinulosa*

Fructification white at first, then clay-color, tomentose, soft and spongy, ½ cm. thick; hymenium gelatinous; known from Jamaica only ..... *5. E. gelatinosa*

1. **Eichleriella Schrenkii** Burt, n. sp. Plate 27, fig. 8.

Type: in Mo. Bot. Gard. Herb. and in Farlow Herb.

Fructifications gregarious, coriaceous, sessile, pezizoid, oblong or rotund, margin free and strongly inrolled, pubescent, smoke-gray; hymenium concave, pale smoke-gray to pallid neutral gray; basidia longitudinally septate, pyriform, 22 × 11 μ; spores white in collection on slide, simple, curved, pointed at base, 12–19 × 6–7½ μ.

Fructifications ½–2 mm. long, ½–1 mm. broad, ½ mm. thick.

On bark of dead limbs of *Prosopis* (mesquite). San Antonio, Texas. February.

The general habit of this fungus resembles that of very small specimens of *Corticium Oakesii,* of large species of *Cenangium,* or of a sessile *Cyphella;* from all of which *Eichleriella Schrenkii* is easily separated by its longitudinally septate basidia which show clearly in sectional preparations. The fructifications are much smaller than those of any other species of this genus heretofore described.

Specimens examined:

Texas: San Antonio, *H. von Schrenk,* type (in Mo. Bot. Gard. Herb., 42579), and also (in Mo. Bot. Gard. Herb., 42580).

2. **E. Leveilliana** (Berk. & Curtis) Burt, n. comb. Plate 27, fig. 9.

Corticium Leveillianum Berk. & Curtis, Hooker's Jour.

Bot. 1:238. 1849.—*Stereum Leveillianum* Berk. & Curtis, Grevillea 1:163. 1873.

Type: type and cotype in Kew Herb. and in Curtis Herb., respectively.

Fructification coriaceous, soft, dry, rather thick, vinaceous fawn at first, whitening with age, resupinate-effused, with the margin free, sometimes narrowly reflexed, concolorous, minutely tomentose; hymenium composed of a surface layer about 30 μ thick of paraphyses $1\frac{1}{2}$–2 μ in diameter and of a layer of basidia under this; basidia longitudinally septate, 10–18 $\times$ 6–12 μ; spores in spore collection, white, simple, curved, pointed at base, 12–16 $\times$ 5–6 μ.

Fructifications often 5 mm. in diameter at first, finally up to 1–5 cm. long, $\frac{1}{2}$–$1\frac{1}{2}$ cm. broad, about $\frac{1}{2}$ mm. thick.

On dead limbs of several species. New York to Texas, Cuba, Jamaica, Central America, and Brazil. November to May.

This is a well-marked species upon which Berkeley made the following excellent graphic comment:

"At first forming little peltate orbicular spots, which, as they dilate, become closely attached to the matrix, with the exception of the margin, which is often free, soon confluent, soft, rather thick; of the colour of raspberries and cream. Hymenium often minutely pitted. Old specimens lose in great measure their ruddy hue, and are of a dead white."

I have seen no specimens having the hymenium minutely pitted.

Specimens examined.

Exsiccati: Ravenel, Fungi Car. II, 35.

New York: Hudson Falls, *S. H. Burnham* (in Mo. Bot. Gard. Herb., 44009, 44170, 44194); Buffalo, *G. W. Clinton.*

South Carolina: *M. A. Curtis, 1220, 92* (types and cotypes in Kew Herb. and Curtis Herb., respectively); *Ravenel,* Ravenel, Fungi Car. II, 35.

Georgia: Tallulah Falls, *A. B. Seymour,* Farlow Herb., C (in Mo. Bot. Gard. Herb., 44608).

Texas: Austin, *W. H. Long, 570,* Cornell Univ. Herb.; San

Antonio, *A. B. Langlois, bd;* same locality, *H. von Schrenk* (in Mo. Bot. Gard. Herb., 42576).

Cuba: San Diego de los Baños, *Earle & Murrill, 296, 356 in part,* N. Y. Bot. Gard. Herb.

Jamaica: Cinchona, *W. A. & E. L. Murrill,* N. Y. Bot. Gard., Fungi of Jamaica, 493.

Brazil: Blumenau, *A. Möller,* comm. by G. Bresadola; Matto Grosso Cuyaba, *G. Malme, 599,* comm. by L. Romell.

3. **E. alliciens** (Berk. & Cooke) Burt, n. comb.

Plate 27, fig. 10.

Stereum alliciens Berk. & Cooke, Linn. Soc. Bot. Jour. **15**: 389. 1876; Massee, Linn. Soc. Bot. Jour. **17**: 201. 1891.

Type: in Kew Herb.

Fructification coriaceous, resupinate, sometimes narrowly reflexed, separable, ochraceous buff, the margin slightly paler, the reflexed portion tomentose; structure in section, 200–300 μ thick, (1) with hyphae next to substratum ochraceous, loosely interwoven and protruded, 3 μ in diameter, similar to those on outer surface of reflexed portion, (2) with intermediate layer 100–180 μ thick, composed of longitudinally arranged hyphae 2 μ in diameter, (3) with hymenium composed of basidia 10 μ below the surface, imbedded in jelly through which rise a few filiform paraphyses or hyphae to the surface; hymenium even, ochraceous buff; basidia longitudinally cruciately septate, pyriform, 12–15 $\times$ 9–10 μ; spores colorless, simple, even, curved, 10–13 $\times$ 3½–5 μ.

Fructifications of type described as several inches long, originally orbicular; Cuban specimen 1 cm. long, 1 cm. broad, reflexed side 1–2 mm. long, 1 cm. broad.

On dead wood in virgin forest. Cuba and Brazil. March.

The fructification resembles in habit and coloration that of a resupinate specimen of *Stereum hirsutum* with a very narrowly reflexed margin. The Cuban collection, of which but a single fructification was communicated to me, is much smaller than the Brazilian type and has the hyphae of the intermediate layer with gelatinously modified wall.

Specimens examined:

Brazil: San Antonio da boa vista, Rio Javary, *Traill, 1,* type (in Kew Herb.).

Cuba: San Diego de los Baños, Pinar del Rio Province, *Earle & Murrill, 405,* N. Y. Bot. Gard. Herb.

4. E. spinulosa (Berk. & Curtis) Burt, n. comb.

Plate 27, fig. 11.

Radulum spinulosum Berk. & Curtis, Grevillea **1**: 146. 1873.—*Radulum deglubens* Berk. & Broome, Ann. and Mag. Nat. Hist. IV. **15**: 32. 1875.—*Eichleriella deglubens* (Berk. & Br.) Lloyd, Letter No. 45: 7. 1893; Wakefield, Brit. Myc. Soc. Trans. **4**: 305. 1914.—*Stereum rufum* of English authors but not *S. rufum* Fries.—*Radulum Kmetii* Bresadola, I. R. Accad. degli Agiati Rovereto Atti III. **3**: 102. 1897.—*Eichleriella Kmetii* Bresadola, Soc. Myc. France **25**: 30. 1910.

Type: in Kew Herb.

Fructifications longitudinally and broadly effused, wood-brown, coriaceous-soft, separable, with the margin whitish, finally narrowly reflexed on the upper side and tomentose, or with margin everywhere free and curved outward; hymenium wood-brown, dry, usually bearing tubercules singly or in small clusters, with pale tips; basidia longitudinally septate, clavate, 25–36×9 μ, arranged between paraphyses with brown tips; spores simple, colorless, cylindric, curved, 15–16 × 6 μ.

Fructifications range up to 6 cm. long by 1–2 cm. wide and may be larger by confluence, about 700 μ thick; tubercules about $\frac{1}{2}$–1 mm. long.

Alabama. On bark of dead *Populus trichocarpa,* Idaho, and Oregon. July to September.

This species is distinguished by having a hymenium with configuration of a *Radulum* and cruciate basidia. The tubercules are often simple and cylindric, sometimes deformed and multifid. The wide distribution and yet the extremely local occurrence of this species together with the absence, until recently, of observations on its basidia have resulted in a very interesting synonymy. It is remarkable that this species, which occurs on *Fraxinus, Populus,* etc., in several countries of Europe, should have been collected in the United

States in Alabama, Idaho, and Oregon only. I am greatly indebted to Mr. L. Romell for a preparation from the type of *Radulum spinulosum* which makes possible the reference to this species.

Specimens examined:

Sweden: Stockholm, *L. Romell, 327*, and three unnumbered collections.

Alabama: *Peters*, Curtis Herb., 4543, preparation from type (in Kew Herb.).

Idaho: Kaniksu National Forest, Priest River, *J. R. Weir, 55.*

Oregon: Eugene, *C. J. Humphrey, 1103.*

5. E. gelatinosa Murrill, n. sp. Plate 27, fig. 12.

Type: in N. Y. Bot. Gard. Herb. and in Burt Herb.

Fructification coriaceous, effuso-reflexed, white when young, finally clay-colored, tomentose, soft to the touch, margin obtuse; context soft, spongy, zonate; hymenium tough, gelatinous, drying Hay's brown, even; basidia longitudinally septate, 13 × 11 μ; spores simple, colorless, even, flattened on one side, 8–10 × 6 μ.

Reflexed portion of fructification 1½–2 cm. long, 2½ cm. wide, ½ cm. thick.

On rotting wood in wet, wooded regions. Jamaica. December and January.

Only two collections of one fructification each were made. That of December 17 is a white, young specimen, with no basidia developed, which shows the general habit and early characters of the species, but would not have been determinable except for the later collection of January 12–14, which shows the darker coloration assumed at maturity. The thick, spongy, soft pileus of the mature fructification distinguishes this species from others known at present.

Specimens examined:

Jamaica: Troy and Tyre, Cockpit country, *W. A. Murrill & W. Harris*, N. Y. Bot. Gard., Fungi of Jamaica, 1087, type (in N. Y. Bot. Gard. Herb.), a portion in Burt Herb.; Blue

Hole, Priestman's River region, *W A. Murrill,* N. Y. Bot. Gard., Fungi of Jamaica, 180, immature specimen.

SEBACINA

Sebacina Tulasne, L. R. and C., Ann. Sci. Nat. V. **15**: 223–226. *pl. 10. f. 6–10.* 1872; Linn. Soc. Bot. Jour. **13**: 35. 1873; Brefeld, Untersuch. Myk. **7**: 102–106. *pl. 6. f. 22–26.* 1888; Patouillard, Essai Taxon. Hym. 24, 25. 1900 (with the exclusion of section *Hirneolina*).—*Exidiopsis* Brefeld, Untersuch. Myk. **7**: 94. *pl. 5. f. 20–22.* 1888.—*Stypella* Möller, A., Bot. Mitth. a. d. Tropfen. 8, Protobasidiomyceten 166. *pl. 4. f. 6, 7.* 1895.

Fructification coriaceous, membranaceous or floccose, gelatinous, waxy or pulverulent, resupinate, with habit of *Corticium;* basidia longitudinally septate, close together or scattered, sometimes between bushy conidiophores; spores colorless, producing in germination a similar spore or a cluster of conidia.

The type species of the genus is *Corticium incrustans* Pers. *Sebacina incrustans* occurs sometimes on the ground and incrusting herbaceous stems and various erect objects but is often on decaying wood; *S. Helvelloides* occurs on the ground and incrusting erect objects; *S. chlorascens* has been observed incrusting the mossy bases of living trees; the other species have been recorded only on dead wood and bark. A few members of this genus are thick and spongy and were originally included in *Thelephora;* usually the species are thin and *Corticium*-like in general habit and were in several instances published under *Corticium.* In the dried conditions some species of *Sebacina* may be tentatively recognized as such by having the hymenial surface glassy or resembling dried cartilage; but such a separation from *Corticium* is very uncertain, for some species of *Sebacina* dry with a dull, soft surface and some true Corticiums assume the appearance of dried cartilage in drying.

It seems probable that it will always be difficult to determine resupinate species of *Hymenomycetes;* it is not possible to do so from the descriptions alone of the earlier botanists. European authors have recently been enlarging such descrip-

tions by giving spore characters, dimensions of basidia, cystidia, and hyphae, and the presence or absence of clamp connections. Such additional characters may often be obtained quickly by microscopic examination of a portion of the fructification which has been teased out and crushed down in dilute potassium hydrate solution; by these helpful additional characters, some species may be recognized with reasonable accuracy, but there are comparatively few such species. Structure in section of the fructification affords important characters for the identification of resupinate species. In practical work with these species, a microscopical mount of a sectional preparation of a type specimen is the next best thing for purposes of comparison to having the type itself.

My method of determining a resupinate specimen is to observe closely its general habit and characters, such as consistency, adnation, thickness, surface, margin, substratum, and color. Color is an important character when given in terms of an adequate color standard. The color which the specimens retain in drying is often the only color character available; it is more constant, fortunately, than is commonly appreciated, for it has to be the color factor in the comparison of herbarium specimens. The preliminary observation may suggest that the species is one of several of somewhat similar habit which may be of the same genus or of various genera. The sectional preparations, which are now made, may present (*a*) a uniform, homogeneous arrangement of similar hyphae from substratum to hymenium, (*b*) dissimilar hyphae or organs distributed uniformly throughout the whole fructification, (*c*) a layered, heterogeneous arrangement of various types with the layers more or less sharply differentiated from one another, (*d*) a stratose arrangement having the first stratum extend from the substratum to the upper surface of the first hymenium, the second stratum a repetition of the first and borne on the first, and so on. Under *a* there are characteristic varieties of structure, constant for each species, such as all the hyphae in erect position extending from substratum to hymenial surface, or all interwoven, or all procumbent, and there are also constant

differences in regard to whether the hyphae are crowded close together or are loosely arranged. Under *c*, a conspicuous example would be one in which the layer next to the substratum is composed of longitudinally arranged hyphae (that is, parallel with the substratum) crowded closely together; from this layer, a few branches might extend outward at right angles to the first layer and form a layer of loosely arranged, erect hyphae — the second layer; the hyphae of the second layer might branch abruptly at its outer surface and bear a compact hymenial layer. Some species invariably form a loosely interwoven layer next to the substratum, and on the surface of this layer form a dense hymenial layer, as, for example, *Sebacina incrustans, S. chlorascens,* and *S. Helvelloides.* Sterile fructifications may frequently be determined by their general characters and structure in section.

The preparations which reveal structure in section, give also spores, basidia, paraphyses, and other organs. From the combination of general characters, structure in section, and details of spores and noteworthy organs, the species becomes manifest. Our species of *Sebacina* are described in accordance with this method in the following pages.

Key to the Species

Fructifications on the earth, running up and incrusting the bases of living stems and trunks as well as dead objects 1
Fructifications confined to bark and wood of dead branches and trunks ... 2

1. Sometimes passing into branches or ascending flaps; hymenial layer drying warm buff, 60–150 μ thick; paraphyses densely crowded and somewhat interwoven or adglutinated ..... *1. S. incrustans*
1. Pileate branches drying cream-color with a glaucous tint, imbricated, the apices spiculose or fimbriate; hymenial layer drying vinaceous brown, 140–240 μ thick ..... *3. S. chlorascens*
1. Not forming free branches or flaps; hymenial layer 200–300 μ thick; paraphyses straight and rod-like; basidia 20–25×15 μ ..... *4. S. Helvelloides*
2. Fructifications white or whitish when dry 3
2. Fructifications not white 4
3. Hymenium composed of unbranched, flexuous, even-walled, deeply staining, clavate organs 40–45×6 μ, in addition to few-branched paraphyses and basidia ..... *5. S. Shearii*
3. Hymenium composed of paraphyses and basidia; fructification 300–400 μ thick; margin thick, not closely adnate to substratum ..... *6. S. macrospora*
3. Hymenium composed of basidia and paraphyses; fructification 50–150 μ thick, shining white at first; margin very thin and closely adnate .. *7. S. calcea*
3. Hymenium composed of basidia and paraphyses; fructification 200–300 μ thick, dirty whitish; hyphae incrusted in upper two-thirds of fructification; margin thin and closely adnate ..... *8. S. monticola*

4. Drying ochroleucous, basidia at or near the surface in tissue not sharply differentiated as a layer from tissue near substratum; much crystalline matter about 100 μ below surface. On *Alnus*, South Carolina ..... *9. S. scariosa*
4. Drying some variety of brown 5
4. Drying fuscous to black 6

5. Drying cacao-brown (testaceous of Saccardo's 'Chromotaxia'); separable from substratum; resembling *S. incrustans* but with margin soon detached and spores 6–7×4½–5 μ. On juniper, Alabama ..... *2. S. deglubens*
5. Blue-purple when fresh, drying tawny olive to Saccardo's umber where directly on the wood; adnate to substratum; 30–45 μ thick; basidia 7–10×6–8 μ; spores 6–7×3–5 μ ..... *10. S. podlachica*
5. Drying cinnamon-brown; adnate to substratum; 100–140 μ thick; scattered paraphyses with bushy-branched, brown tops rise 45–60 μ above the basidia. On *Magnolia*, Delaware ..... *11. S. cinnamomea*
6. Hay's brown when moist, drying fuscous, the margin pale cartridge-buff; separable from substratum; 500–600 μ thick. On *Populus*, Idaho ..... *12. S. adusta*
6. Drying blackish plumbeous; adnate to substratum; 150–200 μ thick, the margin indeterminate. On *Populus*, Washington ..... *13. S. plumbea*
6. Grayish when moist, drying dark mouse-gray and shining; adnate to substratum; 50–160 μ thick, the margin indeterminate. On very rotten wood, New England ..... *14. S. atrata*

1. Sebacina incrustans Pers. ex Tulasne, Ann. Sci. Nat. Bot. V. **15**: 225. *pl. 10. f. 6–10.* 1872; Linn. Soc. Bot. Jour. **13**: 36. 1873. Plate 27, fig. 13.

Corticium incrustans Persoon, Obs. Myc. **1**: 39. 1796.—*Thelephora incrustans* Persoon, Syn. Fung. 573. 1801; Fries, Syst. Myc. **1**: 448. 1821.—*Thelephora sebacea* Persoon, Myc. Eur. **1**: 155. 1822; Fries, Elench. Fung. **1**: 214. 1828; Hym. Eur. 637. 1874; Saccardo, Syll. Fung. **6**: 540. 1888.—*Corticium sebaceum* Massee, Linn. Soc. Bot. Jour. **27**: 127. 1891.—*Merisma cristatum* Persoon, Syn. Fung. 583. 1801.—*Thelephora cristata* Fries, Syst. Myc. **1**: 434. 1821; Hym. Eur. 637. 1874; Saccardo, Syll. Fung. **6**: 539. 1888.—*Sebacina incrustans* Tul. ex Bresadola, in part (Hym. Hung. Kmet.), I. R. Acad. Sci. Agiati III. **3**: 117. 1897.

Illustrations: Tulasne, *loc. cit.*—Persoon, Com. Fung. Clav. *pl. 4. f. 4;* Berkeley, Outlines Brit. Fung. *pl. 17. f. 6;* Brefeld, Untersuch. Myk. **7**: *pl. 6. f. 22–26.* Hennings in Engl. & Prantl, Nat. Pflanzenfam. (**I.** 1 **)**: 91. *f. 59 C, D;* Nees, System *pl. 34. f. 256 B;* Patouillard, Tab. Anal. Fung. *f. 155;* and Essai Tax. Hym. 25. *f. 17 a, b;* Soc. Myc. Fr. Bul. **5**: *pl. 7. f. 11.*—See Saccardo, Syll. Fung. **20**: 945 for references to some additional illustrations which I have not seen.

Type: authentic specimens of *Thelephora incrustans* and *Merisma cristatum* from Persoon in Kew Herb.

Fructifications coriaceous-fleshy, varied in form, creeping on the ground and ascending and incrusting small erect objects and forming little columns and free branches, the apices somewhat awl-shaped or fringed, or effused and resupinate on bark, whitish, drying warm buff; structure in section, 250–400 μ thick, (1) with a broad layer of very loosely interwoven rather stiff hyphae, 2–2½ μ in diameter, which divide above into fine branches and form (2) a densely interwoven layer about 60–150 μ thick with the basidia in the upper 40–90 μ among the very fine (1½ μ in diameter), densely crowded, somewhat interwoven filaments from the subhymenium; basidia longitudinally septate, ovoid or pyriform, 12–20 × 9–14 μ; spores colorless, simple, even, flattened on one side or curved, 12–14 × 6–8 μ.

Fructifications 5–6 cm. long, 2–5 cm. wide, ascending objects 2–5 cm.; pileate flaps, when present, ½–1 cm. long.

On the ground in woods and incrusting objects, and resupinate on logs. Canada to Louisiana and westward to Missouri. June to October. Common.

S. incrustans is the common incrusting *Sebacina* of Eastern North America. It may usually be recognized at sight by coriaceous-fleshy consistency, occurrence on earth and running up and incrusting living objects, and pallid color. The thinner hymenial layer, paraphyses less rod-like in form, and finer and thinner-walled hyphae of layer next to the substratum afford structural characters separating specimens of this species from those of *S. chlorascens* and *S. Helvelloides.*

I exclude from the synonymy of *S. cristata, Clavaria laciniata* of Bulliard's 'Hist. Champ.' 1:208. *pl. 415. f. 1,* because in the absence of authentic specimens and observations in regard to spores and basidia, it is not certain that *C. laciniata* Bull. is *Merisma cristatum.* Bulliard's figures represent quite as well an incrusting European fungus communicated to me by Bresadola under the name *Thelephora fastidiosa* (Pers.) Fr., which has simple basidia and colorless echinulate spores. This species is the *Thelephora cristata*

of Patouillard's 'Tab. Anal. Fung.' No. 559, and *Cristella cristata* of his 'Essai Taxon. Hym.' *f. 28.* Patouillard notes that *Clavaria laciniata* is a synonym of the species which he figures. Because of the uncertainty as to whether figures of *Thelephora cristata* by European authors represent the true *Merisma* [*Sebacina*] *cristatum* Pers. or the echinulate-spored *T. fastidiosa* (Pers.), I have refrained from citing any illustrations except that of Persoon, of whose species I have studied an authentic specimen.

Specimens examined:

Exsiccati: Ellis, N. Am. Fungi, 513.

The specimen in Thuemen, Myc. Univ. 2009, under the name *Thelephora sebacea,* collected in France, is *Thelephora mollissima* Pers.

Europe: authentic specimens of *Thelephora incrustans* and *Merisma cristatum* from Persoon in Kew Herb.

Sweden: sterile specimen determined as *Thelephora cristata* by E. Fries (in Fries Herb.); Stockholm, *L. Romell, 54.*

Canada: *J. Macoun, 5, 10.*

Quebec: Hull, *J. Macoun, 203, 313.*

Ontario: near Ottawa, *J. Macoun, 40* (in Can. Geol. Surv. Herb.); London, *J. Dearness.*

Maine: Portage, *L. W. Riddle.*

New Hampshire: Shelburne, *W. G. Farlow* (in Farlow Herb.).

Vermont: Middlebury, *E. A. Burt,* two collections.

Massachusetts: Williamstown, *W. G. Farlow* (in Farlow Herb.).

New York: Hudson Falls, *S. H. Burnham, 2* (in Mo. Bot. Gard. Herb., 43995).

Pennsylvania: *Michener, 5821* (in Curtis Herb.); Trexlertown, *W. Herbst.*

District of Columbia: Rock Creek, *C. L. Shear, 793.*

North Carolina: Asheville, *H. C. Beardslee, 03126.*

South Carolina: *Ravenel, 1619* (in Curtis Herb.).

Louisiana: St. Martinville, *A. B. Langlois, F, 2015;* the same locality and collector, (3022 in Lloyd Herb.); Baton Rouge, *Edgerton & Humphrey, 667.*

Ohio: *A. P. Morgan* (in Lloyd Herb., 2655, 2656); Cincinnati,

C. G. Lloyd, 4198; Loveland, *D. L. James* (in U. S. Dept. Agr. Herb.).

Wisconsin: Blue Mounds, *E. T. and S. A. Harper, 864, 879, 880;* Madison, *W. Trelease* (in Mo. Bot. Gard. Herb., 5145, 44779); *C. J. Humphrey, 2146* (in Mo. Bot. Gard. Herb., 44784).

Illinois: Riverside, *E. T. and S. A. Harper, 698.*

Missouri: Creve Coeur, *E. A. Burt* (in Mo. Bot. Gard. Herb., 44763).

2. S. deglubens (Berk. & Curtis) Burt, n. comb.

Corticium deglubens Berk. & Curtis, Grevillea **1**: 166. 1873.

Type: type and cotype in Kew Herb. and Curtis Herb.

Fructification resupinate, effused, coriaceous, separable, white beneath, drying about cacao-brown, the margin very narrow, white, byssoid, soon detached; structure in section 250–300 μ thick, (1) with a very loosely interwoven layer 180–200 μ thick, having hyphae $1\frac{1}{2}$–2 μ in diameter which branch and form (2) a very densely interwoven layer 80 μ thick with the basidia in the upper 30 μ, not quite reaching to the surface, among the very fine, densely interwoven filaments from the subhymenium; basidia longitudinally septate, 15 $\times$ 10–12 μ; spores colorless, simple, even, flattened on one side, 6–7 $\times$ $4\frac{1}{2}$–5 μ.

On juniper, Alabama.

This fungus has the same type of structure which is found in resupinate specimens of *Sebacina incrustans.* It differs from the latter in having the hymenium darker, all the spores found in a sectional preparation a little smaller, and the hyphae of the layer next to the substratum a little smaller and more flaccid than those of *S. incrustans,* and the margin was described as soon detached. These differences may be merely the variation from specific type of a single collection, or they may be those of a subspecies of *S. incrustans* which has taken on the saprophytic life on dead wood, prevalent for most species of *Sebacina.* Until other collections, referable to *S. deglubens* are made, the former view appears the more probable.

Specimens examined:
Alabama: *Peters,* Curtis Herb., 4557, type (in Kew Herb.).

3. S. chlorascens Burt, n. sp. Plate 27, fig. 15.

Type: in Mo. Bot. Gard. Herb. and in Farlow Herb.

Fructification coriaceous, drying cream-color with glaucous tint, effused, ascending and incrusting the mossy bases of trees and forming imbricated, free, pileate, sterile branches, the apices spiculose or fimbriate; hymenium gelatinous, drying vinaceous brown, occurring in somewhat scattered spots on the lower portions of the fructification; structure in section 800 μ thick, with (1) a broad, spongy layer next to the substratum of loosely interwoven, rather rigid, even-walled hyphae $2\frac{1}{2}$–3 μ in diameter, which bear (2) a sharply differentiated hymenial layer 140–240 μ thick, composed of rod-like paraphyses 2 μ in diameter, between which occur basidia throughout the outer 60 μ of the layer; basidia longitudinally septate, pyriform, 15–18×12 μ; spores simple, colorless, flattened on one side, 10–$10\frac{1}{2}$× 6–7 μ.

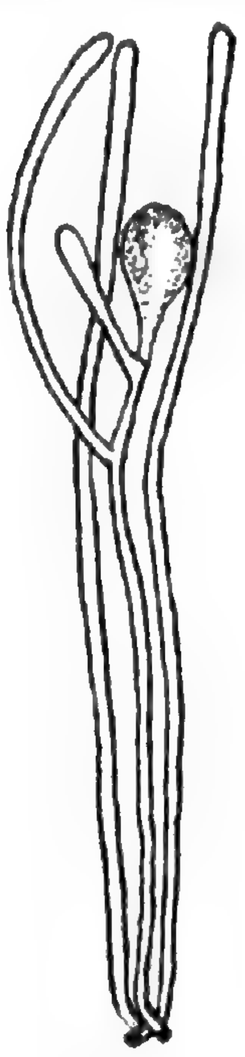

Fig. 1
S. chlorascens
Paraphyses, basidium×540.

Ascending objects 2–4 cm., 1–2 cm. broad; free branches up to 5 mm. long.

On mossy bases of living trees. Florida. Autumn.

As shown by the figures in pl. 27, the pileate branches of *S. chlorascens* do not resemble those of *S. incrustans.* The structure in section is different in every detail from that of specimens of the latter species and approaches more closely that of *S. Helvelloides,* but the fructification is thinner than that of the latter, has smaller basidia and spores, and the basidia distributed from the surface to about 60 μ below the surface, and forms free pileate branches.

Specimens examined:
Florida: Cocoanut Grove, *R. Thaxter, 98,* type (in Mo. Bot. Gard. Herb., 43923, and in Farlow Herb.).

4. S. Helvelloides (Schw.) Burt, n. comb. Plate 27, fig. 14.

Thelephora Helvelloides Schweinitz, Naturforsch. Ges. Leipzig Schrift. **1**: 108. 1822; Am. Phil. Soc. Trans. N. S. **4**: 168. 1834; Fries, Elenchus Fung. **1**: 193. 1828; Epicr. 541. 1836–1838.—*Corticium Helvelloides* Massee, Linn. Soc. Bot. Jour. **27**: 153. 1891.—*Corticium basale* Peck, N. Y. State Mus. Rept. **43**: 69 (23). 1890.

Type: in Herb. Schw. and portions in Curtis Herb. and in Kew Herb.

Fructification coriaceous, spongy, effused, convex, closely adnate and incrusting, on ground in mosses and on bark at bases of living trees, at first whitish, drying honey-color to warm buff; structure in section, with (1) a very thick spongy layer next the substratum, of loosely interwoven, branched, rather rigid, even-walled, brownish hyphae, 3–3½ μ in diameter, which bear (2) a fertile layer 200–300 μ thick made up of great numbers of erect, straight, cylindric paraphyses 2 μ in diameter, between which occur the basidia at about 40–50 μ below the surface; basidia longitudinally septate, pyriform, 20–25 $\times$ 15 μ; spores colorless, simple, flattened or slightly curved on one side, 12–13 $\times$ 6 μ.

Fructifications 3–15 cm. long and wide, drying about ½–2 mm. thick to 9 mm. thick in type which covers a cushion of moss plants.

On ground and bark at bases of living trees. New York to North Carolina. July and August.

Specimens of this species have somewhat the habit of thick specimens of *Coniophora puteana* but are of very different structure. The abundant, erect, unbranched, cylindric paraphyses often 200 μ long which compose the greater part of the hymenium, and the large basidia are reliable characters for identifying *Sebacina Helvelloides* when sections are studied; the coarser and colored hyphae of the species give an additional character separating it from *S. incrustans* when the latter occurs strictly resupinate.

The type specimen is abnormal in thickness and ridged surface by running over and incrusting a bed of moss. The hanging rootlets referred to in the original description are

moss stems. The specific name is rather fanciful and misleading.

Specimens examined:

New York: Whitehall, *C. H. Peck,* type of *Corticium basale* (in Coll. N. Y. State); Alcove, *C. L. Shear, 1221.*

North Carolina: Salem, *Schweinitz,* type (in Herb. Schw., in Curtis Herb., and in Kew Herb.).

5. **S. Shearii** Burt, n. sp. Plate 27, fig. 16.

Type: in Burt. Herb., and in Shear Herb.

Fructification coriaceous, effused, dull white, drying pale olive-buff, cracked, the margin determinate, entire; structure in section, 140–200 μ thick, with (1) a broad and dense layer next to the substratum of longitudinally arranged, slightly brownish, even-walled hyphae 1½–2 μ in diameter, which branch and curve outward at a right angle and form (2) a fertile, less compact layer 60–75 μ thick of suberect, few-branched paraphyses 3 μ in diameter, of basidia at about 15–20 μ below the surface, and of scattered, even-walled, flexuous, cylindric-clavate organs—perhaps gloeocystidia—40–45 × 6 μ, not emergent above the surface; basidia longitudinally septate, pyriform, 15 × 9 μ, with sterigmata 18 × 3 μ; spores colorless, simple, curved, 9–15 × 4½–6 μ.

Fig. 2
S. Shearii.
Paraphysis
at left,
organ ×540.

Fructifications in crevices of bark at first, 2 × 1 mm., at length, by confluence, 7 cm. long, 1 cm. broad.

On dead *Berberis vulgaris.* District of Columbia. October.

This species is well characterized by the presence in the hymenial layer of flexuous, even-walled organs, which are either latex or gloeocystidia, and by the broad layer of longitudinally arranged hyphae which shows relationship to *Eichleriella,* although the margin is not distinctly free. A few small granules are present on the hymenial surface but I do not know that they are a constant character.

Specimens examined:

District of Columbia: grounds U. S. Dept. Agr., Washington, *C. L. Shear, 1238,* type.

6. S. macrospora (E. & E.) Burt, n. comb.

Corticium macrosporum Ell. & Ev., Torr. Bot. Club Bul. **27**: 49. 1900.

Type: in N. Y. Bot. Gard. Herb.; specimens from type collection in Lloyd Herb., and in Burt Herb.

Fructification coriaceous, appressed, thin, dull white, cracked, the narrow, white, cottony margin sometimes narrowly involute; structure in section, 300–400 μ thick, with (1) a very broad layer of longitudinally arranged and somewhat obliquely ascending crowded hyphae $1\frac{1}{2}$ μ in diameter, colorless next to substratum but brownish in upper part of layer, which pass into (2) the hymenial layer 60–100 μ thick, consisting of erect, bushy paraphyses and of basidia; basidia longitudinally septate, pyriform to subglobose, 15×9–12 μ; spores colorless, simple, flattened on one side or curved, $10\frac{1}{2} \times 4\frac{1}{2}$–$6$ μ.

Appearing at first in orbicular patches 3–5 mm. in diameter, at length confluent and up to 4 cm. long, $1\frac{1}{2}$ cm. broad.

On pine (*Pinus Strobus*) limbs. Ohio. September.

This species is near *Sebacina calcea,* but the single collection which has been studied seems distinct from the latter by the thick, determinate margin, sometimes free and slightly upturned, by the greater thickness of the fructifications, by the brown hyphae of the middle region, and by walls of hyphae not gelatinously modified as in *S. calcea.* A relationship to *Eichleriella* is manifest in the broad layer of longitudinally arranged hyphae and in the tendency of the margin to be slightly free. The original description gives this species as on *"Fraxinus?"*, but the limbs are *Pinus strobus.* The spores are not exceptionally large; the specific name was probably based on immature basidia.

Specimens examined.

Ohio: Linwood, *C. G. Lloyd, 3113,* type collection.

7. S. calcea (Pers.) Bresadola, Fungi Tridentini **2**: 64. *pl. 175.* 1892. Plate 27, fig. 17.

Thelephora calcea Persoon, Syn. Fung. 581. 1801; Myc. Eur. **1**: 153. 1822.—*Thelephora calcea c. albido-fuscescens*

Fries, Elenchus Fung. **1**: 215. 1828.—*Thelephora acerina* forma *Abietis* Fries, Syst. Myc. **1**: 453. 1821.—*Corticium Abietis* (Fr.) Romell, Bot. Not. **1895**: 72. 1895.—*Xerocarpus farinellus* Karsten, Finska Vet.-Soc. Bidrag **37**: 139. 1882.

Illustrations: Bresadola, *loc. cit.;* Patouillard, Essai Taxon. Hym. 25. *f. 17b.*

Fructification effused, closely adnate, crustaceous, slightly pulverulent, shining white at first, at length darkening in the central portion from cartridge-buff to pale drab-gray, cracked, the margin much thinner and farinaceous; structure in section, 50–150 μ thick, (1) with hyphae next the substratum interwoven, 2 μ thick, the wall gelatinously modified, (2) hymenial layer 40–60 μ thick, composed of basidia and of paraphyses branched at the apex into very fine branches loaded with minute granules; basidia more abundant in the lower portion of the hymenial layer, longitudinally septate, 14×9 μ; spores colorless, simple, cylindric, curved, $8–12 \times 4–5$ μ.

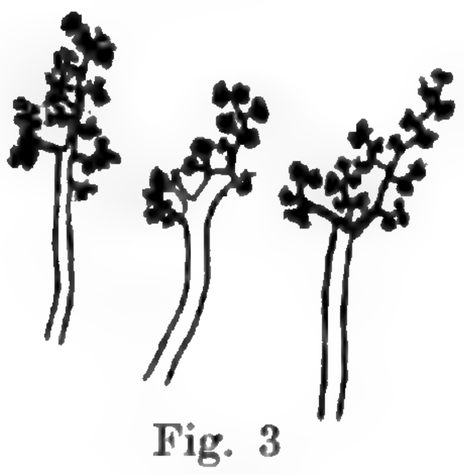

Fig. 3
S. calcea.
Paraphyses × 540.

Fructifications 3–9 cm. long, 1–3 cm. broad.

On bark and wood of dead branches of spruce, pine, hemlock, white cedar, oak, ash, elm, maple, and elder. Canada, northern New England, and New York to Georgia, and in Washington. March to January—perhaps throughout the year.

As good distinctive macroscopic characters this species has: chalky white color with central portions ashy; powdery surface under a lens; thinness on drying and margin still thinner, so that it appears mealy under a lens rather than membranous. The fine branches and granules at the tips of the paraphyses show best in lactic acid preparations; potassium hydrate solution has a solvent action here. I have not been able to study an authentic specimen of *Thelephora calcea* Pers. and accept Bresadola's conclusion on this point.

Specimens examined:

Exsiccati: Romell, Fungi Exs. Scand. 129.

Austria: *G. Bresadola.*

Sweden: *L. Romell, 58, 59;* Stockholm, *L. Romell,* Fungi Exs.

Scand. These specimens are under the name *Corticium Abietis.*

Norway: Christiania, *M. N. Blytt* (in Herb. Fries and determined by Fries as *Corticium calceum*).

Finland: Mustiala, *P. A. Karsten,* under the name *Xerocarpus farinellus.*

Canada: *J. Macoun, 30, 33.*

New Hampshire: Chocorua, *W. G. Farlow,* two collections.

Vermont: Middlebury, *E. A. Burt,* two collections; Ripton, *E. A. Burt;* Little Notch, Bristol, *E. A. Burt.*

New York: Alcove, *C. L. Shear, 1134, 1208;* Hague, *C. H. Peck, 10;* Clear Water, *G. F. Atkinson,* Cornell Univ. Herb., 5049.

Georgia: Tipton, *C. J. Humphrey, 177;* Savannah, *C. J. Humphrey, 5106* (in Mo. Bot. Gard. Herb., 15081).

Washington: Bingen, *W. N. Suksdorf, 695, 711, 763, 765, 864.*

8. S. monticola Burt, n. sp.

Type: in Mo. Bot. Gard. Herb.

Fructification coriaceous, resupinate, cracked, dirty whitish approaching pale smoke-gray, the margin closely adnate; structure in section 200–300 μ thick, with hyphae colorless, 3–4 μ in diameter, ascending obliquely from substratum to surface, densely crowded together, more interwoven and little incrusted in the lower third of the fructification, but more loosely arranged and heavily incrusted in the whole upper two-thirds, terminating in incrusted paraphyses which are either simple or 2–4-branched and with the hyphal body about $2\frac{1}{2}$ μ in diameter under the incrustation; basidia about 40 μ below the surface of the hymenium, longitudinally septate, 15–20 $\times$ 9–12 μ; spores simple, colorless, even, cylindric, straight or curved, 9–$10\frac{1}{2}$ $\times$ 5–$5\frac{1}{2}$ μ.

The portion of the fructification described is 5 cm. long, about $1\frac{1}{2}$ cm. wide.

On bark of log of *Picea Engelmanni,* altitude 8,500 ft., Pike's Peak, Colorado. August.

This species belongs in the group with *Sebacina calcea* and *S. macrospora;* it is distinguished from both of these by the

incrustation of its hyphae and by simpler paraphyses, which are either unbranched or with only about 2–4 branches not branching repeatedly and becoming so attenuated as to be nearly invisible except for the granules which they bear.

Specimens examined:

Colorado: Pike's Peak, *G. G. Hedgcock,* comm. by C. J. Humphrey, 2571, type (in Mo. Bot. Gard. Herb., 15157).

9. S. scariosa (Berk. & Curtis) Burt, n. comb.

Corticium scariosum Berk. & Curtis, Grevillea **2**: 3. July, 1873.—*Corticium secedens* Saccardo, Syll. Fung. **6**: 635. 1888.

Type: type and cotype in Kew Herb. and Curtis Herb., respectively.

"Forming a thin, oblong, membranous stratum, without any distinct border; hymenium pulverulent ochroleucous."

—Original description.

Structure in section 300–600 μ thick, with hyphae 2 μ in diameter, branched, very loosely interwoven, extending from substratum to basidia, with walls gelatinously modified, imbedded in jelly, much crystalline matter about 90–120 μ below the hymenial surface; basidia at or near the surface, longitudinally septate, pyriform to subglobose, 12–15 $\times$ 9–12 μ; no spores found.

On alder, South Carolina.

The type specimens of this species have the general habit of *Peniophora gigantea,* which they also resemble in being separable and in cracking and peeling up from the substratum, but they are more lemon-yellow in color than specimens of the latter species. The structure in section is distinctive and suggestive of that of *Eichleriella alliciens.* Authors have sometimes confused *Corticium scariosum* B. & C. with *Corticium scariosum* B. and Br., published from Ceylon a few months later in the same year. The types of these fungi are not of the same genus, the American specimens having longitudinally septate basidia.

Specimens examined:

South Carolina: Society Hill, *M. A. Curtis, 4916* (type and cotype in Kew Herb. and Curtis Herb.).

10. S. podlachica Bresadola, Ann. Myc. 1:117. 1903.

Type: in Bresadola Herb. and a portion in Burt Herb.

Fructification effused, closely adnate, described as "e pallido-caerulea caesio-hyalina," drying tawny olive to Saccardo's umber where directly on the wood; structure in section 30–45 μ thick, with hyphae 2 μ in diameter closely crowded together and rising obliquely from substratum to the surface; basidia in upper 15 μ of fructification among the hyphal filaments, longitudinally septate, pyriform, 7–10 $\times$ 6–8 μ; spores colorless, simple, even, curved, 6–7 $\times$ 3–5 μ.

Covering areas 5 cm. long, 2 cm. broad.

On decaying coniferous wood, Massachusetts; on decaying beech wood, Russian Poland.

The Massachusetts collection was noted as blue-purple when fresh; in some places algae coating the wood have been covered by the fructification and the modified color of this algal layer is seen through the dried fructification; where the fungus coats the wood directly, the color of specimens which have been several years in the herbarium is the tawny olive. The American collection agrees closely with that communicated by Bresadola.

Specimens examined:

Russian Poland: on beech wood, *Eichler*, comm. by Bresadola, part of type.

Massachusetts: on coniferous wood, *W. G. Farlow*.

11. S. cinnamomea Burt, n. sp. Plate 27, fig. 18.

Type: in Burt Herb.

Fructification effused, coriaceous, dry, closely adnate, drying cinnamon-brown, the margin determinate, thick, entire; structure in section 100–140 μ thick, with (1) a layer 10–30 μ thick next to the substratum of longitudinally arranged, densely interwoven hyphae 2–2½ μ in diameter, which bear (2) the hymenial layer composed of basidia at the lower side of the layer, and of loosely arranged, highly branched, bush-

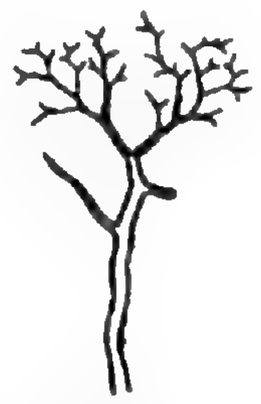

Fig. 4
S. cinnamomea.
Paraphysis $\times$ 540.

shaped paraphyses with brown branches of zigzag form, which rise 45–60 μ above the basidia and give the characteristic color of the hymenium; basidia 15–20 $\times$ 9–11 μ, longitudinal septation not positively made out; no spores found; paraphyses 75 μ long, trunk $1\frac{1}{2}$–2 μ in diameter, sweep of branched top about 20 μ.

Fructification 4 cm. long, 1 cm. broad.

On limbs of dead *Magnolia glauca.* Maryland. December.

It is not certain that this fungus is a *Sebacina,* for none of its basidium-like organs show longitudinal septa, although in a very few there is arrangement of the protoplasm suggestive of such septation. The specimen is a little too immature for generic reference but is probably a young *Sebacina* in my opinion. The species is distinct from others in possible genera by cinnamon-brown color, paraphyses scattered as to trunks but with such brown, bushy-branched tops as to form a compact surface of the color stated.

Specimens examined:

Maryland: Takoma Park, *C. L. Shear, 1339,* type.

12. S. adusta Burt, n. sp. Plate 27, fig. 19.

Type: in Burt Herb.

Fructification broadly effused, coriaceous, separable from the substratum, Hay's brown when moist, drying fuscous, the margin pale cartridge-buff, fibrillose-fimbriate; structure in section, 500–600 μ thick, composed of densely interwoven and obliquely ascending hyphae 3 μ in diameter, the walls not gelatinously modified, which bear the basidia at the surface of the hymenium; basidia longitudinally septate, pyriform, 12–16 $\times$ 8–10 μ; spores colorless, simple, curved, 10–12 $\times$ 4–5 μ.

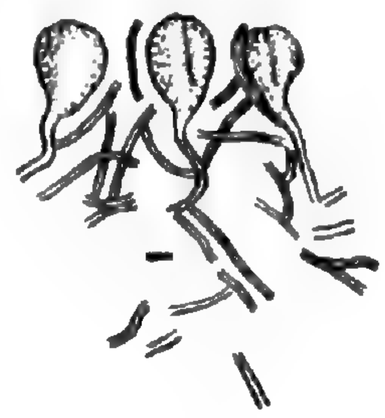

Fig. 5
S. adusta.
Basidia and
hyphae $\times$540.

Fructification 12 cm. long, 4 cm. broad.

On decorticated trunk of *Populus trichocarpa.* Idaho. July to September.

In the single collection of this species which has been received the margin is everywhere closely applied to the substratum and shows no tendency towards becoming free or

reflexed, hence the species must be included in *Sebacina*. The distinguishing specific characters are easy separation as an unbroken membrane of the moist fructification from the substratum, thickness of fructification, and position of the basidia at the surface of the hymenium.

Specimens examined:

Idaho: Kaniksu National Forest, Priest River, *J. R. Weir, 12,* type.

13. S. plumbea Burt, n. sp. Plate 27, fig. 20.

Type: in Burt Herb.

Fructification effused, closely adnate, drying blackish plumbeous, pruinose, the margin indeterminate; structure in section, 150–200 μ thick, with (1) a broad layer next to the substratum containing much crystalline matter in the interspaces between the interwoven suberect hyphae $1\frac{1}{2}$–2 μ in diameter, the wall gelatinously modified, and (2) a hymenial layer about 60 μ thick consisting of basidia, and of hyphae which branch and form a densely interwoven hymenial surface; basidia about 30 μ below the surface of hymenium, longitudinally septate, pyriform, 15–18 × 10–13 μ; spores colorless, simple, even, curved, 13–15 × $4\frac{1}{2}$–6 μ.

Fig. 6
S. plumbea. Basidia and hyphae × 540.

Fructification 4–8 cm. long, $\frac{1}{2}$–1 cm. broad.

On blackened wood of *Populus trichocarpa.* Washington. November.

The coloration and habit of specimens of this species agree closely with those of the European *Corticium plumbeum* Fr. which have been received from Karsten, but the internal structure is wholly different from that of the latter.

Specimens examined:

Washington: Bingen, *W. N. Suksdorf, 862,* type.

14. S. atrata Burt, n. sp. Plate 27, fig. 21.

Type: in Burt Herb. and in Farlow Herb.

Fructification effused, somewhat gelatinous, closely adnate, grayish when moist, drying dark mouse-gray and shining, the margin thinning out and indeterminate; structure in section,

50–160 μ thick, with even-walled hyphae 3 μ in diameter, densely interwoven next to the substratum, then curving outward to form a hymenial layer 50–90 μ thick, consisting of erect, parallel, rod-like paraphyses 2 μ in diameter and of basidia about 30 μ below the surface of the hymenium; basidia longitudinally septate, pyriform, about 18×12 μ; spores colorless, simple, somewhat flattened on one side, 8–10 $\times$ 6–7 μ.

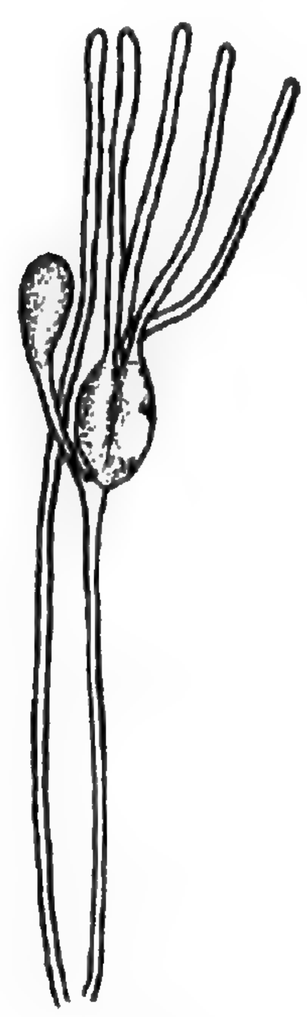

Fig. 7
S. atrata.
Paraphysis,
basidia $\times$ 540.

Fructifications $2\frac{1}{2}$ cm. long, $1\frac{1}{2}$ cm. broad.

On very rotten coniferous and frondose wood. New Hampshire and Massachusetts. May.

When bits of dried specimens of this species are moistened, they become softer and more gelatinous than is usual with those of other species of the genus, but walls of the hyphae do not show gelatinous modification in sectional preparations. The paraphyses are as noteworthy as those of *Sebacina Helvelloides*, being arranged close together side by side in a palisade layer. They are sometimes simple rods, sometimes divided into equal branches which rise side by side to the surface of the hymenium.

Specimens examined:

New Hampshire: Chocorua, *W. G. Farlow*, two collections (of which No. *a* is in Mo. Bot. Gard. Herb., 44782).

Massachusetts: Magnolia, *W. G. Farlow*, type.

(To be continued.)

Explanation of Plate

PLATE 26

The figures of this plate have been reproduced natural size from photographs of dried herbarium specimens.

Fig. 1. *Tremellodendron Cladonia.* *a*, from specimen collected in Canada by J. Macoun, 78; *b*, collected at Hague, New York, by C. H. Peck, 7; *c*, collected at Cincinnati, Ohio, by A. P. Morgan, Lloyd Herb., 32.

Fig. 2. *T. Cladonia*, from the type of *Thelephora gracilis*, collected in Alabama by F. S. Earle, 13.

Fig. 3. *T. candidum.* Collected at Newfane, Vermont, by C. D. Howe. *a* agrees closely with the type and is my standard for comparison; *b* could be separated without fracture into three portions, each having form of *a*.

Fig. 4. *T. merismatoides.* *a*, from specimen collected at York County, Pennsylvania, by N. M. Glatfelter; *b*, single fructification from the cluster *a*; *c*, from a very fasciculate specimen having stems grown together and branches still fimbriate at apex, collected at Haddonfield, New Jersey, by T. J. Collins.

Fig. 5. *T. simplex.* From type collected in Porto Rico, by J. R. Johnston. The fructification on the right is inverted.

Fig. 6. *T. pallidum.* *a*, from specimen collected at Middlebury, Vermont, by E. A. Burt; *b*, from specimen in Mo. Bot. Gard. Herb., 712370, collected at St. Louis, Missouri, by N. M. Glatfelter. Both show the growth together of the flattened pileate divisions.

Fig. 7. *T. tenue.* *a*, from type, collected at Chester Vale, Jamaica, by W. A. and E. L. Murrill, 400; *b*, from specimens collected at Cinchona, Jamaica, by the same collectors, 614.

BURT—THELEPHORACEAE OF NORTH AMERICA

1 AND 2. TREMELLODENDRON CLADONIA.—3. T. CANDIDUM.—4. T. MERISMATOIDES.—5. T. SIMPLEX.—6. T. PALLIDUM.—7. T. TENUE.

COCKAYNE, BOSTON.

EXPLANATION OF PLATE

PLATE 27

The figures of this plate have been reproduced natural size from photographs of dried herbarium specimens, except in the cases noted otherwise.

Fig. 8. *Eichleriella Schrenkii.* From the type collected at San Antonio, Texas, by H. von Schrenk. *a*, photograph of a piece of limb bearing many fructifications, and *b*, drawing of median longitudinal section of single fructification, × 16.

Fig. 9. *E. Leveilliana.* From specimens collected at San Antonio, Texas, by H. von Schrenk.

Fig. 10. *E. alliciens.* From specimen collected at San Diego de los Baños, Cuba, by Earle and Murrill, 405, in part.

Fig. 11. *E. spinulosa.* From specimen collected at Priest River, Idaho, by J. R. Weir, 55.

Fig. 12. *E. gelatinosa.* From specimens collected in Jamaica by W. A. Murrill and W. Harris. *a*, upper surface of No. 180; *b*, type specimen, 1087, split longitudinally to show thickness of pileus and structure.

Fig. 13. *Sebacina incrustans.* *a*, from specimen collected at Middlebury, Vermont, by E. A. Burt; *b*, from specimen with pileate flaps, collected at Asheville, North Carolina, by H. C. Beardslee, 03126.

Fig. 14. *S. Helvelloides.* From specimen collected at Alcove, New York, by C. L. Shear, 1221. *a* shows upper surface; *b* is a vertical section from the same fructification to show thickness.

Fig. 15. *S. chlorascens.* From type specimen collected at Cocoanut Grove, Florida, by R. Thaxter, 98.

Fig. 16. *S. Shearii.* From type specimens collected at Washington, District of Columbia, by C. L. Shear, 1238.

Fig. 17. *S. calcea.* From specimen on white cedar bark, collected at Middlebury, Vermont, by E. A. Burt.

Fig. 18. *S. cinnamomea.* From type specimen collected at Takoma Park, Maryland, by C. L. Shear, 1339.

Fig. 19. *S. adusta.* From type specimen collected at Priest River, Idaho, by J. R. Weir, 12.

Fig. 20. *S. plumbea.* From type specimen collected at Bingen, Washington, by W. N. Suksdorf, 862.

Fig. 21. *S. atrata.* From specimen collected at Chocorua, New Hampshire, by W. G. Farlow.

BURT—THELEPHORACEAE OF NORTH AMERICA

8. EICHLERIELLA SCHRENKII.—9. E. LEVEILLIANA.—10. E. ALLICIENS.—11. E. SPINULOSA.—12. E. GELATINOSA.—13. SEBACINA INCRUSTANS.—14. S. HELVELLOIDES.—15. S. CHLORASCENS.—16. S. SHEARII.—17. S. CALCEA.—18. S. CINNAMOMEA.—19. S. ADUSTA.—20. S. PLUMBEA.—21. S. ATRATA.

COCKAYNE, BOSTON.

ENZYME ACTION IN THE MARINE ALGAE

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In a previous contribution from this laboratory[1] attention has been called to the difficulties experienced in demonstrating enzyme action in *Fucus vesiculosus*. Because of the negative results there obtained it was deemed worth while to extend the study to certain representative forms of the three great groups of marine algae, the "greens," the "browns," and the "reds"; first, to ascertain whether this apparent inactivity were generally characteristic of the algae, and second, because of the light such an investigation might shed upon the general metabolism of the group.

Historical

Knowledge concerning enzyme activity and the distribution of enzymes in the algae is extremely meagre. The few papers that have found their way into the literature have been, for the most part, by-products of other studies and as such have dealt merely with isolated phases of the subject. From time to time, previous to actual demonstration, the presence of enzymes has been suggested by the work of various investigators. Arber ('01), attacking the problem of carbon assimilation in *Ulva latissima*,[2] found that the accumulation of starch in the tissue disappeared very slowly when the plant was subjected to darkness. This would suggest the presence of a diastase acting slowly. Spargo ('13) observed that *Chlamydomonas* began growth more slowly when the medium contained sucrose as a source of carbon than when dextrose was supplied. She suggests that the sugar is probably assim-

[1] Duggar, B. M. and Davis, A. R. Enzyme action in Fucus vesiculosus. Ann. Mo. Bot. Gard. 1:419–426. 1914.

[2] The binomials used throughout the historical review are those employed by the original investigators, no attempt being made to have them conform to any different existing nomenclature.

ilated in the hexose form and that sucrose must be split by invertase before becoming available. It is a well-known fact that diverse fresh-water algae can be grown in pure culture on media where asparagin and peptone are sources of nitrogen. It is hardly conceivable that the large protein molecule is assimilated directly and, *a priori,* this would argue for the presence of both an ereptase and a desamidizing enzyme.

ENZYMES FOUND IN THE MARINE ALGAE

Few workers have demonstrated enzymes present in either the fresh- or salt-water algae. Fischer ('05), working on the storage carbohydrates of *Anabaena* and *Oscillatoria,* found that the specific carbohydrate involved, which he named anabaenin, disappeared when the algal tissue was autolysed at 40°C. Microchemical tests showed glycogen split off. The action here, if it be due to ferments of the alga, is interesting in that the action was inhibited by .1 per cent acetic acid, by 1 per cent carbolic acid, and still more strangely, by concentrations of ethyl alcohol as low as 5 per cent. One per cent carbolic acid is quite often used as an antiseptic in enzyme experimentation, and the resistance of enzymes to even high concentrations of alcohol is common knowledge. No attempt was made to isolate the enzyme or to carry on experiments outside the cell.

Teodoresco ('12) found that *Chlamydomonas* in pure culture gave rise to an extracellular enzyme that decomposed sodium nucleate with the liberation of phosphorus. Later, ('12[a]) he demonstrated nucleases present in certain "blue-greens," "browns," and "reds." Unfortunately, differences in methods do not permit a true comparison of activity with that of the nuclease isolated by Dox ('10) from *Penicillium camemberti,* nor with that determined by Zaleski ('07) in the growing tips of *Vicia faba,* yet even a crude comparison is interesting. Dox added 2 grams of mold powder to 100 cc. of a 2 per cent solution of yeast nucleic acid, and maintaining his flasks at a temperature of 35–37°C. for forty-five days, found 51 milligrams of phosphorus (calculated as phosphoric acid) liberated. Teodoresco used a .5 per cent solution of sodium

nucleate with an unstated amount of crushed seaweed. The temperature during the incubation period varied from 21 to 26°C. for the different forms used. The following are his results for 100 cc. of substrate:

TABLE I

Alga	Days	Phosphorus as P_2O_5 mgms.
Cladophora frusta.....	57	54.3
Ceramium rubrum.....	51	76.6
Griffithsia setacea.....	37	62.5
Phormidium sp.....	15	90.0

Zaleski crushed growing tips of *Vicia faba,* added water and an antiseptic, and allowed this material to autolyse at 34°C. for 4 days. At the end of that time the control flask showed a free phosphorus content of 13.6 milligrams and the one containing the active enzyme 51.2 milligrams. We have no means of knowing even the relative amount of enzyme present in any of these experiments and yet it seems that the algal nuclease compares very favorably with that isolated from the fungi and the higher plants.

The classes in plant physiology at the Marine Biological Laboratory, Woods Hole, for several years past have qualitatively determined diastase in *Ulva lactuca.* Bartholemew ('14), working on the question of starch in the *Florideae,* conclusively demonstrated diastase present in such "reds" as *Polysiphonia variegata, Dasya elegans, Agardhiella tenera,* and *Ceramium sp.* In order to isolate the enzyme, he used the ordinary method of precipitation by alcohol from an aqueous extract of crushed tissue. Starch as paste was hydrolysed rather slowly to an undetermined reducing sugar, presumably dextrose, 5 cc. of .25 per cent starch paste with a relatively large amount of the enzyme material requiring from 6 to 9 days for the completion of hydrolysis. Microscopic observation of the attacked starch grain showed corrosion similar to that caused by the translocation diastase of the barley. Torup (Krefting and Torup, '09) had previously isolated an enzyme from fresh *Laminaria* that hydrolysed the characteristic storage carbohydrate of that alga, laminarin, to dextrose.

Atkins ('14) investigated the oxidases and peroxidases of twenty-nine diverse algae. Using guaiacum as a reagent, oxidases were demonstrated in but one—*Furcellaria fastigiata*—while peroxidases were shown present in seven. Alpha naphthol gave negative reactions for all the forms studied, while with it peroxidases could be determined in but two—*Delesseria sanguinea* and *Furcellaria fastigiata*. He calls attention to the reducing power of the tissues of certain algae and suggests that such agents may be responsible for the failure to obtain positive tests in the other forms. Reed ('15, '15[a]), on the other hand, holds that many of these algae may show a specific oxidative ability. Like Atkins, he found that the ordinary reagents, such as gum guaiac, alpha naphthol, and aloin, gave negative results in all but one or two instances. When, however, alpha naphthol and para-phenylenediamine, para-phenylenediamine alone, or the hydrochlorides of these two were used in the presence of peroxide, positive tests were very generally obtained.

As earlier indicated, the results obtained by Duggar and Davis ('14) for *Fucus vesiculosus* were very generally negative. This was true even though a great variety of substrates were used under varying conditions, and only vigorously growing plants, fresh crushed, or dried and powdered, were employed for enzyme action. The results are exceedingly difficult to explain. It might well be that the enzymes were present but in such small amounts as to escape detection by the ordinary methods. Methods of enzyme isolation are still crude and they undoubtedly involve some loss of the ferments. Another factor suggested in the preliminary paper, was that the death of the cell might liberate certain substances which would then be free to unite with the enzyme complex, throwing it out of the sphere of action.

SOME STORAGE PRODUCTS OF THE ALGAE

It is often assumed that the presence of storage products in the plant is generally linked with the presence of specific enzymes—starch with diastase, inulin with inulase, fats with lipase, hemicelluloses with cytase, etc. These enzymes may be present at all times, as the diastase of the potato tuber and

the diastase and maltase of the barley grain, or they may only arise when there is food transformation and translocation, as in germinating seeds. However, in the light of such possibilities of association, it is worth while to call attention briefly to some of the work that has been done on the chief storage products of the algae.

The carbohydrates have been more worked over in this respect than has any other chemical group, but much confusion still exists regarding their exact status in assimilation. Much of the study has been on the cleavage products, obtained by acid hydrolysis, of undetermined carbohydrates. These, however, are not a true index of the distribution and more restricted chemical nature of assimilable carbohydrates in the living plant; one must look rather to the work of those who have limited themselves to the isolation and determination of unaltered carbohydrates.

CHLOROPHYCEAE

Polysaccharides.—Nägeli ('63) reported "sphärokristalle" in *Acetabularia* which Leitgeb ('87) later showed were inulin. The former worker also demonstrated the presence of this carbohydrate in various members of the *Dasycladaceae.* Küster ('99) has more recently found characteristic crystal formations in *Derbesia* and *Bryopsis* which, from the many reactions they gave, appear to have been inulin. Famintzin ('67) and Krause ('70) worked on the effect of light on starch formation in *Spirogyra,* and within recent years, Timberlake ('01) has contributed observations on the starch of *Hydrodictyon.* Oltmanns ('05, p. 147) speaks of starch accumulation in the *Conjugales, Volvocales, Ulotrichales, Charales, Siphonocladiales,* and some of the *Siphonales.* He considers it the first visible product of assimilation, but thinks that it may also function as a reserve. Starch in the marine forms seems to be quite widely distributed. In the work of Arber ('01), to which reference has already been made, starch accumulation in the tissues of *Ulva, Cladophora,* and *Enteromorpha* was easily demonstrated by means of iodine. Swartz ('11) isolated starch from *Ulva* but was unable to prove its presence in *Enteromorpha,* a closely re-

lated genus. She concluded that the carbohydrates existed in the form of hemicelluloses, probably as pentosans.

Glycogen, although frequently found in the "blue-greens," where, as held by some authors (Fischer, '05), it functions as the chief reserve carbohydrate, has been demonstrated in but one case, as far as is known, in the *Chlorophyceae,* and that by Beyerinck ('04) in *Chlorella variegata.*

Simple sugars.—The nature of the simple sugars in the group is indefinite. Klebs ('96) reported a substance in the cells of certain *Heterokonteae* that reduced Fehling's solution, but this means little since most algae contain non-carbohydrate reducing substances made up chiefly of tannins and tannoidal bodies. Tihomirov ('10) used the phenylhydrazine method as modified by Senft ('04) for the detection of osozone-forming sugars in algal tissues in this group, chiefly those of *Codium bursa* and *C. tomentosum.* After a period of thirty days, for these two forms, yellow amorphous deposits appeared in the cells indicating a sugar reaction. The definite sugars these osozones represented could not be determined, but he suggests the possibility of dextrose and d-galactose. It seems evident that they must be present in very small quantities in the tissues investigated.

PHAEOPHYCEAE

Polysaccharides.—Starch is conspicuously absent from the great group of "browns," but there are, however, certain less highly condensed polysaccharides present. Schmiedeberg ('85) speaks of a dextrin-like compound which he isolated from *Laminaria.* He gave to it the name "laminarin" and the general formula, $10(C_6O_{10}O_5)$-$9H_2O$. There seems, however, to be some confusion regarding his method of arriving at these figures. Torup ('09) was able to extract a dextrin from *Laminaria sp.* with warm water, that gave dextrose on hydrolysis. This could be isolated only during the winter months. He called it "kreftin." Kylin ('13), extracting crushed *Laminaria saccharina, Fucus vesiculosus,* and *Ascophyllum nodosum,* obtained a dextrin-like compound similar to that described by Schmiedeberg and he retained Schmiede-

berg's name, "laminarin." He showed also that Torup's "kreftin" was without doubt a modification of "laminarin." Kylin ascribes to "laminarin" the same physiological function that starch performs in the higher plants, i. e., that of a reserve product. In a more recent paper ('15) he shows that there is an accumulation of the "laminarin" in the tissues of the algae during the summer months, while during the winter and spring this reserve is drawn upon by the young fronds until by the end of March very little of it is demonstrable.

Kylin was also able to clear up much of the confusion that has attended observation of the light-refracting granules present in the cells of many members of the group. They had been variously considered as of fatty nature, proteinaceous, tannin-like, and glucosidal. Reinke ('76) demonstrated fat-like bodies in the cells of *Fucus* that he looked upon as the first visible products of assimilation, a point of view later supported by Hansen ('93). Schmitz ('83) claimed two distinct bodies present, one of which, although it did not react with iodine, he called "phaeophyceenstärke," the other giving the ordinary reactions for fats. Hansteen ('92) had observed bodies in the same plant which he maintained were of carbohydrate composition and to which he applied the term, "fucosankörner." Crato ('92, '93), the same year, investigating the fat globules observed by Schmitz, suggested that they were either phloroglucin or a derivative of it, since they colored red with vanillin-hydrochloric acid. This conception was held by Bruns ('94) as well. In a later paper, Hansteen ('00) observed that the "fucosankörner" were formed in the presence of light, and this to his mind indicated that they function as the first assimilable products. Hunger's ('02) work two years later pointed to Hansteen's "fucosankörner" as being glucosidal in nature, the carbohydrate attached being bound up with phloroglucin, or at times, with tannic acid. Some of the larger "körner" gave fat reactions, some protein. Kylin found three definite bodies in the cell, the nature of which had been confused by earlier workers—fat globules, proteinaceous particles, and tannin-like bodies—these latter probably representing the "fucosankörner" of

Hansteen. He holds that none of these are to be considered the first visible products of assimilation, and suggests that here, as in most phanerogams, carbohydrates function in that rôle.

Simple sugars.—As far as is known, Tihomirov ('10) was the first to definitely demonstrate simple sugars in these plants. He used the same phenylhydrazine method employed with the "greens," but as was the case there, was unable to connect the osozones with definite sugars. The osozones took considerable periods of time to form, in some cases as long as five months, evidence pointing to the low concentration of sugars in the cell. It is a question, too, whether during this long period of incubation some of the more highly condensed carbohydrates in the cell were not hydrolysed far enough to give the sugar tests. Using the same method, Kylin ('13) was unable to substantiate these results. However, by using 40 per cent alcohol as an extracting agent, precipitating the inorganic material with lead acetate, and then purifying with alcohol, he was able to obtain reducing sugars from several of the *Fucoideae,* particularly *Laminaria digitata, L. saccharina, Ascophyllum nodosum,* and *Fucus vesiculosus.* In all cases Seliwanoff's test for fructose was positive, while dextrose was demonstrated by its osozone. These sugars he considers the first products of assimilation referred to above.

RHODOPHYCEAE

Polysaccharides.—The so-called Florideae-starch has been the source of many investigations, from the time of Nägeli ('58) and Van Tieghem ('65) to the present day. Although not identical perhaps, it is very similar to the starch of the higher plants, and as very generally held, it undoubtedly functions in the same manner. Meyer ('95), Kolkwitz ('00), and Bartholemew ('14) hold the opinion that it represents a combination between true starch and dextrin, while Bütschli ('03) suggests the possibility of its being a transitional stage between amyloporphyrin and amyloerythrin. Kylin ('13) considers it as standing midway between starch and dextrin. This investigator succeeded in isolating

Florideae-starch from *Furcellaria fastigiata,* that was readily hydrolysed to dextrose by malt diastase, and it will be remembered that Bartholemew ('14) isolated diastase from several of the "reds" that split phanerogamic starch to reducing sugars.

Simple sugars.—Very little work has been done on the di- and monosaccharides of the "reds." Tihomirov ('10) succeeded in obtaining the same yellow amorphous osozone deposits in the tissues of *Sphaerococcus crispus* and *Gigartina mamillosa* that he had in certain members of the "greens" and "browns," but here, as in the other groups, the specific osozone involved could not be determined.

FATS AS STORAGE PRODUCTS

Many observations have made it evident that fats in some form or other are generally present in the algae, their peculiar rôle, however, having been very little investigated. In some of the siphonaceous forms, particularly *Vaucheria,* they seem to replace carbohydrates. Whether fats are to be regarded as the first visible products of assimilation in these forms is disputed. Some workers hold them to be reserve products, some by-products of metabolism. If they are utilized as a reserve or storage product in any of the forms, one might expect to find evidences of lipolytic action, yet none has been reported so far.

As stated by Czapek ('13, p. 761), Loew and Bokorny find that *Spirogyra* and other filamentous forms contain 6 to 9 per cent of the dry weight as fat. This probably includes lecithin. The same authority gives the following results as obtained by Sestini, the figures being percentages of the dry weight:

Vaucheria pilus	2.94
Ulva latissima	.21
Fucus vesiculosus	.67
Valonia aegagropila	.15
Gracilaria confervoides	.11

König and Bettels ('05) made a large number of analyses of the dry tissues of a variety of marine algae and found a fat

content ranging from .20 per cent in *Enteromorpha* to .98 per cent in *Porphyra*.

RELATION OF THE ALGAE TO NITROGEN

Some of the recent work on pure culture methods with fresh-water algae, such as that of Beyerinck ('90), Charpentier ('03, '03[a]), Chick ('03), Artari ('13), Spargo ('13), and Schramm ('14) have conclusively proved that these forms can utilize organic nitrogen. Furthermore, the work of Letts and Hawthorne ('11), and Foster ('14) point to the fact that the marine forms may have this capacity as well. Letts and Hawthorne and also Letts and Richards ('11) showed that *Ulva latissima* grew better in sewage-contaminated sea-water than in water from the open sea. Foster placed strips of *Ulva lactuca* in normal and artificial sea-water, containing in addition compounds of nitrogen in varying concentrations. When urea or ammonium sulphate was added to either solution an accelerated growth took place.

The current conception concerning the assimilation of organic nitrogen by the animal organism is that the protein and amino acid molecule must be completely desamidized before the building-up process can begin. In the absence of definite information to the contrary, we can conceive of a parallel situation existing in the plant. The question at once arises in regard to the algae, whether this be due to the agency of amidases formed by the tissue, or to the activity of desamidizing bacteria, the presence of which Brandt ('99), Gran ('02), Baur ('02), Reinke ('03), Benecke and Keutner ('03), and others have shown to exist abundantly in harbor waters. Neither Letts and Hawthorne nor Foster worked with pure cultures, and these bacteria may have been the agency in their experiments to render the amino-nitrogen assimilable.

CARBOHYDRATES AND CARBOHYDRATE CLEAVAGE PRODUCTS OF ALGAL SLIME

Besides the carbohydrates that may be directly assimilable, we find those whose function in metabolism is more or less disputed. The so-called algal slime is made up chiefly of such products.

Chemical composition.—Greenish ('81) found agar from *Fucus amylaceus* to consist of 37.21 per cent gelose (probably galactan since it passed to galactose on hydrolysis) and that from *Sphaerococcus crispus* of 60 per cent of the same carbohydrate. König and Bettels ('05) give the carbohydrate composition of agar-agar from *Gelidium* as 33 per cent galactans and 3.1 per cent pentosans; by hydrolysis, d-galactose and levulinic acid were split off. Günther and Tollens ('90) found fucosan in *Fucus* from which the methyl-pentose, fucose, was split off. Galactose was also demonstrated. Sebor ('00) obtained galactose, glucose, and fructose from the slime of *Chondrus crispus* by acid hydrolysis. He held that the slime is a very complex carbohydrate of high molecular weight, made up chiefly of galactosan, glucosan, and fructosan.

The cleavage products of *Porphyra laciniata,* as investigated by Oshima and Tollens ('01), were found to consist chiefly of l-galactose and mannose, but glucose, fucose, and other pentoses were also obtained. Müther and Tollens ('04) found methyl-pentosans in several of the *Fucaceae.* König and Bettels ('05), working on the carbohydrate hydrolytic products of various species of *Porphyra, Gelidium, Laminaria, Cystophyllum,* and *Enteromorpha,* found them to consist of such hexoses as galactose, dextrose, and fructose, as well as several pentoses, chiefly methyl-pentoses. *Enteromorpha* yielded a pentose—rhamnose. The results of Swartz ('11) agree with those above, namely, that for all forms studied, representatives of the "greens," "browns," and "reds," pentosans were always present, and galactans frequently so. Kylin ('13), by direct extraction with warm water of crushed *Ceramium, Furcellaria,* and *Dumotia,* obtained substances that gave the mucic acid test for galactose, as well as the phloroglucin test for pentosans. Substances giving pentosan reactions alone were isolated from the slime of *Ascophyllum nodosum, Fucus vesiculosus,* and *Laminaria sp.* He was apparently unable to substantiate the finding of galactan in *Fucus* by Günther and Tollens, and this negative result also conflicts with the statement of Swartz, who says that the gelatinization in the algae is due to the galactan groups.

Kylin ('14) and others have also demonstrated pectin-like compounds forming the middle lamella in various members of the *Fucaceae*. These exist as the calcium salts of pectic-like acids which Kylin designates "Fucinsäure" and "Alginsäure."

PHYSIOLOGICAL SIGNIFICANCE OF ALGAL SLIME

It is seen that algal slime is made up chiefly of the anhydrides of hexoses and pentoses—carbohydrates that must be broken down to simpler form before assimilation by the plant would be possible. Two questions naturally arise: (1) Do the algae concerned form enzymes that will hydrolyse these highly condensed carbohydrates to assimilable form? (2) Does the slime itself arise through the breaking down of the hemicelluloses of the cell wall through enzymic or other causes, or does it represent a final stage in the condensation of those hemicelluloses?

Algal slime as a reserve product.—Galactanases and mannases have been demonstrated in the phanerogams and in the fungi by Bourquelot and Hérissey ('99), Grüss ('02), and Hérissey ('03). The last worker especially has clearly shown the distinct rôle that galactans and mannans may play as reserve products in the tubers of the *Orchidaceae* and in many of the *Leguminoseae*. It is significant that Gran ('02[a]) was able to isolate a marine bacillus, *B. gelaticus*, that acted on part of the constituents of agar-agar to give a reducing sugar. From the standpoint of a possible symbiosis it would be interesting to know if this organism has the ability to fix free nitrogen. Saiki ('06) experimented with a number of algal and lichen preparations containing a large proportion of carbohydrates as galactans and pentosans, and concluded that the latter could not be transformed into sugars readily by carbohydrate digesting enzymes of animal origin and scarcely more so by the vegetable enzymes, either of the higher plants or of bacteria.

Still less is known of the digestion of pentosans by the higher plants. Schöne and Tollens ('92) found no decrease in the amount of pentosans during germination and conclude

that they cannot function as reserves. Cross, Bevan, and Smith ('95) consider the pentosans as by-products of metabolism and once formed remain unalterable. Ravenna and Cereser ('09), on the other hand, in some very interesting experiments, found that when dextrose was supplied as the sole nutrient to the leaves, pentosans increased greatly, especially in the light. If, however, the function of chlorophyll is inhibited, a decrease in the amount of pentosans takes place. These results form the basis for their conclusion that pentosans may sometimes function as reserves.

The origin of algal slime.—The question concerning the origin of the slimy and gummy constituents of cells, whether they arise through enzyme action or through other causes, has provoked much discussion. There is considerable doubt whether such gums can arise directly from true cellulose or whether they are, at least in the case of the plant mucilages, laid down as such.

One might roughly group the plant gums into those arising as a result of some external excitant, such as, for example, cherry gum, acacia gum, gums of citrus, etc., and those which seem to be normal constituents of the plant, as the mucilages found in the epidermis of many seeds and plant organs. The former arise as a result of a pathological condition; the latter, as far as we know, are normal physiological products and as such are more nearly comparable to the algal slime.

Klebs ('84), investigating slime formation in some of the lower algae, particularly some of the *Desmidiaceae,* held that it was not a conversion product of cellulose. Hauptfleisch ('88) substantiated the conclusion of Klebs, and going further, states that it arises in this particular case through the activity of the protoplasm, being excreted through pores. Oltmanns ('04, p. 76) illustrates very clearly the arrangement of these pores. Tschirsch ('89) differentiates these slimes or mucilages into those giving a cellulose reaction and those not doing so, the former having some relation perhaps to the cellulose, but the latter being laid down on the cell wall as such by the protoplasm. He holds the epidermal slime of *Spirogyra* to be of this latter type, which he calls "echter Schleim." In

the same work the author concludes the slime of the *Fucaceae* and of the *Florideae* to be of the "echter" type, occurring here, however, not as a layer laid down on the inner cell wall, but as an intercellular substance. Guignard ('93) held much the same view, and in an excellent histological investigation, clearly demonstrated the presence of slime or mucilage ducts in the *Laminariaceae*.

Mucilages very similar in nature and origin to the algal slimes occur in the higher plants, and much more work has been done with them than with those occurring in the algae. It is hardly necessary to go into the historical aspect of this phase of the work. The current conception of its origin is voiced by Walliczek ('93), who, investigating rather fully the location of different types of normal mucilages by means of suitable stains, found that in almost all cases they were laid down as such. According to him, the slime forms secondary layers on the cell wall which he designates "Membranverdickungsschichten"—layers that in many instances almost completely fill the cell. Where the epidermal layer of seeds becomes gelatinous, as, for example, in those of flax, mistletoe, various *Cruciferae*, etc., it is this inner cell wall which Walliczek holds to be the seat of slime formation. Upon contact with water the slime swells remarkably, filling the cell and at times even bursting it. There may or may not be an actual hydrolysis of the true cellulose, but if there is it seems rarely to enter into mucilage formation.

Experimental

Forms used.—The algae to be used for enzyme investigation were collected in the vicinity of Woods Hole, Massachusetts, during the summers of 1913–14, at which time the plants were also dried for winter work at the Missouri Botanical Garden. Work with the fresh tissue was carried on at the Marine Biological Laboratory, Woods Hole, during the latter summer. The selection of forms with which to work was limited to those relatively abundant in the neighboring waters, a further limiting factor in selection being relative freedom from adhering marine organisms. Only those plants

were selected that were "clean." This was an important precaution, since many adhering organisms have been found to be quite active enzymatically, and the presence of even a few might well lead to serious errors in the final results. The following forms lent themselves most readily to the work:[1]

Chlorophyceae
Ulva lactuca (L.) Le Jolis
Enteromorpha intestinalis (L.) Link

Phaeophyceae
Laminaria Agardhii Kjellm.
Ascophyllum nodosum (L.) Le Jolis
Mesogloea divaricata (Ag.) Kutz

Rhodophyceae
Ceramium rubrum (Huds.) Ag.
Agardhiella tenera (J. Ag.) Schmitz
Rhodymenia palmata (L.) Grev.
Chondrus crispus (L.) Stack.

Preparation of algal material.—In addition to the question of cleanliness, great care was taken to select only plants that were in a young, vigorously growing condition. These were brought into the laboratory, placed in large aquarium jars containing salt water, picked over, and all detectable foreign matter removed. A thorough washing in running salt water for two hours was then given, after which, with the exception of one or two forms that rapidly gelatinized, the plants were placed in running fresh water for 10 or 15 minutes. This fresh water treatment was very efficacious in causing small snails and other minute marine organisms to loosen their hold.

The plants so washed were either crushed and used at once with the substrate for enzyme action, or they were dried for future use. In either case, two general ways of using the ma-

[1] With the exception of *Laminaria Agardhii* and *Agardhiella tenera*, these binomials conform to the nomenclature as given by Farlow (Marine algae of New England, pp. 1–210. *pl. 1–14.* 1881); these two forms are as given by De Toni (Sylloge Algarum **3:** p. 349. 1895) and Engler and Prantl (Nat. Pflanzenfam. 1^2:371. 1896), respectively.

terial for such action were employed. The tissue was added directly to the substrate, or it was extracted with water by the method to be described later and a water-diffusion used of the alcohol precipitate. If the fresh tissue were to be used directly, it was ground in a meat chopper two or three times, then pounded in a large mortar with an equal amount of fine, clean, quartz sand. This treatment gave a very homogeneous pulp, one in which a large number of the cells were broken down. If desired for future use, the plants were either dried at room temperature or dehydrated by the following modified Buchner "dauerhefe" process:

3 volumes	95 per cent alcohol	for 15 minutes.
3 volumes	acetone	for 15 minutes.
3 volumes	95 per cent alcohol	for 10 minutes.
3 volumes	acetone	for 5 minutes.
2 volumes	absolute alcohol or ether	for 5 minutes.

After each treatment, the dehydrating liquid was pressed out through two thicknesses of cheese cloth by making a tourniquet. Upon the removal of the absolute alcohol or ether, the tissue was spread out on adsorbent paper, either filter paper or paper toweling, until all the dehydrating agent had evaporated. A uniformly dry, brittle, easily crushed material usually resulted that was roughly broken up and stored in tightly stoppered bottles for future use. Those plants that were dried at room temperature were simply wrapped in paper or placed in paper bags until needed.

The crushing of the dry material was accomplished in the same manner as was the fresh. Usually it was ground twice or more in an ordinary meal mill, then pounded in a mortar with an equal weight of quartz sand until a very fine powder was obtained. The sand was dispensed with if the tissue were easily crushed.

Methods of isolating the enzymes.—As indicated above, there were two general methods of using the material for enzyme action: first, adding the crushed tissue directly to the substrate, either as fresh pulp or as "dauerhefe" powder;

second, by extracting the tissue with water and precipitating the protein-enzyme complex with several volumes of 95 per cent alcohol. Wherever possible the first method was used, since it was thought that in this way the maximum enzymic activity would be obtained. However, the fresh pulp and the powdered material contained a substance, or substances (probably tannoidal bodies), that reduced copper from Fehling's solution, and so in all experiments where sugar determinations were involved, it was found necessary to use the extraction and precipitation method; by this means all the unknown reducing substances were avoided. The method was as follows:

To a known amount of the crushed, fresh algal material, 3–5 volumes by weight of distilled water were added; to the powdered tissue, 8–10 volumes. The amounts varied owing to the differences in viscosity produced by the different algae. In some forms a relatively large amount of water was necessary in order to overcome difficulties in handling due to this high viscosity. Two per cent toluene was generally added as an antiseptic, or in some cases, 1 per cent chloroform-thymol mixture was used (5 per cent thymol dissolved in chloroform), and the extraction allowed to go for 12 hours at room temperature, or for 4 hours at 35° C. The water extract, if at all viscous, was then filtered off through two thicknesses of cheese cloth and the algal tissue pressed out as completely as possible by making a tourniquet of the cloth. Filtering through cotton was tried at first, both with pressure and without, but the method had the disadvantage of slowness and also that of adsorption by the cotton. Neither did filter paper lend itself efficiently to the filtration of such viscous liquids, a drier residue being obtainable in a shorter time by the cheese cloth-tourniquet method. A press would have been desirable but none was at hand. If the medium were not viscous, it was filtered with pressure through a thin layer of cotton or a coarse filter paper in the bottom of a Buchner funnel.

The protein-enzyme complex was precipitated with 3 volumes of 95 per cent alcohol. After a few moments the

coagulum either came to the top or settled to the bottom of the vessel—if to the top, it was usually very much aggregated and little difficulty was experienced in the filtering, if to the bottom, it was generally in a very finely divided condition and unless care was exercised in the decantation of the supernatant liquid the pores of the filter soon became clogged, resulting in extremely slow filtration. Time was therefore given for a complete settling out (15 minutes to half an hour sufficed) and all the clear fluid filtered off before the coagulum reached the filter paper.

A homogeneous diffusion of the precipitate was made by placing the filter paper with the attached coagulum in a known volume of distilled water. The paper could soon be removed without loss of material, and the weight of the original fresh or dry tissue represented by an aliquot portion of the solution easily reckoned. If the precipitate were not required immediately, it was dried on a filter paper at room temperature and stored in stoppered jars. In none of the experiments was the enzyme material purified further.

When dissolved in water, the precipitates behaved differently. Some, especially those where much slime had been noticed in the extraction, gave an extremely viscous suspension, others a suspension of low viscosity. In *Laminaria* and *Chondrus,* where the extract had been quite viscous and slimy, the protein was caught up in the precipitated slime in such a way as to make the freeing of it practically impossible. The precipitate in these cases was very large and when diffused in water gave a suspension difficult to handle. *Rhodymenia, Ceramium,* and *Enteromorpha,* on the other hand, gave a finely divided precipitate that produced no viscosity.

Glassware, antiseptics, solutions, etc.—With few exceptions, the various experiments were set up in 125 cc. Erlenmeyer flasks. All glassware was thoroughly cleaned with strong soap and then with chromic-sulphuric cleaning mixture, after which it was rinsed several times with tap and distilled water.

Solutions were made up from either Merck's or Kahlbaum's "guarantiert" chemicals.

Three general antiseptics were used—toluene, alcohol to 20 per cent, and 5 per cent thymol in chloroform. Toluene was, in general, the most satisfactory. Usually it was used to 2 per cent concentration, but where large surfaces were exposed, as high as 4 per cent was found necessary. The chloroform-thymol was also very efficacious, but in the carbohydrate experiments chloroform could not be used because of its power of reducing copper. In the lipase work the substrate was made up to 20 per cent alcohol since the action seemed to proceed best in the presence of this antiseptic. In all cases where the experiments were maintained over a considerable period of time, it was necessary to add additional antiseptic from time to time.

Checks were set up in all experiments—on the substrate, on the material used to demonstrate enzyme action, and on the substrate plus such enzyme material boiled to destroy any ferments that might be present.

CARBOHYDRASES OF THE ALGAE

In these experiments the alcohol precipitate from an aqueous extract of crushed, fresh or dried, algal tissue was employed as an enzyme source, this precipitate being diffused in such a volume of distilled water that one gram of the original material was represented by 5 cc. of the diffusion. Thus one can more closely compare the amounts of enzyme present in definite amounts of different algal tissue. The number of cubic centimeters of diffusion will be noted in connection with each set of experiments.

Substrates.—Starch, dextrin, inulin, sucrose, maltose, lactose, glycogen, and in one or two cases, laminarin isolated from *Laminaria Agardhii,* were used as substrates. These were made up in 1 per cent concentrations with the exceptions of maltose and glycogen, where .25 per cent, and laminarin, where .5 per cent concentrations were employed.

Of the many suggested methods for making up starch paste, the following one used by Clark ('11) was found to give the best satisfaction. Ten grams of potato starch were weighed out and placed in a beaker with 250–300 cc. of distilled water.

This was brought to a boil with constant stirring, and when an opalescent solution resulted the paste was transferred with rinsing to a 2-liter flask containing about 500 cc. of boiling water. The lot was boiled under a reflux condenser for two hours, cooled, and made up to a liter. Although, as is stated by Clark, this treatment is very effective in breaking down the starch grain physically, no detectable hydrolysis takes place, and the additional advantage is gained in obtaining a paste that will not settle out, even after long standing. Two per cent toluene was employed as an antiseptic if the starch were not to be used immediately.

Since all dextrin obtainable contained some reducing sugar, it was found necessary to purify it by making a concentrated solution in hot distilled water, and then precipitating out with several volumes of 95 per cent alcohol. The dextrin was caught on a filter paper and dried at a low constant temperature.

Laminarin, a dextrin-like carbohydrate found in many of the *Fucaceae,* was isolated from *Laminaria Agardhii* according to the method employed by Kylin ('13), with some few slight modifications. Freshly collected *Laminaria* was crushed in the usual way and 1,680 grams of the pulp were boiled with 7 liters of water for 24 hours, water being added from time to time to replace that lost through evaporation. The extract was then filtered off through a double thickness of cheese cloth, and the residue pressed out with a tourniquet. About 3,000 cc. of a dirty brown filtrate were obtained which was divided into three lots of 1,000 cc. each. To the first of these was added a concentrated $Ba(OH)_2$ solution until the precipitation of the inorganic matter was complete. The precipitate was caught on a cotton filter in a Buchner funnel, the filtrate being a clear, golden-colored liquid. The inorganic material in the other two lots was precipitated with basic lead acetate, the liquid filtered off through cotton, and the excess of lead removed with H_2S. The solutions were filtered while hot through double filter paper to remove the lead sulphide, and then the excess of H_2S was driven off with heat. The three portions were first evaporated to about one-

third their volume, when the scum that formed was filtered off; this filtrate was then further evaporated to about one-fifth the original volume on the water bath. At this point the two lead acetate portions were placed together. Ninety-five per cent alcohol was added to each of the lots to about 80 per cent concentration when a flocculent precipitate came down rather slowly. With the $Ba(OH)_2$ portion this was copious, with the lead acetate, slight. After two hours the precipitates were filtered off, washed with absolute alcohol, redissolved in a small amount of distilled water, and then reprecipitated with 4 volumes of absolute alcohol, the resulting precipitate being dried over $CaCl_2$. From the $Ba(OH)_2$ portion, 4.2 grams of a creamy white powder were obtained that gave a very slightly reddish tinge with iodine, did not reduce Fehling's, and was easily soluble in water, giving a clear solution. Upon hydrolysis with weak H_2SO_4 a reducing sugar was split off. The lead acetate portion gave but two grams of the same material. This powder was taken to be the laminarin described by Kylin.

The determination of reducing sugars.—The reduction of copper, or in the case of maltose and lactose, the increase in the reducing value of the substrate plus the enzyme over that of the checks, was taken as the measure of carbohydrate hydrolysis. In this determination the permanganate titration method, as modified and described by Shaffer ('14), was used, it being possible with it to determine amounts of sugars as low as 2 milligrams[1] very accurately and quickly. Shaffer's description may not be generally available to plant workers who may desire to use this really splendid method, and so the various steps in the process as used here are set down in some detail.

Ten cc. of the carbohydrate-enzyme substrate were placed in a large test-tube containing 5 cc. of water, and just brought to a boil. At this point a drop of 50 per cent acetic acid was added. When the slight protein precipitate formed, 5 cc. of

[1] Shaffer determines values below two milligrams, but as used here, consistent results could not be obtained where less than that amount was involved. Below this point the relative increase in the experimental error is large.

colloidal iron (Iron dialysed, Merck) were pipetted in and the tube well shaken, the iron then being flocked out with .25 gram of Na_2SO_4. Upon the addition of this latter the mixture was again thoroughly shaken and the iron precipitate thrown down by centrifuging, the resulting clear, supernatant liquid then being decanted off through a small filter. This filtrate was entirely free of proteins or other substances which, through oxidation later, would lead to errors in the permanganate values. Ten cc. of this filtrate were placed in a 50 cc. lipped centrifuge tube, and standard Fehling's solution added, the copper content of which was in excess of that reducible by the sugar present.[1] The tube was then placed in a boiling water bath for 10 minutes, at the end of which time it was centrifuged at a moderate speed for 2 minutes, the supernatant unreduced Fehling's carefully decanted off, a like volume of distilled water added, and the cuprous oxide again thrown down by a 2-minute centrifuging. All but 1 or 2 cc. of this wash water was carefully decanted off, and the copper dissolved in the smallest amount necessary of a mixture of equal parts of 10 per cent ammonium ferric sulphate and 50 per cent sulphuric acid. It was found that if the copper were stirred up with a glass rod just before dissolving, it went into solution more readily. The dissolved copper was titrated directly in the centrifuge tube against N/50 $KMnO_4$.[2]

By calculation it is found that 1 cc. of N/50 $KMnO_4$ is equivalent to 1.27 milligrams of copper, and for the conversion of this into glucose use was made of the table prepared by Shaffer.[3]

As stated by Shaffer, care must be observed on the three following points: (1) to eliminate all oxidizable substances other than sugar, (2) to titrate the cuprous oxide immediately after dissolving, (3) to use poor conductors of heat as containers of the centrifuge tubes in the water bath, else many broken tubes will result. As employed here, circular wire

[1] In the determinations made here this amount never exceeded 10 cc.

[2] It is necessary to titrate immediately after dissolving because of the danger of oxidation of the cuprous oxide. If larger amounts of sugar are concerned, N/10 $KMnO_4$ may be used.

baskets having wooden bottoms and tops were used, the tops containing holes large enough for the free insertion of the centrifuge tubes, and the bottoms, slight depressions into which the tubes might rest. It is always necessary to run blanks with Fehling's solution since some reduction always takes place. The cuprous oxide solvent must be free from ferrous iron, and this can be assured by the addition of a trace of permanganate.

Method of setting up experiments.—Fifty cc. of the substrate to be used were placed in 125 cc. Erlenmeyer flasks with 2 per cent toluene as an antiseptic. If the series were maintained longer than six weeks, another 2 per cent toluene was added. As previously noted, in these carbohydrate experiments the material used for enzyme action was an alcohol precipitate from a water extract of algal powder or pulp. This was diffused in water so that 10 cc. of the diffusion represented 2 grams of the original tissue. Usually this amount was added to the substrate to be tested. Duplicates and checks were set up in accordance with the following model series for starch:

1. 50 cc. starch, 10 cc. enzyme diffusion.
2. 50 cc. starch, 10 cc. enzyme diffusion.
3. 50 cc. starch, 10 cc. boiled enzyme diffusion.
4. 50 cc. starch, 10 cc. boiled enzyme diffusion.
5. 50 cc. starch, 10 cc. distilled water.
6. 50 cc. starch, 10 cc. distilled water.

[3] To make this table more generally available, it is printed here in full.

Shaffer's table of copper-glucose equivalents

mgms. copper	mgms. glucose	mgms. copper	mgms. glucose	mgms. copper	mgms. glucose
0.7	.47	6.0	2.74	20.0	9.71
1.0	.62	7.0	3.21	25.0	12.25
1.5	.88	8.0	3.68	30.0	14.80
2.0	1.11	9.0	4.15	35.0	17.40
2.5	1.32	10.0	4.65	40.0	20.00
3.0	1.50	12.0	5.61	50.0	25.00
3.5	1.67	14.0	6.61	60.0	30.10
4.0	1.82	16.0	7.61	80.0	40.40
5.0	2.27	18.0	8.65	100.0	50.70

In addition, at the end of a complete carbohydrate series there were included for each alga the following checks:

1. 50 cc. distilled water, 10 cc. enzyme diffusion.
2. 50 cc. distilled water, 10 cc. enzyme diffusion.
3. 50 cc. distilled water, 10 cc. boiled enzyme diffusion.
4. 50 cc. distilled water, 10 cc. boiled enzyme diffusion.

Where the enzyme diffusion referred to above actually contained carbohydrases, it was extremely difficult to render them inactive by heating—10 minutes at the boiling point not being sufficient in most cases to more than slow down the action. This was probably due to the impurities contained, the relatively large amounts of protein and slime present tending to protect the enzymes. Those extracts relatively richer in such constituents proved the more difficult to render inactive. The expedient was finally adopted of placing the enzyme material in the autoclave and bringing the pressure in the latter up to 15 pounds. This proved quite effective.

THE CARBOHYDRASES OF ULVA LACTUCA

The effect of an extract of Ulva lactuca on different starches.—Since starches were to be used in many of the following

TABLE II

THE ACTION OF ULVA LACTUCA "DIFFUSION-EXTRACT"* UPON CERTAIN STARCHES

Starch 50 cc. 1 per cent	15 days		30 days	
	Sugar as glucose in 5 cc.† mgms.	Iodine test	Sugar as glucose in 5 cc. mgms.	Iodine test
Potato	10.1	Blue, trace red	17.4	Complete hydrolysis
Arrowroot	9.8	Blue, trace red	16.9	Complete hydrolysis
Wheat	9.9	Blue, trace red	17.1	Complete hydrolysis
Corn	6.3	Blue	10.8	Reddish purple
Soluble	8.7	Blue	15.9	Traces dextrin
Inulin	....	.....	Trace‡	.....

* Wherever the term "diffusion-extract" is employed, it refers to a diffusion in water of the alcohol precipitate from an aqueous extract of the alga under discussion.

† The sugar values in this and the following tables are net, i. e., sugar values for all checks have been deducted.

‡ In all the following experiments an amount of sugar below 2 mgms. is designated a "trace."

experiments, it was desired to know which, if any, were the most favorable substrates for the diastases of the algae. The action of diastase from *Ulva lactuca* was taken as an index. Potato, arrowroot, wheat, corn, and soluble starch, as well as inulin, were made up in 1 per cent concentrations in the manner previously described. To 50 cc. of each of these substrates were added 10 cc. of a diffusion of an alcohol precipitate from a water extract of dehydrated *Ulva lactuca*. Two per cent toluene was added as an antiseptic, and the flasks maintained at a temperature of 35°C. for 30 days. The results of the experiments are given in table II.

The data show but slight differences in the rate of digestion of the starches with the exception of corn starch, and the reason for this is not clear. One would expect it to be due to some impurity in the starch rather than to an inherent difference in the granule. The action on inulin was so slight as not to warrant the assumption of hydrolysis due to inulase.

The action of an extract of Ulva lactuca upon various carbohydrates.—A series was arranged using a "diffusion-extract" from *Ulva lactuca* with the following substrates: potato starch, dextrin, glycogen, sucrose, maltose, and lactose. Ten cc. of the "diffusion-extract" were added to each flask with 50 cc. of substrate, 2 per cent toluene used as an antiseptic, and the flasks maintained at a temperature of 35°C. for 30 days. The data are given in table III.

TABLE III

THE ACTION OF AN EXTRACT OF ULVA LACTUCA UPON VARIOUS CARBOHYDRATES

Substrate	Sugar as glucose in 5 cc. mgms.	
	15 days	30 days
Starch	10.20	15.50
Dextrin	6.30	9.95
Glycogen	2.25	3.50
Sucrose	.....	Trace
Lactose	.....	.....
Maltose	.....	Trace

The two polysaccharides, starch and dextrin, are very readily attacked even though the action is slow. Glycogen, which is hydrolysed by most diastatic enzymes with about the

same ease as starch, seems very slightly acted upon by the carbohydrases of *Ulva*. The failure of action on sucrose and lactose is not so surprising as is that on maltose, for one would expect the action on polysaccharides to continue to what is generally held to be directly assimilable sugars, i. e., the hexoses.

THE CARBOHYDRASES OF ENTEROMORPHA INTESTINALIS

This series (table IV) was run under exactly the same conditions as the one preceding. The "diffusion-extract" was from dehydrated tissue about two months old. Ten cc. of this were used with each 50 cc. of substrate, toluene added as an antiseptic, and the flasks kept at a temperature of 35°C. for 30 days.

TABLE IV

THE ACTION OF A "DIFFUSION-EXTRACT" FROM AIR-DRIED ENTEROMORPHA TISSUE UPON CERTAIN CARBOHYDRATES

Substrate	Sugar as glucose in 5 cc. mgms.	
	15 days	30 days
Starch	9.7	13.1
Dextrin	5.1	9.8
Glycogen	2.8	3.9
Inulin	Trace	Trace
Sucrose	....	Trace
Lactose	....	....
Maltose	....	....

The results for this closely related form are consistent with those obtained for *Ulva,* the action in the present case, however, being somewhat slower. The more common polysaccharides are acted upon while the disaccharides are not attacked.

THE CARBOHYDRASES OF LAMINARIA AGARDHII

The water extract from air-dried Laminaria tissue was extremely viscous and upon addition of alcohol, a very heavy precipitate was thrown down that contained a large amount of algal slime. When water was added to this precipitate in the usual ratio a very viscous diffusion was obtained. Ten cc. of the "diffusion-extract" were used with 50 cc. of the substrate and 2 per cent toluene added as an antiseptic. The flasks were kept at a temperature of 20–22°C. for 100 days,

portions being removed and sugar determinations made at the definite intervals noted in table v.

The carbohydrases in this form appear to be limited to those acting on starch and dextrin, and with these the hydrolysis proceeds much more slowly than was true with either of the preceding "greens." The lower temperature at which the hydrolysis occurred does not explain completely the lessened action. Inhibiting substances or else an actually smaller concentration of the enzyme seem to be important factors.

TABLE V

THE ACTION OF A "DIFFUSION-EXTRACT" FROM AIR-DRIED LAMINARIA TISSUE UPON CERTAIN CARBOHYDRATES

Substrate	Sugar as glucose in 5 cc. mgms.			
	15 days	45 days	75 days	100 days
Starch	Trace	3.25	4.7	6.5
Dextrin	Trace	4.1	6.85	8.3
Glycogen	Trace	Trace	Trace	Trace
Inulin	....	....	Trace	Trace
Sucrose	....	....	Trace	Trace
Lactose	....	....	....	....
Maltose	....	....	Trace	Trace

Another series (table VI) of flasks was set up with the same form, using a "diffusion-extract" from the fresh tissue. Ten cc. of this diffusion represented 6 grams of the Laminaria pulp. In addition to the usual substrates, .5 per cent laminarin was used. Toluene was added and the flasks maintained for 60 days at room temperature (22–23°C.).

TABLE VI

THE ACTION OF A"DIFFUSION-EXTRACT" FROM FRESH LAMINARIA TISSUE UPON CERTAIN CARBOHYDRATES

Substrate 100 cc.	Sugar as glucose in 5 cc. mgms.				
	7 days	15 days	30 days	45 days	60 days
Starch	.....	Trace	2.7	4.2	5.35
Dextrin	Trace	Trace	3.6	5.15	7.40
Laminarin	Trace	2.4	3.9	5.4	5.65
Glycogen	Trace	Trace	Trace	Trace	Trace
Inulin	.....	.....	.....	Trace	Trace
Sucrose	.....	.....	Trace	Trace	Trace
Lactose	.....	.....	.....	.....	.....
Maltose	.....	.....	Trace	Trace	Trace

The diastases of fresh *Laminaria* seem slightly more active than those isolated from the dried tissue; however, no other carbohydrases were evident than those shown in the previous table.

THE CARBOHYDRASES OF ASCOPHYLLUM NODOSUM AND MESOGLOEA DIVARICATA

The Mesogloea material was dehydrated as soon as brought into the laboratory, the preliminary fresh-water washing being omitted because of the rapid gelatinization of the tissue. The crushed dried tissue, extracted in the usual way, gave a very heavy, stringy precipitate with alcohol, consisting, as did that from *Laminaria,* mostly of slime. This, when diffused in the usual volume of water, gave a very viscous mixture. Crushed fresh *Ascophyllum* was extracted directly. The viscosity of the extract was high, but the alcohol precipitate from it came down in a flocculent mass that gave only a slightly viscous diffusion with water.

Experiments were set up with the various carbohydrates heretofore employed, including laminarin, and in the different series, amounts of the "diffusion-extract" were used varying from 5–15 cc. As was true with the *Fucus* reported in the previous study, in no case were there evidences of hydrolysis even after 60 days at room temperature.

THE CARBOHYDRASES OF RHODYMENIA PALMATA

The air-dried Rhodymenia tissue proved to give rise to one of the most viscous extracts encountered in the algae, 20 volumes of water being necessary to make handling possible. With alcohol, a very rubbery, white precipitate came down that was made up of a large proportion of algal slime. This diffused very slowly, giving an extremely viscous mixture. Ten cc. of the "diffusion-extract" were used with the substrate to determine action, and toluene was added. The flasks were kept at a temperature of 21–22°C. for 100 days, sugar determinations being made from time to time, the results of which are given in table VII.

The results here are quite comparable to those obtained with *Ulva* and *Enteromorpha,* the same carbohydrates being

acted upon, although perhaps a little more slowly. This action is definitely progressive with starch, dextrin, and laminarin, but with glycogen it takes a sudden jump during the 15–45-day period, then remains practically stationary for the rest of the time the series is being maintained. As was true of the results shown in the previous tables, this carbohydrate was less favorable as a substrate than any of the other polysaccharides employed.

TABLE VII

THE ACTION OF A "DIFFUSION-EXTRACT" FROM AIR-DRIED RHODYMENIA TISSUE UPON VARIOUS CARBOHYDRATES

Substrate	Sugar as glucose in 5 cc. mgms.			
	15 days	45 days	75 days	100 days
Starch	9.2	12.2	14.8	18.2
Dextrin	8.25	9.7	10.3	11.1
Glycogen	Trace	6.1	6.4	6.7
Laminarin	4.7	7.3	9.6	10.5
Inulin	....	....	Trace	Trace
Sucrose	....	Trace	Trace	Trace
Lactose	....	....	....	Trace
Maltose	....	....	Trace	Trace

THE CARBOHYDRASES OF AGARDHIELLA TENERA

The very succulent nature of the freshly collected material compelled its partial dehydration immediately. Two 15-minute treatments with 95 per cent alcohol were used, then the tissue spread out on paper toweling to dry at room temperature. After drying, it was very easily powdered without the aid of quartz sand. The alcohol precipitate from a water extract of this powder was quite fine and flocculent, differing much from that of *Rhodymenia,* both in amount and in nature.

TABLE VIII

THE ACTION OF A "DIFFUSION-EXTRACT" FROM DEHYDRATED AGARDHIELLA TISSUE UPON CERTAIN CARBOHYDRATES

Substrate	Sugar as glucose in 5 cc. mgms.			
	15 days	45 days	75 days	100 days
Starch	6.35	9.4	14.5	20.9
Dextrin	7.00	10.5	15.95	19.7
Glycogen	2.35	6.15	6.65	6.85
Laminarin	5.8	8.3	11.6	13.2
Inulin	....	Trace	Trace	Trace
Sucrose	Trace	Trace	Trace	Trace
Lactose	....	....	....	Trace
Maltose	....	....	Trace	Trace

It diffused readily in water with no resulting viscosity. Ten cc. of the "diffusion-extract" were used for enzyme action, toluene added, and the flasks kept at a temperature of 21–23°C. for 100 days. The data here obtained are given in table VIII.

Dextrin here more nearly approaches starch as a favorable substrate, differing from the action evidenced by the other algae with the exception of *Laminaria,* where all action was slow. There is also a slightly increased action over that evidenced by *Rhodymenia,* for all the carbohydrates hydrolysed.

THE CARBOHYDRASES OF CERAMIUM RUBRUM

As was the case with *Rhodymenia,* it was necessary here to use 20 volumes of the water-extracting medium, not, however, because of the great viscosity, but on account of the great adsorption of water by the tissue particles. The alcohol precipitate was copious and finely flocculent. It diffused in water rather slowly, giving a mixture that was only slightly viscous. Ten cc. of the "diffusion-extract" were used for action, the usual percentage of toluene added, and the flasks maintained at a temperature of 21–23°C. for 100 days. The data are given in table IX.

TABLE IX

THE ACTION OF A "DIFFUSION-EXTRACT" FROM FRESH CERAMIUM TISSUE UPON CERTAIN CARBOHYDRATES

Substrate	Sugar as glucose in 5 cc. mgms.			
	15 days	45 days	75 days	100 days
Starch	6.85	8.1	11.75	16.9
Dextrin	11.5	15.0	17.5	19.6
Glycogen	Trace	6.2	7.3	8.85
Laminarin	7.2	9.4	12.1	12.2
Inulin	....	....	Trace	Trace
Sucrose	....	Trace	Trace	Trace
Lactose	....	....	....	Trace
Maltose	....	Trace	Trace	Trace

Dextrin proved the most favorable substrate for the carbohydrate enzymes of this alga, the hydrolysis being about the same as that evidenced by *Agardhiella.* With the exception of glycogen, the other carbohydrates showed a decreased hydrolysis when compared with this latter form, and when

compared with *Ulva* the difference is quite marked. As in the other algae, *Ceramium* showed no ability to hydrolyse the disaccharides used.

A COMPARISON OF THE DIASTATIC ACTIVITY OF ULVA LACTUCA WITH THAT OF LEAF TISSUE FROM SOLANUM TUBEROSUM

One of the very evident facts brought out by the data in the preceding tables was the relative slowness with which hydrolysis was carried on. This point made it seem worth while to compare, in a general way, the activity of such a form as *Ulva* with the starch-forming leaf tissue of a higher plant, one from which diastase could be isolated rather easily. The potato (*Solanum tuberosum*) was chosen.

The Ulva tissue was from an air-dried lot that had been tried out earlier and had been found quite active. Fresh potato tops were brought into the laboratory, and both these and the *Ulva* given the "dauerhefe" treatment. After dehydrating and drying at room temperature, both lots were ground in a mill, then reduced to a fine powder in a mortar. Exactly 18.5 grams of each were extracted with 250 cc. of water for 12 hours at room temperature with toluene added as an antiseptic, and then the protein-enzyme complex precipitated with 2.5 volumes of 95 per cent alcohol. The Ulva precipitate was the characteristic heavy white mass to which attention has been called before, while that of the potato was finely divided and dark.

The entire amount of each precipitate was diffused in 60 cc. of water. The Ulva precipitate gave a rather viscous diffusion, due to the adsorption of water by the protein particles; that from the potato did not all go into solution, making it necessary to shake the flask so that a true sample might be obtained. Five cc. of the "diffusion-extract" represented 1.84 grams of the original dehydrated tissue, and this volume was used with 50 cc. of a starch and dextrin substrate. Toluene was added as an antiseptic, and the flasks kept at a temperature of 31°C. for 42 days. Portions of the substrate were removed from time to time and sugar determinations made, the results of which are shown in table x.

The action of the potato extract upon starch was about two and one-half times that of *Ulva,* and its action on dextrin about twice in all of the determinations made. For some unknown reason the hydrolysis of dextrin by the diastase from *Ulva* ceased after the twenty-eighth day.

TABLE X

A COMPARISON OF THE DIASTATIC ACTIVITY OF ULVA WITH THAT OF POTATO LEAF TISSUE

Substrate 50 cc.	Sugar as glucose in 5 cc. mgms.									
	14 days		21 days		28 days		35 days		42 days	
	Ulva	Potato	Ulva	Potato	Ulva	Potato	Ulva	Potato	Ulva	Potato
Starch....	8.7	18.1	9.6	26.3	11.8	28.1	12.9	33.5	13.8	35.5
Dextrin...	10.5	17.3	11.5	25.1	17.8	27.5	17.9	30.3	17.9	31.9

ACTION OF VARIOUS ALGAL EXTRACTS UPON THE CARBOHYDRATE CONSTITUENTS OF AGAR-AGAR, AND OF VARIOUS GUMS, AS WELL AS EXPERIMENTS UPON THE AUTOLYSIS OF ALGAL SLIME

Because of the large amounts of carbohydrate-containing slime formed by many algae, and because of the rôle this might play as a reserve product, it was deemed advisable to try out the various algae for enzymes capable of hydrolysing such complex carbohydrates to assimilable sugars. It was assumed on the basis of the work done by König and Bettels ('05) and others, that such hydrolytic products would be reducing sugars, in all probability galactoses and pentoses.

A series was set up with each of the several algae, using 50 cc. of .25 per cent agar as a substrate and varying amounts of a "diffusion-extract" from fresh tissue. The agar substrate was slightly viscous in the cold, but when kept at a temperature of 40°C., the optimum temperature for diastase, this was not noticeable. Toluene was used as an antiseptic. The flasks were shaken at regular intervals during a 30-day period and at the end of that time aliquot portions were removed and tested for reducing sugars. There was no reduction in any case.

As a parallel series, thin strips of agar were placed in test-tubes and 20 cc. of "diffusion-extract" added. Toluene was used as an antiseptic and the tubes kept at a temperature of 40°C. for two months. At the end of that time no hydrolytic

action was observable, either by reduction of Fehling's or by microscopical examination.

In the experiments on the hydrolysis of various poly- and disaccharides, checks were set up in which the usual amount of "diffusion-extract" was placed in distilled water. This was to determine the reduction of copper, if any, due to the "diffusion-extract" itself. In no case was there more than a very slight trace that might have been due to other causes than enzymic. However, it was thought that a self-digestion series would more definitely determine whether the hydrolysis of the carbohydrates of the slime could be brought about by specific algal enzymes. With this in mind, a series was arranged in which the flasks contained 50 cc. of a water extract from each of the forms investigated. Checks were set up in which the "diffusion-extract" was inactivated in the autoclave. Toluene was used as an antiseptic and the flasks maintained at a temperature of 22–23°C. for two months. Aliquot portions removed from time to time failed to show the slightest trace of hydrolysis.

It will be remembered that Tihomirov ('10) had found osozone-forming sugars in the conceptacles of *Ascophyllum* and *Fucus* that he thought might be dextrose and d-galactose, possibly also fucose and arabinose. Thinking that these might possibly have arisen from their corresponding anhydrides contained in the conceptacle slime, a self-digestion series was set up with an extract from the abscised, crushed conceptacles of those two forms. The *Fucus* was in a fruiting state. The series were set up in duplicate, one kept at room temperature and the other at 32–33°C. Fehling's test showed no hydrolysis after a month.

Pentosans alone were then used as substrates. Two series of flasks for each of the algae investigated were set up, each containing a .5 per cent solution of gum arabic.[1] To one series was added 10 cc., to the other 20 cc. of "diffusion-extract," and the flasks placed at room temperature with toluene as an antiseptic. No hydrolysis was apparent either

[1] The gum arabic was dissolved in water, then precipitated with several volumes of 95 per cent alcohol to get rid of reducing sugars.

by the phloroglucin test or by sugar determinations, even after 60 days.

THE ACTION OF ALGAL "DIFFUSION-EXTRACTS" UPON CELLULOSE AND HEMICELLULOSE

Experiments were carried out to determine the presence or absence of cellulose hydrolysing enzymes in the algae, and to this end several methods were employed. First, strips of filter paper were placed in test-tubes and entirely covered with 20 cc. of "diffusion-extract." Checks were maintained with distilled water and also with the "diffusion-extract" alone. The series were set up in duplicate—one kept at room temperature and the other at 35°C., both with toluene as an antiseptic. After definite intervals during a 60-day period, the contents of the tubes were tested for reduction. None was observable in any case, and microscopic examination of the filter paper failed to reveal any decomposition whatsoever.

A double series was then set up in a similar way, except that 2 grams of fresh, crushed algal tissue were added to the tubes instead of the "diffusion-extract," together with 20 cc. of distilled water. At the periods noted above, microscopic examination revealed no attack. It was thought an inherent difference between algal and filter paper cellulose might be responsible for this absence of action. Accordingly, cellulose was prepared from the tissue of *Ascophyllum* after the method described by Fowler ('11, p. 159) and used by Cooley ('14). Fifty grams of air-dried tissue were placed in a liter flask, 500 cc. of distilled water added, and the lot placed in the autoclave at 15 pounds for 15 minutes to destroy any cellulase that might be present, and also to extract as much as possible of the water-soluble substances. The water was filtered from the tissue, fresh water added, and the flask placed in an incubator at 35°C. It was kept at this temperature with daily changes of water for 10 days, at which time the water-soluble constituents seemed to be almost entirely removed. The treatment from here on was the same as that described by Cooley. To the tissue was added a liter of potassium-chlorate-nitric-acid solution made up in the proportion of 30 grams of potassium chlorate to 520 cc. of nitric

acid (sp. gr. 1.1). The flask was kept in the ice-box for two weeks, when the oxidizing mixture was changed and the new lot allowed to remain another fortnight. At the end of this time a yellowish white tissue was obtained, representing fairly pure algal cellulose. This was filtered off, washed well with distilled water, and dried in the oven at 75–80°C. The final product weighed 19.7 grams.

This cellulose was used in a way similar to the filter paper in the first series. One gram was placed in each flask and well shaken up with 50 cc. of distilled water. A concentrated "diffusion-extract" was prepared from *Ascophyllum, Laminaria, Ulva,* and *Chondrus,* 10 cc. of which represented 5 grams of the original dried tissue. This volume was added to the flasks, and the series set away at 30°C. with toluene as an antiseptic. At the end of two months no reduction of Fehling's was observable and under the microscope there seemed to be no decomposition of the cellulose particles.

Action on hemicelluloses.—Hemicellulose was used from two sources—from date seeds, and from the seeds of the wild persimmon, *Diospyros virginiana.* In both cases the experiments were essentially the same. The horny coats were broken and the embryos removed. Small pieces of the hemicellulose were then taken, placed in a flask with water, and heated in the autoclave at 15 pounds for 15 minutes to kill the cytase present. Upon removal from the autoclave the pieces were washed several times in distilled water, being left in the last wash water for several days with toluene as an antiseptic—this to get rid of any reducing sugars present. Two of these washed pieces were placed in test-tubes with 10 cc. of the concentrated "diffusion-extract" used in the experiments with cellulose. Another lot was covered with 10 cc. of distilled water and 2 grams of the dried algal powder added. In a third series shavings of the hemicelluloses were mounted in a Van Tieghem cell with a drop of enzyme solution. All the algae under investigation were tried out, but in no case was there the slightest trace of decomposition, either microscopically or by the reduction of copper.

Results.—These negative results do not necessarily argue against the production of slime through the agency of enzymes. It is impossible to exactly reproduce the conditions of the cell *in vitro*, and enzymes which might act upon cellulose in the living tissue to produce slime might easily be inhibited from action on cellulose or hemicellulose under the conditions of the experiments. Grüss ('10) found that fresh cherry gum contained cytase, but that none was demonstrable in the older gum. He also found that malt diastase would not act upon such gum until the tannins had been removed. It is known that the algae do contain tannins or "tannoidal" bodies, the writer having demonstrated a "tannoid" content in *Ascophyllum* of 1.1 per cent of the dry weight. These, or other agents, could be involved in the partial or complete inhibition of cytolytic action. On the other hand, indirect evidence, at least, points to the presence of the galactan and pentosan groups as due to their being laid down as such, that is, they do not arise as the direct result of hydrolytic enzyme action, but probably represent the final step in the condensation of those particular hemicelluloses. Tschirsch ('89) and his students have shown that the algal slime exists as an intracellular substance, and they hold that in most instances, at least, it does not arise from the cellulose. This seems to be the logical view, and we in turn seem justified in looking upon the galactan and pentosan groups in the algae as normal products of the plant's metabolism, present at all stages in the plant's growth, and capable of giving rise to gelatinization at any time upon the adsorption of water. If one examines, for instance, such forms as *Fucus, Mesogloea,* and *Chondrus,* the slime is hardly detectable when the plants are growing under normal conditions, but when brought into the laboratory and placed in fresh water, a rapid adsorption begins at once. The dissolved salts in sea-water are undoubtedly the inhibiting factors in such adsorption under normal conditions.

That this inhibition is not bound up with the living cell may be shown by the simple experiment of killing two fronds of *Chondrus,* for example, and placing one in fresh, the other

in salt water, with toluene to keep down bacterial action. Very slight, if indeed any, gelatinization is evident with the frond placed in salt water, while that in fresh water begins to gelatinize immediately. It is also a well-known fact that in histological or cytological work with these forms, the killing fluids must be made up in sea-water or water containing a high percentage of salts, else gelatinization interferes. These facts, together with the apparent absence of cellulase and cytase, tend to show that the galactan and pentosan groups are always present as final condensation forms of their particular "generic" carbohydrate line, and that sliming in the marine algae, at least, is the result of the adsorption of water by these already existing carbohydrate groups.

DISCUSSION OF RESULTS OF CARBOHYDRASE EXPERIMENTS

It is seen from the data presented in the foregoing tables that carbohydrases in the algae, at least those that can be isolated by standard methods, are very few. Furthermore, in all cases where such carbohydrase action is evident, it is limited to the polysaccharides—starch, dextrin, laminarin, and glycogen. In no case were the disaccharides hydrolysed. As groups, the "greens" are more active than the "reds," while of the "browns," *Laminaria* is the only form in which carbohydrate action is demonstrable. Moreover, the action here is extremely slow and is limited to starch, dextrin, and laminarin. *Mesogloea* and *Ascophyllum* are similar to *Fucus* in failing to show the presence of carbohydrases. Within the groups there is little difference in the rate of carbohydrase action. This is especially true in the "greens." Of the "reds," *Agardhiella* is a little more active than the other forms investigated, while *Ceramium* is slightly the slowest. Bartholemew ('14), in the work already referred to, also found that *Ceramium* was less active than the other "reds" with which he worked.

The various polysaccharides, with two exceptions, prove favorable as substrates for the various algae in the same order, viz., starch, dextrin, laminarin, and glycogen. The carbohydrases of *Ceramium* act more rapidly upon dextrin than upon starch and this is also true of *Laminaria,* although

to a lesser extent. Glycogen, which is very generally hydrolysed by diastase, is here decidedly less readily attacked than the other polysaccharides. This would seem to indicate that we are dealing with a distinct enzyme, one that might be placed in the same category with dextrinases. These latter always occur with the diastases but are held by many workers to be distinct.

Some of the substrates tested for hydrolysis do not, as far as we know, occur in the plants investigated. This is true of sucrose, lactose, and inulin. However, although this might reconcile us to the failure to find their specific enzymes, it does not argue conclusively against such enzymes being formed. It is well known that tissues do form ferments that have no detectable substrates upon which to act—the rennen of the bird's stomach and the urease of the Soja bean being notable examples. Inulin, as pointed out previously, does occur in certain "greens," as in *Acetabularia* and members of the *Dasycladaceae*. Unfortunately, none of these forms were available for investigation.

The absence of lactase and sucrase is not so significant as is that of maltase. It is very generally considered that in the plant, as well as in the animal organism, poly- and disaccharides must be hydrolysed to simple sugars before assimilation can take place. It is hardly possible that the algae are an exception to this general rule and yet it is difficult to account for this important negative result. It is known that inhibiting agents do not affect all enzymes alike, and it may be here that if such agents are liberated on the death of the cell, the maltase might prove more sensitive to them than the other carbohydrate enzymes. According to the findings of Kylin ('13), both dextrose and fructose have been demonstrated in the tissues of *Ascophyllum, Fucus,* and *Laminaria,* but in extremely small quantities. These results would tend to convince one that an enzyme giving rise to them is probably present in the algal cell.

Such carbohydrates as galactans, pentosans, and mannans, are very frequently met with in the algae and are potentially capable of being split to assimilable sugars. That they are

not so split, however, seems evident, at least not through the activity of demonstrable algal enzymes, and in the face of the negative evidence obtained, we would consider them as by-products of metabolism rather than as playing the rôle of reserves. As such, they would not be so comparable to the reserve carbohydrates of the date as they would be perhaps to the mucilaginous constituents of various seeds, as those of flax, mistletoe, etc. These latter adsorb water readily with gelatinization, and as far as is known, never function as reserves but act in a purely mechanical way (Czapek, '13, p. 705).

LIPASES IN THE ALGAE

The almost universal presence of fats in the marine algae led to the question of their assimilation. Accordingly, experiments were set up to determine the lipolytic activity upon emulsions of neutral fats as well as upon certain esters of the lower fatty acids. For the neutral fats olive oil was chosen as a substrate, and two general methods were employed in forming the emulsion.

The first, an olive oil-casein emulsion was made up after a method described by Bloor ('14). Four grams of casein were placed in a warm mortar on a water bath and water added until the whole formed a paste of medium viscosity. A drop of phenylphthalein was added, then N/1 NaOH poured in and stirred with the casein until the latter had been dissolved, this point being indicated by a permanent pink tinge of the mixture. Eight cc. of olive oil were stirred into the hot solution and then ground with a pestle until all the oil globules had disappeared. At this point the mortar was removed from the bath and the emulsion cooled. During the cooling it was found necessary to stir the mixture occasionally. The thick, creamy mass resulting was diluted up to the required concentration by the careful addition of water. If this dilution is too great, the oil globules tend to rise to the surface.

The second method was also suggested by Doctor Bloor, but, as far as is known, has not been described. Eight cc. of olive oil were dissolved in the smallest amount of absolute alcohol necessary. This solution was run through a hot fun-

nel to which a drawn-out piece of glass tubing had been attached, into about 100 cc. of cold distilled water, the water being stirred constantly while the olive oil was being run in. A milk-white emulsion made up of extremely small suspended globules of oil resulted. In an emulsion carefully made, most of these globules are small enough to show Brownian movement. The alcohol was driven off finally by heating and the emulsion made up to the desired concentration.

Both emulsions stand up well. In the latter, however, there is a tendency toward flocking out by some of the smaller particles upon the addition of any salt-containing substance, such as, for instance, algal powder; but, on the other hand, it has the advantage of being more easily checked up because of its simpler composition.

TABLE XI

LIPOLYTIC ACTION OF THE SEVERAL ALGAE UPON OLIVE OIL-CASEIN EMULSION

Alga	Number cc. of N/10 NaOH to neutralize 10 cc. of substrate											
	4 days				10 days				15 days			
	Emulsion + tissue	Emulsion	Water + tissue	Net acidity	Emulsion + tissue	Emulsion	Water + tissue	Net acidity	Emulsion + tissue	Emulsion	Water + tissue	Net acidity
Ulva	....	....	....	....	1.3	.25	.1	.95	....	....	.....	.....
Enteromorpha	....	....	....	....	1.25	.2	.1	.95	....	....	.....	.....
Mesogloea	.6	.00	.1	.5	1.00	.1	.1	.8	2.2	.6	.075	1.525
Ascophyllum	....	....	....	....	1.50	.05	1.0	.45	....	....	.....	.....
Laminaria	....	....	....	....	.4	.00	.05	.35	.6	.1	.025	.475
Chondrus	1.2	.00	.05	1.15	1.85	.00	.05	1.8	2.3	....	.1	2.200
Agardhiella	....	....	....	....	.3	.00	.05	.25	....	....	.....	.....
Ceramium	....	....	....	....	1.6	.00	.1	1.5	....	....	.....	.....
Rhodymenia	.3	.1	.05	.15	.9	.2	.15	.55	....	....	.....	.....
Champia	.2	.1	.05	.05	.35	.3	.05	.00	....	....	.....	.....

In all the lipolytic experiments, algal powder or fresh algal tissue crushed with fine quartz sand, was used as a source of enzyme action. In some of the original series the olive oil-casein emulsion was employed, but on account of the danger arising from a possible hydrolysis of the casein with a resulting increase in acidity, the alcohol emulsion was used in the later work.

Lipolytic action of the several algae upon olive oil-casein emulsion.—In this experimental series (table xi) flasks were set up containing 50 cc. of olive oil-casein emulsion as a sub-

strate, 5 grams of crushed algal tissue for enzyme action, and 10 cc. of 95 per cent alcohol as an antiseptic. Checks were employed wherein the flasks in one case contained the emulsion alone, and in another case, the same weight of algal pulp in distilled water. The flasks were maintained for 15 days except for the forms especially noted. At intervals 10 cc. portions were removed and titrated against N/10 NaOH with phenylphthalein as an indicator.

Lipolytic action on alcohol-water-olive oil emulsion.—Because of the possibility of the hydrolysis of the casein in the emulsion used in the preceding experiments, a series (table XII) employing the alcohol-water emulsion was set up as a check. This emulsion alone was practically neutral but a slight acidity was produced by the addition of the algal powder. A negligible amount of the oil globules ran together and collected at the surface of the liquid after some days, but the bulk of the emulsion stood up well. As in the preceding series, 5 grams of the fresh tissue were used as a source of lipolytic activity, and the alcohol in which the olive oil had been dissolved served as an antiseptic. Fifty cc. of the emulsion were used as a substrate, and the flasks maintained at a temperature of 22–23°C. for 10 days.

TABLE XII

LIPOLYTIC ACTION OF THE SEVERAL ALGAE UPON ALCOHOL-WATER-OLIVE-OIL EMULSION

Alga	Number cc. N/10 NaOH to neutralize 10 cc. substrate after 10 days				
	Emulsion + tissue	Emulsion alone	Water + boiled tissue	Water + tissue	Net acidity
Ulva	.9	.00	.05	.05	.85
Enteromorpha	.8	.00	.025	.1	.7
Mesogloea	.65	.00	.05	.075	.575
Ascophyllum	.2	.00	.15	.15	.05
Laminaria	1.15	.00	.02	.3	.85
Chondrus	1.45	.00	.1	.35	1.10
Agardhiella	.25	.00	.05	.05	.20
Ceramium	.85	.00	.1	.20	.65
Rhodymenia	.525	.00	.05	.15	.375
Champia	.125	.00	.15	.15	.00

Lipolytic action on triacetin.—The lipolytic activity of dry tissue powder of *Ulva, Mesogloea,* and *Chondrus* was tested, using a .5 per cent solution of triacetin as a substrate. Two

grams of the tissue powder were used, otherwise the series (table xiii) was arranged exactly as the preceding and kept at room temperature for 25 days.

Action on other esters.—A series was set up with methyl acetate, ethyl acetate, and ethyl butyrate in .25 per cent solution, using 2 grams of algal powder with 50 cc. of the substrate in 20 per cent alcohol. Titrations were made from time to time against N/10 NaOH with phenylphthalein as an indicator. Even after 60 days at room temperature no increase in acidity was observable over the checks.

TABLE XIII

THE ACTION OF POWDERED TISSUE FROM CERTAIN ALGAE UPON TRIACETIN

Alga	Number cc. of N/10 NaOH to neutralize 10 cc. substrate after							
	10 days				25 days			
	Triacetin + tissue	Water + tissue	Triacetin alone	Net acidity	Triacetin + tissue	Water + tissue	Triacetin alone	Net acidity
Ulva	.3	.025	.1	.175	.5	.15	.15	.2
Mesogloea	.25	.05	.1	.1	.4	.2	.15	.05
Chondrus	.55	.35	.1	.1	.8	.4	.15	.25

General results for experiments with lipases.—The results serve to show that, although slight, there is distinct lipolytic activity in most of the forms investigated. The various groups of algae are not so distinct regarding this activity as was the case with the carbohydrases, nor does the activity of the individual alga in this case relate itself particularly to the activity shown by the form in its carbohydrase action. *Agardhiella* hydrolyses the polysaccharides more rapidly than any other alga, yet its lipolytic activity is very low. Likewise, *Laminaria,* so inactive in the previous group of enzymes, is among the most active on fats. *Fucus,* on the other hand, was found in previous work to have no action on either carbohydrates or fats.

The action is especially evidenced by use of the olive oil-casein emulsion. In general, the increases were less where the alcohol-water emulsion was used—a difference probably ex-

plainable on the ground that the casein gave rise to a slight acidity.

Specificity of action might explain the failure to obtain action on most of the esters. Euler ('12) differentiates the lipases into true lipases and esterases, the former acting on neutral fats particularly, the latter on the methyl and ethyl esters of the lower fatty acids. Even in this latter restricted field, great specificity may be shown. Reed ('12) found that ethyl acetate was quite rapidly acted upon by an esterase isolated from *Glomerella rufomaculans,* while ethyl butyrate was only slightly hydrolysed.

THE PROTEINASES

The proteolytic activity of the various algae was tested on albumin, casein, legumin, peptone, gelatin, and in certain cases, on proteins isolated from the algal tissue—most of these under acid, alkaline, and neutral conditions. The first four were made up in 1 per cent concentrations. Albumin and peptone went into solution quite readily; legumin and casein, being insoluble in water, were either weighed out directly, or dissolved in N/10 NaOH. The albumin and gelatin were also tested in the form of Mett's tubes, and the gelatin alone in test-tubes where it was held at a temperature high enough to keep it in a liquid state while in contact with the algal powder. In all cases, algal tissue was used directly, either fresh crushed, or dry powdered—usually 2 grams of the powder or 5 grams of the fresh tissue to each 50 cc. of substrate.

Determination of hydrolysis.—Proteolytic action was determined in several ways, each acting as a check on the others. The biuret test was used for the demonstration of tryptic action, the proteins being precipitated by $(NH_4)_2SO_4$ in saturated solution and the test applied in the usual way. The tryptophane test was employed for ereptic action and this also furnished a check on the action of trypsin. In this, 1 cc. of the protein solution was placed in a small evaporating dish, a drop of glacial acetic acid added, and then a few drops of strong chlorine water. The hydrolysis to the amino acid stage

was also demonstrated in two other ways—by the formaldehyde-titration method of Sörenson ('08), and the determination of the amino-nitrogen by the micro-Kjeldahl method of Folin ('13). The Sörenson method consisted in adding 2 cc. of formalin, made alkaline to a faint pink tinge with N/20 NaOH, to 10 cc. of the filtered protein solution, made alkaline to the same color. Upon mixing, the color disappeared and the acidity resulting was titrated against N/50 NaOH, using phenylphthalein as an indicator.

In the determination of the amino-nitrogen by the "micro" method of Folin, the protein in a 5 cc. filtered portion of the solution was precipitated with 2 cc. of a 25 per cent solution of phosphotungstic acid in 5 per cent H_2SO_4. The precipitate was filtered off and a 2 cc. portion of the filtrate removed for the determination of the nitrogen. Duplicate determinations were made in all cases. These portions were placed in Jena test-tubes, 20×200 mm., 1 cc. concentrated H_2SO_4 added, then 1 gram of K_2SO_4, and a drop of 5 per cent $CuSO_4$. The digestion was carried on over the flame from a micro burner, the fumes being carried away by the fume adsorbers described by Folin. Usually 20 minutes sufficed for the completion of the digestion, although in a few instances 25 minutes were required. After cooling slightly, 6 cc. of distilled water were carefully added. The tubes were then transferred to the distilling apparatus where concentrated NaOH was added to alkalinity, and the tube contents distilled over for three minutes, the NH_3 being collected in a known volume of N/10 HCl. The acid in the collection flask was titrated against N/10 NaOH with alizarin red (alizarin sulfonsäure Natrium, Merck), and the amount of nitrogen represented by the acid neutralized, determined.

In the method originally described by Folin, the NH_3 was not distilled but was forced over from an alkaline solution by a strong air current. However, students in his laboratory have made use of a micro distilling apparatus, and the suggestion for the ones employed here owes its origin to one of Folin's assistants. Distillation has the advantage of quickness, and from the writer's experience, of accuracy as well,

at least where suction instead of compressed air is employed in the air method. The results with the air current were very often below the theoretical. The distilling tubes used were made in the laboratory from glass tubing, the outer jacket measuring 40×2 cm., and the inner being 5 mm. in diameter. The lower end of this latter, where it dipped into the collection acid, was fitted with a larger tube 14 mm. in diameter—this to prevent a back flow of the acid; to the upper end of this inner tube was attached a safety bulb made from a 10 cc. pipette, and this in turn fitted into the Jena tube containing the distilling mixture, by means of a two-hole rubber stopper. Through the second hole in this stopper was a small piece of glass tubing closed at the upper end with a bit of rubber tubing and a pinch clamp; it was through this that the alkali was added after the apparatus was connected up for distillation.

Considerable trouble was experienced at first with bumping, especially after the digestion mixture had become concentrated. Neither bits of glass nor pebbles would overcome it. Finally the expedient was adopted of using short pieces of glass tubing sealed at one end and this end placed uppermost. These were of such a diameter that after digestion, the digestion mixture drawn up into them by the cooling of the contained air, would easily drain out when the boiling tube was forced up on the side of the test-tube by a quick downward motion.

The action of Enteromorpha, Mesogloea, and Chondrus powder upon various proteins.—Fifty cc. lots of casein, legumin, albumin, and peptone were used as substrates in this series—all in 1 per cent concentrations. The albumin and peptone were dissolved directly in distilled water, the legumin and casein in N/10 NaOH. Two grams of air-dried tissue powder were used for proteolytic action, with the exception, however, of *Mesogloea,* which, as before stated, was partially dehydrated before being air-dried. The various substrates were made neutral by the addition of N/10 alkali and then acid or alkaline by further addition of 2.5 cc. of N/10 HCl or NaOH. In the formaldehyde titrations 10 cc. of the sub-

TABLE XIV

THE ACTION OF TISSUE POWDER FROM CERTAIN ALGAE UPON VARIOUS PROTEINS

Substrate 50 cc.	Weight algal powder gms.	Reaction* of substrate	*Enteromorpha*				*Mesogloea*				*Chondrus*			
			Formol titration†		Biuret	Trypto-phane	Formol titrations		Biuret	Trypto-phane	Formol titrations		Biuret	Trypto-phane
			15 days	30 days			15 days	30 days			15 days	30 days		
Albumin	2	neut.	2.20	3.70	+	+	1.40	2.30	+	+	2.70	5.10	+	+
	.....	neut.	.30	.40	—	—	.50	.70	—	—	.40	.65	—	—
	2	acid	.80	1.90	+	—	.70	.90	—	—	1.65	2.85	—	—
	.....	acid	.40	.55	—	—	.40	.40	—	—	.65	.80	—	—
	2	alk.	2.75	4.95	+	+	2.15	4.80	+	+	2.10	4.35	+	+
	.....	alk.	.25	.30	—	—	.45	.55	—	—	.75	.75	—	—
Peptone	2	neut.	3.25	7.10	.....	+	2.70	5.75	.....	+	4.95	12.05	.....	+
	.....	neut.	.90	1.10	.....	—	.75	.80	.....	—	.90	1.05	.....	—
	2	acid	1.35	4.75	.....	+	1.50	4.35	.....	+	1.75	3.80	.....	+
	.....	acid	1.15	2.05	.....	—	.80	.95	.....	—	.60	.60	.....	—
	2	alk.	4.50	9.30	.....	+	3.55	7.90	.....	+	5.30	12.55	.....	+
	.....	alk.	.95	1.20	.....	—	1.10	1.10	.....	—	.85	1.20	.....	—
Casein	2	neut.	3.175	11.80	+	+	2.30	2.45	—	—	3.10	7.15	+	+
	.....	neut.	2.40	2.70	—	—	2.50	2.55	—	—	2.20	2.25	—	—
	2	acid	2.75	3.40	—	—	2.10	2.35	—	—	2.75	2.65	—	—
	.....	acid	2.60	2.70	—	—	2.40	2.45	—	—	2.80	2.95	—	—
	2	alk.	4.65	12.30	+	+	2.60	2.75	—	—	5.30	10.15	+	+
	.....	alk.	2.10	2.45	—	—	2.30	2.20	—	—	2.10	2.35	—	—
Legumin	2	neut.	2.10	4.95	+	+	1.55	1.70	—	—	2.10	2.45	—	—
	.....	neut.	1.80	1.95	—	—	1.90	2.00	—	—	1.85	1.65	—	—
	2	acid	2.00	3.60	+	+	1.40	1.65	—	—	1.70	2.30	—	—
	.....	acid	1.60	1.65	—	—	1.65	1.75	—	—	1.55	1.60	—	—
	2	alk.	3.35	7.10	+	+	1.95	2.15	—	—	2.90	5.85	+	+
	.....	alk.	2.10	2.05	—	—	1.50	1.90	—	—	.40	.80	—	—
Water	2	.....	.20	.25	—	—	.35	.30	—	—	.65	.75	—	—

*The substrates were made N/200 acid or alkaline with N/10 HCl or NaOH.
†The values represent the cc. of N/50 NaOH to neutralize 10 cc. of the substrate used.

strate were titrated against N/50 NaOH. One per cent chloroform-thymol was used as an antiseptic, and the flasks were kept at a temperature of 22–23°C. for 30 days.

The forms used in table XIV show a general ability to hydrolyse proteins. All four proteins employed were acted upon by one alga or another, but peptone and casein in neutral and alkaline solution were the most readily attacked. *Enteromorpha* split albumin and legumin but poorly; *Chondrus* acted upon legumin only in alkaline solution, and then slightly; *Mesogloea* failed to hydrolyse casein and legumin, and its action on albumin and peptone was very slow.

The action of Ulva, Laminaria, and Agardhiella powder on peptone and casein in alkaline and neutral solution.—Indications in the preceding experiment seemed to point to the fact that peptone and casein were more easily acted upon than the other proteins—and these more especially in neutral and alkaline solution. Accordingly, a series was set up with these two substrates, similar in all respects to the preceding one, except that the acid substrate was omitted and that *Ulva, Laminaria,* and *Agardhiella* were used for proteolytic action. Five grams of air-dried tissue were employed with 100 cc. of substrate. One per cent chloroform-thymol served as an antiseptic, and the flasks were kept at 35°C. for 30 days. Formaldehyde titrations were made after 15 and 30 days and tryptophane tests and amino-nitrogen determinations after 30 days. In the titrations 10 cc. of substrate were titrated against N/50 NaOH, and the amino-nitrogen represents that in 2 cc. of the filtrate from phosphotungstic precipitated protein.

The data in table XV tend to substantiate that of table XIV concerning the hydrolysis of peptone and casein. The higher temperature at which the flasks were maintained undoubtedly had something to do with the larger amounts of amino acids split off from these two proteins than was the case in the preceding series, yet if we can judge by the action on carbohydrates and fats, we are dealing here with the more active members, enzymatically, of their respective groups.

On the whole, peptone and casein seem to be the most favorable substrates of those used for proteolytic activity, and

TABLE XV

THE ACTION OF POWDERED TISSUE FROM CERTAIN ALGAE UPON PEPTONE AND CASEIN

Substrates 100 cc. 1 per cent	Weight algal powder gms.	Reaction of substrate	*Agardhiella*				*Ulva*				*Laminaria*			
			Formol* titrations		Trypto-phane test	Amino-N† in 2 cc. mgms.	Formol titrations		Trypto-phane test	Amino-N in 2 cc. mgms.	Formol titrations		Trypto-phane test	Amino-N in 2 cc. mgms.
			15 days	30 days			15 days	30 days			15 days	30 days		
Peptone	5	neut.	4.35	15.00	+	1.68	2.80	6.75	+	1.06	2.25	5.65	+	1.14
	.....	neut.	.70	1.00	—	.07	.70	1.00	—	.07	.70	1.00	—	.07
	5	alk.	5.30	18.00	+	1.84	3.05	8.35	+	1.19	2.30	4.15	+	.39
	.....	alk.	.55	.85	—	.00	.55	.85	—	.00	.55	.85	—	.00
Casein	5	neut.	8.70	22.00	+	1.49	6.40	17.70	+	.92	5.95	15.60	+	.98
	.....	neut.	5.55	6.10	—	.48	5.55	6.10	—	.49	5.55	6.10	—	.49
	5	alk.	8.60	23.15	+	1.56	6.25	26.35	+	1.10	5.70	14.50	+	.83
	.....	alk.	5.20	5.70	—	.35	5.20	5.70	—	.35	5.20	5.70	—	.35
Water	5	.....	.40	.95	—	.08	.90	1.65	—	.11	1.05	1.40	—	.09

* Values represent the number of cc. N/50 NaOH to neutralize 10 cc. of substrate.

† The amino-nitrogen in 2 cc. of filtrate from phosphotungstic precipitated protein represents 1.4 cc. of the original substrate.

these in neutral and slightly alkaline solution. This was shown in the formol titrations[1] and in the determination of the nitrogen in the amino acids split off. Albumin was slowly acted upon by *Enteromorpha, Mesogloea,* and *Chondrus.* The first and last also hydrolysed the vegetable protein, legumin, to a slight extent—an action that was not shared by *Mesogloea.*

The action of algal powder on the proteolysis of gelatin and albumin in Mett's tubes.—Two lots of Mett's tubes were made up, one containing coagulated egg-white, and the other, 15 per cent gelatin. In each of a series of flasks containing 50 cc. of distilled water, N/200 NaOH and N/200 HCl respectively, were placed one tube each of egg-white and gelatin. Two grams of the powdered tissue from each of the several forms under investigation were added for enzyme action and the usual percentage of toluene used as an antiseptic. The several series were kept for two months at room temperature. At the end of that time the albumin tubes in the alkaline solution containing the algal powder of *Ulva, Enteromorpha, Chondrus,* and *Agardhiella* showed a slight digestion. The checks in the alkaline solution alone showed swelling. However, although this was indicative of action, it was not definite, since the great length of time the protein was in contact with the complex constituents of the tissue may have been a factor in either causing a slight hydrolysis or a contraction of the albumin. On the other hand, *Laminaria, Ascophyllum, Mesogloea,* and *Ceramium* caused no such action. The gelatin tubes showed no evidences of action even after 60 days.

The effect of proteinases on the hardening of gelatin.—Dox ('10) describes a method for testing the hydrolysis of gelatin which consists in keeping the protein in a liquid state during contact with the material being tested for proteolytic activity, then at the end of a stated period noting whether the gelatin congeals when placed in cold water. This method was used in the following way: Five cc. of 20 per cent gelatin were placed in each of a series of test-tubes, and 5 cc. of the standard

[1] The formaldehyde titrations, as used here, were satisfactory only in a general way, i. e., to show relative rather than exact differences in the amounts of amino acids split off. The differences brought out by the amino-nitrogen determinations are much more exact.

"diffusion-extract," described under "carbohydrases," used for action. The contents of the tubes were made neutral, and acid and alkaline to N/200, as was done in the other proteolytic experiments. Five drops of chloroform-thymol were added as an antiseptic. Checks were set up containing the gelatin together with 5 cc. of boiled "diffusion-extract." The tubes were placed in an incubator at 35°C. for a week, at which time they were removed and cooled in running water. All tubes hardened in a short time, showing that no hydrolysis had taken place.

General results for experiments on proteolysis.—The proteolytic activity, although slow, as was the case with the other enzymes investigated, is definite enough to warrant the statement that proteinases and peptases are very generally present in the algae. When present, such enzymes act best under neutral and alkaline conditions. This last finding is interesting in the light of the existing differences of opinion regarding the relative value of acid and alkaline substrates for vegetable proteinases. It will be recalled that Vines ('97) found that acidity favored the proteinase contained in the leaf pitchers of *Nepenthes,* and in a later paper, he states that peptase (hydrolysing albumoses and peptones to amino acids) always act best under faintly acid conditions. Emmerling ('02), on the other hand, demonstrated that the papain of *Carica papaya* acted more rapidly when the substrate was alkaline. Euler ('12) states in a general way that peptases require a neutral or faintly alkaline substrate, and proteinases (tryptases) an acid one.

Of the proteins employed, solutions of casein and peptone prove the most favorable substrates. Albumin in solution is acted upon slowly, but when employed in the form of Mett's tubes, doubt exists regarding its digestion. Legumin appears to be slowly hydrolysed by *Enteromorpha* and *Chondrus,* but not by *Mesogloea.* Gelatin, either in the liquid state or in the form of Mett's tubes, is not attacked. As groups, the "reds" appear more active in proteolysis than do the "greens," while, as was true for carbohydrases, the "browns" show the least activity.

THE AMIDASES

The tissues from the several algae were tested for their ability to split NH_3 from such amino and amido compounds as urea, acetamid, asparagin, and methyl amine. These compounds were used in 1 per cent concentrations. Series were set up in which 50 cc. of the substrate to be tested were placed in flasks together with 2 grams of the powdered tissue and chloroform-thymol as an antiseptic. Checks were used with the nitrogen compounds alone and with the algal tissue in distilled water. The flasks of duplicate series were kept at room temperature and at 35°C. respectively, for 30 days, at the end of which time Folin's method was employed for the determination of any NH_3 that might have been split off. In the collection of the NH_3, Friedrich's improved gas washing bottles containing 250 cc. of N/50 HCl were used. Air was bubbled through by means of a suction pump for two hours, then 25 cc. portions of the collection acid were removed and titrated against N/50 NaOH, with alizarin red as an indicator. In no case was there any action over that evidenced by the checks.

These results are extremely interesting, in the case of *Ulva* especially. This form, as has been shown, thrives in waters where the organic nitrogen content is high. The question would at once arise whether this increased growth were due to the ability of the *Ulva* to break down the protein molecule and thus obtain an increased supply of nitrogen as NH_3, or whether it were due to the activities of the denitrifying bacteria rendering available a larger assimilable supply. That such bacteria are relatively abundant in sewage-contaminated water has been shown in the review of literature. We can conceive of another factor entering in—that of selective formation of enzymes. It might well be that with plenty of the amino-nitrogen available through the activity of bacteria, no amidases would be formed. The possibility of shedding some light on this point led to the experiments following.

Experiments on amidase formation by Chlamydomonas.—*Chlamydomonas* was grown in pure culture upon two different media; one (with one or two modifications, that used by

Schramm ('14)), containing $(NH_4)_2SO_4$ as a source of nitrogen, the other with nitrogen supplied as peptone and asparagin. These media complete were as follows:

A.		B.	
Agar	10.00 grams	Agar	10.00 grams
$(NH_4)_2SO_4$	.25 grams	Peptone	4.00 grams
$MgSO_4.7\ H_2O$	.10 grams	Asparagin	1.00 grams
K_2HPO_4	.10 grams	$MgSO_4.7\ H_2O$	.10 grams
$FeSO_4$	trace	K_2HPO_4	.10 grams
Glucose	10.00 grams	$FeSO_4$	trace
Distilled H_2O	500.00 cc.	Glucose	10.00 grams
		Distilled H_2O	500.00 cc.

These media, designated "A" and "B," were placed in 125 cc. Erlenmeyers, about 25 cc. to each flask, and the flasks placed horizontally until the agar hardened. A relatively large surface was obtained in this way and the harvesting of the alga later was facilitated. In inoculation, the alga was smeared over the surface of the agar to give an even growth. After a growth of thirty days, it was harvested by scraping from the agar surface with a stiff, platinum needle. The cells were then dehydrated with alcohol, acetone and ether, dried, and ground with an equal weight of fine quartz sand. Flasks were set up in duplicate in Wollf wash bottles, using 1 per cent asparagin as a substrate, with an amount representing .35 grams of sand-free algal powder. Checks were run on both the asparagin and the algal powder alone. One-half the series was taken down at the end of 7 days, the other half at the end of 15 days, and the NH_3 split off determined by the Folin method previously employed. The flasks were kept at a temperature of 35°C. The results are given in table XVI.

TABLE XVI

THE ACTION OF DEHYDRATED CHLAMYDOMONAS CELLS UPON ASPARAGIN

Substrate 50 cc. 1 per cent	Weight algal powder	Nitrogen as NH_3 in 50 cc. substrate mgms.			
		7 days	Net N	15 days	Net N
Asparagin	.35 grams "A"	.36	.16	.45	.21
	.35 grams "B"	1.17	.96	1.84	1.60
	.....	.18	.....	.22	.....
Water	.35 grams "A"	.02	.....	.02	.....
	.35 grams "B"	.03	.....	.04	.....

The amount of nitrogen in the checks is so small as to be well within experimental error. The NH_3 split off by powder

"B" would be almost negligible were the findings not so consistent. There is a definiteness about the increase over the checks that can hardly be ignored. In order to get further evidence on this point, however, another series (table XVII) was set up, using urea and asparagin in 1 per cent concentrations as substrates. The flasks were maintained at a temperature of 35°C. for 30 days.

TABLE XVII

THE ACTION OF DEHYDRATED CHLAMYDOMONAS CELLS UPON ASPARAGIN AND UREA

Substrate	Weight algal powder	Nitrogen as NH_3 split off in 30 days mgms.	Net nitrogen mgms.
Asparagin	.5 grams "A"	1.15	.20
	.5 grams "B"	3.10	2.20
	.....	.65	.....
Urea	.5 grams "A"	1.45	.17
	.5 grams "B"	3.70	2.47
	.....	.98	.....
Water	.5 grams "A"	.30	.....
	.5 grams "B"	.25	.....

In this, as in table XVI, the evidence goes to show that although the desamidization is practically negligible where the alga is grown with $(NH_3)_2SO_4$ as a source of nitrogen, it is definite where the nitrogen is supplied in the amino and amido form. The actual splitting is small in any case.

On the basis of the above, we can simply reason by analogy, and yet this analogy points to the fact that the probable reason for the failure to demonstrate amidase in *Ulva* lies in the failure to form that enzyme. This in turn would indicate that the great growth of *Ulva* in sewage-contaminated waters is probably due to the abundance of desamidizing bacteria which those waters maintain—bacteria which break down the protein molecule with the ultimate setting free of NH_3. Nitrogen, as such, becomes directly available to the plant.

NUCLEASES

The presence of nucleases in the algae has already been reported by Teodoresco ('12), but since he investigated only

one of the forms falling within the scope of this study, experiments were carried on to determine the presence or absence of nucleases in one representative of each group, *Ulva, Ceramium,* and *Ascophyllum.*

One-half per cent nuclein was dissolved in N/10 NaOH, the complete solution of the compound being shown by a drop of phenylphthalein. One hundred cc. of this neutral solution were added to each flask together with 3 grams of air-dried algal powder. Toluene was added as an antiseptic. Checks were set up by adding autoclaved algal powder to the nuclein and also by using nuclein solution alone. The flasks were placed at 35–36°C. for 38 days, at the end of which time the phosphoric acid split off was determined as P_2O_5 by the uranium-acetate method.[1] Five cc. of a sodium acetate solution[2] were added to 25 cc. of the nuclein substrate, this brought to a boil and titrated while hot. Potassium ferrocyanide was used as an indicator—a drop of the titration mixture being removed from time to time and brought into contact with a drop of the indicator on a porcelain plate. The results obtained are given in table XVIII.

TABLE XVIII

THE ACTION OF POWDERED TISSUE FROM CERTAIN ALGAE UPON NUCLEIN

Substrate 100 cc. 1 per cent	Weight algal powder	Free H_3PO_4 as P_2O_5 in 100 cc. in 38 days mgms.	Net amount P_2O_5 in 100 cc. mgms.
Nuclein	3 gms. *Ceramium*	70.00	56.25
	3 gms. *Ceramium* boiled	13.75	.....
	3 gms. *Ulva*	56.70	39.20
	3 gms. *Ulva* boiled	17.50	.....
	3 gms. *Ascophyllum*	17.25	.35
	3 gms. *Ascophyllum* bld.	16.90	.....

These findings substantiate those of Teodoresco ('12) regarding the general presence of nucleases in the algae. The values for *Ceramium* agree very well with those he obtained for the same form, i. e., 56.25 milligrams in 38 days at 35°C., as compared with 76.6 milligrams in 51 days at 22–26°C. *Ulva*

[1] The standard solution of the uranium acetate contained 8.8652 grams of the salt in 250 cc. of water, and each cc. by calculation was equivalent to 5 milligrams of P_2O_5.

[2] The sodium acetate solution contained 25 grams of sodium acetate and 25 cc. of 30 per cent acetic acid in 250 cc.

shows less nuclease activity than does *Ceramium,* while *Ascophyllum,* true to its reputation for inactivity, gives a value so small as to be negligible.

An interesting point is brought out by the use of nuclein—one that proves a check on some of the previous proteinase experiments. Nuclein is composed of nucleic acid bound up with some protein (according to Abderhalden, '11, this is albumin) which must be split off by a proteinase before the nuclein residue is exposed to the attack of the nuclease. That unmistakable nuclease activity was evident, only serves to show again the presence of proteolytic enzymes.

OXIDASES AND CATALASES

Oxidases.—Direct and indirect tests for oxidase action, that is, for the oxidases and the so-called peroxidases, were carried out in all cases with fresh tissue. The general method described by Clark ('10) was employed, using guaiacum, alpha naphthol, and phenylphthalin as reagents. Five grams of the fresh tissue, crushed with an equal weight of fine quartz sand, were extracted for half an hour with 25 cc. of distilled water. The extracting fluid was then filtered off, the tissue residue pressed out, and the filtrate made up to 50 cc. Five cc.-portions were placed in test-tubes, and for the direct test, ten drops of the reagent were added; for the indirect test, this amount plus 1 cc. of fresh 3 per cent hydrogen peroxide. In only two cases was direct oxidization observable—with *Agardhiella* and *Ulva.* With the former, direct action was strong with all three reagents, and when peroxide was added an immediate deepening of the color occurred, showing the presence of peroxidases as well. With *Ulva,* however, both direct and indirect tests were only weakly positive. Atkins ('14), it will be remembered, obtained direct tests with but one of twenty-nine diverse algae investigated and indirect tests with but seven. He thought that reducing substances prevent the demonstration of oxidases in other forms. As brought out in the review of literature, Reed ('15[a]) has since demonstrated indirect oxidation of the alpha naphthol-para-phenylenediamine group of compounds by many of these

forms. In the filamentous forms he showed the presence of oxidases by the formation of colored granules within the cells surrounded by these reagents. Reed concludes that oxidases of specific oxidative ability are very generally present in the algae, and where negative results are obtained, either the necessary specific compound is not present or other factors enter in, such as the destruction of the oxidase equilibrium of the cell upon crushing.

Catalases.—Both fresh and air-dried tissue were used for catalase demonstration. In a preliminary series, the addition of 5 cc. of 3 per cent hydrogen peroxide to about a gram of fresh crushed algal tissue showed evolution of oxygen in all cases except one, that of *Mesogloea*. Later, a series (table XIX)

TABLE XIX

CATALASE ACTIVITY OF CERTAIN ALGAE

Alga	Number cc. O_2 evolved at 21.5°C.		
	2 minutes	5 minutes	10 minutes
Ascophyllum	.3	.9	.9
Laminaria	1.4	2.3	2.3
Mesogloea	0.0	0.0	0.0
Ulva	.2	.4	.5
Agardhiella	3.3	4.6	5.6
Chondrus	.4	2.0	2.5
Rhodymenia	.9	1.4	2.0
Ceramium	3.7	5.9	8.2
Potato leaf tissue	22.6	....	....

was set up in which 1 gram of powder was placed in 125 cc. Erlenmeyer flasks, 10 cc. of 3 per cent hydrogen peroxide added, and the oxygen evolved collected in a gas burette over water. The flask in which the action was taking place was shaken every 15 seconds, and the volume of oxygen evolved read at the end of 2, 5, and 10 minutes. The temperature of the room was practically constant during the experiments and no especial precautions were taken to control the temperature of the flask other than keeping the hands away from it during the action. The results are not meant to be quantitatively exact, but they do give the relative catalase activity of the several forms. In addition, air-dried potato leaf tissue that had been in the laboratory about the same length of time as the algal tissue was tested for comparison.

Catalase, so wide-spread in all plant tissues, is found here in all the forms investigated except *Mesogloea.* The "reds" prove more active than the "browns," and these latter slightly more active than the "greens." No alga is strikingly active, however, when compared with potato leaf tissue. Strangely, *Ulva,* most active in regard to the other enzyme groups, is one of the least so here.

General Discussion and Conclusions

The data obtained in the foregoing investigation serve to show that the number of enzymes in the algae that can be isolated, by standard methods at least, is quite limited. This is especially true of the "browns," in two forms of which, *Ascophyllum,* and the *Fucus* of the earlier study, such action is limited to catalase alone. In this group the demonstrable carbohydrases are restricted to very slowly acting diastases in *Laminaria;* in neither *Ascophyllum* nor *Mesogloea* is there the slightest trace of what might be termed carbohydrate hydrolysis. Moreover, negative results are obtained in these forms for most of the other enzymes sought. *Laminaria* shows lipases and catalases (it was not tested for proteolytic or nuclease activity), and action in *Mesogloea* is restricted to lipases and proteinases, both tryptic and ereptic. On the other hand, very general enzymic activity is demonstrable in the "greens" and the "reds"—diastases, dextrinases, lipases, proteinases (tryptic and ereptic), nuclease, and catalase being isolated from the crushed tissue. Oxidase is shown present in one "red," *Agardhiella,* and in one "green," *Ulva.* Such action, as a whole, appears a little more rapid in the "reds" than in the "greens," but no enzyme stands out as being specific for either a group or an alga within a group.

The carbohydrases demonstrated are restricted in their action to those hydrolysing starch, dextrin, glycogen, and laminarin of the polysaccharides used as substrates, and in *Laminaria,* such action was further limited by a failure to act upon glycogen. In no case, in any member of the three groups was there evidence of disaccharides being attacked. While

this is not so surprising perhaps for sucrose and lactose, it is difficult to understand the failure of enzymic hydrolysis of maltose. The results obtained by Kylin ('13) indicate that both dextrose and fructose are found in algal tissues, and reasoning from results found for plant and animal tissues in general, it seems, as is true in those cases, that in the algae, maltose must be broken down to glucose before assimilation can take place. The failure to isolate this enzyme points to the possible presence of some inhibiting factor, rather than to the non-formation of the ferment.

Lipases, acting very slowly, appear wide-spread in algae, being demonstrable in all the forms used in this study excepting *Ascophyllum*. Along with the fact that fats are very generally found in the algae, these results are significant in that they indicate the importance of the rôle these compounds may play as assimilatory products. It is not thought, as was advanced by Reinke ('76), Hansen ('93), and others, that these fats function as the first products of assimilation, but rather, that they act as storage products of more or less importance.

The algae, in general, show the presence of enzymes capable of hydrolysing certain proteins. Casein and peptone in alkaline and neutral solution prove the most favorable substrates of those tested, although legumin and albumin are also slightly attacked. The "greens" and the "reds" are about equally active in this way, the "browns," as usual, acting more slowly. The fact that both native proteins and peptones were hydrolysed, points to the presence of both tryptic and ereptic enzymes. Still further evidence of the presence of the first of these was the splitting of the protein molecule from nuclein preceding the action of nuclease.

Amidases seem not to be formed by any of these algae. The results obtained with *Chlamydomonas,* from which the amidases were isolated when the alga was grown on a medium containing asparagin and peptone as a source of nitrogen but not when the nitrogen was in the form of ammonium sulphate, indicate that such amidase formation may depend upon the nature of the supply of assimilable organic nitrogen. This has a distinct bearing upon the reason for the increased growth of

Ulva in sewage-contaminated waters. In order to break down the proteins present in the surrounding waters and even those in close contact with the plant itself, it would be necessary for the *Ulva* to secrete an extracellular enzyme, since the large protein molecule is not diffusible into the cell. If so secreted, the enzyme would be quickly dissipated in the large volume of surrounding water. Desamidizing bacteria, on the other hand, have been demonstrated in harbor and shore waters where such algae abound. They can come into much more intimate contact with the protein than can the plant, and undoubtedly play an important rôle in rendering available at all times an abundant supply of organic nitrogen.

The demonstration of nucleases acting upon the previously split nuclein molecule, substantiates the findings of Teodoresco for this enzyme. Both *Ulva* and *Ceramium* showed the presence of the ferment, while *Ascophyllum,* the only representative of the "browns" investigated, gave negative results. Where such enzymes were formed, they compared more favorably with enzymes of fungi and higher plants than do any of the other algal ferments.

None of the "browns" studied showed the presence of oxidative enzymes, while in the "reds" and the "greens" but one form gave the characteristic reactions. It is interesting to note that these algae, *Agardhiella* and *Ulva,* were the most enzymatically active forms studied. The oxidase reactions with guaiacum, alpha naphthol, and phenylphthalin were very positive, both directly, and indirectly with hydrogen peroxide.

In all cases where enzymes were demonstrated, the action was very slow, being with the exception of nuclease, much less rapid than in the higher plants. The reason for this is not clear, but it cannot in all instances be due to inhibiting substances set free upon the death of the cell. Arber ('01), as has been mentioned before, found that *Ulva, Cladophora,* and *Enteromorpha,* placed in the dark but under otherwise presumably normal conditions, required from two weeks with *Ulva,* to two months and more in the case of *Enteromorpha* for destarching. This indicates the presence of a very slowly acting diastase in the cells of these algae. The metabolism

of the algae is also probably slower than that of the higher plants and one might expect, *a priori*, the enzymes also to be less rapid in their action. Although the algal enzymes may be inherently slow, it seems that there may also be substances set free on the death of the cell which either partially or entirely inhibit enzyme action. The writer has found evidence in some preliminary experiments, that the action of taka diastase upon starch is directly proportional to the amount of free tannin present. In connection with this, it was also found that *Ascophyllum* had a "tannoidal" content of 1.1 per cent of the dry weight. It is possible that such tannoids, if in an uncombined state, may after the death of the cell unite with an enzyme to throw it out of the sphere of action. That diastases are demonstrable in tissues having a high tannin content may perhaps be explained on the basis that they are bound up in such a way as to render them incapable of uniting with the ferments. Still other organic inhibiting compounds may be present, and the point opens up a very interesting problem concerning inhibition, not only in algal tissues, but in those of many higher plants as well.

Summary

1. Using standard methods of enzyme isolation and determination, the following enzymes have been found in fresh or dried algal tissue:

a. Carbohydrases hydrolysing the polysaccharides, starch, dextrin, glycogen, and laminarin, but not those hydrolysing the several disaccharides employed as substrates.
b. Lipases acting upon neutral fats but not upon the esters of the lower fatty acids.
c. Proteinases (tryptic and ereptic) acting best under neutral and alkaline conditions.
d. Nucleases.
e. Oxidases and peroxidases (in but two forms—*Agardhiella* and *Ulva*).
f. Catalases.

2. Negative results were obtained for cellulase, cytase, maltase, lactase, sucrase, amidase, and esterase.

3. The action of all the enzymes isolated was very slow.

It is a pleasant duty to acknowledge indebtedness to those who in various ways have lent support to this investigation. Such acknowledgments are due Dr. George T. Moore for the privileges of the Missouri Botanical Garden, especially its library and laboratories; to Dr. Benjamin M. Duggar, at whose suggestion the problem was undertaken, and under whose direction and constant kindly interest it has been pursued; to Dr. Phillip A. Shaffer, of the Biochemical Laboratories of the Washington University Medical School, for suggestions and advice concerning biochemical methods, and for the courtesy of his laboratory from time to time; and finally, to the Woods Hole Biological Laboratory, for the privileges extended during the summers of 1913–14.

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