





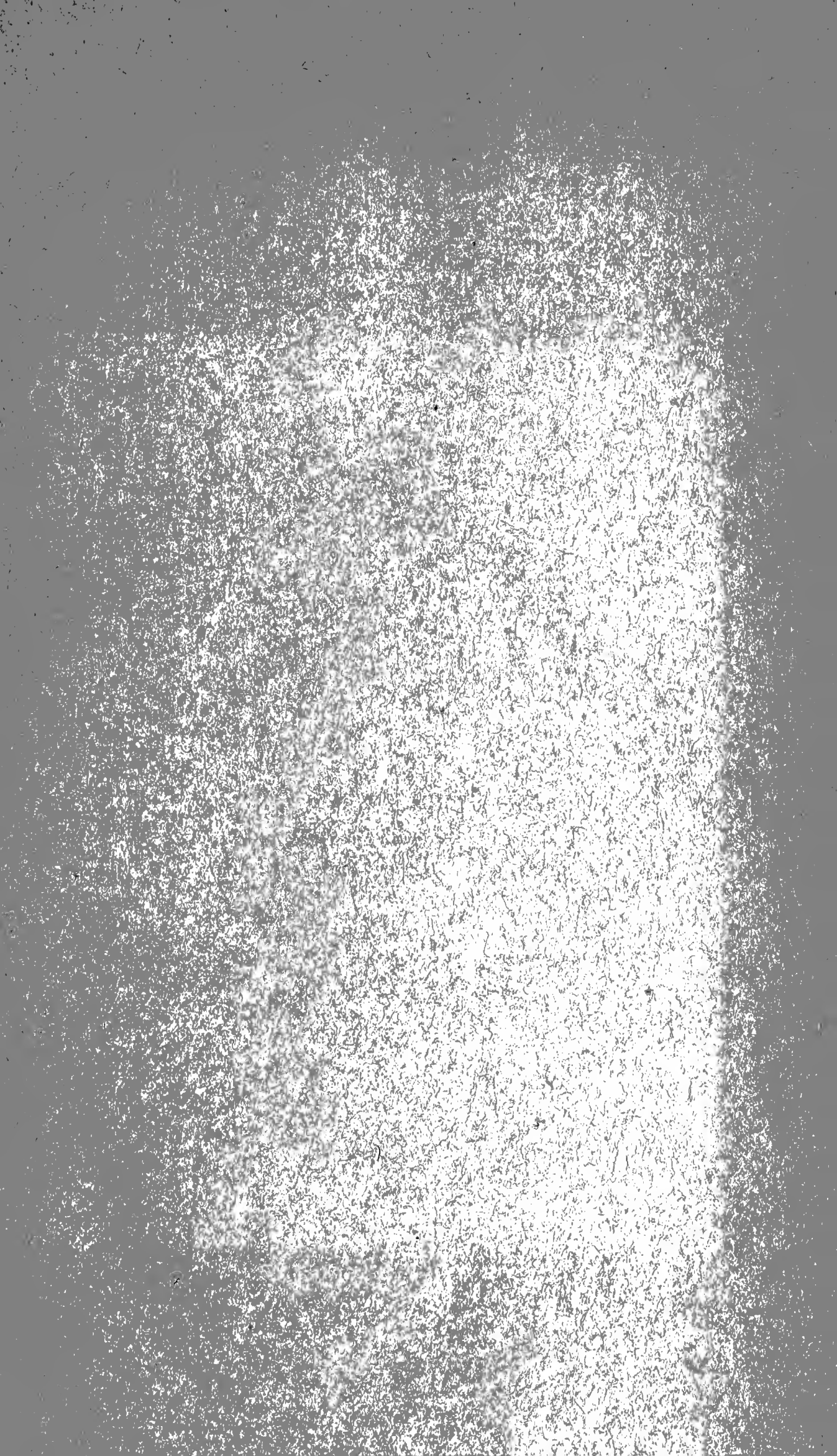
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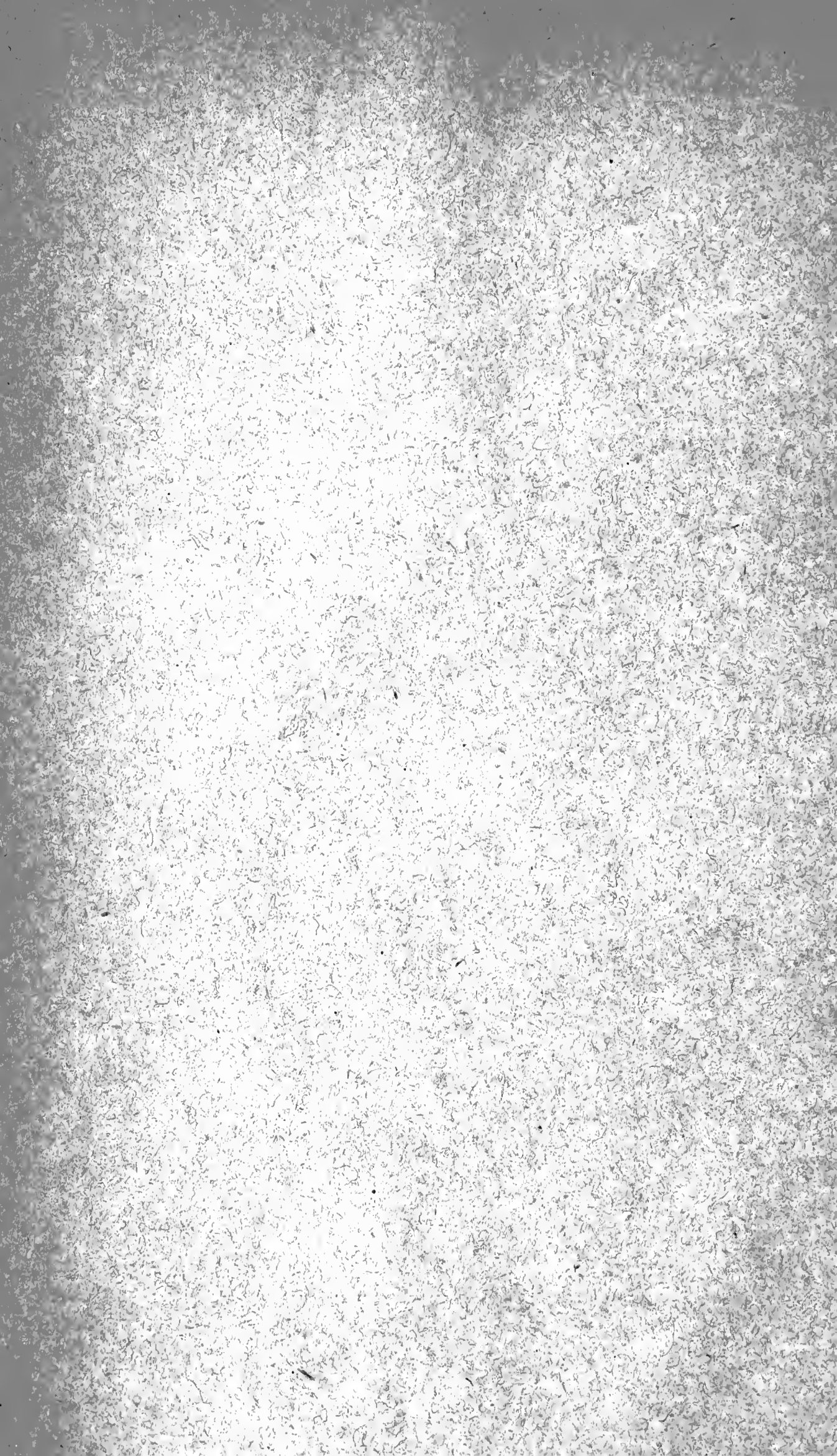
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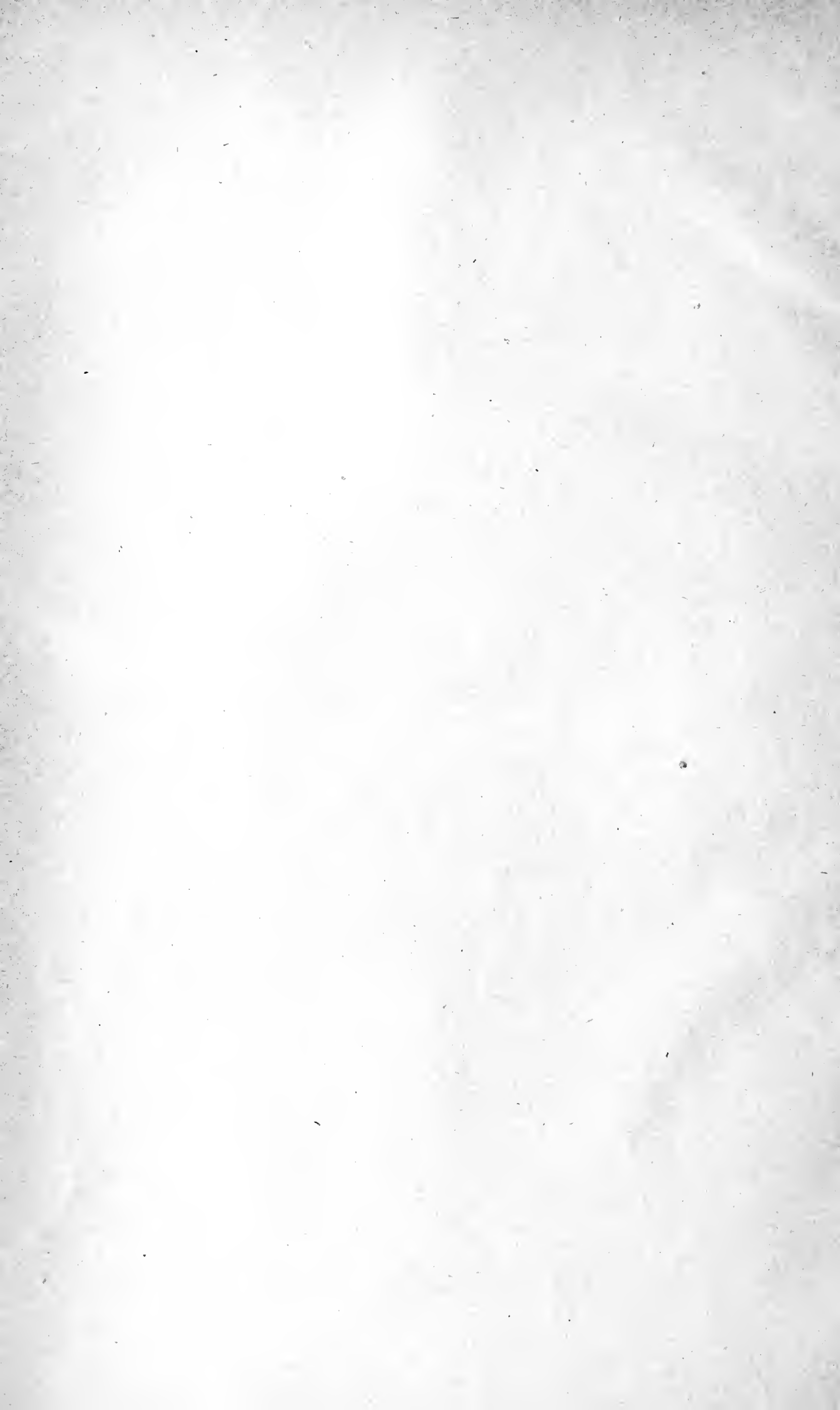
Proceedings of the Boston Society of Natural History.

VOL. 33, No. 1,

p. 1-8.

PROCEEDINGS OF THE ANNUAL MEETING, MAY 2, 1906.

BOSTON:
PRINTED FOR THE SOCIETY.
JULY, 1906.



PROCEEDINGS

OF THE

Boston Society of Natural History.

VOL. XXXIII.

WITH THIRTY-EIGHT PLATES.

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GARDEN.

BOSTON:
PRINTED FOR THE SOCIETY.
1906-1907.

PUBLISHING COMMITTEE.

CHARLES S. MINOT,
WILLIAM G. FARLOW,

DOUGLAS W. JOHNSON,
JAY B. WOODWORTH,

GLOVER M. ALLEN.

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No. 1.— PROCEEDINGS OF THE ANNUAL MEETING,
MAY 2, 1906.

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BOTANICAL
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By order of the Library and publishing committee the following abstract of the proceedings of the annual meeting, May 2, 1906, is published.

ABSTRACT OF REPORT BY THE CURATOR, CHARLES W. JOHNSON.

The past year has been a very favorable one for the Society, and considerable progress has been made towards completing the arrangement of the New England collections. Two large cases for the moose, deer, and caribou, and two smaller ones for bird groups have been built. A fine pair of moose from Maine has been secured and placed in one of these cases. The cow moose was shot accidentally in Washington County and was purchased from the State through the kindness of Mr. L. T. Carleton, chairman of the Commissioners of inland fisheries and game of Maine. A New York weasel was presented by Mr. V. D. Lowe, from Randolph, N. H. From a specimen of the common dolphin, taken off No Man's Land, a model has been made and the skeleton preserved. On March 2, there came ashore at Wells Beach, Maine, a bottle-nosed whale (*Hyperoodon ampullatum*) 15 feet long, and through the kindness of Mr. Robert W. Lord, on whose property it came ashore, the Society was able to obtain the skeleton and a cast of the specimen.

The collection of New England birds has been increased by 43 specimens representing 33 species, and two groups including the black and white warbler and redstart, from the gift of Mr. Augustus Hemenway. Mr. William A. Jeffries presented 13 species including the blue goose — the only Massachusetts record — Baird's sandpiper, parasitic jaeger, Eskimo and Hudsonian curlews, and other interesting species; and from the collection of J. A. Jeffries 40 species including a hoary redpoll. Mr. D. Robinson presented an interesting variation of the black duck; Mr. F. H. Kennard nests and eggs of the barred and long-eared owls, broad-winged, sharp-shinned, and sparrow hawks, and the brown creeper. The nests being *in situ*, form six very attractive groups arranged in two new cases. Six species, including the prairie

JUL 31 1906

horned lark, Acadian sharp-tailed sparrow, and Ipswich sparrow were presented by Dr. C. W. Townsend.

The collection of New England fishes has been entirely rearranged, cases altered, and specimens removed from the blue boards and placed directly on the backs of the cases. This change not only makes a much neater appearance but saves much space.

The collection of New England insects has been largely augmented by donations from members of the Society and the Cambridge entomological club. Mr. H. H. Newcomb presented the Emily L. Morton collection of Microlepidoptera containing 195 species and 755 specimens. The collection which was largely made in the vicinity of Newbury, N. Y., forms a valuable series by which to determine New England species. Dr. George Dimmock presented 48 species, 145 specimens, of Diptera and other insects; Mr. L. W. Swett, 54 species of Lepidoptera and a number of Coleoptera; Mr. E. J. Smith, 104 specimens of moths representing about 36 species, among them many new to the collection; Dr. F. W. Russell, about 53 moths and other insects; Mrs. Annie T. Slosson, several interesting Diptera from Mt. Washington; Dr. W. E. Britton, a number of Diptera from Connecticut; Mr. Owen Bryant, a large series of moths and other insects mostly from Cohasset; Dr. H. F. Perkins, two specimens of a walking-stick (*Aplopus mayeri*) from the Tortugas, Florida, with the twigs of its food plant, *Suriana maritima*, an interesting case of protective resemblance. Specimens have also been received from Messrs. G. M. Allen, F. Blanchard, P. G. Bolster, W. D. Denton, N. S. Easton, J. H. Emerton, C. H. Fernald, C. A. Frost, B. H. Malden, A. P. Morse, H. M. Parshley, W. P. Pearmain, J. H. Rogers, Jr., A. C. Sampson, S. A. Shaw, W. H. Souther, and M. T. Thompson.

Mr. Cushman, during his summer work at Wood's Hole, obtained about 85 species of Crustacea most of which were unrepresented in the collection. Mr. A. S. Pearse presented 10 microscopic slides of the types of *Epischura massachusettsensis*, also types of *Dioptomus pygmaeus* and *D. spatulocrenatus*, and other New England copepods. Through the kindness of Dr. P. B. Hadley the Society obtained a series of the lobster from the egg to the twelfth stage.

About 50 species of shells from various localities were presented by Miss Susannah Minns; Mr. John Ritchie, Jr., gave two species of Helices from the Bahamas; Mr. Owen Bryant a number of New England shells including cotypes of *Paludestrina salsa* from Cohasset.

Specimens of the last were also received from Rev. H. W. Winkley. Seventy species have been donated by the Curator. Rev. R. K. Smith presented 7 specimens of brittle stars from Maine, Mr. Dwight Blaney a specimen of the sun star (*Crossaster papposus*) from Frenchman's Bay, and Mr. S. N. F. Sanford fine specimens of *Caudina arenata* from Newport, R. I. Mr. Cushman has also added considerable material to the collections of New England invertebrates.

The New England collection of paleontological specimens has been rearranged and considerable additional material obtained from Gay Head. A series of fossils from Sankoty Head has been received from the Nantucket Maria Mitchell association.

From the herbarium of the late Miss Frances C. Prince 840 species have been selected about one half of which were from New England. Dr. A. Fredholm presented 101 species of plants from Florida, Mr. Cushman 45 specimens of New England plants, Mr. Laurence Brooks a beautiful specimen of the fungus, *Hydnum coralloides*, Mr. Owen Bryant an interesting example of the so called witches' broom, and Mr. C. M. Mead cones from the cedar of Lebanon.

ABSTRACT OF REPORT BY THE SECRETARY AND LIBRARIAN,
GLOVER M. ALLEN.

During the year 1905–1906, the Society has lost by death two Honorary Members — Albert von Kölliker and Ferdinand von Richthofen — and two Corresponding Members — Emile Oustalet and Henri de Saussure. Five Corporate Members have died during the year — T. W. B. Clark, James C. Davis, Roland Hayward, Nathaniel S. Shaler, Edward S. Wood. Eight Corporate Members have been dropped and nine have resigned. The class of absent members has been abolished so that the total membership is lessened by about fifty.

Eight new Corresponding Members have been elected — J. A. Allen, William H. Dall, Joseph S. Diller, Richard E. Dodge, J. Walter Fewkes, William F. Ganong, Frederick H. Newell, Warren Upham. Ten new Corporate Members have been elected and the name of

Alexander Agassiz has been added to the list of Patrons. The present membership consists of 12 Honorary, 121 Corresponding, and 387 Corporate Members, a total membership of 520. There are 15 Patrons.

Fourteen regular meetings of the Society have been held during the year. The number of persons present has varied from 13 to 61, with a total attendance of 539 and an average of about 38. Seventeen formal communications have been made by as many persons, and seven papers have been presented by title.

During the year eight numbers of the Proceedings have been issued: Development of ascus and spore formation in Ascomycetes, by J. Horace Faull. Vol. 32, no. 4, 37 pages, 5 plates.

Proceedings of the annual meeting, May 3, 1905. Vol. 32, no. 5, 29 pages.

Alimentary canal of the mosquito, by M. T. Thompson. Vol. 32, no. 6, 58 pages, 6 plates.

Birds of the southern Lesser Antilles, by Austin H. Clark. Vol. 32, no. 7, 110 pages.

Anatomy of *Boophilus annulatus* Say, by S. R. Williams. Vol. 3, no. 8, 22 pages, 5 plates, 3 figures.

Circulatory and respiratory systems of *Desmognathus fusca*, by Anne Barrows Seelye. Vol. 32, no. 9, 23 pages, 4 plates, 4 figures.

Marine Ostracoda of Vineyard Sound and adjacent waters, by Joseph A. Cushman. Vol. 32, no. 10, 27 pages, 12 plates.

Squamosal bone in tetrapodous Vertebrata, by F. W. Thyng. Vol. 32, no. 11, 39 pages, 4 plates, 19 figures.

Under Mr. Samuel Henshaw's editorship have appeared two more numbers of Vol. 7 of the Occasional Papers devoted to lists of New England animals: No. 5, List of the Crustacea, by Mary J. Rathbun, 117 pages; No. 6, List of the Odonata, by P. P. Calvert, 43 pages.

The additions to the library during the year are as follows:—

| | Svo. | 4to. | Folio. | Total. |
|------------------|------|------|--------|--------|
| Volumes | 419 | 109 | 20 | 548 |
| Parts of volumes | 2035 | 588 | 18 | 2641 |
| Pamphlets | 1089 | 55 | 28 | 1172 |
| Maps and photos | | | 696 | 696 |
| Total | 3543 | 752 | 762 | 5057 |

These additions include numerous pamphlets from the Cambridge entomological club, books and pamphlets from Mr. S. H. Scudder, and 668 plates of Muybridge's "Animal locomotion" from Prof. W. P. Wilson of Philadelphia. During the year 715 books and 1810 pamphlets have been bound. There have been borrowed from the library 698 volumes in addition to 261 loaned for use in the building. Six new exchanges have been added during the year, and three others have ceased. The library contains May 1, 1906, 32,196 volumes, 1439 current or otherwise incomplete volumes, and 25,045 pamphlets.

REPORT OF THE TREASURER, EDWARD T. BOUVÉ.

ANNUAL STATEMENT, MAY 2, 1906.

| | | | | | |
|---|-------------|--|--|-------------|-----------|
| 1905, May 1. To balance April 30, 1905, belonging to General Expense Account... | | | | | |
| 1906, Apr. 30 To cash received from income, | \$1648.16 | | 1906, Apr. 30 By cash paid for | | |
| General Fund..... | 7556.91 | | Fuel and Light..... | | \$509.36 |
| Bulfinch Fund..... | 1721.68 | | General Expense..... | | 1903.33 |
| Flint Fund..... | 195.93 | | Insurance..... | | 185.00 |
| Pratt Fund..... | 550.27 | | Museum..... | | 1848.88 |
| Wolcott Fund..... | 407.11 | | Library..... | | 1698.62 |
| Saltonstall Fund..... | 928.52 | | Publications..... | | 2563.36 |
| Waterston Fund..... | 450.96 | | Salaries..... | | 7840.00 |
| Walker Fund..... | 1882.59 | | Walker Prize Advertising... | | 49.50 |
| Randall Fund..... | 250.00 | | Walker Prizes..... | | 125.00 |
| Billings Fund..... | 805.00 | | Janitor Services Lecture Hall | | |
| Special Museum Fund..... | 103.27 | | renting..... | | 26.00 |
| Special Fund for Large | | | Repairs..... | | 44.49 |
| New England Mammals | | | Trustees for Insurance Sink- | | |
| Mass. Inst. Technology..... | 1897.00 | | ing Fund..... | | 476.00 |
| Admission Fees..... | 200.00 | | Large New England Mam- | | |
| Annual Assessments..... | 50.00 | | mals..... | | 1398.00 |
| Museum Fees..... | 1485.00 | | Balance carried to new ac- | | |
| Sales of Publications..... | 150.70 | | count; this belongs to | | |
| Rent of Lecture Hall..... | 174.35 | | Library..... | \$576.49 | |
| Interest on deposit Shawmut | 127.00 | | Museum..... | 282.82 | |
| Bank..... | | | Publications.. | 235.97 | |
| Donation to Museum..... | 68.37 | | N. E. Mammals | 1750.76 | 2846.04 |
| Refund for broken glass | 159.50 | | | | |
| (Museum)..... | 16.50 | | | | |
| General expense sale rags | | | | | |
| and paper..... | .30 | | | | |
| Trustees, balance paid them | | | | | |
| April 30, 1905, returned.. | 684.46 | | | | |
| Total, | \$21,513.58 | | Total, | \$21,513.58 | |
| TEACHERS' SCHOOL OF SCIENCE. | | | | | |
| 1905, May 1 To balance from old account..... | \$14.27 | | 1906, Apr. 30 By cash paid for Lectures and Supplies | | \$3354.77 |
| 1906, Apr. 30 Cash rec'd from A. L. Lowell, Trustee | 3060.00 | | | | |
| Donations..... | 265.00 | | | | |
| Cash rec'd to balance account..... | 2.41 | | | | |
| Interest on deposit Shawmut Bank... | 13.09 | | | | |
| Total, | \$3354.77 | | Total, | \$3354.77 | |
| ARMS FUND. | | | | | |
| 1905, May 1 To balance from old account..... | \$1780.39 | | 1906, Apr. 30 By balance to new account..... | | \$1816.00 |
| 1906, Apr. 30 Interest on deposit Shawmut Bank... | 35.61 | | | | |
| Total, | \$1816.00 | | Total, | \$1816.00 | |

ABSTRACT OF REPORT ON TEACHERS' SCHOOL OF SCIENCE,
BY PROF. G. H. BARTON, CURATOR OF THE SCHOOL.

During the year the usual field and laboratory courses have been given.

The field courses in botany, under the charge of Mr. Hollis Webster, were mainly devoted to a study of the relationships of the flowering plants. The average attendance was 21 in the spring and 12 in the autumn.

The field work in zoology, under the charge of Mr. A. P. Morse, was devoted to the study of insects in the spring, and in the autumn, to the study of the native mammals. The average attendance during the spring was 9, and in the autumn, 15.

The course in field geology, supported by a friend of the School, is under the charge of the Curator of the School. The spring work was devoted mainly to a study of structural geology, and the autumn lessons consisted of a definite course of instruction in erosion of the earth's surface. The average attendance for the spring was 34, and for the autumn 53.

The laboratory courses in botany and zoology, which finished their four years with the winter of 1904-05, were each extended over a fifth year so that new classes for a four years' course could be formed. This additional year gave an opportunity in botany to try the experiment of a course in plant physiology. The average attendance for the term was 23.

The laboratory work in zoology was devoted to the study of vertebrate anatomy, with an average attendance of 21 for the seventeen lessons.

Two classes are now conducted in laboratory geology. The one is two years in advance of the other in its work, and this year took up the subject of historical geology. The average attendance for this course was 62. The other class, now in its second year, took up the subject of lithology, with an average weekly attendance of 38.

In addition to the regular work of the School, a course of eight lectures on the topographic features of the United States was given by Dr. D. W. Johnson of the Massachusetts institute of technology, with an average attendance of 98. The expense of this extra course was

furnished by contributions from Miss Marian C. Jackson and Prof. A. L. Lowell. A course of six lectures, each in a separate department of science and each by an authority on his subject, was given in Huntington Hall under the auspices of the Teachers' school of science association.

In direct connection with the work of the School, a course of lectures and laboratory exercises in advanced physics has been carried on during the winter at the Massachusetts institute of technology under the direction of Prof. H. E. Clifford. The average attendance in this has been about 50.

On the recommendation of the Walker Prize committee the two annual prizes were awarded as follows: a Walker first prize of \$100 to Prof. A. W. Grabau of Columbia university, for his essay entitled "The interpretation of stratigraphic series by the principles of sedimentary overlap," and a Walker second prize of \$50 to Prof. Douglas W. Johnson of the Massachusetts institute of technology for his essay on "Drainage modifications in the Tallulah district; a study in river capture."

The following officers were elected: —

PRESIDENT,

CHARLES SEDGWICK MINOT.

VICE-PRESIDENTS,

CHARLES P. BOWDITCH.

HENRY W. HAYNES.

EDWARD L. MARK.

SECRETARY,

GLOVER M. ALLEN.

TREASURER,

EDWARD T. BOUVÉ.

COUNCILLORS FOR THREE YEARS,

CHARLES F. BATCHELDER.

N. T. KIDDER.

HUBERT L. CLARK.

WILLIAM L. UNDERWOOD.

WILLIAM M. DAVIS.

ARTHUR W. WEYSSE.

W. L. W. FIELD.

Miss MARY A. WILLCOX.

Printed July, 1906.

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VOL. 33, No. 2,

p. 9-42, pl. 1-11.

TERRACES OF THE WEST RIVER, BRATTLEBORO, VERMONT.

BY E. F. FISHER.

BOSTON:
PRINTED FOR THE SOCIETY.
OCTOBER, 1906.



No. 2.—TERRACES OF THE WEST RIVER, BRATTLE-
BORO, VERMONT.

BY E. F. FISHER.

INTRODUCTION.

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THE flights of stepping terraces which border our New England rivers are of singular interest and add much to the beauty and charm of the river topography. The almost level terrace plains and especially the low-lying meadows are agriculturally the most fertile in New England. They represent river-deposited and carved remnants of the clays, sands, and gravels which once occupied in larger volume than to-day the rock-floored valleys of still earlier origin. They are but transitory waste forms on the way to the sea. The meadows, irrigated each year by the floods and hence the richest of these terrace plains, are steadily increasing or decreasing in extent as attacked by the river, and all the time some of the flood plain is being washed down the valley toward the sea.

The river terraces of New England may be accounted for by the behavior of meandering and swinging streams slowly degrading previously aggraded valleys without necessary change in volume and by the control exerted here and there over the lateral swinging of the streams through the discovery of rock ledges. The rivers are essentially graded, with reference to sea level, to the main stream or to a local rock barrier, though all the while actively swinging, slowly degrading streams. Prof. W. M. Davis has most ably stated and discussed this river-terrace theory and its deduced consequences, defining terraces in early, middle, and late stages, and also the various patterns produced by free-swinging rivers constrained by rock barriers.

The purpose of this investigation is to test the above theory by applying it to a new locality. As a whole, the theory stands. A few modifications of special features are suggested. The West River in Vermont, at its junction with the Connecticut at Brattleboro, was chosen as offering varied and distinct illustration of numerous terrace patterns and as showing the importance of rock barriers. Furthermore, the valley of this West River is narrow and can be studied

within a limited area, as the river in its wandering and degrading discovered a large number of rock ledges which defend the higher and older terraces and prevent their erosion.

In consideration of the variety of terrace forms developed by the West River, it seemed advisable to survey with transit and stadia an area covering about two square miles at the junction of the West and Connecticut Rivers. The area surveyed was plotted on the scale of four hundred feet to the inch. Terrace scarps have been hachured and the different levels of the plains noted by heights (in feet) above mean sea level, and in groups by shading. The map (pl. 1) reveals the destructive postglacial work of the West River in the constructive postglacial filling of its valley.

Another portion of the field work has been the measuring, with a Locke level, of terrace scarps here and there (at frequent distances) for about two hundred miles along the Connecticut River from Saybrook to Brattleboro. From such measurements taken in different sections of the valley, it may be possible to determine by means of their variations whether an even regional uplift or a tilting was chiefly responsible for the activity of the river in degrading its valley. Such dimensions will give direct proof as to the kind of movement by which the process of terracing was initiated, and will possibly confirm the evidence already at hand regarding the nature of postglacial movement in New England. The results of this portion of the field work will be presented at another time.

For valuable suggestion and advice in this study the writer gratefully acknowledges indebtedness to Prof. W. M. Davis, and also takes the present opportunity of thanking Dr. S. E. Lawton of Brattleboro, Vt., for unfailing kindness in the furtherance of the field work.

PRELIMINARY INQUIRY.

Terraces in the cycle.— A typical section of one of the terraced river valleys in New England (represented in the accompanying text-figure A) shows a broad rock valley, aggraded with drift, and partially degraded by a swinging river checked in its lateral cutting here and there by the discovery of rock ledges. These ledges act as barriers against which the river is practically powerless. The river terraces are deposits of stratified sands and gravels temporarily delayed on their way to the

sea, and indicate an interruption in the cycle of river development. The rock valleys represent the work accomplished, before the ice age, by the mature rivers in sculpturing our hills and valleys.

During the glacial period, the valleys became filled with abundant drift material, and the subsequent changes of level in the earth's surface forced the rivers to erode, stratify, and carve the unconsolidated material into the form of terraces. Postglacial time has allowed the rivers to swing widely in their valleys and thus remove more and more of the unconsolidated material, a task which is as yet very incomplete because of the rock ledges, which have served as barriers, preventing erosion and so protecting the higher alluvial plains. Should the rivers succeed in removing all the valley drift,—or in cutting down to the floor of the preglacial rock valleys,—they would not have advanced beyond the preglacial stage of their cycle of development. Davis ('02, p. 285) has clearly shown that "terraces are examples of the forms assumed by waste that still remains in its stopping-place after part of its volume has been swept forward again."

Terrace pattern.—A river terrace is a plain terminated backward by an escarpment which rises to the terrace above, and forward by

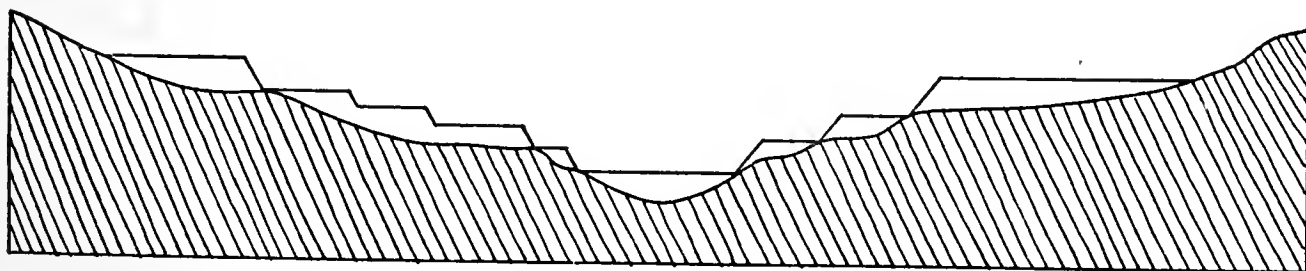


FIG. A.— Typical section of a terraced river valley in New England. Shows a broad rock valley, aggraded with drift and partially degraded by a swinging river checked in its lateral cutting here and there by the discovery of rock ledges.

an escarpment which falls to the terrace below. The surface of a terrace is rarely level, but slopes gently toward the sea, since it has been deposited by the gradually falling river. Further, the terrace floor slopes toward its river bed as an even or as an undulating surface. Occasionally the plain rises toward its river on account of accumulations from heavy floods.

The most significant line of the terrace is not the conspicuous front edge where the plain drops by an escarpment to a lower terrace, but rather, the line to the back and at the base of the rising escarp-

ment, since this line is determined by the carving action of the stream, while the conspicuous frontal edge of the terrace has oftentimes been affected by the simple processes of drainage. A characteristic feature of some terraces is a line of drainage at the back of the plain and at the foot of the rising escarpment. This line of drainage, or brook, flows down stream, cutting a gorge to the plain below and spreading there a fan-like delta deposit.

The width of the terrace plain is variable. Commonly, terraces present, toward the river, scarps which here and there show a series of concave curves meeting in pointed cusps.

It is clearly recognized that the curved terrace fronts have been sculptured by successive encroachments of a winding stream which at some time must have swung against the base of the rising scarp; and

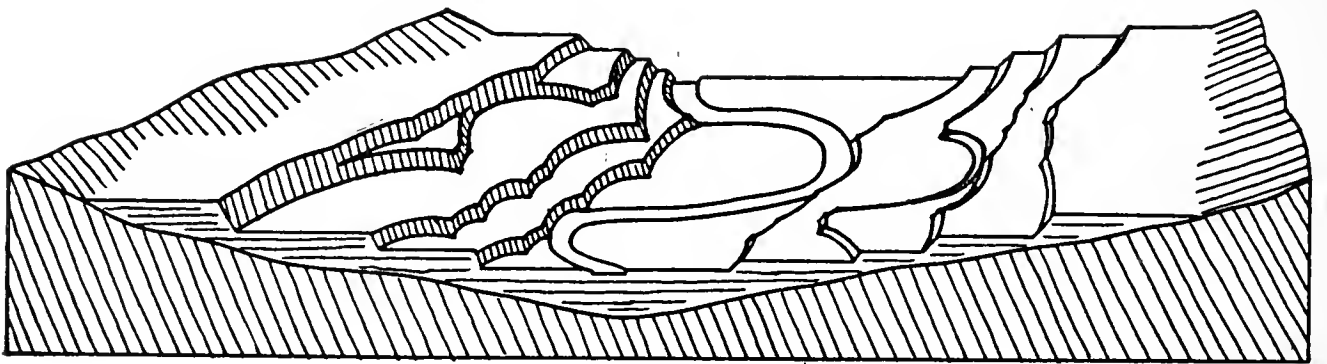


FIG. B.—Valley showing middle stage of terrace pattern. Terraces vary in width, have curved, concave scarps meeting in pointed cusps, and exist because of the discovery of defending rock ledges at lower and lower levels.

it is believed that the stream has swung laterally at least as many times as there are terraces.

Terrace scarps are steepest where the eroding stream has most recently done its work. In a series of stepping terraces, one would find the steepest slopes in the lowest and youngest, and the more gently and more deeply weathered slopes in the highest and oldest terraces. The oldest terraces not only weather to a gentler slope but, also, their edges are rounded off, which means that a convex slope of erosion is formed above and a concave slope of deposition below. Very excellent examples of this may be found by a careful study of the terraces in our valleys where the dissection of the highest and oldest terraces has been so excessive as fairly to separate them into individual plains severed by sharp and deeply incised valleys of erosion. At first sight they appear like delta sand plains with lobate margins.

Origin of river terraces in New England. — The stepping terraces of our valleys suggest a narrowing meander belt, a broad valley floor for the carving of the higher and older terraces, and a narrower valley floor upon which the rivers are to-day meandering (see profiles, plate 2). Three theories offer an explanation of this shrinkage of the meander belt. The first theory assumes a diminution of stream volume during and after the uplift which caused the rivers to degrade. It is supposed that the greater volume of the rivers necessitated a greater arc of curvature and a broader space on which to swing. To-day the streams are weakened by the loss of much of their former volume, and therefore swing with shorter arc of curvature over a more limited area, and in consequence have not the power to undercut and remove the terraces of earlier date.

The second theory postulates that the lower and lower terraces are the result of successive uplifts of the region. The river revived by each uplift cuts its channel beneath its former flood plain until grade is reached and the river swings laterally. Allow less and less time to elapse between successive uplifts, and there would be a diminution in the amount of lateral swinging as the valley was worn deeper.

The third theory (suggested by Miller, '83) points to a slow regional uplift as the cause of valley erosion and then calls attention to the rock ledges discovered by a wandering river at successively lower and lower levels producing narrower and narrower interscarp terrace plains and the observed shrinkage of the meander belt. It is this third theory which is competent to account for the occurrence and pattern of our New England terraces. The importance of this theory has been recognized and fully demonstrated by Davis ('02; '02a).

Terminology of winding rivers.— It may be well to summarize the terms used in considering the processes of river terracing. A meander belt covers the area included between tangents drawn outside of the bends or meanders of a stream. This belt widens as the meanders push outward or wear away their banks. It may also collapse locally in the case of a cut-off or short-cut. As the river moves laterally, the process is known as swinging. The meanders may be said to sweep progressively down the valley. "Up-stream" and "down-stream" refer as usual to the motion of the current, whereas "up-valley" and "down-valley" indicate a more general direction than that of the circuitous channel of the stream. The terms "right" and "left" relate to the down-stream direction of the current.

The compound movement of meanders sweeping in a swinging meander belt is called wandering. The whole breadth of the valley floor, which may be worn down by the stream, is known as the belt of wandering,— a belt which corresponds to our familiar flood plains. It is now recognized that the meanders sweep down the valley and therefore pass progressively any given point; and since at the same time the river is degrading, each successive meander must pass at a slightly lower level. The amount of difference in level is comparatively little. In the much longer time necessary for the entire river to swing across its wandering belt, the river degrades more markedly, carving a deeper scarp. Ordinarily the scarp separating terraces is a measure of the amount of down-cutting the river has accomplished in swinging across the valley and back (profiles, plate 2). The terraces left after the river has swung several times across its valley will vary in width, and they stand as remnants of the flood plains.

According to Davis ('02, p. 298), the behavior of a wandering river rests upon four postulates: “(1) The degrading stream continually maintains an essentially graded¹ condition. (2) The lateral swinging of the meandering channel is very much faster (a hundred fold, for example) than the degradation of the valley floor. (3) The breadth over which a free river (not constrained by ledges) tends to swing laterally is greater than the breadth of the meander belt (the belt included by tangents to the meandering channel). (4) An individual meander tends to enlarge its radius and to work its way down the valley until it may be abandoned at season of high water for a short-cut across a flood-plain lobe, or at any season (but usually at high water) for a cut-off through the narrowing neck of a lobe.” To these postulates may be added a fifth: any departure of the thread of the current from the delicate adjustment of its symmetrical curves, caused by change of volume, cut-off, short-cut, rock barrier, accidental natural obstruction, or artificial construction, deflects the curving thread of the current throwing it into a new series of meanders.

THEORY OF RIVER TERRACES.

In order better to appreciate the work which the West and Connecticut Rivers are accomplishing, it may be well at this point to review the

¹ It may be pertinent to state that a river is graded, if at high water it falls in a gentle unbroken slope to the sea. A graded river may at low water reveal rapids, for a river though practically graded, is slowly degrading.

processes of river action according to the accepted theory and its deduced consequences. To this end, the lateral movement of a meandering river may be considered.

So far as these processes have been presented, they are: (1) the meander process, (2) the cut-off process, (3) the short-cut process.

Lateral swinging by meander process.— Considering the first point, — the work of a meandering stream (Davis, '03) is that of erosion upon the outer bank of its meander where the current strikes with greatest force, and of deposition upon the inner bank where the water is shallow. The current is not only swinging laterally, but is also flowing down-stream, degrading its channel to sea level. Consequently the erosion is not only at the outermost portion of the bend, but the downward motion of the water carries the current strongly against the outer and lower side. Hence the deposit is continuous and forms an even plain, sloping toward the river. Attention is called to the accompanying text-figure C, illustrating in plan the work accomplished by the meandering river, and showing that by equal erosion on one bank and deposition on the opposite bank, the entire channel of the river without changing width may move laterally across the valley, while the stream is steadily moving down the valley.

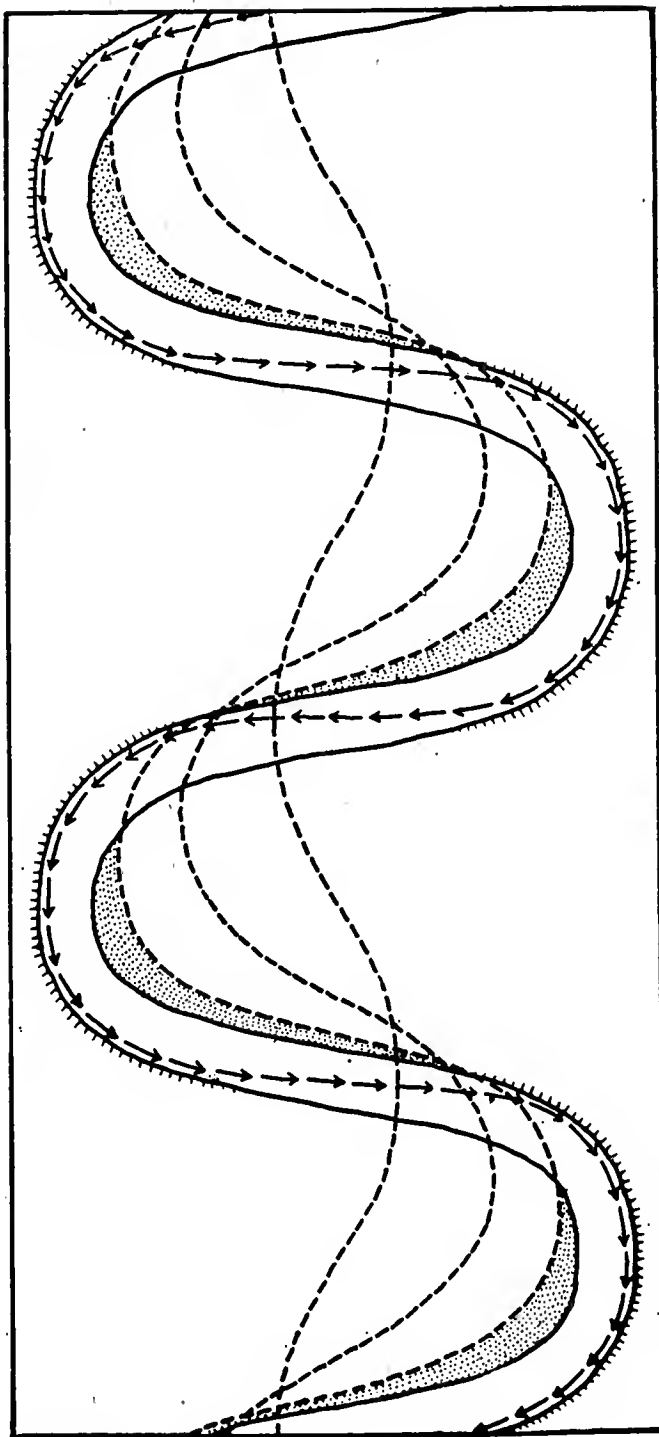


FIG. C. — River flowing forward in normal symmetrical curves. Meander belt widening by equal erosion on outer bank of the meanders and deposition on the inner bank. Erosion is strongest on outer and lower side of each meander hence the entire channel of the river moves laterally while meanders move progressively down-stream.

Lateral swinging by cut-off process.— The second, or cut-off process (Tower, '04) may be thus briefly stated: when the meanders of a river become closely compressed and widely lobate, it is possible for the stream to cut off a lobe, desert its old meander course, and follow the straighter channel to the sea. Innumerable examples of this type have been noted, and may be recognized, if recent, by a lagoon-shaped lake, silted at the ends, closing toward the river; and later by the dry and deserted crescent-shaped channel.

Lateral swinging by short-cut process.— By the third process, widely curving meanders of the river may be deserted during flood season through the formation of a new flood-made channel which gives a short-cut across the flood plain. Nothing is more evident on the low meadows which border our rivers in New England, especially in the central and northern portions where the floods are severe, than to find channels which have been rudely and quickly carved. These channels do not cut entirely across the plains, but often extend a few or several hundred feet into them. The channel banks are vertical or caving, with evidence of small land slides caused by the undercutting of a strong, rapid current, which has eaten its way under heavy pressure a certain distance, and which in another flood season may extend through the flood plain and so serve as a short-cut. Thus the river after slowly and elaborately making for itself a wide swinging meander will suddenly desert it for a steeper course to the sea. These processes of cut-off and short-cut are very common.

Lateral swinging by partition process.— There is, perhaps a fourth process by means of which a river swings across its belt of wandering. This may be called the process of river partition, or the partition process. The process is of singular interest. It is by the growth of a sand bar within the stream channel that an island is formed and the river parted thereby. Eventually the deeper channel acquires the entire stream. Thus the deserted channel and the one-time island are added to the growing flood plain, and the river has moved laterally on its journey across the valley. The formation of other islands would again and again part the river, causing it to depart successively from the less prosperous channels and so continue to move laterally.

In order better to understand the formation of the sand bar, it is well to consider the meandering habit of a river. The current of any river tends to sweep down its valley in a series of systematic curves or

meanders (text-figure C) so long as there is nothing to cause a departure of the current from the normal. The radius and arc of curvature of each meander are definitely controlled by the simple law of deflection. As the meanders of the river sweep down-stream, they gradually deposit on the inner and lower side of each bend a plain sloping gently toward the river. Probably no river to-day shows a perfect type series of meanders developed by the systematic deflection of the thread of fastest current. That the river does not show this systematic arrangement is due to the departure of the current from its delicate adjust-

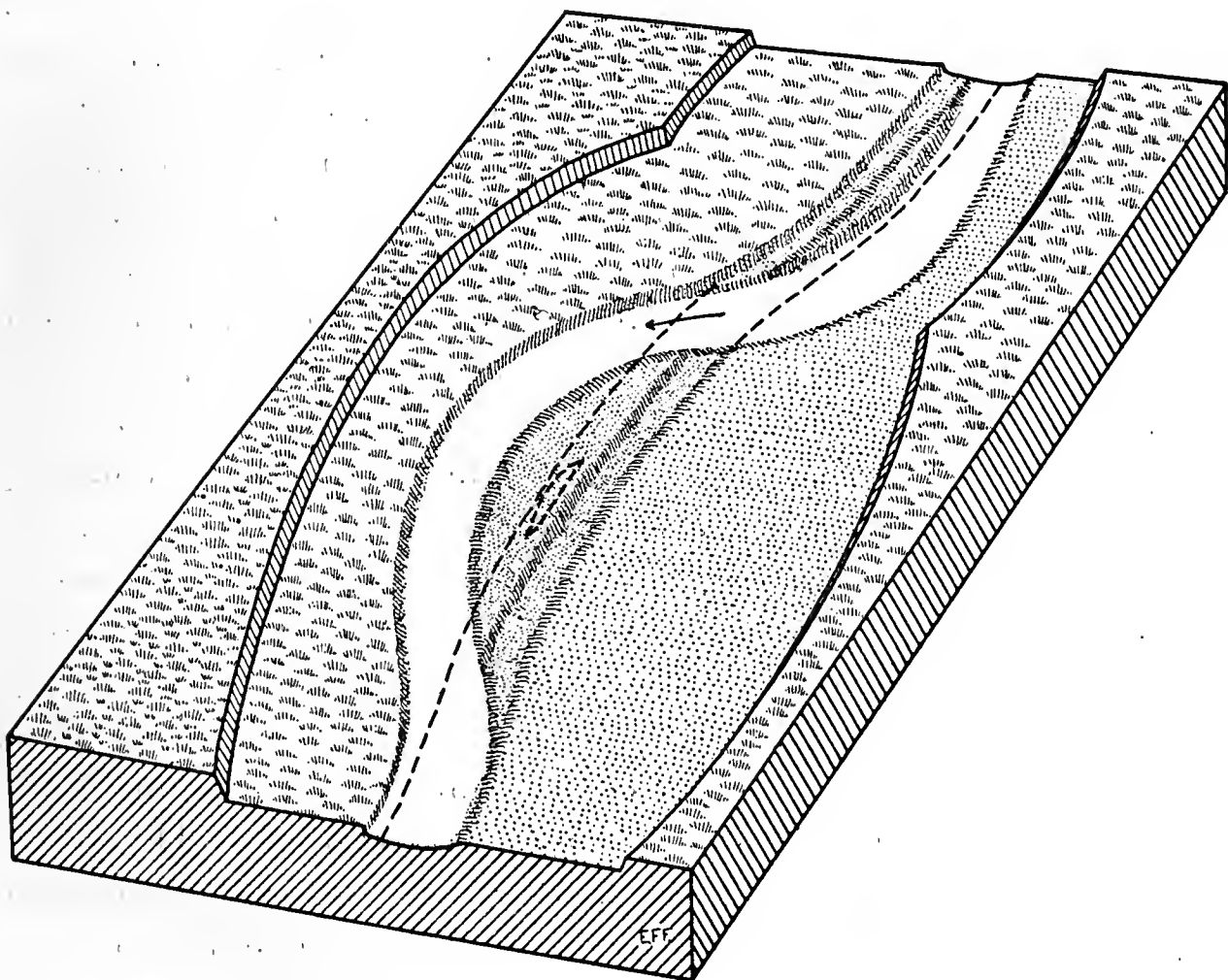


FIG. D.—Partition process of lateral movement; early stage. River adjusting its meanders to a new deflection of the current. By the growth of one sand-bar island, the river parted and has entirely departed from the weaker channel. Old channel is indicated by the dotted lines.

ment, incident upon change of volume, cut-off, short-cut, rock barrier, accidental natural obstruction, or artificial construction. Any one of these controls causes the deflection of the thread of the current, forcing the establishment of a new series of curves which cannot coincide with the former series. Any change in the direction of the strongest current

causes it to withdraw from former banks of erosion; the water there becomes shallow, and determines an area of deposition (away from the formerly eroded bank) building a sand bar which in time becomes an island. The deposition cannot be continuous with the deserted bank, as the thread of the current has been so suddenly withdrawn to the opposite side of the river. In consequence the island grows within the channel of the river near the bank from which the current has been withdrawn by its new deflection. Whenever out of adjustment, the river swings with unusual vigor, and yet is unable to re-establish itself until assisted at times of excessive flood, when the river suddenly increases its erosion and so withdraws rapidly from the existing sand bar, depositing another sand bar (text-figure G). The partition type of plain would be deposited until the new meanders were well adjusted to the new deflection. Considering the nature and the number of the causes which influence the course of streams, it is evident that a river will rarely have an opportunity to develop symmetrical, systematic meanders. But there will always be some portion of the river producing a new series of curves, and in consequence, within such portions of the river the flood plain will be forming by the partition process.

Of these controls, change of volume is probably the most influential in bringing about deflection of the stream. Any change of volume alters the radius and arc of curvature of the meanders, thus disturbing the former adjustment and initiating the establishment of another series of curves. Furthermore, many chance obstructions such as ledges, fallen trees, ice blocks, etc., encountered by the sweeping flood, throw the current into widely divergent courses. New channels are carved, and the short-cut or cut-off may be the result. The floods which at least annually sweep through the river channel are forceful agents of erosion, tearing away the unconsolidated material until the passing of the highest water, when in consequence of the decreased velocity the deposition of the transported material instantly begins in the form of sand bars. After the attainment of symmetrical curves the deposited material is regularly added to the extending meander lobes. During the development of a new series of curves, the excessive floods cause an unusual amount of erosion and a correspondingly sudden withdrawal from the filling-in bank. Moreover, the current of every stream is at least yearly thrown more or less out of adjustment by change of volume.

The short-cut and cut-off may be cited as causing the river suddenly

to desert a given channel for a distinctly different one, and so definitely to change both the position and the direction of its current. These processes are not in themselves constructive. They stop (at one place) the deposition of flood-plain layers,— let us say, of the normal type,—

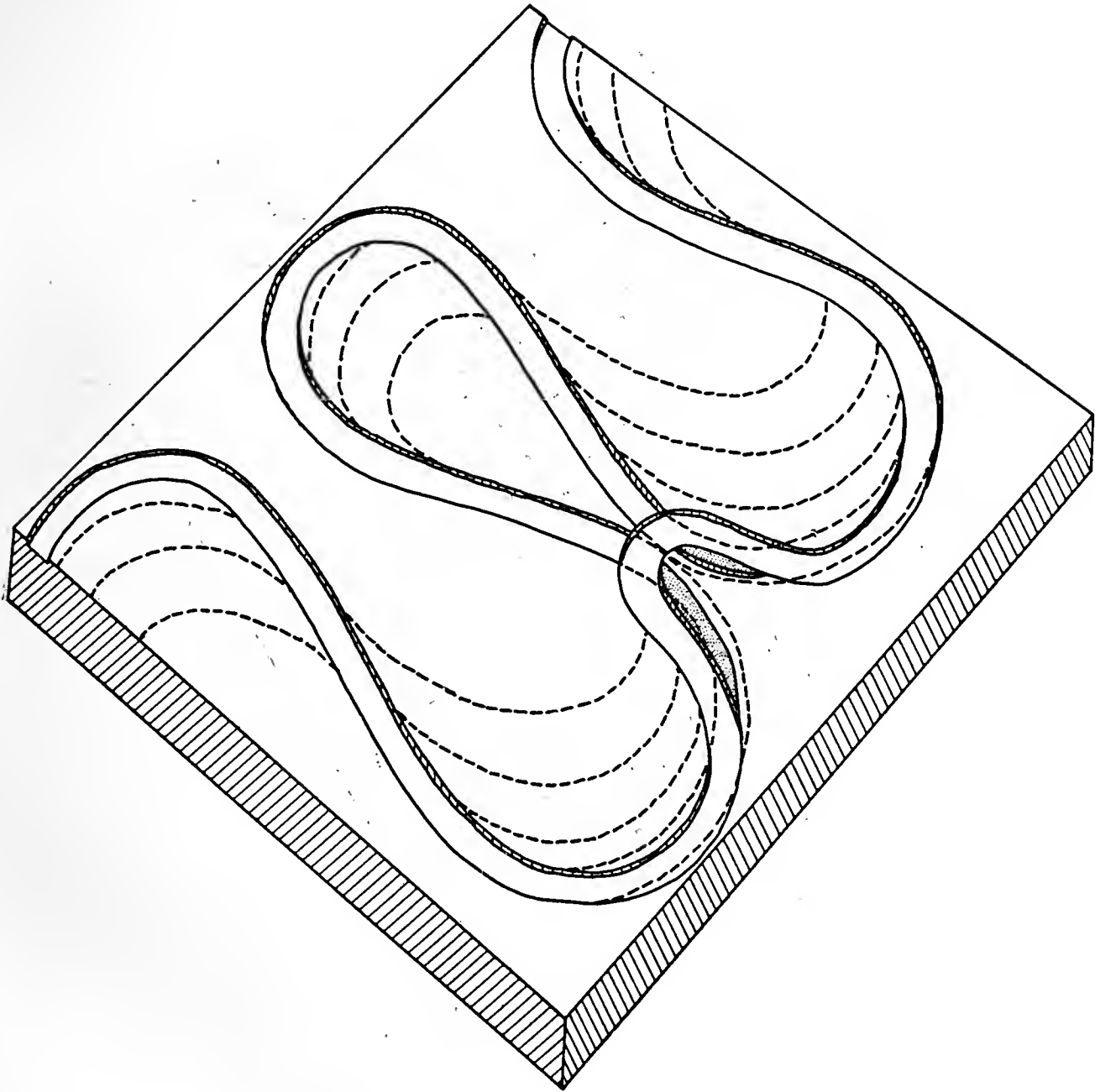


FIG. E.— Early stage of stream deflection due to cut-off process of lateral movement. The river in adjusting itself to the new bend has withdrawn from former banks of erosion by the growth of sand bars — the early stage in the partition process. The cut-off checked the formation of the flood plain by the meander-built process to allow its continuation elsewhere by the partition process.

only to start elsewhere the deposition of flood-plain layers, and this time of the 'partition' type. A river swinging in systematic curves would regularly and continuously add layer after layer to the inner and

lower side of each meander, thus extending the normal, meander-built flood plain. The short-cut or cut-off destroys the normal curves and so causes the river to adjust itself to a new series as clearly demonstrated by Tower ('04). The new channel instantly deflects the thread of the current, and causes the formation of sand bars just

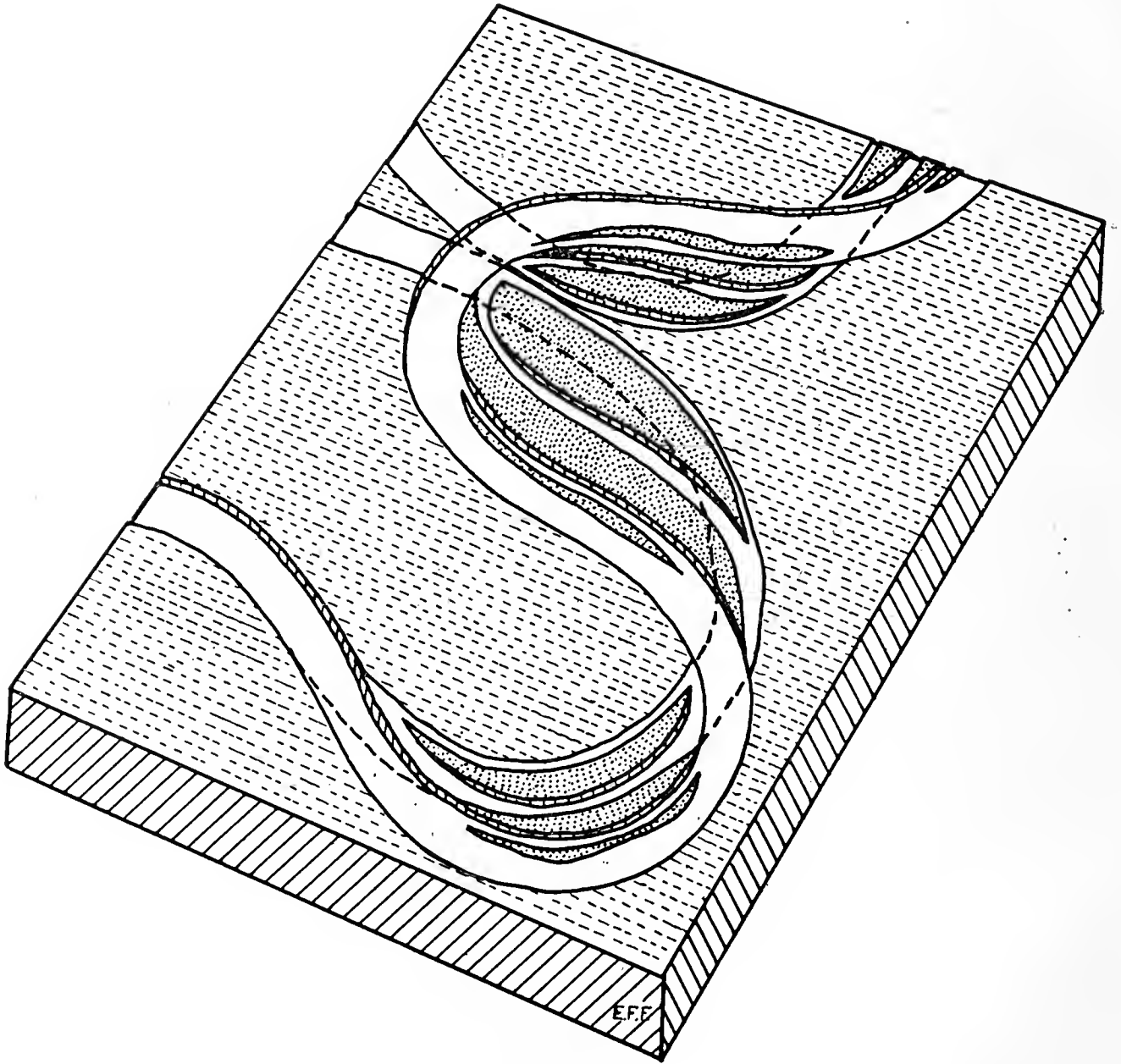


FIG. F.—Stream deflection due to cut-off. Later stage of E in adjustment of the river to the new meanders by the partition process. River has been successively parted by three sand-bar islands.

above and below the short-cut or cut-off. The accompanying figure illustrates the change in the work of the current, initiated by cut-off.

Tower ('04, p. 593), in describing the shallow water deposits resulting from a cut-off, speaks of these deposits as "fills," and says: "Fills may or may not be continuous with the former banks; for the sudden

change of the current may on the first fill down valley from the neck cause a deposition away from the bank and separated from it by a narrow strip of water or slough." Tower also cites a recent cut-off at Cole's Point on the Mississippi where the down-stream fill from the cut-off appears "as a distinct island, with a slough behind it, indicating a rapid change in the position of the current."

A rock barrier likewise deflects the thread of the current causing a readjustment of meanders. The sign of the readjustment, *viz.*, the partition process, is always more noticeable above and below the obstruction and grows less and less prominent up and down stream. If a rock barrier is encountered near the apex of a meander, the river by withdrawing slightly to the center of its valley may succeed in slipping past. The withdrawing and the slipping past indicate a necessary deflection of the thread of the current. Consequently the river impinges below the ledge and must withdraw from the channel cut above. Sand-bar islands appear when the withdrawal is sudden, and the river forms a new series of curves. Should a rock ledge be discovered below the apex of a meander, the river is unable to slip past, and is strongly compressed above the ledge. Again the normal sweep of the meander is prevented, therefore the river above and below the compressed curve must conform to the new deflection. Sand bars and partition plains are the result.

Any accidental natural obstruction, which temporarily fills a portion of the channel, such as a fallen tree, a slipping down of the sod, a piling up of logs, an accumulation of surface debris, etc., effectually deflects the current and initiates a new adjustment of meanders.

The effect of any such artificial obstruction as a pier, dam, or bridge is to prevent the river from continuing its normal swinging. The river must therefore spend its energy in cutting new meanders and filling the deserted portions of its course with deposits and possibly sand bars. The new curves established as the result of a bridge differ from curves formed by a cut-off deflection, since a bending must occur above and below the bridge, while by cut-off a new meander develops, growing outward and down-stream from the cut-off meander.

A clear example of the partition process exists about seven miles from Brattleboro where the Putney road crosses a young meandering brook known as Canoe Brook just south of Canoe Brook farm (see photographic illustrations, plate 11). The current has withdrawn by successive deflections from a rather well developed series of right- and

left-hand meanders to a winding but much straighter course and each deflection has been so rapid as to leave a series of four distinct islands of less and less curvature from the former meanders to the present almost straight course (as illustrated by the photograph, pl. 11, fig. 1). These resultant, undulating plains will be described under the development of partition plains. Other series of equally good sand-bar islands and one-time channels appear along the brook. These deflections have resulted from a large quantity of fallen tree trunks and brush, that initiated a left-hand deflection about a hundred feet up-stream from the road. At flood season short-cuts have been carved as a result of the new adjustment. At the lower end of the photographed meander, special sand-bar forms were constructed resulting from the discovery of a barrier of clay made firm by the roots of trees. This barrier chanced to be below the apex of a left-hand meander. The meander became more and more compressed causing the brook to bend up-stream to encircle the barrier, and that deflection enforced a withdrawal from the compressed bend and the formation of sand bar after sand bar until the brook flowed comfortably by the barrier. The entire brook for several hundred feet has successively withdrawn more and more from its meanders by a combination of the partition and short-cut processes.

Development of the partition plain.—A deflection of the current by any of the afore-named processes causes rapid erosion and the consequent widening of the channel. The river in struggling to withdraw rapidly from the opposite bank deposits on that side, and yet away from it, a sand bar which soon develops into an island. Continued outward cutting by the thread of the current causes the river to withdraw more and more from its shallow bank (see text-figure D). The downward cutting of the thread of the current deepens the wider and stronger channel, thus drawing the water off from the more shallow channel. Erosion continues gradually until flood season, when suddenly more erosion takes place and much material is deposited, forming sand bars which part the river. As the current departs from its weaker channel, this abandoned course and the one-time island are added to the growing partition plain; and the river has moved laterally an appreciable amount.

The continued deflection of the current allows, at times of excessive flood, the formation of another and yet another sand-bar island, which upon the departure of the river from the weaker channels are succes-

sively added to the growing, undulating plain. The growth of such plains is more rapid immediately following the change in the deflection of the thread of the current, and slowly decreases as the river approaches the series of normal curves. Since the rivers, though

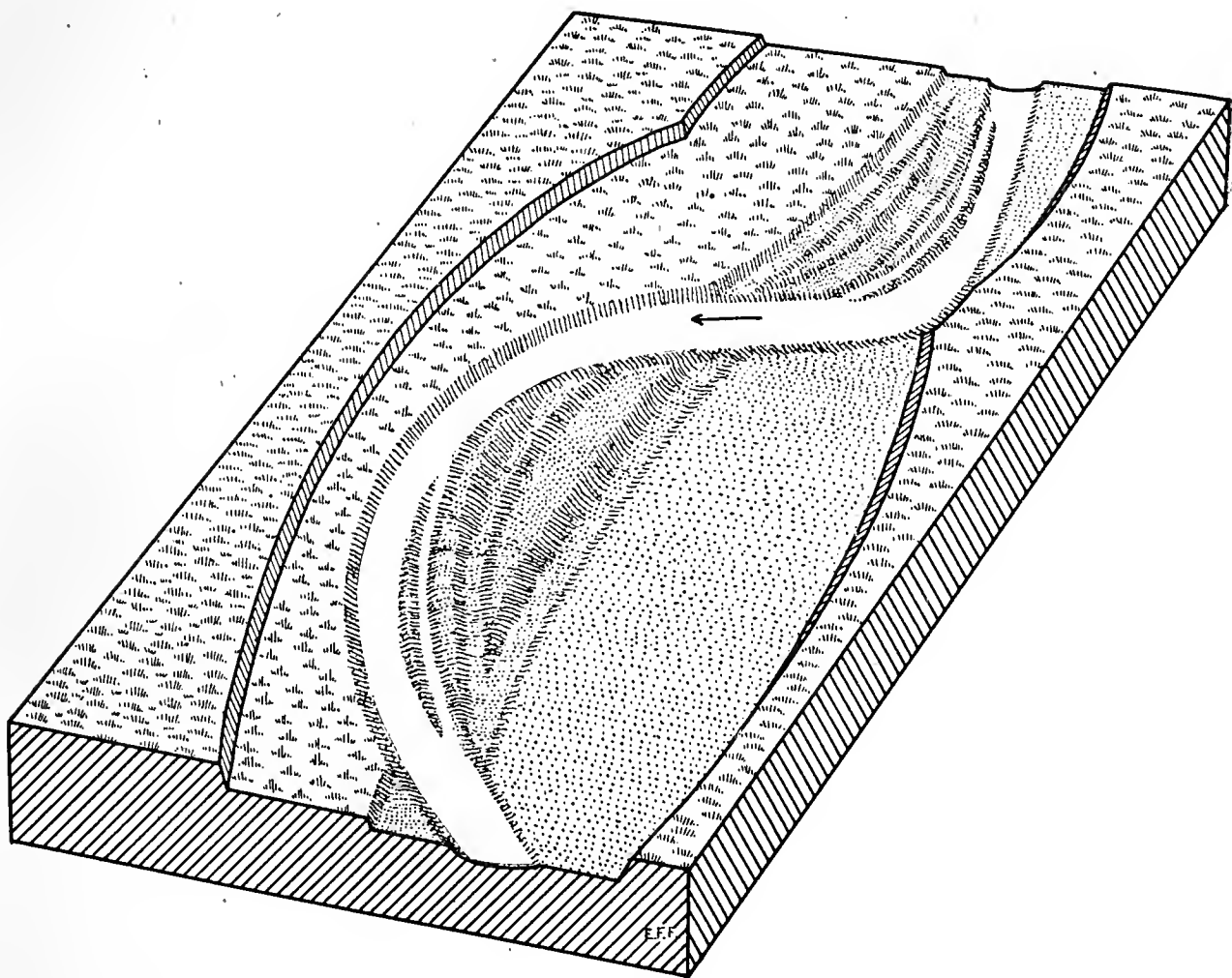


FIG. G.— Partition process of lateral movement; later stage of Fig. D, showing three islands which have successively parted the river. At times of successive erosion the deposition has been withdrawn from the former bank, causing the growth of the sand bars.

graded, are constantly degrading, the deserted channels and the islands are successively lower and lower, and the flood plains though undulating, slope slightly toward the river.

Such sand bars may be formed in any meandering river whether degrading, graded, or aggrading. By degrading, the more active streams drain the water from the growing partition plain, and by the continued deepening of the main channel the successive sand bars are exposed. They are narrow and show rather strong parallelism with the old and new river banks. The sand bars of the less active, more mature rivers accumulate slowly and form much more permanent islands. They are large in extent, often forest-covered and

receive additions where the current is not strong, usually along the filling channel and at the up-stream end. Observations upon our essentially graded New England rivers show the prevalence of these sand-bar islands. The West River as it flows into the Connecticut shows three islands of varying sizes and the younger, less mature streams that descend from the valley sides into the West and Connecticut Rivers exhibit many such islands. The island though usually of systematic sand-bar formation may be accidentally the result of short-cut. Islands of this type will be considered later.

The West River is to-day parted by a sand-bar island at the 205-foot level (see plate 1). This island is the first of a series by means of which the current of the river is adjusting itself to a comparatively recent deflection caused by short-cut from the base of the Retreat Meadow. The thread of the current and consequently the deeper channel are on the right. At low water the left-hand channel is dry, and the pebbly, gravelly material covering its floor, grades gradually to the level of the island. During the subsiding floods, the up-stream current, entering the shallower channel, is more or less checked, and therefore deposits, gradually building up the floor of the soon-to-be-deserted channel. With continued wash-filling, the old channel will be recognized not by a perfect river bed but by a valley-like depression.

Two other islands occur in the West River before it reaches the Connecticut, and the Connecticut is parted by a large island at Brattleboro. The current of the Connecticut flows through the wider right-hand channel. At low water, the left-hand channel is almost deserted, and inevitably it will be abandoned in the future. The river will then have moved materially to the right. Its further progress in this direction cannot be great because of the artificial constructions. Innumerable other instances of partition and the resulting lateral movement of the Connecticut might be cited. The process, however, may be studied more simply if reference be made to the younger, more energetic side streams. Just before Canoe Brook seven miles north of Brattleboro, reaches the main stream, an island, unquestionably of sand-bar formation, appears in the middle of its course and the water divides to flow around it (plate 10). The thread of the current, deflected to the right, has cut down so vigorously as to produce a fall of water. Continued erosion of the stream will cause the fall to move headwards, and the two streams will exist until the waterfall has retreated far enough to acquire the more shallow

stream causing it to depart from its channel,—a change which is inevitable because of the lower grade attained by the more vigorous stream. As a result, the left-hand channel will be deserted, a sand bar added to the left-hand widening flood plain, and the river moved

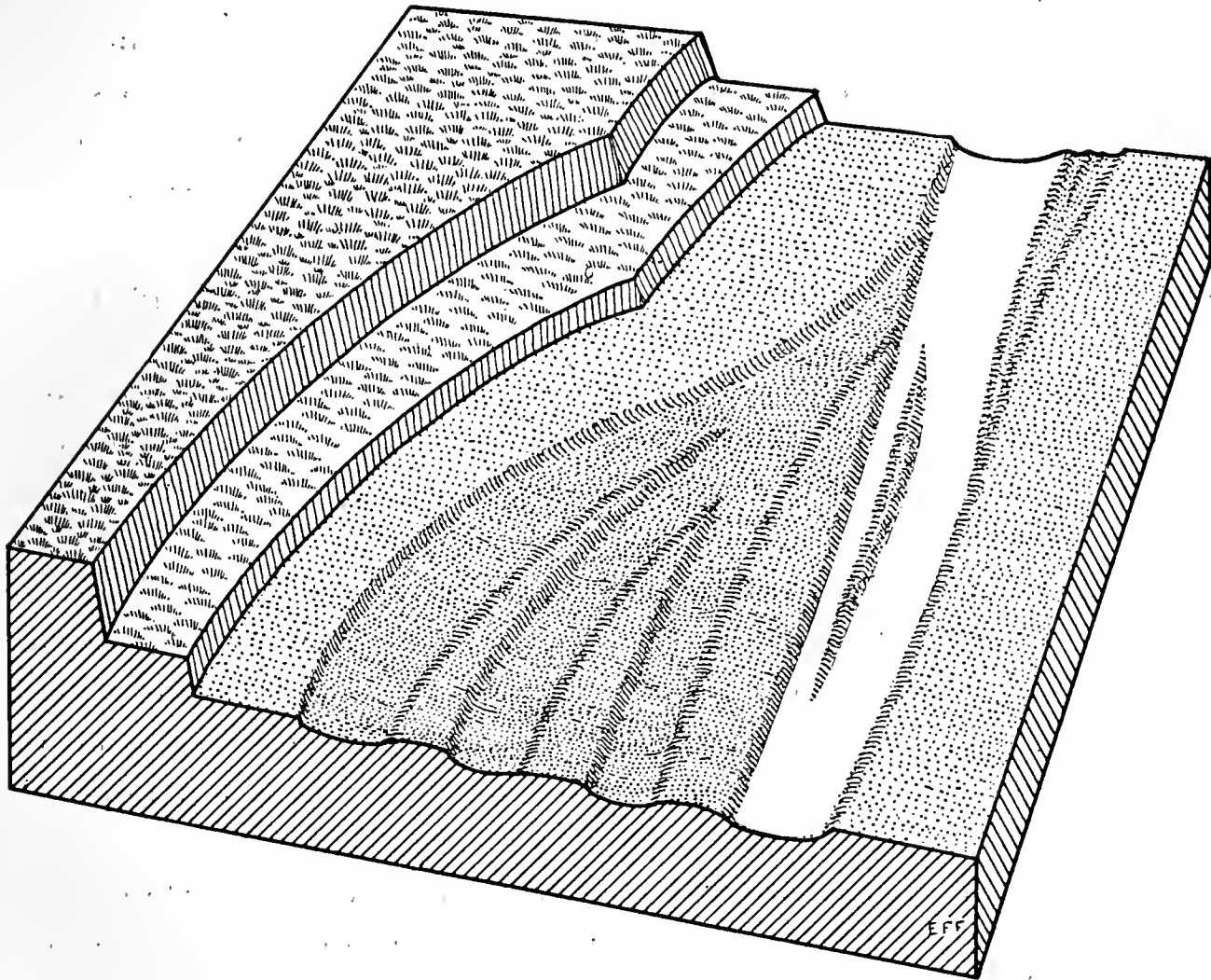


FIG. H.—Diagram of the mature stage of the partition flood plain built by Canoe Brook seven miles from Brattleboro, Vt. Ridges represent the one-time sand-bar islands and the valleys the deserted river channels. Current flows toward top of figure.

to the right; and thus one stage of the process will be complete. So long as the new curves are being developed, the position of the river channel, noticeably at flood time, may be greatly changed, and there will be a repetition of the island process. A few hundred feet up the brook just referred to, there is a good illustration of the same process in a more mature development (plate 11 and text-figure H). To the left of the stream, four deserted river channels are found separated

by ridges, former sand bars. And so recent are these changes that the entire process is clearly demonstrated. The material of the sand bars and channels is coarse gravel. The deserted river channels are not well defined with flat bottoms and steep sides, but the plain is undulating. The entire surface is swept at flood, and further deposits may tend to obliterate these irregularities. The undulations are no greater than appear upon many of our broad flood-plain areas. At Hadley, the Connecticut at its great right-hand meander has left a series of islands on the up-stream side of the down-stream portion of the bend, which give to the plain an undulating surface, as pointed out by Emerson ('98). In describing the Sunderland, Hatfield, Hadley, and Northampton meadows, Emerson says: "The plain that seems so perfectly level when seen from above, proves on closer inspection to be made up of a series of broad, low ridges, like the long, low swell that comes in on the coast after a distant storm and the curved grooves which separate these ridges run approximately parallel to the bank of the stream but with greater or less curve. This is due to the composite nature of the terrace itself Each of these low bars represents one of the elements out of which the terrace is built and has passed through the stages of bar, island, and 'glacis terrace'¹ as it has added itself to the previously formed plain, while the groove on the outside of each ridge, (out from the river) is the unfilled remnant of the waterway which separated the island from the former shore.

"The surface of the broad terrace plain north of North Hadley and extending up to Sunderland shows this most strikingly, and when seen from the hill just north of Hatfield, each separate island of which the terrace was built by the westward swing of the river can be picked out."

With reference to the topography of the meadow at Brattleboro,—the area is wide in extent, and from a distance appears like a level plain. A careful survey, however, shows elevations and depressions, comparatively distinct to-day, notwithstanding the fact that the entire surface has been ploughed and re-ploughed for agricultural purposes. At the base of the Retreat scarp is the brook drainage characteristic of many such flood plains. A closer examination of the high and low areas reveals the existence of a series of valleys, representing channels

¹ Hitchcock, "Surface geology," 1860, p. 5.

from which the parted river departed on its passage to the right across the meadow. A natural conclusion would be that the West River, having reached the Retreat scarp by the partition process, was withdrawn by a short-cut to its present position, from which it is again moving to the right by the island process.

At flood season the entire meadow is covered with water. As the water subsides, the old channels left by the partition process are occupied by the lingering water, and thus mark with some clearness the positions which the stream may have held as it gradually moved to the right. Some of the higher levels observed along the banks of the West River must have been produced by flooding. The floods are strongly marked within this area. Not uncommonly it happens that trees are uprooted or lose their bark. The water descends with great suddenness, transporting huge blocks of ice for long distances and often twenty feet or more above the present meadow level. As the water subsides, such a flood would deposit much material, therefore increasing the height of the river banks, and adding to the sand bars.

It is quite possible that the swinging of a river from one side of its meander belt to the other may be accomplished by a combination of short-cut and partition processes. A series of short-cuts produced at flood causes the stream at low water to follow in part its old channel and in part its new short-cut channel. Such a flood-plain island determines the parting of the river and is a measure of its lateral movement. The flood plain exposed on the left-hand side of the West River is deeply eroded and cut into at flood season. Should any one of these cuts be carved entirely across that flood plain, incision might be below the level of the West River channel and so cause a further parting of the river around a short-cut island. The largest island in the West River, because of its structure, size, and forest vegetation, may be a portion of the flood plain separated by a left-hand short-cut.

The partition plain may be defined as young, mature, or old. The young plain is characterized by clearly defined ridges and channels of sand-bar material slightly elevated above the water level. So recently abandoned are these plains that they show no signs of erosion, are rarely grass-covered,—indeed, the probability is that they are still swept by floods, receiving additional flood-plain deposits. The mature plain is more gently undulating, because the floods have so frequently swept over it as to fill in the valleys with fine silt and possibly to remove the crests of the ridges. The mature plain is dry, not covered by water,

and often the river has swung broadly away from it. The old plain is more wavy than undulating. The sand bars and the intervening channels are no longer distinct. It is difficult and practically impossible to define the positions of the courses from which the river successively departed. It is probable that the plain will be elevated above the river which, since the formation of this plain, has degraded to lower and lower levels, forming younger and lower plains. Such elevated old partition plains will show signs of weathering and dissection.

As a result of these processes, two types of terrace plains are constructed, the meander built and the partition built. The first type is formed by the regular deposition at the inner and lower side of the down-stream sweeping meanders. Such a terrace is even and nearly level, sloping gently toward the meander, and is the type generally recognized as the normal flood plain. A second constructive type is produced by the partition process. A terrace so formed slopes gently toward the river, but is undulating, with elevations and channel-like depressions, representing the former islands and the intervening deserted channels. The other processes of lateral movement check deposition in one place to start it elsewhere. They straighten the river locally, and by destroying the existing curves, deflect the current, forcing it to establish a new systematic series of meanders. The new deflection of the thread of the current withdraws the stream from former erosion banks by the deposition of a series of sand-bar islands, leaving partition plains.

TERRACES OF THE WEST RIVER VALLEY.

Terrace pattern, early stage.—Terraced valleys show different stages of development: the early stage, the middle stage, and the late stage, corresponding to the stages of youth, maturity, and old age. In the early stage, the river valley has commonly but one or two terraces, perhaps one completed terrace and one low flood plain. They show clear cut, simple forms, few in number, wide in extent. The terrace pattern is without the complexities of middle life and has the most immature development of terrace drainage, if any. Any terracing brook furnishes a good example of this early stage, showing forms

which have suffered no weathering and only slight undercutting by the swinging of the brook. This simple ideal type, represented in text-figure I, shows at least one distinct terrace, with scarp concave toward the brook, and more or less cusped,— the cusps formed between the concave incision of the meanders of the brook. As each meander sweeps down the brook valley, it probably diverges sufficiently from

its original angle of incision to make a series of these concave cuts, uniting in noticeable cusps. These cusped edges are most apparent when the terrace scarp faces the brook, and are entirely wanting when the terrace scarp has been carved by the forward extension of an arm of the meander. The text-figure I shows that such sweeps of the terrace scarp face up-stream. An illustration may be seen on plate 1. The low terrace facing the right side of the meadow is distinctly cusped just before it makes the long, concave curve of the Retreat scarp. A meander of the West River carved the deeply compressed Retreat scarp after it had successively cut the right-hand cusps.

Three of the early stages in the development of the West River terraces may be traced as shown by diagrams (pl. 3, figs. 1, 2; pl. 4, fig. 3), which are necessarily more or less hypothetical, since it is impossible to-day to locate with absolute definiteness the positions occupied by the river thousands of years ago. The West River has been swinging and slowly degrading its aggraded valley since the glacial period. In following its left-hand wanderings, there are rem-

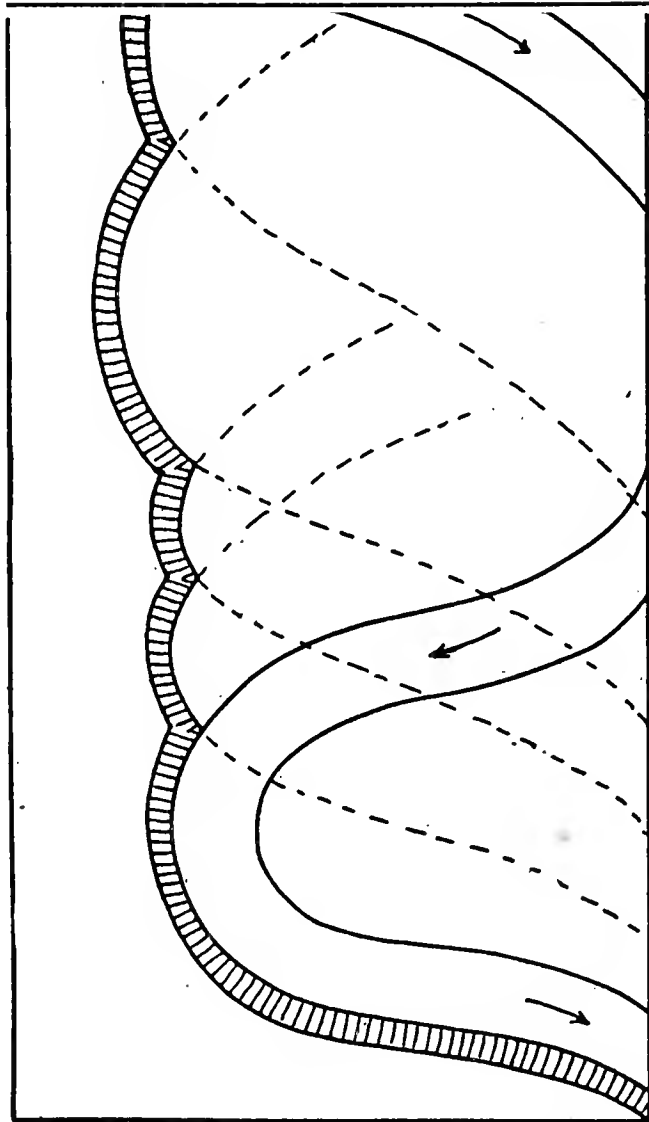


FIG. I.— Ideal terrace pattern; early stage. As each meander progresses down-valley, it vacillates sufficiently to carve the curves and cusps characteristic of the early stage of terrace scarps.

nants of seven terrace levels marking at least as many and probably more left-hand swings. The earliest record is given by the highest 347-foot level (pl. 3, fig. 1). That plain, now limited in extent, skirts the left-hand rock hill — the limit of swinging. The once more extensive plain was nearly consumed by the river as it swung to the left later at the 304-foot level (pl. 3, fig. 2) carving a scarp in the higher 347-foot terrace. That scarp, the oldest to the left of the river, is now weathered with rounded edges and deeply incised transverse valleys, but thousands of years ago when the river flowed at its base, and the entire valley was filled to the 304-foot level, that high terrace scarp was young, with a sharply defined straight edge. A third time as the river swung to the left it eroded the 304-foot plain leaving a scarp descending to the 291-foot flood plain (pl. 4, fig. 3). This third position of the river is the most hypothetical, and is based only upon the two limited scarps at the back of the triangular 291-foot plains (plate 1). The remnants of these early plains are assuming old forms. They distinctly represent the highest plains in the valley, and those that were first formed.

Terrace pattern, middle stage.— Allow the river to continue its sweeping and swinging, and a terrace pattern of some complication may result. It is possible that the river may cross and recross its valley many times. On the northeastern side of the river (plate 1) are shown the results of at least eight swings including the present position of the West River; and this is probably not a full count.

Having carved the three highest terraces, the river continued to degrade and to swing back and forth across its valley, carving and depositing four terraces at successively lower and lower levels as accidentally determined by rock barriers, short-cuts, or cut-offs. The complexity of terrace pattern of the middle stage is determined by the remnants of the three early and four later flood plains as represented in diagrams (pls. 3, 4, 5, 6). At a later return of the river to this side of the valley (pl. 4, fig. 4) it was flowing from 279 to 280 feet above the sea, and succeeded in almost completely removing the remnants of the 291-foot flood plain. The two small triangular areas shown on the fourth diagram (pl. 4, fig. 4) represent all that remains of the formerly more extended 291-foot flood plain. So perfect are these triangular areas to-day that they seem almost like models. When the river returned for the fifth time to the northern side of its valley, it was flowing at the 262- or 263-foot level, and the scarp cut was 18

feet. The river must have been meandering in great loops, extending one meander far into the 280-foot terrace, then curving broadly to the other side of the meander belt and returning so as to make a more extensive cut into the same flood plain. The evidence of this is most clear. A rock barrier held the first meander mentioned, at its lower side, and prevented the cutting away of the long spur of the 280-foot flood plain. This necessarily deflected the river broadly to the western side, and returning, it cut the extensive bend, represented to-day by a distinct ox-bow channel, a course from which the river was withdrawn by a short-cut. It is interesting to note that the outer bank of this great meander bend is distinctly cusped, which would seem to indicate that the current impinged with varying force upon the bank of erosion. On the sixth return (pl. 5, fig. 6), the river apparently cut to the 225-foot level, which produced a scarp of 38 feet. This scarp is distinctly deeper than the other one-swing scarps of the valley. Presumably the same amount of time was necessary for the river to swing across its valley; therefore if the power for degrading remained the same, this scarp is not a one-swing but more probably a two- or a three-swing scarp. Evidence from the other side of the valley may tend to prove in the absence of intervening levels, whether this is a one- or more-swing scarp. The small terrace which appears at the northwestern end of this 225-foot level is so insignificant — only one or two feet above the 225-foot plain — that it is more probably a two-sweep terrace and does not indicate a swing of the river. On the seventh return (pl. 6, fig. 7) the river flowed at the back of the 209- to 214-foot level. Evidently as the river moved from this position, it swung strongly to the right, reaching the base of the Retreat scarp, — chiefly by the partition process. By short-cut, across the narrowing flood plain, the river was withdrawn to its present position on the left side, and is flowing now at the 200-foot level. This last short-cut disturbed the adjustment of the current, deflecting it to the right and causing the formation of the large island at the 205-foot level.

The form and position of the 291-foot cusps (pl. 4, fig. 4) are accidental, carved by the intersection of two lines having no particular relation to each other. All the elements of these cusps are variable, influenced in some other way than by a common control. They may be considered typical cusps formed by an unguided, swinging river. A definite arrangement and grouping of cusps is recognizable

at the two extremities of the 225-foot plain, where the rock outcrops produce a series of stepping terraces. No such definite arrangement of cusps, one back of another, could exist by accident. A better example is found (plate 1) west of the meadow, in the vicinity of the farm buildings, where the curving terraces terminate and are replaced by the rock ledges which—as will be later explained—form the control for the systematic arrangement.

Terraces of such complications frequently show a perfectly developed system of terrace drainage. This system exists upon the Retreat plain and the meadow plain. A line of drainage follows the back of the Retreat plain to its lower end. There the brook has eroded for itself a valley to the meadow plain and deposited on the floor below a fan-like delta. The Retreat plain slopes to this line of drainage, indicating that the plain was built while the river occupied the position of the present brook and that the river was finally withdrawn by short-cut or partition. At the foot of the Retreat scarp on the meadow is another brook, following what may have been the old course of the West River and now emptying into the present river.

Such complexity of terrace pattern as exists within the West River valley is typical of the middle stage, because rock ledges were discovered to defend and preserve positions of the many terrace plains. Moreover, the remnants of the higher terrace plains are few and small, since they have been repeatedly undercut and destroyed; and the lower plains are larger, more numerous, and better preserved because time enough has not elapsed for them to be frequently attacked by the river.

Terrace pattern, late stage.—When the power of a river to degrade weakens, it devotes its energy to swinging repeatedly to and fro across its valley. In the absence of rock ledges, even the basal terraces disappear, and the intermediate plains may be completely swept away. The river thus swings until it reaches the limit of its wandering belt; and the whole descent from the high-level terrace to the existing flood plain is made in one deep escarpment.

Three conditions may bring about this weakened ability to degrade, as Davis ('02) has shown: first, the attainment of nearly fixed values of volume and load, such as might be reached when a glacial climate had given way to a milder climate and the latter had become well established; second, the cessation of any slow uplift by which degradation had been initiated or aided; third, superposition of the stream

on a strong rock sill on which corrosion is very slow. Any one or two of these conditions may have weakened the ability of our New England rivers to degrade. And they are essentially graded for long stretches and therefore devote their energy to swinging. The river-terrace topography such as is found along the Connecticut in the vicinity of Holyoke and Springfield suggests that possibly here the river has been prevented from degrading lower, and (in the absence of more controlling rock ledges) has left high, strong escarpments on either side with a few low terraces in the more central portion of the valley.

Were there no controlling elements, it would be surprising to find

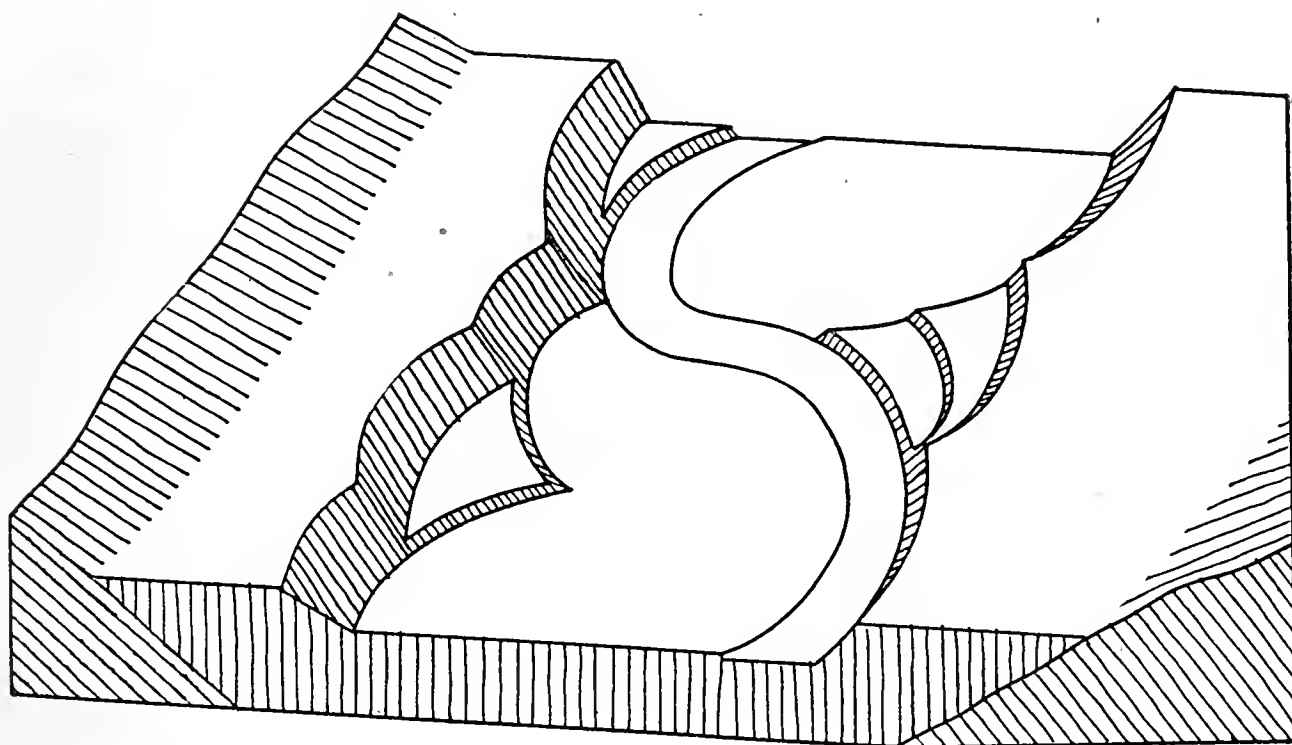


FIG. J.— Ideal terrace pattern; late stage. Absence of rock ledges has made it possible for river to wander broadly, removing the intermediate terraces. Descent from the highest terrace to the flood plain is concentrated in a single high scarp. Central portion of valley shows a few low basal terraces.

preserved a series of eight stages in any such valley as that of the West River at Brattleboro. Evidently the factor which has made possible the preservation of the remnants of these terraces must be due to another and eminently important cause, *viz.*, the rock ledges.

Influence of rock barriers upon the form and preservation of the West River terraces.— It has been stated that a free-swinging river in an aggraded valley will by degrading discover the rock prominences or reefs of its floor; and the outcrops of ledges so discovered will be constantly at lower levels and nearer the center of the valley. These

ledges defend and protect the higher terraces. Only a small portion of the flood plains, however, is left back of such defended cusps. There may extend down-stream a long trail of the same flood plain to mark its more widespread extent; and the trail only exists there because of the up-stream and possible down-stream cusp which has prevented the river from swinging more widely and so consuming the entire terrace. The extent of such terraces from the point of protection will vary from a few feet to several hundred. If the ledge discovered lies near the apex of a down-sweeping meander, the meander may succeed in slipping past it by withdrawing slightly toward the center of its valley. The obstacle is thus avoided, and the river impinges deeply on the down-valley side. An example of this type is seen where the West River slips by the rock on its right bank at the pumping station, and is now sweeping broadly to the right. By slipping past this and other rock barriers the river succeeded formerly in making the entire sweep of the meadow (plate 1).

To the west of the meadow and south of the farm buildings there is a strong rock control. At three succeeding stages, when the meander reached this point, the rock ledge was discovered below the apex of the meander. In such a position the meander could not slip by, but was forced to bend outward and cut a curved re-entrant in the terrace front next up-stream from the ledge. The meanders farther up-stream continued their advance down-stream, which compressed the meander next to the ledge to a relatively strong curvature. This sharpened the defended cusp and caused it to point up-stream. The features which represent this control are the rock ledges to the south, the sharp bend or the deep concavity of the terraces to the north of the defining ledge, and the sharp cusp of the ledge pointing up-stream. The area of the West River just described is of special interest since it shows that the form and outline of the terrace front have there at least been wholly controlled by the definite rock ledges and the accidental position which they held with reference to the meanders of the river. Three times it happened that the defining ledge was on the tangent between two meanders or at the point of river inflection; and the last time as the river was sweeping around the meadow, the defining ledge chanced to be near the apex of the meander. In the first instance the stream could not slip past, whereas at another time, slipping past, it did its greatest work below the defining ledge. Examples of rock control on the left side of the valley have been cited. It frequently

happens that ledges which have been of greatest importance in controlling the deflection of streams are not visible because of wash deposits which could most easily cover and apparently obscure them. Yet the terrace patterns which appear, make it absolutely evident that a ledge existed there. Otherwise the left-hand, 280-foot alluvial spur would have been swept away by any river swinging strongly against its northern up-stream side. The positions of the rock ledges on the map give many other illustrations of rock control, though possibly not so striking as these. For instance, as the West River swung to the left at the back of the 220-foot level, its meanders impinged against the alluvial material and would probably have eroded more to the left had it not been for the existence of the rock ledges. As the West River swung southward across the meadow, its passage to the right was definitely limited by rock ledges.

Diminished swinging of the meander belt.— While rivers are flowing at high levels in their drift valleys, they may not be expected to encounter ledges. As they cut deeper, the possibility of encountering rock grows greater, and rock ledges are constantly nearer and nearer the axis of the valley and so tend to narrow the meander belt. As the valley deepens, the number of defended cusps tends to increase; and as the meandering belt is narrowing because of the rock barriers, the horizontal distance between low-lying scarps must be less than between the high-level scarps,— a principle which is of great interest in this connection because it shows that the narrowing of the valley must be a normal result due to the discovery of rock ledges and not referable to diminution in volume as according to the earlier but discarded theories.

Since there is no normal distribution of reefs of rock upon the valley floor, their discovery is not only accidental but without systematic arrangement. Consequently the rock reefs which appear on both sides may chance to be near the axis, and so narrow the valley, or may be widely separated, and so enable the meander belt to cover a broad area. There may be stretches along any river comparatively free from ledges, or if not free, in which the ledges lie so low as to have little influence and to allow a broadly open valley. Under such circumstances, few of the middle terraces will be preserved, and on either side will be a high, strong escarpment with a few low-lying escarpments protected by ledges. The Holyoke-Springfield district may again be mentioned as an example of this type. Such types, however, attract comparatively slight attention, since it is the existence of step-

ping terraces, and not the absence of them, which arouses interest. The Whetstone Brook at its junction with the Connecticut River at Brattleboro, is a vigorous, active stream, swinging within a comparatively narrow, rock-bound valley. In its swinging and degrading, the brook has uncovered ledges at each lower level, thus successively narrowing the width of its wandering belt. Consequently a most excellent example of stepping terraces occurs, being of sufficient width to allow the construction of a street and its houses with cross-roads ascending the terrace scarps. This topography is recognized as a unique feature of the town.

The distribution of high and low scarp terraces as typically developed

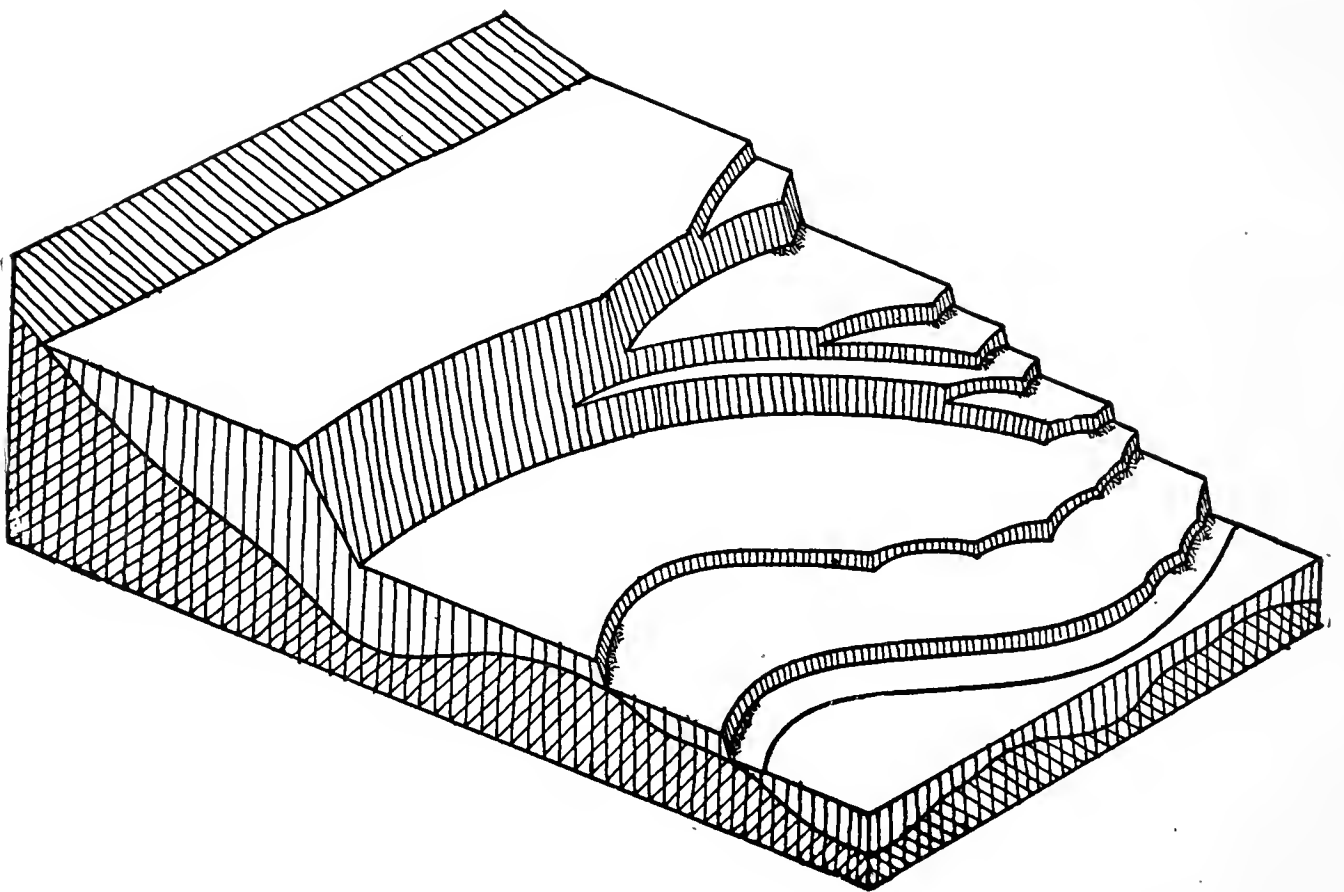


FIG. K.— Distribution of high-scarp and low-scarp terraces as controlled and defended by rock ledges.

is illustrated by text-figure K. Assume that a low-scarp terrace is first formed along one border of the belt of wandering. After a few swings, a ledge is discovered, consequently all the terraces of earlier swings lying back of this ledge are preserved. Every later swing of the river is checked nearer and nearer the axis of the valley, because of the sloping surface of the buried rock ridge. A flight of stepping terraces is formed as a result of the defended cusps. Down-stream

from the defended cusps, successive terraces may be consumed, until by chance a lower rock ledge may be discovered. Such a lower ledge would protect the last flood plain and the high escarpment back of it. Davis ('02, p. 320) has concluded "that low undefended, high-level terraces of early swings are most likely to be preserved back of defended cusps of later swings; that the undefended terraces of early swings would probably be swept away in the production of a single high scarp terrace wherever broad swinging at low levels is not prevented; and that when high scarps occur in a flight of stepping terraces they are more likely to be found at or near the top than at the bottom of the flight."

It is therefore evident that the preservation of the many flights of stepping terraces has been made possible by rock ledges — an eminently important control — as was suggested by Miller, as Davis has clearly demonstrated and as is proclaimed by almost every river terrace in New England.

Relation of terrace pattern on two sides of valley.— It is a generally accepted fact that the terraces on the two sides of the valley of an essentially graded river slowly degrading, do not necessarily agree in number or in height. The complete swing to and fro across the valley results in an appreciable amount of degradation. In the Brattleboro region, twelve feet appears to be a characteristic one-swing scarp. The difference need not necessarily be always maintained, since by the cutting-off process the river is immediately withdrawn to a new position. Much evidence has been given to prove that the number of terraces remaining on opposite sides must be accidental as determined by constraining ledges, so that the same number or a widely differing number may exist on the two sides,— assuming always that they were systematically formed on both sides, but that one or more may have been completely removed. Another fact with reference to the terrace plains is that they slope with the stream; if the grade of the river is a strong slope, the difference in the up-stream and the down-stream ends of the plain will be appreciable. The West River (see profiles, plate 2) at Brattleboro shows a fall of ten or twelve feet in a distance of a half mile, consequently the meadow shows a grade of probably ten or twelve feet within the same distance. Such a down-stream slope of the flood plain makes it difficult to correlate the terraces on opposite sides of a steeply graded river, because any change of grade would have directly affected the slope of the flood plain. Granted

that there has been no change in grade, the distance and the fall per mile must be calculated so as to correlate the order of deposit of the flood plains on the two sides.

The profile map (plate 2) gives two actual cross sections, one from east to west along the line A-B, and the other from northeast to southwest along the line C-D. The scale of profile does not admit the showing of the more delicate slopes and undulations of the plains. The cross sections emphasize any possible relations existing between the plains on either side of the river. These, in connection with the ideal profile, show a difference in the number and levels of plains on the two sides. The higher scarps are the sum of two or three scarps of lower plains which were consumed by the river as it swung more widely than on previous swings across its valley. Perhaps the greatest value of the profiles lies in the fact that they indicate that while the river is swinging laterally it is also always steadily approaching sea level. Could we stand for untold ages and observe the river, we would see meander after meander progressively passing gradually by, and we would also see the entire river channel move or swing back and forth within its narrowing meander belt.

HISTORY OF THE WEST RIVER VALLEY.

This West River branch of the Connecticut rises among the hard crystalline Green Mountain hills of southern Vermont, and flows southward and eastward across the metamorphic rocks to the Connecticut. A valley narrowing up-stream had been carved preglacially in these rocks. During and at the close of the glacial period, the valley became aggraded with more or less wash drift to the elevation of the highest plains which now rest against the rock boundaries of the valley. The river has since then by wandering and degradation carved the present valley topography, wandering at first freely in the unconsolidated material until at lower levels the rock reefs were encountered and served as a defence for the remnants of higher flood plains. The highest plain within the valley, *viz.*, the Golf Links area, is not of simple origin. Its surface is rolling, consisting of morainic and kame-like material. The upper layers are of coarse gravel, then sand, and below, clay,— a clay outcropping at an elevation of 375 feet. These deposits may have been continuous across the valley at the

early stage when the river began its degrading work. The general appearance and character of the deposit would suggest that the high area is one of local out-wash from the higher ground during the period of aggradation. The area may be considered as a delta surface, built up in standing water, perhaps the flooded West River. As we descend from this delta plain and its lobate slopes, we pass successively younger and younger terrace patterns. The older and higher ones show deeply incised valleys, rounded edges, and long wasting slopes of erosion. At the bottom of the series, in contrast, we have sharp terrace edges and steep terrace scarps with few or no evidences of erosion.

The terrace patterns of the West River are ideal young and middle-stage patterns, showing free and defended cusps. The strong defending rock ledges south of the Retreat farm buildings, at the pumping station, and the strong rock barrier east of the meadow are good illustrations of the influence of such accidental barriers. The wandering belt of the river has been constantly narrowing by reason of the discovery in its swinging of rock barriers nearer and nearer the axis of the valley. The flood plains of the West River valley are both meander-built and partition-built. The 262-foot plain on the left side of the river is a typical meander-built plain, and the meadow is a good example of a partition plain.

It is evident that in the future the river, if undisturbed, will abandon the left-hand course about its large sand-bar island for the deeper right-hand course. It will thus swing to the right unless another deflection causes a change in the direction of the current. At present flood-carved gullies cut deeply into that left-hand flood plain, and their further extension through the plain will produce a short-cut thereby preventing the right-hand incision of the meander and thus straightening the course of the river.

CONCLUSION.

Obviously the conclusion to be deduced from the foregoing study is the one already suggested,— that Miller's theory of defending ledges affords a better explanation than any other for the terraces of our New England valleys. These terraces are not in every instance defended, though all the flights of terraces exist in consequence of defending ledges. A lessening of the river volume and interrupted uplifts appar-

ently have not had great effect in confining the swinging and slowly degrading river to more and more restricted belts. The narrowing of the valleys results rather from the confining influence of rock ledges discovered successively nearer and nearer the center of the valley. Another conclusion, moreover, is that the curves and scarps of river terraces may be most minutely accounted for, and that the action of a meandering and swinging river fully explains every detail of terrace forms. The West River terraces not only confirm the theory but also the entire train of consequences as deduced by Davis.

Further, and a far more important conclusion from this study of a meandering and swinging river, is a better knowledge of the controls which determine the behavior of such a river. A river of definite volume swinging freely in unconsolidated material tends to flow forward in symmetrical curves. During the approach and after the attainment of the symmetrical curves of this normal type, continuous deposits are formed on the inner and the lower side of each downstream-sweeping meander causing the growth of an even plain sloping slightly toward the river — the meander-built plain. Such a perfect series of river curves is rarely if ever developed because of the many accidents which by new deflection cause a departure of the current from the normal delicate adjustment of its symmetrical curves. Such a departure of the current may be caused by change of volume, cut-off, short-cut, rock barrier, accidental natural obstruction, or artificial construction. Any one of these controls may so throw the river out of adjustment as to initiate the formation of a new series of meanders. The sudden deflection of the current forces the river to withdraw suddenly from some banks by the formation of sand bars. The sand bars appear up and down stream from the cause of deflection. In many instances their formation can be definitely anticipated and located. The addition of successive sand bars is at times of excessive floods. Other islands, portions of the flood plain, are often severed at flood season by new short-cut channels. The sand-bar and flood-plain islands have invariably been a source of trouble and expense in river navigation. It is possible that having in mind the controls which cause the departure of the current of a river, we may foresee where the islands will form along our rivers and thereby simplify navigation.

This process of lateral swinging due to a deflection of the current from the normal curves is recognized by the formation of sand-bar

islands and may be called the partition process. The result is the partition plain, likewise sloping toward the river, but undulating, with elevations representing the island walls which successively parted the river, and with intervening channels representing the abandoned courses of the river. And furthermore, it may be said, in consideration of the four processes which account for the lateral swinging of a river, that while the short-cut and the cut-off processes stop deposition at certain places to allow it to begin elsewhere, the other two processes are constructive, depositing the meander-built plain and the partition plain. The meander-built plains have long been recognized as the ordinary flood plains, although many so classified are in reality undulating partition plains. The partition plains are of frequent occurrence and are typically represented along our New England rivers. Doubtless every meandering river is swinging in some portion of its course by the partition process.

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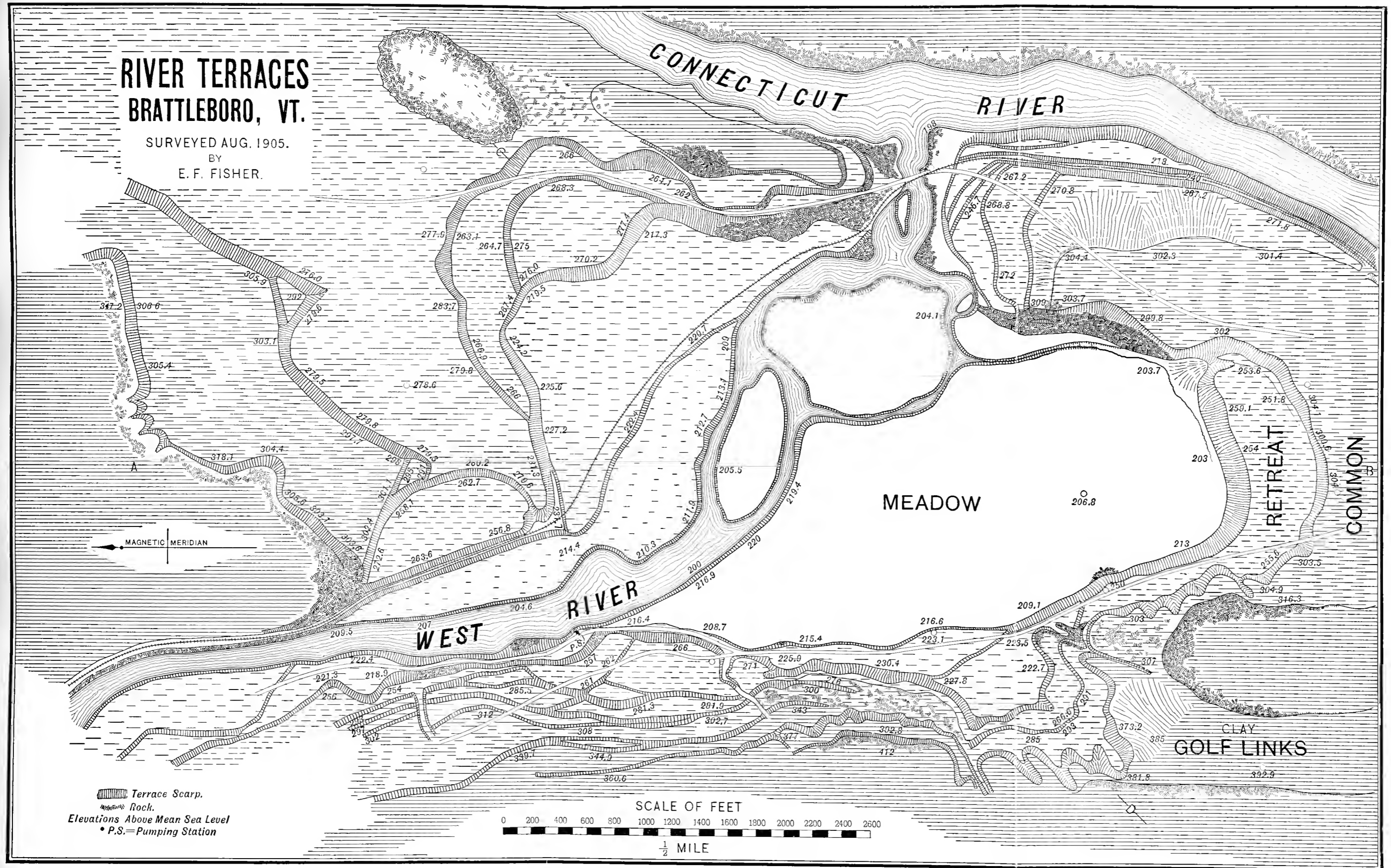


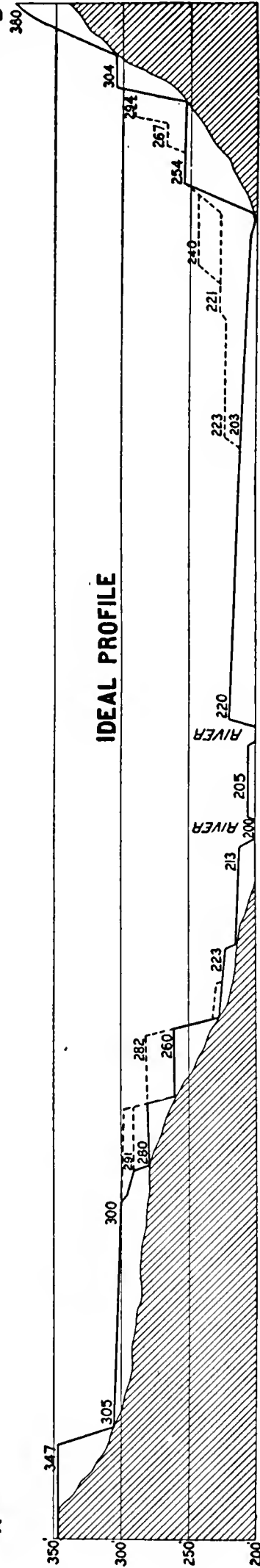
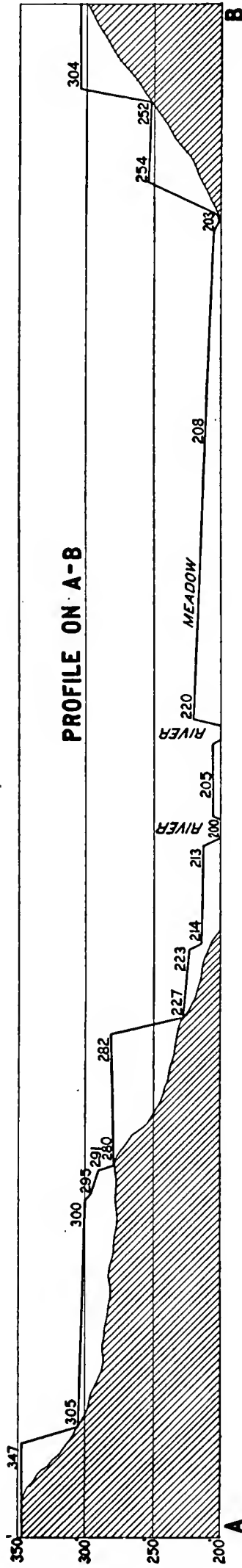
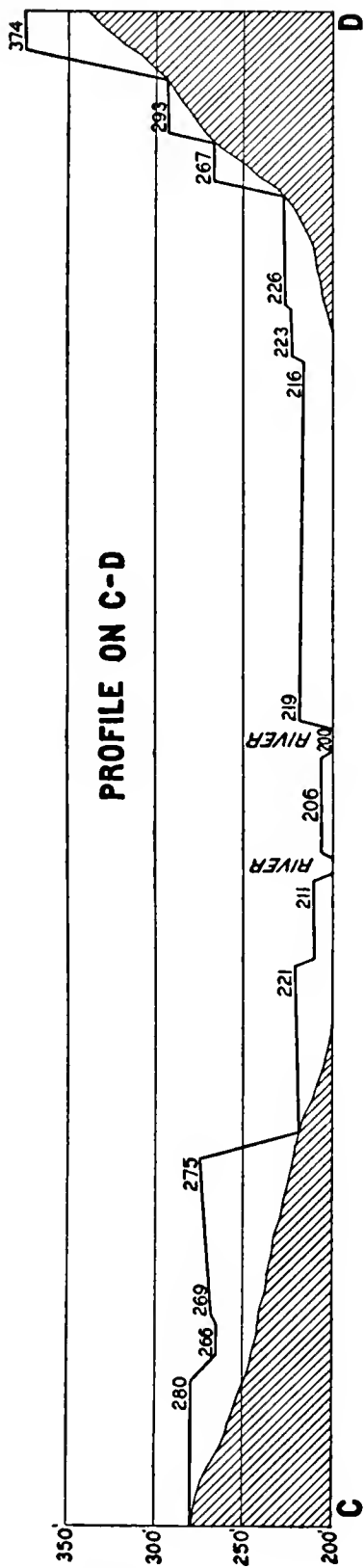
PLATE 2.

Profiles of West River terraces.

Sections made from survey map (plate 1). Show that terraces left after the river has swung several times across its valley will vary in width, and that they stand as remnants of the flood plains. Also they show that the lateral swinging of the meandering channel is very much faster than the degradation of the valley floor.

The ideal profile, showing terrace levels along the lines A-B and C-D, demonstrates that high scarps are the sum of two or more lower scarps. They are produced when the river swings more widely, undercutting the lower terrace plains.

PROFILES OF RIVER TERRACES



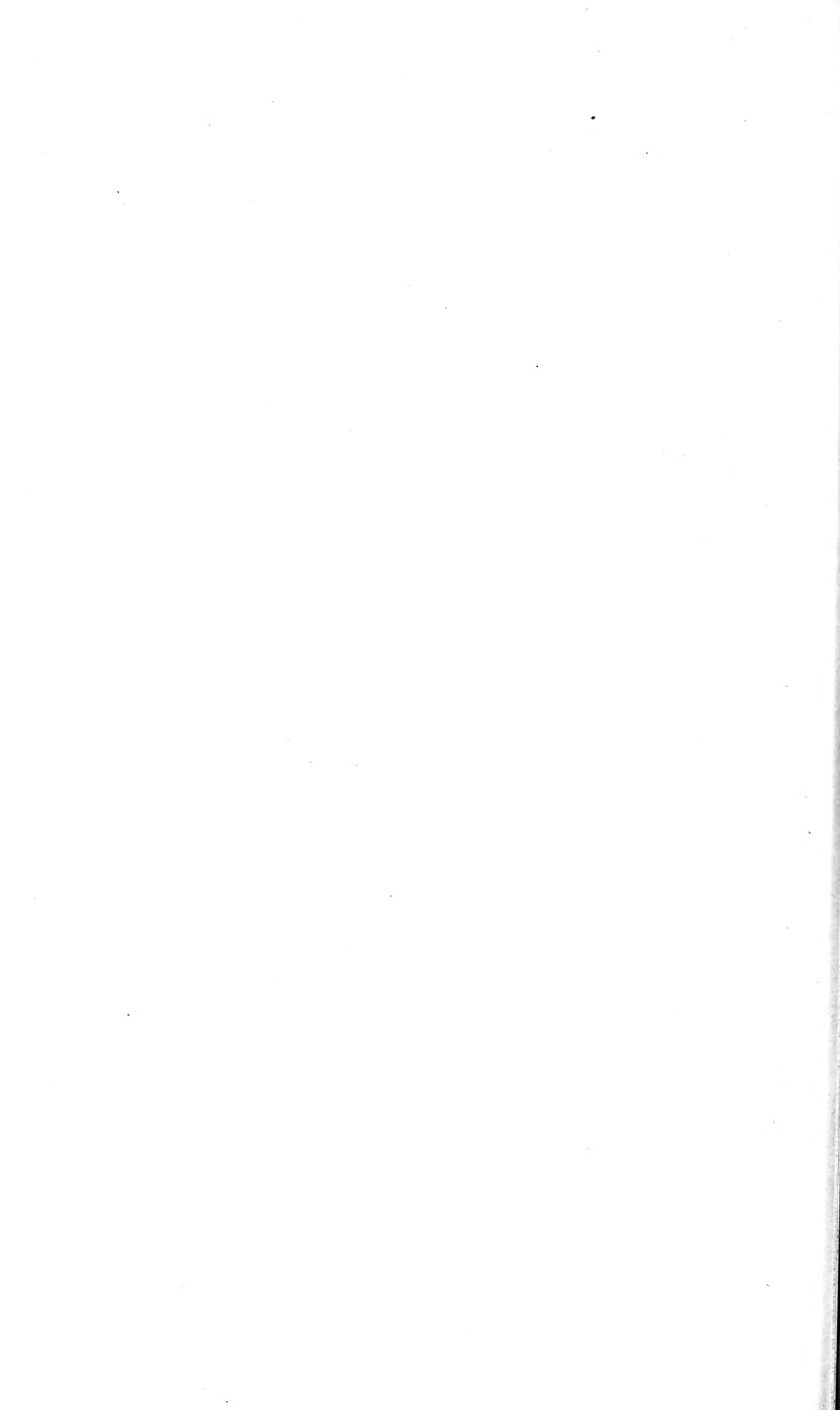
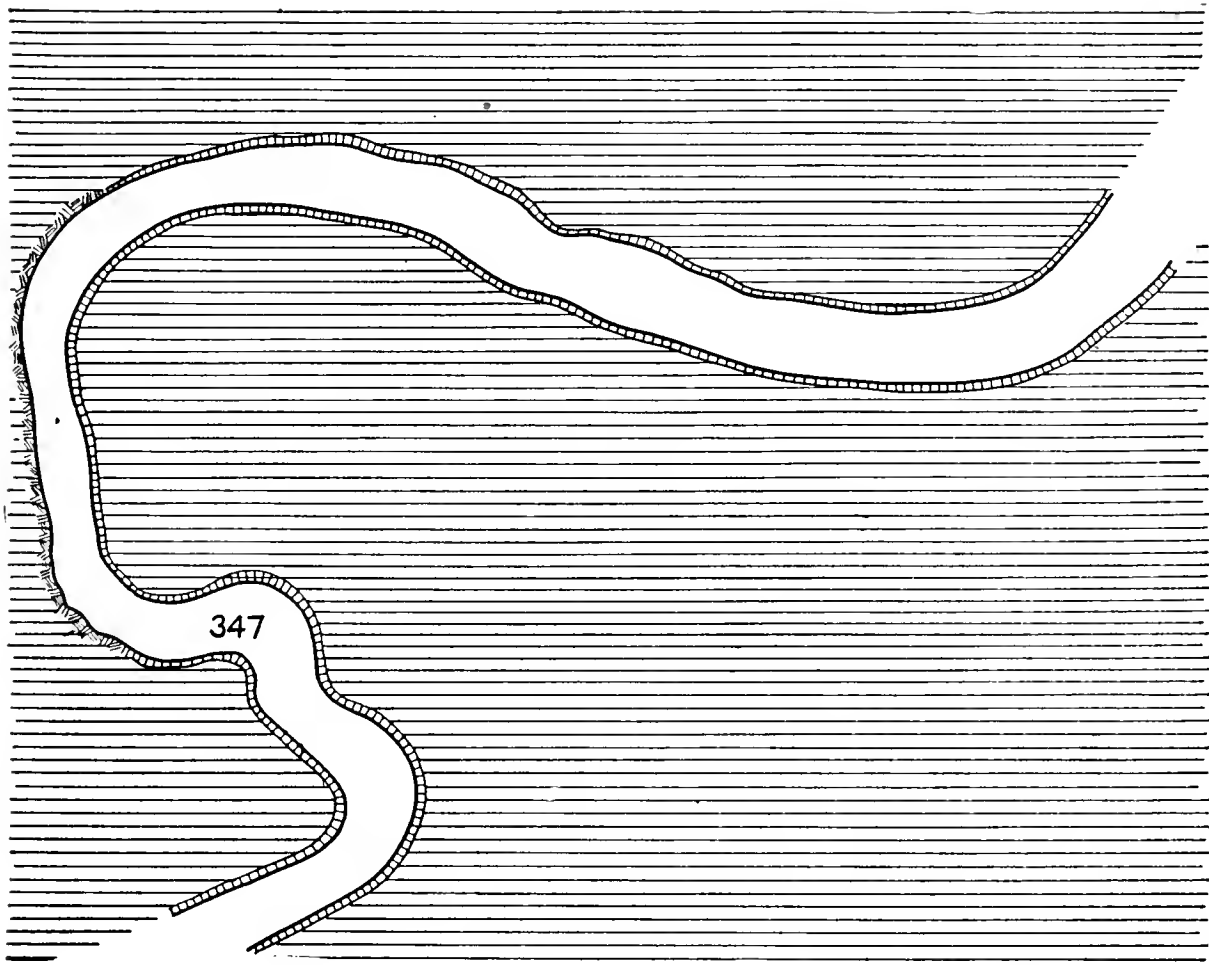


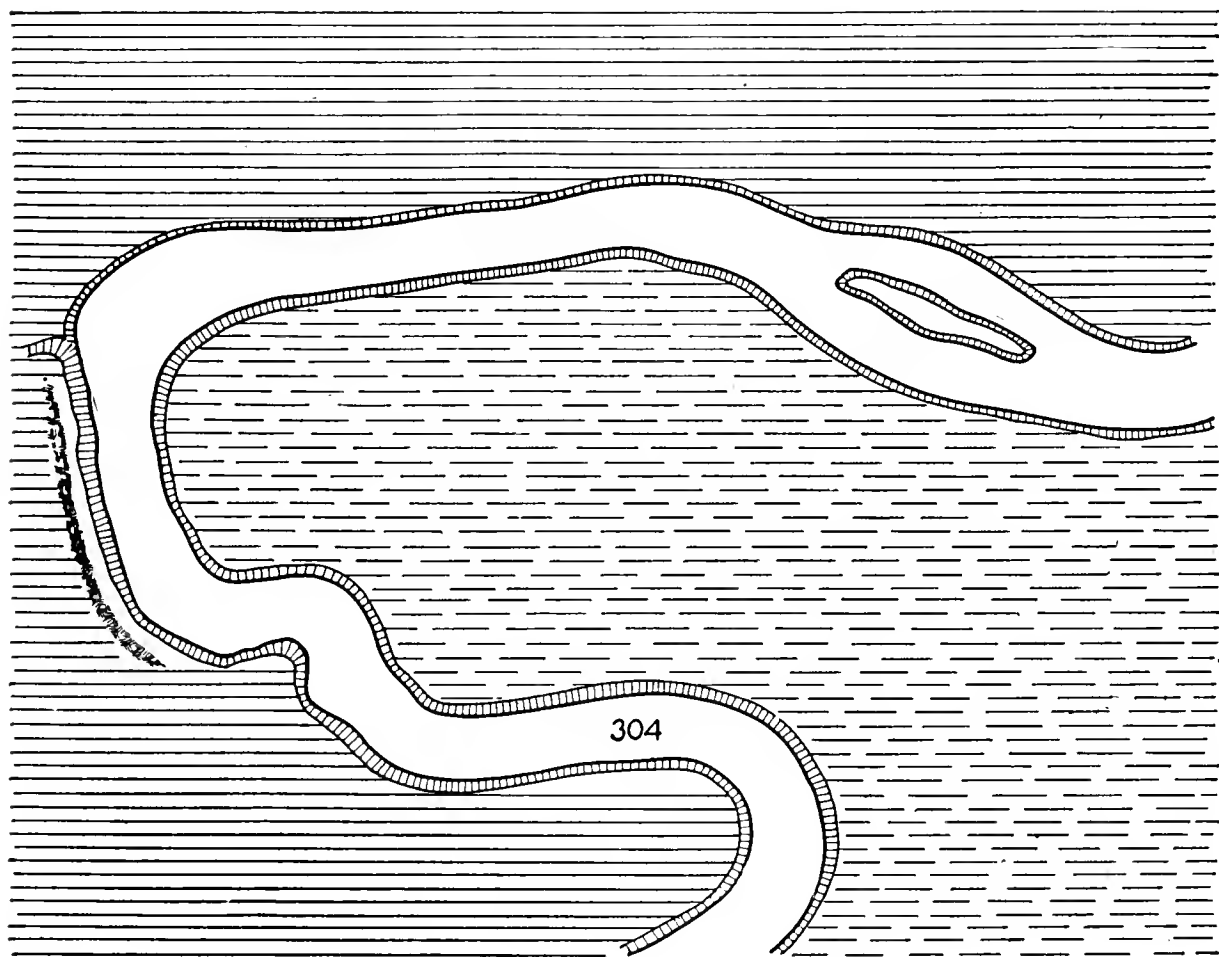
PLATE 3.

Various left-hand swings of the West River since the ice age.

Figs. 1, 2, represent three (more or less hypothetical) positions of the river in the early stage of terrace pattern.



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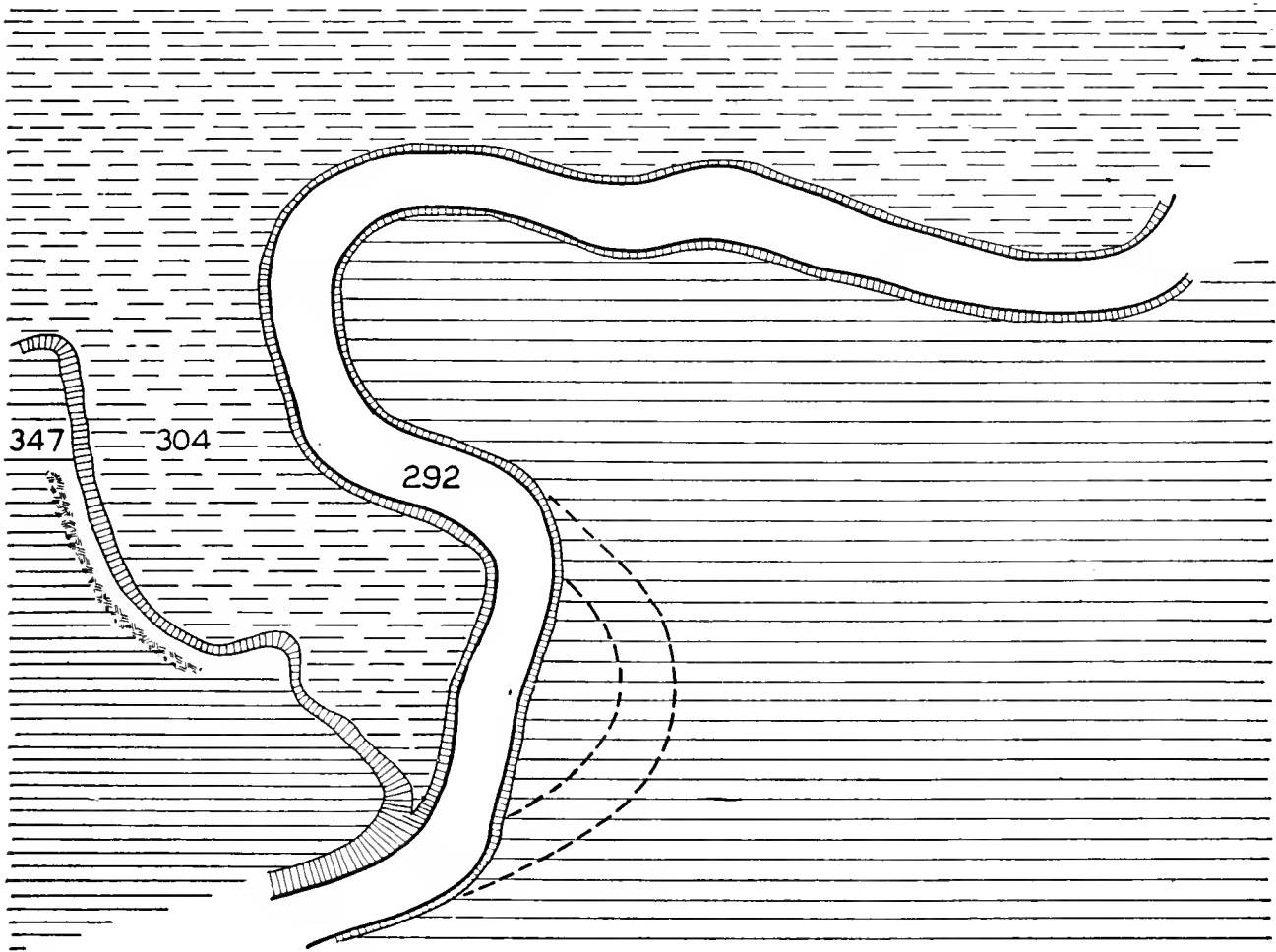
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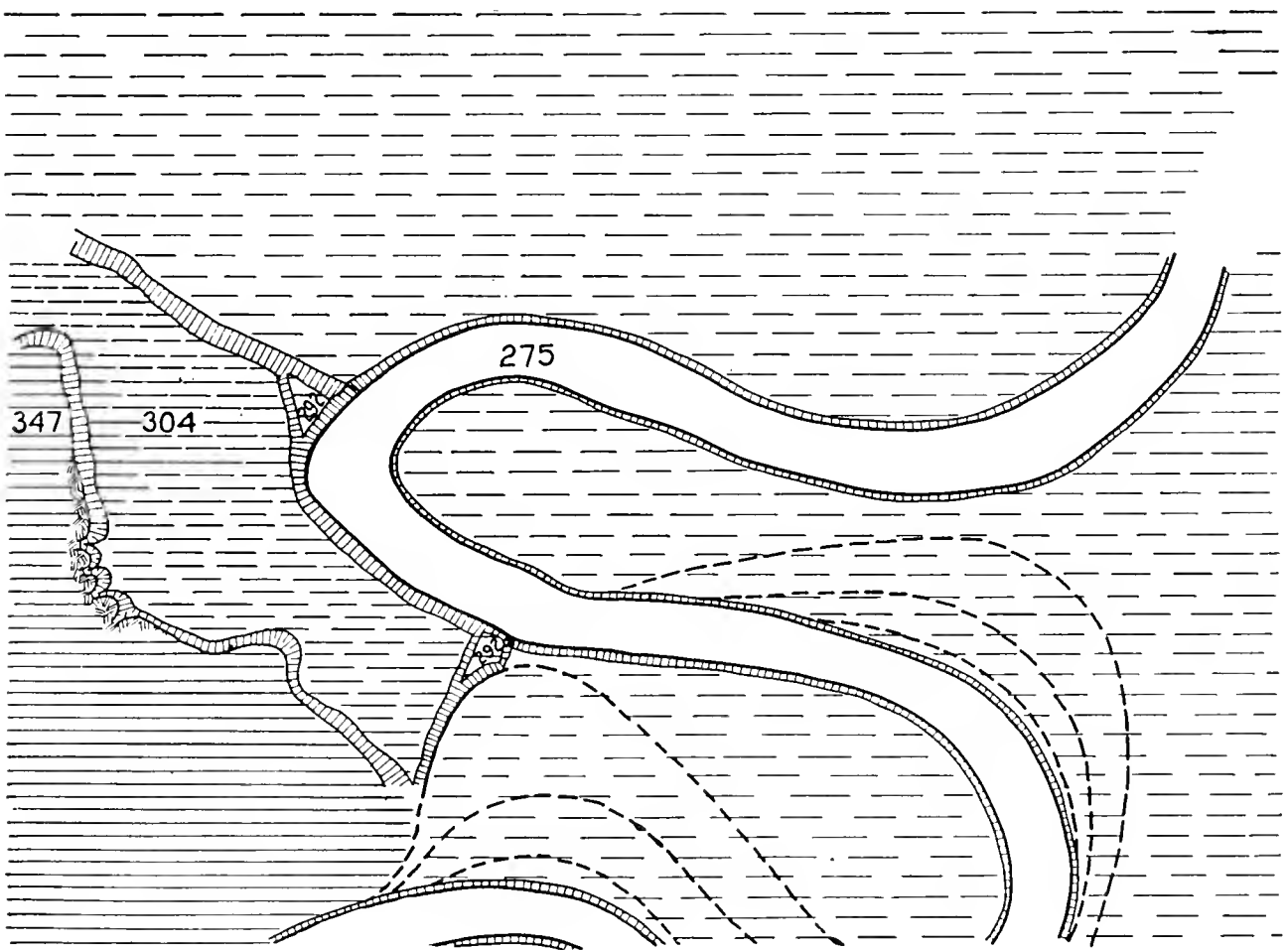
PLATE 4.

Various left-hand swings of the West River since the ice age.

- Fig. 3 (like figures 1 and 2) represents a more or less hypothetical position of the river in the early stage of terrace pattern.
- Fig. 4 represents a later swing of the river, showing compressed meanders. Positions of the river have been located by the existing scarps. Elevations above mean sea level. Dotted lines represent possible changes in the course of the river.



3



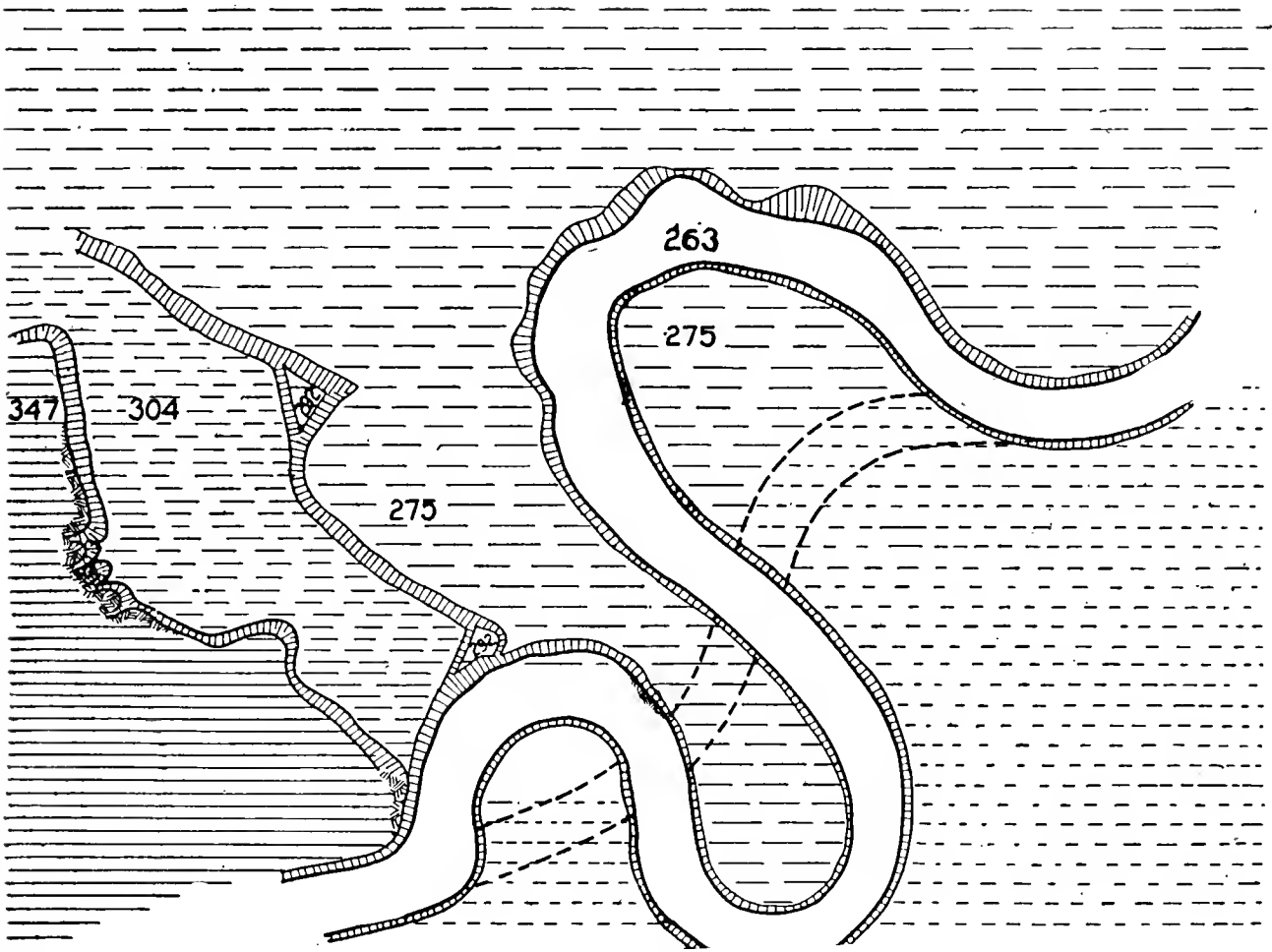
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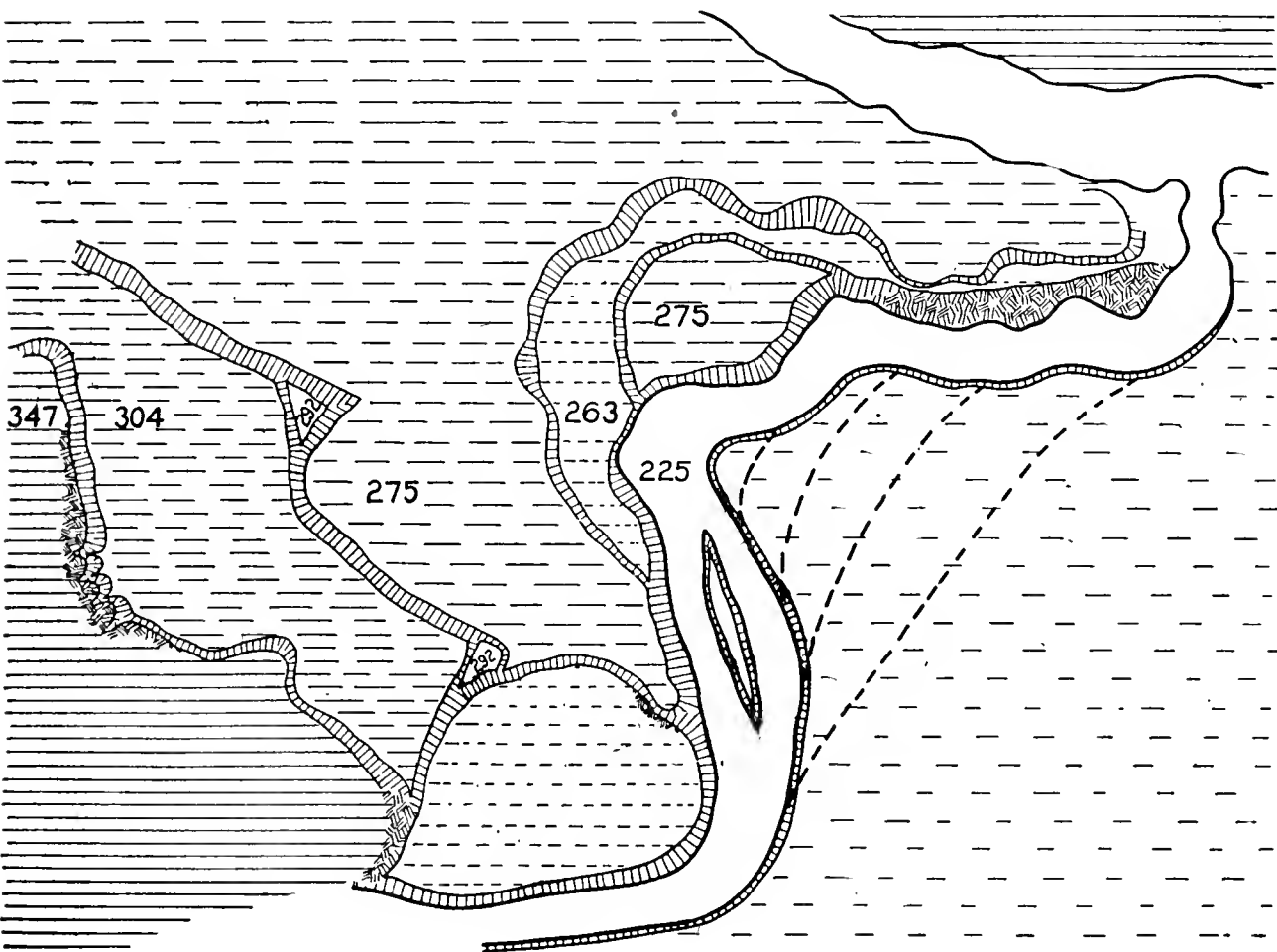
PLATE 5.

Various left-hand swings of the West River since the ice age.

- Fig. 5 shows two deeply compressed meanders enforced by the rock barriers on the down-stream side of each bend. River was suddenly withdrawn from the larger bend by cut-off or short-cut, leaving a very definite river channel.
- Fig. 6. Same rock controls prevented the river at the 225-foot level from eroding further to the left.



5

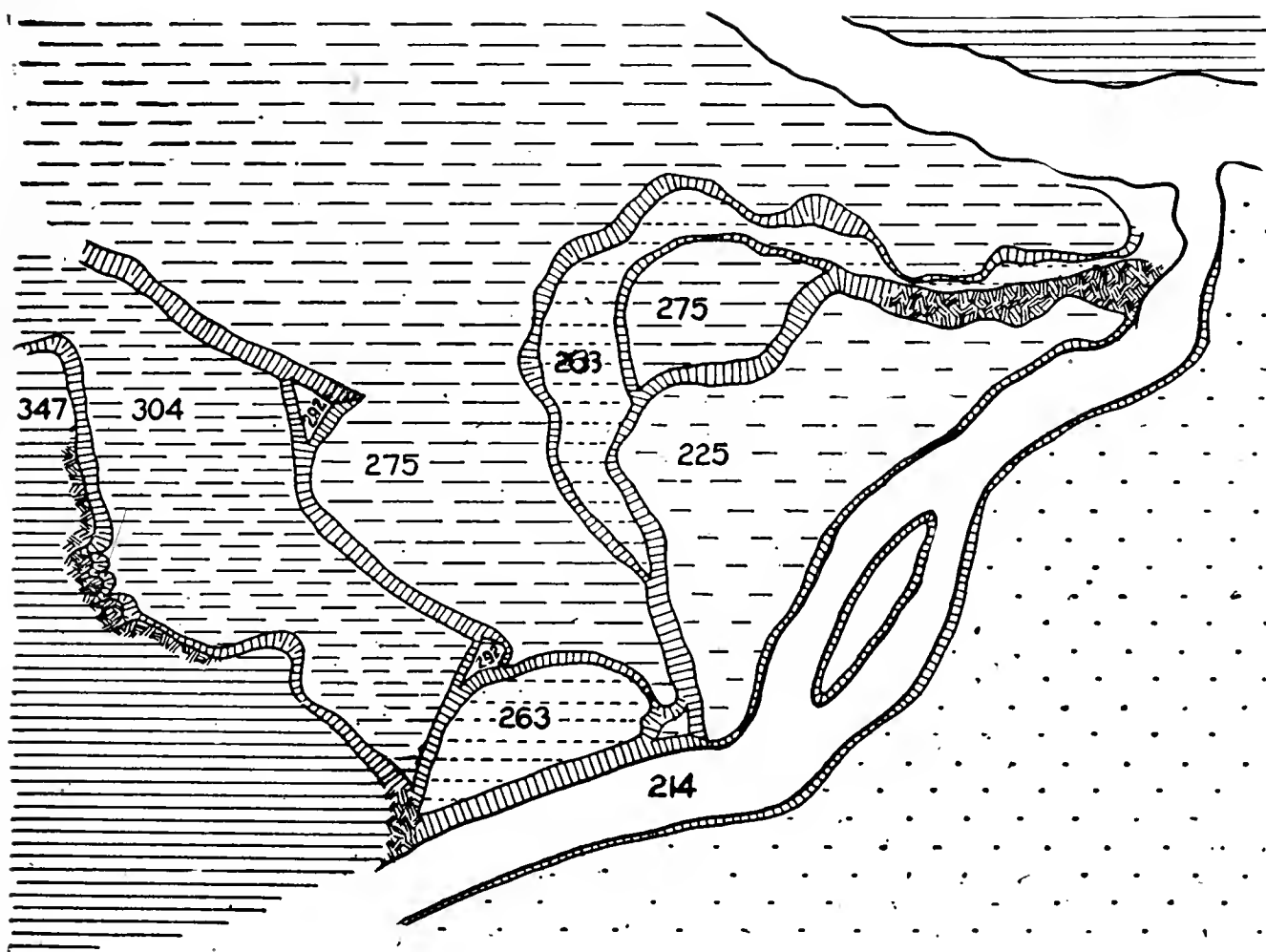


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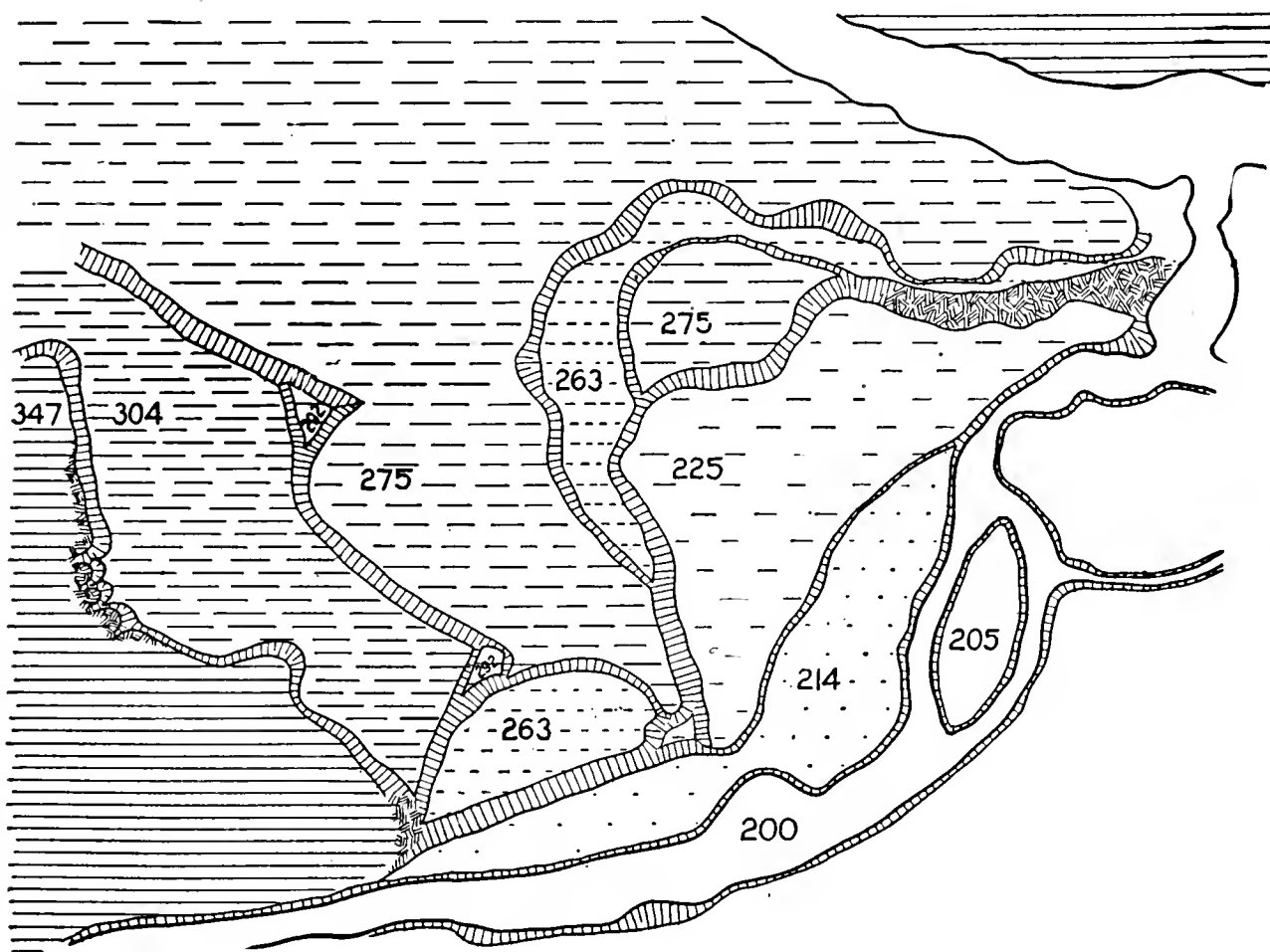


PLATE 6.

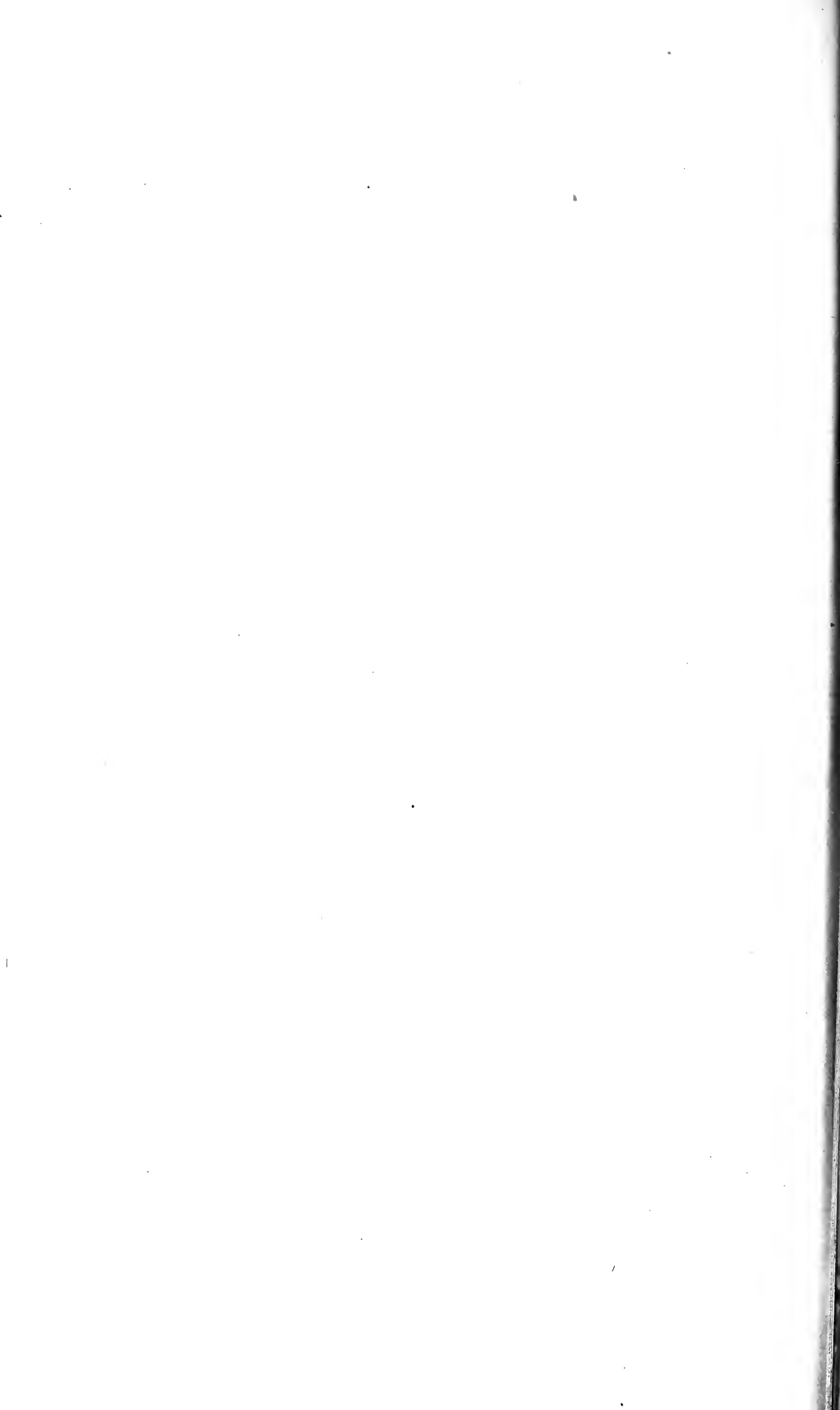
- Fig. 7. Position determined by rock controls. River moving to the right by the partition process.
- Fig. 8. Represents the typical middle stage of terrace pattern produced by the seven earlier swings. River is again swinging to the right by the partition process.



7



8



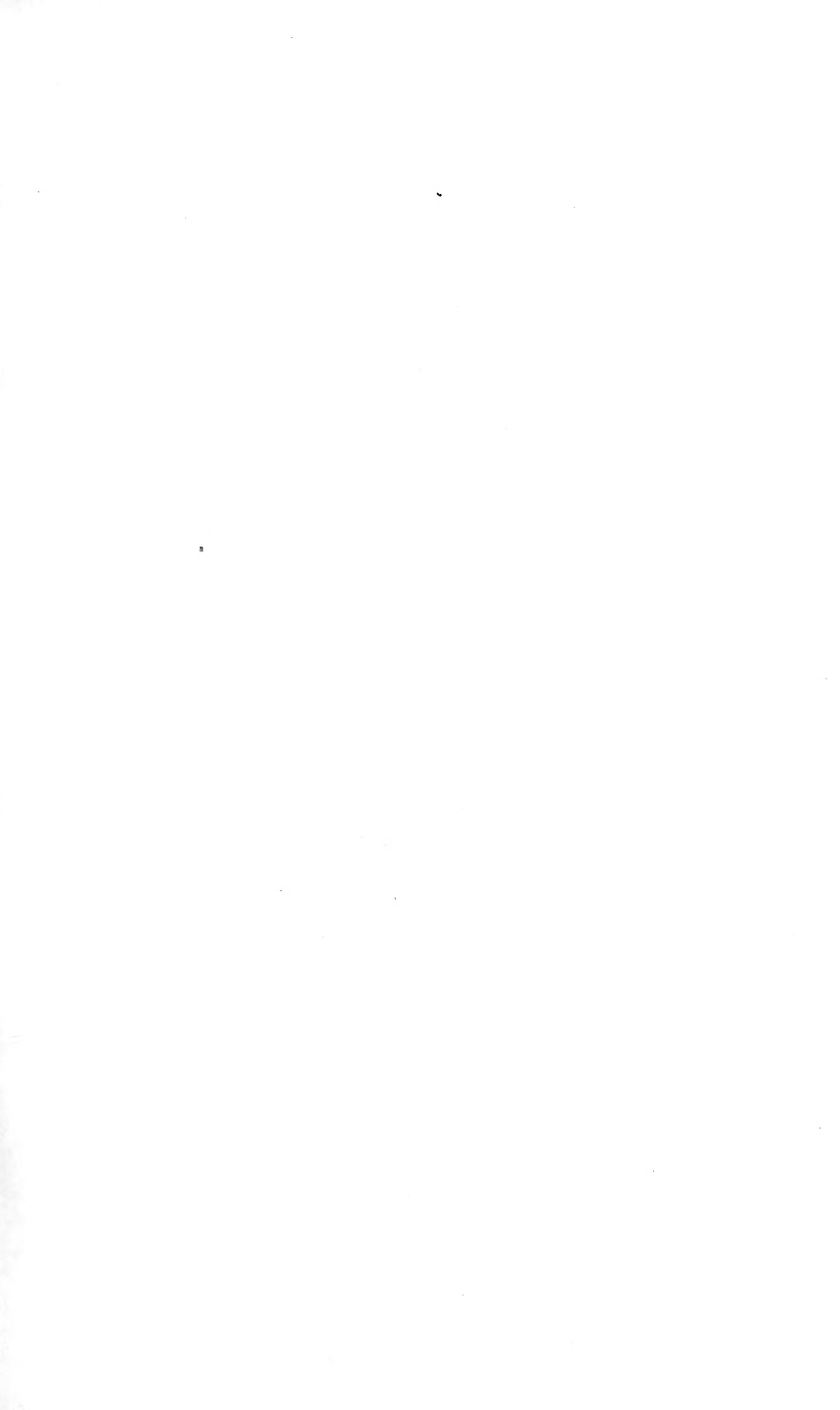
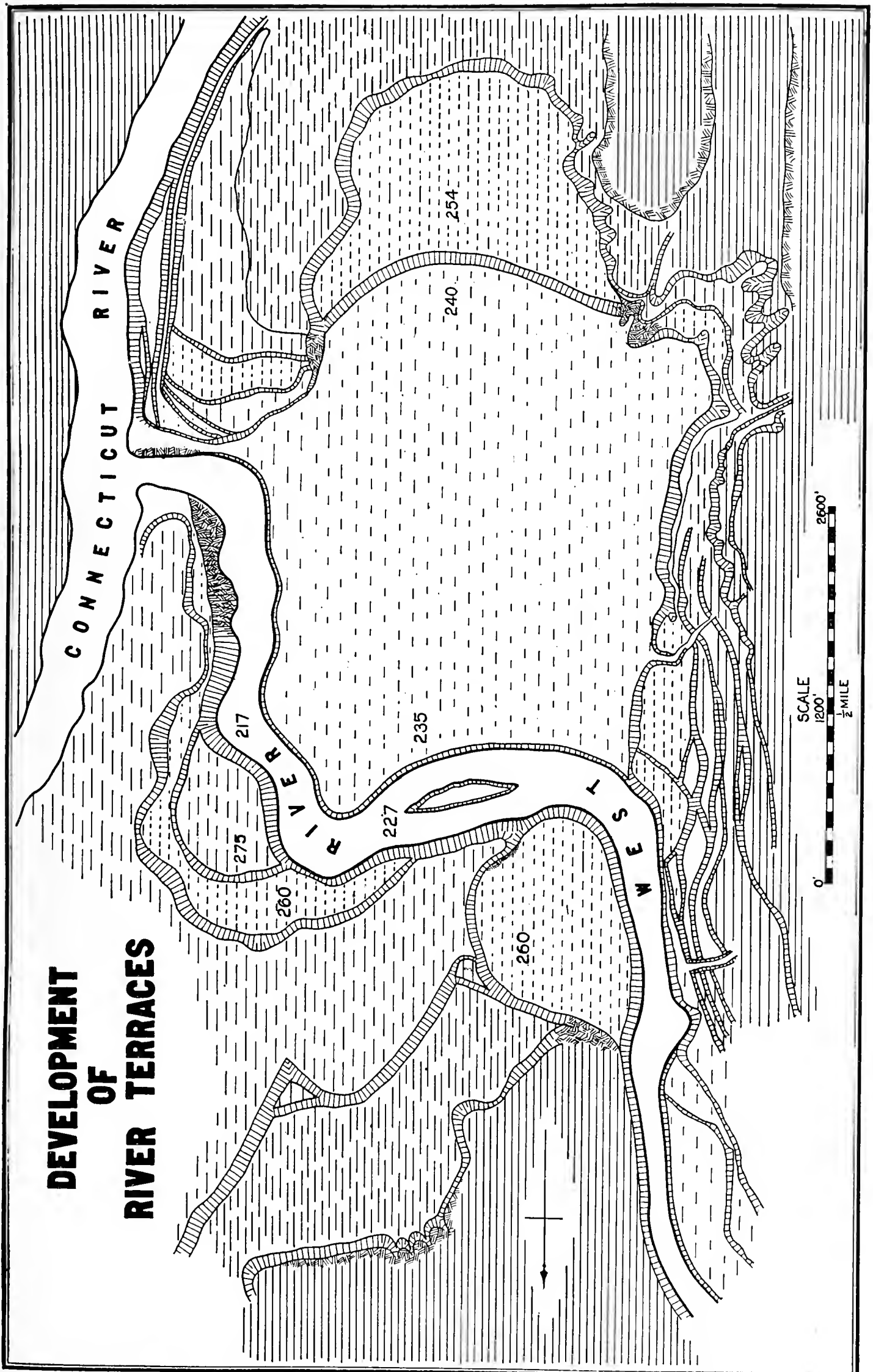


PLATE 7.

Plates 7, 8, 9 show that the West River, during the later stages of its degrading, has swung between nodes determined by rock barriers at the Pumping station and at the junction of the West River with the Connecticut. The right-hand swinging has been, in general, accomplished by the partition process, and the left-hand swinging by the more direct short-cut process.

Plate 7 illustrates the possible terrace pattern of the West River valley at the time when the river made the left-hand swing at the 225–217-foot level.



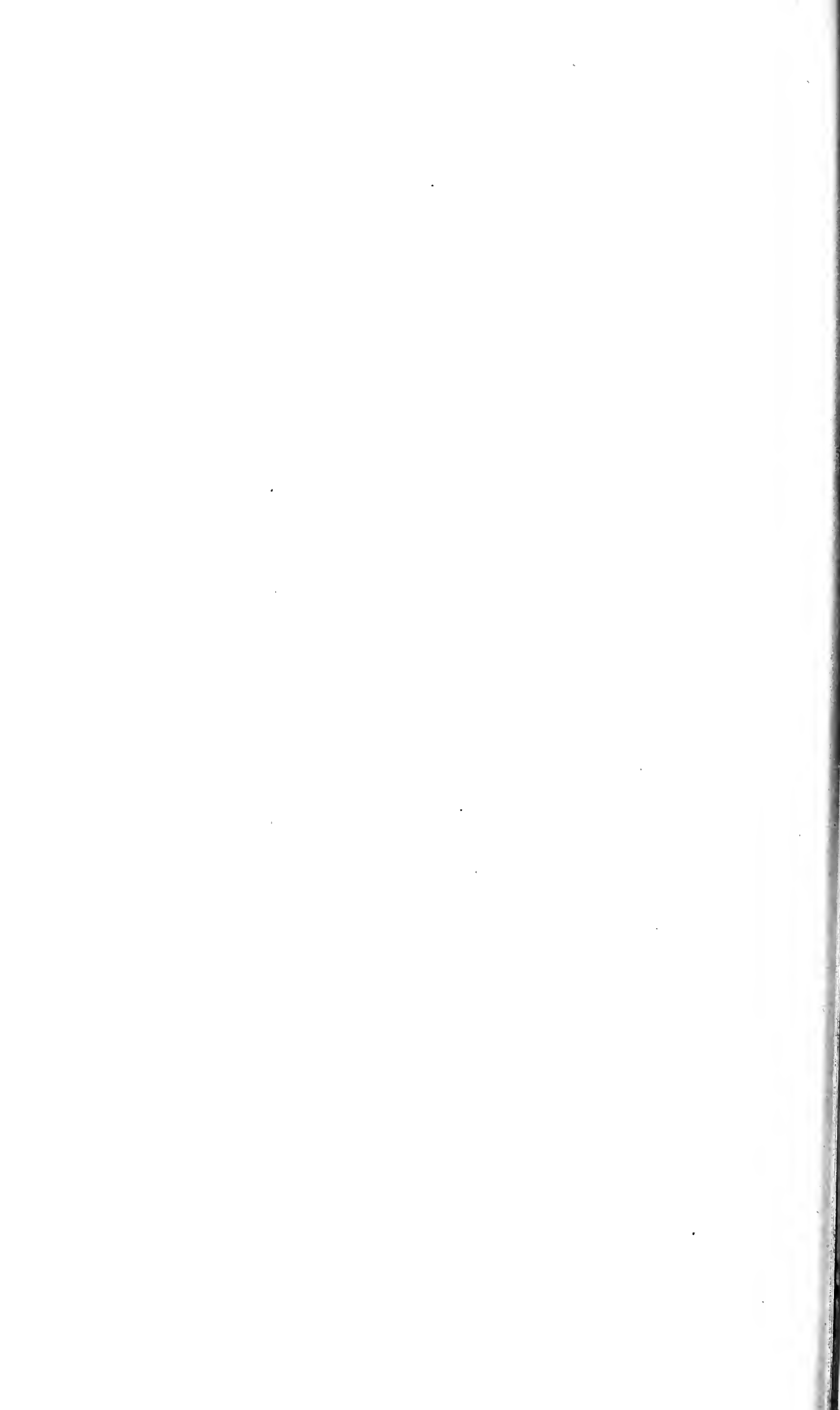


PLATE 8.

As the West River swung to the right from the 225-217-foot left-hand position, it made the possible 240-foot scarp, a position from which it was withdrawn by short-cut to the above left-hand 214-foot level, shown on this plate.

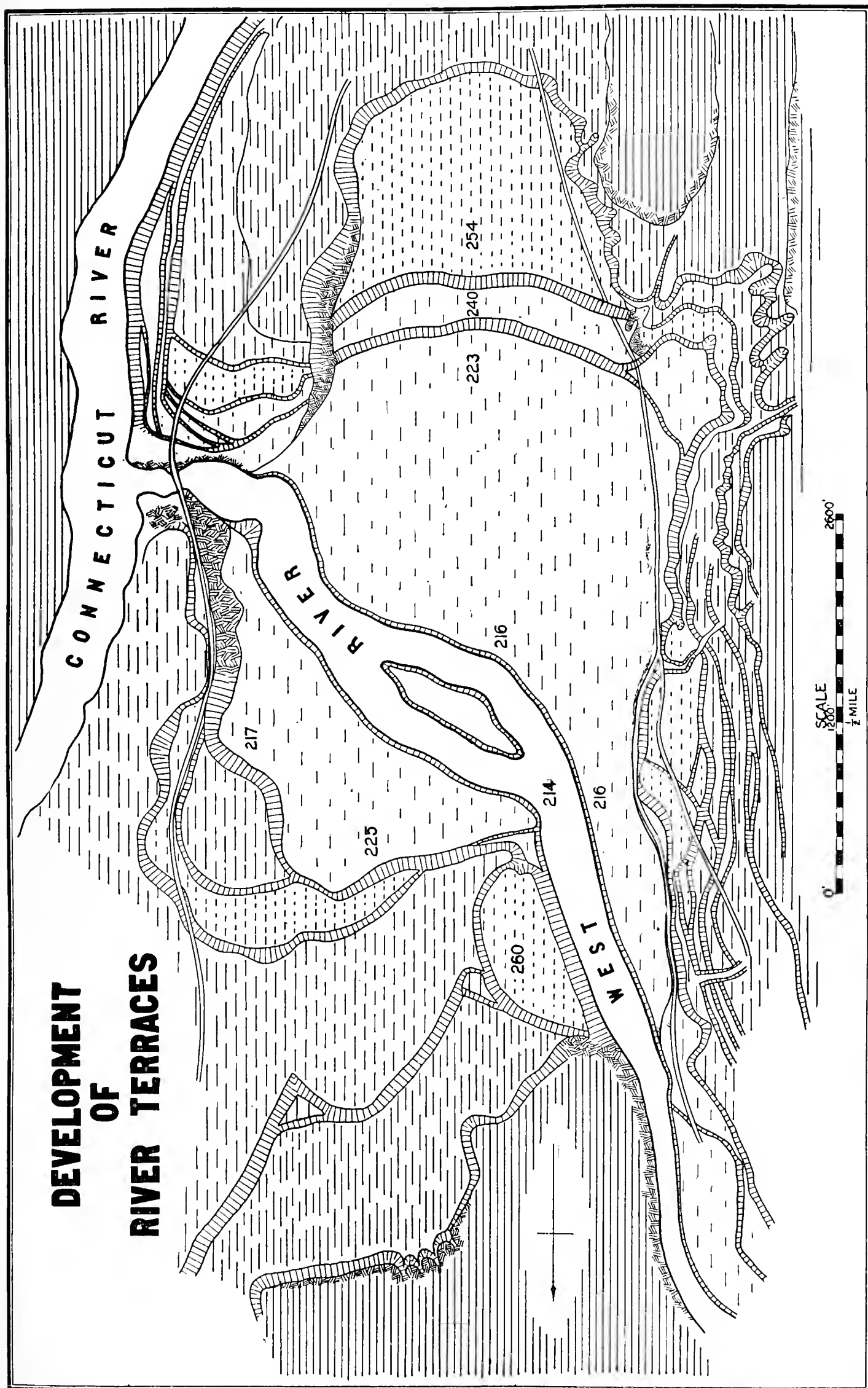




PLATE 9.

From the 214-foot level (plate 8) the West River moved by the partition process to the 203-foot level at the base of the Retreat scarp shown on this plate. By short-cut the river was withdrawn to its present position shown on plate 1, and it is again moving to the right by the partition process.

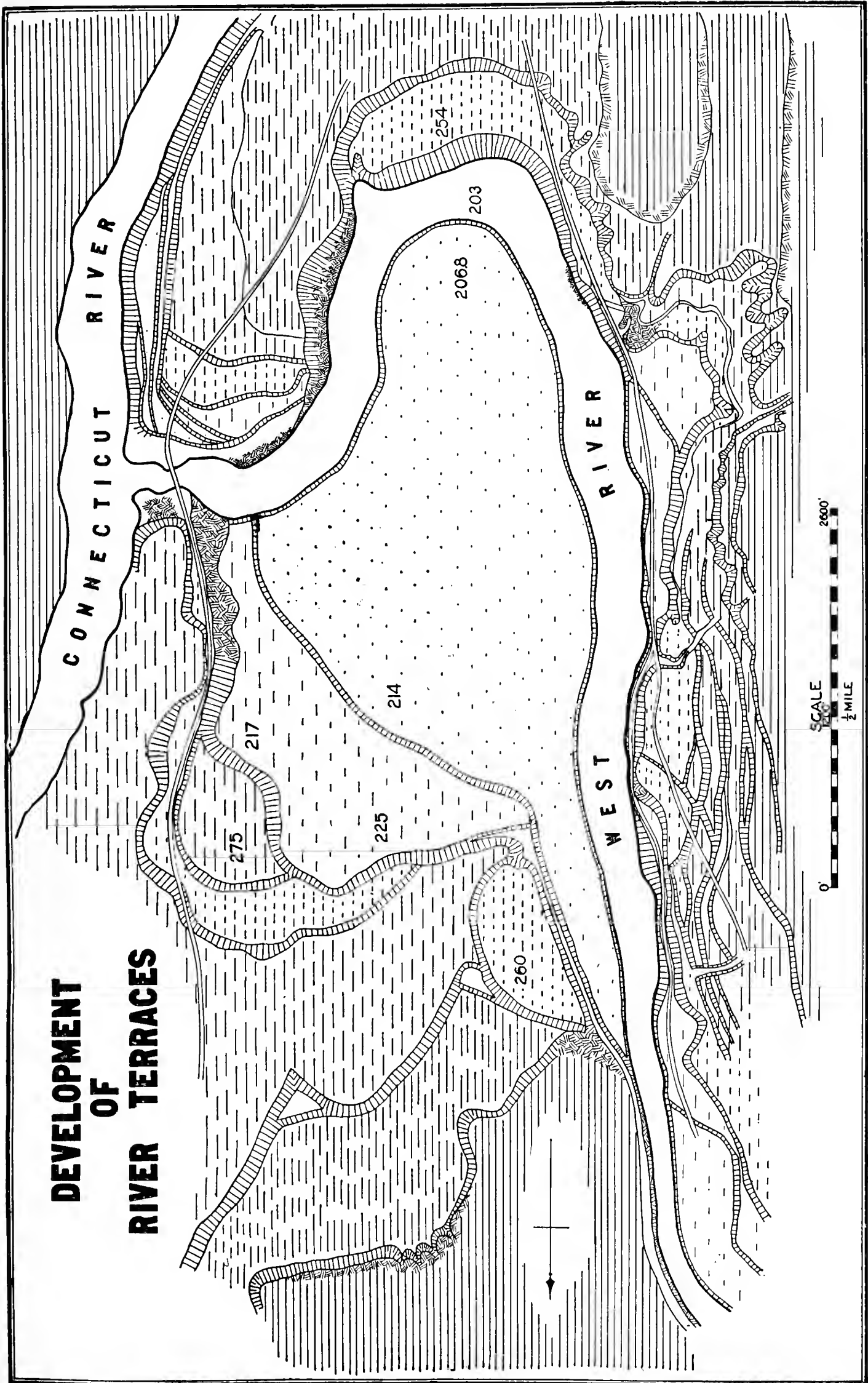




PLATE 10.

Canoe Brook crossed by Putney road, seven miles from Brattleboro, Vt. Illustration of early stage of partition process in which the brook is increasing its meander. The current, deflected to the right, is adjusting itself to a new series of curves. Rapid withdrawal from the left bank has resulted in the sand-bar island. The river is parted thereby, and in time the right channel will acquire the whole stream.

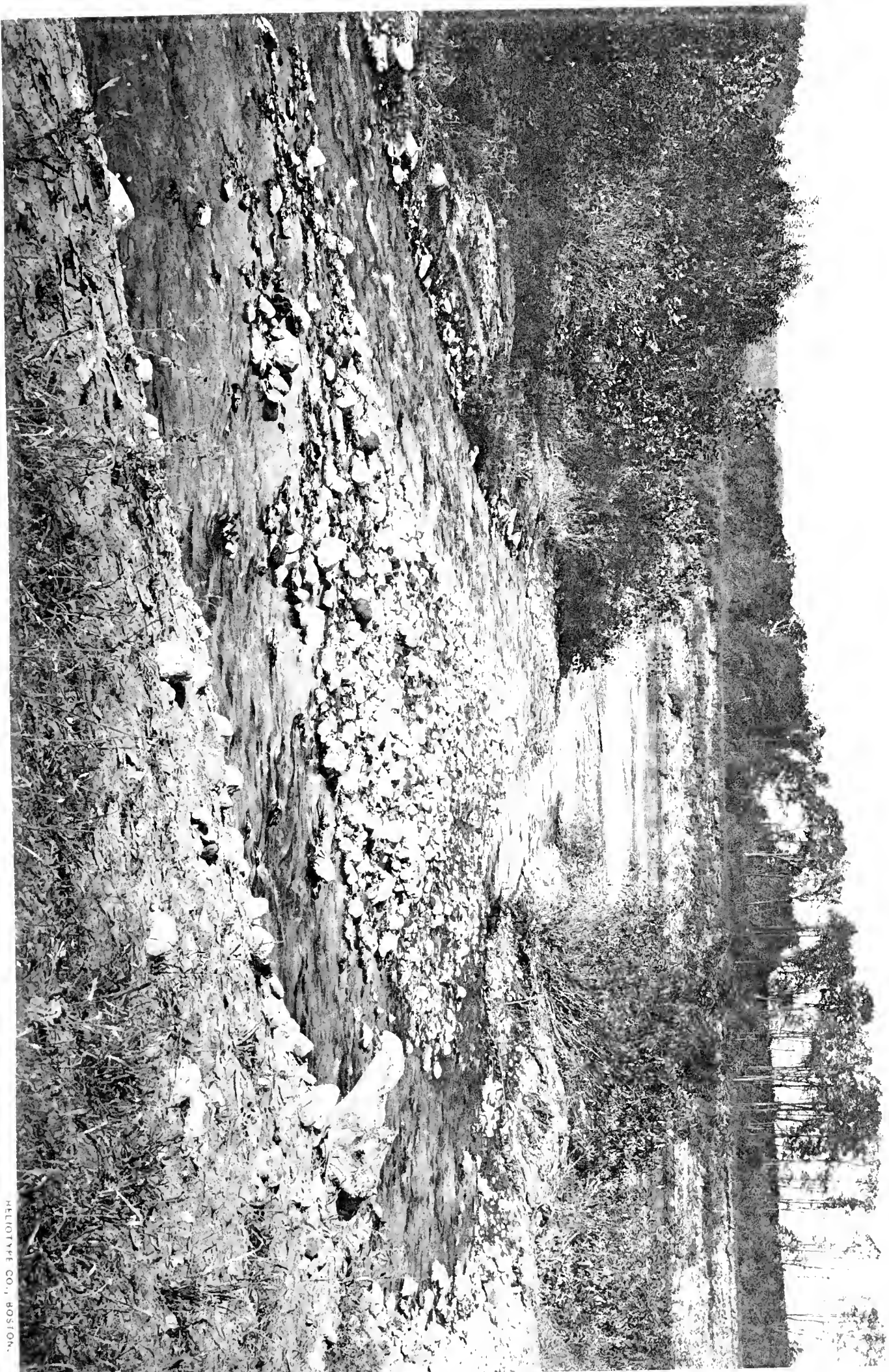


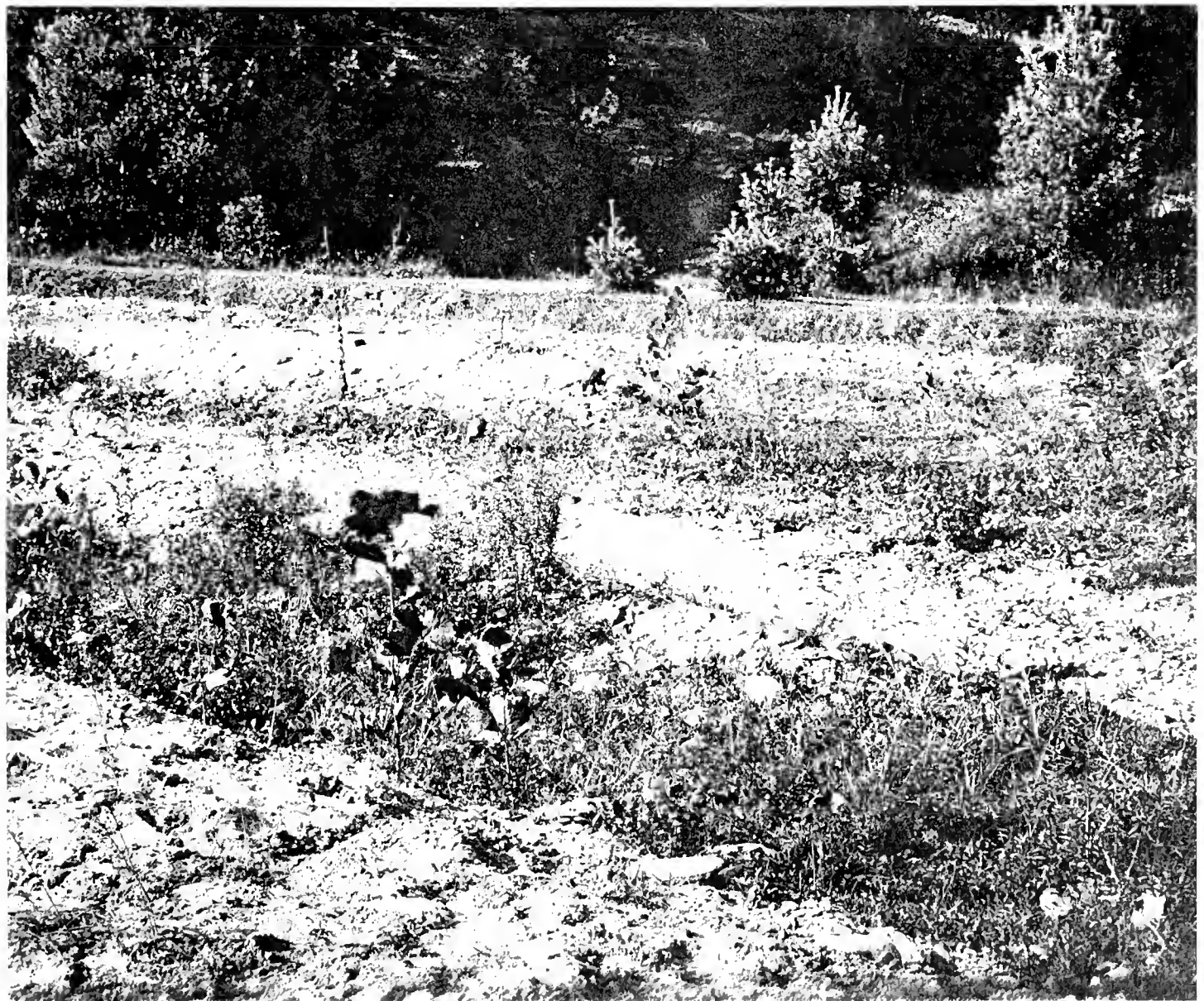


PLATE 11.

- Fig. 1. Illustration of middle stage of partition process in which the brook has withdrawn from a left-hand meander. The partition plain shows four ridges (former islands) separated by valleys (former channels).
- Fig. 2. Illustration showing undulations of a young partition plain. The elevations represent the island walls which successively parted the river, and the intervening channels represent the abandoned courses of the river,

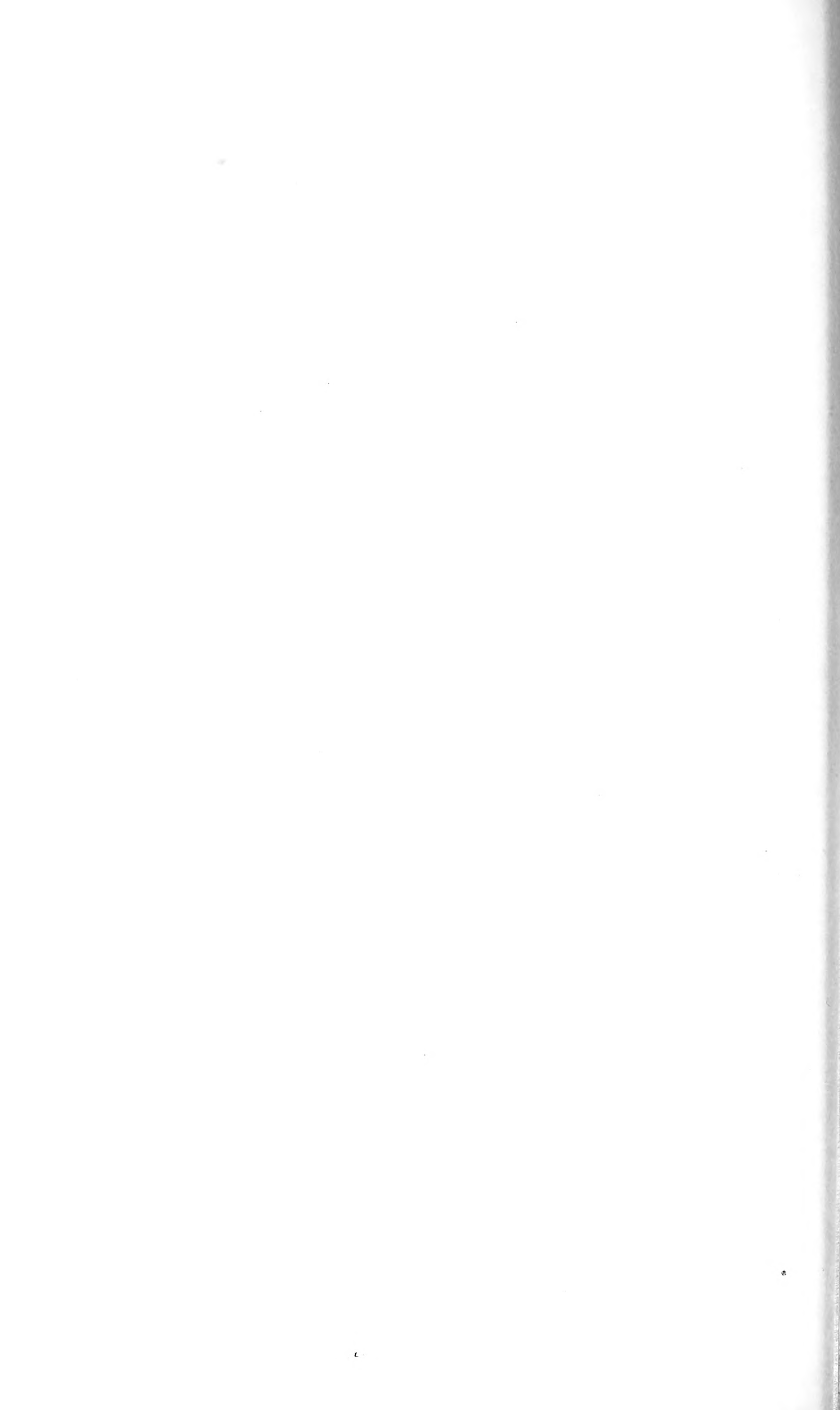


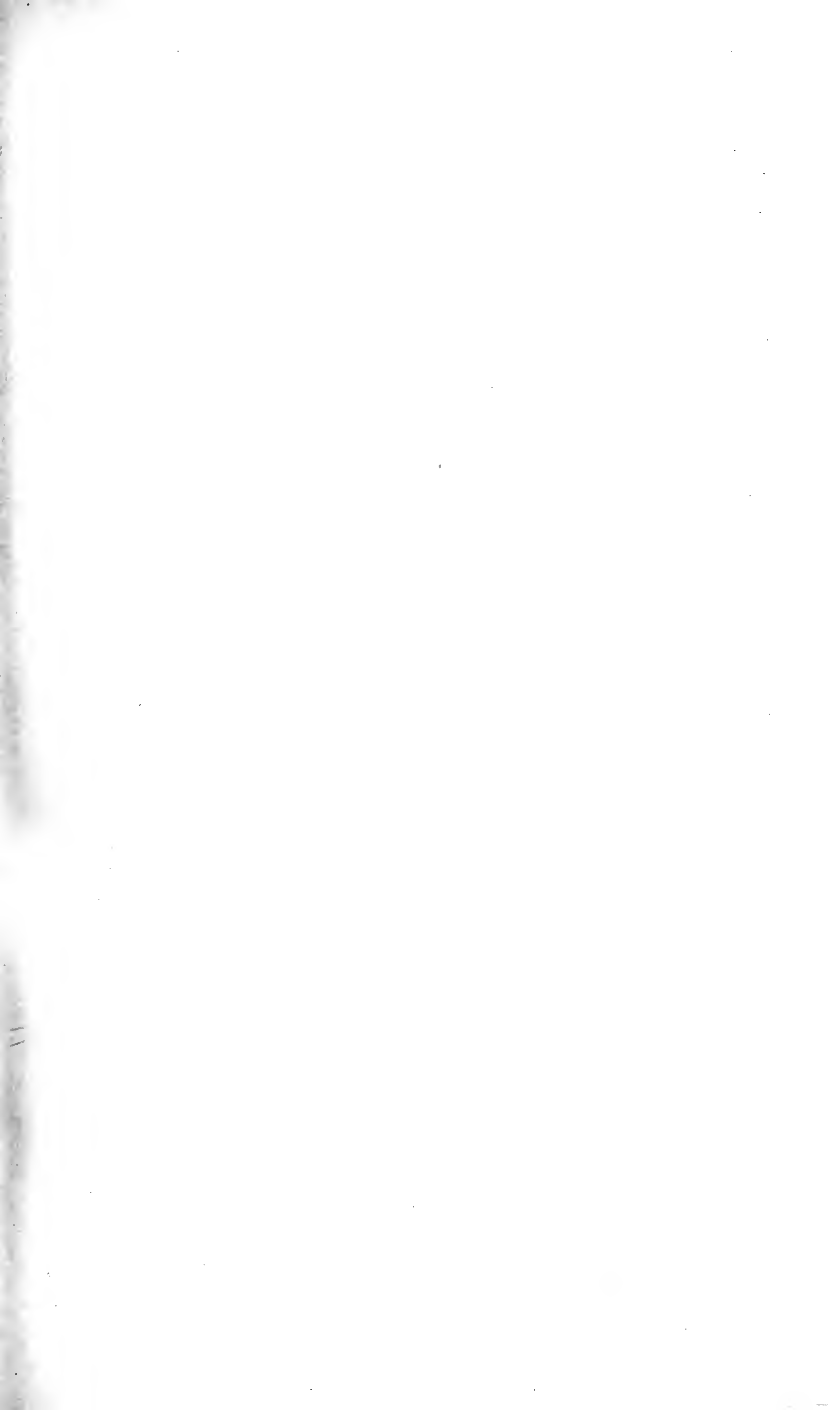
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PLATE II. CO. BOSTON.





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SPERMATOGENESIS OF THE BUTTERFLY, *PAPILIO RUTULUS*.

BY JOHN P. MUNSON, PH.D.

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No. 3.— SPERMATOGENESIS OF THE BUTTERFLY,
PAPILIO RUTULUS.

BY JOHN P. MUNSON, PH. D.

INTRODUCTION.

“SPERMATOGENESIS of Lepidoptera” is frequently referred to in cytological literature. Yet there is hardly anything that can be called a complete account of any one form. The work of early observers is especially fragmentary and scattered, so much so that it now can have but a historical interest, showing as it does the effect of superficial observation and poor technique, as well as lack of acquaintance with the more fundamental cell problems which recent development of the science has brought so prominently to mind.

More recent writers show considerable improvement in most of these respects, yet I believe that it may be affirmed of insect spermatogenesis as a whole that observers have been so preoccupied with some one special problem such as the phase of reduction for instance, as to make their work incomplete in other respects. In many of these later works, too, judged by their plates, the irregular outlines and distorted internal structures of the cells suggest imperfect fixation.

For a number of years I have been studying the spermatogenesis of *Papilio rutulus* (pl. 12, fig. 1) not with any one single problem especially in view, but with the aim of ascertaining the entire life history of its sperm cell, its various phases of development, its mode of growth and differentiation, the history of its several parts, and its relation to the organism.

The sperm cell, it seems to me, is a most instructive cell for such a study, for it shows remarkable external and internal changes, leading up to a highly specialized form well adapted to its special function. Its connection with a gland, also, ought to commend it to the attention of those who do not hesitate to publish startling conclusions regarding life in general from studies on secretion products.¹

¹ Says Matthews ('99): “The foregoing hypothesis makes possible a picture of cell life which avoids altogether the assumption of any peculiarly ‘vital’ substance, as distinct from lifeless, and also, as I believe, that of any peculiar supra-molecular living units, such as the ‘physiological units,’ ‘pangens’ or ‘biophores.’”

OCT 26 1906

I was led to undertake this study while engaged in the microscopic study of the circulation of the blood through the excised heart of this butterfly—a study which revealed not only innumerable small bodies in the blood resembling corpuscles, but also the fact that the periodic contraction of the heart, the heart beat, is not confined to the heart, and is not controlled by the ventral nerve cord. While engaged in this study, I pierced the testis, and was impressed with a remarkable quivering of its contents, due, as I supposed, to contact with the air, but more probably an electrical effect which I have never been able to witness since, notwithstanding repeated attempts to study it more minutely.

The following is primarily an account of my observations. I have not deemed it necessary to review extensively published memoirs on cytology, because I assume that my own observations will show their bearings on work already published by other workers in this field, who are, of course, already familiar with what has been done in their special subject. The necessity of keeping my paper within prescribed limits for publication, also permits only a brief historical survey of the literature.

I wish to express my gratitude to the librarians of the University of California, of the Leland Stanford university, and of the California academy of sciences for their kindness in facilitating my work by allowing me free access to their respective libraries. Professor Ritter has also shown me courtesies for which I wish to thank him.

METHODS.

1. Teasing testis on slide, and studying with hot stage in normal fluids of the testis and normal salt solution. (Pl. 13, figs. 30, 31; pl. 14, figs. 43, 44; pl. 17, figs. 151, 152.)

2. Teasing, fixing, and staining on the slide (pl. 12, fig. 9–23), picrosulphuric and Delafield's haematoxylin.

3. Killing, hardening, imbedding, and sectioning in usual way.

By applying various killing reagents to teased material on the slide, and noting the effect under the microscope while the reagent was acting, I very soon discovered that the most perfect fixation was secured by a concentrated solution of corrosive sublimate to which is added between one and two percent acetic acid.

Without teasing the testis, it is placed perfectly fresh into this fluid,

and allowed to remain from fifteen to twenty minutes after which it is transferred to 50 percent alcohol and carried gradually up to 95 percent alcohol. It is then dehydrated and imbedded in paraffin in the usual way. I have used both the Toma and the Minot microtome, making the sections as thin as possible, usually from four to six μ .

Besides the corrosive acetic mixture which has been most satisfactory, I have, of course, used many others — picronitric and picrosulphuric. Unusually clear asters and spindles can be obtained also, by first leaving the fresh testis in normal salt solution for fifteen minutes and then transferring to corrosive sublimate (pl. 16, figs. 111, 112).

Staining has been done almost exclusively on the slide after fixing to the slide by means of Myer's albumen fixative. Corrosive sublimate material I have allowed to remain in a 50 percent alcoholic solution of iodine for about ten minutes either before or after staining.

The following stains have been found useful, about in the order named: (1) Grenacher's haematoxylin, (2) Delafield's haematoxylin, (3) saffranin, (4) eosin, (5) acid fuchsin, (6) lithium carmine, (7) Biondi-Ehrlich's triple mixture, (8) Haidenhain's iron-haematoxylin, (9) orange G, (10) blue lumière, (11) borax carmine, (12) Weigert's picrocarmine, (13) Bismark brown, (14) iodine green, (15) Congo red, (16) dahlia violet, and others.

The larva and chrysalis have been studied entire without dissecting out the testis. By placing in the fixing fluid the fourth to the eighth abdominal segments, good fixation is secured.

THE DRAWING.

On comparing my drawings with those of Henking ('91), Paulmier ('99), Wilcox ('95), Bessels ('67), Meyer ('49), and some earlier writers on insect spermatogenesis, I notice that my figures appear diagrammatic. But a comparison of my drawings with the living cells of a freshly teased testis will prove to anyone that nothing can well be more diagrammatic than those cells in their normal living state. As all my figures with the exception of figures 1, 2, 3, 7, (pl. 12) were drawn with a camera of the latest and most perfect construction, I consider the regularity of my drawings as indicating perfect fixation. In fact, I know this to be the case, for I have studied the effect of my reagents by applying them to the living cell under the microscope. Many killing and hardening reagents ordinarily used, especially if allowed to act

too long, produce very abnormal effects, causing not only extraordinary shrinkage, but also lateral pressure between the cells resulting in angular outlines. Imperfect development of the asters of the spermatocytes is also evidence of imperfect methods, unless the achromatic figures differ markedly in different orders of insects, which is hardly probable. As my figures show, the asters involve practically the entire cytoplasm, an effect which, of course, could not be attributed to reagents.

The achromatic figures can be studied with the greatest ease in the living dividing cell. I have studied them thus for hours at a time on a hot stage. But I have found it impracticable to study the whole process of mitosis in this way, because of the evident rapidity with which some phases are passed through and the unusual slowness of other phases. This is especially true of the telophase of mitosis, particularly of the last maturation division.

MATERIAL.

For purposes of comparison, I have studied *Grapta silenus* Edwards, a smaller butterfly, also native to the North Pacific coast region, and which, in the adult form, strikingly mimics in color the bark of trees on which it feeds. Being a hibernating form, its life history differs as much as possible from that of *Papilio rutulus*, and I find that while, in the main, the spermatogenesis agrees, yet there are minor differences which have aided me considerably in understanding some difficult matters in *Papilio*. When not otherwise specifically stated, *Papilio rutulus* is the form referred to in this work.

Papilio rutulus is one of the largest, most beautiful, and most striking insects on the Pacific coast of North America. Being especially abundant here at Ellensburg, Washington, it has proved a very favorable subject for study.

I have seen no evidence of dimorphism, yet it resembles very much the tiger swallowtail, *Papilio turnus*, of southeastern United States.

The female of *Papilio rutulus* measures nearly five inches extended, the male about four inches. It is deep yellow with conspicuous black markings on body and margins of wings, the internal posterior parts of the hind wings being also shaded with a patch of brown and two shades of blue. Underneath the hind wings there are also two brown spots and a line of blue spots extending parallel with the posterior

margin of the wing. Close to the posterior margin, which is black, there is a line of yellow dots which underneath form a continuous band on the fore wing. This latter character differentiates it from its close relative, *Papilio turnus*.

ECOLOGICAL OBSERVATIONS.

Papilio rutulus makes its appearance each year between the middle of May and the first of June, and remains with us throughout June, July, and August. I have never seen it after the first of September. The females seem to come earlier than the males. They are easily caught while visiting their favorite flowers, as pansies, milkweed, or while resting on branches or leaves of trees, especially in the early part of the day. They are on the wing most of the time during the middle of the day, flying with stately ease and grace always in a zigzag course. A very large percent of those caught during the early part of the season, say the first of June, are females, while those caught the latter part of July were with only few exceptions males.

I have always gathered a considerable number of larvae in the fall and kept the chrysalids during the winter in my laboratory where the temperature is somewhat variable yet always higher than out of doors. The confinement in a warm room does not seem to hasten the development into the mature butterfly, for they come out no sooner than those outside.

The larva (pl. 12, fig. 2), I believe, feeds primarily on the leaves of the willow. It is green and not easily found in Nature while feeding. Between the first of September and the first of October, they leave their feeding places, and wander about apparently in search of suitable places for pupation. They are most frequently seen after the first autumn frost when the leaves begin to fall. They are then seen on sidewalks, on fences, and in wood piles. Soon after leaving their feeding grounds, and a week or two before pupating, their color changes from a bright green to a deep brown apparently in imitation of the leaves changing to a similar color from the effects of heavy frosts. The caterpillar is often found on early frosty mornings on some exposed plank or fence, clinging motionless with its prolegs while raising the anterior part of its body in an almost vertical position with its front legs folded under its head, an attitude which under the circumstances, seems pathetic enough.

The change in color begins underneath and gradually spreads upward, the green passing gradually into yellowish which assumes a dirty gray and finally a deep velvety brown.

They seem to eat little or nothing after this change of color and usually pupate in a few days when put into the cage. After moving about uneasily for some time, they come to rest. A silken thread is spun, attached to the wire of the cage, and passed around the body between the sixth and seventh segments. While the caterpillar is thus suspended the cuticle hardens gradually, the head drops off, the color changes to a mottled gray and brown presenting a rough irregular surface strikingly resembling old weatherbeaten boards or bark, the usual objects to which they are attached in Nature. I have found the chrysalis (pl. 12, fig. 3) thus suspended from the edge of the siding on the most exposed wall of an old unpainted house, which it strikingly resembled in color. I had passed by it for several months during the winter, but had not noticed it till I saw a sparrow fly at it but fail to get it.

These changing colors to suit first the green leaves, then the brown withered leaves, and finally the gray, somber shades of weatherbeaten support and cloudy winter weather are certainly adaptations in themselves marvelous, but doubly so, because of the brief period of time (a week or two) in which the changes are brought about, corresponding to equally rapid changes in the autumn temperature. Yet the frost which kills the leaves and thus causes the deep brown of such leaves, is not responsible for the change from green to brown in the caterpillar, since the same change occurs when the larva is kept in the laboratory at a uniform temperature of about 70°.

Besides this seasonal correspondence in color between the larval stages of this butterfly and the plants on which it lives, there is a deeper correspondence between the general life processes of the two. And if the change in color from green to deep brown is due in the caterpillar to changes in the physiological processes, it seems not unreasonable to assume that the transformation in color of autumn foliage may likewise be due to internal physiological changes in the plant rather than to variations in the external temperature.

The life phenomena in the young butterfly resemble, broadly speaking, the life phenomena in the willow on which the caterpillar lives at this autumnal season of the year, in the following particulars: (1) in both, growth ceases; (2) both approach a season of rest when the

active vital processes are at their lowest ebb, for I find that at this stage mitosis is practically arrested even in the germ cells; (3) in both, the outer cuticle thickens and hardens, causing in the willow falling of the leaves by the formation of a corky ring around the base of the petiole, and causing in the larva the shedding of its head probably by a similar hardening of the cuticle. The changes of color in both are apparently due to this thickening of the cuticle, the withdrawal of fluids to deeper parts, the hardening and stiffening of the cells covering the body, and even to a certain extent affecting the internal metabolism of the deeper tissue cells, causing changes in the optical properties of the cell pigments.

DEVELOPMENT OF SEX.

I have not studied the embryology of *Papilio rutulus*. The facts regarding the early development of the genital organs in both sexes, I can only infer from what I have seen in the fully formed larva, both male and female. It is often affirmed that sex is not inherited, and that its determination depends on external conditions such as temperature and food. The experiments of Treat ('73) certainly suggest such a conclusion.

In this form the sex is determined early, as in the larva it is an easy matter to distinguish between ovary and testis. It is evident that originally the two must be very similar, for both have the general characters of a gland, a right one and a left one, each consisting of a simple tube or duct, the oviduct or vas deferens, leading from four simple chambers or follicles, which constitute the ovary as well as the testis. In the ovary these follicles remain distinct and elongate into tubes, while in the testis, they become closely applied to one another, and are invested (like the ovary) with three coats forming one spherical body. Then the right and left testes finally become closely applied to each other, constituting thus a double organ characterized by a deep red coloration arising from pigment developed in the inner investing coat, really the original epithelium of the gland.

Although the female is the first to emerge in the spring, the ovary in the larva is comparatively less developed than is the testis. I have found in the male larva the sex cells in the spermatid stage when the oldest egg was in its first stages of growth. Possibly the phenomena

of cell multiplication and cell growth may, when sufficiently understood, give us a clue to this obscure matter of sex differentiation. From my observations I am led to believe that the male elements develop earlier than do the female elements, and further that this precociousness leads later to an arrested development as shown not only by the inferior size of the adult male, but also in the inferior development, so far as size is concerned, of the male germ.

Sexual maturity in the male not only extends over a greater period of time than in the female but is also attained earlier. Mature spermatozoa were found in the chrysalis on April 12, at least one month before the last moult. I have found no mature spermatozoa before the fifteenth of February. It is perhaps safe to say that the male is sexually mature at about the middle of its pupation period.

THE TESTIS.

In the larva the right and left testes (pl. 12, fig. 6) are separated. They lie in the fifth and sixth abdominal segments, between the heart on the dorsal side and the alimentary canal.

The vas deferens (pl. 12, fig. 7, *v. d.*) is a bent tube connected with the copulatory organ on the postero-ventral side, and passing thence upward and forward, increasing considerably in diameter to form a spacious receptaculum seminis. In the adult this is usually filled with spermatozoa either separate or in bundles (pl. 14, fig. 55).

The vas deferens is lined with a columnar epithelium of large cells having very large oval or slightly irregular nuclei very rich in chromatin. This epithelium forms five longitudinal folds or elevations which are very prominent throughout its entire length. It seems clear that the vas deferens is homologous to the duct of a racemose gland, but the epithelial cells lining it evidently have a secretory function. Originally this duct divides, I believe, into four branches. In *Grapta silenus* this division is very evident (pl. 12, fig. 8b). In *Papilio*, the division is not so marked (pl. 12, fig. 5, *v. d.*). But in both it is continued by four short tubes, the follicles.

The follicles of each testis are separated by a single layer of cells in the form of a rather thick membrane provided with large oval nuclei. This same layer surrounds the follicles peripleurally, and thus binds the four follicles into a single organ containing four chambers (pl. 12, fig. 8).

As the two testes grow they gradually approach each other (pl. 12, fig. 6), and finally fuse into a spherical body, the right and left halves of which are indicated externally by a groove as shown in plate 12, figure 7, *t*. The two vasa deferentia also become intimately united at the point of insertion into the testis proper (pl. 12, figs. 5, 7). The two testes then become surrounded by a continuous, comparatively thick connective-tissue layer, the tunica propria (pl. 12, fig. 8, *cn. l.*) which extends also down between the two halves, but does not dip down between the follicles. Outside the tunica propria, there is finally a thin epithelial investing membrane, tunica adventitia, which is also continued over the vas deferens (pl. 12, figs. 5, 8, *pt. m.*).

The inner lining of the follicles early becomes richly pigmented, and this red pigment resisting to a remarkable degree the decolorizing effects of reagents, gives the whole organ a bright red appearance, which facilitates considerably this study, since the testes can easily be seen with the naked eye even in the unstained larva sectioned *in toto*. In teasing the testes the pigmented lining epithelium (pl. 12, fig. 8, *p. l.*) and the tunica propria (*cn. l.*) rupture easily. But the outer tunica adventitia (fig. 8, *pt. m.*) is quite tough and elastic, allowing the spermatozoa and cysts to accumulate between it and the tunica propria.

I have been unable to arrive at any definite conclusion as to how this union of the two testes, and their final inclusion within a continuous membrane is brought about. I assume that it results from the increase in size. As the two testes grow they encroach on the surrounding connective tissue of the body which finally becomes compressed between them and crowded over the surface till it constitutes a comparatively thick investing membrane.

I find these relations of the testes to each other and to the surrounding stroma to be the same in *Grapta silenus* (pl. 12, fig. 8 b). Here, as in *Papilio rutulus*, there are four follicles in each testis. In *Grapta silenus*, however, the inner pigmented layer is relatively more developed and the nuclei much more stainable and prominent, but the tunica propria is less developed (compare pl. 12, fig. 8 and fig. 8 b).

NOMENCLATURE.

We are indebted to La Valette St. George for the terminology usually employed in this subject. I use this terminology so far as it suffices; but, as there are some facts brought to light in my work

which are new, it seems necessary for the sake of clearness, to use some terms that may need definite explanation.

1. The germinal material in the embryo is supposed to consist of individual cells forming a layer, the germinal epithelium — *primordial germ cells*.

2. At a given period in the development of the larva, these primordial germ cells begin to multiply and continue to do so during the so called *period of multiplication*.

3. At the beginning of multiplication these primordial germ cells are called *primary spermatogones*.

4. After the first division of the primary spermatogone, they are called *secondary spermatogones*.

5. After a certain number of divisions in the division period they are said to enter on a *period of growth*. In this stage of their history the cells are called spermatocytes.

6. From the beginning to the end of the growth period the cells are called *primary spermatocytes* or *spermatocytes first order*.

7. The spermatocytes of the first order divide twice in succession, and while thus dividing, they are called *secondary spermatocytes* or *spermatocytes second order*.

8. These last two divisions, corresponding to the maturation divisions of the ovum are called the *maturation divisions* of the maturation period.

9. At the end of the maturation divisions, the cells become *spermatids*.

10. The spermatids then develop into the fully formed *spermatozoa*, the final product.

11. As soon as the primary spermatogone begins to multiply, a colony of similar cells results, which is surrounded by a cellular capsule which is called a *cyst*.

12. The cells of this cyst undergo marked changes during the development of the germ cells into mature spermatozoa. It seems desirable to have a name for these different stages.

New Terms.

13. I therefore propose: to call (*a*) a cyst containing spermatogones a *gonocyst* (pl. 12, fig. 9-13); (*b*) those cysts containing spermatocytes, *cytocyst* (pl. 13, fig. 35-38); (*c*) those cysts containing spermatids and spermatozoa, *spermatocyst* (pl. 12, fig. 14-23).

14. In the stages of *Papilio rutulus* that I have studied there is no true germinal epithelium, but as will be pointed out farther on, the original germinal material from which primary spermatogones arise, has the character of a large primordial germ cell (pl. 12, figs. 4, 8b; pl. 15, fig. 56), which I have called the *grandmother stem cell*.

15. The grandmother stem cell has connected with it numerous smaller cells (pl. 15, fig. 57a), which I have called the *mother branch cells*.

16. The grandmother stem cell and the mother branch cells are surrounded by minute nuclei which I have called *cortical nuclei*.

17. Finally, I have distinguished two kinds of spermatocytes, the *ordinary* and the *giant spermatocytes*, and *ordinary* and *giant spermatids*.

GROWTH ZONES OF THE FOLLICLES.

In the youngest larva which I have studied, and while the right and left testes are still separated, the gonocysts are already formed. They practically fill each follicle, the spermatocysts not yet having been formed. In the pupa of about the 15th of February, four months before the last moult, cytocysts are formed, some having even passed the maturation period and entered on the spermatocyst stage (pl. 12, fig. 6). But no fully formed spermatozoa exist. These appear about one month before the last moult.

In the mature testis the larger portion of each follicle is filled with spermatocysts in various stages of development (pl. 12, fig. 5, *sp. c.*). In such a testis, therefore, there is at the periphery, next to the pigmented inner lining of the testis, a series of variously developed gonocysts. This is the *multiplication zone* of the follicle. Within these there is usually a zone of cytocysts, the *growth zone*, and scattered within that again are cysts in which maturation is taking place, *maturation zone*. Finally within these, and next to the opening into the vas deferens, are the variously developed spermatocysts, the mature ones being nearest the vas deferens.

While it is possible, therefore, to distinguish, in a very general way, these various zones, they are not distinctly separated. It follows that as the spermatozoa become mature and are discharged, the inner zones encroach more and more on the outer ones. Hence late in the season

the peripheral or first multiplication zone, the second growth zone, and even the maturation zone have disappeared, the gonocysts and cyto-cysts having all been converted into spermatocysts variously developed (pl. 12, fig. 5, *f.*).

Each follicle of the testis seems to mature independently of the rest. Thus I often find some follicles in which nothing but mature spermatocysts remain as in plate 12, figure 5, *f.*, while neighboring follicles may still have the original multiplication and growth zones of gonocysts and cyto-cysts. I shall show later that this difference is due to the presence in the latter follicles, of grandmother stem cells from which new gonocysts arise. It is quite probable, therefore, that one part of the testis may become quite functionless, while other parts may continue to produce spermatozoa, the spermatogones in the former being exhausted.

GONOCYSTS.

In those follicles where no grandmother stem cell exists, I have been unable to find the first stages or two-cell stage of the gonocyst. Even in the youngest larva examined by me where the right and left testes are still separated by a considerable space, and still comparatively small, all the gonocysts are in an advanced stage, judging by the number of spermatogones they contain, *i. e.*, not considering those follicles containing a grandmother stem cell.

I feel justified in inferring from this that all the primary spermatogones begin their multiplication at about the same time, in a given zone of the follicle and that this multiplication begins near the vas deferens, the proximal area of the follicle, and extends gradually towards the periphery, the distal termination of the follicle. The question then naturally arises how are new spermatozoa produced when all the primary spermatogones are thus developed into advanced gonocysts at this early period of larval life?

For a long time this question was a mystery, for there was nothing suggesting a solution in published accounts of other insects, and I did not at first understand the real significance of the grandmother stem cell. There is nothing in the plates of Henking ('92), Wilcox ('95), or Paulmier ('99), showing that these writers have solved the problem. It seems clear that the same problem exists in those insects, but the

matter seems to have been given no attention. As to the origin of the cyst cells; which was so much discussed by the earlier writers, Meyer ('49), Bessels ('67), and others, without finding any proof or giving any satisfactory explanation, the later writers dismiss it with mere conjectures. My studies on the grandmother stem cell, to be related presently, give, I believe, a complete explanation of the problem.

The number of cells in a gonocyst increases by division till there are between one hundred and one hundred and fifty cells. The cysts are approximately spherical. They are surrounded by a thin membrane, that was thought by earlier writers to be the mother cell which by endogenous cell multiplication had given rise to the contained spermatogones. The cyst wall or membrane is composed of a few very thin broad cells with distinct nuclei. Surrounding the nucleus there is usually a thick zone of cytoplasm, the peripheral parts of each cell being so thin as to be scarcely visible in section. There is no evidence of mitosis in these nuclei after the cyst is formed. Their number is probably determined very early, a fact that is sustained by the small number of these cells that become so prominent in the developed spermatocyst (pl. 12, fig. 14-23; pl. 13, figs. 43, 44, 48, 49, 50, 51, 54). A comparison of the different forms represented in these figures shows that one of these gonocyst cells becomes the head nurse-cell of the spermatocyst, while the rest become enveloping cells of the bundle of mature spermatozoa. The origin of these cyst cells is explained later in connection with the grandmother stem cell, and the origin of the primary spermatogone. It will there be seen that they divide by the usual mitosis in that early stage.

The gonocysts increase in size as the cells multiply, and as the cells in this period of multiplication lie closely packed, there being no internal cavity, there must be some growth of the cells after each division, a conclusion which is sustained by a comparison of the relative size of the spermatogones in the younger and older cysts. I do not consider it strictly true, therefore, that all growth is confined to the "period of growth" just preceding maturation. This is illustrated in the following diagram (text-fig. A).

Degenerating gonocysts.— Both in the early stage of the larva and in the mature butterfly, some follicles occasionally contain degenerating gonocysts. These can be recognized by the fact that the contained cells vary greatly in size, some being several times larger than others (pl. 13, fig. 33). They can also be known by the nuclei which are

small, compact, spherical bodies staining very intensely in nuclear stains. The chromatin seems to be compacted into a solid mass. The larger cells contain from two to several such nuclei (pl. 13, fig. 33).

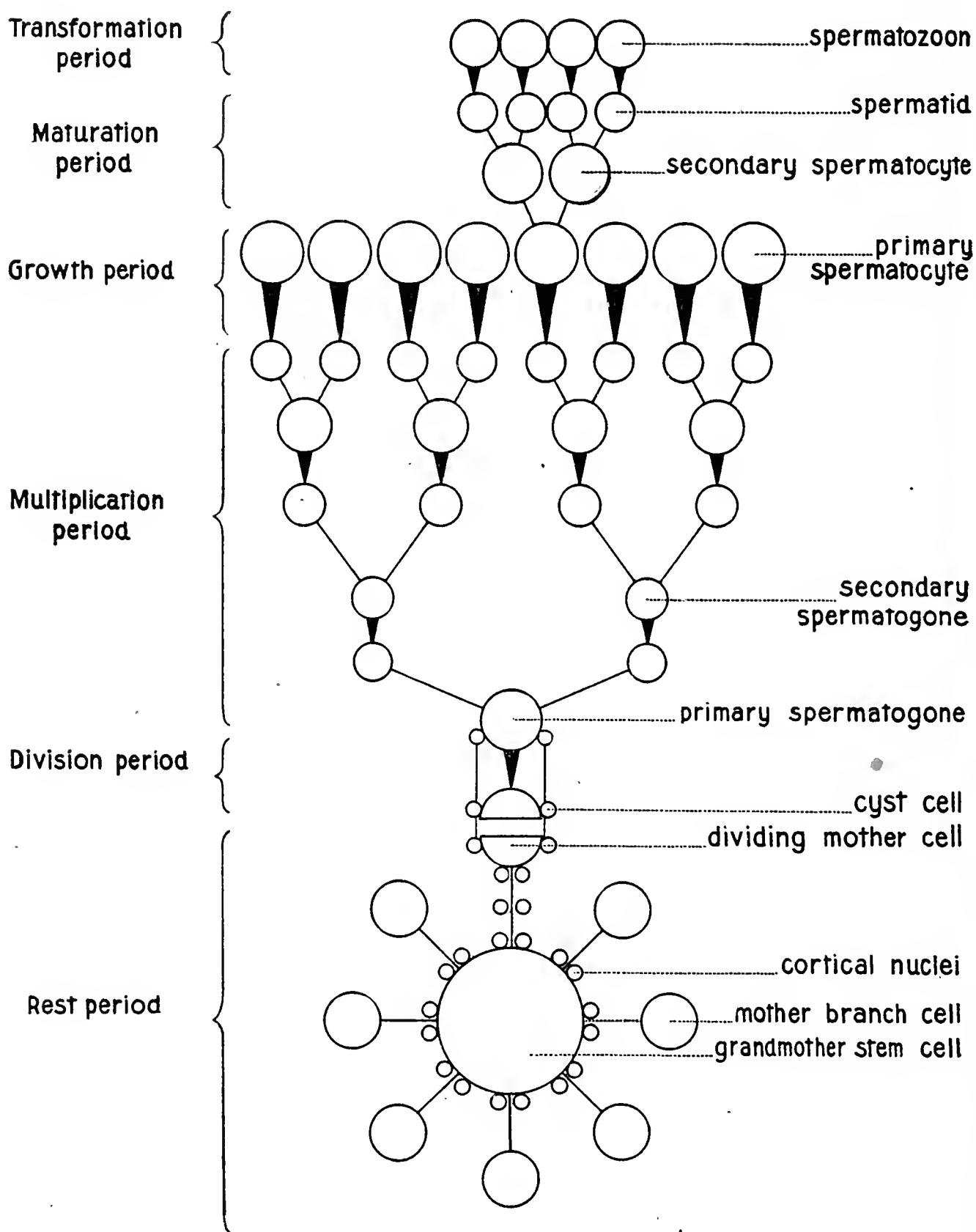


FIG. A.

There is no evidence of nuclear fragmentation, and none to suggest that the multinuclear condition is brought about by amitosis. Writers often insist that amitosis is evidence of degeneration, as it is often

found in cells whose function has been discharged, and which are to be eliminated. Of course no such cause could be assigned here. The multinuclear condition of the larger of these cells certainly suggests that nuclear division has taken place, while division of the cytoplasm has not followed in the usual way. The compact condition of the nuclei and the consequent capacity for staining suggest an inertness on the part of the chromatin, which in the normal cells becomes separated soon after mitosis by the secretion within and the accumulation around it of the hyaline karyolymph. In these cells the karyolymph seems not to be produced.

In my work on *Clemmys* ('04) and also in my work on *Limulus* ('98), I came to the conclusion that through the action of the chromatin directly, or indirectly through chromatin nucleoli, a nuclear matrix, nucleoplasm, was formed as a result of chemical action; that this nucleoplasm enters the cytoplasm and acts as a digestive fluid on substances entering the cell as food from without. As a result of this, metaplast (a form of archoplasm) arises, and is the culture medium of the living substance, *i. e.*, the result of synthetic metabolism which most resembles the living formed substance itself, and which consequently alone can serve as food.

If those conclusions are correct (they are based on evidence), then the degenerating cells of these gonocysts are simply dying from starvation resulting from indigestion, the chromatin having lost the power, as we see, to generate the necessary karyolymph.

Every trace of nuclear membrane and cell membrane disappears; the cytoplasm becomes granular, and finally seems to crumble into fragments; the whole cyst finally is dissipated in the fluids of the testis, and probably serves to enrich the latter with nutritive material for the support of other cysts. This degeneration also occurs later during the period of growth and even during maturation. There may be several such degenerating cysts in the same follicle. Usually all the cells in degenerating cysts are equally affected; but occasionally some cells still have their normal appearance. They all, however, ultimately degenerate and crumble to pieces.

THE CYTOCYST.

Like the gonocyst the cytocyst continues spherical. But unlike the gonocyst, it is a hollow vesicle (pl. 12, fig. 5, *cy. c.*; pl. 13, fig. 35-39). If we compare the gonocyst to the morula of a developing egg,

the cytocyst may be compared to the blastula, so far as the relation of the cells to the enclosed cavity is concerned. The causes for the hollow condition may be the same in both cases. Loeb has attempted a physical explanation of the hollow condition of the blastula, by assuming that the cells acquire a peculiar affinity for water, and hence favor its accumulation in the form of a large water vacuole in the center. Such an explanation is probably altogether inadequate. In the living material of teased testis, it appears more like an electrical phenomenon, the similar spermatocysts having been previously, as secondary spermatogones, crowded together 'as if attracted to one another, now, as division ceases and growth begins, being suddenly repelled from each other, and attracted by the unlike cyst cells. Mutual repulsion on the part of the spermatocysts, and attraction between them and the dissimilar cyst cells would, of course, produce the hollow vesicle. The suggestion may perhaps be pardoned, purely theoretical as it is, that during karyokinesis, the opposite poles of each spermatogone are differently charged electrically; hence the mutual attraction of the cells at the spermatogone stages; while during the growth period the entire cell is similarly charged, hence the repulsion between them. Such repulsion may, for aught we know, favor the expansion of the cell, and hence be one of the leading factors in absorption and nutrition. This hypothesis of an electrical charge is partly sustained by the singular movements already described at the close of the introduction to this paper as being one inciting cause of my undertaking this study.

When the spermatocytes enter on their maturation divisions, the cytocyst is often very large (pl. 13, fig. 35-39). The size, however, varies. In the same testis, and on the same slide, but usually in different follicles there are cytocysts varying greatly in size while the contained spermatocytes are in the same phases of maturation. In the large cysts the cells are correspondingly large. They give rise to giant spermatids (pl. 13, figs. 36, 39; pl. 14, fig. 46; pl. 17, fig. 138).

SPERMATOCYSTS.

Soon after maturation, the spermatids begin to elongate and the spermatocysts lose their spherical form. At one pole the cyst cells are crowded out, and the cyst becomes oval or ovate in outline (pl. 12, fig. 14). From this stage on, the cyst elongates, finally becoming

cylindrical with one end rounded, the other pointed (pl. 12, fig. 15-23; pl. 14, fig. 40-43).

The cyst cell at the rounded end of the cyst finally develops into a very large cell, the head nurse-cell (pl. 14, figs. 43, 44, 48, 54). With this head nurse-cell the heads of the developing spermatozoa finally become connected (pl. 14, fig. 43). At first it is a very much flattened cell, in no way differing from the other cyst cells, but as the spermatids develop, they seem to shift their position, so that all have their nuclear end turned toward or connected with one cyst cell only. This then increases in thickness (pl. 14, fig. 50), occasionally appearing oval as in plate 14, figure 49. (Compare also pl. 14, figs. 49, 50, 54, *h. n.*) While this head nurse-cell curves slightly to include the heads of the growing spermatozoa (pl. 14, figs. 48, 50, 54), the other cyst cells grow into the form of a hollow cylinder enclosing the bundle of spermatozoa. Plate 14, figure 52, shows one of these in section transverse to the long axis of the spermatocyst. (Compare with this also pl. 14, fig. 43, *c. c.*) From the anterior head nurse-cell, the cyst cells diminish in thickness backward, till they become so thin as to be scarcely visible. I have occasionally found one of these cells at the tail end of the cyst in the early stage of development, but that is an exception rather than the rule.

The head nurse-cell varies considerably in shape during the development of the spermatocyst; but it ultimately becomes the largest cell and more or less spherical in shape. It has a large oval or irregular, rarely spherical nucleus (pl. 14, figs. 43, 44, 48, 54, *h. n.*). The nucleus is rich in chromatin arranged in the form of a network, which is sometimes massed irregularly (pl. 14, fig. 54). There is usually a condensation of the chromatin at one point, which can hardly be called a true nucleolus, though it is the only body present to suggest one. The cytoplasm is greatly developed. In the living cyst it is bright and nearly transparent (pl. 17, fig. 151). In preserved material, it shows a distinct and well developed cytoreticulum. The other cyst cells agree in these respects (pl. 14, fig. 54, *c. c., h. n.*).

ABNORMAL SPERMATOCYSTS.

Very rarely spermatocysts are found having the appearance represented in plate 14, figure 45. It consists of a spherical mass of nuclei with little or no cytoplasm surrounding each, and with little or no

trace of an enclosing membrane. The central portion of this mass is more compact and the nuclei much less distinct. Indeed the nuclei in the central portion seem more or less disorganized, appearing more like a granular central portion with nuclei at the periphery.

Into this mass are inserted the heads of a bundle of fully formed spermatozoa. I am unable to explain this except on either of two suppositions. It seems to be a case where only a few of the spermatids have developed into spermatozoa, the remainder being gradually absorbed as food. Possibly this may be due to a failure of the cyst cells to develop properly, which is quite evident. The central solid portion may be the head nurse-cell, which has become imbedded in the mass of undeveloped spermatids.

I have thought that possibly also a number of mature spermatozoa, having been discharged from the cyst, but not finding their way into the vas deferens, have taken possession of an undeveloped gonocyst or cytocyst.

Fate of the spermatocyst.—When the spermatozoa are mature, the spermatocyst is discharged into the vas deferens. But just before this, the cyst cells seem to dissolve, allowing the spermatozoa to escape either singly (pl. 14, fig. 51), or collectively (pl. 14, fig. 53). Remnants of the cysts are found near the entrance to the vas deferens often crowded into masses of debris between the stalked cells (pl. 12, fig. 5). Traces of cyst cells are also found in the vas deferens, but usually only parts of the head nurse-cell to which the heads of the spermatozoa are still attached (pl. 14, fig. 55). I have never found a complete spermatocyst in the vas deferens, though the spermatozoa frequently occur adhering in bundles (pl. 14, fig. 55), as they are also found within the testis after being discharged from the cyst (pl. 14, fig. 53; pl. 12, fig. 5).

HISTORY OF INDIVIDUAL CELLS.

That part of the vas deferens which penetrates the testis, and which in *Grapta silenus* divides into four branches, one for each follicle, is lined with a modified epithelium differing in some respects from that lining the vas deferens proper. The cells are more spherical and the nuclei are unusually large, spherical, and very rich in chromatin (pl. 12, figs. 5, Sb, v. d.).

Stalked cells.—Apparently connected with the epithelial cells de-

scribed above, are numerous chains of cylindrical cells placed end to end, the terminal one being spherical (pl. 12, fig. 5, *st. c.*; pl. 15, fig. 68). They are not visible in the testes of the larva or pupa. They seem to develop late in the season, for they are seen only in the older forms. It may be that these chains are only empty spermatocysts remaining temporarily after the spermatozoa have been discharged. Yet for reasons which the following description will make clear, I have not been able to satisfy myself that this is the true explanation of them.

The large terminal cell, which I at first thought to represent the head nurse-cell of a spermatocyst, is spherical (pl. 12, fig. 5, *st. c.*). Their size varies somewhat but they are the largest cells in the testis, larger even than the grandmother stem cell to be described presently. I have found no reference to these stalked cells in literature. They have a large spherical, though often irregular nucleus not especially rich in chromatin. The nucleus is usually located about midway between the center of the cell and its periphery. There is a distinct nuclear reticulum with stainable bodies at the nodes. These stainable bodies are sometimes aggregated into an irregular mass at one point. There are often, also, one or two paler bodies, probably representing nucleoli (pl. 15, figs. 68, 69, 77).

The cytoplasm is slightly granular, and a cytoreticulum is visible, but not always equally distinct. In the center of the cytoplasm, there is a spherical body having the appearance of archoplasm with a central condensed portion containing a granule. That a relation exists between this attraction sphere and the nucleus is suggested by figures 68, 77 (pl. 15) where the nucleus is indented on the side facing the sphere. The body is also surrounded by zones which are in relation with the nucleus (pl. 15, fig. 68). I am forcibly reminded, in this case, of the cytocenter and the cytoceol of the ovarian egg of *Clemmys* (Munson, '04).

Occasionally similar cells are found free in the fluids of the follicle (pl. 12, fig. 5, *x*). In plate 15, figure 69, is represented such a free cell. Besides the nucleus and sphere which in this case are near the center, there are in the cytoplasm several irregular bodies resembling the yolk nucleus of the tortoise egg. In fact, these cells resemble eggs very closely. In figure 83 (pl. 15) another such free cell is represented, having a more distinct cytoreticulum and likewise a spherical body near the nucleus. Two large vacuoles partly surround it. Figure

84 (pl. 15) represents two such free cells considerably smaller but lying side by side as if originated by division of a free stalked cell. Partly imbedded in the nucleus is a mass of archoplasm (*arch.*) which in the second cell (*b*) has divided into two masses as if preparing for cell division. In plate 15, figure 85, is represented another free cell, apparently of the same kind, in the metaphase of karyokinesis. The asters are well developed and the spindle is very distinct. The outline of the original nucleus is still visible.

The free cells are found in that part of the follicle where the spermatocysts are fully developed. They are not common. I see no way of accounting for them except on the assumption that they are the spherical end cells of the stalk (pl. 12, fig. 5, *st. c.*) set free. There are no isolated free spermatogones of the usual kind, the primary spermatogones being found in the immediate neighborhood of the grandmother stem cell.

If we compare figure 85 (pl. 15) with the next (pl. 15, fig. 86), a spermatocyte — a spermatocyte from the unusually large cytocysts already referred to (pl. 13, fig. 36) and which give rise to the giant spermatid (pl. 14, fig. 46; pl. 17, fig. 138) — the question arises whether these free stem cells do not give rise to the giant spermatocytes. There are good reasons for assuming that such is the case. Yet I do not feel that the evidence in this case is sufficient to justify a definite statement. It needs further investigation in other forms.

Should the above hypothesis prove true, we would here have a case where the primordial germ cell grows like an egg without dividing and finally segments into a number of cells, spermatocytes, the period of growth — unlike the usual mode — preceding the division period as is the case with a segmenting egg.

THE GRANDMOTHER STEM CELL.

In some follicles a very large cell is found which deserves special attention. Unlike the free stalked cells considered above, this cell is usually surrounded by a compact mass of small cells forming, as it were, a heap, in the center of which the large cell is invariably found. I have named it the grandmother stem cell. I have never found more than one of these in a follicle, and never more than four in a testis (pl. 12, fig. 5, *g. m. c.*). As there are eight follicles in a

double testis, all follicles do not have one of the cells. My first impressions consequently were that this is an abnormal growth of one of the gonocysts. From the general appearance of the grandmother stem cell and its connection with surrounding cells resembling an egg follicle; I suspected that it was a case of primary spermatogones growing from the first, instead of dividing, as an oocyte or young egg.

An examination of the developing ovary of a young larva reveals indeed a striking resemblance between the grandmother stem cell and the young growing egg. Excepting the irregular ones in the grandmother stem cell, the nuclei are strikingly similar, and the cytoplasm of the young growing egg very strikingly resembles that of the grandmother stem cell. I found even that the young egg, like the grandmother stem cell, sends out protoplasmic processes to the surrounding follicle cells, and seems thus to have a protoplasmic connection with each follicle cell. So far the resemblance is certainly striking. But in some transverse sections of the young ovarian tube — of which there are four, corresponding to the four follicles of the testis — the food or nurse cells (few in number and highly specialized, particularly as regards the nucleus), occupy the position held by the cortical nuclei in the grandmother stem cell.

The fact that each testis has at least one, sometimes two, three, or four of these grandmother stem cells (pl. 12, fig. 8 b) seemed not to sustain the view that it is merely an abnormal or accidental growth of a spermatogone; while, the fact that every follicle does not seem to have such a cell, forbade me, as I thought, from assigning any great importance to it. Yet the origin of the primary spermatogones and the origin of the cyst cells surrounding the already developed gonocysts remained a mystery, as no free primary spermatogones or primordial germ substance could be seen.

The significance of the grandmother stem cell assumed an entirely different aspect when I began to suspect that the testis has originally but a single lumen, and that the partitions separating the testis into four chambers or follicles appear gradually as the testis enlarges, so that the already formed gonocysts are included in each chamber. Consequently it does not matter much in which of these follicles the grandmother stem cell finally becomes lodged. The fact, too, that it is always close to the inner pigmented lining — (I have found only one instance where it was removed slightly from the peripheral wall) — seemed to suggest some original origin or function of this cell.

The latter hypothesis assumed the certainty of a fact in my mind when I discovered that the bodies imbedded in the outer cytoplasm of the cell are real nuclei (not granules as I had supposed) and further that immediately connected with the grandmother stem cell, there are cells which divide, one product of division being in fact a primary spermatogone. I found further that only in this region immediately surrounding the grandmother stem cell, a single cell can be found dividing, something to be found nowhere else, as all the cells of a gonocyst divide at the same time. More careful examination showed that each primary spermatogone is accompanied by at least one small nucleus at its periphery, which proved to be the "anlage" of the future cyst cells.

The grandmother stem cell is irregular in outline, the cytoplasm all over its surface being prolonged into cytoplasmic processes which on a superficial examination seem to extend out between the numerous smaller cells surrounding it. Its general outline is about the same in whatever plane looked at, the main body of the cell being a sphere (pl. 15, fig. 56). It has a large nucleus which is usually regular and spherical or oval. In many cases, there is on one side of the nucleus, an unstained portion resembling a vacuole, as large as or even larger than the nucleus itself. Within this area, there is often a spherical body suggesting a sphere with its archoplasm, but more frequently a mass of granules resembling chromatin in staining reaction (pl. 12, fig. 4). Occasionally this is double and looks as if it might be part of a fragmented nucleus, but less rich in chromatin than the main part of the nucleus (pl. 15, fig. 57a). In most cases, the chromatin forms a network, but occasionally it is compacted into a mass (pl. 15, fig. 56). Granules resembling chromatin are sometimes to be seen also in the cytoplasm, usually contained in rather small vacuoles.

The cytoplasm of these cells is very much the same in all. It is distinguished from that of all other cells of the testis by its resistance to stains. It is apparently devoid of those cytoplasmic granules which take the stain as it seems also devoid of cytoreticulum and cytomicrosomes. In appearance the whole cytoplasm resembles archoplasm. It stains well in saffranin, but remains practically unstained in haematoxylin and borax carmine and most nuclear stains that I have used. In this, too, it resembles archoplasm. I consider it the most undifferentiated cell in the testis. I shall present other good reasons for believing this to be the real original germ cell, for which reason I have called it the grandmother stem cell.

The cortical nuclei.—Surrounding the grandmother cell and apparently imbedded in its peripheral cytoplasm are numerous nuclei of various sizes, mostly very minute. They extend also along the protoplasmic projections or branches of the grandmother cell, and seem to surround those branches like a mantle. I have called these *cortical nuclei*. As they do not stain readily and are so variable in size and often very minute, they are easily overlooked, if the right kind of stain is not used. In this resistance to stains, they resemble the cytoplasm of the grandmother cell. In material prepared according to my method, they are made clear and prominent by means of saffranin, much less so by means of haematoxylin.

As the whole surface of the grandmother cell is studded with the protoplasmic processes or branches, these cortical nuclei become crowded in between the branches, making it difficult to understand their real nature except in very favorable cases. Out of the large number of these remarkable cells which I have carefully examined and compared, I have had several such favorable specimens from which my drawings are made (pl. 12, fig. 4; pl. 15, fig. 57a). They have shed a flood of light on the whole very complex and obscure problem regarding this cell colony and the origin of the primary spermatogones, of the gonocysts, and of the cyst cells.

The mother branch cells.—At their termination, the protoplasmic strands (branches) proceeding from the grandmother stem cell, are connected with cells about the size of a primary spermatogone, whose nuclei are many times larger than these cortical nuclei. I have called them mother branch cells (pl. 15, fig. 57a, *br. c.*). These cells are ovate or partly cuneate, with the nucleus located in the broad peripheral end and the apex turned inward toward the grandmother stem cell. Each protoplasmic branch (pl. 15, fig. 57a, *b.*) divides at or near its termination into several finer branches, each of which becomes inserted into the apex of the mother branch cell. Evidently the cytoplasm of the grandmother stem cell is continuous through the numerous protoplasmic branches with the cytoplasm of all the mother branch cells. Taking into consideration the great size of the grandmother stem cell as compared with the short diameter of the mother branch cell, the great numbers of the latter, thus connected, can be readily conceived, closely packed as they are.

Considering the intimate relation between the grandmother stem cell, the mother branch cells, and the cortical nuclei, a primitive germi-

nal syncytium is suggested, out of which the cortical nuclei are being organized into cells, while the mother branch cells are completely differentiated with the exception of their protoplasmic connection with the stem cell.

I have never seen the grandmother stem cell divide, there being never more than one in a follicle (pl. 12, fig. 8b). The nucleus, however, often presents appearances suggesting amitotic division (pl. 15, fig. 57a). Yet, aside from the granules resembling chromatin in the cytoplasm (pl. 15, fig. 56) I find nothing suggesting an origin of the cortical nuclei from the nuclei of the grandmother cell.

The cortical nuclei are usually elongated, compressed, and irregular, and it may be possible that they multiply amitotically, their minuteness preventing a definite determination of that matter. I have never seen any evidence of karyokinesis in these nuclei, though I have seen it in their descendants, the young cyst cells, soon to be considered. On the other hand, the mother branch cells present beautiful mitotic figures (pl. 12, fig. 4; pl. 15, fig. 57a). It is necessary to consider very carefully whether the nucleus of the mother branch cell may not be merely developed cortical nuclei, and the whole mother branch cell in fact a developed cortical cell to be replaced by the latter as they develop. Facts do not sustain this hypothesis. The cortical nuclei not only surround the protoplasmic processes or branches, but extend also over and between the mother branch cells, where they are apt to be overlooked except in most favorable preparations. At the distal end of the mother branch cell, the cortical nuclei are generally considerably larger (pl. 15, fig. 57a).

Karyokinesis of the mother branch cell.— During rest the mother branch cell is more or less conical, the apex being in all cases turned toward the grandmother stem cell, which is the point of attachment with the branch. Near the center of the proximal pointed pole there is often seen a body suggesting a centrosome and sphere with archoplasm.

The nucleus in the resting state is comparatively large, spherical, and rich in chromatin (pl. 15, fig. 57a, *br. c.*). The latter is in the form of a network evenly distributed with spherical, deeply staining chromosomes near the periphery, and an irregular aggregation of deeply stained granules near the center — the only representative of a nucleolus.

When division ensues, the nucleus is transformed into a compara-

tively large and distinct spindle, having the twenty-eight spherical chromosomes arranged perfectly in the equatorial plate. This phase is very common (pl. 15, fig. 57a, *d*). The chromosomes then split, each half being drawn to an opposite pole of the spindle. The separation and the movement toward the poles is accomplished with the utmost regularity, making beautiful dyasters. The anaphase is evidently passed through much more rapidly than the metaphase or telophase, as it is rarely seen (pl. 15, fig. 57a, *e*). The telophase (pl. 15, fig. 57a, *f*) is frequently to be seen, the beautiful intermediate fibers of the spindle remaining apparently for a long time after the separation of the chromosomes is completed. In only one instance have I seen as many as four mother branch cells belonging to the same grandmother cell dividing at the same time (pl. 15, fig. 57a). Usually only one is seen in mitosis.

Without exception, the spindle is arranged in the long axis of the cell, and consequently vertically to the surface of the grandmother stem cell. This arrangement of the spindle results, as the cytoplasm constricts at the equator, in the division into two unlike and unequal parts — a distal spherical cell (*p. g.*), and a proximal conical cell (*i.*), connected as was the original mother cell with the central grandmother cell.

The peripheral, spherical daughter cell (*p. g.*) becomes detached from its sister, and is, in fact, a primary spermatogone. The proximal daughter cell retains the original character of the mother stem cell, occupying the same position and still connected with the grandmother cell. After growing to its original size it evidently divides in the same manner again and again thus giving rise to a succession of primary spermatogones somewhat as a branch of some trees gives rise to new buds to replace those that drop off, a single tree thus becoming the parent of a forest.

As the primary spermatogone is thus pinched off in karyokinesis from its sister cell — the mother branch cell — one or more of the cortical nuclei also accompany it, and are later developed into the cyst cells (pl. 15, fig. 57a, *k*). A section through the cells (*br. c.*) in the plane indicated by the dotted line is represented in plate 15, figure 57b, where the relation of the mantle nuclei to the mother branch cells is clearly seen. They form a circle of three or four nuclei around each cell. The same relation is, of course, obtained in a similar section through primary spermatogones.

This constant pinching off of the primary spermatogones in this way accounts for their accumulation here in the neighborhood of the grandmother stem cell, and for their absence in all other parts of the testes. It explains, too, how the production of new spermatozoa is possible in the adult butterfly even though all gonocysts are already well developed in the very young larva.

Summary on the grandmother stem cell.— I am not aware that an account has ever been published of a similar case, and I consequently anticipate on the part of my readers a scepticism no less hostile than has been my own during my study of this subject. I therefore summarize the facts on which my conclusions are based:—

1. There is at least one, but may be as many as four grandmother stem cells in a testis (pl. 12, fig. 8b).

2. There are no free spermatogones except in the immediate vicinity of this cell (pl. 12, fig. 4).

3. Follicles that do not contain such a cell, soon have all their contents converted into mature spermatocysts (pl. 12, fig. 5, *f.*).

4. Follicles containing this cell continue to function to the end of the breeding season (pl. 12, fig. 5, *g. c.*, *g. m. s.*).

5. The cell exists in the immature testis of the young larva (pl. 15, fig. 56) as well as in that of the adult near the end of the breeding season (pl. 12, fig. 5).

6. The body of the cell though very large is apparently undifferentiated resembling archoplasm in its homogeneity (pl. 12, fig. 4).

7. The nucleus sometimes shows signs of amitotic division (pl. 15, fig. 57a).

8. The cell is amoeboid in outline, sending out protoplasmic strands all over its spherical surface (pl. 15, fig. 56).

9. Apparently imbedded in its peripheral protoplasm are numerous minute nuclei, cortical nuclei, which because of their variable size and shape are easily mistaken for granules surrounding the central cell (pl. 12, fig. 4).

10. Attached to the end of each protoplasmic process or branch is a conical cell (mother branch cell), with its apex turning inward toward the central grandmother cell (pl. 12, fig. 4).

11. The conical branch cell divides independently of other cells by mitosis (pl. 12, fig. 4).

12. The position of the spindle is invariably in the long axis of the cell, the spindle axis being in line with the protoplasmic branch

and consequently vertical to the body of the grandmother cell (pl. 12, fig. 4).

13. Division of the branch cell, consequently, results in two unequal daughter cells, a proximal attached portion (pl. 15, fig. 57a, *i.*), and a distal free spherical cell, the primary spermatogone (pl. 15, fig. 57, *p. g.*).

14. The cortical nuclei not only surround the protoplasmic strands or branches, but extend also around the branch cell, the one at the distal end becoming especially developed (pl. 15, fig. 57, *c.*).

15. When the branch cell divides, some of the mantle nuclei including the large distal nucleus (*c.*) are pinched off with the primary spermatogone.

16. The nuclei thus associated with the primary spermatogone become the cyst cells (pl. 15, fig. 57b).

17. The proximal attached sister cell grows after division to the normal size of the mother branch cells and then divides again.

18. Chains of three or four spherical primary spermatogones can thus be seen directly in line with each mother branch cell, having been pinched off from it, as it were, like so many buds, but by a process of karyokinesis (pl. 12, fig. 4).

19. Beyond these chains of primary spermatogones may be seen isolated spindles, the first division of the spermatogone into a two-celled gonocyst.

20. It is only in this vicinity that I have ever found isolated dividing cells and gonocysts in the two-celled or four-celled stage (pl. 12, fig. 4, *c, d, e*).

21. In the advanced gonocysts, all cells divide at the same time (pl. 13, figs. 30, 31). Hence single spindles cannot be seen, except where primary spermatogones begin their first division (pl. 12, fig. 4, *b*).

22. Soon after the primary spermatogone divides, the cortical nucleus accompanying it may also be seen to divide mitotically (pl. 12, fig. 4, *f*).

23. The spindle of the primary spermatogone does not have that constant position which the mother branch spindle has with reference to the grandmother stem cell (pl. 12, fig. 4, *b*).

24. Beginning with the grandmother stem cell as a center and drawing a line radially outward as in plate 12, figure 4, there are, *first*, the mother branch cell; *second*, one or more primary spermatogones;

third, a dividing spermatogone; *fourth*, a gonocyst in the two-celled stage; *fifth*, a gonocyst in the four-celled stage; *sixth*, a gonocyst in the eight-celled stage, sixteen, thirty-two, etc., stages.

25. The grandmother stem cell group is always found close to the inner pigmented layer, at the periphery of the follicle (pl. 12, fig. 4, *g*), never in the center of a follicle nor near the vas deferens where the mature spermatozoa and the stalked cells are found (pl. 12, fig. 5).

When all the above facts are considered together, it will be conceded that my conclusion in regard to the character and function of the grandmother stem cell is fully justified. The subject certainly deserves further study in other forms. As I find this cell also in a different genus of butterfly, *Grapta silenus*, I am surprised to find no mention of it by Henking ('92), Paulmier ('98), or Wilcox ('95) in their work on other insects. Paulmier claims to have studied *Papilio*, and draws one of his most important conclusions concerning the centrosome from it.

A suggestion.—In my "Researches on the oogenesis of *Clemmys marmorata*" ('04) I found that the follicle cells are the sister cells of the egg, having originated from the same primordial oogonium. The relation of the mother branch cells to the grandmother stem cell resembles very much the relation of follicle cells to the egg. This, I have already pointed out, is suggested when we examine an ovary of the butterfly larva. Without running the risk of drawing unwarranted conclusions, it may be suggested, at least, that we seem to have in this grandmother stem cell a singular reversal of function. In the female the central cell functions as the germ cell, while in the male, the peripheral cells corresponding to the follicle cells of the ovary become the germ. If there is any homology between this grandmother stem cell and the Sertoli cell of the mammalian testes, then may not the Sertoli cell be homologous with the ovum of the mammalian ovary?

HISTORY OF THE SPERMATOGONIA.

In the preceding account of the grandmother stem cell, I have given the evidence for my conclusion that the primary spermatogones originate from the mother branch cell by division of the latter (pl. 15, fig. 57, *f*). The distal half becomes a free primary spermatogone,

while the proximal half grows and divides alternately, giving rise thus successively to a series of primary spermatogones.

At the same time one or more cortical nuclei (pl. 15, fig. 57, *k*) are pinched off with the primary spermatogones and become the cyst cells (pl. 15, fig. 58).

The nucleus of the primary spermatogone is large and regularly spherical. The cytoplasm is not especially abundant. The cyto-reticulum is distinct. At one pole of the nucleus an irregular mass of archoplasm can be seen when properly stained (pl. 15, fig. 58).

Period of multiplication.—When the spermatogone prepares for division the chromatin of the nuclear reticulum is aggregated into spherical chromosomes, arranged near the periphery. There are twenty-eight chromosomes. They preserve their individuality to a remarkable extent throughout the history of the cell.

The archoplasmic mass elongates and finally divides, each half moving to opposite poles of the nucleus (pl. 15, fig. 59), where two large asters, with minute but distinct centrosomes, are developed. The nuclear membrane disappears while the nucleus is being converted into a spindle with the chromosomes at the equator (pl. 15, fig. 60). The spherical chromosomes are then split and each half is drawn towards its respective pole (pl. 15, fig. 57a, *e*). The metaphase and the telophase are most frequently seen, the prophases and anaphase being passed through rapidly. The details of the prophases are more readily made out in maturation, where they are described more fully. The chromosomes having reached their respective poles, the cytoplasm constricts through the equator of the spindle, forming two equal cells which owing to the persistence of the intermediate fibers remain united for some time (pl. 15, figs. 61, 62). The chromosomes then begin to separate owing to the formation of karyolymph, a new nuclear membrane appears (pl. 15, fig. 63), the intermediate fibers gradually disappear, and the two-celled stage is attained (pl. 15, fig. 64).

They are surrounded by the cortical cells (pl. 15, fig. 64), which also divide a few times by karyokinesis, forming a distinct spindle like that just described (pl. 12, fig. 4, *a, f*). I infer that these cortical cells, now the *cyst cells*, divide only in this early period, because I have never seen them divide in the larger and more developed cysts.

A second division of the two spermatogones (pl. 15, fig. 64) soon ensues, leading to the four-celled stage (pl. 15, fig. 65). During their

period of rest, the spermatogones seem to grow slightly, which is evident from the gradual increase in size of the cyst as a whole. (Compare pl. 15, figs. 64, 65, 66.)

At rest the nuclei are large and spherical. An indistinct nuclear network is present, but the spherical chromosomes are arranged chiefly around the periphery (pl. 15, figs. 65, 66, 70). There is usually an indistinct, irregular, feebly staining body representing a nucleolus (pl. 15, fig. 65). But usually nothing can be seen except a deeply staining irregular mass of chromatin granules — a chromatin nucleolus. In mitosis this body disappears. It is probably an aggregation of chromosomes which assume their position at the equator of the spindle like the rest.

Even these small spermatogones in the four- or eight-celled stage of the cyst show distinct and beautiful mitotic figures (pl. 15, figs. 66, 67). Sections through the equator show twenty-eight chromosomes (pl. 15, fig. 66a).

While in nearly all cases all the cells of a cyst are in the same phase of mitosis, there are occasional exceptions (pl. 15, fig. 66b). These exceptions have aided me considerably in determining the rather obscure sequence of events.

The original boundary of the nucleus can sometimes be seen after the nuclear membrane has disappeared and the spindle is fully formed (pl. 15, fig. 66c). There is no reason whatever to doubt that the part of the spindle lying between the outer circle of the centrosome is derived entirely from the nucleus. This will be seen to be even more evident in the first maturation division.

There is represented in plate 15, figure 67, an unusually distinct preparation showing the circles of microsomes surrounding each centrosome and the relation of the chromosomes to those circles.

Synapsis.—When the cells of a cyst are nearing the end of the multiplication period, they pass through a series of changes which I have called synapsis, a term used by Moore ('95) to designate similar appearances in elasmobranchs.

Up to this time, the spermatogones have remained spherical. Now they become crowded and consequently in tangential section regularly five-sided (pl. 15, fig. 70). They also become regularly arranged, acquire a conical shape, the apex being turned toward the center of the cyst, the base or broad end in contact with the enclosing cyst wall. In this broad outer part of the cell, the large spherical nucleus is invariably found (pl. 13, fig. 25).

In the preceding spherical condition of the spermatogones, the chromatin is in the form of a network with chromosomes arranged around the periphery, and an irregular chromatin mass near the center (pl. 13, fig. 24). Now the chromatin is all massed at the inner pole of the nucleus, close to the nuclear membrane (pl. 13, fig. 25). I have come to the conclusion that this is not the effect of reagents. It occurs in the best preserved material, and regularly in cysts of that particular stage. The nucleus shows no sign of shrinkage as it is regularly spherical. But owing to the massing of the chromatin at the inner pole of the nucleus, the latter has the appearance of a large vacuole (pl. 13, fig. 25). The chromatin then gradually expands into the vacant part of the nucleus, the chromatin strands growing out along the periphery, and finally turns out to be a much coiled single thread with regularly arranged small chromosomes (pl. 13, fig. 26). At first this coil appears near the periphery of the nucleus leaving a clear vacant space in the center. But this, too, becomes obliterated, and the nucleus finally presents the appearance represented in plate 13, figure 27. The cells have now again become spherical (pl. 13, figs. 26, 27), the nucleus has increased in size causing the cytoplasm to appear less abundant than in the first synaptic stage (pl. 13, fig. 27). The chromatin is now again in the form of a network, but the linin fibers are very delicate, and intersect one another at variable angles. At these points of intersection, the spherical chromosomes, now greatly reduced in size, are found. The whole network has the appearance of being in a state of tension, caused by the expansion of the nucleus (pl. 13, fig. 27).

These cells now proceed to divide mitotically. Two centrosomes each with an indistinct aster appear at the opposite poles of the nucleus; the nuclear membrane disappears, and the nuclear contents are converted into a spindle (pl. 13, fig. 28). The chromosomes are arranged at the equator of the spindle. They are spherical and apparently single (pl. 13, fig. 28, *a*). They soon split (pl. 13, fig. 28, *b*). Each half chromosome moves to its respective pole (pl. 13, fig. 28, *c*). I have seen only one fiber attached to each chromosome. As the halves separate, the intermediate fibers connect the halves, but these fibers seem much more delicate than the original spindle fibers (pl. 13, fig. 28). I shall refer to this again in connection with the maturation division, some phases of which are represented in plate 13, figures 29, 30, 31. I feel certain that figures 25, 26, and 27 represent prophases

leading up to the division represented in figure 28. It is of course next to impossible to determine just what happens. But it seems to me that there is first a conjugation of chromosomes (pl. 13, fig. 25), then a re-formation of mixed chromosomes (pl. 13, fig. 26), then a pulling apart of those new chromosomes into double the original number (pl. 13, fig. 27). A reunion of different halves is then brought about in the formation of the spindle, thus restoring the original number of twenty-eight chromosomes. I have seen nothing in these stages suggesting a pseudoreduction. It may have something to do with the comparatively long period of rest and growth which follows. The efficiency of the chromatin in metabolism of the cell may be enhanced by this new equilibrium of its chromosomes brought about by rearrangement of their constituent units.

Pseudomitosome and abnormal spermatogones.—At the close of this synaptic mitosis, the spindle, or intermediate fibers, disappears more slowly than usual, and consequently gives rise to a body corresponding to the “nebenkern” of the spermatid. This pseudonebenkern gradually melts away at the periphery causing a large spherical vacuole extending partly if not completely around the nucleus (pl. 13, fig. 32). It is about the size of the original nucleus just before the formation of the spindle (pl. 13, fig. 27). At one pole of this vacuole lies the compact spherical nucleus (pl. 13, fig. 32, *c*) apparently without nuclear membrane, and evidently with little or no karyolymph. The original spindle substance, mitosome, gradually diminishes till nothing remains but a small spherical body in appearance not unlike an attraction sphere (pl. 13, fig. 32, *b*). This occasionally has one or two central bodies suggesting centrosomes (pl. 13, fig. 32, *a*).

As this occurs in cysts which I have to interpret as gonocysts and in cells of the size of spermatogones in synapsis, I have to select one out of two possible conclusions. Either there is here an abortive attempt of the spermatogones to form spermatids, thus omitting the spermatocyte stage, and hence the usual maturation divisions, or else it is a pathological condition of the cells, a fact which is suggested by the peculiar position and behavior of the nucleus.

It is of course possible that the nucleus (pl. 13, fig. 32, *c*) may expand till it ultimately fills the vacuole, thus restoring the cell to its original resting condition. In that case the centrosome and sphere remaining after the pseudomitosome is absorbed, would lie close to the nuclear membrane between the nucleus and cytoplasm,— a posi-

tion which it actually does occupy in the normal spermatocyte (pl. 13, fig. 36, *c*).

That which gives these cells their pathological aspect is the compactness of the nucleus. I have already called attention to similar nuclei represented in plate 13, figure 33, where their pathological nature is very evident since these cells actually crumble to pieces. In those cells, too, the nuclei are compact, deeply staining bodies devoid of karyolymph. I assume that the chromatin, for some reason, has ceased to function, inasmuch as the karyolymph — which I have found in other cells to be a product of chromatin, *i. e.*, nuclear activity — is no longer produced. I should hesitate to consider as pathological, the somewhat similar nuclei represented in plate 13, figure 32, were it not that in most cases after mitosis, the daughter nuclei are soon re-formed and expanded.

The large cells in plate 13, figure 33, with several nuclei suggest that while the nuclei have divided into two, four, or even six distinct nuclei, the cytoplasm has evidently failed to constrict. The general appearance of this cytoplasm is certainly pathological; but it is difficult to decide whether the disorganization is due to the nucleus or to the cytoplasm. The evidence will hardly permit the conclusion that synapsis is a diseased condition leading up to the final disorganization represented in plate 13, figure 33. (Compare pl. 13, figs. 24, 25, 26, 27, 28, 32, 33.)

Period of growth.—It seems certain, judging from the gradual increase in size of the gonocysts, that there is a slight period of growth after each mitosis during the division period. But it is equally clear that there now intervenes a considerable rest period in which the spermatogone, now a spermatocyte, simply grows. I have sought to represent these facts in the diagram (text-fig. A).

The size finally attained by the spermatocytes varies greatly. At maturation most spermatocytes are comparatively minute (pl. 13, figs. 29, 30, 31). These minute ones are usually found near the periphery, the cytocysts being scattered among the gonocysts. Occasionally, in the same testis with the former, there are found, nearer the center of the follicle, and among the mature spermatocysts, enormously developed cytocysts with unusually large spermatocytes. Hence there are ordinary spermatocytes and giant spermatocytes (pl. 13, figs. 35, 36, 37, 38; pl. 15, figs. 76, 78, 79, 80).

Under the heading "Stalked cells," and in connection with cyto-

cysts, it has already been pointed out that a possible connection may exist between these giant spermatocytes and the stalked cells (compare the series, pl. 15, figs. 68, 69, 77, 83, 84, 85 and figs. 86, 87, 88, 89, 78, 79, 80, the former being free cells, possibly originally stalked like fig. 68, the latter, giant spermatocytes in process of maturation).

Aside from their origin, the giant spermatocyte and the ordinary smaller ones differ in no particular except size. The end product, too, turns out to be identical. I have discovered no difference in the spermatozoa, but the spermatids differ greatly as to size.

Because of their size the giant spermatocytes are especially favorable for the study of the phases of mitosis and reduction, as well as for the various problems connected with the transformation of the spermatid into a mature spermatozoon.

SPERMATOCYTE FIRST ORDER.

When the spermatocyte begins to grow, its relation to the other cells of the cytocyst changes. For, whereas during the multiplication period, the spermatogones form a solid cyst like the morula of a segmenting egg, the spermatocytes form a hollow cyst resembling a blastula. Under the heading "Spermatocysts" a physical explanation of this has already been suggested. All the spermatocytes assume a definite relation to the surrounding cyst cells. Each spermatocyte now has one pole in contact with the cyst wall, the opposite pole free and next to the center of the cyst. On all other sides they are subjected to pressure from neighboring cells. Consequently they are elongated radially. Transversely to the long axis the outline of the cells is similar to that of the spermatogone in some phases of its development (pl. 15, fig. 70). In the radial axis, they show a flattened base next to the cyst wall, and a free rounded side next to the lumen of the cyst (pl. 13, figs. 35, 36). At this smaller, free pole the spherical nucleus always lies (pl. 13, figs. 35, 36, 37).

The chromatin network resembles that of the spermatogone at rest, but the arrangement of the chromosomes is not so definitely peripheral. An irregular, deeply staining body is also present here. It has a somewhat variable position near the center of the nucleus.

Relatively, the cytoplasm increases more than the nucleus though the latter also exceeds the nucleus of the spermatogone (compare

fig. 35 with fig. 24, pl. 13). A distinct reticular structure with cytomicrosomes can be seen in the cytoplasm of the resting cell. In this respect, as in many others, these spermatocytes differ very markedly from the grandmother stem cell. From the latter up to the spermatocyte, there seems to be a gradual evolution of the cytoreticulum, as even the cytomicrosomes, practically invisible in the grandmother stem cell, seem also to increase in size with the growth of the cell. While the cytoplasm is distinctly granular, there is nothing that could be compared to the yolk of eggs.

The centrosome of spermatocyte.—Although often impossible to see, favorable preparations reveal a centrosome. Its position is somewhat variable (compare pl. 13, fig. 35, *a, b, c, d, e*, with fig. 36, *c*). In the spermatocytes of *Papilio rutulus*, the centrosome, in the resting cell, is imbedded in the nucleus, causing an indentation in the latter, by which it can often be located (pl. 13, fig. 36, *c*; pl. 15, figs. 71, 75). This, however, seems not to be the case in *Grapta silenus* (pl. 13, fig. 35). In *Papilio*, it is usually found on the inner free pole of the nucleus. In material preserved as indicated in the "method," it is a clear unstained vesicle or archoplasmic body very regularly spherical, but sometimes more irregular. In *Grapta silenus*, the centrosome or small sphere has a more variable position (pl. 13, fig. 35).

Giant spermatocytes.—At the end of the growth period, the spermatocytes of the same cyst are remarkably uniform in size, though as already pointed out the size varies greatly in different cysts (compare pl. 13, figs. 29, 30, 31 with figs. 35, 36, 37).

I have never found these giant spermatocytes in the larval testes. They occur in the mature butterfly chiefly late in the season, when, as already shown, the stalked cells and the free cells (pl. 15, figs. 68, 69, 77, 83, 64, 85) are also found. Consequently there seems to be some correspondence between the growth of the spermatocytes and the general maturity of the insect. No such difference exists between the spermatogones of the larva and the adult.

PERIOD OF MATURATION.

Having completed their growth, the spermatocytes enter on their two final divisions to form spermatids. The first indication of approaching division appears in the centrosome (pl. 13, fig. 35, *a, b*).

Even in the resting stage, the centrosome is apparently double (fig. 35, *c*). But in most cases this is not evident (pl. 13, fig. 36, *c*; pl. 16, fig. 90). No changes can, as yet, be discovered in the nucleus.

Prophases of mitosis.—The two centrosomes separate. As yet, there is no evidence of an aster, and there is no spindle uniting the two centrosomes as they separate (pl. 13, fig. 35, *d*). Each centrosome moves around the nucleus through an angle of ninety degrees. The original position of the centrosome is usually in the long axis of the cell, the axis vertical to the tangent at the cell's base or cyst membrane. Consequently the line joining the two centrosomes when they have reached their destination at opposite poles of the nucleus is at right angles to the vertical or long axis of the cell.

Shortly before arriving at their respective poles (pl. 13, fig. 36, *e, f*) or immediately afterward, an aster is developed around each centrosome (pl. 16, fig. 92).

The aster.—Usually both asters are developed at the same time, but a case has been seen where one aster was well developed while the other was not (pl. 13, fig. 37, *a, c*), the centrosome without an aster having apparently not yet reached its destination.

The aster is developed entirely at the expense of the cytoreticulum, the entire cytoreticulum being involved (pl. 16, fig. 92). All fibers of the cytoreticulum converge at the two opposite poles of the nucleus, from which point they radiate in straight lines to the very periphery of the cell.

Owing to the constant eccentricity of the nucleus, near the inner free pole of the cell, the asters are necessarily unsymmetrical, *i. e.*, the rays on one side are very much longer than those on the opposite side (pl. 16, fig. 92; pl. 13, fig. 36, *d, e, f*). The archoplasm theory of the astral rays finds no support here. There is no evidence of a gradual outgrowth from the centrosome or spheres of the astral rays. The microsomes of which they are composed seem smaller than those of the former cytoreticulum.

The study of these asters inclines one more and more to favor the view of an actual splitting of the original cytoreticulum and cytomirosomes. There is a very evident crossing of the astral rays in the larger proximal pole of the cell (pl. 16, figs. 92, 93, 94, 95, 96, 97). But there may be a connection at the periphery of the cell between the long fibers of one aster and a corresponding short fiber of the other. This might produce the crossed appearance, and would not necessa-

rily imply a new formation of the astral rays. In the immediate neighborhood of the centrosome the rays are so crowded as to obscure the centrosome entirely, and cause a dark cloudy effect which can be seen with a magnification too low for the entire aster to be seen.

The centrosome.—In specially favorable preparations, the centrosome can be seen with the highest magnifying power as a minute dot at the focus of the astral system (pl. 16, fig. 111). It is surrounded by an inner circle of microsomes. At an equal distance outside this is a second circle which barely touches the nuclear membrane (pl. 15, fig. 75), and outside this a third circle which intersects the nucleus (pl. 16, fig. 92). Viewed from the pole the aster appears regular and symmetrical, showing the same thickenings of the fibers which give the three-ringed appearance (pl. 16, fig. 112). In these preparations, which are especially clear, the astral rays seem to proceed directly from the centrosome. That being the case, the minuteness of the centrosome, *i. e.*, the central granule, is remarkable. If the centrosome were the result of coalescence of many cytomicrosomes of the ordinary kind, it ought to be larger. It scarcely exceeds a single microsome. It is only in the most favorably preserved material, consequently, that it with its circle of microsomes can be seen. Figure 111 and figure 112 (pl. 16) were drawn from material left for fifteen minutes in normal salt solution, then transferred to a concentrated solution of corrosive sublimate for fifteen minutes more, after which a one-percent solution of acetic acid was added and allowed to act for ten minutes. Before staining in saffranin, it was left for ten minutes in a fifty-percent alcoholic solution of iodine.

The nucleus.—While the asters have thus been fully developed, the nucleus has remained practically unchanged. The distance of the centrosome from the nuclear membrane is usually very constant, the second ring of microsomes apparently touching the nuclear membrane, which is still as prominent as ever. The nucleus is regularly spherical (pl. 15, figs. 78, 86; pl. 16, fig. 92). It is rarely elongated in the direction of the centrosomes (pl. 15, fig. 81); but on the other hand frequently indented at one pole (pl. 15, figs. 71, 75), or at both poles, being compressed laterally (pl. 15, figs. 76, 82). To suppose that this indentation is due to a pushing in of the astral rays as they shoot out from the centrosome is about as absurd a proposition as could well be made—absurd even if no account be taken of the fact that such indentation exists often before the rays are developed (pl. 15, fig. 84; pl. 16, figs. 90, 91).

History of the chromatin.—The chromatin nucleolus has now disappeared, but the nuclear network seems still unchanged. The chromosomes are still irregularly scattered throughout the nucleus; and apparently connected with the linin strands. These are granular as usual.

A change now ensues. The loose wavy linin strands become converted into a well defined system of straight intersecting threads by which the chromosomes are suspended about equidistant from one another. The linin threads seem stretched, and the chromosomes are more regular and more clearly defined than previously (pl. 16, fig. 93).

Formation of the spireme.—What up to this time appeared as a network, has now been converted into a single coil, with the chromosomes arranged like a bead string. The coil is wavy and as it does not lie in the same plane, it is difficult to understand and even more difficult to represent in a drawing (pl. 16, fig. 94).

The thread then becomes closely packed in a solid mass at one pole of the nucleus (pl. 16, fig. 95). The point of condensation seems to vary as it is not always found at the same pole, considering the position of the asters.

This mass then moves into the center of the nucleus (pl. 16, fig. 96). It now consists of a double thread — two parallel rows of chromosomes — which viewed in the right plane has more or less the shape of a horseshoe or imperfect circle. This then elongates (pl. 16, fig. 97) and the result is a second doubling of the thread, making a thread of four chromosomes lying side by side (pl. 16, fig. 98). Very little of the linin is to be seen between the chromatin. The rest of the nucleus is a clear vacuole. I have discovered no definite relation between the position of this chromatin thread and the axis uniting the two centrosomes.

Formation of tetrads.—The chromatin thread now begins to break up, and the fragments separate gradually (pl. 16, figs. 99, 100). Each fragment consists of four chromosomes (pl. 16, fig. 101). As they do not all lie in the same plane, they are not all visible at the same time. Hence some of the chromosomes of a tetrad seem less distinct than others. No clear linin fibers connecting the tetrads are visible.

The tetrads are thus formed from a single chromatin thread doubled twice on itself. There being originally twenty-eight chromosomes, the thread when thus doubled shows seven chromosomes in a line,

but four chromosomes deep. These seven tetrads are then separated (pl. 16, fig. 101).

Formation of diads.—Slight traces of linin fibers can finally be seen connecting the tetrads, and as they separate more and more, the linin becomes more evident. I assume that in the preceding stages, the linin has been contracted and formed an imbedding mass in which the chromosomes lie.

The tetrads remain distinct as tetrads only for a short time. As they separate they are pulled apart into twos, thus making fourteen diads from the original seven tetrads (pl. 16, fig. 103).

Formation of the spindle.—As the diads become more and more distributed throughout the nuclear space, the linin becomes more distinct, while the individual chromosomes of each diad seem to diminish in size (pl. 16, fig. 104). Slight indications of a polar arrangement of the linin strands can now be seen (pl. 16, fig. 105).

The nuclear membrane now disappears. And this occurs while the first undoubted spindle fibers connecting the two centrosomes are being formed (pl. 16, fig. 106). The original outline of the nucleus is still apparent and the diads are distributed about equally throughout the nuclear area. All the linin fibers are now, however, much more distinct; and a definite polar arrangement is clearly seen. The original nuclear area is now slightly elongated in the direction of the asters (pl. 16, fig. 106).

The central part of the spindle is first to be formed. As the remaining fibers are pulled into place, the chromosomes, also, are brought into line with the spindle axis. In the meantime the distance between the asters seems to increase; hence the oval shape which the spindle finally assumes (pl. 16, fig. 107).

It is very evident that the spindle is of nuclear origin, the entire nucleus being gradually converted into a spindle. But that part of each spindle fiber extending from the centrosome to the second microsome ring of the aster is of course cytoplasmic in origin as the entire asters are. This is seen clearly in plate 16, figure 109, where the original nuclear area is still visible.

Prophase of first maturation division.—The chromosomes still apparently grouped in twos when the first signs of spindle formation appear, are at first scattered equally throughout the nuclear area, and are brought into line at the equator of the spindle as the spindle forms. I infer this from such appearances as are represented in

plate 16, figure 107. I feel obliged to consider this stage as the first maturation division for reasons which appear in the description of the second maturation division (see fig. 117).

In this division the chromosomes never form such a perfect equatorial plate as they do in corresponding phases in division of the spermatogonia (pl. 15, fig. 66). In nearly all cases some of the chromosomes are slightly eccentric.

Metaphase.— The number of chromosomes in the equatorial plate is readily determined in these giant spermatocytes. I have repeatedly counted twenty-eight chromosomes. Sections through the equator of the spindles are common (pl. 16; fig. 110). The spindle is circular in transverse section. In this first maturation division, there is no separation into mantle fibers and central spindle. The chromosomes are regularly distributed, a fact which facilitates the counting of them. In many if not in all cases the chromosomes in the equatorial plate show a marked tendency towards a lineal arrangement (pl. 16, fig. 110), more marked in some cases than in others (pl. 15, fig. 72). There is also a distinct radial arrangement of the granules of the cytoplasm, which represent the cut ends of the astral rays (pl. 15, fig. 72; pl. 16, fig. 110). But this is not nearly so marked as in the case of the aster looked at from the pole (pl. 15, fig. 73; pl. 16, fig. 110).

While the chromosomes still occupy the equatorial plate they split into halves.

Anaphase.— The halves of each chromosome then move to opposite poles. The movement of some segments is faster than that of others, the result being that in this phase, also, it is a rare occurrence to find such perfect diasters as in a corresponding phase of spermatogonia mitosis.

They all reach their respective poles where they become crowded closely together into a more or less crescent-shaped mass partly encircling the centrosome (pl. 16, fig. 113; pl. 15, fig. 74). From what I have seen of this in hundreds of cases both in the living dividing spermatocyte and in the best preserved material, I have been led to the conclusion that the chromosome segments approach the centrosome no nearer than the second microsome ring (pl. 16, fig. 109), which is the limit of that portion of the spindle which is formed from the nucleus. I feel certain that this is also the case in the karyokinesis of the spermatogonia (pl. 15, fig. 67).

As the chromosome segments are thus drawn towards their respective poles, they seem still united by the intermediate fibers which present in general outline the form of the original spindle (pl. 16, fig. 113). The connecting fibers seem finer than the original spindle fibers; and the question naturally arises whether the original fibers are not really composite. I have reason to believe that this is the case; for by the application of acetic acid either in stronger solution or for a longer period of time, the spindle can be made to swell out greatly till it is nearly circular (pl. 13, fig. 38). In this case, the number of spindle fibers seems greatly increased. On several occasions spindle fibers have appeared to be split up into two or more strands; and in still other cases they vary greatly in thickness as if some had been split while others had the strands still united.

This may account for the fact that the intermediate fibers seem finer than the original ones. It may suggest, too, that the separation of the chromatin segments is due to a splitting of the spindle fiber. Assuming that each spindle fiber arising from the original nucleus is really composite from a double folding on itself of a fiber like the letter S, the origin of the intermediate fibers as well as the cause of their thinness could be explained. If the two ends of the compressed S contract, then the two half chromosomes belonging to each arm of the S would be separated, leaving only one third of the original fiber as the intermediate fiber.

Telophase.—Some time after the chromosome segments have reached their respective poles, the cytoplasm begins to constrict at the equator, the constriction reaching the spindle before the latter begins to disappear (pl. 16, fig. 114). In the living cell, I have watched this intermediate spindle for hours, and noted the gradual constriction of the cytoplasm, being impressed by the persistence of these intermediate spindles and their remarkable clearness in the living state.

SECOND MATURATION DIVISION.

Soon after the first division is accomplished, the cell prepares for the second division, apparently before a new nucleus has been developed out of the chromosomes. Even before the first division is completed, and while the intermediate fibers of the first spindle still exist, the centrosomes at the poles divide, each forming two small asters which

gradually separate (pl. 16, fig. 114). The chromatin segments are soon drawn in between the two separating asters, and a new spindle is formed (pl. 16, fig. 115). The separation of the new asters is not always equally rapid in the two daughter cells of the spermatocyte (pl. 16, fig. 115). One spermatocyte second order may even be completely divided, while the other has not yet begun to divide (pl. 16, fig. 116). This may take place while the intermediate fibers of the first division still persist. As a result of this there may be one large cell (spermatocyte second order) connected by half of a divided spindle with each of two smaller spermatids, the latter in turn being also connected by a spindle (pl. 16, fig. 116). This is not at all common. Generally the first division is completed before the second begins.

The achromatic figure in the second maturation division is very much like that of the first division; but the chromosomes have a decidedly different relation to the spindle fibers. In the first place, no equatorial plate is formed. In the second place, it is only the central fibers of the spindle that are attached to chromosomes, the chromosomes being strung along these central fibers from pole to pole. The outer fibers of the spindle are entirely devoid of chromosomes (pl. 16, fig. 117). I take this to be due to the fact that division begins before the nucleus is reconstructed after the first division, and the fact that, unlike the first division, the separation of the chromosomes is not preceded by spireme and tetrad formation. Hence there is in this case no division nor splitting of the chromosomes. There is merely a sorting of them in such a way that one half the original number is drawn toward one pole, the other half number toward the other. This of course results in the reduction of the number of chromosomes to fourteen in each cell, one half the somatic number.

Orientation of cell and spindle.—The cytocyst being a hollow sphere, with the spermatocytes arranged in a single layer next to the cyst wall, the cells acquire an outer broad base, and a narrow inner rounded end turned toward the cyst cavity. The nucleus of the cell has an eccentric position, being always located near the inner, narrow end of the cell. When the spindle develops in the first maturation division, it is always placed in the short axis at right angles to the long or vertical axis of the cell and parallel to the cell's base. This results in the division of the spermatocytes into exact halves.

As the cell is about to constrict, however, it assumes a more spherical shape (pl. 16, figs. 112, 113).

The spermatocytes second order thus formed have a more spherical form (pl. 16, fig. 117), and do not remain so definitely related to the surrounding cyst wall. This is especially true of the small forms of spermatocytes, which are by far the most common (pl. 13, fig. 31).

The above account of the maturation divisions is based on the giant spermatocytes (pl. 13, fig. 35-38). But I have the best of reasons for assuming that the processes in these large ones do not differ from those in the ordinary spermatocytes. They, too, show an eccentric nucleus and a similar orientation of the spindle; they show the spireme thread, the early development of the asters, and a similar disposition of the chromosomes (pl. 13, figs. 29, 30, 31). I have given most attention to the giant spermatocytes for the obvious reason that the more difficult details are there more easily made out. The small spermatocytes are considerably more crowded.

SUMMARY AND CONCLUSIONS ON MATURATION.

1. The centrosome of the growing spermatocyte of *Papilio rutulus* appears as a clear sphere, lying close to the nucleus, causing an indentation in it. In *Grapta silenus* it is more variable in position being sometimes close to the nucleus, sometimes halfway between it and the cell periphery. There are two little granules lying side by side.

2. These granules separate and move to opposite poles of the nucleus.

3. Asters are then developed out of the general cytotreticulum, the astral rays extending in all directions to the very periphery of the cell.

4. At the equator, between the two asters, the astral fibers cross one another, suggesting that they are fibers instead of compressed alveoli.

5. There are reasons for suspecting that not only do the centrosomes divide and separate, but that there is also a division of the fibers of the reticulum and cytomicrosomes, the division of the centrosomes being merely the first of a long series of divisions in both cytoplasm and nucleus (fiber and granule) which finally results in the formation of two cells from one.

6. The centrosome is extremely minute, a mere dot at the point of convergence of the astral rays.

7. The centrosome is surrounded by three circles of microsomes, which are so related to the astral rays that they appear like considerably enlarged cytomicrosomes.

8. The nuclear membrane persists long after the asters are formed.

9. The theory of the individuality of the chromosomes is well sustained in these sperm cells.

10. It seems to me that the chromosomes can be traced from the primary spermatogone to the fully developed sperm cell.

11. The nuclear linin forms a network with which the chromosomes are associated.

12. From what I have seen, I believe that the chromatin and linin are intimately related; that the smaller granules in the linin, forming the stainable nuclear network, resemble the cytomicrosomes, and may in certain states of the linin be added to or subtracted from the chromosomes, causing them to vary in size.

13. In a state of nuclear rest, the granules separate from the aggregated chromosome, and become scattered along the linin fiber, which thus appears granular and stainable.

14. On approaching mitosis, the granules all flow together into their respective large stainable chromosomes, which are united by the clear linin substance, appearing now as if stretched.

15. From this stretching there results a single chain of chromosomes arranged around the periphery of the nucleus.

16. This thread becomes folded by sinking together of the whole chromatin substance at one pole of the nucleus.

17. Out of this compact mass there emerges a double thread, spireme, partly doubled a second time.

18. As the second doubling progresses, there results a thread of four series of chromosomes, seven in a line.

19. This thread finally breaks up or rather separates between each chromosome giving rise to seven groups of four chromosomes, tetrads.

20. By continued separation, the four chromosomes of a tetrad are separated into two groups, diads.

21. Tetrad formation here is consequently a temporary conjugation of chromosomes, in which there may be an exchange of constituent granules or ids.

22. The tetrad formation and the following diad formation lead to a gradual orientation of the nuclear material with reference to the asters and centrosomes.

23. The vacuole-like appearance of the nucleus in the spireme stage may be due to withdrawal of the linin into the chromosomes.

24. The spindle is formed from the nuclear contents.

25. The entire transformation of the nucleus, including the spireme and tetrad formation, into a spindle is accomplished after the large asters are fully formed.

26. The nuclear membrane disappears when the first traces of the spindle appear.

27. The occasional indentation of the nucleus where it is in contact with the aster, is not due to the growing out of the astral fibers, nor does it seem proper to say that the spindle fibers grow into the nucleus and become attached to the chromosomes.

28. The chromosomes are gradually drawn into the equator of the spindle as the latter is being formed.

29. The chromosomes divide but as they are spherical, it is absurd to speak of a longitudinal or a transverse splitting of these chromosomes.

30. The tetrads are formed from separation of the four chromosomes lying side by side in the doubly folded spireme.

31. There is in maturation only one case of undoubted division of a chromosome — the splitting of the equatorial plate in the first maturation division.

32. The first maturation division is an equatorial division, one half of each chromosome being drawn toward its respective pole.

33. The second maturation division sometimes begins before the first has been completed.

34. The spindle in the second maturation division differs from that of the first in that only the central fibers are connected with the chromosomes, and in that no equatorial plate is formed.

35. The second maturation division results only in a sorting of the chromosomes, fourteen being drawn toward one pole, fourteen toward the other.

36. It might be thought that the diads in the first maturation division fuse, were it not that sections through the equatorial plate show twenty-eight chromosomes, the somatic number.

37. I infer, therefore, that each spermatid receives one half the

number of half chromosomes or one fourth the original chromatin mass.

38. With reference to the number of chromosomes, the second maturation division is the reducing division.

39. There are two kinds of spermatocytes as there appear to be two kinds of primary spermatogonia, and, as we shall see, two kinds of spermatids.

40. From the above facts, and also from the sorting of the chromosomes in the last maturation division, it must be inferred that, even if the chromosomes are bearers of heredity, in Weismann's sense, the spermatids and consequently also the mature spermatozoa differ in their hereditary qualities.

41. The equal division of the cytoplasm is as scrupulously accomplished here as is the equal division of the nucleus.

42. The theory of the individuality of the chromosomes is well sustained here.

43. There are reasons for believing that the fibers of the spindle are capable of being split up into smaller fibrils, and that these thin fibrils can reunite into larger fibers.

44. The theory of a special archoplasm giving rise to the astral rays is not at all sustained here.

THE SPERMATID.

As there are giant spermatogonia (stalked cells), and giant spermatocytes, so there are giant spermatids. Excepting their size, there is nothing to show that these giant spermatids are abnormal or pathological. I am convinced that their unusual size is not due to an arrested mitosis during maturation. Degenerating gonocysts have already been noted. The spermatogonia they contain often differ in size as three or four to one. As the largest of these may contain two or even four nuclei (pl. 13, fig. 33), I feel safe in assuming that they are cases of arrested mitosis. Their variable degrees of disintegration in the same cyst or in different cysts are sufficient evidence of their pathological condition.

There are, however, also spermatocytes with two or even three nuclei (pl. 17, figs. 122, 123). All these nuclei are well developed and evidently as normal as those where only one exists. The cyto-

plasm also looks normal. The two nuclei are probably not the result of amitosis, but unusual cases of failure on the part of the cytoplasm to constrict after the anaphase of mitosis. Mention has already been made of those cases in maturation, where the second division has begun before the first is completed and where the two spermatocytes second order differ as to the time in which they prepare for the final division. Normally all cells in a cyst, whether spermatogonia or spermatocytes, are found in almost identical phases of mitosis (compare fig. 24-32, pl. 13). But there are not a few exceptions, and these have been of great service in determining the sequence of events (compare fig. 29 and fig. 34, pl. 13). These are, it must be admitted, exceptions, but there is no reason to suspect that their presence indicates pathological material.

Occasionally a spermatid also with two nuclei has been found (pl. 17, fig. 124). It is not absolutely certain that one of the two bodies is not an enlarged centrosome.

The giant spermatids show no trace of these abnormal features. Their great size offers special opportunity to study their structures and their transformation into spermatozoa (pl. 13, figs. 39, 39a; pl. 16, fig. 119-121; pl. 17, fig. 131; compare these with pl. 17, fig. 126-130).

After the last maturation division, the resulting spermatid can be identified by the presence, in the cytoplasm, near the nucleus, of a large spherical body, the so called *nebenkern*.

While the large cytocysts are hollow spheres, with the spermatocytes arranged in a single layer around the periphery, the spermatocysts have cells also in the interior of the cyst (pl. 13, figs. 39, 39a).

I have already shown that, in the first maturation division, the spindle is always so placed as to lie in the short axis of the cell and consequently parallel to its base. This results in an equal division of the cell (pl. 13, figs. 36, 38).

But in the second maturation division no such relation of the spindle exists. The second division often results in the production of one cell related to the cyst wall, and another occupying the hollow cavity of the cyst (pl. 13, figs. 39, 39a). Those in the lumen are usually spherical, while those in relation with the cyst wall are compressed laterally and of course flattened at the base (pl. 13, fig. 39a).

Origin of the nebenkern.—Owing to the fact that, at the end of the first maturation division, the nucleus is not entirely reconstructed

before the second division to form spermatids begins, the second spindle differs markedly from the first as regards its origin. It has already been pointed out that, whereas in the first maturation spindle, (derived wholly from the nucleus) each spindle fiber is connected with a distinct chromosome, in the second division, the spindle consists of a peripheral portion, whose fibers have no connection with chromosomes, and a central portion to which the chromosomes are attached.

I believe these two parts of the spindle have different origins; the outer "mantle fibers," being derived from the persistent intermediate fibers of the first spindle, while the central spindle is derived, partly at least, from the chromosomes. As there are now only fourteen chromosome segments to be drawn to each pole, only a corresponding number of spindle fibers with chromosomes is formed (compare pl. 16, fig. 111 with fig. 117).

This difference in the outer and inner part of the second maturation spindle becomes manifest in the peculiar behavior of the intermediate fibers of this spindle before and after the final completion of the last division. Before the final separation of the two spermatids (pl. 16, fig. 118), the outer portion of the spindle melts away by breaking up into granules. The central fibers persist till the final constriction of the cytoplasm (pl. 16, fig. 118). As the final constriction of the intermediate fibers occurs, the central fibers contract and withdraw into the center of the cell. Here they form a homogeneous archoplasm-like body close to the chromosomes which have not, as yet, expanded into a new nucleus (pl. 16, fig. 119). The outer granular remnant of the mantle fibers now forms a ring around the central archoplasmic portion, as the cytoplasm closes in at the place of constriction (pl. 16, fig. 119). This concentric striation of the contracted spindle, now the "nebenkern," gradually disappears as the central portion assumes more and more the character and appearance of the outer layers.

The resistance of the maturation spindles to reagents is remarkable. In studying the living dividing cells on the slide, I have seen the cytoplasm gradually disintegrate, become vacuolated, and disappear while the spindles remained as perfect as ever. In testing the effects of reagents, too, I have been able to dissolve practically the whole of the cytoplasm of all the cells of the cyst, while the spindles remained, showing a system of connected spindles throughout the whole cyst.

In the case of the second maturation spindle which is transformed

into the nebenkern (pl. 16, fig. 121), there are various reasons for believing that its persistence is due not only to the fact that the central spindle fibers are derived directly from the chromosomes, causing their considerable diminution in size, but also to the fact that chromatin granules are separated off from the chromosomes as they move toward the poles. Occasionally entire chromosome segments seem to be left behind (pl. 16, fig. 119; pl. 13, fig. 31). Often a few straggling chromosome segments are found scattered along the spindle fibers (pl. 13, fig. 31; pl. 16, fig. 118), or else drawn out into stainable threads parallel with the spindle fiber.

It seems to be the presence of this chromatin gradually shed or eliminated along the path as the chromatin segments approach their respective poles, which gives the nebenkern its staying power.

Relation of nebenkern to nucleus.— I have been led to believe that in mitosis of the spermatogonia, the connective fibers are reabsorbed by the nucleus as it expands, and that it does not merely disintegrate. The nucleus in those cases is active, fully re-formed after each mitosis as the cell also seems to grow. The nucleus becomes large occupying a considerable part of the cell.

At the completion of the last maturation division, too, the nucleus is partly re-formed, but it is different from the original nucleus. It never becomes so large and rich in nucleoplasm as the nuclei of the spermatogones (compare fig. 24 with fig. 39a or with fig. 32, pl. 13). I consider this failure on the part of the nucleus to regain its original size and to acquire a larger supply of karyolymph as evidence of its declining functional activity. This is suggested partly by the fact that no further mitosis is to occur.

In my work on *Limulus* (Munson, '98) and also in that on the tortoise (Munson, '04), I was led to conclude that karyolymph is produced inside the chromatin masses especially in the chromatin nucleoli of the oocyte; and that it is secreted or extruded by these chromatin masses. Thus it accumulates between the chromatin granules, causing the whole nucleus to expand. The large expanded state of the nucleus is therefore, in my mind, evidence of nuclear activity. It may be worth while considering whether the comparative inertness of the chromatin mass, after the last maturation division, is not responsible for the persistence outside the nucleus, but in close contact with it, of the nebenkern. The lagging behind of some chromosomes may be another evidence of this inertness.

Numerous cases, like that represented in plate 13, figure 32, have led me to suspect that in these cases, the large vacuole containing a mitosome derived from the intermediate fibers of the preceding division and the homologue of the nebenkern, is due to a failure on the part of the nucleus to expand and occupy the space which it normally would occupy. I believe that such an expansion would normally take place, and the mitosome consequently be reabsorbed by the nucleus (pl. 13, fig. 32, *b*). Even if in this case the mitosome has a centrosome in its interior as is suggested by the central, condensed portion (pl. 13, fig. 32, *a, b*), the normal expansion of the nucleus would cause it to fill the vacuole in which the mitosome lies and crowd the centrosome into the narrow space between the nucleus and cytoplasm. This narrow space would have the form of a crescent if the kinoplasm surrounding the centrosome were sufficient in amount to spread out as the nucleus expanded.

Considering the mechanism of mitosis, the relative position of the centrosome, chromosomes, and intermediate fibers in the anaphase of mitosis, we should hardly expect *a priori* to find the centrosome associated with the nebenkern derived from the intermediate fibers of the spindle, and, indeed, I find they are often separate bodies (pl. 13, fig. 39). They may lie at opposite poles of the nucleus.

In those spermatids which retain a fixed relation to the cyst wall, already referred to, there is a definite orientation, also, of the nucleus and nebenkern. The nucleus is always nearest the periphery of the cyst, or at the fixed pole of the cell, while the nebenkern is always nearest the free end of the cell. The nebenkern consequently occupies the position which the nucleus has in spermatocytes of the first order, the nucleus having now changed its position from the inner free narrow end to the outer fixed pole of the cell (pl. 13, fig. 39). This, of course, cannot be seen in those cells that lie free in the lumen of the cyst. But all these spermatids later acquire definite relation to the cyst wall, and then they all show this relative position of nucleus and nebenkern (pl. 14, figs. 40, 46).

Relation of centrosome to nucleus and nebenkern.—Immediately after formation of the spermatid, the chromatin segments form a compact mass often slightly crescent-shaped lying between the aster and the intermediate fibers which give rise to the nebenkern (pl. 16, figs. 119, 121). As the nucleus develops, it expands more toward one side than the other, and consequently seems to move out from

between the centrosome and nebenkern, causing these bodies to approach each other. In plate 13, figure 39a, are seen traces of the original mantle fibers of the second maturation spindle, the central spindle having condensed, as described, into a nebenkern. The nucleus is here already expanded and its eccentricity caused by this expansion is also evident. Compare, also, the other spermatids in this cyst (pl. 13, fig. 39) with those in figure 39a. It is here seen that the nebenkern, nucleus, and centrosome rarely lie in the same axis. Writers who have observed this almost invariably attribute the effect to movement of the centrosome, the latter being described as changing its position and moving around the nucleus till it ultimately is thought to become permanently located between the nebenkern and nucleus or even to become imbedded in the nebenkern. I shall show that that is not true in this case; for as the spermatid elongates into the spermatozoon, the nucleus becomes again crowded in between the centrosome and the nebenkern, and the three bodies — centrosome, nucleus, and nebenkern — all assume their fixed position in the long axis of the growing spermatozoon in the order named (pl. 14, figs. 40, 46). Thus the centrosome finally becomes located at the head pole of the nucleus, the nebenkern invariably at its tail pole. This is just what could be predicted from the relation of the three at the close of the second maturation division.

Accidental bodies.— The subject of spermatogenesis has been unnecessarily complicated by writers who describe two or three other bodies under special names such as mitosome, acrosome, and chromophile bodies. In a very few instances I have seen in the neighborhood of the nucleus a minute archoplasmic body resembling a second smaller nebenkern (pl. 17, figs. 133, 134). But I interpret it either as a slight remnant of the first maturation spindle, owing its persistence perhaps to a stray chromatin granule accidentally left behind in the first mitosis, or as a condensed remnant of the astral rays or archoplasm of the centrosome. I have also seen a small body resembling a centrosome in the neighborhood of the nebenkern (pl. 17, figs. 128, 130), which led me to believe that the centrosome divides, one centrosome taking its position at the head pole of the nucleus, the other at the tail pole. A somewhat similar body is also occasionally seen inside the nebenkern. I regard these now as fragments of chromatin left behind in the last maturation spindle, which either become imbedded in the nebenkern as it forms, or are left just

outside developing a vacuole of their own like a pseudonucleus. These as well as the first body are rare exceptions destined ultimately to disappear, and consequently take no part in the formation of the spermatozoon. To give such temporary, accidental bodies a name can only lead to confusion.

DEVELOPMENT OF THE SPERMATOZOON.

With the preceding orientation of the essential parts of the spermatid—centrosome, nucleus, nebenkern, and cytoplasm—in mind, the transformation of the spermatid into a spermatozoon can be expressed in a few words. The spermatozoon is simply a greatly elongated spermatid, consequently a greatly elongated and compressed cell.

The originally spherical spermatid (pl. 13, figs. 39, 39a) early begins to elongate. It becomes irregular, wedge-shaped, and pointed (pl. 17, fig. 125–132). The giant spermatids arising normally from the giant spermatocytes, are almost from the beginning in relation with the cyst wall (pl. 13, fig. 39). They all sooner or later acquire such a relation (pl. 14, figs. 40, 46).

That part of the cytoplasm in which the nebenkern is located, grows out into the tail of the spermatozoon. The cells are now so oriented that the tail grows toward the center of the cyst (pl. 14, fig. 40). As this elongation continues, the cyst bulges out at one point, toward which the growing tails are directed (pl. 14, fig. 41). There is evidently considerable lateral pressure. Growth of the cell is in the direction of the free pole of the cell, which owing to its relation to the enclosing cyst cell and the surrounding spermatids is necessarily the tail end.

The axial filament.—While the cell is thus being compressed into the elongated form, there grows out from the nucleus a fiber which penetrates the nebenkern, and extends apparently along the path made by the original intermediate fibers. It soon emerges from the cytoplasm at the pointed tail end as a long flagellum (pl. 17, fig. 133–135).

Originally there may be three or four of these fibers; but they finally unite; and at the point of union a knot or small enlargement sometimes appears. This is apt to be mistaken for a centrosome. The point of union varies, and consequently the knot is sometimes seen in the center of the nebenkern (pl. 17, figs. 133, 139), at the distal or

tail pole of it (pl. 17, figs. 134, 135), or close to the nucleus (pl. 17, fig. 143). At the point where this axial filament is attached to the nucleus, there is frequently a stainable body, which is easily mistaken for a centrosome. But as it stains like chromatin and is without doubt inside the nuclear membrane, I look upon it as an aggregation of chromatin, caused by the convergence at that point of the fibrils which together constitute the axial filament.

That the axial filament is composed of several threads seems supported also by the fact that the constituent fibrils sometimes separate at various points along their course through the tail of the spermatozoon (pl. 17, figs. 140, 141).

It is not at all improbable that the cytoreticulum is continuous with the nuclear reticulum in other cells, and it ought not to be considered improbable, *a priori*, that the axial filament may have a similar connection with the nucleus.

In my work on the ovarian egg of *Limulus* ('98), I removed the germinal vesicle from the living egg and found that thread-like processes adhered to the nuclear membrane as if the broken cytoplasmic fibers of the reticulum were really continuous with the lining of the nuclear network. Other appearances in the sectioned material of those oocytes, led me to the same conclusion. The phenomena of mitosis, too, support that view.

In my work on *Clemmys* ('04) I have described a division of the cytoplasm into a central portion and a peripheral portion. These two zones, which I also found in the oocyte of *Limulus*, I believe are present in most cells. I have called the line separating them, the cyto-coel.

The cyto-coel in the spermatid is the line between the cytoplasm and the nebenkern. At first the material of the nebenkern fills the inner space completely. But I feel convinced that if the material of the nebenkern could be removed entirely, there would remain some slight trace of a reticulum in the vacuole thus formed. This is supported by the fact that the material of the nebenkern, in numerous instances, does not fill the space entirely (pl. 17, fig. 125). In those cases traces of a reticulum within the nebenkern vacuole can be seen. The fibrils resemble in appearance those which constitute the axial filament.

My conclusion is that the axial filament of the spermatozoon represents the greatly compressed cytoreticulum of that portion of the cell

lying within the cytozoel. As the spermatid elongates into the spermatozoon, the cortical cytoplasm of the spermatid becomes elongated into a narrow tube, the lumen of which is bounded by the original cytozoel. Into this lumen, the cytoreticulum of the central portion of the cell becomes compressed till it looks like a mere fiber. Thus, if the cell represented in figure 125 (pl. 17) were pulled out lengthwise to many times its original length would there not result some such an effect as in the cell represented in figure 143?

Comparing the mass of the spermatid with the mass of the fully developed spermatozoon (pl. 17, fig. 149), there is no ground for supposing that the transformation of the spermatid into the spermatozoon involves an actual increase in the quantity of protoplasm. The comparative inertness of the nucleus at the close of the last maturation division and ever afterward (already considered) would not justify us in assuming that this is a growth period primarily in the history of the spermatozoon; but rather that it is a transformation period of those organs that are already present and fully grown in the spermatid stage. This transformation in all the organs of the cell is merely an elongation such as could be brought about, doubtless, by prolonged equal lateral pressure.

Fate of the nebenkern.— My interpretation of the spermatozoon as being in a sense a tube formed by the cortical cytoplasm, and containing the axial filament representing the greatly attenuated central cytoreticulum of the original spermatid, is supported by some other considerations to be noted regarding the fate of the nebenkern.

The nebenkern has nothing to do with the middle piece of the spermatozoon. Originally the nebenkern always occupies the position where one would naturally expect the middle piece to develop. In this position it remains, too, for some time. Its size apparently varies with the size of the cell. Compare the small spermatids (pl. 14, fig. 40; pl. 17, fig. 126–130) with the giant spermatids (pl. 14, fig. 46; pl. 17, figs. 131, 138). It can be readily seen even in unstained sections. Its staining reaction is cytoplasmic. Its first appearance reminds one forcibly of the cytoplasm of the grandmother stem cell. Like it, too, it is remarkable for its resistance to nuclear stains. It stains, as does the grandmother cell, in saffranin and acid fuchsin. In the large spermatids, especially, it is often many times the size of the nucleus, and apparently perfectly spherical. At first, homogeneous and resembling archoplasm, it gradually becomes more granular, and as the

cell becomes more and more elongated and compressed, it assumes an oval form (pl. 17, figs. 142, 143).

Finally it leaves the nucleus and moves down along the axial filament (pl. 17, figs. 140, 141). It is now a mass of granules suspended in a fluid, which collects at points along the axial filament giving rise to swellings or oval vacuoles at regular intervals (pl. 17, figs. 140, 141, 143, 144, 145). In fresh living material of teased testis, these spherical vacuoles can be seen distributed at regular intervals along the lumen of the tail of the spermatozoon. In this mature state, they look like clear vacuoles. I take these to be temporary accumulations of cytolymph in the lumen of the tail surrounding the axial filament. The granules of the disintegrating nebenkern are evidently dissolved finally in this cytolymph and carried along with it through the cytoceol of the tail of the spermatozoon.

In this respect, the nebenkern behaves very much like the yolk nuclei described by me in the egg of *Clemmys*. It shows many of the chemical and physical properties of those bodies. I came to the conclusion that the yolk nuclei in the oocyte of *Clemmys* represent a kind of metaplast arising in the neighborhood of the nucleus, and by the influence of the nucleus and cytoplasm combined; that after flowing throughout the cytoplasm chiefly in the cytoceol, it is gradually absorbed by the living substance of the egg as food. The nebenkern originates essentially in the same way, but indirectly through the spindle, being partly of nuclear, partly of cytoplasmic origin. Its fate, too, is essentially the same, namely, absorption as food.

In the larger vacuoles formed by the disintegrated nebenkern and combined with cytolymph, the separation of the axial filament into its constituent fibrils can sometimes be seen (pl. 17, fig. 141). I take this to be another proof of my assumption that the axial filament is not a mere fiber but a greatly compressed and attenuated reticulum belonging to the central portion of the original spermatid, but obscured in that stage of the cell by the substance of the nebenkern. That cytolymph may accumulate within the area corresponding to the cytoceol, is suggested by the appearances represented in plate 17, figures 125, 136, 137, 138, and 143, where a clear space is seen around the nebenkern. I do not believe that these are artefacts due to shrinkage, but that they are essentially similar to the vacuoles seen in the living material, along the axial filament of the spermatozoon.

The centrosome.—During the earlier stages of transformation of

the spermatid into the spermatozoon, the centrosome is found close to the nucleus. The latter becomes spherical and expands into a vesicle, with the chromatin arranged chiefly around the periphery (pl. 16, fig. 125). The centrosome becomes unusually prominent at this time. The astral rays have disappeared; and the centrosome is now a comparatively large body occupying the center of a vacuole, which almost equals the nucleus in size (pl. 17, fig. 134). Its position with reference to the nucleus is extremely variable, except that it is always close to the nucleus. In the majority of cases, it occupies the anterior pole of the nucleus (pl. 17, figs. 132, 134, 136). But it may also be found to the right or to the left of it (pl. 17, figs. 133, 135, 137), or even at the posterior pole (pl. 17, figs. 140, 141). Isolated cases like this are apt to be misleading as one might be easily led to conclude that the axial filament grows out from the centrosome at this point, and that later the centrosome is converted into the middle piece of the spermatozoon.

I have already described the origin of the axial filament. Assuming a continuity of the cytoreticulum with the nuclear reticulum for reasons already given, there is no reason why the axial filament should not be connected with the centrosome even though the latter is located at the anterior pole.

The variable position of the centrosome I have already explained as being due not to migration of the centrosome around the nucleus, but to lateral growth of the nucleus as it is reconstructed after the last maturation division. The subsequent history of the spermatozoon shows that wherever the centrosome may be located (pl. 14, figs. 40, 46) at first, it ultimately comes to occupy the anterior pole of the nucleus (pl. 14, figs. 43, 44, 48, 54, c.).

Changes in growth of spermatozoon.— In the earlier stages of transformation and growth of the spermatozoon, the posterior or tail end is the only part which lengthens out, the centrosome, nucleus, and nebenkern being always found near the anterior end close to the enclosing cyst wall (pl. 14, figs. 40, 41, 46). As the spermatozoa increase in length, the cyst is transformed into a greatly elongated, hollow cylinder, with the elongated sperm cell arranged parallel within.

When this transformation of the cyst is accomplished, the head end of the sperm cell begins to elongate, possibly from the increased lateral pressure (pl. 14, fig. 49). At the same time the nebenkern disappears

in the manner described above. The nucleus then moves away from the anterior end of the sperm cell which seems at the same time to sever its connection with the surrounding cyst wall. The cyst then becomes spindle-shaped; and the nuclei of the sperm cells now occupy a zone near the largest part of the cyst.

The nucleus.—Previous to this, the nucleus has been comparatively large and spherical after its reconstruction. Now after the cells have severed their connection with the cyst wall, and the nuclei have moved down from the anterior end, it becomes small and compact. The chromatin takes the form of a crescent, which partly surrounds a large clear vacuole in the center of which there is a stainable body, about the size of the centrosome of earlier stages. The horns of the crescent-shaped nucleus sometimes point forward to the anterior end of the cell, sometimes backward, and sometimes laterally. Hence the stainable body, which I take to be the centrosome (though it may possibly be a nucleolus), is either anterior or posterior or lateral to the nucleus (pl. 14, fig. 49).

Development of the head nurse-cell.—After the separation of the sperm cells from the surrounding cyst, and the transformation of the latter into a compressed cylinder with pointed ends, that cyst cell which occupies the anterior end of the cyst begins to grow rapidly and from now on continues to expand. Its cytoplasm which up to the present time has been so flattened out as to be scarcely visible, now accumulates around the nucleus, being in part relieved of the lateral pull which must exist in the early stage of the spermatocyst (pl. 14, fig. 49). The nucleus, also, increases in size and assumes a more spherical form.

The anterior end of all the sperm cells now becomes attached to this one head nurse-cell. It is in connection with this, that the later development of the head end of the spermatozoon is accomplished. As soon as this new connection between the sperm cells and the head nurse-cell is established, the nuclei of the sperm cells leave their central position and move up close to the nurse cell, at the same time losing their crescent form and becoming small compact deeply staining bodies (pl. 14, fig. 50).

At this time it is difficult to determine the position of the centrosome, as the sperm cells are now extremely elongated and compressed, looking hardly larger than a hair.

Lateral cyst cells.—As the head nurse-cell develops, the other

cyst cells also increase in size. The nuclei in them become large and distinct, fairly rich in chromatin. This forms a loose network.

As one of these lateral cyst cells grows, it gradually surrounds the bundle of sperm cells, and finally coalesces on the opposite side, thus forming a ring or tube (pl. 14, fig. 52, *c. c.*). Hence beginning at the head nurse-cell (pl. 14, fig. 43), there is a single row of these tubular cells gradually diminishing in thickness, but broadening out antero-posteriorly toward the tail end of the cyst. In one or two instances one of these cells has been seen at the extreme end of the cyst, but these are rare exceptions.

HISTORY OF THE HEAD OF THE SPERMATOZOON.

The spermatozoon has now acquired its definite length, and the tail probably is completed. The head of the spermatozoon is now so intimately related to the head nurse-cell, being imbedded in its cytoplasm, that these have to be considered together. While the head nurse-cell is growing rapidly, the original nucleus of the spermatozoon (pl. 14, fig. 50) elongates enormously (pl. 14, fig. 44). The remarkable regularity in the length of these nuclei, their perfectly parallel arrangement, their homogeneous appearance, and their uniform staining in nuclear stains are very striking. I have found it difficult to make my drawings as diagrammatic as these sperm heads, taken together, appear under the microscope.

The acrosome.— At this stage (pl. 14, fig. 44), we find again evidence of the position of the centrosome. The anterior end of the cell has become greatly attenuated and elongated. This has penetrated the spongy cytoplasm of the head nurse-cell till it nearly reaches the nucleus, the nurse cell having at the same time developed greatly. Near the middle of this anterior portion of the sperm cell, the centrosome occupies a little vacuole in a slight enlargement of the cytoplasm. All these taken together form a row running parallel to the anterior ends of the greatly elongated nuclei (pl. 14, figs. 43, 44, 48, 54). They, too, are imbedded in the head nurse-cell. The elongated nuclei take the green of the Biondi-Erlich triple stain; the centrosomes are eminently cytoplasmic, being made distinct by orange G and acid fuchsin and saffranin.

Transverse section through the elongated nuclei is represented in

plate 14, figure 47. A similar section through the centrosomes is represented in plate 14, figure 42. The large nucleus of the large nurse cell sometimes occupies an eccentric position, and hence it is visible in transverse sections. The loose arrangement of the cyto-reticulum of the head nurse-cell is seen to the left in figure 42.

FURTHER GROWTH AND MODIFICATIONS.

It seems that the chromatin substance within the greatly elongated nucleus of the spermatozoon can shift its position. Instead of being pulled out lengthwise as in figure 44 (pl. 14) it may condense near the base of the head nurse-cell as in figure 43. I infer that this represents a more advanced stage than figure 44. This same condensation appears in figure 48; a stage still more advanced.

The mature stage is probably that represented in figure 54 (pl. 14).

In all of these cases the row of centrosomes is visible. In the later stages (pl. 14, fig. 48) the centrosome appears elongated, the vacuole in which it lies having also assumed an oval form.

The greatly elongated nucleus shows distinctly that it is not homogeneous, but composed of granules, probably the chromosomes considerably reduced (pl. 14, fig. 48).

The discharge of mature spermatozoa.—When a spermatocyst is mature, the lateral cyst cells gradually dissolve. This takes place just as the cyst is about to enter the vas deferens. The spermatozoa then escape in a bundle into the vas deferens. Occasionally they are discharged into the follicle of the testis one by one (pl. 14, fig. 51). In that case they show a tendency to associate in bundles forming rings (pl. 14, fig. 53). These appear occasionally to become imbedded by their heads into an unripe gonocyst causing a gradual degeneration of those cells (pl. 14, fig. 45). In the vas deferens the spermatozoa are frequently found in bundles, and even still attached to the partly disorganized head nurse-cell. They usually separate at once, on entering the vas deferens, and probably under the influence of its secretions become wavy and coiled—the only evidence of movement I have seen (pl. 14, fig. 55).

The elongated head now becomes considerably shortened and bent into the form of the letter S, the centrosome forming an enlargement of the anterior filament. In many cases the tail forms a loop just back

of the head (pl. 17, fig. 149); or else the head is considerably more contracted, with a single bend and a slight enlargement at the anterior end — the head piece formed by the centrosome.

In figure 151 (pl. 17) is represented a group of ripe spermatocysts from a teased testis. In such fresh material one occasionally finds a mature spermatocyst discharging its spermatozoa (pl. 17, fig. 152).

GENERAL SUMMARY AND CONCLUSIONS.

1. Each testis originally resembles a simple gland with a duct and a terminal enlargement containing the germinal mass.

2. The germinal mass is surrounded by a layer of cells resembling an epithelium, which early forms septa dividing the original follicle into four approximately equal follicles which, when the gonocysts are formed, differ considerably in size. These four follicles correspond to the four ovarian tubes of the female butterfly.

3. The lining epithelium becomes early pigmented, giving the fully formed testis a bright red appearance.

4. Outside the pigmented layer there is a thick tunica propria. As the right and left testes develop independently, they approach each other and become united in a double organ.

5. The entire testis is surrounded by a thin tough tunica adventitia.

6. The original germinal mass has the appearance of a syncytium out of which there is differentiated in each testis one or more large grandmother stem cells with protoplasmic processes connected with a mother branch cell.

7. Surrounding the grandmother stem cell, its processes, and the mother branch cells, are nuclei probably derived from the original syncytium, the cortical nuclei.

8. The primary spermatogonia are derived from the mother branch cells which divide regularly by mitosis, one half remaining attached to the grandmother cell and continuing thus to divide, the other half being separated and constituting the primary spermatogone.

9. When a primary spermatogone is pinched off in mitosis, one or more of the cortical nuclei accompany it and furnish the "anlagen" of the cyst cells.

10. The grandmother stem cell does not divide by mitosis.

11. There is at least one, but I have seen as many as four grandmother stem cells in a testis.

12. In the later larval and adult stages, the primary spermatogones can be found only in the immediate neighborhood of the grandmother stem cell.

13. The primary spermatogones divide and form secondary spermatogones to the number of one hundred and fifty cells contained in a cyst.

14. The cortical nucleus constricts off with the primary spermatogone, divides by mitosis once or twice, and gives rise to the cyst.

15. In the spermatocyst stage, one of the cyst cells develops into a large head nurse-cell, in the body of which the heads of the mature spermatozoa are imbedded.

16. The various stages of development of the sperm cell can be traced in their regular order only by choosing a grandmother stem cell as the starting point, thus: (*a*) grandmother stem cell, (*b*) mother branch cell, (*c*) cortical nuclei, (*d*) primary spermatogone, (*e*) gonocyst, (*f*) cytocyst, (*g*) spermatocyst.

17. In those follicles having no grandmother stem cell, the above series cannot be found, as the primary spermatogone is here wanting and no new ones are produced.

18. The grandmother stem cell gives rise to new spermatogones, and consequently even late in the season, new spermatogones are produced.

19. This butterfly is sexually mature in the pupa state a month or two before the last molt.

20. The secondary spermatogones are spherical and fill the gonocyst.

21. Near the end of the period of multiplication, probably just before the last spermatogone division, the spermatogones become conical with the large nucleus at the broad external pole.

22. The chromatin becomes massed at the inner pole of the nucleus leaving the remainder of the nucleus a large vacuole. It seems to correspond to the synapsis of writers, but nothing indicates the pseudo-reduction generally attributed to it.

23. After synapsis the chromatin fills again the nuclear vacuole, and appears now as a very delicate loose network of straight intersecting fibers. This is preceded by a spireme.

24. From this nucleus, there is developed a spindle with all the chromosomes arranged very regularly in the equatorial plate. The chromosomes split, form a diaster, and in the anaphase move simul-

taneously in line to their respective poles. Here they soon develop a new nucleus, and the cytoplasm constricts in the usual way.

25. The mitosis of the secondary spermatogones is quite similar to that of the mother branch cell and the primary spermatogones.

26. After the last division of the secondary spermatogones with its peculiar prophases, the cells, now spermatocytes, enter on a period of growth.

27. The cytocyst containing growing spermatocytes differs from the gonocyst in being hollow, the spermatocytes being arranged in a single layer and definitely oriented with reference to the cyst wall.

28. Besides the ordinary small spermatogones derived from the mother branch cell, there are giant stalked spermatogones in the testes of the mature butterfly, especially late in the season. These differ from the ordinary ones in that they are stalked and also in that the period of growth precedes the period of multiplication.

29. After being loosened from its stem, the giant spermatogone gives rise to giant spermatocytes and these to giant spermatids.

30. The end product of the two kinds seems to be similar, as I have found no trace of giant spermatozoa, unless it be those that I have described as forcing their heads into gonocysts and apparently causing their disintegration.

31. Like the synapsis stage of the spermatogones, the spermatocytes have a definite orientation with reference to the cyst wall, the outer pole of the cell being larger than that facing the central cavity. But, unlike the spermatogones, the spermatocytes have the nucleus in the inner narrow end of the cell.

32. In the first maturation division the spindle is transverse or parallel to the cyst wall. In the second maturation the spindle is vertical to the cyst wall, hence one cell resulting from the division lies freely in the cyst cavity.

33. In the prophase of the first maturation division, the centrosome lying in an indentation of the nucleus divides, each of the two resulting centrosomes moving to an opposite pole of the nucleus where asters are formed.

34. A general division or splitting of the cytomicrosomes and cytoreticulum simultaneously with the division and separation of the centrosomes seems not at all improbable.

35. While the nuclear membrane is still intact, and while the asters are fully developed, the chromatin inside the nucleus under-

goes changes as follows: (*a*) the chromatin is massed at one side of the nucleus; (*b*) from this there develops a spireme surrounding the nucleus as a single wavy thread; (*c*) this is then drawn together again at one pole; and, from this, there emerges a double thread partly doubled again on itself — a double thread bent in the form of a horse-shoe; (*d*) by elongation, this second doubling is accomplished; (*e*) this thread separates or segments between the chromosomes giving rise to seven tetrads; (*f*) the tetrads then divide into two, giving rise to fourteen diads.

36. The spindle is developed at this time entirely from the nucleus; but that part of each spindle fiber extending from the centrosome to the second microsome ring is cytoplasmic.

37. The first spindle fibers to appear are the central ones, extending directly from centrosome to centrosome.

38. At first the chromosomes are scattered evenly throughout the nuclear space where the spindle is being formed. But later they are drawn together from all sides; and by the time the spindle is formed, they occupy the equator of the spindle.

39. There are twenty-eight distinct chromosomes in the equatorial plate. As this is the somatic number, the preceding tetrad and diad formation must have some other significance than that usually ascribed to it. It may be a process of conjugation of chromosomes, an interchange of ids, or a phase in the arrangement of the chromosomes for their final division in the metaphase of the mitotic process.

40. The twenty-eight chromosomes split into halves, each half being drawn to its respective pole by a single spindle fiber.

41. As the chromosomes are spherical, and equal in size, it is useless to talk about longitudinal and transverse splitting.

42. That the chromosomes are not bivalent is to be inferred from the fact that there are twenty-eight chromosomes, the somatic number in the equatorial plate of the first maturation division.

43. The second maturation division follows soon after the first. Occasionally the centrosome has divided and asters are formed before the first maturation division is completed.

44. The spindle of the second maturation division, differs from the preceding in that it has: (*a*) mantle fibers formed apparently from the intermediate fibers of the preceding division and consequently devoid of chromosomes; and (*b*) a central spindle developed from the chromosomes, each central spindle fiber being connected with one chromosome.

45. In the second division the chromosomes form no equatorial plate; they are dragged along one by one to each pole, fourteen being drawn to one pole and fourteen to the other.

46. At the close of the second maturation division, the intermediate fibers, especially those of the central spindle, having more or less chromatin granules adhering to them, persist as the nebenkern. The nebenkern consequently is a mitosome.

47. The nebenkern does not form the middle piece of the spermatozoon nor the inner sheath of the axial filament, but persists for a considerable time at the base of the nucleus, after which it is gradually absorbed, moving bodily down along the axial filament forming vacuoles at regular intervals along its path.

48. The axial filament is not a single fiber, but a greatly attenuated central cytotreticulum in connection with the nucleus.

49. The centrosome finally takes up its position at the head of the nucleus; as the latter elongates into the mature spermatozoon head, the centrosome with the anterior part of the sperm cytoplasm, becomes imbedded in the cytoplasm of the head nurse-cell as the acrosome.

50. I have seen nothing that could positively be identified as a middle piece.

51. The mature spermatozoon is a greatly compressed and elongated cell, with its nucleus correspondingly elongated, with its fourteen chromosomes arranged in a row, and the centrosome at the anterior end.

HISTORICAL SURVEY OF THE LITERATURE.

Malpighi is one of the first to give an account of the sexual organs of insects. He studied the silkworm and described the male genital organ of the larva. It was some time before the ovary was discovered, the red pigment of the testis making it more easily seen with the naked eye.

Swammerdam was unable to find the ovary; but he described the testis of *Vanessa urticae* as two kidney-shaped bodies. These he claims could not be found again in the pupa, as he found only a red body occupying about the same position.

Bessels ('67) gives a correct explanation of this in calling attention

to the fact that in *Bombyx*, the right and left testes, which in the larva are separated (as in *Papilio rutulus*), are united in the pupa into one double body as it has been described in the present work.

In an anatomical treatise, Lyonett gives a description of the testis of *Cossus ligniperda* and states his opinion that from this body either the male or the female genital organ is developed, hence suggesting the similarity of the two during the early stages.

Herold ('15) was one of the first to distinguish between the male and the female genital organs. He conjectured that the sexes are differentiated in the early embryo, as he found them well differentiated in the larva just escaped from the egg. Bonnet also claimed to have seen the ovary of the silkworm developed in the larva as completely as in the adult moth.

The first discovery of spermatozoa is often attributed to Louis Ham (1677); but more usually Leeuwenhoek is given credit for this discovery. I find, however, in an old volume by Henry Baker (1743), this interesting statement which needs no comment: "At the beginning of the year 1678, Mr. Nicholas Hartsoeker, of Rotterdam, declared in a Treatise of Dioptries, by him then published, that it was twenty years since he first began to examine the Semen masculinum of several living creatures by the help of Microscopes; that, as far as he knew, he was the first person who had ever done so; that he had found in such semen infinite numbers of Animalcules, most exceedingly minute, almost in the Shape of Tadpoles or young Frogs; and that he had made this Discovery known to all the World in the 30th of the Ephemerides Eruditorum, printed at Paris in the same year 1678.

"Mr. Leeuwenhoek, in the 113th of his Epistles, dated January 1678; is very angry at this claim; and asserts that he himself first discovered the Animalcules in Semine, and sent an account thereof to the Royal Society in November 1677, as he proves by the Philosophical Transactions published in December 1677, and in January and February 1678; Nay, he further affirms, that Letters had past between him and Mr. Oldenburg on this Subject in 1674."

Besides the extensive studies of Leeuwenhoek and Hartsoeker, the subject was studied also by Spallanzani, and at the beginning of the nineteenth century by Prevost and Dumas ('24). All these early observers studied merely the external form and appearances of the spermatozoon. They seem to have been especially interested in its movements and its minuteness as compared with the animals with

which they were familiar; for the spermatozoa were regarded as real independent animals and often looked upon as parasites. Attempts were even made to classify them, some regarding them as Infusoria (Ehrenberg), others as worms. Thus to quote the same author: "It is wonderful to consider the minuteness of these little animals, and particularly the amazing slenderness of their Tails; which must, notwithstanding, be furnished with as many Joints as the Tails of larger creatures, since they are able to move them with great Agility; and, besides, every one of these Joints must be provided with its proper Muscles, Nerves, Arteries, and Veins; and also with Fluids circulating thro' them, and supplying them with Nourishment, Strength, and Motion. In short, the mind loses itself in contemplating a minuteness beyond all human conception; tho' Reason tell us, it certainly must be."

Notwithstanding this conception of spermatozoa as animals, *samenthierchen*, as they were called, no effort seems to have been made to trace their origin and development. For this, their methods were altogether too crude. The true idea of the spermatozoon being a cell could not, of course, be entertained before the announcement of the cell theory. The very able discussion of this theory by Schleiden ('38) and Schwann ('39) gave a new impetus to the study of tissues, though the cell nature of tissues was already known through the researches of Robert Brown, Unger, and others.

It was not before the year 1840 that it became known that these were not animals in a true sense having an individual life of parasitic worms, but rather were gradual formations from undifferentiated cells.

Duvernoy gave them the name of spermatozoids or zoosperms. R. Wagner ('36) is thought to have published the first work dealing especially with spermatogenesis. He studied the spermatozoa of birds. Peltier ('38), Hallmann ('40), Dujardin ('37), and von Siebold ('36) made more or less important contributions also.

That branch of cytology which we call spermatogenesis really began with the first work of Kölliker ('41). He described the spermatozoa of several invertebrates, replacing the name *samenthierchen* with *samenfäden*. He showed that they are developed from the cells of the testis, but he thought that the nucleus was primarily involved. He was doubtless influenced by the theory of a cytoblastema of Schwann which assumed that the nucleus or even the nucleolus is first to arise,

the rest of the cell being precipitated much as crystals are formed. Our present conception of the cell dates from 1860 when Max Schultze gave us our present definition of a cell. Even as late as 1885, Kölliker seems to have believed that the head of the spermatozoon proceeds from one part of the nucleus and the tail from another part of it.

On the other hand, it was maintained by many at that time that the nucleus disappears and has nothing to do with the formation of the spermatozoon. Zenker thought that to be true in the case of isopods, and Remak ('54) at about the same time thought it true also of amphibians. A similar view was held by Metschnikoff ('68) in the case of crayfish, and by Balbiani ('69) in the spermatozoa of Aphis. The spermatozoon of amphioxus was thought by Langerhans ('76) not to develop from the nucleus, but from a body at the side of the nucleus possibly what we now know as the nebenkern.

Says Sabatier ('90): "Les grains de nucléine du noyau deviennent vésiculeux et forment une groupe de vésicules dites nucléaires, qui en se fusionnant et en perdant leur affinité pour les colorants nucléaires, constituent la coiffe céphalique en forme d'ancre. Elles représentent ce qui reste du noyau qui s'est donc altéré et a perdu ses caractères nucléaires. La dégénérescence du noyau comme noyau est donc un des traits principaux de la spermatogénèse des Locustides."

On the other hand, Bessels ('67) speaking of Lepidoptera (the forms related to the subject of the present work) says: "Wir haben es hier mit einer bildung der spermatozoon aus den zellkerns zu thun deren entstehung ausserhalb der kerneliegenden theile des zelleninhalts wie das Weismann vermuthet, ich in abrede stellen muss."

We thus have had what might be called respectively the nuclear and the cytoplasmic view of sperm formation. But several early observers were able to show the presence of the nucleus in the spermatozoa supposed to be devoid of them, thanks, doubtless, to improved methods and technique. Nussbaum ('84) and likewise Gilson ('85-'88) showed the presence of the nucleus in Crustacea.

But even considerably earlier than these discoveries, our present view with regard to the function of the nucleus and cytoplasm was not without its advocates. Among the first to insist on the presence of both nucleus and cytoplasm in the formation of the spermatozoon was Henle ('66). Even as early as 1865, Schweigger-Seidel ('65) concluded that the spermatozoon is an entire cell which has merely been transformed. It is interesting to note that he even made out

three divisions — the head derived from the nucleus, the middle part and the tail, both derived from the cytoplasm.

We owe to La Valette St. George the most satisfactory theory — that at least which is now most generally accepted by writers on spermatogenesis. To him also we are indebted for the nomenclature now most generally used, and that which I have adopted in the present work. In a series of articles (“Ueber die genese der samenkörper,” ’67, ’78, ’86, ’87) he has given as a general law, the following succession of cells with their names, here quoted from Waldeyer: —

1. Spermatogonien = anfangszellen.
2. Spermatozyten = produkten der ersten teilung.
3. Spermatoziden = endzellen = produkte der letzten teilung.
4. Spermatozomen = direkten umformungsprodukten der endzellen = samenfäden.

In the present work it has seemed desirable to define more clearly the term spermatogonia and spermatozyte, for it is useful to distinguish the primary spermatogonia (those before division begins) and the secondary spermatogonia (those which finally form the growing spermatozyte). It has also seemed desirable to distinguish more definitely than did La Valette St. George between the cyst containing spermatogonia, and that containing spermatozytes; hence the terms gonocyst and cytocyst introduced in this work.

Recent literature.—The following statement by Biondi (’85) expresses the condition of the subject at the present time: “Noch vor wenigen jahren war es nicht schwierig sich nach dem stande unserer damaligen kenntnisse über die spermatogenese eine bestimmte und klare vorstellung zu verschaffen. Heutzutage können wir das nicht mehr sagen; durch zahlreiche neue arbeiten sind zwar unsere kenntnisse bezüglich dieses vorganges ausserordentlich vermehrt, aber unter bedeutender einbusse an klarheit und einigkeit in den anschauungen.” In the body of this paper, it has been suggested that much of this confusion is due to the naming of accidental and transient bodies. This tends to obscure the most essential fact that the spermatozoon is merely a greatly elongated cell with centrosome, nucleus, and cytoplasm.

One of the bodies which causes unnecessary confusion is the so called nebenkern. The first discoverer of this body is supposed to be La Valette St. George. According to Wilson (’02) it was first described by Bütschli (’71). La Valette called it the nebenkörper.

The principal question concerns its nature and origin, and the part it plays in the formation of the sperm. Says Wilson ('02): "The confusion that has arisen in this difficult subject is owing to the fact that the spermatid may contain, besides the nucleus and centrosomes, no less than three additional bodies, which were endlessly confused in the earlier studies on the subject. These are the *Neben-kern*, the attraction-sphere idiozome (Meves) and the chromatoid nebenkörper (Benda)."

La Valette first came to the conclusion that the nebenkern originates in the cytoplasm, a view which was later accepted by Nussbaum ('84) in the crayfish, by Keferstein ('66) in pulmonates, by Lenhossek ('98) in the rat, — by Bütschli ('71), Balbiani ('69), and Metschnikoff ('68) in arthropods, and by Auerbach ('96) in Paludina.

On the other hand it has been held by many that the nebenkern has a nuclear origin. Van Beneden and Julin ('84) attributed such an origin to it in *Ascaris*, Grobben ('78) in decapods, and Lee ('88) in *Sagitta*. Attempts have been made to homologize the nebenkern with the yolk nucleus of eggs, and consequently it has been thought to have a similar origin. So far as I have been able to ascertain there is no similarity between the two as regards origin, but the history of the two is precisely the same, namely, absorption as food.

It appears that the majority of writers now take the view that the nebenkern is a remnant of the achromatic spindle after the last division of spermatocytes to form spermatids. This is the conclusion which my preparations have led me to adopt. The evidence is so strong that there is scarcely any room for doubt.

Platner ('86) has shown that the nebenkern of authors has meant different things; that it consists of two parts, the centrosome at the pole of the spindle, and the remnant of the achromatic spindle which he names, very appropriately it seems to me, the *mitosome*. Prenant ('87) in a series of studies on pulmonates and reptiles has arrived at the same conclusion; also Meves ('97a) in *Salamandra*. Henking ('91) attempts to show that in *Pyrrhocoris*, the nebenkern is derived from a yolk-like substance existing in the cytoplasm and especially surrounding the nucleus, which gradually aggregates into a sphere after karyokinesis. I have seen no evidence of yolk bodies such as these in *Papilio rutulus*. Wilcox ('96) professes to have seen, in *Caloptenus*, evidence of the yolk-like substance forming at least part of the nebenkern, and the same seems to be inferred in Paulmier's ('99) work on *Anasa*.

Another important question which has attracted considerable attention, and given rise to much confusing discussion is the relation of the centrosome to this nebenkern and the part which either of these plays in the formation of the spermatozoon. Says Wilson ('02): "The nebenkern sometimes takes a definite part in the formation of the tail envelopes and of the acrosome (insects) but in many cases it seems to be wholly wanting." In *Papilio* it takes no such part, and the fact that in many cases it is wholly wanting is easily understood when its ultimate fate in *Papilio* is considered. He says further: "The idiozome is in some cases an undoubted attractionsphere derived from the aster of the last division, and at first containing the centrosome as shown by Calkins, ('95) and Erlanger, ('96, 4) in the salamander and guinea pig, Meves ('96, '99), and in *Helix* according to Korff ('99), though in later stages the centrosomes usually pass out of the body of the idiozome. In some cases the idiozomes of adjoining cells remain for a time connected by bridges of material representing the remains of the spindle, and hence corresponding to a nebenkern (*e. g.*, salamander, Meves, '96), and the distinction between nebenkern and idiozome here fades away."

From my observations already recorded it is self evident that some of Wilson's ('02) statements are misleading when he maintains that in insects the nebenkern takes a definite part in the formation of the tail envelopes and acrosome. Neither can the broad statements of La Valette St. George ('85) and Bütschli ('71) be strictly true when they maintain that in insects, the nebenkern forms the middle piece. As I have shown that the nebenkern finally dissolves in the cytoplasm, as Prenant ('88) also found in pulmonates, the general statement that the nebenkern forms the headpiece as maintained by Keferstein ('66), La Valette St. George ('67), Metschnikoff ('68), Duval in molluscs, Grobben ('78) in decapods, and by Nussbaum ('84) is not confirmed by the facts in *Papilio*.

I have shown that it originates primarily from the intermediate spindle fibers of the last maturation division and that its persistence seems to be due to the elimination of chromatin granules during the last maturation division, which if it were not for the maturation divisions themselves would strongly suggest that it has something to do with reduction. This has also been suggested by van Beneden and Julin ('84) in *Ascaris*. Both Waldeyer ('87) and Weismann ('64) have favored such an interpretation.

In what has become regarded as a typical spermatozoon, the following parts are usually thought to be present: (1) acrosome, head, middle piece, tail; in the tail there is thought to be (2) axial filament, inner tail envelope, outer tail envelope. From what parts of the spermatid do these various parts arise? Wilcox ('96) found that in *Caloptenus* the middle piece arises from the centrosome. Paulmier ('99) says: "A strict application of the term *nebenkern* (defined as a body formed from the spindle fibers and yolk granules) would include the acrosome, shortly to be described; for that also in insects appears to have a common origin with the part forming the tail sheath." Of the centrosome, Paulmier says: "It thus seems quite certain that in *Anasa* it does not move around the nucleus, as Wilcox ('96) describes in *Caloptenus*, and as I have myself observed in *Papilio*. Later however, a centrosome appears in the *nebenkern*, lying on the nuclear membrane."

It seems unfortunate that Paulmier has yielded to the temptation of drawing some of his most important conclusions, not from *Anasa*, the subject which he studied primarily, but from *Papilio*, a form which he appears to have examined only incidentally. My observations on *Papilio rutulus* do not confirm these conclusions.

There is a very extensive recent literature on the question of tetrad formation, reduction, and maturation. Henking ('92), Henneguy ('98), Wilcox ('95), and Paulmier ('99) have discussed this literature in their interesting studies. It is so well known by students of cytology, that I feel justified in omitting any discussion of it. Observations on reduction are stimulated by the theory of Weismann. To argue extensively about the longitudinal and transverse splitting of the spherical chromosomes of insects such as I find in *Papilio* only suggests that facts are in danger of being suited to the theory rather than the theory to the facts.

Mention must be made here of the so called Verson's cell of the silk worm which the above authors do not mention, and which is evidently so closely related to the grandmother stem cell of the present work.

Erico Verson ('89) first described in *Bombyx mori* an enormous cell, located in the peripheral end of each follicle. According to him, it has an eccentric nucleus and the cytoplasm spreads out radially. The cell divides amitotically and gives rise to all the formed elements of the testis. He regards it, consequently, as the true spermatogone.

Cholodkovsky ('94) likewise found a large cell in the blind end of the testis follicle of *Laphira*, which he took to be the spermatogone from which all the contents of the follicle originate. He saw radial processes proceeding from this cell in which numerous nuclei were imbedded. It contained, not a single nucleus, but several, which he took to be the result of mitotic division. He found the same cell in various Lepidoptera, Hemiptera, and Neuroptera.

Spichardt ('86) found in the testis of *Liparis dispar* a giant cell with scattered nuclear substance. This nuclear substance, derived from the nucleus, was thought to generate new nuclei at the periphery.

Erlanger ('96) came to the conclusion from his own observations that the cell divides amitotically; but he regards it as a supporting cell.

Toyama ('94) found the same cell in the silk worm and other Lepidoptera, both in the testis and (as he thought) also in the ovary. He found, in studying the early stages that originally both the ovary and the testis have but one lumen. This finally becomes indented and in each compartment thus formed, there is a cell which acquires a connection with the rest of the germ cells. He concluded that it has nothing to do with the formation of germ cells, and that it is primarily a supporting cell. In this Cholodkovsky did not agree.

Vom Rath ('93) basing his opinion on Verson's description, considered the cell a degenerating sex cell. Somewhat earlier, both he and Ziegler considered it as a supporting cell whose nucleus multiplies amitotically. They regarded the small peripheral nuclei not as daughter cells of the large cell, but as sister cells of the spermatogones.

Finally La Valette St. George ('97) gives his opinion, from his study of the silk worm, *Bombyx mori*, that in the testis as in the ovary, these cells have nothing to do with the multiplication of spermatogonia or of oogonia. According to him, they serve as supporting cells. They are not mother cells, but sister cells of the primordial germ cells. He says: "Wenn ich mich über die herkunft diese zelle äussern soll, so kann ich nichts anders annehmen als dass sie als eine umgewandelte spermatogonie aufzufassen sei." It does not appear, however, from his plates that he had studied the matter very carefully. Even if they were supporting cells, their absence in some cases would be as difficult to explain as if they were primary spermatogones. I have shown that in *Papilio*, the cell in the ovary resembling the grandmother stem cell, is the growing egg.

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EXPLANATION OF PLATES.

ABBREVIATIONS.

| | |
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| <i>a. f.</i> axial filament. | <i>n.</i> nucleus. |
| <i>ac.</i> acrosome. | <i>n. c.</i> nerve cord. |
| <i>al. c.</i> alimentary canal. | <i>n. k.</i> nebenkern. |
| <i>arch.</i> archoplasm. | <i>p. ct.</i> primary spermatocyte. |
| <i>br. c.</i> mother branch cell. | <i>p. g.</i> primary spermatogone. |
| <i>c.</i> centrosome. | <i>p. l.</i> pigmented layer. |
| <i>c. c.</i> cyst cells. | <i>pt. m.</i> tunica adventitia. |
| <i>cn. l.</i> tunica propria. | <i>s. ct.</i> secondary spermatocyte. |
| <i>cy. c.</i> cytocyst. | <i>s. g.</i> secondary spermatogone. |
| <i>ep.</i> epithelium. | <i>sp. c.</i> spermatocyst. |
| <i>f.</i> follicle. | <i>spz.</i> spermatozoon. |
| <i>g. c.</i> gonocyst. | <i>st.</i> spermatid. |
| <i>g. m. s.</i> grandmother stem cell. | <i>st. c.</i> stalked cell. |
| <i>h.</i> heart. | <i>t.</i> testis. |
| <i>h. n.</i> head nurse-cell. | <i>tr.</i> trachea. |
| <i>m.</i> muscle. | <i>v. d.</i> vas deferens. |
| <i>m. n.</i> cortical nucleus. | <i>x.</i> free stalked cell. |

PLATE 12.

- Fig. 1. *Papilio rutulus*, reduced $\frac{1}{4}$.
Fig. 2. Larva of *Papilio rutulus*, reduced $\frac{1}{4}$.
Fig. 3. Pupa of *Papilio rutulus*, reduced $\frac{1}{4}$.
Fig. 4. Grandmother stem cell with branch cells and cortical nuclei.
Fig. 5. Longitudinal section of adult testis.
Fig. 6. Transverse section of pupa of *Papilio rutulus*.
Fig. 7. Dissected abdomen of adult Papilio showing testis and vas deferens.
Fig. 8a. Transverse section of adult testis, showing right and left testis and the four follicles of each.
Fig. 8b. Transverse testis of *Grapta silenus*.
Fig. 9-23. Stages of developing spermatocysts from teased testis.

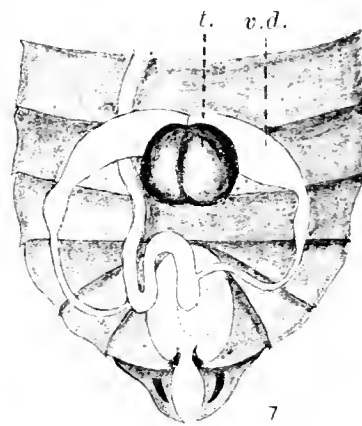
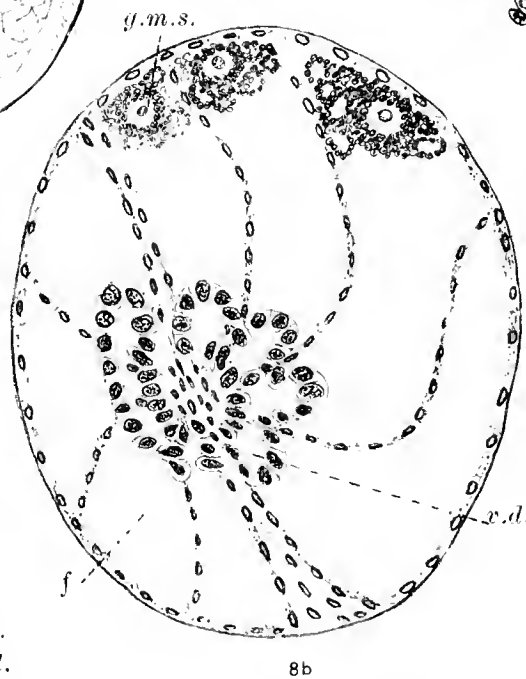
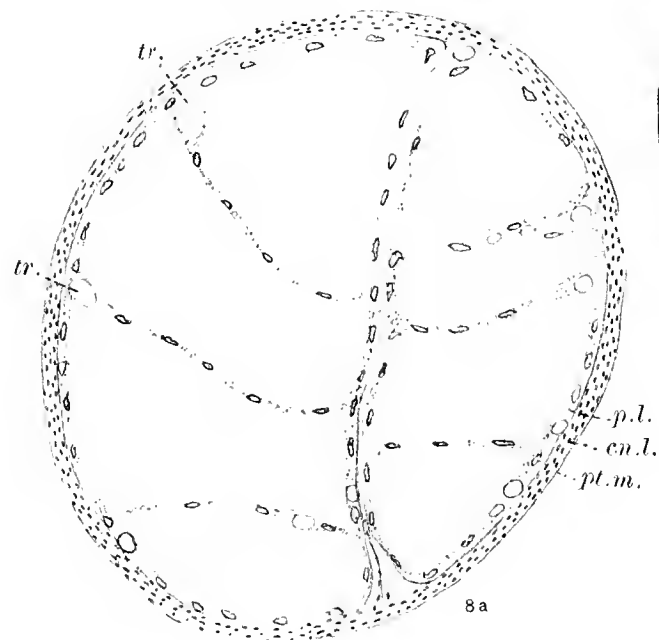
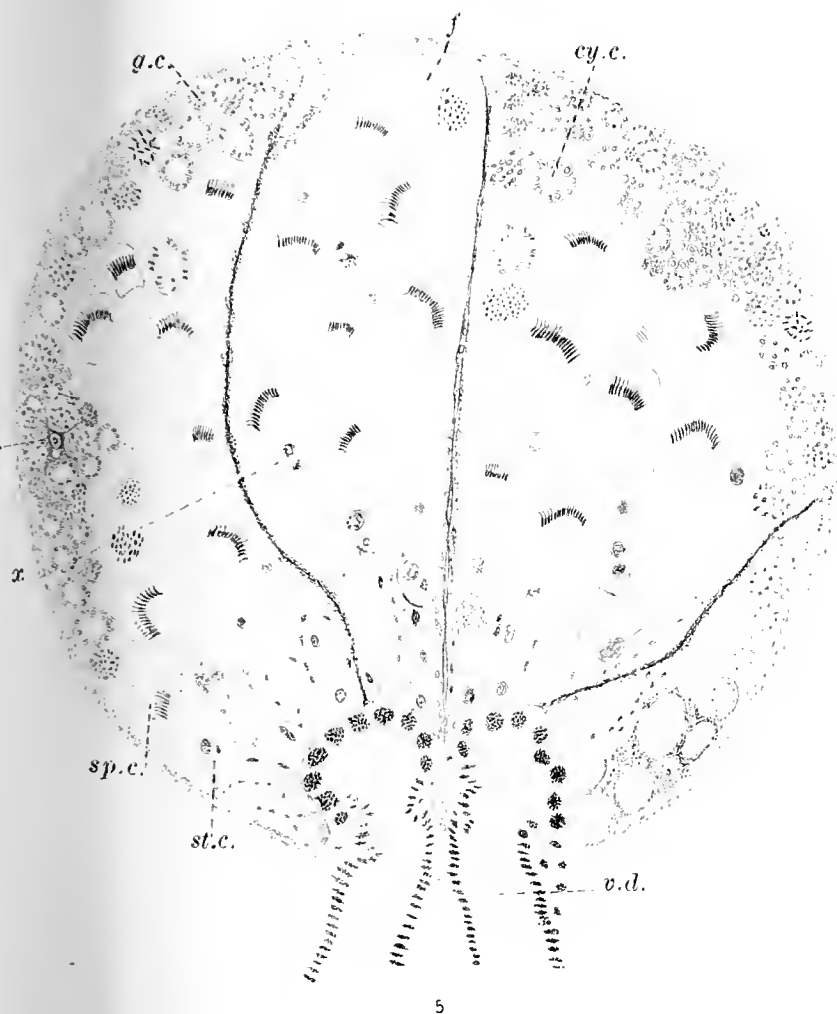
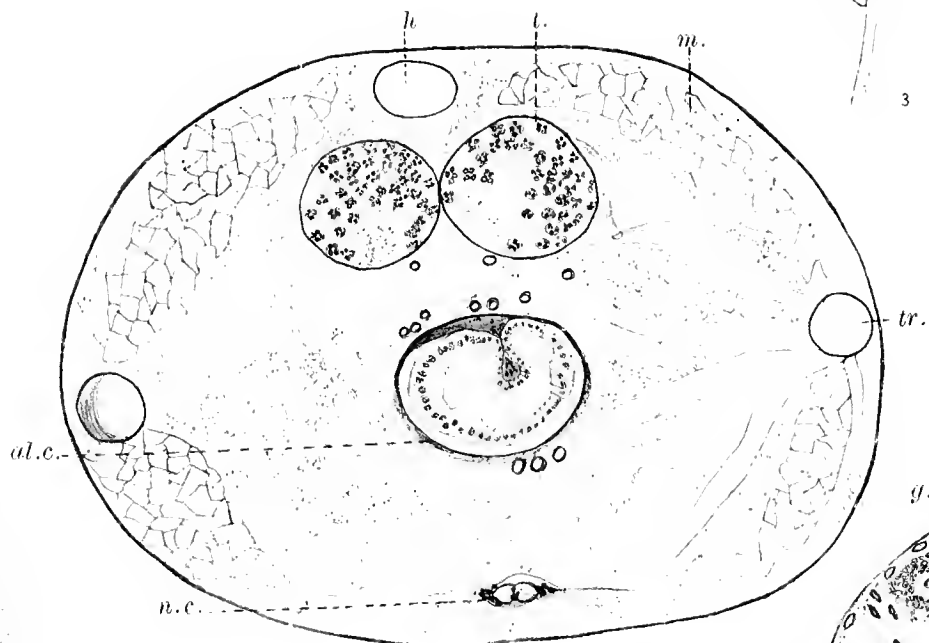
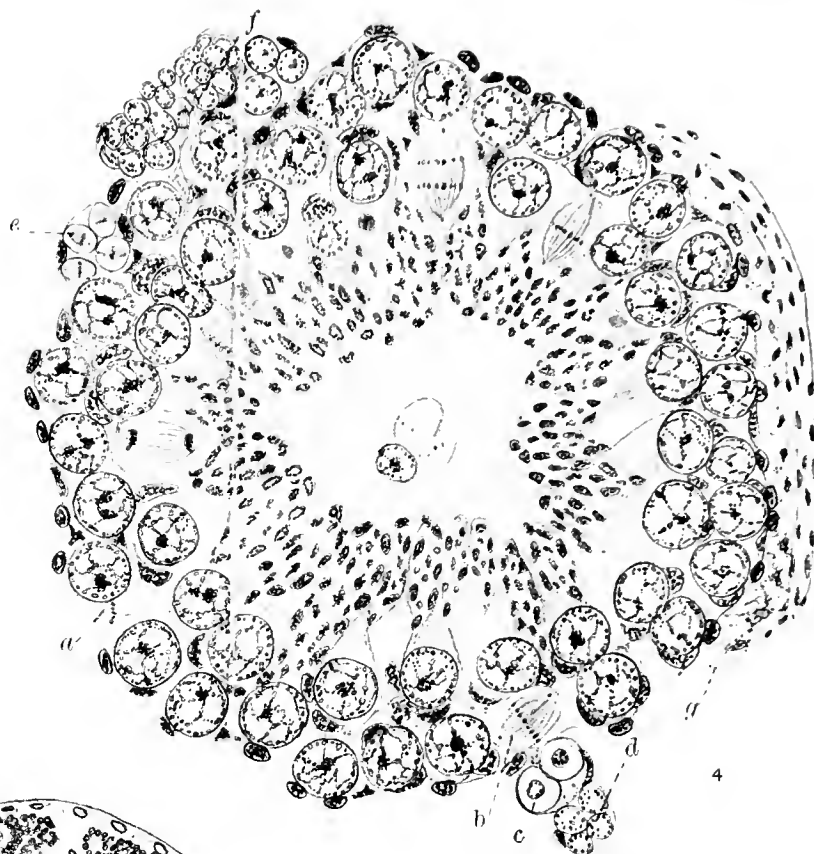
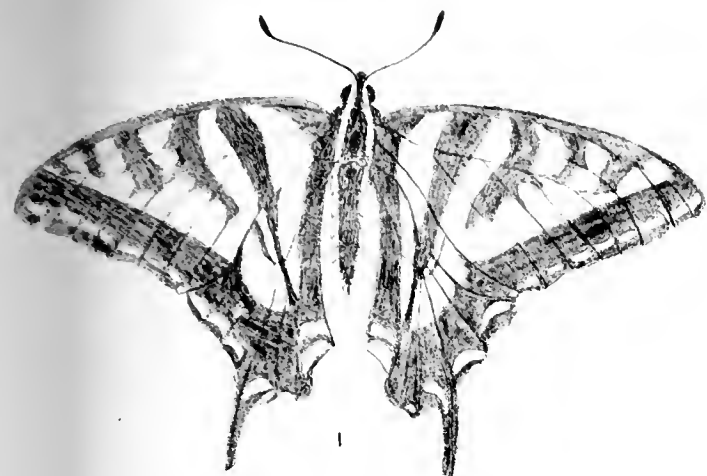
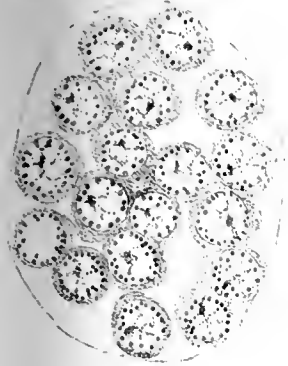


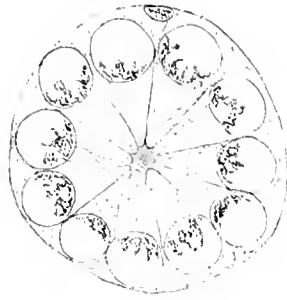
PLATE 13.

Drawn with camera, obj. $\frac{1}{12}$, oc. 1, oil immersion.

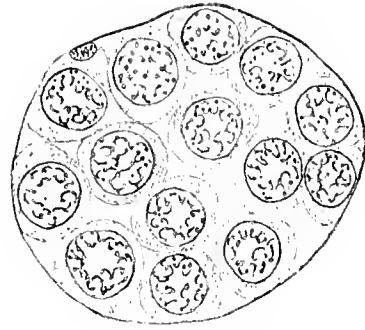
- Fig. 24. Gonocyst, showing spermatogones at rest.
- Fig. 25. Gonocyst with spermatogones in synapsis stage.
- Fig. 26. Gonocyst with spermatogones in the spireme stage.
- Fig. 27. Gonocyst showing spermatogones just before the formation of spindle.
- Fig. 28. Gonocyst with dividing spermatogones, anaphase.
- Fig. 29. Gonocyst with spermatogones much older than the preceding, in various phases of mitosis.
- Fig. 30. Gonocyst with spermatogones in metaphase of karyokinesis.
- Fig. 31. Gonocyst with spermatogones in telophase of karyokinesis.
- Fig. 32. Gonocyst with spermatogones showing pseudonebenkern.
- Fig. 33. Degenerating spermatogone.
- Fig. 34. Various phases of mitotic division of spermatocytes first order.
- Fig. 35. Resting spermatocytes first order of *Grapta silenus*.
- Fig. 36. Spermatocytes preparing for the first maturation division.
- Fig. 37. Spermatocyst with prophases and metaphases of first maturation.
- Fig. 38. Spermatocytes in first maturation division, telophase.
- Fig. 39. Part of spermatocyst showing giant spermatids.
- Fig. 39a. Newly formed spermatids showing nebenkern.



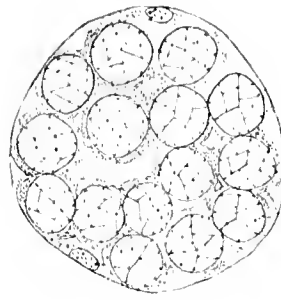
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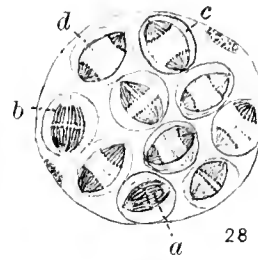
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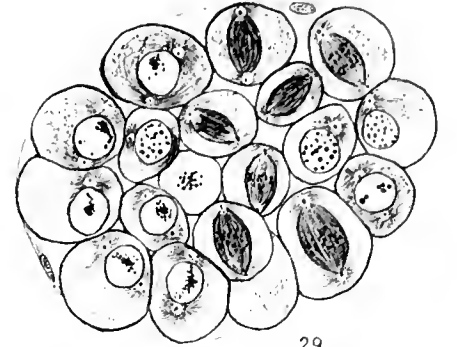
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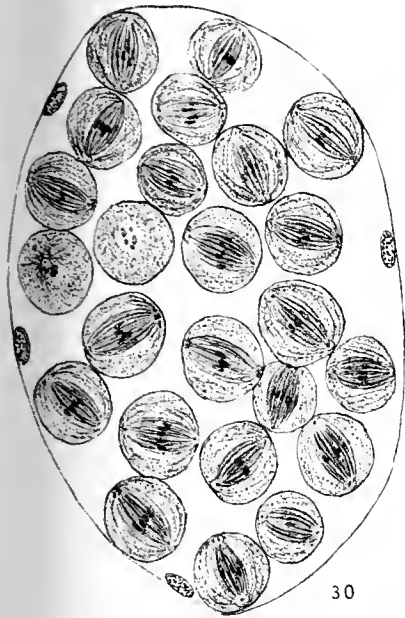
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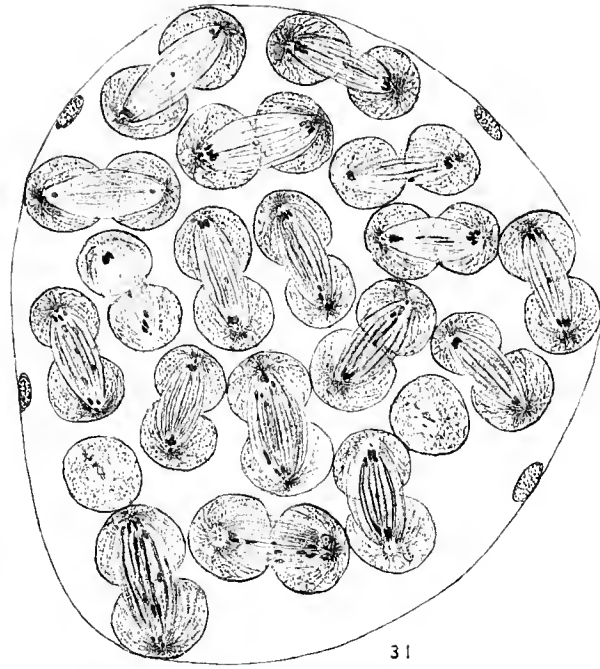
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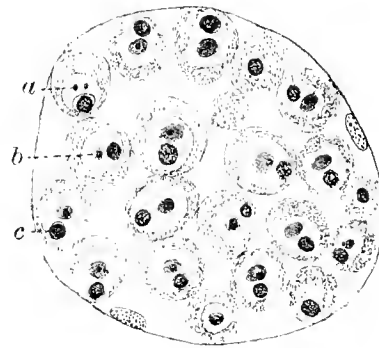
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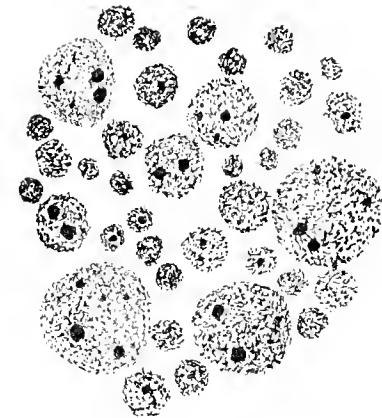
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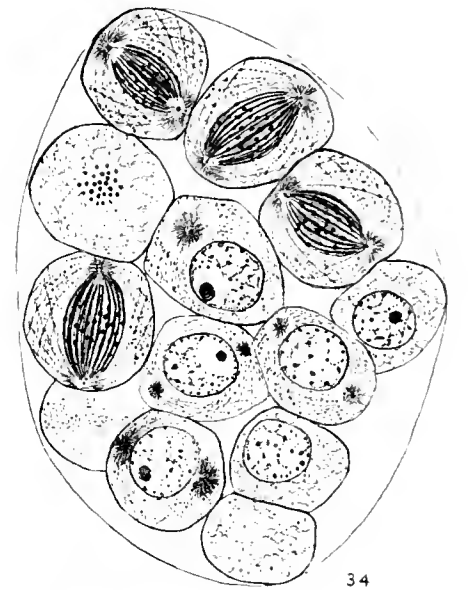
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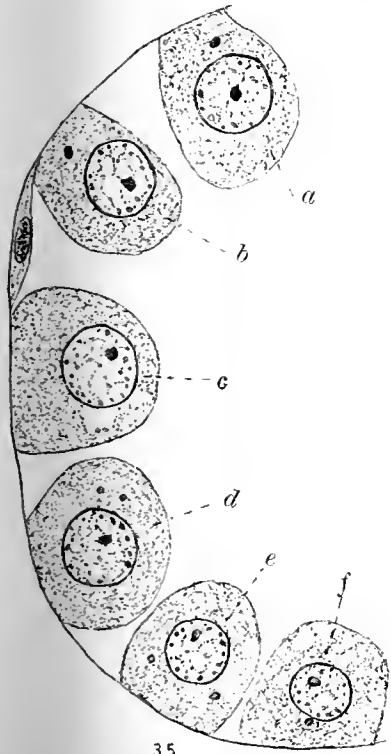
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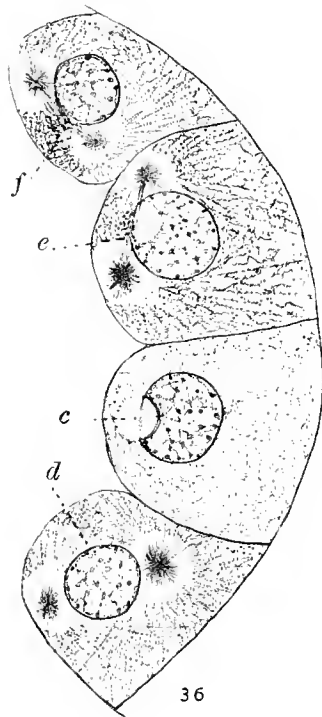
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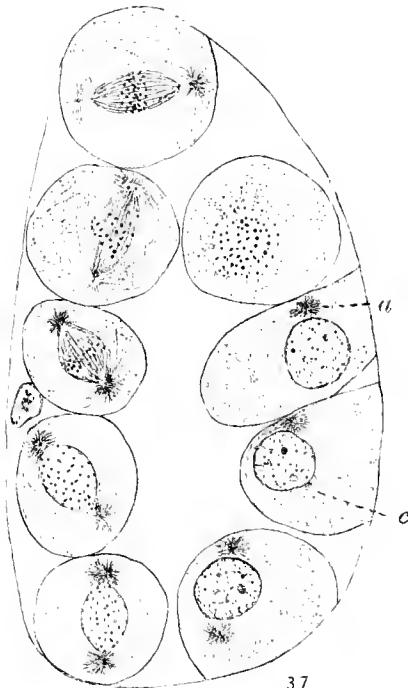
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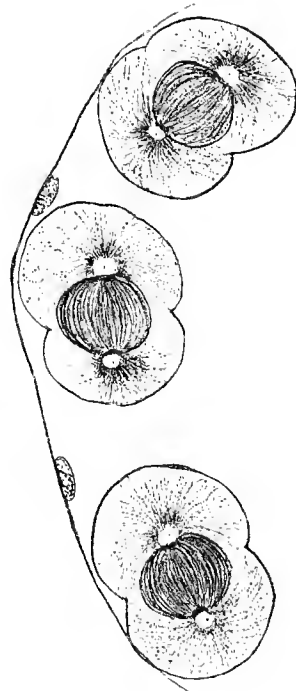
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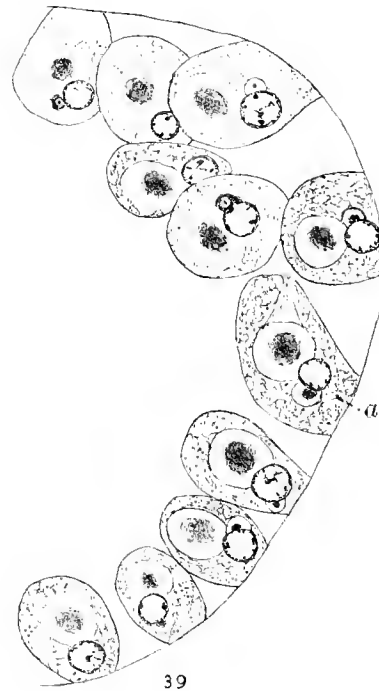
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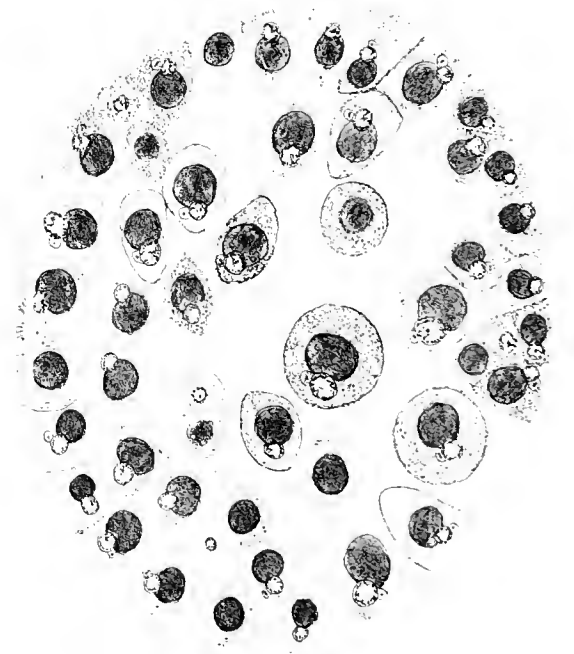
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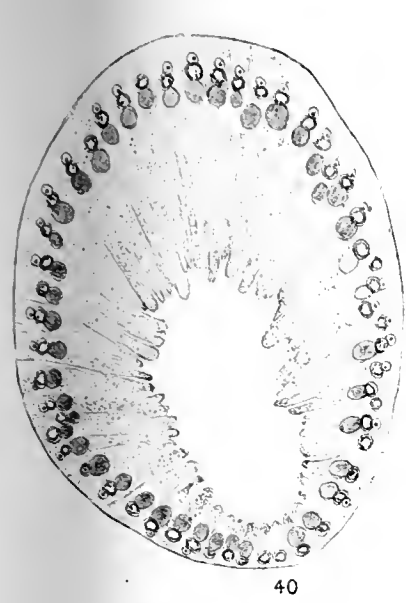


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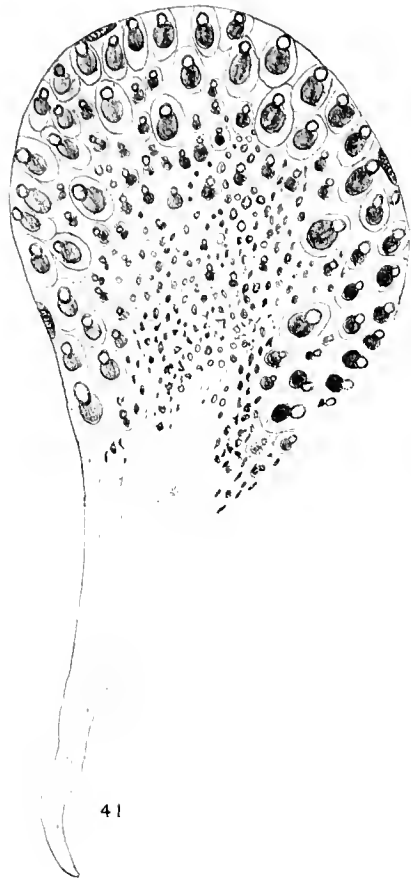


PLATE 14.

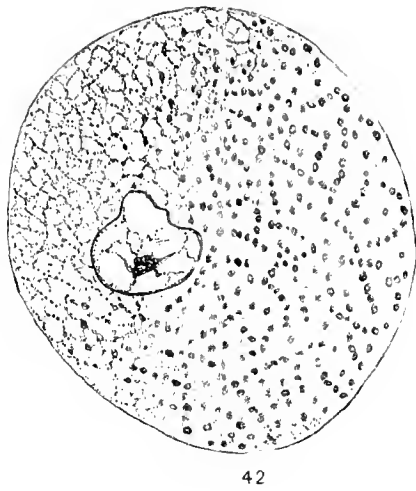
- Fig. 40. Spermatocyst with spermatids forming first stages of spermatozoa.
Fig. 41. Spermatocyst with spermatids growing into spermatozoa — from *Grapta silenus*.
Fig. 42. Section through the head nurse-cell showing insertion of the heads of spermatozoa. Cf. fig. 43.
Fig. 43. Spermatocyst with developed spermatozoa.
Fig. 44. Section of head end of spermatocyst showing relation of spermatozoa to the head nurse-cell.
Fig. 45. Bundle of developed spermatozoa imbedded in gonocyst.
Fig. 46. Part of section of spermatocyst showing development of giant spermatids into spermatozoa.
Fig. 47. Transverse section of a developed spermatocyst represented in figure 45, and showing section of the heads of spermatozoa.
Fig. 48. Section of head end of developing spermatocyst showing extension of nucleus, and imbedding of centrosome (*c.*).
Fig. 49. Section of spermatocyst showing early stage in development of head nurse-cell.
Fig. 50. Section of spermatocyst showing early development of head nurse-cell, and a spherical sperm nucleus.
Fig. 51. Mature spermatocyst showing its gradual absorption and liberation of spermatozoa.
Fig. 52. Transverse section of the body of a spermatocyst represented in figure 43.
Fig. 53. Bundles of free spermatozoa in testis, recently discharged from cyst.
Fig. 54. Section of head end of spermatocyst with fully developed spermatozoa.
Fig. 55. Section of vas deferens showing secreting epithelium and bundles of spermatozoa recently arrived in the proximal end of vas deferens.



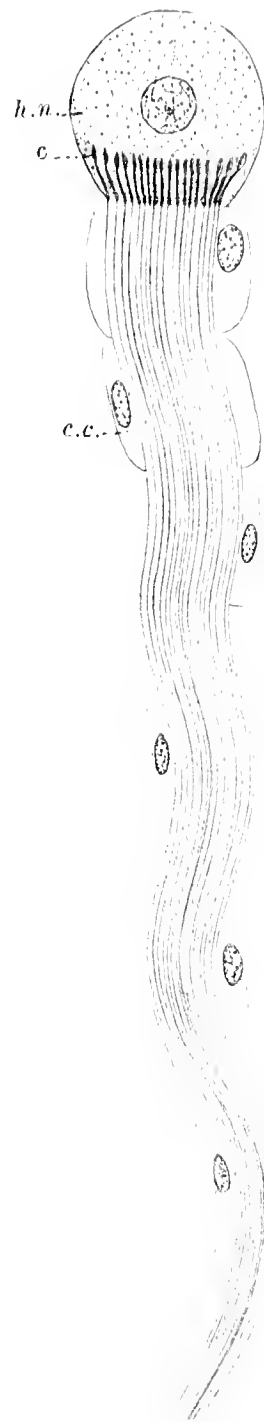
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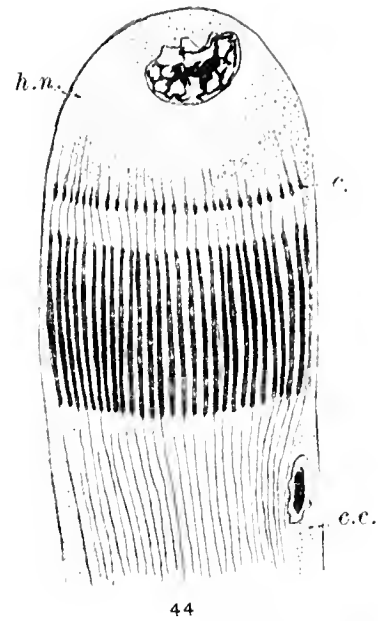
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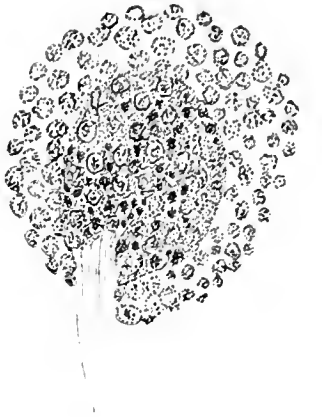
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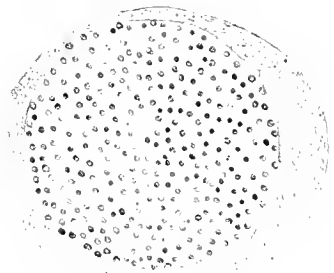
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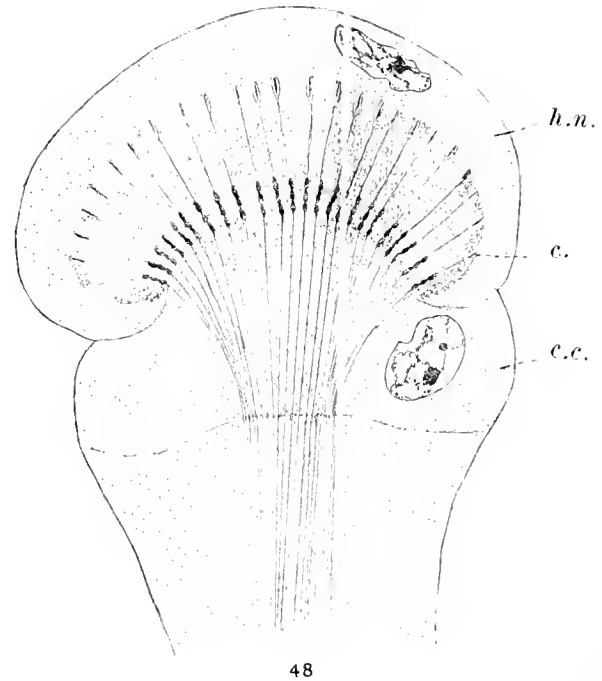
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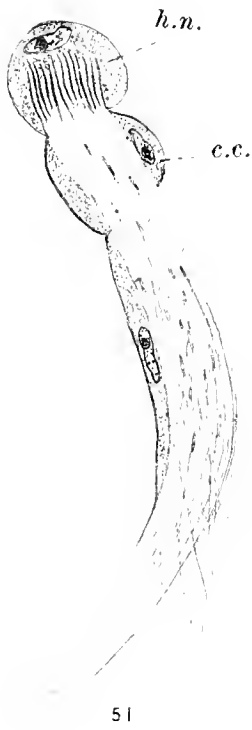
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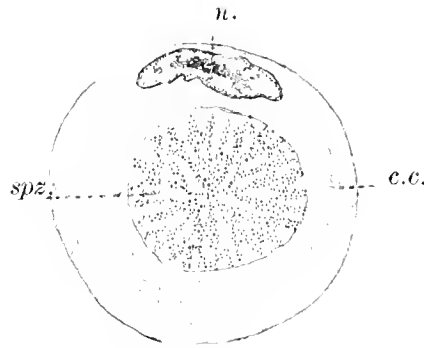
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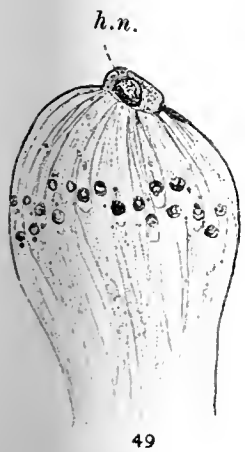
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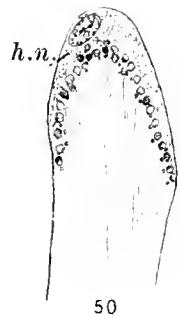
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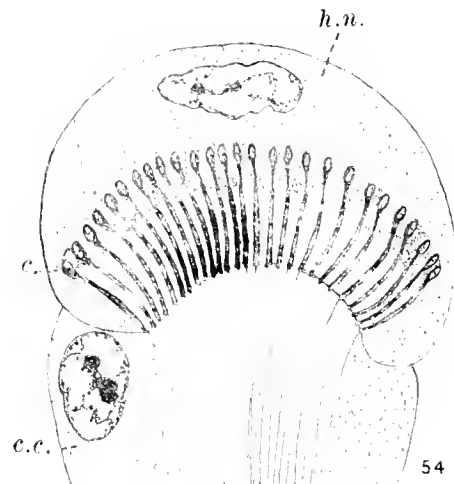
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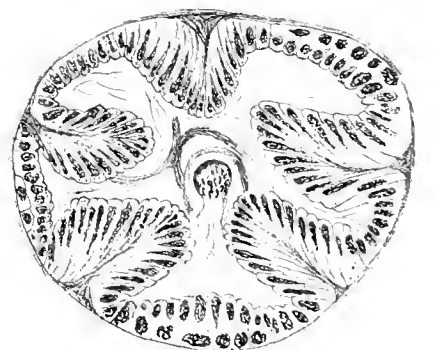
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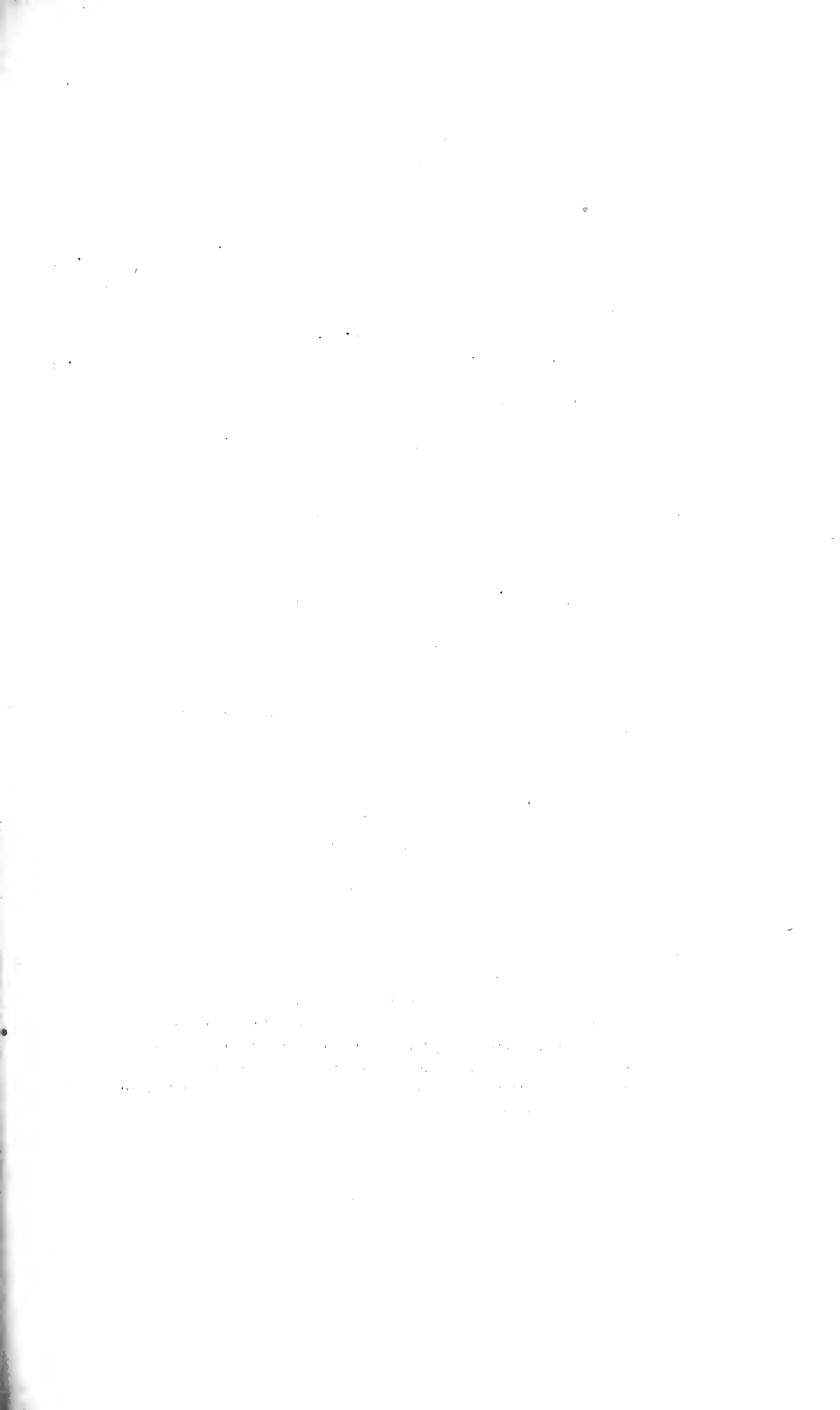


PLATE 15.

- Fig. 56. Grandmother stem cell, from pupa, Feb. 15th.
Fig. 57a. Grandmother stem cell with branch cells and cortical nuclei.
Fig. 57b. Transverse section of branch cells showing cortical nuclei.
Fig. 58. Spermatogone with peripheral nucleus.
Fig. 59. Spermatogone with dividing centrosomes.
Fig. 60. Spermatogone in metaphase of mitosis.
Fig. 61. Spermatogone in anaphase of mitosis.
Fig. 62. Spermatogone in telophase of mitosis, and showing remnant of first spindle.
Fig. 63. Spermatogone in telophase of mitosis.
Fig. 64. Gonocyst in two-celled stage.
Fig. 65. Gonocyst in resting eight-celled stage.
Fig. 66. Gonocyst of sixteen-celled stage in mitosis.
Fig. 67. Part of gonocyst showing anaphase of mitosis.
Fig. 68. Stalked cell.
Fig. 69. Stalked cell set free.
Fig. 70. Spermatogonium in resting state.
Fig. 71. Resting spermatogonium preparing for division.
Fig. 72. Section through equatorial plate showing chromosomes.
Fig. 73. Aster of spermatogone seen from pole.
Fig. 74. Spermatogone in telophase of mitosis.
Fig. 75. Growing spermatogone (spermatocyte).
Fig. 76. Spermatocyte, prophase of first maturation division.
Fig. 77. Stalked cell.
Fig. 78. Spermatocyte, prophases of first maturation division.
Fig. 79. Metaphase of mitosis, spermatocyte first order.
Fig. 80. Telophase of mitosis, spermatocyte first order.
Fig. 81. Division phases of spermatocytes.
Fig. 82. Division phases of spermatocytes.
Fig. 83. Free stalked cell.
Fig. 84. Free stalked cell divided.
Fig. 85. Free stalked cell in metaphase of karyokinesis.
Fig. 86. Prophase of spermatocyte first maturation division.
Fig. 87. Spermatocyte first order with only one developed aster.
Fig. 88. Spermatocyte in metaphase of first maturation division.
Fig. 89. Section of dividing spermatocyte through equatorial plate, showing lineal arrangement of chromosomes.

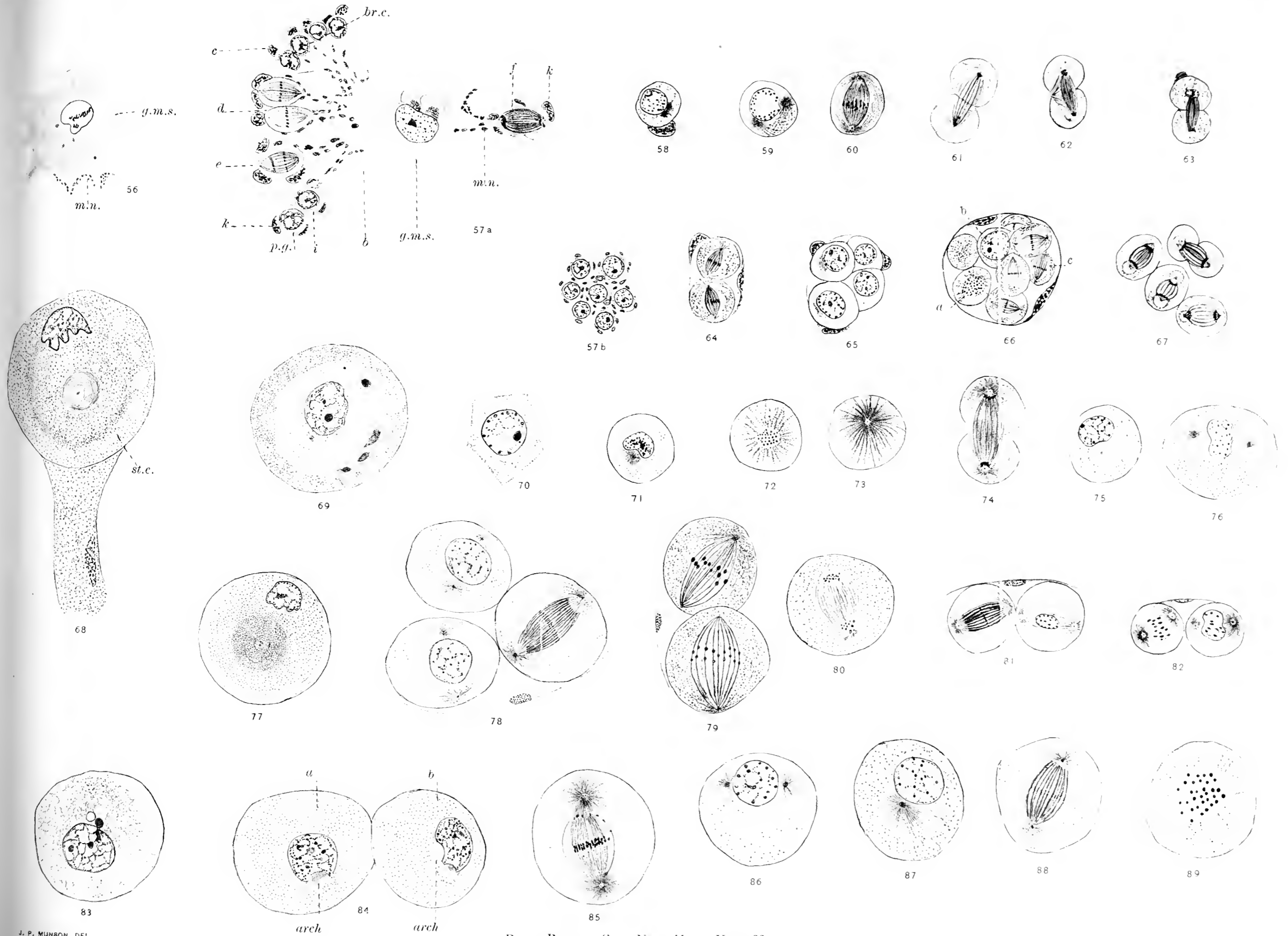


PLATE 16.

Maturation divisions of spermatocytes.

- Fig. 90. Spermatocyte first order at rest.
- Fig. 91. Spermatocyte first order with dividing centrosome.
- Fig. 92. Spermatocytes first order with developed asters.
- Fig. 93. Spermatocyte first order with aster and indented nucleus.
- Fig. 94. Spermatocyte with spireme of first maturation division.
- Fig. 95. Spermatocyte with contracted spireme.
- Fig. 96. Spermatocyte with double spireme.
- Fig. 97. Spermatocyte with second doubling of the thread.
- Fig. 98. Spermatocyte with segmenting spireme.
- Fig. 99. Spermatocyte with dividing spireme.
- Fig. 100. Spermatocyte showing tetrad formation.
- Fig. 101. Spermatocyte with distributed tetrads.
- Fig. 102. Spermatocyte tetrads and connecting fibers.
- Fig. 103. Spermatocyte with diads.
- Fig. 104. Spermatocytes with distributed diads.
- Fig. 105. Spermatocyte with diads showing polar arrangement of fibers.
- Fig. 106. Spermatocyte with disappearing nuclear membrane and first stages of spindle.
- Fig. 107. Spermatocyte first order, prophase of mitosis.
- Fig. 107a. Spermatocyte first order, metaphase of mitosis.
- Fig. 108. Spermatocyte in metaphase of first maturation division.
- Fig. 109. Spermatocyte in metaphase of first maturation division, showing aster and original boundary of nucleus.
- Fig. 110. Section through equator of spindle showing twenty-eight chromosomes in equatorial plate.
- Fig. 110a. Spermatocyte first order showing polar view of aster.
- Fig. 111. Spermatocyte in metaphase of first maturation division.
- Fig. 112. Spermatocyte first order in anaphase of first maturation division.
- Fig. 113. Telophase of first maturation division.
- Fig. 114. Telophase of first maturation division and preparation for the second maturation division.
- Fig. 115. Spermatocyte in telophase of first maturation division and in anaphase of second maturation division.
- Fig. 116. First and second maturation division of spermatocyte of first and second order.
- Fig. 117. Spermatocyte second order showing anaphase of second maturation division.
- Fig. 118. Spermatocyte second order, telophase of second maturation division showing formation of nebenkern.
- Fig. 119. Formation of spermatids with nebenkern.
- Fig. 120. Spermatocyte second order showing constriction of cytoplasm, and the formation of nebenkern.
- Fig. 121. Forming spermatids with nebenkern.

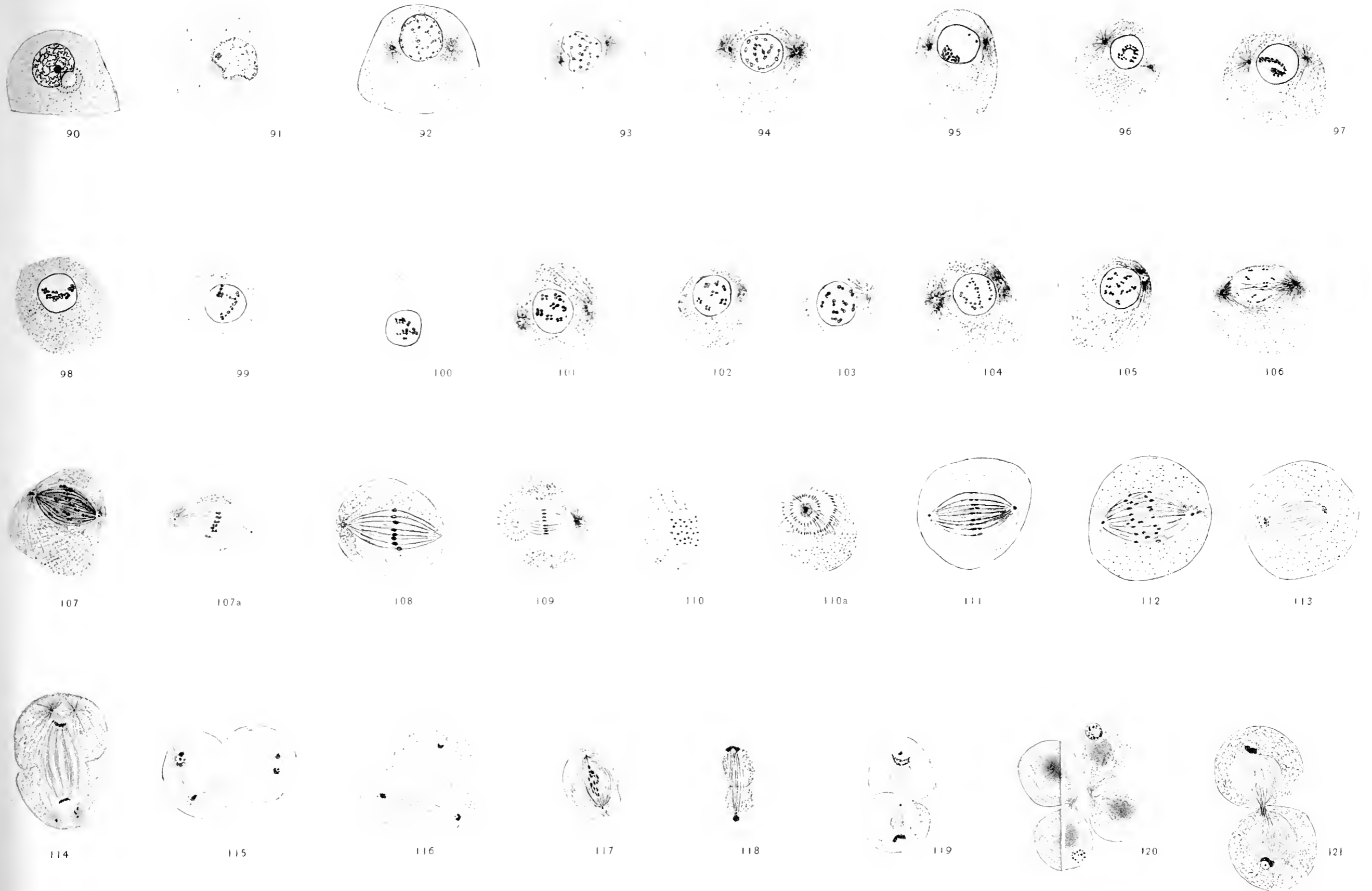




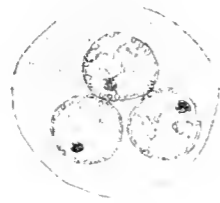


PLATE 17.

- Fig. 122. Abnormal spermatid with two nuclei.
Fig. 123. Abnormal spermatid with three nuclei.
Fig. 124. Abnormal spermatid with two nuclei and nebenkern.
Fig. 125. Typical spermatid with centrosome and nebenkern.
Fig. 126-127. Typical spermatids of the small kind.
Fig. 128. Spermatid with two centrosomes and nebenkern.
Fig. 129. Slightly elongated spermatid.
Fig. 130. Elongated spermatid with two centrosomes and nebenkern.
Fig. 131. Giant spermatid with centrosome, nebenkern, and mitosome.
Fig. 132. Growing spermatozoon with centrosome, nebenkern, and axial filament.
Fig. 133. Growing spermatozoon, with centrosome, mitosome, nebenkern, and axial filaments.
Fig. 134. Growing spermatozoon with centrosome, mitosome, nebenkern, and divided axial filament.
Fig. 135. Growing spermatozoon with centrosome, nebenkern, and axial filament.
Fig. 136. Growing spermatozoon with the axial filament apparently passing through the nucleus.
Fig. 137. Growing spermatozoon with centrosome, small mitosome, nebenkern, and axial filament.
Fig. 138. Growing giant spermatozoon.
Fig. 139. Growing spermatozoon as it appears at a constant period of growth.
Fig. 140. Growing spermatozoon with centrosome, axial filament, axial vacuole, and migrating nebenkern.
Fig. 141. Growing spermatozoon with centrosome and migrating nebenkern.
Fig. 142. Growing spermatozoon with centrosome and elongated nebenkern.
Fig. 143. Growing spermatozoon with centrosome, nebenkern, axial filament, and axial vacuoles.
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Fig. 146. Spermatozoon with elongated acrosome centrosome, but the chromatin still forming a spherical mass.
Fig. 147. Spermatozoon with elongated acrosome and distributed chromatin, into an elongated head.
Fig. 148. Spermatozoon with elongated head showing distinct chromosomes or chromatin granules and an elongated body (centrosome) in the acrosome.
Fig. 149. Spermatozoon from the vas deferens not yet entirely discharged from spermatocyst; acrosome still imbedded in the head nurse-cell.
Fig. 150. Spermatozoon from vas deferens, lower third.
Fig. 151. Mature spermatocysts from teased material.
Fig. 152. Spermatozoa just set free from a single mature spermatocyst (teased preparation).



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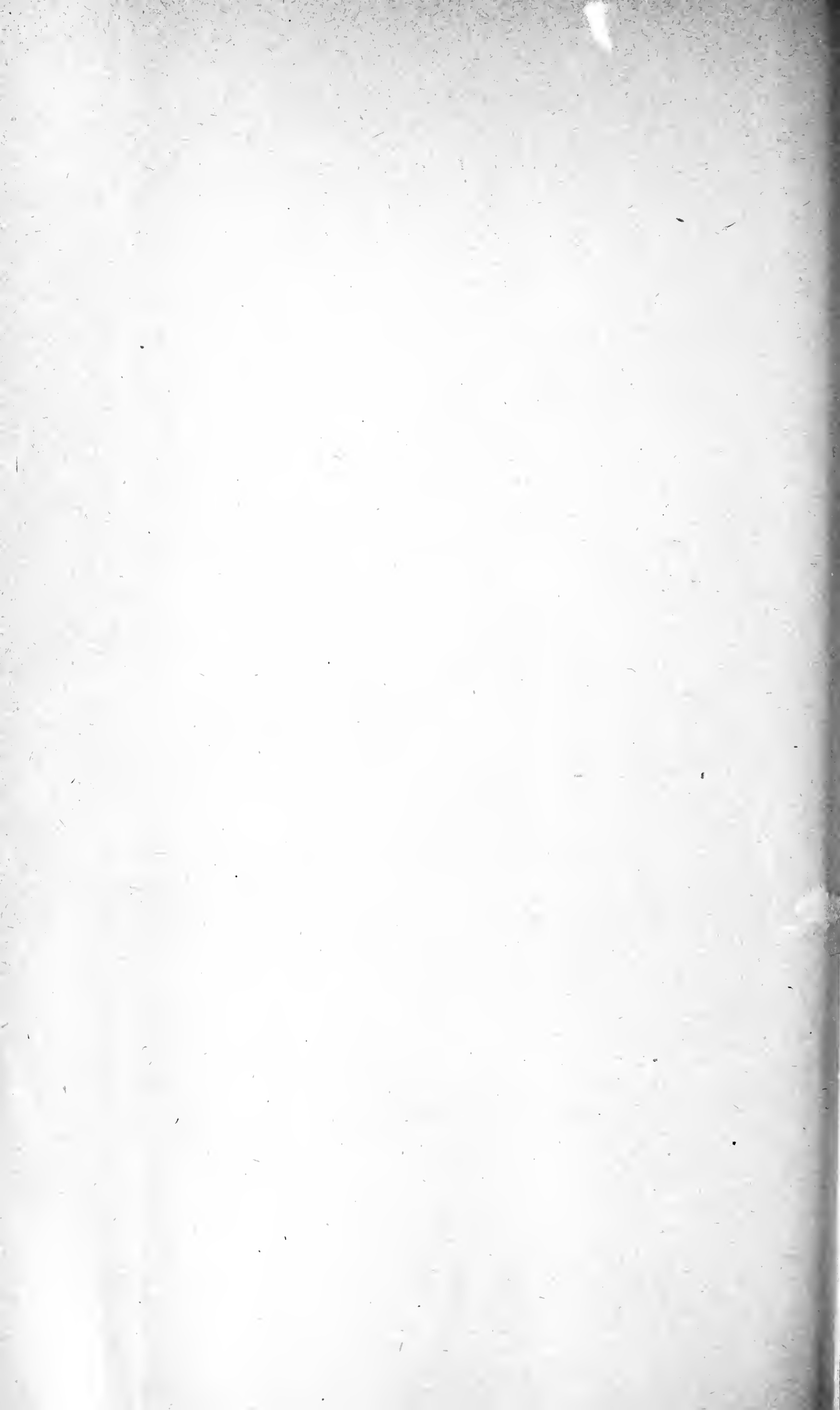
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CULTURE STUDIES ON POLYMORPHISM OF HYMENOMYCETES.

BY GEORGE RICHARD LYMAN.

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No. 4.—CULTURE STUDIES ON POLYMORPHISM OF
HYMENOMYCETES.¹

BY GEORGE RICHARD LYMAN

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INTRODUCTION.

THE life histories of most groups of Basidiomycetes are but imperfectly understood at the present time, and consequently we have but a meager knowledge of the nature and extent of polymorphism in this class of fungi. The group which has been studied most extensively in cultures is the Uredineae, and the development of a considerable number of species has been carefully followed out; but the rusts,

¹ Contributions from the Cryptogamic laboratory of Harvard university.—LXIV.

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although generally regarded as Basidiomycetes, are so far removed from the Hymenomycetes under discussion that they will not be extensively considered in this paper. Our acquaintance with other divisions of the Basidiomycetes is much more imperfect. It is true that we have a general conception of the course of development in the majority of genera, but in the case of very few species do we as yet possess a sufficiently minute knowledge, based on cultural study, to permit a clear understanding of all portions of the life history, particularly the occurrence and importance of secondary methods of reproduction. This is especially true of the Hymenomycetes. Although the existence of secondary spore forms has been reported in many species of this group, the descriptions of the alleged spores, in many instances, are very brief and inaccurate, and the necessary illustrations either indefinite or wanting. Moreover, few of the writers who report these conidia have attempted to germinate them and to obtain cultural knowledge of their nature and importance.

Owing to the need of further investigation concerning the life histories of Basidiomycetes, the writer has undertaken, at the suggestion of Professor Roland Thaxter, a cultural study of certain Hymenomycetes, giving especial attention to woody and encrusting species. The primary object of this research has been to obtain further knowledge of polymorphism in this group. The investigation was begun in the Cryptogamic laboratories of Harvard university, and completed in the botanical laboratory of Dartmouth college.

The writer takes pleasure in acknowledging, at this point, his indebtedness to those who have assisted him in the prosecution of this research: to Professor Thaxter, especially, under whose immediate supervision the first part of the work was accomplished, for his constant advice and encouragement, and for his assistance in obtaining a portion of the material; to Professor W. G. Farlow for many helpful suggestions at the time of completing the work and for the use of his herbarium and of a number of papers from his private library; to Professor E. C. Jeffrey for assistance in preparing the photomicrographs; to Professor E. A. Burt for naming a large number of the species studied; to Dr. G. P. Clinton and Mr. A. H. Chivers for the contribution of basidiomycetous bulbils.

Before recording the results of these studies it will be well briefly to review our present knowledge of the nature and extent of polymorphism among the Basidiomycetes.

THE NATURE OF POLYMORPHISM AMONG THE BASIDIOMYCETES.

The primary reproductive body of the Basidiomycetes is the basidiospore, borne on the basidium, which is the characteristic organ of the group. All other spore forms, *i. e.*, those not borne on basidia, will be classed in this paper as secondary or imperfect spores. No consideration will be given to purely vegetative multiplication due to the spreading of the mycelium in the substratum, or to the formation of such enduring parts as rhizomorphae, etc. Nor will the production of sclerotia by many species receive attention here save in the case of the small definitely formed bodies which Eidam called bulbils. These are reported for the first time in this paper as occurring among the Basidiomycetes. Secondary spores thus far known to belong to species of Basidiomycetes are of four types: (*a*) chlamydospores,—encysted vegetative cells; (*b*) oidia,—the dissociated cells of vegetative hyphae; (*c*) budding cells,—produced by yeast-like growth; and (*d*) conidia,—exogenously abjoined cells which show more uniformity of size and shape than do the other types of spores mentioned, and are usually produced on more or less characteristic structures called conidiophores.

In "Kryptogamen-flora von Schliesen, pilze," heft 1, p. 87, Schröter ('85) says that the polymorphism so richly shown by Ascomycetes is disappearing among Hymenomycetes, and the conidia still seen in individual cases are in process of degeneration. But Brefeld ('89, p. 187) asserts that as a result of his extensive culture studies this view must be abandoned, since Basidiomycetes are in no way inferior, as regards polymorphism, to Ascomycetes or other classes of fungi. Both of these views seem extreme in the light of our present knowledge. The investigations of Brefeld and others have revealed a considerable number of imperfect spore forms (largely oidia and chlamydospores) not known to Schröter, but the number and variety of well differentiated forms, at least among the Autobasidiomycetes, do not appear to warrant Brefeld's statement. Among the Phycomycetes and Ascomycetes, secondary spore formation is probably present in the majority of species; the secondary spores are produced in immense numbers and in varied fashion, and are of such great importance in reproduction that in many species the formation of zygospores or ascospores is resorted to at certain times only, or under special condi-

tions, while the great burden of propagating the species falls upon the secondary spores. On the contrary, among the Autobasidiomycetes secondary spores are less commonly known, are less varied in character, and where present, frequently appear to be of slight value in propagation, so that in this group the basidiospore is the main, and in many cases the sole agent of reproduction.

The literature bearing upon this subject is very unsatisfactory, as has already been pointed out. Writers have reported spores, or spore-like cells, in addition to the basidiospores, in a large number of species; but in many instances these reports are based upon very superficial examinations of the fungi concerned, and the alleged spores were found merely upon the basidiosporic fructifications. In the absence of accurate and sufficient descriptions and illustrations, and particularly of culture study of the alleged conidia, such reports are open to a two-fold criticism: first, that the conidia may belong to foreign fungi growing parasitically upon or together with the Basidiomycetes; and, second, that even though it be admitted in any instance that the conidia are produced upon the same mycelium with the Basidiomycete, it has not been shown that the alleged spore is capable of reproducing the fungus, and that it is not a purely vegetative structure produced as a result of unnatural or abnormal conditions of environment. Such criticisms can only be satisfactorily answered, and the correct status of the conidia established, by the germination of the latter in cell cultures, with subsequent cultivation to the production of normal basidiomycetous fructifications. Careful investigations of this character have been made in comparatively few instances.

The most extensive culture study of Basidiomycetes is that of Brefeld, who has made a notable contribution to our knowledge of polymorphism in this class of fungi. In his "Untersuchungen aus dem gesamtgebiete der mykologie," hefte 3 ('77), 7 ('88), and 8 ('89), he records the results of his cultivation of more than two hundred species, including about sixty-five genera belonging to various groups of Basidiomycetes. Brefeld emphasizes strongly the necessity of beginning the culture with the germination of a single spore, but he kept his cultures, thus started, on open slides under a bell-jar. Although he exercised great care in removing the slides to the stage of the microscope for examination, keeping the atmosphere of the room damp and free from air currents, nevertheless it is obvious that there is danger of contamination of the unsealed cultures. This danger

is well illustrated by his own account ('83, heft 5, p. 68) of the discovery of smut sprout cells in a majority of his cultures after a fructification of corn smut had been dropped in the room.

REVIEW OF PRESENT KNOWLEDGE OF POLYMORPHISM AMONG THE BASIDIOMYCETES.

In the following review, Brefeld's division of the Basidiomycetes into Protobasidiomycetes and Autobasidiomycetes will be followed, the former including the Uredineae, the Auriculariineae, the Tremellineae, and the angiocarpic Pilacraceae; the latter including the forms usually grouped under the Hymenomycetes and the Gasteromycetes. A very brief statement will be given as to the extent of polymorphism in the Protobasidiomycetes and the Gasteromycetes, followed by a more detailed summary in the case of the Hymenomycetes. References will be made to such papers as the writer himself has seen.

PROTOBASIDIOMYCETES.

Polymorphism is well developed among the members of this group. Typical oidia and chlamydospores have not been found, but yeast-like cells or conidia are practically universal. Three types of polymorphism may be recognized: that of the Uredineae, that of the Auriculariineae and Tremellineae, and that of the Pilacraceae.

The Uredineae possess polymorphism of a very highly developed character, and of a type quite unlike that shown by any other group of Basidiomycetes. The rusts are so far removed in this respect from the Hymenomycetes under discussion that it is obviously not important or advisable to attempt to discuss in this paper the many interesting problems connected with their life histories.

The Auriculariineae and Tremellineae regularly produce imperfect spores, according to the researches of Brefeld ('88), Möller ('95), and others. These spores are usually clusters of conidia or bud cells formed upon the germinating basidiospore, upon the mycelium, within the hymenium or other parts of the fructification, or even in specially formed pycnidia-like cavities, as in *Craterocolla cerasi* (Schum.) Bref. (Brefeld, '88, pl. 6). Indications of a bud-cell nature

are shown by all the imperfect spores of these two groups; this character is very clearly defined in the genus *Tremella*, where the germinating basidiospores produce abundant bud cells. The conidia and bud cells may immediately reproduce themselves by sprouting or they may produce normal mycelia and basidiosporic fructifications. Although these imperfect spores are probably normal and important factors in the reproduction of the Auriculariineae and Tremellineae, they are by no means so highly differentiated morphologically as are the spores of the Uredineae, nor is the life history in these groups complicated by the regular succession of spore forms commonly seen in the rusts.

In *Pilacre petersii* B. & C., Brefeld ('88) found, in addition to four-spored basidia of the *Auricularia* type, numerous non-septate conidiophores resembling the basidia in form, but bearing many spores. On account of the similarity between these two organs, Brefeld believes that the basidium of *Pilacre* has arisen from the conidiophore by the development of septa, and by the reduction of the spores to the fixed number four, and that this genus marks one of the several points of origin of the Basidiomycetes from the Hyphomycetes. Möller ('95) found a fungus in Brazil which is similar to the European *Pilacre petersii* but produces no conidia. He also describes from Brazil a new species of *Pilacrella*, a genus which bears some resemblance to *Pilacre*. This species produces conidiophores which show all gradations into normal basidia, and bear conidia which are indistinguishable from the basidiospores; in addition to these large conidia, small spermatium-like cells are abjoined from the ends of certain hyphae.

It is not certain where the genus *Pilacre* should be classified, and the position of *Pilacrella* seems still more uncertain. Saccardo ("Sylloge fungorum," vol. 4) places *Pilacre* among the Stilbeae of the Hyphomycetes, while Boudier ('88b), finding indications of ascus formation, classes a number of the species under the Discomycetes. Brefeld ('88), Lindau ('00), and Patouillard ('00) place the genus under the Protobasidiomycetes near *Auricularia*. This classification is supported by Istvanffi ('95) who says: "The young basidium of *Pilacre petersii* has a nucleus which later divides into four daughter nuclei that migrate into the young spores." Further study of this organ is necessary before its character is clearly understood, and before the basidiomycetous nature of *Pilacre* is definitely proven.

AUTOBASIDIOMYCETES.

The development of polymorphism in this group is much inferior to that shown by the Protobasidiomycetes. True conidia have been found in but few species, and although oidia and chlamydo-spores are tolerably common, very many species apparently produce basidiospores only.

Gasteromycetes.

So far as can be determined from our present knowledge, there is almost no polymorphism among the angiocarpic Autobasidiomycetes. The only examples which have come to the writer's notice are the two mentioned below. But few cultures have been made of the basidiospores, however, and hence little is known of the nature of the mycelium and of its possible methods of reproduction.

In *Sphaerobolus* (Fischer, '84) the interior of the mature fructification becomes a mass of mucilage in which are embedded basidiospores and cells which Fischer called gemmae. The latter are described as isolated, thin-walled, one- or few-celled pieces of the trama, and perhaps partake of the nature of oidia. The principle burden of reproduction appears to fall upon these gemmae, for they are rich in protoplasm and germinate at once in moist situations, while the basidiospores rarely put forth germ tubes in Fischer's cultures.

Eidam ('76) and Brefeld ('77) found that in impure or badly nourished cultures of the spores of Nidulariaceae the young hyphae show a tendency to break up into oidia.

Hymenomycetes.

Since this group is the special object of consideration in the present paper, the citation of reported cases of polymorphism is as full as the writer has been able to make it, although it is not presumed that the list is complete.

Dacryomycetaceae.—According to Brefeld ('88), Möller ('95), and others the basidiospores in all genera of this family germinate by dividing into several cells which at once produce tufts of conidia having more or less of the bud-cell nature. Clusters of similar spores are produced abundantly upon the young mycelia. In addition, Brefeld

found in his cultures of *Dacryomyces deliquescens* (Bull.) Duby, a definite fructification of considerable size composed entirely of gemmae, which are formed by the hyphae breaking into one- or two-celled portions, each capable of vigorous germination. These gemmae should probably be classed as oidia.

Exobasidiaceae.—The whole life history of a Basidiomycete was first followed by Woronin ('67) in *Exobasidium vaccinii* (Fuckel) Woronin, a species later cultivated by Brefeld ('89) and Richards ('96). If the basidiospores germinate on a substratum less favorable than a leaf of the host plant, the germ tubes at once produce clusters of rather elongated, fusiform bud cells, which continue to sprout and form similar cells at their extremities. This process may continue indefinitely with unimpaired vigor, as is shown by Brefeld who followed it in his cultures for more than a year. In *Exobasidium andromedae* Peck, Richards found not only these "small acicular spores borne on much branched hyphae among the basidia," but also a second type of conidium, which is larger and is "borne singly on rather stout hyphae not occurring with the basidia." On germination both types of conidia produce acicular secondary spores like those produced by the germinating basidiospores.

The Dacryomycetaceae and the Exobasidiaceae are placed among the Autobasidiomycetes on account of their unseptate basidia. Yet in many respects they are unlike other Autobasidiomycetes and similar to the Protobasidiomycetes. Their type of polymorphism, especially, recalls that of the Auriculariineae and Tremellineae, *viz.*, in the immediate formation of tufts of bud cells or conidia on germination of the septate basidiospores, and in the formation of similar bud cells or conidia on the young mycelia. Hence, in the succeeding parts of this paper these two families will not be considered further in the discussion of the polymorphism of the Hymenomycetes.

Hypochnaceae.—All the genera of this family are of interest in the present discussion, since some possess definite conidia, and the exact nature of others is rendered uncertain by peculiarities and variations of the basidia.

The most interesting conidia are found in *Tomentella*, a genus which closely resembles *Hypochnus*, for Brefeld ('89, p. 9) asserts that "the distinction between the two genera consists solely in the possession of conidial fructifications by *Tomentella*," and that the discovery of conidia in other species may "enrich *Tomentella* at the

expense of *Hypochnus*." P. Hennings ('97) also recognizes the possession of conidia as a distinctive mark of this genus. In both species of *Tomentella* which Brefeld examined he found Botrytis-like conidiophores that resemble the basidia in form, but bear spores over the whole surface. The conidia differ from the basidiospores only in being slightly smaller. These conidial fructifications had already been described as species of Botrytis,—*Botrytis argillacea* Cooke, belonging to *Tomentella flava* Brefeld, and *Botrytis gemella* Sacc., to *Tomentella granulata* Brefeld. In August or September, Brefeld found only conidiophores on the mycelium; later in the autumn basidia appeared, and finally entirely replaced the conidiophores. He was unable to germinate either conidia or basidiospores, but asserts that he observed the production of both kinds of spores on branches of the same hypha, thus proving their connection. He believes this to be another instance of the preservation of the ancestral conidiophore in connection with the derived basidium.

Many species of the hyphomycetous genus *Zygodesmus* show a very striking resemblance to *Hypochnus* or *Tomentella*, as is pointed out by Saccardo in "Sylloge fungorum," vol. 4, p. 283, and vol. 6, p. 653, and by Lindau ('00, p. 462). It is possible that certain forms of *Zygodesmus* may be conidial stages of species of *Hypochnus*.

Patouillard ('87a) describes swollen cells which replace the basidia in *Hypochnus anthochrous* and *Hypochnus acerinus*, and bear on their tapering summits single large colored conidia; these bodies are quite unlike the small colorless basidiospores which he says are rare in the former species and unknown in the latter. Brefeld ('89) cultivated *Hypochnus anthochrous* together with several other members of this genus, but found no conidia, obtaining in all cases only sterile mycelia. Spores of the character described by Patouillard in the above species of *Hypochnus* seem not uncommon, for they have been reported in several other genera of Hymenomyces (*cf. Corticium marchandii*, p. 136); they are probably produced by degenerate basidia in which three of the spores have been aborted. Apparently these conidia have never been made to germinate.

According to Boulanger ('93), the normal basidia of *Matruchotia varians* Boul. are two-spored, but may be replaced by one-spored conidiophores. This change in number of spores seems dependent on the nature of the culture medium used. Ferry ('96) found that this species and also *Matruchotia complens* Möll., whose basidium is four-

spored, possess conidiophores bearing from one to five spores in addition to the normal basidia. He believes that both species have descended from the same conidial ancestor. But the mere variation in the number of spores on the basidium cannot be considered of great importance in this connection for it is of common occurrence in various species, *e. g.*, *Exobasidium* has from three to eight spores on a basidium, *Corticium alutaceum* (Schrad.) Bres. has from four to eight spores, etc. Moreover, in species where the number of spores on a basidium is practically constant under normal circumstances, variations become frequent under unnatural conditions of growth, as in artificial cultures. Hence this fact in itself can hardly be regarded as of phylogenetic significance.

The morphology of the basidium and basidiospore of *Pachysterigma* Ols., and of *Muciporus* Juel, is a disputed matter. According to Patouillard ('88) the primary outgrowths from the basidium are huge sterigmata which correspond to the divisions of the four-parted basidium of *Tremella*; these bear basidiospores which become detached from the sterigmata and germinate by the formation of short promycelia, each bearing a single conidium. This opinion is also held by Brefeld ('89) and Hennings ('97), while Juel ('97, '98), after a study of the nuclear processes in the basidium, interprets the large sterigmata of Patouillard as sessile basidiospores which germinate *in situ* and produce secondary spores (the basidiospores of Patouillard) on short promycelia. If we accept the conclusions of Juel, we have the interesting phenomena of two generations of promycelia and conidia intervening between the basidiospore and the normal mycelium.

The germination of the basidiospore by the formation of a promycelium bearing one or more conidia is the distinguishing characteristic of Patouillard's Basidiomycètes hétérobasidiés, a division which includes all the Protobasidiomycetes, together with the Dacryomycetaceae and the genera *Pachysterigma* and *Muciporus* of the Autobasidiomycetes. The Exobasidiaceae also frequently show this phenomenon, although Patouillard does not include them in the above group. Brefeld also reports the same method of germination in *Radulum laetum* (see p. 137).

Hemigastraceae.—Juel ('95a, '95b) describes from Upsala a new genus, *Hemigaster*, which he places near the Hypochnaceae, in the new family Hemigastraceae. The mature fructification is angiocarpic, and externally resembles *Pilacre*, but the younger stage has a

pileus with ventral smooth hymenium. The edges of the growing pileus curve under and finally join the stipe, thus enclosing a central cavity which is lined with the hymenium and traversed by the stipe as a columella. From its method of development, Juel regards the fungus as a Hymenomycete rather than a Gasteromycete. In the mature condition the cavity becomes filled with chlamydosporic hyphae, and the fructification somewhat resembles that of *Ptychogaster*. The chlamydospores are produced in abundance, either singly or in chains on the hyphae. Juel was unable to distinguish detached chlamydospores from basidiospores. In cultures of spores he found no conidia, but in spontaneous cultures on rabbit dung there were numerous chains of conidia which he thought belonged to *Hemigaster*, although he was unable to prove it, for the conidia on germination produced only conidia-bearing mycelia.

Thelephoraceae.—According to Eichelbaum ('86), specimens of *Stereum hirsutum* kept for several days in a damp chamber produce a white mouldy growth of hyphae from the palisade zone of the hymenium. On these hyphae numerous roundish conidia are borne terminally or laterally. Eichelbaum's attempts to germinate the spores yielded only yeast-like budding. The same spores were seen by Masee ('90-'91) in specimens of this species grown in moist situations. In such cases the hymenium presented a velvety appearance due to the presence of small compact bundles of hyphae which branched in an irregularly verticillate manner, each branch bearing at its end a small colorless spore. "In very dilute alkaline solutions the gonidia made feeble attempts at germination." Marshall Ward ('97), however, found no conidia in his thorough study of this fungus, nor did Brefeld ('89), who also cultivated eight other species of *Stereum*, obtaining only sterile mycelia in all cases. The conidia reported by Eichelbaum and Masee in *Stereum hirsutum* belong to a class of wet-weather spores found in a number of Hymenomycetes (*cf.* *Solenia*, p. 136, *Pleurotus*, p. 139, *Mycena*, p. 140, *Polystictus*, p. 142). Until these spores have been more thoroughly investigated, we must regard their nature as uncertain, and their occasional production as of doubtful importance to the fungus.

Doubtless the bodies referred to in the following extract from a letter from Professor Burt are of the same nature as those mentioned above: "In young stages *Corticium roseum* Pers. bears a crop of minute spore-like bodies, presumably conidia. The conidiophores

may generally be found later as characteristic organs between the basidia."

So far as can be judged from the inadequate descriptions, the oval spores mentioned by Fuckel ('71) as occurring on the hairs of *Solenia caulium*, and the ovoid colorless bodies which Patouillard ('89b) found terminating the hairs on young cups of *Solenia anomala*, may be of similar nature to the spores reported in *Stereum hirsutum*. Unfortunately, no figures are given and the spores were not germinated.

The hymenium of *Stereum disciforme* Fr., according to Patouillard ('94b), contains cells larger than paraphyses, but smaller than basidia, each bearing terminally either a single conidium, or two conidia separated by a constriction. These are produced all over the hymenium and even mingled with the marginal hairs. Similar conidia, produced in simple or branched chains, were seen by Richon ('77) and Patouillard ('87a) in the hymenium of *Corticium amorphum* Fr. The nature of these alleged conidia cannot be definitely determined from the imperfect descriptions and illustrations, but they are apparently moniliform paraphyses, or chlamydospores formed in modified basidia (cf. *Pterula multifida*, p. 137, *Hydnum*, p. 137, *Fomes bambusinus*, p. 142).

The hymenium of *Corticium marchandii* Pat. contains a few basidia bearing small colorless basidiospores, but is mainly composed of stout nodulose conidiophores (Patouillard, '83a), each bearing terminally a single large colored body which Patouillard calls a conidium (cf. *Hypochnus anthochrous*, p. 133).

Massee ('90-'91) speaks of "large elliptical gonidia produced singly on thick gonidiophores" in *Aleurodiscus (Corticium) oakesii*, but Peirce ('90) did not see these large gonidia, and thinks that Massee must have been misled by the moniliform paraphyses of this species, or by occasional monosporic basidia in which the other spores have been aborted. Peirce found that "when the plant is not producing basidial spores, that is, when it is young or after basidial spores have ceased to form, the bristles of the paraphyses often bear at their tips clear, highly refringent, colorless, spherical bodies about 0.82 μ in diameter, which are doubtless conidial spores." He did not germinate these tiny conidia.

Clavariaceae.—Oidia of the type seen in many of the Agaricaceae occurred in Brefeld's ('77) cultures of species of *Typhula*; but the majority of the members of this family have never been studied in cultures and nothing is known of the character of the young mycelia.

Polymorphism is reported by Patouillard ('83a, '87a) in three species of this family in connection with the basidio-fructification, as follows:—

The hymenium of *Pterula multifida* Fr. contains cells similar to paraphyses, whose upper part is alternately inflated and constricted with a wall at each constriction. These enlarged cells may become separated, and are doubtless chlamydospores similar to those found in *Stereum disciforme* (see p. 136).

On the hymenium of *Pistillaria rosella* Fr., var. *ramosa* Pat. are small tubercles composed of slender, articulate, diverging hyphae, each terminated by a large ovoid conidium.

The sclerótium of *Pistillaria bulbosa* Pat. may give rise to a pezizoid cup bearing a thick layer of two- to three-septate, staff-shaped bodies, which become disarticulated as cylindrical conidia. In both species of *Pistillaria* the exact nature of the conidia should be determined by culture-study.

Hydnaceae.—The hymenium of *Hydnum coralloides* Scop. contains thick-walled microconidia produced endogenously in chains or grouped in clusters on branching hyphae (de Seynes, '91). Macroconidia are also produced terminally on slender conidiophores. De Seynes compares the spore formation in this species with that seen in *Polyporus biennis*. Similar spores occur in *Hydnum erinaceus* Bull. (Richon, '81, and Patouillard, '94a). Undoubtedly both micro- and macroconidia, so called, are chlamydospores formed in the elements of the hymenium or subhymenium, a phenomenon which is apparently not uncommon in the Hymenomycetes (*cf.* *Stereum disciforme*, p. 136).

Brefeld ('89) cultivated species of *Grandinia*, *Radulum*, *Phlebia*, and *Irpex*. *Grandinia* yielded only sterile mycelia, but *Phlebia* and *Irpex* formed abundant oidia. The mycelium of *Radulum* produced short side branches with a beaded appearance as in the formation of oidium chains, but the parts of the chain did not germinate or separate to form oidia. The basidiospores of *Radulum laetum* (Fries) germinated by the formation of promycelia and secondary spores (*cf.* *Pachysterigma*, p. 134).

Agaricaceae.—Oidia are very common in this family, having been reported in the majority of the species thus far investigated. In most species they germinate readily, and form normal mycelia. Falck ('02) cultivated a considerable number of the *Agaricaceae* through

the formation of oidia to the mature fructification, and concluded that the oidium form is a definite stage in the life cycle of many of the higher fungi. In certain species almost the whole mycelium becomes disarticulated to form oidia; in other species only certain hyphae produce oidia during a limited period of the growth of the mycelium; while in still more specialized cases, the oidia are formed in particular places, and more or less differentiated clusters are produced, as in species of *Psilocybe*, *Psathyra*, *Coprinus*, etc. In such cases the oidia frequently seem to be incapable of germination, and were thought by Hoffmann ('56), Reess ('74), Eidam ('75), Van Tieghem ('75a), and others to be spermatia or male cells. A little later Van Tieghem decided that they had no sexual significance since he had observed their germination, and moreover, had seen the development of normal basidiosporic fructifications in the entire absence of the supposed spermatia. From the experiments of Van Tieghem, Brefeld ('77, '89), and others, it seems clear that these alleged spermatia are merely oidia of more specialized type which appear to have lost the power of germination in many instances.

Chlamydospores have not been reported in many genera of the Agaricaceae. Fayod ('89a) mentions them as occurring in the stipe or pileus of a number of species, but Brefeld ('89) found them only in *Nyctalis*. This interesting genus has been studied by many investigators. In the mature fructification of *Nyctalis asterophora* Fr., the whole upper part of the pileus is composed of thick-walled stellate chlamydospores which form a yellowish brown layer about one millimeter or more in thickness. In smaller specimens, especially, this layer of chlamydospores encroaches so far as to hinder the formation of basidia and gills below. In *Nyctalis parasitica* (Bull.) Fr., the chlamydospores are found in the subhymenium, the thick swollen lamellae of mature specimens being composed almost entirely of narrowly ellipsoid, smooth chlamydospores, so that the production of basidiospores is nearly or quite suspended. The chlamydospores of *Nyctalis* have given rise to considerable controversy. Tulasne ('60) was the principle advocate of the theory that the chlamydospores are organs of species of *Hypomyces* growing parasitically upon certain agarics. De Bary ('59), on the contrary, held that the chlamydospores are not due to parasitism, but are organs of two natural species of *Nyctalis*, and the truth of this theory is conclusively proven by other observers. Krombholz ('31) sowed chlamydospores on the pileus

of *Russula* and obtained normal fructifications of *Nyctalis*. Brefeld ('89) repeated Krombholz's experiment, and, in addition, found that the mycelia from germinating basidiospores produced the characteristic chlamydospores and also oidia in abundance. Finally, Costantin ('91) germinated the chlamydospores in a variety of culture media, and traced their development to the formation of basidia.

Conidia have been reported in several species of this family as described below, but they seem to be of small importance in the life histories of the fungi concerned, and the more interesting forms need to be investigated further that their basidiomycetous nature may be fully demonstrated.

Conidia were observed by Patouillard ('80, '81, '87a) in specimens of *Pleurotus ostreatus* grown under conditions unfavorable to perfect development. The stalks and caps become villous with short septate simple or branched hairs, some of which, particularly those about the margin of the pileus, produce small colorless conidia, which are borne singly on each cell on terminal or lateral sterigmata. Brefeld ('89) cultivated *Pleurotus ostreatus* and found oidia, but makes no mention of conidia. Matruchot ('97), however, corroborates Patouillard's observations, finding such conidia on the margin of the pileus and in the hymenium. The latter region also contains numerous bodies which he calls cystidia, each bearing one, two, or three sterigmata with terminal swellings. Moreover, in eight-days-old cultures the mycelia produce cells (called pseudoconidia) similar to the conidia of the pileus. Matruchot found gradations between these three different spore forms, and regards all the conidiophores as modified basidia. So far as he could tell, the various spores are incapable of germination.

According to Heckel ('80) the glands of *Pleurotus glandulosus* are composed of basidia transformed into long hairs that bear spores laterally in varying number.

In *Pleurotus craterellus* the stalk is represented by a small tubercle covered by hairs whose swollen ends produce one to several oval conidia, borne side by side (Patouillard, '87a).

Eichelbaum ('86) says that a conidial modification of the basidium may be induced in any agaric by keeping it for some time in a damp chamber. The basidia lengthen into slender threads, each bearing at its extremity a large round cell which occasionally shows yeast-like budding *in situ*. All gradations between these slender conidiophores.

and normal basidia are especially well seen in *Agaricus (Mycena) rugosus* Fr.

None of these alleged spores reported in species of *Pleurotus* and other agarics have been germinated and grown in cultures, hence their functions and importance remain problematical. They are evidently of the same type as the spores produced in *Stereum hirsutum* (see p. 135) as the result of unfavorable conditions of growth, especially dampness. In the cases described by Eichelbaum the conidiophores are evidently modified basidia; in *Pleurotus* the morphology is less clear, although Matruchot and Heckel believe that here also the spores are produced by degenerate basidia.

In his "Text-book of comparative morphology" (p. 334 of Eng. transl.) de Bary says: "The slender stipe of *Agaricus (Collybia) racemosus* Pers. is beset throughout its whole length with short hair-like spreading branches which were compared by Fries ('36, p. 90) and Berkeley ('57, p. 365) to the sporophores of the form-genus *Stilbum*, because like them they abjoin at their extremities numerous spores (gonidia) arranged in rows and forming together a small gelatinous head." The presence of these spores is confirmed by Stefan ('05), who says the sporophores are collected into "ein *Stilbum*- oder *Pilacre*-ähnlicher Köpfchen," which usually bears a water drop. The spores are regularly ellipsoidal, and are borne singly or in rows on the ends of the hyphae; they germinate readily in culture cells. Stefan called these bodies chlamydospores, although they are thin-walled, and from his description would seem to be more of the nature of oidia. Brefeld ('89, p. 61) found numerous oidia on the mycelium of this species, but no chlamydospores or conidia.

A very interesting conidial form has been described by Oersted ('65) as belonging to *Agaricus (Claudopus) variabilis* P. Short, non-septate, erect sporophores arise from the mycelium and abjoin ellipsoidal spores simultaneously in a small head at their extremities. The author compares the conidiophores with Corda's form-genus *Cephalosporium*. Unfortunately, Oersted did not prove the connection of the *Cephalosporium* with *Agaricus variabilis* by culture study. Brefeld obtained only sterile mycelia in his cultivation of this species. Hence it seems probable that the *Cephalosporium* is a parasite on the mycelium of the Basidiomycete, an interpretation which is strengthened by the presence of certain large cells and adjacent slender branches, organs regarded by Oersted as oospheres and antheridia respectively, but which give the appearance of parasitism.

Zukal ('89) found on the decaying leaves and fruit of the olive a fungus externally resembling a *Marasmius*. No spores were produced on the ventral face of the pileus, but on the dorsal surface a hymenium was formed, which consisted of hypha ends, each swelling to form a thick-walled roughened spore whose germination was not observed. This hymenium had a great resemblance to the uredo-fructification of the Uredineae, especially when, as occasionally happened, the stipe remained undeveloped. Zukal believes this to be a peculiar Hymenomycete in which the conidiophore has not yet become specialized into a basidium. In the opinion of Fayod ('89b) it is a conidial stage in the development of some agaric. But in the absence of further knowledge of this peculiar fungus, we must regard its affinity to the Basidiomycetes as very doubtful.

Polyporaceae.—*Oidia* are not so common in this group as in the *Agaricaceae*, although Brefeld ('89) found them in certain species of *Daedalea*, *Trametes*, and *Polyporus*.

Chlamydospores, on the other hand, occur in many species, and have been reported by Tubeuf ('02) on the mycelium of *Merulius lacrymans*, by Fayod ('89a) in the hymenium of *Polyporus (Fomes) lucidus*, by Farneti ('01) in the hymenium of *Boletus briosianus* Far., and by other writers in species of *Polyporus* and related genera, where they sometimes occur in such abundance as to form definite fructifications of their own,—the basidio-fructification in some species is unknown or only occasionally recognizable. A chlamydosporic formation of this character was named *Ptychogaster albus* by Corda ('38), and has been variously classified with the Myxomycetes, with Pilacre, with the Lycoperdaceae, as a case of parasitism or cohabitation of two species, as a conidial stage of a species of the Ascomycetes, and as a monstrous form of *Polyporus* (Corda, '38, Tulasne, '65, Tulasne, L. R., and E., '72, Cornu, '76, de Bary, '87, etc.). Ludwig ('80) found a *Polyporus* hymenium in *Ptychogaster albus*, and renamed the plant *Polyporus ptychogaster*. Boudier, Patouillard, de Seynes, and others have described a considerable number of species of *Ptychogaster*, some of which have been definitely connected with the *Polyporaceae* by culture study and by the discovery of basidiosporic hymenia, while the identity of others is still unknown. Brefeld ('89) made the new genus *Oligoporus* to include species of *Polyporaceae* with copious formation of chlamydospores, corresponding to the genus *Nyctalis* among the *Agaricaceae*; while Saccardo in "Sylloge fun-

gorum" and Hennings in "Die natürlichen pflanzenfamilien" retain the name *Ceratomyces* of Corda ('37) for such *Ptychogaster* species as have not yet been certainly connected with a basidiosporic form. But in many species there is no doubt of the systematic affinities, since the formation of chlamydospores is not so copious as materially to modify the normal basidiosporic hymenium or the normal basidiofructification may occur together with the *Ptychogaster* form; *e. g.*, *Polyporus biennis* Bull. (Boudier, '88a, and de Seynes '88), *Trametes rubescens* Fr. (Patouillard, '82), *Polyporus sulfureus* Bull. (de Seynes, '78, '84, '88), and *Fistulina hepatica* (de Seynes, '64, '74, and Brefeld, '89). In the species last named, the young fructification consists almost entirely of chlamydosporic hyphae; later, tubes may begin to form below and the mass of chlamydospores may become pushed up to the upper side and spread out in a thick layer.

Conidia similar to those reported in *Stereum hirsutum* and *Pleurotus ostreatus* are said to occur in a number of species of this family when grown in wet or other unfavorable conditions; *e. g.*, in *Polystictus versicolor* (Patouillard, '83a, '83b), and *Polystictus zonatus* (Eichelbaum, '86).

Conidia are described by Patouillard ('91a, '00) in *Polyporus (Fomes) bambusinus* from China. The conidiophore is an erect hypha, simple or very little branched, arising from the margin of the fructification, and bearing chains of from three to ten russet spores, the oldest at the end. Patouillard compares the method of formation of conidia with that in *Poria mollusca* (Patouillard, '90 — not seen by writer). In the absence of a more adequate description it seems probable that these conidia are chlamydospores, perhaps produced in elements of the hymenium, as in *Stereum disciforme* (see p. 136).

In species of *Fomes* and related genera the upper surface of the basidiofructification is sometimes thickly dusted with spores (Patouillard, '87a, '87b, '89a, and Schulzer von Müggenburg, '78, '80, '83) which have been interpreted both as conidia and as basidiospores. Patouillard found the dorsal surface of *Fomes fulvus* producing both normal basidia and others more or less modified into one- or two-spored conidiophores. On the pileus of *Fomes applanatus* are irregularly branched hyphae bearing terminally or laterally one or more spores (Schulzer von Müggenburg, '80), and similar sporophores also arise from the hymenium. This formation of spores on the dorsal surface of a number of species has not yet been sufficiently investi-

gated, but it seems probable that the sporophores are degenerate basidia.

According to Fuckel ('73), *Polyporus (Poria) metamorphosus* at first produces only yellow conidia of the type of *Sporotrichum* or *Botrytis*. Unfortunately no figures accompany the brief description.

The most important and interesting conidial form thus far reported among the Basidiomycetes is that which Brefeld ('89) discovered in his cultivation of *Polyporus annosus*. In cultures of basidiospores, after six to eight days the mycelium produces club-shaped conidiophores of the *Oedocephalum* type which bear numerous spores exactly similar to the basidiospores. These conidia germinate readily and produce typical mycelia. The conidiophores show considerable variation in form and size, and, when the number of spores is reduced to four, they are externally indistinguishable from isolated basidia. On account of these conidia, Brefeld removed this species from the genus *Polyporus* and placed it in the new genus *Heterobasidion*. He regards the conidiophore as the original form of the basidium, and believes that in this species as in *Pilacre* and *Tomentella*, there is still preserved the ancestral hyphomycetous form from which the Basidiomycete has been derived.

Summary.

It will be seen from the above statement that polymorphism appears to be very general among the Protobasidiomycetes, the secondary spores taking the form of very simple conidia or bud cells; typical oidia and chlamydospores have not thus far been found. Confining our attention to the Hymenomycetes, and excluding the Dacryomycetaceae and the Exobasidiaceae from the discussion on account of their resemblance to the Protobasidiomycetes, we may review the known occurrence of the four types of secondary spores as follows:—

(a) Bud-cell formation occurs only in isolated cases where the spores have apparently germinated under unfavorable conditions.

(b) Oidia are extremely common in the Agaricaceae, occasional in the Polyporaceae, Hydnaceae, and Clavariaceae, and unknown in the other families. They are found on the mycelium, never forming a fructification of their own, although in certain species of agarics they occur in rather definite tufts or clusters.

(c) Chlamydospores are known in *Hemigaster*, in a few agarics

(especially in *Nyctalis*), and reach their highest development in the Polyporaceae, where they occur in many species, frequently forming definite fructifications, and nearly or quite replacing the basidiospores. It is probable also, that the conidia reported by Patouillard in *Stereum disciforme*, *Corticium amorphum*, and *Pterula multifida*, and by several writers in species of *Hydnum*, are chlamydospores. Aside from these doubtful cases, chlamydospores are not known to occur in the Hydnaceae, Clavariaceae, or Thelephoraceae. In distinction from oidia, chlamydospores occur in the hymenium or other parts of the fructification, having been found on the mycelium only in rare instances.

(d) Conidia have been reported in all families of the Hymenomyces, and for convenience may be divided into the following five classes:—

(1) Spores formed on a promycelium produced by the germinating basidiospore. This is the type of conidium most commonly seen in the Protobasidiomycetes, but is known only in *Pachysterigma*, *Muciporus*, and *Radulum lactum* of the Autobasidiomycetes.

(2) Spores produced by modified basidia. Examples of this type are common, especially in artificial cultures and under unnatural conditions of growth. This modification may merely mean an increase or decrease in the number of spores on the basidium, as in *Matruchotia*; or it may also carry with it such a change in the shape of the basidium and in the character of the spores that the sporophore can no longer be certainly recognized as a basidium. Examples of this kind are seen in *Corticium marchandii*, and in species of *Hypochnus*, *Pleurotus*, *Fomes*, etc.

(3) Spores produced by branching hyphae upon the basidio-fructifications of certain species, probably as a result of unfavorable conditions, particularly excessive dampness; *e. g.*, in *Stereum hirsutum*, *Pleurotus ostreatus*, *Polystictus versicolor*, etc. These wet-weather spores have never been germinated and studied in cultures, and it is not certain whether they are produced by modified basidia as in class (2) above, or are true secondary spores. They are apparently not of great importance in the propagation of the species possessing them.

(4) True conidia produced upon the mycelium. These are at present certainly known only in *Tomentella* and in *Polyporus annosus*.

(5) Spores of interesting character reported in a number of species, but which are not sufficiently known to merit unqualified acceptance as polymorphic stages of Basidiomycetes; *e. g.*, the conidia reported in *Pistillaria*, *Claudopus variabilis*, *Poria metamorphosus*, etc.

Of the five classes mentioned above, the fourth seems to be of the greatest importance in the present discussion of polymorphism. Conidia of the first class are characteristic of the Protobasidiomycetes, and the Hymenomycetes which possess them, *Pachysterigma* and *Muciporus*, are in many ways allied to the Protobasidiomycetes; hence this method of germination of the basidiospore is interesting as indicating possible affinities of the genera in question. Brefeld reports this method of germination also in *Radulum laetum*, but it seems doubtful whether this is the normal method in this species. The spores of the second class, being produced by modified basidia, are intrinsically basidiospores and not conidia; hence they belong more properly to the realm of teratology and should not be given great weight in this discussion of polymorphism. The third class of spores may also come in the same category as the second, and even if it be shown that they are true secondary spores and not modified basidiospores, their occasional production as the result of certain unfavorable conditions of growth, and the apparent absence of power of germination in most cases, would seem to indicate that they are neither normal nor important factors in the life histories of the fungi concerned.

The more highly differentiated spores of the fourth and fifth classes are of greatest importance in the present discussion. Unfortunately, the basidiomycetous nature of spores of the fifth class needs to be demonstrated by further study; hence there remains only the fourth class, *viz.*, the well differentiated conidia found in the genus *Tomentella* and in *Polyporus annosus*. The exact status of the conidia of *Tomentella* has not been proven by culture study, but Brefeld's testimony as to their connection with the basidiosporic fungus seems to have been accepted and confirmed by other writers. The author of this paper has been so fortunate as to obtain fresh specimens of *Polyporus annosus*, and the mycelia from the germinating basidiospores produce in abundance the interesting conidia described by Brefeld. The latter's observations upon this species were confirmed in all essential particulars.

Thus, in the light of our present knowledge, it appears, that in the great majority of Hymenomycetes there are no secondary spores; that where present, these spores usually take the form of mycelial oidia as in many of the Agaricaceae, or of chlamydospores produced upon or within the basidio-fructification as in certain of the Polyporaceae; that conidia of a more or less doubtful character are reported in a

number of species, but only in *Tomentella* and in *Polyporus annosus* are regularly occurring and well differentiated conidia known to exist.

CULTURE METHODS.

The germinating basidiospore was the starting point of every culture used in the present investigation. In many instances pure cultures were obtained in other ways, as by transferring with a sterile knife a bit of the subhymenium to the culture medium, but such cultures were employed merely as checks, and were never made the basis of extensive experiments. The basidiospore was regarded as the most logical point of departure in culture study, and the possibility of error was less than though the culture was obtained in some other way; moreover, it was thought that the young mycelium arising from the basidiospore might possess properties and means of reproduction not seen in the more mature stages of the fungus.

To obtain the basidiospores, specimens of the fungus with fresh hymenia were collected in the field, carefully wrapped in clean paper or placed in sterile boxes and brought as quickly as possible into the laboratory. The fructification, with hymenium turned downward, was suspended over a sterile plate on which were lying sterilized slips of mica. The whole was covered with a bell jar in order to prevent the entrance of foreign spores, and to ensure a moist atmosphere suitable for the continued development of basidiospores. After a considerable number of spores had been deposited on the mica, the slips were removed and placed in sterile vials stopped with cotton plugs. When the cultures were made a tiny drop of water was placed upon the mica slip in the vial, and the spores, loosened from the mica, could then be removed with a platinum needle.

The basidiospores of many species retain the power of germination but a short time, especially when dry; hence cultures were made immediately from the spores on the mica. Carefully sealed Van Tieghem cells were used in which were placed hanging drops of a weak decoction of some fresh vegetable, dried fruit, etc., rendered solid by agar-agar. All materials and instruments employed in the construction of these cells were carefully sterilized. No extensive experiments were conducted to secure the germination of refractory spores, but attention was given to those species whose spores germinated readily under ordinary culture conditions.

Brefeld has rightly insisted that every culture should be begun with the germination of a single spore. To secure this end, the writer transferred a few spores with a platinum needle from the mica slip to a drop of sterile water, where they were diluted sufficiently so that a single spore could, in the course of several attempts, be carried on the point of a needle to the hanging drop in the culture cell. Almost insuperable difficulty was experienced in this operation in the case of species with extremely minute and colorless spores, for even careful microscopic examination of the hanging drop failed to demonstrate with certainty the number of spores present; such spores commonly enlarged greatly on germination, however, and thus became clearly visible.

Inasmuch as the percentage of germination in most species is low, at least considerably below 100 percent, it will be seen that a large proportion of the cells thus laboriously made showed no growth. Hence, to reduce the amount of unproductive labor, a preliminary test was made, using a culture cell in which many spores were sown. Then other cells were made containing few spores,—the approximate number depending upon the percentage of germination shown by the first cell; the spores in each cell were carefully examined and identified so far as possible as belonging to the species in hand. All cells showing the germination of more than one spore were discarded. In case but one spore germinated, the growth was carefully watched until the hyphae had spread out beyond the ungerminated spores when a bit of the mycelium-bearing agar was transferred to a new drop culture. In this way pure cultures were secured. In the case of species which proved to be of especial interest, however, pains were taken to secure the germination of isolated spores, and the discussion in the following pages is based upon cultures thus obtained. The danger of error was reduced by carrying numerous cultures as checks, and all important results were verified by cultures obtained from later collections of the basidio-fructifications in the field.

From the hanging drop, bits of mycelium were taken to start cultures in test tubes and jars upon nutrient agar, and sterilized wood, vegetables, etc. In the majority of species studied the writer was able with more or less difficulty to raise basidiosporic hymenia in the laboratory, thus completing the life cycle, and giving a supply of basidiospores of unquestioned purity for further experiments. All the more important species discussed in this paper have been kept under culti-

vation for several years and the complete life histories followed through many times.

DESCRIPTION OF CULTURES.

The writer has restricted his studies largely, although not entirely, to prostrate and encrusting species of Hymenomycetes, as they have been least studied in cultures. Considerably over one hundred species of Thelephoraceae, Hydnaceae, and Polyporaceae were collected and attempts made to germinate the spores. About seventy-five species were successfully cultivated. Six of this number possess secondary methods of reproduction of especial importance: *Corticium effusatum* and *Corticium roseo-pallens* produce mycelial conidia of great interest; *Aegerita candida* is the imperfect form of a new Peniophora; *Michenora artocreas* is the secondary reproductive condition of *Corticium subgiganteum*; the mycelium of *Corticium alutaceum* forms bulbils in great profusion; *Lentodium squamulosum* produces peculiar conidia about the margin of the pileus and upon the protruding hyphae of the trama. Each of the species above mentioned will be discussed in detail in the following pages. In addition to these more definitely characterized methods of reproduction, either oidia or mycelial chlamydospores were found in a considerable number of species, but in no case did the same species possess both.

Unfortunately, in removing the writer's effects from Cambridge, Massachusetts, to Hanover, New Hampshire, the notes were lost which described the germination and cultivation (including the formation of oidia and chlamydospores) of almost two thirds of the seventy-five species studied; consequently the information which can be presented as to the occurrence of these simpler types of spores is more incomplete than it would otherwise have been.

The records are preserved for the following twenty-eight species: — *Corticium vagum* B. & C., *C. effusatum* C. & E., *C. roseo-pallens* Burt, *C. subgiganteum* Berk., *C. alutaceum* (Schrad.) Bres., *C. roseum* Pers., *C. atrovirens* Fr., *Coniophora suffocata* Peck, *Peniophora candida* (Pers.) Lyman, *P. pertenuis* (Karst.) Burt, *Stereum gausapatum* Fr., *Hydnum* sp. (?), *H. ochraceum* Pers., *Irpex* sp. (?), *Phlebia* sp. (?), *Radulum tomentosum* Fr., *Fomes leucophaeus* Mont., *Polyporus fumosus* Fr., *P. adustus* (Willd.) Fr., *P. brumalis* (Pers.) Fr., *Polystictus conchifer* Schw., *P. versicolor* (L.) Fr., *Poria* sp. (?), *P. spissa*

Schw., *P. incrustans* B. & C., *Daedalea unicolor* Bull., *Lenzites betulina* (L.) Fr., *Lentodinium squamulosum* Morg.

OIDIA.

Of the twenty-eight species named above, five (all belonging to the Polyporaceae) possessed oidia,—viz., *Daedalea unicolor*, *Lenzites betulina*, *Polyporus fumosus*, *Polystictus conchifer*, and *Polystictus versicolor*; oidia were not seen by the writer in the Hydnaceae although Brefeld found them in species of *Phlebia* and *Irpex*; nor did they appear in the Thelephoraceae. Thus the writer's results agree with those of Brefeld, viz., that oidium formation is present in a large proportion of species in the higher families of Hymenomyces, but is not known in the lower families,—*Corticium alutaceum* being the only known case among the Thelephoraceae, and here the bodies produced may more properly be called conidia than oidia (see p. 163).

The method of formation is well described by Brefeld ('89, p. 25). They arise by the division of a hypha into many cells which become separated from one another to form thin-walled, short-cylindrical bodies with rounded ends and usually with dense refractive contents (pl. 18, fig. 1). The retention of vitality by oidia is short, but if transferred to drop cultures when fresh they germinate readily in case of the species studied by the writer, enlarging greatly in most cases, and producing germ tubes at one or both ends.

CHLAMYDOSPORES.

Chlamydospores were produced in abundance in the writer's cultures upon the mycelia of the following species: *Lentodinium squamulosum*, whose position is midway between the Agaricaceae and the Polyporaceae; *Poria incrustans* (?) of the Polyporaceae; *Radulum tomentosum*, two undetermined species of *Irpex* (or *Hydnum*), and one of *Phlebia* of the Hydnaceae; *Corticium vagum* and *Corticium effusatum* of the Thelephoraceae. Moreover, the spores of *Michenera artocreas*, which is now shown to be an imperfect state of *Corticium subgiganteum*, are chlamydospores of a specialized nature.

Brefeld ('89) found chlamydospores only in *Ptychogaster* and *Fistulina* of the Polyporaceae, and in *Nyctalis* of the Agaricaceae,—three genera in which there is a copious formation of chlamydospores

encroaching on the basidiosporic fructification. He makes no mention of them in describing his cultures of other species. The writer finds chlamydospores to be of much wider distribution than Brefeld had supposed, particularly upon the vegetative mycelium. Further culture study will assuredly add many names to this list and show the wide distribution of chlamydospores among all families of Hymenomyces. They are undoubtedly important reproductive organs of the vegetative mycelium in many species.

The formation of the chlamydospore agrees with the process known in other groups of fungi, as in *Mucor racemosus*, but the development will be outlined here for purposes of comparison with the spores of *Michenera artocreas* (see p. 155). The method of development does not vary in the species examined, and is well illustrated in *Corticium effuscatum* and *Lentodinium squamulosum* (pl. 21, fig. 80-83, and pl. 22, fig. 110-114). Any cell of the mycelium may form a chlamydospore, hence the position is either terminal or intercalary; and in species which produce them profusely they are thickly strewn along the hyphae, and the intervening spaces are spanned by the empty hypha walls (pl. 21, fig. 80). In the process of formation the protoplasm of the hypha becomes vacuolate, certain cells losing their contents entirely, while in others which are to produce chlamydospores the condensing protoplasm draws away from the ends of the cell and concentrates in the middle region where the side walls bulge to receive it (pl. 21, fig. 82). Here a resistant wall (endospore) forms about the encysting cell within and adnate to the hypha walls on each side, and cuts off the empty portion of the parent cell at each end. Continued contraction of the protoplasm may cause the abandonment of these end walls, and the formation of new walls farther in (pl. 21, fig. 83; pl. 22, fig. 111). The mature chlamydospore is thick-walled, with dense, granular, refractive contents becoming vacuolate with age. The usual form is lemon-shaped, but great variation is shown on account of different degrees of contraction of the protoplasm. Hence in the same culture we may find all shapes from spheres to cylindrical cells whose walls have become resistant; the latter function in every way as normal chlamydospores (pl. 22, fig. 112-114). The mature spores are freed only by the decay of the empty portion of the parent hypha, and are able to withstand adverse conditions for a considerable period. In drop cultures they germinate at once by the formation of from one to several germ tubes (pl. 21, fig. 84-85; pl. 22, fig. 115).

A further consideration of the nature of oidia and chlamydospores is reserved for a later page (see p. 194), after the discussion of the six species mentioned above as possessing more highly developed secondary reproductive methods.

CORTICIUM SUBGIGANTEUM Berk.

(*Michenera artocreas* B. & C.)

Pl. 18, fig. 2-21; pl. 26, fig. 137.

It has for some time been suspected that an organic connection exists between *Michenera artocreas* and the *Corticium* which usually accompanies it. In order to test this point, specimens of *Michenera* and the associated *Corticium* were collected in swamps at Kittery Point, Maine, and at Bedford and East Billerica, Massachusetts, on dead limbs of *Acer*. The spores of both *Michenera* and *Corticium* were germinated and grown in cultures and the connection which had been suspected between the two forms was conclusively proven. This *Corticium* was distributed by Ellis & Everhart in North American fungi, no. 3102, as *Corticium ochroleucum* Fr., var. *resupinatum* E. & E. The label bears the following note: "*Michenera artocreas* B. & C. is usually found associated with this and growing out of it." But after examining the writer's material Professor Burt says: "Your specimen is certainly *Corticium subgiganteum* of Berkeley. This species was distributed by Ellis & Everhart as *Corticium ochroleucum* Fr., from which it is quite different according to an authentic specimen in the Kew Herbarium."

Corticium subgiganteum.— This species was described by Berkeley in "Notices of North American fungi," (*Grevillea*, vol. 2, p. 3, July, 1873). Masee, in his *Thelephoreae* ('90-'91), transfers the species to *Peniophora*, but without having seen a specimen. It has been reported from a number of widely separated regions of the United States, particularly near the Atlantic coast, from Maine to Florida, and as far inland as Ohio. It occurs principally upon species of *Acer*, but is also found upon *Magnolia* and *Carya*.

The fructification sometimes forms small patches, but is usually effused; it is smooth, of rather tough, fibrous consistency, and becomes corky when dry. The color is described by Berkeley as "at first cream-colored, then acquiring a brownish tint, especially toward the

margin." On the contrary, in the dried specimens observed by the writer the whole surface acquired the brownish tint equally, except the margin, which remained whitish or cream-colored. The hymenium rests upon a thick trama composed of interlacing uniform hyphae of small size, which appear to pass up through the subhymenium and mingle with the basidia in the form of slender branching paraphyses about 1.5μ in diameter (pl. 18, fig. 2). No cystidia were found although certain bodies about the size of young basidia but with attenuated apex were occasionally seen. The basidia are club-shaped and of large size,— $14.5 \times 40 \mu$ (pl. 18, fig. 2). The spores are very large ($14 \times 19 \mu$), globose, apiculate, with very granular contents and usually a single large refractive globule (pl. 18, fig. 3).

Michenera artocreas.— This fungus was first described by Berkeley & Curtis in "Cuban fungi," (Journ. Linn. soc. London, vol. 10, p. 333, 1869), on dead trunks of trees (black oak). Berkeley & Broome ('75) use the name *Artocreas micheneri* B. & C., and Masee in his "Thelephoreae" ('90-'91) calls it *Aleurodiscus micheneri*. The species is not common, but has been reported from a considerable number of localities in the eastern United States, also from Cuba (Wright), upon species of *Acer*, *Quercus*, and *Fraxinus*.

The fructification has the form of a cup, from 3 to 20 mm. in diameter with whitish or brownish tinted sides and projecting rim; in mature specimens this cup is nearly or quite filled with reddish brown spores which cohere in a compact mass that becomes hard and cracked when dry. These cups are solitary, grouped together, or even more or less completely fused (pl. 26, fig. 137). In a longitudinal section three distinct regions may be recognized (pl. 18, fig. 6): the sides and base of the cup composed of interlacing hyphae, the hymenium lining the whole interior, and the brown mass of mature spores which frequently fills the cup to the brim. The sides and base of the fructification are composed of small colorless branching hyphae, woven into a loose spongy tissue. Near the exterior the hyphae are faintly brownish tinted, and layers of the same color traversing the tissue of the cup show that in many cases the development has been by intermittent periods of growth. In the inner region this spongy tissue passes into a denser zone of a yellowish or brownish color, the subhymenium. From this zone arise the sporophores and paraphyses which compose the hymenium. The sporophores (pl. 18, fig. 8-9) are branching clusters of hyaline filaments of varying length, each branch bearing

terminally a single, smooth, ellipsoidal or lemon-shaped spore (pl. 18, fig. 13), which is attached to the sporophore by a persistent shank or stipe, and bears at the apex, opposite the stipe, a slender, tapering lash. The body of the mature spore is yellowish to deep reddish, very thick-walled, 10–15 μ wide by 12–20 μ long, and contains dense protoplasm with one or more prominent vacuoles. The stipe is empty, of the same diameter as the sporophore (3–4 μ), about as long as the inflated portion of the spore, and is usually lighter in color than the latter. The lash is flexuous, hyaline, empty, 1.5–2.5 μ in diameter and frequently very long (20–75 μ). The paraphyses which are intermingled with the sporophores, are long, slender, hyaline, non-septate hairs, of about the same diameter as the sporophores among which they arise, and are undoubtedly of the same nature with them, for abnormalities are present showing all gradations between paraphyses and normal sporophores with fully developed spores.

Cultivation of basidiospores.—Some difficulty was experienced in securing germination in most media tried, but moderate success was attained with prune decoction. The large spores germinate in two or three days, usually producing two or more germ tubes (pl. 18, fig. 4–5). The young mycelium is composed of hyaline hyphae of rather small size (1.5–3 μ), which are devoid of clamps, and without any distinguishing peculiarities. The substratum becomes covered with a cottony growth which is at first white, and later frequently shows brownish red spots and patches, the color being located partly in the hyphae and partly in excreted material. Clamp connections are apparently not formed in this fungus, as repeated search has failed to reveal them. No oidia, chlamydospores, or conidia were found upon the mycelia, although occasionally certain enlargements of the hyphae at first seemed indicative of the formation of chlamydospores, but they always failed to develop. In potato-agar tubes one month old the brownish red spots mentioned above become especially numerous and often enlarge to form pustules of considerable size; examination shows that they frequently contain many *Michenera* spores. Wood cultures also yield abundant *Michenera* fructifications. Thus far the writer has not been able to secure the completion of the life history by the production of basidiosporic hymenia in pure cultures. Portions of the mycelium sometimes assume the color and appearance of a hymenium, but examination of these regions has always failed to reveal basidia.

Cultivation of Michenera spores.— Germination of the thick-walled mature spores was obtained in but few instances; very strongly concentrated potato-agar gave the best results. Younger spores germinate much more readily; in fact, if the spore is not fully mature and some protoplasm still remains in the shaft or appendage, this frequently puts forth a hypha, while the spore proper remains unchanged (pl. 18, fig. 14). This should not be regarded as germination of the spore, but merely as a continuation of the vegetative growth. From three to four days are normally required for the germination of mature spores. The number of germ tubes is frequently as high as three or four from a single spore, one commonly making its appearance through the empty shaft (pl. 18, fig. 15). The mycelium produced is indistinguishable from that arising from a basidiospore, and, like it, soon forms *Michenera* fructifications, but has not thus far produced basidiosporic hymenia. Although the chain of evidence is incomplete through the absence of this last link, yet the identity of *Corticium subgiganteum* and *Michenera artocreas* as stages in the development of one fungus seems sufficiently demonstrated by the absolute similarity of the mycelia, and especially by the constant and regular production of *Michenera* fructifications in cultures of the basidiospores.

Development of fructification and spores of Michenera artocreas.— The spores grown in agar tubes agree perfectly with those produced under natural conditions in the field, but are heaped up in a pustule without the formation of a cup. In wood cultures, too, the sides of the cup are much lower than in Nature and frequently appear only when the fructification is sectioned, being completely submerged by the copious production of spores. In such cases the general appearance of the fructification strongly resembles that of *Hypoxylon*. Culture conditions appear to disturb the normal process of development, and to produce a stimulation of spore formation at the expense of the sterile parts of the cup. Hence the following account of the development of the fructification is taken from specimens collected in the field.

The first appearance of the cup is a small pyramidal growth of hyphae, faintly brownish tinted on the exterior. A longitudinal section frequently reveals concentric brownish layers which mark the successive periods of growth in the intermittent development of the pyramid. The hymenium originates at the apex of the pyramid where the hyphae begin to form spores and a brown spot appears.

This spot becomes sunken, due to the continued upward growth of the surrounding sterile tissue to form the raised sides of the cup. Patouillard ('91b) observed a young cup of this age with edges nearly meeting above, and supposed that the cup was primarily closed, and hence that the development of the hymenium was angiocarpic. The writer has in no instance observed the formation of spores within a closed fructification. The origin of the hymenium is superficial and its development entirely gymnocarpic, for the cup makes its appearance by the continued upward growth of the tissue at the margin of the hymenium, not by the rupture of an originally closed vessel. The diameter of the fructification increases by the continued expansion of the hymenium, which develops not only in the bottom but also up the sides to the margin of the cup. The spores are produced continuously, and since their dissemination is retarded by the long paraphyses and by the entangling lashes of the spores themselves, they collect in the cup in a thick red-brown mass.

The sporophore is a short hyaline filament of nearly twice the diameter of the sterile hyphae below, and bears a single terminal spore. The origin of the sporophore in the subhymenium is difficult to trace in the compact mature fructification, but is easily determined by the examination of very young hymenia formed in cultures, which may be dissected out under the microscope (pl. 18, fig. 8-9). The normal vegetative hyphae, with diameter of 1.5-2.5 μ , give off large branches (3.5-4.5 μ in diameter) which act as sporophores. Frequently the increase in size is gradual and the hypha may branch repeatedly before it bears spores, forming a cymose cluster. After the formation of the first spores repeated basipetal branching takes place either just at the bases of the spores or from lower parts of the sporophores.

In a young hymenium spores in all stages of development are met with, together with many abnormalities. The process of development of the spore is as follows (pl. 18, fig. 10-13). The end of a young sporophore, rich in protoplasm, enlarges to form the lemon-shaped spore. Meantime growth continues from the upper end of the enlargement to form the slender appendage or lash, which has about one half the diameter of the sporophore. As the spore approaches full size it is cut off from the sporophore by a septum some distance below the swollen portion, thus forming the stipe. The terminal appendage and basal stipe become vacuolate and finally emptied of their protoplasm as it gradually concentrates in the body of the spore. The

mature spore has a thick wall consisting of an episore, which is the wall of the original hypha and which also forms the walls of the stipe and the appendage, and an endospore which surrounds the inflated portion only. The endospore is formed during the period of concentration of the protoplasm. Therefore the stipe and base of the appendage frequently show thin, curving, transverse septa, abandoned as the protoplasm shrinks inward, which belong to the endospore and mark the successive stages in the concentration of the spore's contents (pl. 18, fig. 13). As the spore matures the color deepens and finally becomes yellowish to deep reddish brown, the color being partly in the walls and partly in the spore contents. Usually the stipe is of lighter hue than the body of the spore, while the appendage is hyaline, although all three may be of the same shade.

Among the mass of perfect spores may be observed many abnormalities (pl. 18, fig. 16-21). Occasionally the appendage is entirely absent, or two are seen on one spore, or the single appendage although of normal diameter is branched one or more times. Again the appendage may retain the size of a sporophore, grow on irregularly, branch, and produce other spores which are sometimes separate and sometimes more or less fused. Or the spore may enlarge and color normally but not form an endospore, the body of the spore remaining in open communication with stipe and appendage. Such a development resembles a paraphysis, a likeness which is still closer where the enlargement of the body of the spore is slight and the appendage has the diameter of a paraphysis. In fact, all gradations are found between normal spores and paraphyses, showing the morphological similarity of the two structures.

Is the spore of Michenera artocreas a chlamydospore? — This interpretation has been suggested by Peirce ('90) and Patouillard ('00). There is a very suggestive resemblance between the spores of *Michenera* and typical chlamydospores, both in the appearance of the mature spores and in their method of formation. In both cases the protoplasm shrinks into the inflated central portion of the cell leaving empty walls above and below. The successive stages in this process are marked by abandoned curving layers of the thickening endospore (see p. 150 for description of chlamydospore formation).

There are two principal distinctions between these spores and ordinary chlamydospores. The first of these is seen in the position of the spore in the hypha and in the character of the empty portions

of the parent cell. In the case of typical chlamydospores any cell may produce a spore, and the walls of the abandoned portions of the cell remain unchanged and finally disappear. In the case of this species, however, the spore is normally formed in a terminal cell, and the empty portions of the parent cell are differentiated into stipe and appendage which persist as permanent parts of the spore. When the typical chlamydospore chances to be formed subterminally the resemblance is more exact, as the empty end of the parent hypha simulates the appendage of the *Michenera* spore. This subterminal position has become habitual with the *Michenera*, resulting in the formation of the characteristic attenuated appendage. But every fructification shows many exceptions to this rule, in the case of spores in which the appendage is absent or has developed vigorous growth, perhaps with the formation of other spores beyond; in the latter instance the spore has an intercalary position like an ordinary chlamydospore.

The second distinction between these spores and typical chlamydospores is that the former are grouped into definite fructifications. In agar cultures of *Michenera* isolated spores are frequently produced by the mycelium independent of any fructification, but under more natural conditions the spores are collected in a highly differentiated structure with a well defined hymenium. No such condition is known in the case of undoubted chlamydospores, but the nearest approach is found in *Nyctalis*, *Ptychogaster*, and *Fistulina*, where extensive chlamydosporic fruit bodies are formed, though there is no definite hymenium and the fructifications are formed through the usurpation by the chlamydospores of what were primarily basidiosporic fructifications.

It seems impossible to avoid classing these bodies as chlamydospores since their method of formation is chlamydosporic. They are, however, more highly organized than other spores of this nature, and in assuming the habit of forming definite fructifications, they have developed many of the characteristics of the higher types of spores.

History of Michenera artocreas.—This fungus has, by common consent, been given a place among the Thelephoraceae, although the justification for this classification is not apparent. It is true that there is a certain external resemblance between the *Michenera* fructification and a circumscribed basidiosporic hymenium of the type seen in certain species of *Corticium*, but the likeness is entirely superficial,—the spores are quite unlike any known basidiospores, the sporophores

do not resemble basidia, nor has the basidiomycetous nature of the fungus been proven in any way. Yet the authors of systematic treatises of the Thelephoraceae (Saccardo, '88, in the "Sylloge," and Hennings, '97, in "Pflanzenfamilien") assume that the spores, hymenium, etc., of *Michenera* are homologous with structures of the same name in *Corticium*, and the two genera are placed side by side. This error is due to the acceptance of the descriptions and classification given by the first observers of this plant who had but a very imperfect knowledge of it.

A careful examination of the structure and development of *Michenera artocreas* proves conclusively that its spores are not basidio-spores, nor is there any internal evidence of a basidiomycetous nature. It is true that a *Corticium* hymenium is usually found in the neighborhood of the *Michenera*, but the only argument thus far advanced in proof of their connection is the inconclusive one of contiguity. Peirce ('90, p. 308) made a study of herbarium specimens and concluded that such neighboring hymenia "have nothing whatever to do with *Michenera artocreas*," and that "the basidial stage of *Michenera artocreas* either does not exist at all, or it is so completely replaced by the conidial stage (represented by the flask-shaped cells) that it very seldom appears." Patouillard ('91b) examined material collected by Wright in Cuba, and decided that the species should be removed from the Thelephoraceae and placed among the Uredineae on account of the character and method of formation of its spores. In a later paper ('00, p. 67), however, Patouillard abandons this view and says: "Le genre *Michenera*, Berk. & Curt. doit être rattaché à *Corticium* comme forme conidifère." He observed a *Corticium* growing closely about the *Michenera*. "Ce *Corticium* présente une trame filamenteuse d'hyphes identiques à celles de la paroi des cupules de *Michenera* et en continuité avec cette paroi." On this account he unhesitatingly connects the two forms and agrees with Peirce in calling the peculiar spores of the *Michenera* chlamydo-spores of the *Corticium*. The writer has also observed the absolute similarity between the tissue forming the base and sides of the *Michenera* cup and the medulla of an adjacent *Corticium* hymenium, but it is impossible to trace the continuity of the interlacing hyphae with sufficient certainty to establish an organic connection between the two fungi.

The *Corticium* appears on the under side of the host branch, and the *Michenera*, when present, on the upper side. On fallen branches,

however, where the *Corticium* chanced to lie uppermost, *Michenera* cups may appear rising directly from the hymenium, not as if breaking through from below like a foreign fungus, but actually fused with the tissue of the *Corticium* whose hymenium overruns the bases and sides of the cups. It was doubtless such specimens as this that Patouillard had before him when he asserted that the *Michenera* is a conidial form of the *Corticium*. This presumption is strengthened by an experiment performed by Dr. Thaxter, the results of which he has made known to the writer. He reversed the position of several branches, bringing the *Corticium* uppermost, and found that this change was frequently followed by liberal production of *Michenera* cups arising from the hymenium (pl. 26, fig. 137). This was true even in specimens which did not originally show any *Michenera* fructifications (pl. 26, fig. 137, lower figure). This line of proof, however, does not absolutely demonstrate the organic connection of the two fungi, and conclusive evidence must come from culture study where the complete life history can be followed out.

Other species of Michenera.—The only other representative of this genus is *M. poroniaeformis*, described in 1875 by Berkeley & Curtis from Ceylon. After a study of its structure and development, Masee ('88) decided that it has no affinity whatever with the Hymenomyces. He renamed it *Matula poroniaeformis*, and made it the type of the *Matuleae*, a new order of Gasteromycetes, intermediate between the *Nidulariaceae* and the *Hymenogastraceae*. "The leading features of the plant are: (1) a peridium closed above by an epiphragm until all differentiation is completed; (2) a gleba broken up into numerous cavities or loculi by dissepiments bearing basidia on their free surfaces." The basidia are described as "very primitive in structure, being slightly or not at all thickened at the apex, and producing usually a single spore which at first appears as an obovate terminal cell attached by a broad base. . . . While the spores are still young and obovate they are set free by the total disappearance of the basidia, afterward becoming spherical and increasing considerably in size."

It seems extremely doubtful whether the plant described above should be regarded as the perfect state of a Basidiomycete, for, as in the case of *Michenera artocreas*, the structural resemblances may be merely superficial and accidental. Until further information is at hand demonstrating the nature of the monosporic "basidia" which Masee describes, it is safer to regard them as conidiophores of a fungus whose perfect condition is yet unknown.

The removal of this species from *Michenera* leaves *M. artocreas* as the sole type of the genus, which now sinks to the status of a form genus whose only representative is the imperfect condition of *Corticium subgiganteum* Berk.

CORTICIUM ALUTACEUM (Schrader) Bresadola.

Pl. 19, fig. 22-43.

Bresadola (Hym. Hung. Kmetiani, p. 46 (110), 1897) gives the synonymy of this species as follows: *Thelephora alutacea* Schrader, Spic. Fl. Germ., p. 187, 1794; *Thelephora radiosa* Fr., Obs., vol. 2, p. 277; *Corticium radiosum* Fr., Epicr., p. 560; Icon. Sel., tab. 198, fig. 1; *Corticium citrinum* Pers., Myc. Europ., vol. 1, p. 136; Fr., Hym. Europ., p. 655.¹

This species was collected several times during two successive years in the vicinity of Cambridge, Massachusetts, on well rotted oak logs, although never in large quantities. Material sent to Professor Burt was pronounced by him to agree well with European specimens in his herbarium from Bresadola. In the writer's cultures two secondary methods of reproduction appeared which will be described below.

The specimens collected by the writer were effused, thin, closely adnate, with rather indeterminate sometimes fibrillose margin, and varied in color from whitish or cream-colored to faintly ochraceous. The basidia are apparently not compacted into a dense hymenium; they are rather short ($5-7 \mu \times 20-40 \mu$), only slightly clavate, 4-8 spored (usually 5-6), and arise from septate, clamped, nodosely branched hyphae (pl. 19, fig. 22). The spores are hyaline, ovoid to lemon-shaped, slightly inequilateral, $3.8-4.5 \mu \times 5.8-6.5 \mu$, with granular contents and often one or more guttulae (pl. 19, fig. 23).

Germination of basidiospores.—An unusually large proportion of the spores was found to be capable of germination, and, although thin-walled, many retained this power even after remaining for more than three months in a dry condition.

Germination is very rapid in drop cultures. The spore enlarges to several times its original volume and in from twelve to fifteen hours

¹ In addition to the synonymy given by Bresadola, Streinz and Fries mention as synonyms: *Athelia ochracea* Pers., Myc. Europ., vol. 1, p. 84, and *Ganoderma radiosum* Hoffm., Veg. subterr., vol. 15, pl. 10, fig. 2.

produces the first germ tube, which is normally followed some hours later by a second germ tube from the opposite end of the spore (pl. 19, fig. 24). The germ tubes grow rapidly into an extensive primary mycelium composed of small hyphae about $3\ \mu$ in diameter and devoid of clamps. After five or six days the hyphae of the primary mycelium give off branches of large size which average $6\ \mu$ in diameter and possess abundant clamps (pl. 19, fig. 25-26); these hyphae constitute the secondary or mature mycelium, which at first grows intermingled with the primary mycelium and sometimes anastomoses with it. The latter, however, soon loses its contents and disappears from the culture; it is not again produced although frequently branches of limited growth from the secondary mycelium resemble the primary hyphae both in size and in absence of clamps. This change in the character of the mycelium takes place regularly in all cultures and is apparently not influenced by the nature of the culture medium or by other external conditions.

Reproduction in cultures.—No chlamydospores or chlamydosporic cells were observed in any of the writer's cultures; all the cells of the vegetative mycelium remained thin-walled, and lost their protoplasm with equal rapidity. In old cultures the distal ends of many cells of the secondary mycelium become enlarged (pl. 19, fig. 27), and somewhat resemble developing chlamydospores. These enlargements, however, do not have thickened walls, nor is the protoplasm retained beyond other parts of the mycelium; they are not reproductive and are perhaps due to imperfect nutrition.

Typical oidia were not observed in this species, but in drop cultures from six to ten days old, small conidia appear, frequently in considerable abundance, which do not differ greatly from oidia. Moreover, in nutrient-agar tubes and in cultures upon sticks of wood, bulbils are formed in such profusion as to cover the substratum and completely obliterate the mycelium.

Finally, in old cultures, there is occasionally a development of basidiosporic hymenium, thus completing the life history; but, although normal in appearance and structure, the hymenium was always very limited in extent in the writer's cultures.

Conidia.—In drop cultures from six to ten days old, tiny conidia appear about the margin of the drop on clampless conidiophores which either arise directly from the primary mycelium, or, more rarely, are slender clampless branches from the secondary (pl. 19,

fig. 28). The conidiophore is slender, 2–3 μ in diameter, either simple or branched, and bears laterally several to many conidia irregularly distributed along its length. The conidia are thin-walled, hyaline, cylindrical or slightly curved, 1.8–2.6 μ in diameter by 4.5–6.7 μ in length, and average $2 \times 5.5 \mu$ (pl. 19, fig. 29). They arise with but slight regularity of sequence or position as lateral, branch-like outgrowths from the conidiophore, and are generally of the same diameter with it. Each conidium is cut off by a curved septum, and soon falls away, at first leaving a depression in the conidiophore corresponding to its convex base (pl. 19, fig. 29). When the conidiophore is immersed in the nutrient drop, or rests on its surface, the conidia show a tendency to assume right and left positions parallel to the surface of the drop (pl. 19, figs. 28, 30); but when the fertile hypha extends out into the air the conidia are produced radially on all sides of the conidiophore (pl. 19, fig. 32). In any case there is a tendency for adjacent conidia to assume a parallel direction in groups of two or more. As the old conidia fall away new ones may develop from other parts of the conidiophore (pl. 19, fig. 29) or all may mature at once without any subsequent growth. The total number of conidia produced on a single conidiophore varies from one to more than twenty.

After the formation of conidia, the conidiophore soon loses its protoplasm and disappears, but a single conidium is frequently first cut off from its distal end (pl. 19, fig. 30). In exceptional cases, a considerable length of the old conidiophore may, after the formation of the lateral conidia, break up into a chain of two or more spores, thus resembling the formation of oidia (pl. 19, fig. 31).

Germination of conidia.—Germination begins at once in cell cultures, the conidium swelling enormously and giving off two or more germ tubes. The whole conidium may enlarge and become lemon-shaped or nearly spherical (pl. 19, fig. 33a), but more frequently the swelling is unequal at the two ends and the spore becomes pear-shaped (pl. 19, fig. 33b). In the former case germ tubes are usually given off from both ends at once (pl. 19, fig. 34a), while in the latter the first germ tube appears at the larger end and may be subsequently followed by one or more others from the sides or smaller end (pl. 19, fig. 34b–34c).

The germ tubes develop into small-sized, clampless hyphae constituting a primary mycelium which is not externally distinguishable from that arising from a basidiospore. In certain respects, however,

it differs from the latter; first, in its greater duration, the secondary or clamped mycelium not appearing for from ten to twelve days; and, second, in the increased production of conidia, which are frequently formed sparingly in cultures from basidiospores, but always in abundance when the culture originates from a conidium. In succeeding generations of cultures from conidia the formation of these spores becomes more and more copious, and the appearance of the secondary mycelium is longer and longer delayed, until in some cases the clamped hyphae fail to appear at all during the entire life of the drop culture. If transferred to an agar tube, however, the secondary mycelium finally develops, and is followed by the production of bulbils as in the case of cultures from basidiospores. Thus it appears that the conidia belong essentially to the primary mycelium, because they are produced by primary hyphae, or by branches from the early growth of the secondary mycelium which resemble primary hyphae, because they invariably give rise to primary mycelia on germination, and because continued cultivation of conidia causes the characteristics of the primary mycelium to become intensified, and separates the latter more sharply from the secondary mycelium. The significance, if there is any, of this separation into primary and secondary mycelia has not been determined.

The nature of the conidia.— It is evident that in certain respects these bodies, which we have called conidia, closely resemble oidia. The occasional breaking up of the whole hypha into a chain of spores is exactly comparable to the formation of oidia; but such a case is the exception, not the rule. Moreover, the cutting off by a mere septum, without the formation of a constriction or sterigma, of a cell having the same diameter and appearance as the parent hypha, is a type of spore formation which is decidedly inferior to that ordinarily pertaining to conidia, and closely resembles the production of oidia, which are merely segments of the parent hypha. On the other hand, the character of true conidia is shown (1) by the differentiation of a rather definite sporophore which may be quite easily distinguished from the vegetative hyphae; (2) by the early disappearance of the sporophore after the separation of the spores, while the latter retain their vitality for a slightly longer period, thus indicating that we have here not merely vegetative cells, but a definite reproductive mechanism showing some differentiation; (3) by greater uniformity in shape, size, and general appearance of the spores than is usually seen in oidium

formation; and (4) by the formation of the spores separately and laterally on the sporophore in most cases, together with a tendency for adjacent spores to assume a definite position with regard to one another. Hence the writer is of the opinion that we here have to do with reproductive bodies which have advanced beyond the grade of oidia, and, while not coming strictly within our definition of conidia, merit the latter title rather than the former. The significance of this interpretation will be seen in the discussion to follow concerning the nature of oidia and chlamydo-spores (see p. 194).

Bulbils.—In nutrient-agar tubes and in cultures upon wood, the secondary mycelium after a few days' growth produces small bulbous sclerotia or bulbils. These are formed in such quantities in well nourished cultures as to cover the substratum, completely effacing the mycelium from view, and forming a layer from 1 to 3 mm. in thickness. Bulbils never appear on the primary mycelium but invariably occur upon the secondary, without reference to whether the culture originates from a basidiospore, a conidium, a bulbil, or a transfer of vegetative mycelium. They appear on all media, even a very attenuated decoction producing a moderate quantity. Hence we may say that bulbils are normal and unfailing productions under all culture conditions, and the same appears to be true under natural conditions also, for careful examination of the basidiosporic fructifications collected in the field by the writer revealed bulbils accompanying the hymenium and partially overrun by it.

The bulbils (pl. 19, fig. 40) are reddish brown or chocolate-colored clusters of cells, more or less globose in shape, and usually 65–80 μ in diameter, although ranging as high as 220 μ . The cells composing the cluster vary in diameter from 10–25 μ , and have thick brownish walls, and very dense granular contents; although angular through mutual pressure they are not closely enough compacted to obliterate entirely the intercellular spaces (pl. 19, fig. 41). The bulbils are frequently very irregular in shape due to the unsymmetrical arrangement of the cells, and to the bulging of the free outer walls. There is no distinction between internal and external cells of the cluster. The external cells first lose their contents through age, and hence old bulbils frequently present the false appearance of having an irregular cortex of empty cells; but at the time of maturity the cells of the cluster are quite undifferentiated as regards size, shape, contents, or power of germination.

Formation of bulbils.—A sparse mycelium develops over the surface of the culture medium, and after about ten days it takes on a powdery appearance under a hand lens. Microscopic examination shows that the hyphae of the secondary mycelium are putting forth numerous, short, knotted outgrowths (pl. 19, fig. 35–37), which branch profusely and bulge irregularly to form close bundles of a highly distorted appearance. The knotted closely compacted elements of each bundle become cut up into cells which adhere to one another, and all trace of the original branch is soon lost (pl. 19, fig. 35–40). The cells enlarge and thicken their walls, and the bundle becomes a globose or irregularly shaped cluster of brown thick-walled cells. The production is so profuse that many bulbils may appear on one hypha, either forming on short lateral branches, or engulfing the hypha itself, which in this case does not run through the bulbil as an axis but completely loses its individuality in the elements of the developing cluster. Practically the whole visible mycelium may thus become swallowed up. Occasionally neighboring clusters become fused, due to pressure at time of formation, but usually adjacent bulbils remain independent and preserve their unity of origin from a single branch.

Mingled with the perfect bulbils of globose form, are many of abnormal appearance as to shape, size, arrangement of cells, etc., some being reduced to a straight or curved row of several cells, which have the size and appearance of bulbil cells, but are not compacted into a cluster (pl. 19, fig. 42). Such numerous variations in the character of the bulbils are to be expected from their method of formation. There is no characteristic primordium in this species like the coiled hypha of *Helicosporangium* (see p. 196), which would naturally yield a more uniform product. The initial hypha may sometimes chance to bend on itself in a helicoid fashion (pl. 19, fig. 35), but there is no general regularity in its appearance or behavior. The bulbil arises simply as the result of a close irregular branching and knotting of the parent hypha.

Cultivation of bulbils.—The exact length of time during which bulbils will retain the power of germination was not determined, but it is considerable. Those taken from a dried-up agar tube nearly three years old still germinate vigorously. The process of germination is very rapid in all media; ten to twelve hours are sufficient for the formation of germ tubes as long as the diameter of the bulbil (pl. 19, fig. 43). Germ tubes not only arise from the external cells,

but others force their way out from the cells below, and an extensive secondary mycelium is quickly formed which again produces bulbils in profusion. Thus it is seen that the bulbil belongs entirely to the secondary mycelium, since it is invariably formed on a clamped hypha, and gives forth germ tubes which bear clamps immediately.

No conidia have been seen in cultures of bulbils although the writer has repeatedly sought for them. As stated above, it appears that the conidia belong to the early period of development of the fungus,— to the primary mycelium and the first growth of the secondary — while the bulbils succeed them, and are such a successful means of reproduction that the conidia are not again resorted to.

Other bulbils belonging to Basidiomycetes.— The writer has under cultivation two other kinds of bulbils which are proved to belong to species of Basidiomycetes, inasmuch as the mycelia are profusely clamped and basidiosporic hymenia are produced in pure cultures. Unfortunately the writer has thus far succeeded in producing only very imperfect specimens of hymenia with scattered basidia, from which specific diagnosis is impossible. The bulbils of one of these species were found by Dr. G. P. Clinton in the vicinity of Cambridge, Massachusetts, on a fragment of an old newspaper in a field. They are of about the same size as those belonging to *Corticium alutaceum*, but are somewhat lighter-colored, the component cells are smaller and more closely and evenly compacted, and the form is more regularly spherical. The method of formation of these bulbils agrees exactly with that described above for *Corticium alutaceum*, except that in the early stages the branching is more loose and open. Arising from the normal clamped mycelia in drop cultures are many freely branching hyphae of smaller caliber which produce conidia in considerable abundance of the type found in *Corticium alutaceum*. In wood cultures small rhizomorphic strands are at first formed thickly upon the substratum, but these are soon covered and partially concealed by the innumerable bulbils.

The bulbils belonging to the second species mentioned above were discovered by Mr. A. H. Chivers in a gross culture of bits of wood, paper, etc., from the floor of a woodshed in Hanover, New Hampshire. This species is very similar in most respects to that just described, but is readily distinguished in cultures, even with the naked eye, by the much lighter rusty-cinnamon color of the bulbils, and by the very numerous, white, fibrous strands of hyphae which radiate

thickly over the substratum and are never completely covered by the subsequent formation of bulbils even in old cultures. In rare instances conidia were seen of the type described above.

These two kinds of bulbils thus agree very closely with each other and also with those of *Corticium alutaceum* in appearance, and in method of development and of germination. Moreover, the same type of conidium is associated with all three. Hence it seems probable that they belong to closely related species of *Corticium*, but, as is mentioned above, this point cannot be determined until more perfect hymenia are obtained.

Several other varieties of bulbils have been cultivated by the writer but have given no indication of basidiomycetous relationships. Further discussion of these forms and of the nature of bulbils in general is reserved for a later page (see p. 196).

PENIOPHORA CANDIDA (Persoon) Lyman.

(*Aegerita candida* Persoon.)

Pl. 20, fig. 44-55; pl. 26, fig. 138.

The small white fructifications of *Aegerita candida* are common upon damp prostrate sticks of alder and other wood about the wet margins of ponds and along brooks. On a favorable stick the fructifications may be closely packed together side by side, in which case they strongly resemble insect eggs in form, size, and general appearance. Frequently there is associated with the *Aegerita* a delicate whitish, pearl-colored or creamy Basidiomycete of the *Corticium* type. A connection between the two forms was suspected on account of this companionship, and, although the *Aegerita* frequently occurs alone, prolonged search failed to reveal any well developed specimens of the Basidiomycete which were not more or less closely accompanied by the *Aegerita*. The identity of the two forms as stages in the life history of one species was definitely established by culture study, as will be explained below.

Specimens of the Basidiomycete were sent to Professor Burt, who pronounced it a new species of *Peniophora*, which is described below as *Peniophora candida* (Persoon). It is a very delicate form, pure white or frequently pearl-colored when moist, and becoming faintly cream-colored when dry. It appears first in the form of small circular

patches surrounding or in the immediate neighborhood of *Aegerita* fructifications. These patches spread and become confluent, finally forming an effused area which is, however, never of great extent. The thickness is so slight that when dry the hymenium is easily overlooked, and it often appears like a subiculum on which rest *Aegerita* sporodochia. Cystidia are scattered, few in number, and appear only in well developed hymenia (pl. 20, fig. 44).

Peniophora candida (Persoon) Lyman.

Thin, inseparable from the substratum; commencing as small patches with indeterminate margin, which soon become confluent and form effused areas. Hymenium very minutely velvety; white or pearl-colored, often becoming faintly cream-colored. Cystidia scattered; cylindrical or attenuated upward; $5-8 \mu \times 40-60 \mu$. Spores globose or ellipsoidal with a small apiculus; $5 \times 6 \mu-6.5 \times 8.5 \mu$, average $5.8 \times 7 \mu$; containing from one to many refractive guttulae of varying size.

Imperfect form is known as *Aegerita candida* Persoon (Syn. meth. fung., p. 684, 1801). Sporodochia crowded, granular; subglobose to egg-shaped or short-cylindrical; sessile, superficial, usually with a delicate, whitish subiculum; pure white when fresh, turning yellowish and sometimes greenish when old and dry; at first glabrous, then becoming minutely mealy with the numerous conidia; $0.1-0.25 \times 0.15-0.35$ mm. Conidiophores hyaline; short, rather thick, wavy, irregularly branched, forming a loose spongy tissue. Conidia hyaline; globose, ellipsoidal or pear-shaped; $7 \times 9 \mu-10 \times 15 \mu$; terminal and solitary, or rarely in chains of two or three; forming a close, nearly smooth layer which gives the sporodochium the appearance of having a cellular cortex.

Host.— On pieces of pine boards, and fallen branches of *Alnus*, *Populus*, *Acer*, etc., in wet places; the hymenium is always accompanied by the conidial form.

Aegerita candida is found widely distributed in North America and Europe, also in Ceylon. Thus far the perfect condition has been reported only from Cambridge, Massachusetts, and Hanover, New Hampshire.

Germination of basidiospores.— Germination takes place readily in from 24 to 36 hours, the spore producing one or sometimes two germ tubes without appreciable enlargement (pl. 20, fig. 46). The hyphae are hyaline, non-granular, vacuolate, and branch freely, but the branches normally arise some distance below the septa, not immediately below, as is the rule with most of the other Hymenomycetes studied. The mycelium is at first devoid of clamps, but on the fourth or fifth day after germination these begin to develop and

finally appear at practically all septa even out to the extremities of the hyphae. All subsequent growth is fully provided with clamps.

Reproduction in cultures.—No indication of spore formation of any kind was observed in drop cultures of either basidiospores or conidia, although various media were used and the cultures were kept for weeks until the hyphae lost their contents. Nutrient-agar tubes, also, usually produced only a sparse growth of sterile mycelia, although in rare instances a few sporodochia were formed on hard potato-agar. No oidia or chlamydospores were seen in any culture of this fungus.

In cultures on sticks of *Alnus* or *Salix* in jars and large test tubes, *Aegerita* sporodochia were produced in abundance. There was no difference observable between a culture originating from the germination of a basidiospore and one from a conidium, save the temporary distinction that the latter was usually a little more tardy in beginning the formation of sporodochia. The first sporodochium was observed after four to five weeks, from which time the formation increased steadily until, at the end of three months, the production in many cultures was equal to the most abundant ever found in the field. Portions of the stick were whitened by the sporodochia, and even the sides of the vessel over which the mycelium had spread were thickly dotted with them (pl. 26, fig. 138). Moreover, an elementary formation of basidiosporic hymenium made its appearance after three or four months in all the wood cultures started from basidiospores, and in some, although not all of those started from conidia.

Thus the complete life history has been followed in pure cultures beginning with both the basidiospore and the conidium; and the connection between the *Peniophora* and the *Aegerita* is conclusively shown by the appearance of both types of fructification in the same culture, whether the starting point be the basidiospore or the conidium.

Development of the sporodochium.—Inasmuch as only sterile mycelia were produced in drop cultures, it was not possible with the microscope to follow a single sporodochium through all stages of its development. The process is easily understood, however, from the study of wood cultures in large test tubes. In the latter the mycelium soon spreads from the wood over the sides of the tube and forms a copiously branched, anastomosing network (pl. 26, fig. 138). A portion of this network scraped off and mounted on a slide shows young sporodochia in all stages of development.

The first step in the process is the formation, near the end of a hypha,

of several branches of peculiar and characteristic appearance (pl. 20, fig. 47-48). This primordium is easily distinguished from normal vegetative hyphae. Its elements are bent and twisted, irregularly gnarled and uneven in diameter, and are filled with denser, more granular protoplasm than are the neighboring cells. The branching increases (pl. 20, fig. 49) until there is formed a dense tangle of irregular hyphae in which no details can be traced out. Other branches are given off from the lower parts of the original hypha, and these participate in the formation of the sporodochium. Frequently branches from neighboring hyphae become involved so that the fructification may have a multiple origin. But in any case, the origin, whether simple or multiple, is finally obscured by the presence at the base of the sporodochium of a loose tangle of anastomosing hyphae (pl. 20, fig. 50), which may be merely the branches from the single original hypha, or may contain branches from neighboring hyphae.

Frequently when the formation of sporodochia is rapid and copious, two or more primordia may be so closely situated as to become entangled, and the resulting fructification is a twin, or an irregular composite of several fused sporodochia. Hence it is seen that this conidial fructification may lack strict unity of origin, as Harper ('02, p. 9) has pointed out in the case of basidiosporic fructifications. The sporodochium may be built up by the ramifications of a single hypha, or it may originate from several hyphae belonging to the same or to different mycelia.

The elements of the young sporodochium are of irregular lengths and project unequally from the surface, but as the mature size is reached this unevenness is lost; the tips of the branching hyphae become approximately even, while the terminal cells enlarge and become closely placed side by side to form a cortical layer of conidia. Hence the external aspect of the young sporodochium is changed from that of a tangled web of hyphae to that of a compact, nearly smooth, cellular body having a sclerotoid appearance (pl. 20, fig. 50). The spongy interior of the mature fructification (pl. 20, fig. 51) is composed of loosely radiating, copiously branched hyphae, whose cells are short, irregular, and sometimes bear clamp connections (pl. 20, fig. 54). Each hypha or conidiophore is terminated by a single spore, or rarely by a chain of two or more spores (pl. 20, fig. 53-55). These spores are of a very simple nature, being merely the enlarged terminal cells; they show no specialization of wall or contents,

are not set off from the parent hypha by sterigma or constriction, and show great variation in size and shape. Yet their spore nature seems to be conclusively proven by their separation from the parent hypha at maturity, and by their retention of the power of germination long after other parts of the sporodochium have lost all vitality.

Germination of conidia.—A whole sporodochium transferred to the hanging drop, in twenty-four hours gives forth many germ tubes. When such a specimen is crushed to separate its elements, the origin of the germ tubes from the ends or sides of the conidia is clearly seen (pl. 20, fig. 52–55). Only in the case of immature sporodochia, in which the conidiophores still retain some protoplasm, do germ tubes arise from any but the terminal cells (conidia), except in the rare instances where two or three conidia are borne in chains (pl. 20, fig. 53).

The germ tube from a conidium produces clamps immediately at all septa, while the mycelium from a basidiospore shows clamps only after four or five days of growth; but after the formation of clamps the mycelia in the two cases are quite indistinguishable.

Formation of basidiosporic hymenium.—The hymenium first appears in the form of small, thin, white patches on the surface of the wood or bark. These patches enlarge, become confluent, and overrun and immerse the sporodochia encountered, finally forming an effused layer. The process observed in the writer's cultures does not differ from that which takes place in the field, so far as can be judged from the examination of specimens collected. The very young patches of hymenium are composed of erect hyphae grouped in cymosely branched clusters, the end cells forming basidia. The method of growth of these clusters appears to be similar to that described by Harper ('02, p. 8) and de Bary ('87, p. 301) for *Hypochnus*, where by a process of basipetal branching, cymose clusters are formed. As the patches enlarge and become confluent with their neighbors, the hymenial layer increases in thickness, and becomes compacted until it is impossible to separate the cohering elements from one another or to trace the process of branching, but it is undoubtedly a continuation of that described above. Cystidia appear only in well developed hymenia; they vary considerably in size and shape, sometimes being regularly attenuated upward, but frequently cylindrical or irregular.

History of Aegerita.—The genus *Aegerita* has a large synonymy, and various writers in the past have regarded it as related to widely

different groups of fungi,— to the Discomycetes, the Pyrenomycetes, the Myxomycetes, the Ustilagineae, various divisions of the Hyphomycetes, etc. This has undoubtedly been due to two factors: first, to the great variety of forms which have from time to time borne the name *Aegerita*, and, second, to the lack of careful microscopic examination of these fungi by the earlier writers, and to ignorance of their method of development. By recent writers the genus is referred to the Tubercularieae of the Hyphomycetes. About twenty species have been described. “Five species are reported from North America, of which some are rather doubtful” (Pound & Clements, '97).

In “*Symbolae mycologicae*,” Fuckel refers to the close association, upon wet sticks, of *Aegerita candida* and a *Corticium* which he calls *Corticium lacteum* Fr. On account of this contiguity, and the close resemblance of the hyphae and spores, Fuckel was convinced of the generic connection of the two fungi. He believed that the mycelium from the germinating basidiospore produced either *Aegerita* fructifications or *Corticium* hymenia, according to weather conditions, especially as regards moisture.

The identity of two fungi cannot be positively affirmed, however, merely on account of contiguity and mycelial resemblances. This fact can be absolutely demonstrated only by growing the fungi in pure cultures, a line of proof which the writer has followed in the present investigation. The Basidiomycete concerned appears to be a new species of *Peniophora*, and not *Corticium lacteum* Fr., as Fuckel supposed.

Aside from this note of Fuckel's, no statement bearing upon the affinities of this species has come to the writer's notice, and, so far as he is aware, no other species of this genus has been connected with the perfect form of any fungus.

Other species of Aegerita cultivated.— Knowing the basidiomycetous nature of *Aegerita candida*, it seemed not unlikely that other species of this genus might have similar affinities. Hence two undetermined species were cultivated by the writer, but without important results. The first was with difficulty induced to grow in the laboratory, and finally the culture was lost. The other species has very large hyphae, devoid of clamp connections, and has as yet given no clue to its relationships. Apparently, however, these species are not Basidiomycetes since the habit of the mycelia is quite unlike that common to most members of this class.

CORTICIUM ROSEO-PALLENS Burt.

Pl. 20, fig. 56-73.

Collections of this species from well rotted oak logs at Stony Brook, Massachusetts, resemble *Corticium rubro-pallens* Schw., but were pronounced by Professor Burt to be a new species as yet undescribed, which he has previously known only in two collections of his own at Middlebury, Vermont, and in one by Professor Atkinson at Ithaca, New York.

The hymenium is thin, rather broadly effused, pale rosy salmon-colored when fresh, but fading to almost white in dried specimens. The spores are small, $2-2.5 \times 4-5 \mu$, allantoid, with thin walls and clear refractive contents (pl. 20, fig. 57).

Germination of basidiospores.—Although small and thin-walled, the basidiospores show great retention of vitality, a considerable percentage being still capable of germination after having been kept for six months in the laboratory in a dry condition. Germination in drop cultures is rapid, the spore swelling at once to several times its original volume, while the contents become more granular and develop one to several refractive guttulae (pl. 20, fig. 58). The first germ tube appears in from twenty to thirty hours, and is followed a little later by a second in the majority of cases; the spore finally becomes indistinguishable from the hypha or is marked only by a slight enlargement at the junction of the two germ tubes (pl. 20, fig. 59-62).

Nature of the mycelium.—The character of the mycelium arising from the germinating basidiospore varies. In some instances clamps appear at once on the germ tubes (pl. 20, fig. 60), but in the majority of cases no clamps are produced (pl. 20, figs. 59, 62). This primary clampless mycelium sometimes produces clamps after a period of growth, but more commonly the clampless condition persists during the entire life of the cell culture until the mycelium becomes exhausted by the production of conidia and growth ceases. The hyphae with clamps are somewhat larger, averaging $3-3.5 \mu$ in diameter, while those without clamps average $2.5-3 \mu$. Growth is equally rapid and of the same character in both cases except that the formation of conidia is slightly more tardy on the clamped mycelia. On the latter, conidia first appear on unclamped branches of somewhat smaller diameter,

but their formation soon spreads to the clamped hyphae, and the spore production in a short time becomes as copious as on the clampless mycelia.

This variation in the character of the young mycelia is not dependent on differences in the culture media or on other conditions of environment, since the two types of mycelia may arise from neighboring spores in the same drop culture, or both types of hyphae may arise together,— a germ tube with clamps appearing at one end of the spore, and one without clamps at the other end (pl. 20, fig. 61). Thus it is seen that primary and secondary mycelia, which are so clearly defined in *Corticium alutaceum*, are not sharply differentiated in this species. It is possible, however, that cytological study may reveal some fundamental distinction.

Reproduction in cultures.— In drop cultures the growth of the mycelium is very limited, being soon checked by the copious production of conidia on which the entire vitality of the culture is expended. In agar tubes, also, the mycelium does not form an extensive growth on most media. Prune decoction seems especially suited to vegetative development, and here, in addition to the usual abundant formation of conidia, an imperfect basidiosporic hymenium is frequently produced at the upper end of the tube. In wood cultures there is a sparse development of superficial mycelium followed after about two months by a fairly extensive development of basidiosporic hymenium. This hymenium agrees in every way with that collected in the field. No oidia or chlamydospores were observed in any culture.

Conidia.— Conidia are produced on all mycelia, appearing on the fourth or fifth day in the case of mycelia without clamps and one or two days later on clamped mycelia. The formation is abundant in all media, even a very attenuated decoction producing them liberally, while in drop cultures in which a medium of fair concentration is used, the formation is so copious that the vegetative growth of the mycelium is checked and the surface of the hanging drop becomes clouded by the mass of discharged spores.

The conidia are hyaline, thin-walled, allantoid, and agree with the basidiospores in every particular save that they more frequently contain refractive guttulae and are longer, being 2–2.7 μ in diameter by 6–9 μ in length (pl. 20, fig. 70). They occur in groups of from two to ten borne on low elevations on the sides of the hyphae (pl. 20, fig. 69). These groups are at first scattered here and there over the mycelium,

but become more and more thickly disposed as the production increases.

Development of conidia.— The several conidia composing one group are formed successively in the following manner (pl. 20, fig. 68 a–f): a papilla appears on the hypha, and elongates into a tubular projection which later becomes club-shaped at the extremity. The tubular base forms the sterigma, while the enlarged terminal portion develops into the spore by continued elongation. As the spore enlarges it becomes curved into an allantoid form, and is finally cut off from the sterigma by a septum. As the first spore approaches mature size, a second sterigma appears at the base of the first, or sometimes from its side, and a second spore is formed, to be followed by others successively. Thus there is rapidly formed a group or tuft of from two to many spores, each being borne on a short sterigma, while all are carried on a common elevation from the side of the parent hypha. This elevation or conidiophore may be low and dome-shaped, capitate, or irregularly shaped (pl. 20, fig. 63–66, 69). In case the mycelium bears clamps, the conidiophore frequently arises from the convex surface of a clamp connection (pl. 20, fig. 69). Figure 62 (pl. 20) represents a young mycelium which has begun the formation of conidia, and in which the majority of the conidiophores have as yet produced but one spore. One hypha from such a young mycelium showing various stages in the development of conidia is shown in figure 67 (pl. 20) on a somewhat larger scale.

The conidia seldom grow submerged in the substratum, but develop on aerial hyphae, and especially on those which lie on or just beneath the surface; in the latter case the spores project away from the substratum into the air. Hence it frequently occurs that the conidia are all situated on the same side of the hypha (pl. 20, fig. 69). The most copious production of conidia is on those hyphae which have spread over the moist surface of the cover glass beyond the limits of the hanging drop. If a young conidium becomes submerged before it reaches maturity, its development as a spore is frequently arrested, and it grows into a vegetative branch.

Germination of conidia.— During germination the behavior of the conidium agrees very closely with that of the basidiospore. It swells to twice the original diameter, and two or more guttulae appear which were frequently not visible before (pl. 20, fig. 71–73). The mycelium also is in no way to be distinguished from that arising from a basidio-

spore; the germ tubes may or may not bear clamps, but in either case conidia are copiously produced, and in wood cultures very extensive basidiosporic hymenia are developed.

CORTICIUM EFFUSCATUM Cooke & Ellis.

Pl. 21, fig. 74-95; pl. 22, fig. 96-105.

The writer collected this species in abundance in several localities near Cambridge, Massachusetts, on fallen logs of *Quercus*, *Populus*, *Acer*, etc. It proved to be an extremely interesting species for on cultivation the mycelium developed not only chlamydospores but also an abundance of conidia of the *Oedocephalum* type, similar to those found by Brefeld ('89) in *Polyporus annosus*.

This species was described by Cooke & Ellis in "New Jersey fungi," (*Grevillea*, vol. 9, p. 103, 1881). It appears to be rather widely distributed in the eastern United States. The hymenium is effused, sometimes forming broad encrusting areas. The color when fresh is reddish tawny to reddish orange, but fades to a dirty pallid ocher when dry. The young hymenium is fragile, waxy, and smooth, but is soon rendered pulverulent by the discharged spores, great numbers of which become embedded in the hymenium as the latter increases in thickness. The clavate, 4-spored basidia (pl. 21, fig. 74) are about $5.5-7\ \mu$ in diameter, and project $8-12\ \mu$ from the surface. The basidiospores are spherical to ellipsoidal, sometimes slightly inequilateral, $5.5-8\ \mu \times 7-10\ \mu$. The spore wall is slightly thickened and the contents are granular with one or more large oil drops (pl. 21, fig. 75). In a mass the spores are concolorous with the hymenium, but when viewed singly under the microscope they appear pale lemon yellow.

Cultivation of basidiospores.—Germination was not so easily obtained in this species as in many others, not more than 1-1.5% of the basidiospores producing germ tubes in any culture medium used. Usually but one germ tube is produced (pl. 21, fig. 76-77) and this makes its appearance only after about forty-eight hours. Subsequent growth, however, is fairly vigorous; the germ tube grows into a copious, much branched primary mycelium of clampless hyphae which average $3-3.5\ \mu$ in diameter, but may range as low as $1.5\ \mu$ and as high as $4.5\ \mu$, all sizes being intermingled in confusion. The primary mycelium persists only five or six days and is then gradually replaced by the secondary mycelium; the latter arises by the direct continuation of the

growth of the former and is distinguished from it only by the presence of numerous clamps, not by increased size of the hyphae, as is the case in *Corticium alutaceum* (see p. 161).

Conidia and chlamydospores are produced in abundance (pl. 21, fig. 78), but oidia were not observed in any culture. The life history is completed, after five or six weeks, by the production of extensive basidiosporic hymenia. In agar tubes, especially in strongly acid decoctions of prunes or other dried fruits, the hymenium first develops on the surface of the agar and afterward spreads far over the glass walls of the tube. Very extensive hymenia are also formed on wood cultures on *Populus*, *Acer*, *Quercus*, etc. The hymenia thus produced appear to be perfectly normal and agree in every way with specimens collected in the field. Indeed, this species produces hymenia more readily and extensively than any other species which the writer has cultivated.

Chlamydospores.— On the next day after germination chlamydospores begin to develop, and soon become numerous in all cultures, appearing on both primary and secondary mycelia in equal profusion. A young primary mycelium which has formed both chlamydospores and conidia is shown in figure 78 (pl. 21). In well nourished cultures there may be an extensive vegetative growth of the mycelium before the formation of chlamydospores, but in drop cultures made from an attenuated decoction of horse dung the mycelium is reduced to one or two hyphae, and chlamydospores occur close to the germinating basidiospore (pl. 21, fig. 79). In many cultures the production is so copious that old hyphae may possess rows of chlamydospores, adjacent ones being frequently separated by less than their own length of the empty hypha walls (pl. 21, fig. 80).

The method of formation (pl. 21, fig. 81–83) agrees with the general description of basidiomycetous chlamydospores already given (see p. 150). In general appearance, also, they are quite typical, save that they present an unusual degree of uniformity in size and shape. They are very regularly ellipsoidal or spherical with comparatively few imperfectly or abnormally developed individuals. In size they vary from $8.5 \times 11.5 \mu$ to $16 \times 17 \mu$, averaging about $11 \times 13 \mu$. As was stated above, chlamydospores are produced on both primary and secondary mycelia indiscriminately, but on germination they invariably produce secondary mycelia. Germination is rapid in drop cultures, eighteen to twenty hours being sufficient for the production

of from one to several germ tubes (pl. 21, fig. 84–85), all of which bear clamps at once and develop into a mycelium indistinguishable from that arising from a basidiospore.

Conidia.—Conidia appeared in all the writer's cultures of this species, usually in great abundance. They belong to Preuss's form-genus *Oedocephalum*, and strongly resemble the conidia discovered by Brefeld in his study of *Polyporus annosus*, save that they are of much smaller size and the conidiophores regularly branch and proliferate repeatedly. These conidia are produced by both primary and secondary mycelia, beginning within forty-eight hours after germination, and continuing throughout the life of the mycelium. They appeared on all media employed, although the production was diminished on very concentrated or very dilute decoctions. It was not possible in most drop cultures to follow the hyphal connection between the germinating basidiospore and the conidium, on account of the extensive interlacing of the hyphae; but by the use of very dilute liquid media this connection was incontestibly demonstrated. In such a culture vegetative growth is greatly abridged, and the entire development of the mycelia from basidiospore to chlamydospore and conidium is evident at a glance, without possibility of error arising through impurity of the culture and consequent intermingling of foreign hyphae (pl. 21, fig. 78).

The typical conidiophore (pl. 21, fig. 86) is a hyaline, erect, club-shaped hypha, from one and one half to two times the size of the vegetative hypha (*i. e.*, 3.5–4.5 μ in diameter) and ending in a terminal enlargement or capitulum, 8.5–11 μ in diameter. The upper half (or slightly more) of the rounded capitulum bears sterigmata whose number varies within wide limits, in normal cases being from 20 to 40, although frequently conidiophores with as few as 5, 4, or even 1 are seen. The sterigmata are slender, cylindrical, or slightly attenuated upwards, and usually about two thirds the length of the spores, although considerable variation is shown and the spores are sometimes almost sessile. The conidia (pl. 22, fig. 99) are hyaline, thin-walled, spherical or egg-shaped with a slight apiculus, 2.5–3 $\mu \times$ 3–3.5 μ , and with finely granular contents.

Development of conidiophores and conidia.—Conidiophores appear on the older hyphae on the second or third day after the germination of the spore. They increase rapidly in numbers, and spread to all parts of the mycelium.

The first appearance of the conidiophore is a hypha of large size, with dense, refractive contents, which usually grows away from the substratum into the air, although in liquid media it is not infrequently submerged; this hypha becomes capitate by a terminal enlargement. When the capitulum has attained about three quarters the mature size, the sterigmata appear as minute papillae which rapidly elongate into tubular projections. Each sterigma becomes capitate and develops a spore at its apex, by whose enlargement the sterigma is reduced to about two thirds the original length. This entire process from the first appearance of the sterigmata to the full development of the spores requires from one and one half to two hours. Successive stages in the process are shown in figures 87 to 91 (pl. 21).

Branching and proliferation of conidiophores.—The older vegetative hyphae in drop cultures soon lose their cell contents; but many of the conidiophores remain filled with dense, refractive protoplasm even after spore formation is complete. This protoplasm may be very limited in extent, being confined to the capitulum and to the part of the conidiophore immediately below it (pl. 21, fig. 95), but yet it is the center of active, vigorous growth; on account of it, the conidiophore branches and rebranches repeatedly, the branches occasionally growing into vegetative hyphae of considerable length, but usually soon producing secondary capitula. Moreover, proliferations through the capitulum occur which at once produce secondary capitula in almost all cases, and these proliferate in turn, thus forming Arthrobotrytis-like fructifications (pl. 21, fig. 92–95; pl. 22, fig. 96–97). The results of such growth are very striking in old drop cultures, for although the vegetative mycelium may have nearly or quite lost its protoplasm so that the empty hypha walls are barely visible, these points of vigorous growth are very prominent in the form of complex, tree-like systems which may have arisen through repeated branching and proliferation of a single conidiophore. Proliferation appears to be a perfectly normal process, since it occurs in all cultures, although its greatest development is seen in rather attenuated decoctions where the vegetative growth is less luxuriant.

The similarity existing between this imperfect form of *Corticium effuscatum* and that which Brefeld discovered in *Polyporus annosus* has already been referred to. The writer has been so fortunate as to secure fresh material of *Polyporus annosus* and has grown it in pure cultures, confirming in all essential particulars the observations of Brefeld. The most apparent differences between these conidia and

those found in *Corticium effusatum* are the smaller size of the latter species, and the greater tendency of its conidiophore to become compound. Brefeld describes branching and proliferation of the conidiophore in *Polyporus annosus*, particularly in old cultures, but these phenomena are only occasional. Indeed, in the writer's study of this species, he has almost never seen any signs of either branching or proliferation in cell cultures, while under exactly similar conditions *Corticium effusatum* always shows both in abundance. Hence this may be regarded as the normal and characteristic method of growth in the latter species, while it is more unusual in the former and is rather the result of external conditions than inherent in the species.

Cultivation of conidia.—The conidia of *Polyporus annosus* germinate readily. On the contrary considerable difficulty was experienced in securing germination of the conidia of *Corticium effusatum* although many different media of various degrees of concentration were employed. Only occasionally did a spore show any signs of germination, and in these cases the development seldom progressed beyond the formation of a germ tube from 10 to 15 μ in length, the growth being not infrequently stopped by the formation of a chlamydospore (pl. 22, fig. 103–104).

In cases where successful germination was secured (pl. 22, fig. 100–102), the process was slow,—both in the first appearance of the germ tube (after from two to five days) and in its initial growth,—facts which apparently indicate low vitality. Moreover, contrary to the rule in the case of such small spores, the conidium does not swell appreciably in germination. Hence the germ tube is necessarily small, 2.5 μ in diameter, but it soon, sometimes immediately, produces hyphae of normal size. This increase in diameter is sometimes secured by a gradual broadening as the germ tube grows in length (pl. 22, fig. 101), and sometimes by a bulbous terminal enlargement from which a hypha of normal size arises a little later (pl. 22, fig. 102). This period appears to be a critical one, and the majority of germinating spores perish at this point, although vitality may be preserved by the formation of a small chlamydospore in the germ tube, as was stated above. If the increase in size is safely secured, more rapid growth follows, and a normal primary mycelium results (pl. 22, fig. 105).

Frequently conidia germinate *in situ* when they chance to be submerged, putting forth germ tubes while still attached to the conidiophore (pl. 22, fig. 98). From this it was thought that the small percentage of germination in cell cultures might be due to early loss.

of vitality by the conidia. Hence cultures were made of conidia which had apparently barely attained the mature size, but even then few put forth germ tubes and many were seen to be incapable of germination in that they contained little or no protoplasm. It was found that a much larger percentage of germination is obtained by transferring a mixture of conidia and basidiospores to the drop culture, or by placing in the cell a bit of mycelium-bearing agar from a tube culture. The presence of the growing hyphae appears to exercise a stimulating influence on the conidia.

From his experiments the writer inclines to the belief that the conidia have partially lost the power of germination, and that they are not now of great importance in the reproduction of the plant. It seems probable that the fungus depends for propagation during its mycelial condition on the chlamydospores which are produced in abundance and germinate readily under ordinary conditions, and that the conidia have degenerated through disuse.

As in the case of the chlamydospores of this species, conidia are produced indiscriminately on both primary and secondary mycelia, but unlike the chlamydospores the conidia always give rise on germination to primary (clampless) mycelia which are of much longer duration than are those formed by the basidiospores. Clamps were rarely seen even in very old cell cultures of conidia, although they were finally found in abundance in transfers to agar tubes where the normal secondary mycelium develops. After the clamped hyphae appear, the culture agrees in every way with one originating from a basidiospore,—producing chlamydospores, conidia, and ultimately a basidiosporic hymenium. It is interesting to note that succeeding generations of cultures raised from conidia show a considerable increase in conidial production, and also that conidia from such cultures show a larger percentage of germination,—facts which appear to support the theory that the conidia are degenerating and that by cultivation their function may be recovered, at least in a measure.

LENTODIUM SQUAMULOSUM Morgan.

Pl. 22, fig. 106-125; pl. 23, fig. 126-128; pl. 24, fig. 129-132;
pl. 25, fig. 133-136.

Typical specimens of this peculiar fungus were collected during three successive autumns at Waverley, Massachusetts, where they

were growing upon dead stumps of *Cephalanthus occidentalis* L. Although this fungus does not belong to the class of Basidiomycetes which were under especial investigation in the preparation of this paper, namely, the woody and encrusting species of the Thelephoraceae, Hydnaceae, and Polyporaceae, its peculiar structure gave rise to the hope that it might possess conidia; so it was cultivated, and its life history carefully followed out. The mycelia bore chlamydospores in abundance, but no conidia; the latter were formed, however, upon the young veil and about the margin of the growing pileus. Typical fructifications in abundance were produced in cultures together with many abnormalities which, however, generally retained the essential peculiarities of the *Lentodium* type. A full discussion of the structure and development of the fructification is included in the present paper, since these are so unusual as to seem to merit a more extensive description than has yet been given.

Description of fructification.—The mature fructification (pl. 23, fig. 126) is umbilicate, semiorbicular, with the margin of the pileus curved downward and inward toward the stipe in most specimens. The pileus varies from one to four centimeters in diameter and from three to eight millimeters in thickness. The texture is tough and fleshy-coriaceous when fresh, but becomes hard and woody when dry. Small, dark-colored, hairy scales cover the pileus, and color its surface brownish gray to rufous verging to blackish toward the center. The stipe varies considerably in length, and is central in perfect specimens; it is tough, solid, fibrous, confluent with and of the same texture as the hymenophore, and frequently scaly like the pileus. A thick stratum of tubes and chambers (pl. 24, fig. 131), lined with the basidiosporic hymenium, descends from the hymenophore and is adnate to and decurrent upon the stipe. The tubes branch and anastomose irregularly, and are traversed by veins and divided into chambers by septa. There is frequently a more or less clearly defined radial arrangement of chambers, and some of them may also be elongated radially, particularly in the region of the stipe (pl. 23, fig. 127), but free gills are never present, and in many specimens absolutely no trace of gill arrangement is discernible.

The mouths of the chambers are usually closed by a white, flocculent web of hyphae which arise from the trama (pl. 23, fig. 127; pl. 24, fig. 132). In growing specimens this veil is thin and the pore is faintly discernible; at maturity it becomes much thicker and firmer

and the position of the chambers may be nearly or quite hidden. In his description of this species, Morgan ('95) characterizes this veil as "a thick white floccose membrane, which after maturity splits irregularly in a radiate manner." The term membrane is misleading, for it is never a separable layer, nor is it distinguished in any way from the tissue of the trama from which it has arisen, save that the hyphae may be more loosely compacted. Neither has the writer observed that it splits radially at maturity; on the contrary, as noted above, he finds that the thickness frequently increases and the pores become more completely hidden.

The trama is composed of loosely interwoven hyphae, from which arise branches that turn outward, fork more or less in a cymose fashion, and form the basidia (pl. 22, fig. 106-107). The hymenium is composed entirely of basidia of various ages, there being no paraphyses. It was thought that this peculiar fungus might show great variation in the character of the basidia, and perhaps possess hymenial conidia. This expectation was not realized, however, for the basidia are normal in every way, being clavate in form, and regularly 4-spored.

The basidiospores (pl. 22, fig. 108) are hyaline, elliptic-oblong, apiculate, inequilateral, $2.5-3.5 \mu \times 5-6 \mu$, and usually contain a pair of refractive guttulae. In old specimens the chambers and passages of the hymenial stratum become filled with a mass of mature spores whose free dissemination is prevented by the veil below.

Cultivation of basidiospores.— Germination occurs in from 15 to 20 hours in drop cultures, the spores swelling slightly, and each developing a single germ tube (pl. 22, fig. 109). A primary mycelium is produced with vacuolate, copiously branched hyphae, $1.5-3 \mu$ in diameter. After four or five days numerous chlamydospores are formed and growth in the drop culture is practically suspended. Only in three-weeks-old cell cultures possessing unusually large nutrient drops were any clamped hyphae of the secondary mycelium observed. However, if the young primary mycelium is transferred to an agar tube, the secondary mycelium develops in a much shorter time. Its hyphae are larger than those of the primary mycelium, bear numerous clamps, and produce chlamydospores abundantly. No oidia nor conidia were found upon the mycelium. Basidiosporic fructifications were produced in from four to five weeks on sterilized sticks of *Cephalanthus* and other wood in jars (pl. 23, fig. 128). The development was hastened and increased by adding a little nutrient material, particularly

sugar and beef peptone, to the water in the jar. In agar tubes normal stalked fructifications were only occasionally developed, although sessile convoluted or brain-like growths whose folds and cavities were lined with normal basidiosporic hymenia were frequent.

Chlamydospores.—Both primary and secondary mycelia produced chlamydospores in abundance, but of different sizes,—those formed in drop cultures by primary mycelia averaging about $7 \times 9 \mu$, while those produced in agar tubes by secondary mycelia average $11.5 \times 13 \mu$. These spores (pl. 22, fig. 110–114) are of the usual basidiomycetous type described on page 150, but in a large proportion of cases the usual lemon-shape is not attained, but the cells remain cylindrical or with slightly bulging walls (pl. 22, fig. 113–114). Such imperfectly formed chlamydospores appear to be as retentive of vitality and to possess the same functions as those of more normal form. In drop cultures the chlamydospores, of whatever form, germinate at once (pl. 22, fig. 115) and produce clamped germ tubes which rapidly form secondary mycelia, similar in all respects to those arising from basidiospores.

Development of fructification.—In wood cultures the young mycelium forms a cottony growth which rapidly spreads over the stick, finally obscuring it beneath a thick white layer. Upon this layer in about four weeks appear small dome-shaped elevations,—the first stage in the development of the fructifications. These elevations are commonly grouped, as the fungus is gregarious in its nature. They rapidly elongate into cylindrical white projections (the young stipes) which are either smoothly rounded or slightly tapering at the end. The elongation is due largely to the terminal growth of the component hyphae, which, although interlacing to a considerable extent, run in a generally longitudinal direction. That a certain amount of growth is intercalary, probably due to enlargement of the cells, is shown by the continued elongation of the stipe even after the cessation of terminal growth at the time of formation of the pileus; however, such growth is not extensive, and does not result in appreciable enlargement of the cells such as is seen in many agarics.

As the terminal growth of the stipe ceases, the apex begins to flatten and broaden out owing to the repeated branching of the hyphae, many of which turn outward in a horizontal direction to form the pileus (pl. 24, fig. 129). The hyphae turning off horizontally continue to grow, constantly giving off branches which bend upward, and in turn

cease to elongate, while the parallel extremities form the tissue of the dorsal surface of the pileus (pl. 24, fig. 130). As the fructification matures these parallel hypha ends become brownish-walled and agglutinated into bundles which form the scales or squamules of the pileus. Similar scales may develop on the stipe. Meantime other branches, given off on the ventral side of the growing pileus, turn downward and give rise to the tissue of the hymenial region (pl. 24, fig. 130; pl. 25, fig. 133), which commences to develop near the stipe and extends outward as the pileus grows in diameter.

By the continued downward growth of certain of the hyphae composing the original hymenial surface, anastomosing ridges and plates are formed which enclose irregular areas. From the loosely interwoven hyphae composing the plates, branches arise which turn outward perpendicular to the surface, fork cymosely, and form the elements of the hymenium. Loosely spreading hyphae, continuous with the elements of the trama, radiate outward in all directions from the growing edges of the plates, and, meeting those from neighboring plates, form the thin flocculent veil which closes the majority of pores even in very young fructifications (pl. 24, fig. 131-132; pl. 25, fig. 133). These radiating hyphae appear to be largely responsible for the peculiarities in the further development of the spore-chambers. As precursors of the advancing trama, they may, by becoming massed, divert the growth to one side or another, thus causing the trama to vary in width, to divide, to form a bridge or septum across the spore chamber, etc. (pl. 24, fig. 131-132). The basidia originate directly from the elements of the trama on cymosely-branched hyphae without the formation of a definite subhymenial layer. Apparently any of the elements of the trama may produce basidia in favorable locations, hence an extension of the trama in any direction becomes promptly covered by a hymenium. Where the thickening of the veil has thus led to the closing in of a spore chamber, a new hymenium may develop outside this septum, thus beginning the formation of a new spore chamber which is at first freely open to the exterior as a shallow depression, but which rapidly deepens by the growth of its walls and becomes hidden by the development of the veil as in the case of the original chamber. As the fructification approaches full development, the downward growth of the plates ceases and the veil increases in thickness until the mouths of most of the spore chambers are nearly or quite concealed from view.

Conidia.— Conidia were found only upon the young fructifications, where they appear about the growing margin of the very young pileus, and upon the spreading hyphae of the young hymenial plates (pl. 25, fig. 134). The conidiophores arising from the trama are long attenuated hairs, 1–1.5 μ in diameter, and bear terminally single spores. The conidia are hyaline or slightly brownish, about 3–4 μ in diameter with very slightly thickened walls, and usually bent more or less in a helicoid fashion and divided into from two to several cells (pl. 22, fig. 116–123). Upon the margin of the pileus the conidiophores are shorter and less attenuated, and the conidia are usually shorter and broader, frequently being reduced to a single globose or kidney-shaped cell (pl. 22, fig. 124). In drop cultures the conidia germinate and grow into normal mycelia, each cell being able to put forth a germ tube (pl. 22, fig. 125).

The production of conidia is restricted to a very limited period in the growth of the fungus. They first appear upon the margin of the young pileus as it begins to develop by the expansion of the end of the stipe. The most copious production is upon the hymenial plates as they are arising from the hymenophore. No conidia have been seen upon the older fructifications where the pileus is fairly well developed and there is a copious formation of basidiospores.

Abnormalities.— The writer has cultivated the fungus under various conditions and on many media, and although he obtained numerous variations and abnormalities, these did not affect the nature of the hymenial layer. Indeed, this appears to be more stable than either pileus or stipe, as is shown by the character of the variations. The stipe varies greatly in length, and is sometimes entirely absent; or, it may branch and bear more than one pileus. Occasionally much branched Clavaria-like growths appear, the separate arms of which may or may not produce pilei. In wood cultures to which a considerable amount of beef peptone or other nutrient has been added, the growth of the hymenial stratum is increased so that the margin of the pileus frequently becomes upturned instead of inrolled (pl. 23, fig. 127; pl. 25, fig. 135); occasionally this excessive development of the fertile region results in the complete abortion of the pileus, and the formation of a spherical head which is entirely covered by a thick stratum of the characteristic spore chambers (pl. 25, fig. 136). In agar tubes, but few normal fructifications are produced; the abnormalities commonly take the form of sessile, convoluted, cavernous growths with an

abundant production of basidiospores. Upon very hard agar tubes which contain but a small amount of nutrient material and upon sand to which some nutrient agar has been added, the convoluted, brain-like growths do not appear, and normal fructifications occasionally develop. Hence it seems evident that concentration of the substratum stimulates the fungus to an excessive development of the hymenium at the expense of the sterile parts of the fructification. But it is to be noted that the variations cited always belong to the pileus or to the stipe, not to the hymenial layer. Culture conditions may modify the copiousness of the latter, but not its character.

History of Lentodium.—The first notices of this peculiar fungus occur in Lea's "Catalogue of plants of Cincinnati," published in 1849, and Berkeley's "Decades of fungi," 1845. Both writers regarded it as an abnormal development of *Lentinus tigrinus* Fr. Lea (*l. c.*, p. 56) has the following record: "*Lentinus tigrinus*, Fr. on dry stumps. Cincinnati, Nov., 1842," and in a footnote he adds: "The gills have anastomosed in these species to such an extent as to form a solid wood mass." Berkeley (*l. c.*, p. 38 of reprint), speaking of *Lentinus tigrinus*, makes this comment: "A most remarkable state of this fungus has been found by Mr. Lea (No. 245) in which the gills have anastomosed until the whole pileus and gills have become a hard solid mass. At first sight it has quite the appearance of a new genus; but I am convinced that it is merely a very curious, but monstrous state of our European species."

The fungus was met with in a number of localities in the northeastern United States, and finally Morgan ("New North American fungi," Journ. Cincinnati soc. nat. hist., vol. 18, p. 36-37, 1895), after encountering it repeatedly, became convinced of its specific value and described it as *Lentodium squamulosum*, the type of the new genus *Lentodium*, which he placed next to *Lentinus* in the Agaricaceae, at the same time calling attention to its resemblance to *Secotium* of the Gasteromycetes. He says: "I meet with this fungus nearly every season and it always has the form described above. I have never found a species of *Lentinus tigrinus* in this region and I have no information that the present fungus has ever occurred in Europe. I am of the opinion that it is a perfectly normal production; if not, the normal and abnormal conditions must at some time occur together and the abnormal form must be accounted for."

Is Lentodium squamulosum an abnormality or a permanent species?—

The writer is inclined to agree with Morgan that this fungus is a permanent species, and that its two most striking peculiarities, *viz.*, the porose-cellular hymenial layer and the peculiar veil, are normal structures. However, before summarizing the grounds on which this belief is based it will be well briefly to examine certain abnormalities, which more or less closely resemble *Lentodium*. Such abnormalities are not common but have been reported in both Agaricaceae and Polyporaceae.

Anastomosing gills forming tubes and irregular spaces are normally present in a number of accepted genera, as in *Daedalea*, *Lenzites*, *Paxillus*, species of *Marasmius*, etc. They also occur in occasional monstrous specimens of various species, *e. g.*, Patouillard ('98) reports a specimen of *Agaricus campestris* in which the ventral surface of the pileus is decidedly polyporoid; and Boudier ('90) describes a morcheloid specimen of *Cortinarius scutulatus* Fr., in which the ventral surface of the pileus is perfectly normal, but the upper face is covered with alveolar spaces formed by anastomosing plates. These spaces are usually shallow open depressions, but occasionally may form closed chambers. It was doubtless such forms as this that Fries ('36-'38) grouped in the genus *Stylobates*, believing them to be autonomous species; in *Stylobates* both faces of the pileus bear gills, those above anastomosing more or less.

A porose-cellular hymenium is known in a number of forms of doubtful status which have been described as new genera, but which are generally supposed to be merely occasional deformities of species of Polyporaceae. An excellent example is *Myriadoporus* which Peck ('84b) describes as follows: "Hymenium cellular-porous, pores of the surface shallow, open, the others embedded in the hymenium, variously directed, short, closed, inseparable from each other and from the hymenophore. . . . At present represented by two species, both of which are resupinate and bear striking resemblance to certain resupinate species of *Polyporus*. I have not been able to find spores in either species, and can scarcely avoid the suspicion that both may be abnormal developments of species of *Polyporus*." Patouillard ('00, p. 111) in speaking of *Myriadoporus* asserts that "cette monstruosité peut s'observer dans tous les groupes de Polypores." The genera *Bresadolia* of Spegazzini ('86) and *Poroptyche* of Beck ('88) are probably similar to *Myriadoporus*.

It appears from the examples cited above that a hymenial region

somewhat resembling that of *Lentodium* is known in certain fungi generally admitted to be abnormalities of *Agaricus*, *Cortinarius*, *Polyporus*, etc. The unique veil of *Lentodium*, however, is not duplicated in any of these species, but the nearest approach is seen in the morchelloid specimen of *Cortinarius scutulatus* described by Boudier, where a few projecting hyphae give the hymenial plates of the dorsal surface a slightly fuzzy appearance. The existence of these monstrosities in some measure resembling *Lentodium* gives a certain basis for the theory that the latter fungus is also an abnormality, but there is no direct proof to support such a theory. The growths cited which are admittedly abnormal are in some cases known to be caused by parasitism or other environmental conditions; in other instances the cause of the monstrosity is not known, but the abnormal character of the fungus in question is more or less clearly established by its growing with normal specimens of the species, by the presence of intergrading forms, etc. In the case of *Lentodium squamulosum*, however, no such direct proof of abnormality exists. It has been regarded as a monstrous form of *Lentinus tigrinus*, a species which it closely resembles in texture and external appearance of stipe and pileus, and in character of basidia and spores. While such resemblances may possibly indicate phylogenetic connection, they are not sufficient to prove the identity of the two forms in the face of the great dissimilarity in other respects. The author bases his belief in the autonomy of this species on the following grounds:—

(1) Its apparent permanence. This plant has been collected in many widely separated localities during more than sixty years, and, so far as the writer knows, it has never been found growing with *Lentinus tigrinus*, nor have intergrading forms been found which might connect it with this or any other fungus growing in the neighborhood. It is true that the data with reference to this fungus are still very meager, but in the entire absence of proof to the contrary, the presumption is in favor of the autonomy of the species.

(2) The permanence of its essential peculiarities in cultures. As has already been stated on page 186, the author was able by varying culture conditions to secure great variation in stipe and pileus, even to the complete abortion of both; but the nature of hymenial layer and veil remained essentially unchanged. If these latter are of abnormal character, it is to be expected that changed conditions would cause variations, and perhaps reversion to the normal type;

but such was not the case. Hence it may be assumed that the cottony veil and porose-cellular hymenium are normal characters, or, if originally monstrosities, that they have become fixed and permanent.

In studying the development of the hymenium of well established genera of the Hymenomycetes we observe definite habits or laws of growth which are invariable under normal conditions. Thus in the Agaricaceae the originally smooth hymenium becomes broken up by descending folds or lamellae of equal thickness which are radially placed and occur at fixed intervals; in *Polyporus* the downward growth of the hymenium forms tubular pores of approximately regular diameter and arrangement; in *Daedalea* there is a lack of regularity in the original arrangement of the folds on the hymenophore, but these folds, once started, then grow on with considerable regularity and result in the formation of variously shaped spaces and passages, but not of closed chambers. This definite law of growth may be overthrown in a given species as the result of parasitism or other conditions of environment, as may be observed in almost any artificial culture of a Hymenomycete; the result is sometimes a deformity like the anastomosing gills of *Agaricus campestris* reported by Patouillard, or the cellular-porous form of *Polyporus* which Peck named *Myriadoporus*. In distinction to these regular laws of growth *Lentodium* appears to be a genus without any well defined law in the development of its hymenial region. The plates arise from the hymenophore without definite order, thus recalling *Daedalea*; but, unlike the latter, they do not grow downward regularly when the position has once been determined, but branch and anastomose to form the cellular-porous hymenial layer characteristic of the genus. As has already been pointed out, these peculiarities are due to the diffuse habit of growth of the trama which forms the false veil. Such an interpretation removes this fungus from the category of abnormalities, and, until further investigation shall have adduced proof to the contrary, it should, in the opinion of the author, be ranked as an autonomous species.

Systematic position of Lentodium.—Although this genus agrees with the Hymenomycetes in most respects, particularly as regards its development, yet the appearance of the mature fructification seems to suggest gasteromycetous affinities. The thick stratum of closed spore chambers bounded by the pileus above and the thickened veil below strongly resembles the gleba of certain Hymenogastrineae;

but in the opinion of the writer this resemblance is a chance occurrence and cannot indicate any close relationship, since the method of development is totally different in the two cases. In *Secotium*, which most closely resembles *Lentodium* in external appearance and in structure of the mature fructification, the plates of the gleba originate by the differentiation of internal tissue, and are covered by the thick peridium until maturity, when the latter tears away from the stipe below and the gleba becomes exposed. *Rhopalogaster* (*Cauloglossum*) *transversarium* (Bosc) Johnston, also strongly resembles *Lentodium* in its porose-cellular gleba covered by a thin delicate peridium which at maturity becomes pulled apart in many places so as to expose the chambers within; but Johnston ('02) found that the original hyphal upgrowth from the mycelium becomes differentiated into a cortical layer (the peridium) and a medullary portion from which the gleba develops. In these species the development is angiocarpic, the hymenium arising from internal tissue. On the contrary *Lentodium* is gymnocarpic, since the hymenial plates arise from the superficial tissue of the young fructification and are not covered by a peridium at any stage of their development; the cottony veil of *Lentodium* being merely an outgrowth of the trama, is not in any sense homologous with the peridium of Gasteromycetes. Hence the method of development of this fungus definitely excludes it from the latter group and allies it with the Hymenomycetes.

Nor can we place this fungus among the veiled Boleti or agarics. The hemiangiocarpic Hymenomycetes which possess a velum universale, as *Amanita*, can be more exactly homologized with the Gasteromycetes than can *Lentodium*, the veil which envelops the young egg being compared with the peridium. Nor is the velum partiale of *Agaricus*, *Cortinarius*, etc., homologous with the veil of *Lentodium*. This structure originates, according to de Bary ('87, p. 290), as a hyphal outgrowth from the superficial layers of the stipe and the margin of the young pileus; these hyphae unite in a close weft which bridges across and closes the furrow between the stipe and the forming pileus, and is torn in the final expansion of the latter. Hence the origin of the veil is quite distinct from that of the hymenial region. On the contrary the veil of *Lentodium* is formed from interlacing elements of the trama, has the same structure as the latter, and is inseparable from it at all times. Such a growth does not constitute a true membrane, as does the veil in *Cortinarius* and *Agaricus*, and

should be called a false veil. It does not become a permanent structure until the maturity of the fructification.

Hence it seems evident that the false veil of *Lentodium* will not assist us in determining relationships since it is not homologous with the peridium of *Gasteromycetes*, nor with the partial or universal veils of *Hymenomycetes*, and is, so far as the writer knows, a structure peculiar to this species. It is probable that the nearest relatives of *Lentodium* are to be found amongst the purely gymnocarpic *Polyporaceae* and *Agaricaceae*. The porose-cellular hymenial region recalls both these families. In some instances portions of the ventral surfaces of young specimens present the regular pored aspect of a *Boletus* in which the mouths of the tubes are partially concealed by a thin veil; but in the majority of cases the pores are sufficiently radial in arrangement and in elongation to give the impression of anastomosing gills; this arrangement is especially striking near the stipe, and frequently amounts to decurrent ridges.

Saccardo in vol. 14 of the "Sylloge" follows Morgan and places *Lentodium* beside *Lentinus*, but calls attention to the resemblance of its hymenium to that of the *Polyporaceae*. Hennings ("Pflanzenfamilien," vol. 11**, p. 196) deems this resemblance so great that he places the fungus among the *Polyporaceae*, where he labels it an "unvollkommen bekannte Gattung."

The writer would place the genus *Lentodium* between the *Agaricaceae* and the *Polyporaceae*, with no near relatives. Among *Polyporaceae* it most resembles such genera as *Daedalea*, *Favolus*, etc., which possess anastomosing gills, or irregularly shaped pores, but which lack closed spore chambers. In development, structure, consistency, etc., of stipe and pileus *Lentodium* closely resembles *Lentinus*, as has been noted by all previous observers; but no normal species of *Lentinus* has a similar hymenium.

Bubák ('04) regards his new genus *Lentodiopsis*, as a connecting form between *Lentodium* and *Lentinus*. This genus is based on two somewhat dissimilar specimens found growing on roots of living fir trees near Tábör. In most respects they agree with *Lentinus*, but the decurrent lamellae anastomose to a certain extent at the stipe, which is "mit dem Hutrinde durch einen häutigen, ziemlich dicken, weissen Scheier verbunden, welcher sich entweder am Steil ringförmig ablöst und mit dem Hutrinde verbunden bleibt oder in strahlenförmige, beiderseits befestigte Streifen zerreisst." This veil is not

like that of *Lentodium*, but belongs to the type seen in *Cortinarius*. Moreover, the hymenial region is composed of gills which, although anastomosing to some extent near the stipe, do not form closed chambers. Hence this genus, even though it be accepted on the scant evidence of but two specimens, cannot be accounted a near relative of *Lentodium* and the latter genus must, for the present, remain isolated.

GENERAL CONSIDERATIONS.

The vegetative mycelium.— In the greater number of species cultivated two periods are clearly discernible in the development of the mycelium; these are designated in this paper as primary and secondary mycelia. The primary mycelium is the product of the germination of the basidiospore and is distinguished by absence of clamps, and occasionally, as in *Corticium alutaceum*, by smaller diameter of the hyphae. The hyphae of the primary mycelium soon lose their protoplasm and disappear. The secondary mycelium arises from the primary in from one to eight days as the direct continuation of the growth of the latter; it is composed of hyphae of normal size and in the great majority of species produces numerous clamps. In certain species no primary mycelium can be distinguished for the basidiospore gives rise at once to a clamped hypha of normal size. In such cases there is either no primary mycelium or its presence cannot be detected by the customary signs. In *Corticium roseo-pallens* the habit of germination is not uniform, for some basidiospores produce clamped, and others clampless germ tubes. Again, in species like *Corticium subgiganteum* which has no clamps at any time, no division into primary and secondary mycelia is possible by either criterion mentioned above.

Both primary and secondary mycelia produce chlamydospores in equal profusion, but on germination these spores invariably give out clamped germ tubes. In the formation of oidia, both types of mycelia are equally active, although the oidia are not usually formed directly from the clamped hypha, but from smaller branches of the size and appearance of the primary hyphae. On germination, oidia form unclamped germ tubes. Conidia also occur on both types of mycelia, and where they are of a highly differentiated nature they agree with the basidiospores in the character of the mycelia produced on germination; thus the conidia of *Corticium roseo-pallens* sometimes give

rise to clamped and sometimes to unclamped mycelia, while those of *Corticium effusatum* invariably produce unclamped mycelia.

Oidia and chlamydo-spores.—The production of oidia appears to be confined almost entirely to the higher families of the Hymenomycetes, as was indicated by Brefeld. On the other hand the writer's studies have demonstrated that chlamydo-spores are much more widely distributed than was previously known. Aside from *Nyctalis*, *Fistulina*, and *Ptychogaster*, where they occur profusely both upon the vegetative mycelium and upon the basidial fructification, they have been occasionally reported in the hymenium or other parts of the carpophore of several species, but have not been noted as regular and characteristic formations. The writer has seen no record of their occurrence on the vegetative mycelium save in the three genera mentioned and in *Merulius lacrymans*. It has now been shown in this paper that they are formed regularly and abundantly on the mycelia of species belonging to all families of Hymenomycetes, and undoubtedly further culture study will furnish additional evidence of their wide distribution. They are undoubtedly important organs of reproduction in many species (see p. 149).

Brefeld believes that oidia and chlamydo-spores are morphologically but modifications of the same structure, basing this theory largely on his study of *Mucor racemosus* ('89, p. 211–237). This species regularly produces cross walls in the hyphae only where the sporophores are to arise. The section of the mycelium that is to produce the sporophore may be large or very small, depending upon external conditions. In different culture media the hyphae may divide into thin-walled, barrel-shaped cells which he calls oidia, or into similar cells with thick walls, which he calls chlamydo-spores, both forms naturally producing sporophores on germination. Hence in these species the oidium is the simpler, and the chlamydo-spore the somewhat more highly differentiated development of the same "Frucht-anlage," or initial cell of the sporophore. If submerged in the substratum, instead of giving rise to sporophores they may function directly as spores and send out germ tubes. Among the Basidiomycetes although oidia and chlamydo-spores are somewhat farther separated in appearance and development, yet Brefeld regards both as but forms of one and the same structure, — "unentwickelte Fruchtrager-Anlagen," which have entirely lost their former functions, and have become physiologically of the value of spores. This interpretation places oidia and

chlamydospores in an entirely different category from conidia, for the former bodies represent the undeveloped primordia of the conidiophores. Also, says Brefeld, the smut spores of Ustilagineae and the aecidio-, uredo-, and teleutospores of Uredineae are morphologically chlamydospores, and the morphological and systematic relations of these groups cannot be understood until the nature of these spores is understood. The smut spore germinates by the formation of a sporophore, but in the Uredineae the teleutospore alone retains this power, the uredospore and aecidiospore putting forth germ tubes directly, as is the case with the chlamydospores of Hymenomyces.

From his culture studies the writer disagrees with Brefeld in thinking that the oidium and the chlamydospore as exemplified in the Hymenomyces can be satisfactorily interpreted as morphologically identical. He has tried in vain to duplicate with species of Hymenomyces the experiment of Brefeld with *Mucor racemosus*, viz., by varying the culture media and the culture conditions to induce the formation of oidia in species which naturally produce only chlamydospores, and *vice versa*. The copiousness of formation was easily modified, but in no case were both types of bodies produced on the mycelia of one species, under either natural or artificial conditions, nor were transitional states between the two seen.

The two forms differ in many respects, some of which seem quite fundamental. Oidia are merely the cells of the vegetative hyphae which separate from one another but show no especial differentiation of either walls or contents; the retention of vitality is short. On the contrary, chlamydospores are encysted cells formed endogenously in the parent hypha by the contraction of the protoplasm which then becomes surrounded by a resistant endospore in addition to the original cell wall. These spores are very retentive of vitality and are freed only by the decay of the hypha walls. Moreover, while the two types of spores are found on both primary and secondary mycelia alike, oidia produce primary mycelia on germination, while chlamydospores give rise to secondary mycelia, a fact which may indicate some cytological or physiological distinction between them.

Both kinds of spores appear occasionally to approach the dignity of conidia. Such an advance in the development of oidia is seen in *Coprinus*, *Psathyra*, and *Psilocybe* (Brefeld, '77, pl. 6; '89, pl. 3), where the oidia are borne in particular places and form more or less specialized tufts or clumps. In *Corticium alutaceum* the spores

are borne singly along the sides of a sporophore, only occasionally forming oidium chains (pl. 19, fig. 28–32). In this species the spores should undoubtedly be ranked as conidia although with oidium affinities.

A similar approach to conidia is seen in the case of chlamydospores. In species of *Ptychogaster*, and particularly in *Fistulina*, the chlamydospores are grouped on branching hyphae and in external appearance closely resemble clusters of conidia. However, the closest approach to the status of conidia is seen in *Michenera artocreas*, where the formation of the spores is typically chlamydosporic (see p. 155), but they have assumed an habitual subterminal position in the parent hypha, and are formed in a highly developed fructification of their own with a definite hymenium, facts which ally them to higher types of spores.

The writer therefore is of the opinion that the oidia and the chlamydospores of Hymenomycetes are morphologically distinct and are not modifications of the same structure.

Bulbils.—Sclerotia have long been known among the Basidiomycetes, as in *Coprinus stercorarius*, species of *Typhula*, etc. Many species also possess sclerotoid growths of a less definite character than those mentioned above, while rhizomorphae and other enduring structures are common. It is not the purpose of the present paper to attempt any discussion of these forms with the exception of the small definitely formed bodies which Eidam named bulbils, and which are, in some instances at least, sclerotoid in their nature.

Bulbils are now for the first time reported among the Basidiomycetes; one species is definitely connected with *Corticium alutaceum*, and the basidiomycetous nature of two other forms is demonstrated, although they are not specifically located. In examining the literature bearing upon bulbils there appears a great confusion due to the conflicting opinions of those who have observed these forms. This confusion the writer cannot attempt to set straight, but a brief review of other known species may assist in the understanding of those with which this paper deals.

A considerable number of species of bulbils has been described and usually placed tentatively in the genera *Helicosporangium* and *Papulospora*. The method of formation varies. In *Helicosporangium parasiticum* H. Karst., *Helicosporangium coprophilum* Zokal, *Papulospora dahliae* Cost., and most other species, a short branch rolls up spirally in one plane, and the terminal (or subterminal) cell of the

spiral enlarges to form a central cell (or cells) which becomes surrounded by a cellular cortex formed by the other cells of the spiral or by branches from below. The cortical cells become empty owing to the absorption of their contents by the central cell. Considerable variation is observed in this process, both in the central cells, and in the development of the cortex, which may be entirely absent. In *Papulospora aspergilliformis* Eidam, there is no distinction between cortical and central cells, and the primordium varies from an evident spiral or screw to a mere gnarled and knotted hypha. This latter method of formation closely resembles that seen in the basidiomycetous bulbils described in this paper (see p. 165). Zokal ('86) describes bulbils belonging to species of *Peziza* which originate from branching hyphae that become swollen, filled with protoplasm, and woven tightly together. The writer has under cultivation a species of bulbil found by Dr. Thaxter running over cultures of Cuban cotton flowers. It has the appearance of an erysipheaceous perithecium, but sections reveal no differentiation of the internal cells. It is formed from an interlacing weft of several different hyphae.

The opinions held regarding the nature and the systematic affinities of these bulbils are very diverse. Karsten ('65) affirms that the central cell of *Helicosporangium parasiticum* sometimes functions as an ascus containing eight spores, and that the bulbil is a perithecium belonging to the Erysipheae. Eidam ('77; '83), in studying what he supposed to be the same fungus, but which Karsten ('88) declares to be another species and names *Baryeidamia*, says that the central cell functions as a spore, not an ascus, and after comparing the bulbil to the perithecium of the Erysipheae and the spore balls of *Urocystis*, decided that the species should be regarded as a transitional form between the Ustilagineae and the Erysipheae. Harz ('90) regards the central cells in *Helicosporangium* and *Papulospora* as oogonia and creates the new order *Leptoomycetes* for these genera midway between the Oomycetes and the Zygomycetes and coordinate with them.

In *Papulospora aspergilliformis*, Eidam ('83) believes that the bulbils are immature ascocarps which have stopped short of ascus formation, a view also held by Costantin ('88) in the case of *Papulospora dahliae*. In an article on the morphological value of fungus bulbils, Zokal ('86) comes to the same conclusion as Eidam, *viz.*, that the bulbils he examined are not sclerotia, but ascocarps arrested in develop-

ment. In his study of *Melanospora fimicola* Hansen, Zukal found that the normal condition of a young perithecium at a certain stage is indistinguishable from a bulbil. Sometimes this bulbil stage of the ascocarp is retained permanently. This occurrence, which is occasional in this species, becomes habitual in certain fungi, as in species of *Peziza* which Zukal investigated, where the primordium of the bulbils and their development correspond exactly to early conditions of the ascocarp, and frequently a large well nourished bulbil may change into an ascocarp by the gelatinization of the cortical cells and the formation of a hymenium on the upper side. Mattiolo ('86) finds bulbils in connection with certain species of Hypocreaceae.

Dr. Thaxter informs the writer that pezizoid apothecia are produced in abundance in cultures of *Helicosporangium coprophilum* from Jamaica, both apothecia and bulbils arising from the same mycelium but quite independently. In this case the bulbils are not arrested primordia of apothecia but definite sclerotoid propagula.

Of the bulbil species known, some are thus seen to be clearly ascomycetous, while the systematic affinities of others are matters of conjecture only. It seems clearly evident from the brief discussion above that the convenient term bulbil is applied to very diverse structures, referring sometimes to imperfectly developed ascocarps of *Discomycetes* or *Pyrenomycetes*, sometimes to bodies of a definite sclerotoid nature, and sometimes to other bodies whose morphology is less evident. The bulbil form and structure may be assumed by very dissimilar organs of widely separated fungi, *e. g.*, compare the bulbils of *Corticium alutaceum* and of *Helicosporangium parasiticum* with the bulbil-like ascocarps of *Erysiphe* and *Penicillium*, and the spore balls of *Urocystis* and *Tubercinia*.

The bulbils of basidiomycetous origin appear to be sclerotoid in their nature. No sharp line can be drawn between them and ordinary sclerotia, although the distinction is usually sufficiently clear to warrant the retention of both names. By sclerotia are usually understood large closely compacted masses of hyphae, irregular in size and shape, with a thick-walled, dark-colored exterior enclosing a central portion which contains reserve food material. They cannot strictly be classed as reproductive bodies, but are dormant vegetative structures which, on resumption of activity usually produce the characteristic fructification of the fungus. On the other hand, the bulbils under discussion are much smaller, are fairly uniform in size and shape, have no dis-

tion of internal and external parts, and on germination produce vegetative mycelia. They may properly be regarded as reproductive bodies. But most distinctive of all is the definite origin of the bulbil from a single hypha, a characteristic not possessed by the sclerotium. Still it must be understood that both bulbil and sclerotium are variations of the same type of structure, which is the compacting into a resistant, dormant mass of a group of vegetative cells or hyphae, which are capable of resuming activity after a period of repose.

The discovery of these bulbils may indicate that this is not a rare method of reproduction among Hymenomyces; the small size of the bulbils and the absence of any massing into a conspicuous fructification accounts for their non-discovery in the field. Bulbil formation would appear to be a very valuable means of propagation, for bulbils combine much of the portability of spores with the power of sclerotia and rhizomorphae to resist unfavorable conditions.

Conidia.—From the author's studies it appears that well differentiated conidia are not common among the Hymenomyces, although they exist in a number of species, and in much greater variety than was previously supposed.

Conidia were found in five species and they are of five distinct types; in *Lentodium squamulosum* the conidia are borne upon the basidiosporic fructification, in *Peniophora candida* they have a definite sporodochium or fruit body of their own, while in the three species of *Corticium* they are borne upon the mycelium in different ways: the conidia of *Corticium alutaceum* are small and somewhat resemble oidia; those of *Corticium roseo-pallens* closely resemble the basidiospores, and are produced successively in nearly sessile tufts upon the hyphae; while the Oedocephalum-like conidia of *Corticium effusatum* are quite unlike the basidiospores but strikingly resemble the conidia found by Brefeld in *Polyporus annosus*.

Furthermore it appears that of the five conidia-bearing species studied,—*Lentodium squamulosum*, *Peniophora candida*, *Corticium alutaceum*, *Corticium roseo-pallens*, and *Corticium effusatum*,—four belong to the Thelephoraceae, three being members of the genus *Corticium*, and one of the nearly related genus *Peniophora*. This circumstance is partially explained by the fact that the majority of the species studied belong to *Corticium* and nearly related genera of the Thelephoraceae. However, a sufficient number of species of Hydnaceae and Polyporaceae was studied to warrant the statement that

conidia, at least upon the mycelia, are less common in these families than in the Thelephoraceae.

As a result of his culture studies, Brefeld developed a theory of the origin of the Basidiomycetes. He believes that the basidium is but a modified conidiophore in which the spores are reduced to the fixed number four. The Basidiomycetes, in his opinion, are not of common ancestry, but originated at several points where the basidium developed from the conidiophore. Pilacre, *Tomentella*, and *Polyporus annosus* are plants in which the ancestral conidiophore is still preserved in connection with the derived basidium.

If Brefeld is correct in assuming that the basidium of *Polyporus annosus* is derived from the Oedocephalum-like conidiophores of that species, then the same relation must exist between the basidium and conidiophore of *Corticium effuscatum*, although here the basidiospores and conidia are more dissimilar than they are in the former species. In *Corticium roseo-pallens* the conidia and basidiospores differ only in length, but the low conidiophores do not much resemble the basidia, and the successive development of the conidia is another point of difference. However, some remote relation between conidiophore and basidium might be advocated in this species also.

This theory of Brefeld's, based largely upon external resemblance of the organs in question, is open to serious objections, and leaves many questions unanswered. It is not the writer's plan, however, to discuss this topic further, for the many interesting and important questions which arise concerning the nature of the Basidiomycetes lie entirely beyond the scope of the present culture study.

SUMMARY.

(1) The basidiospores of about seventy-five species of Polyporaceae, Hydnaceae, and Thelephoraceae (the majority belonging to the last group) were germinated and grown in pure cultures; about 40% of these possess some secondary method of reproduction, usually mycelial oidia or chlamydospores.

(2) Oidia were not found among the Thelephoraceae and Hydnaceae, but were produced by one half of the species of Polyporaceae studied. Hence the writer's results confirm those of previous observers, that oidia are common upon the mycelia in the Polyporaceae and

Agaricaceae, but are rare or wanting in the lower families of the Hymenomyces. In the species mentioned in this paper the oidia retain their vitality but one or two days, but germinate readily when fresh.

(3) Chlamydospores have been known in a few agarics (especially in *Nyctalis*) and in a considerable number of Polyporaceae where they reach their highest development. It is probable also that the conidia reported in the hymenium of species of *Stereum*, *Corticium*, *Hydnum*, etc., are chlamydospores. Aside from these doubtful cases chlamydospores were not known in the lower families of Hymenomyces. The writer has found chlamydospores to be much more common, particularly upon the mycelium, than was previously known, having found them in over one quarter of the species cultivated; they occur in about equal numbers in the three families studied. Undoubtedly further culture study will yield additional proof of their wide distribution among Hymenomyces.

(4) Conidia of a more or less doubtful nature have been reported in a number of species belonging to all families of Hymenomyces, but only in *Tomentella* and *Polyporus annosus* were regularly occurring and well differentiated conidia known to exist. The writer has found conidia or other rather highly specialized secondary methods of reproduction in the following species, all of which belong to the Thelephoraceae except *Lentodium*: —

(a) *Corticium subgiganteum*, whose imperfect form is known as *Michenera artocreas*. The *Michenera* spores are highly specialized chlamydospores which form a definite fructification of their own with a well defined hymenial layer.

(b) *Corticium alutaceum*, which produces conidia of a simple oidium-like nature on the young mycelia, and red-brown spore balls or bulbils in great profusion on the mature mycelium.

(c) *Peniophora candida*, a new species, which is the perfect form of the well known *Aegerita candida*.

(d) *Corticium roseo-pallens*, which produced conidia in great abundance on all mycelia. The conidia closely resemble the basidiospores and are produced successively until groups of from two to ten are formed upon low dome-shaped or capitate elevations on the hyphae.

(e) *Corticium effusatum*, which produces conidia of the *Oedocephalum* type in all cultures, thus recalling Brefeld's *Heterobasidion annosum*. The conidia in this species differ from those of *Hetero-*

basidion principally in their smaller size and in the greater tendency of the sporophores to branch and proliferate. The mycelia also produce abundant chlamydospores.

(f) *Lentodium squamulosum*, which bears helicoid conidia upon long attenuated hairs arising from the young veil and from the margin of the developing pileus. The principal interest attaching to this species, however, lies in the structure and method of development of the basidiosporic fructification. The stipe and pileus are those of an agaric, but the hymenial region is occupied by a thick layer of irregular tubes and chambers whose external openings are more or less completely closed by a white flocculent veil. Diffusely spreading hyphae arising from the trama form this veil and by diverting the direction of growth of the young plates of the hymenium cause the porose-cellular development of the hymenial layer. The writer inclines to the belief that *Lentodium* is an autonomous species, whose systematic position is between the Agaricaceae and the Polyporaceae.

(g) In addition to the bulbils of *Corticium alutaceum* two other species of bulbils were found in the field which produced scattered basidia in pure cultures. Hence the formation of bulbils may be looked for in other species of Hymenomyces.

(5) The quantity of data bearing upon the polymorphism of Hymenomyces is still too limited to make generalizations of much value, but from the facts at hand it appears: (a) that a considerable majority of Hymenomyces possess no secondary spores; (b) that oidia are common among the Agaricaceae and Polyporaceae, and are confined to those two families; (c) that chlamydospores occasionally occur in connection with the basidio-fructification, as in *Nyctalis*, *Ptychogaster*, and *Fistulina*, and are quite widely distributed on the mycelia of all families; (d) that conidia and other highly specialized secondary methods of reproduction are rare, and occur more frequently in the Thelephoraceae than in the higher families.

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EXPLANATION OF PLATES.

The figures of plate 18 to 22 were drawn at the level of the stage with the aid of a camera lucida, using various combinations of Zeiss lenses giving the approximate magnifications mentioned. These plates were reduced in photographing to about $\frac{2}{3}$ their original size, and the magnification given with each figure is the original magnification of the drawing before reduction. Plates 23 and 26 are photographs of living material or of herbarium specimens. Plates 24 and 25 are photomicrographs of sections stained in Heidenhain's haematoxylin.

PLATE 18.

Polyporus fumosus Fr.

Fig. 1. Hypha forming chains of oidia. $\times 550$.

Corticium subgiganteum.

Fig. 2. Section of hymenium. $\times 220$.

Fig. 3. Mature basidiospore. $\times 390$.

Fig. 4-5. Germinating basidiospores. $\times 390$.

Fig. 6. Diagrammatic section through the cup-shaped fructification of *Michenera artocreas*, showing the hymenium and the brownish bands formed by the successive periods of growth. $\times 20$.

Fig. 7. Portion of hymenium and subhymenium of *Michenera* showing spores and paraphyses. $\times 220$.

Fig. 8-9. Groups of sporophores of *Michenera* showing basipetal branching and spores of various ages. $\times 550$.

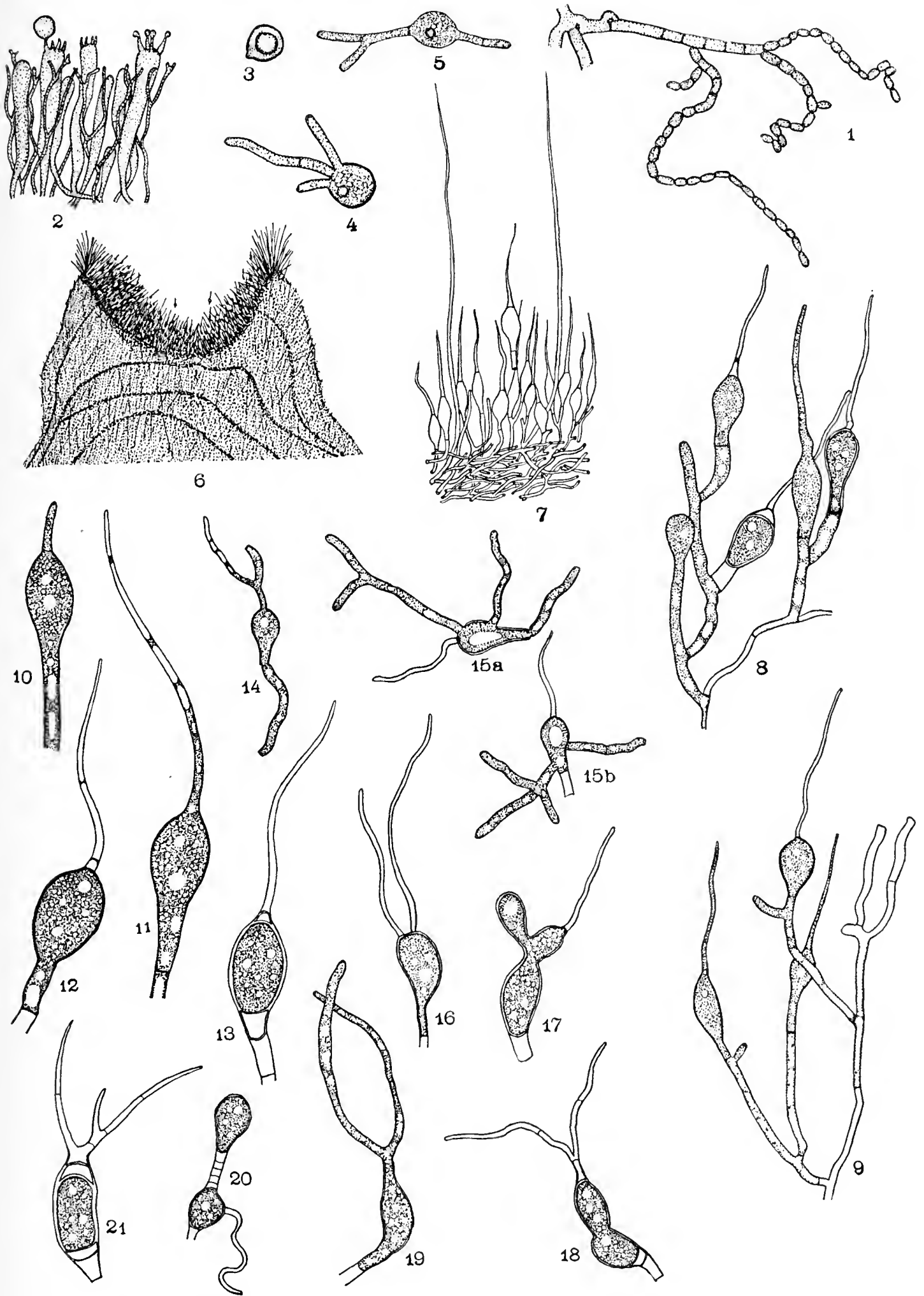
Fig. 10-13. Stages in the development of a *Michenera* spore. $\times 1000$.

Fig. 13. Mature *Michenera* spore. $\times 1000$.

Fig. 14. An immature *Michenera* spore with vegetative hyphae arising from the stipe and appendage. $\times 390$.

Fig. 15. Germinating *Michenera* spores. $\times 390$.

Fig. 16-21. Abnormal *Michenera* spores. $\times 550$.



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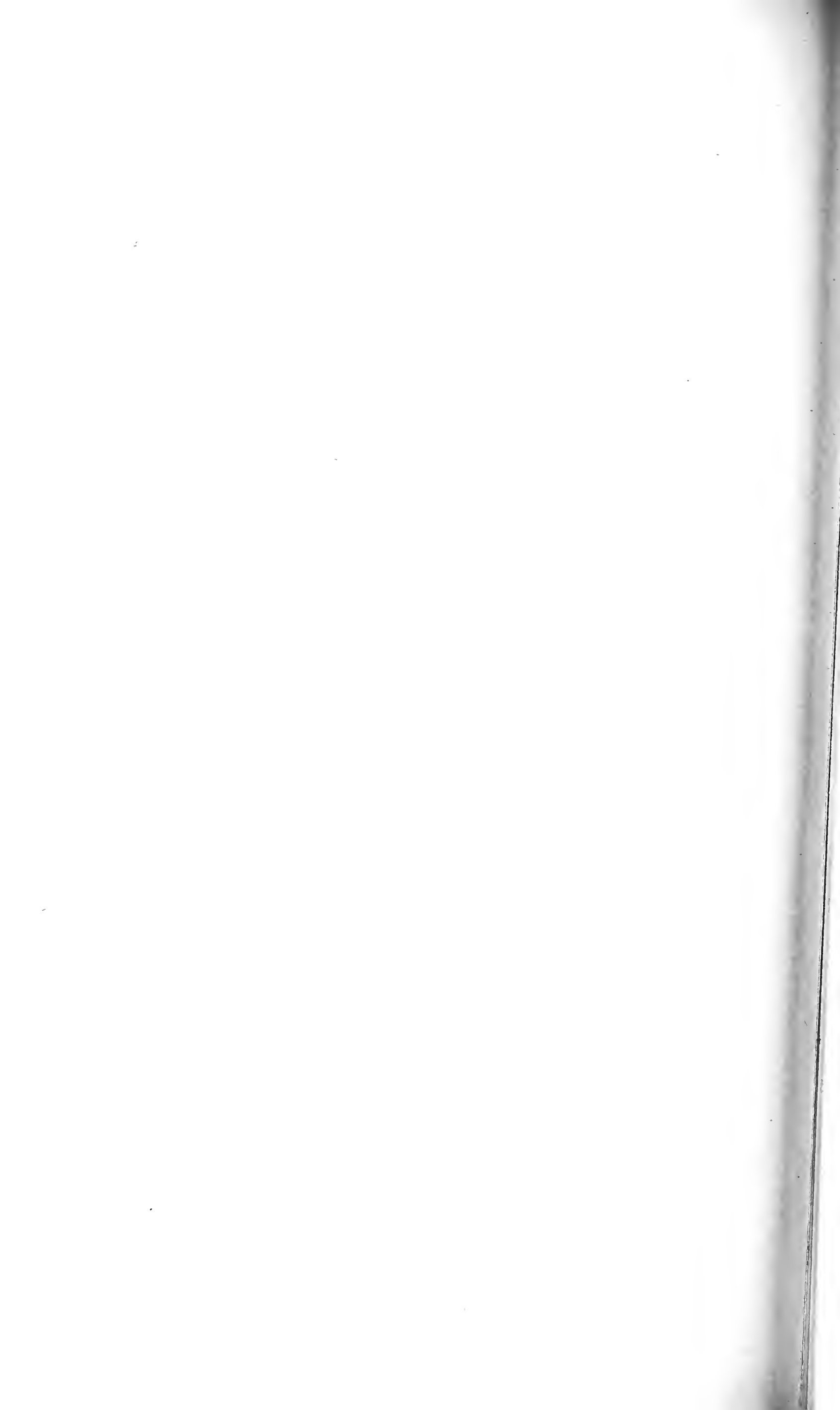
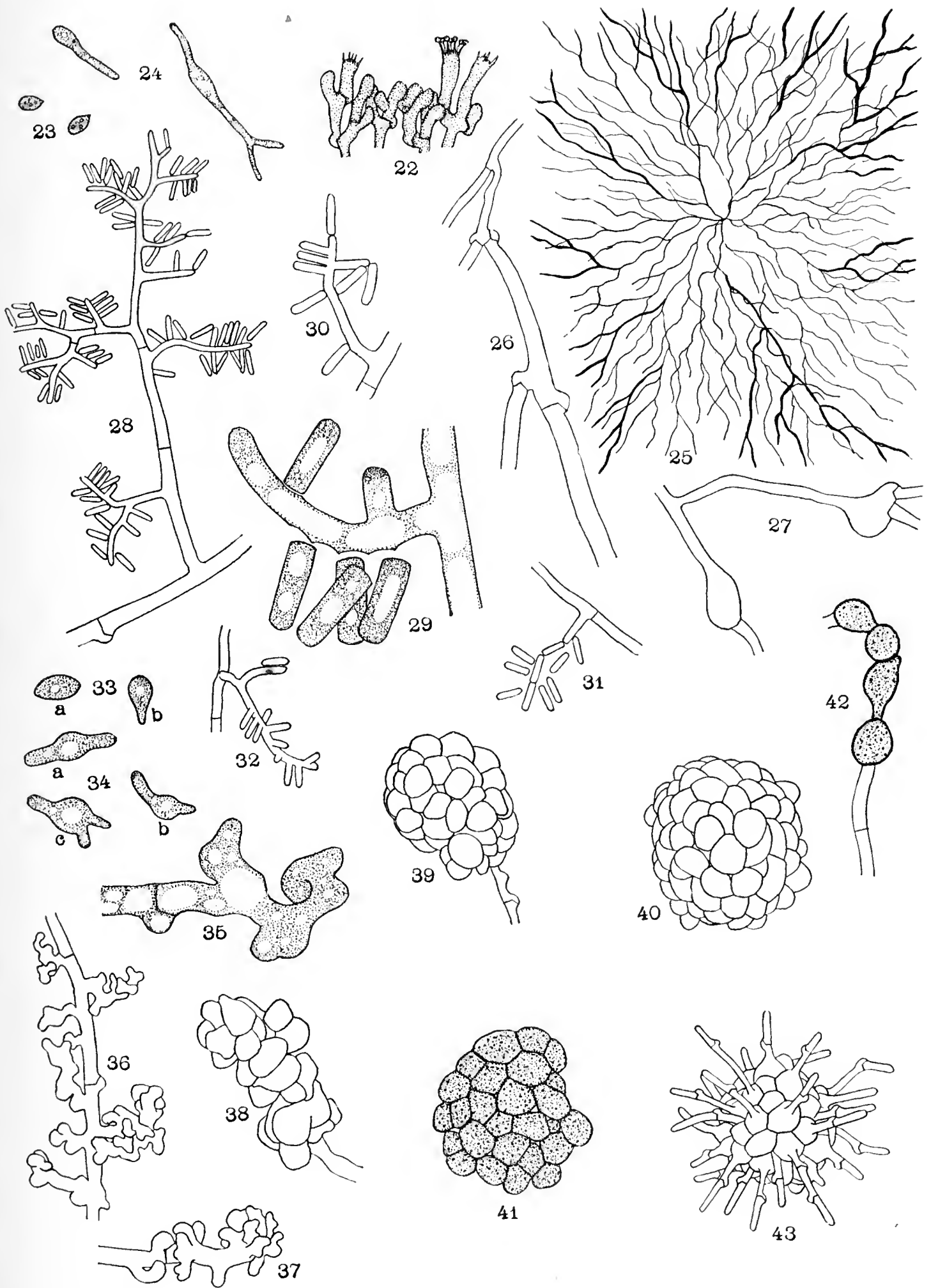


PLATE 19.

Corticium alutaceum.

- Fig. 22. Section of hymenium. Basidia with from 4 to 7 spores. $\times 550$.
Fig. 23. Mature basidiospores. $\times 990$.
Fig. 24. Germinating basidiospores. $\times 600$.
Fig. 25. Diagrammatic representation of primary mycelium showing origin of secondary mycelium. $\times 56$.
Fig. 26. Origin of clamped secondary hypha from unclamped primary hypha. $\times 990$.
Fig. 27. Secondary hypha showing enlarged distal ends of many cells. $\times 550$.
Fig. 28. Conidia-bearing hypha. $\times 660$.
Fig. 29. Conidiophore with several mature conidia becoming detached and one in process of formation. $\times 2300$.
Fig. 30. Conidiophore with terminal conidium. Shows bilateral arrangement of conidia when the conidiophore is immersed in or lies upon the surface of the hanging drop. $\times 990$.
Fig. 31. Old conidiophore breaking up into an oidium chain of spores. $\times 990$.
Fig. 32. Aerial conidiophore showing conidia arranged radially instead of bilaterally, adjacent conidia frequently lying in a parallel direction in groups of two or more. $\times 990$.
Fig. 33. Conidia swelling preparatory to germination. $\times 1200$.
Fig. 34. Germinating conidia. $\times 1200$.
Fig. 35. Primordium of bulbil. End of primordium sometimes curves in helicoid fashion. $\times 2300$.
Fig. 36. Hypha showing numerous bulbil primordia. $\times 550$.
Fig. 37-40. Stages in formation of bulbil. Figure 40 is a mature bulbil. Fig. 37-38, $\times 550$; fig. 39-40, $\times 390$.
Fig. 41. Section of mature bulbil showing dense granular cell contents and small intercellular spaces. There is no difference between internal and external cells. $\times 390$.
Fig. 42. Abnormal bulbil reduced to a chain of cells. $\times 390$.
Fig. 43. Germinating bulbil after 20 hours in drop culture. $\times 220$.



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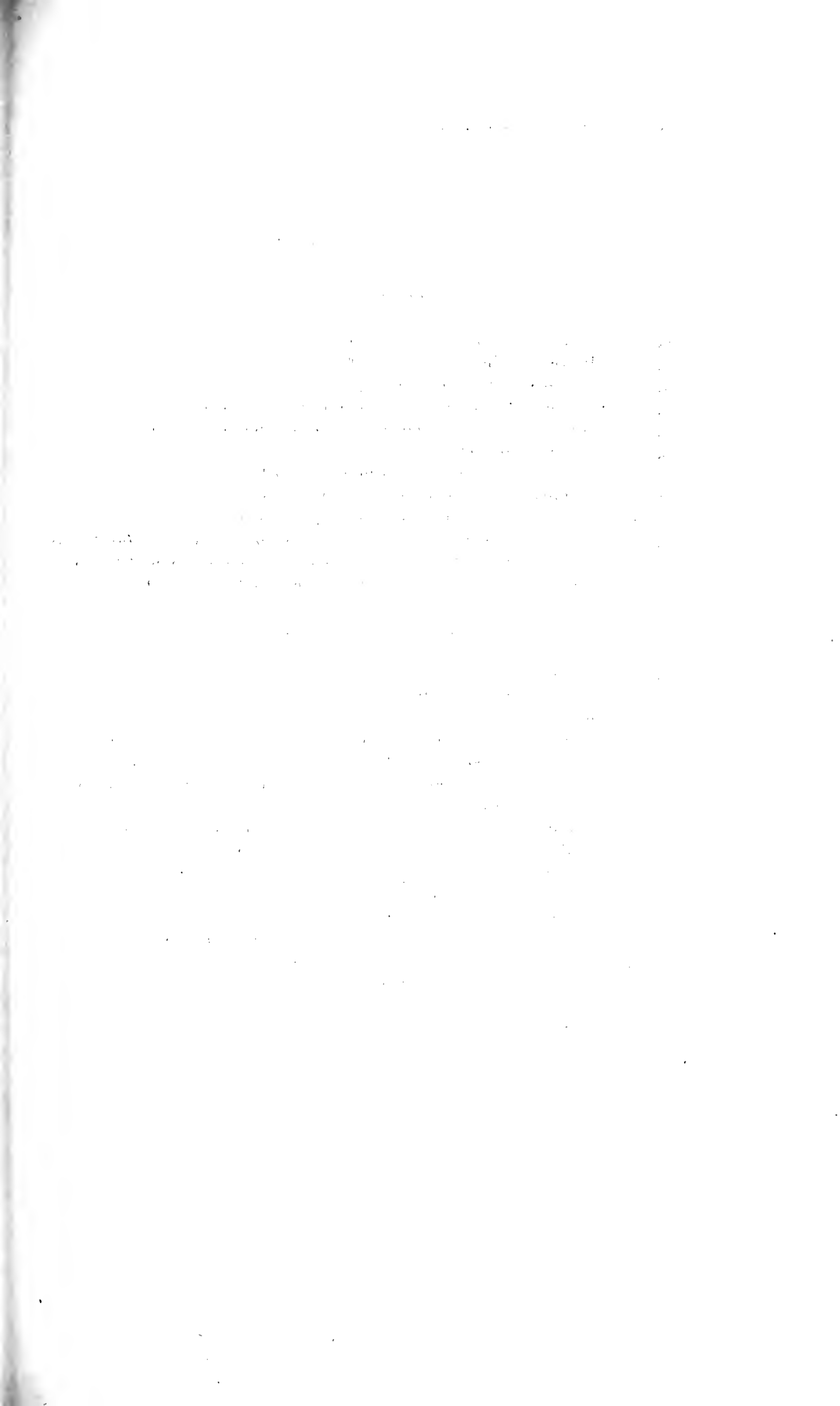


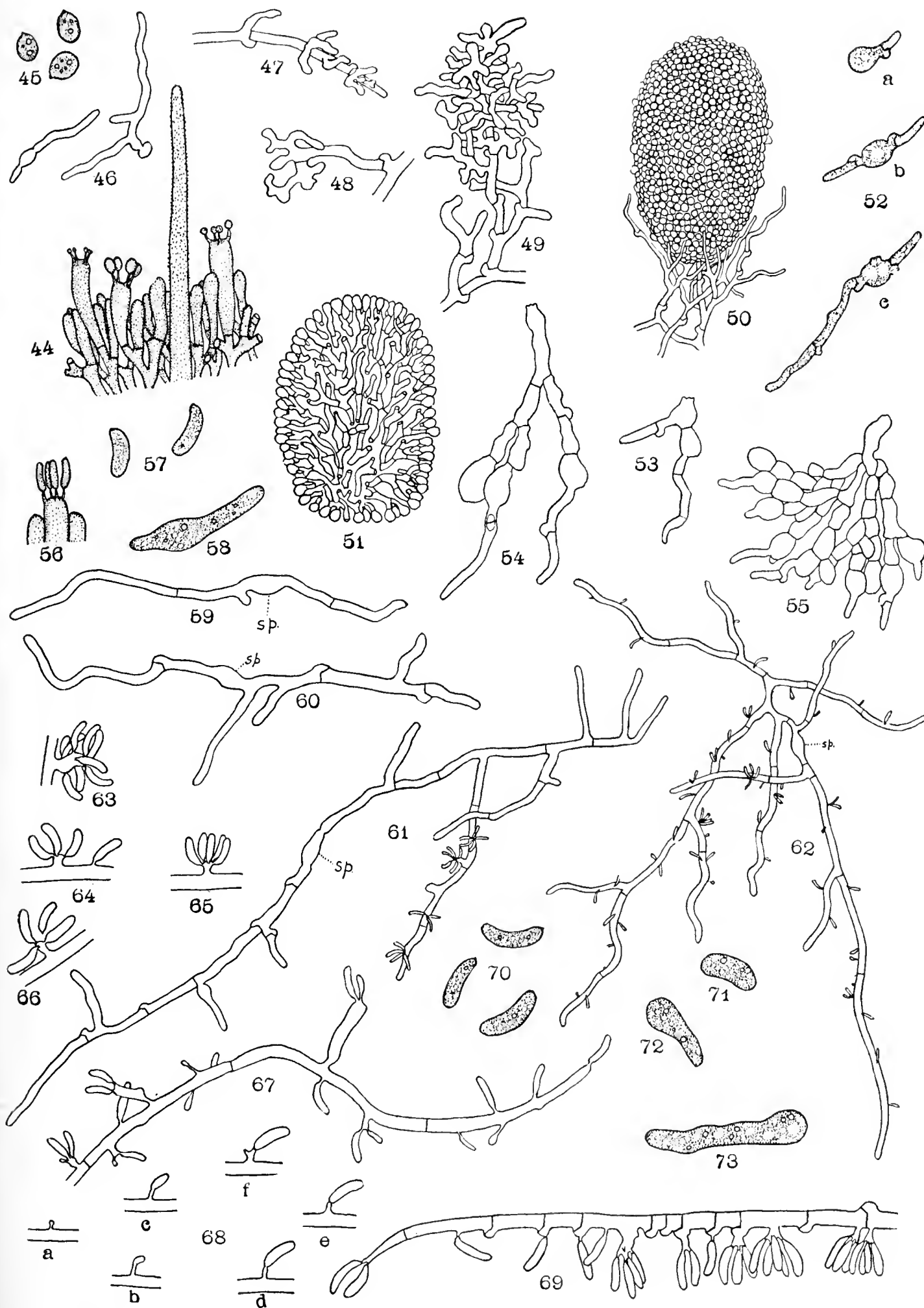
PLATE 20.

Peniophora candida.

- Fig. 44. Section of hymenium. $\times 625$.
Fig. 45. Mature basidiospores. $\times 1000$.
Fig. 46. Germinating basidiospores. $\times 390$.
Fig. 47–48. Primordia of *Aegerita* sporodochia. $\times 390$.
Fig. 49. Later stage in development of sporodochium. $\times 390$.
Fig. 50. Mature sporodochium. $\times 220$.
Fig. 51. Section of mature sporodochium. $\times 390$.
Fig. 52. Germination of detached conidia. $\times 390$.
Fig. 53. Chain of two conidia germinating. $\times 390$.
Fig. 54–55. Some of the elements of a sporodochium placed in drop culture for 24 hours and then crushed out to show the origin of the germ tubes from the ends and sides of the conidia. $\times 390$.

Corticium roseo-pallens.

- Fig. 56. Basidium. $\times 760$.
Fig. 57. Basidiospores. $\times 1300$.
Fig. 58. Germinating basidiospores. $\times 1300$.
Fig. 59. Germinating basidiospore giving rise to a clampless mycelium. *sp.*, basidiospore. $\times 990$.
Fig. 60. Germinating basidiospore giving rise to a clamped mycelium. *sp.*, basidiospore. $\times 990$.
Fig. 61. Germinating basidiospore giving forth a clamped germ tube at one end and a clampless germ tube at the other, the latter producing conidia. *sp.*, basidiospore. $\times 550$.
Fig. 62. Young mycelium beginning to form conidia. $\times 390$.
Fig. 63–66. Sporophores of various shapes. $\times 1000$.
Fig. 67. One hypha from a mycelium of the age shown in figure 62, showing the beginning of conidium formation. $\times 990$.
Fig. 68 a–f. Stages in the development of conidium. In f, the second conidium is appearing. $\times 1000$.
Fig. 69. Hypha lying just at the surface of hanging drop with conidia all projecting downward into the air. Clamp connections frequently produce conidia. $\times 990$.
Fig. 70. Conidia. $\times 1300$.
Fig. 71–73. Germinating conidia. $\times 1300$.



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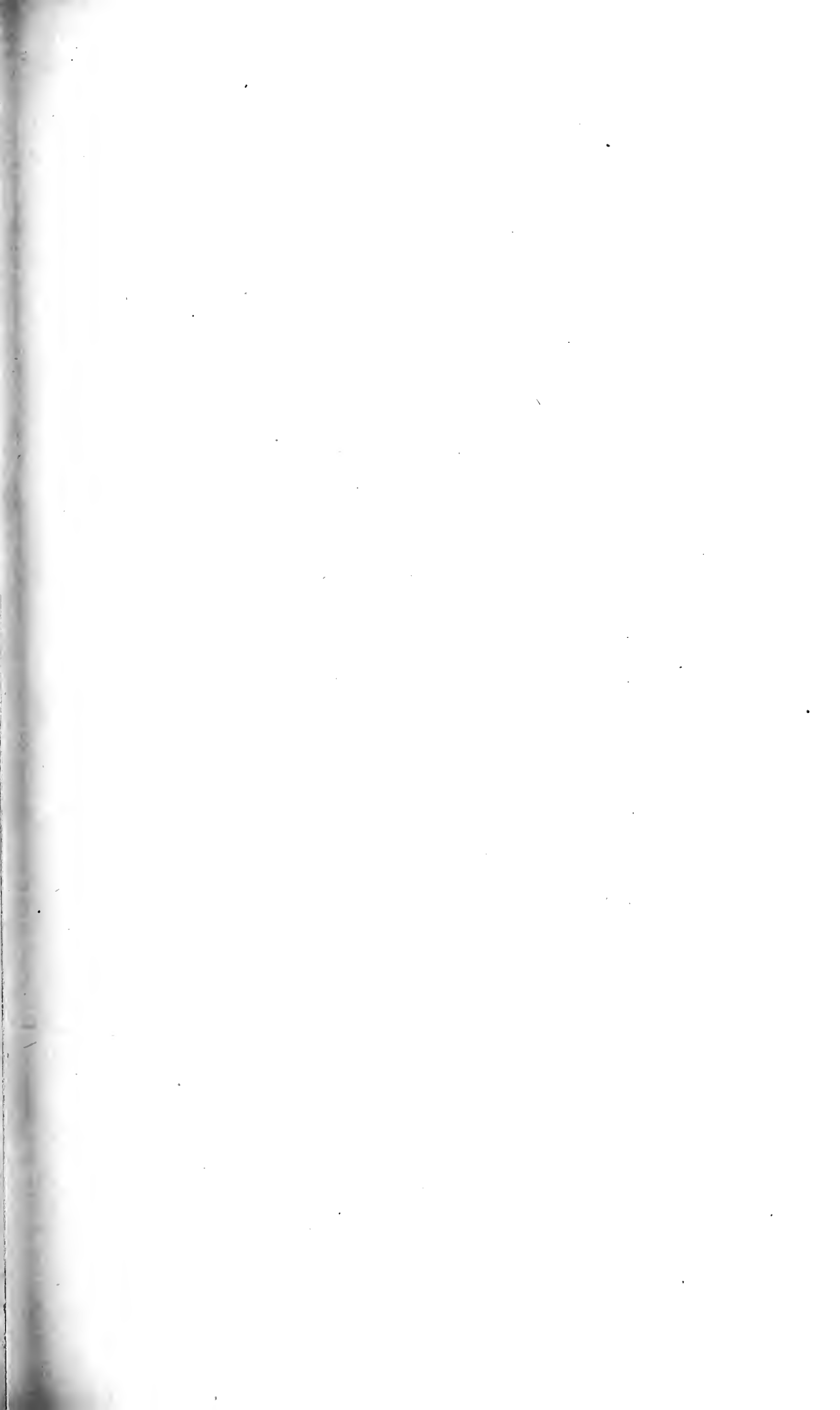
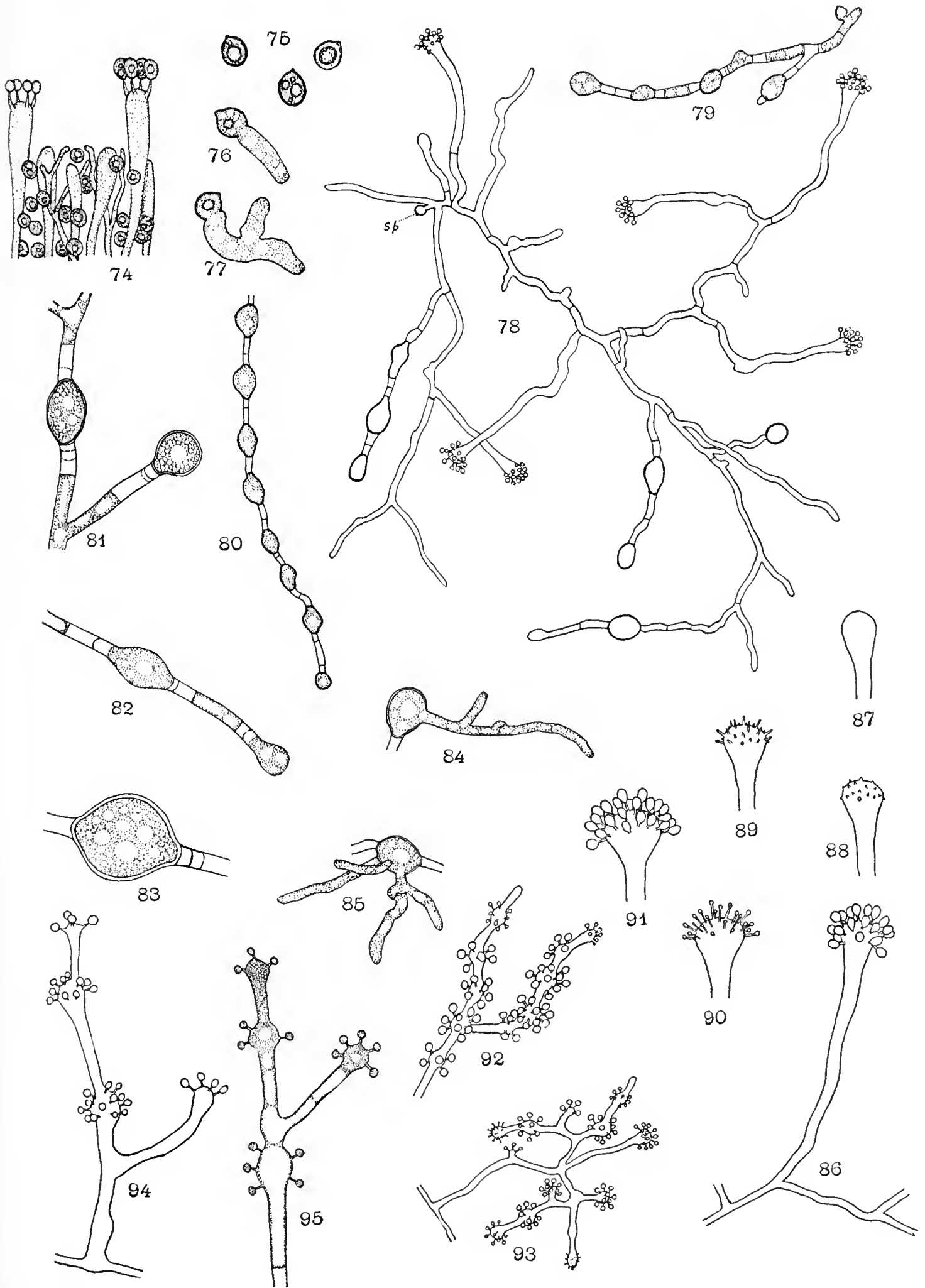


PLATE 21.

Corticium effusatum.

- Fig. 74. Section of hymenium showing discharged basidiospores which are always imbedded in the growing hymenium. $\times 550$.
- Fig. 75. Basidiospores. $\times 1300$.
- Fig. 76-77. Germinating basidiospores. $\times 1300$.
- Fig. 78. Young mycelium from germinating basidiospore (*sp.*) showing production of chlamydospores and conidia. $\times 390$.
- Fig. 79. Chlamydospore formation on germ tube in dilute decoction of horse dung. $\times 390$.
- Fig. 80. Row of chlamydospores. $\times 390$.
- Fig. 81-82. Developing chlamydospores. $\times 1000$.
- Fig. 83. Mature chlamydospore. $\times 1300$.
- Fig. 84-85. Germinating chlamydospores. $\times 625$.
- Fig. 86. Typical conidiophore arising from vegetative hypha. $\times 550$.
- Fig. 87-91. Stages in the development of conidiophore and conidia. $\times 760$.
- Fig. 92-94. Proliferation and branching of conidiophore. Fig. 92, $\times 390$; fig. 93, $\times 315$; fig. 94, $\times 550$.
- Fig. 95. Optical section of proliferating and branching conidiophore showing the dense protoplasm in the growing portion. $\times 550$



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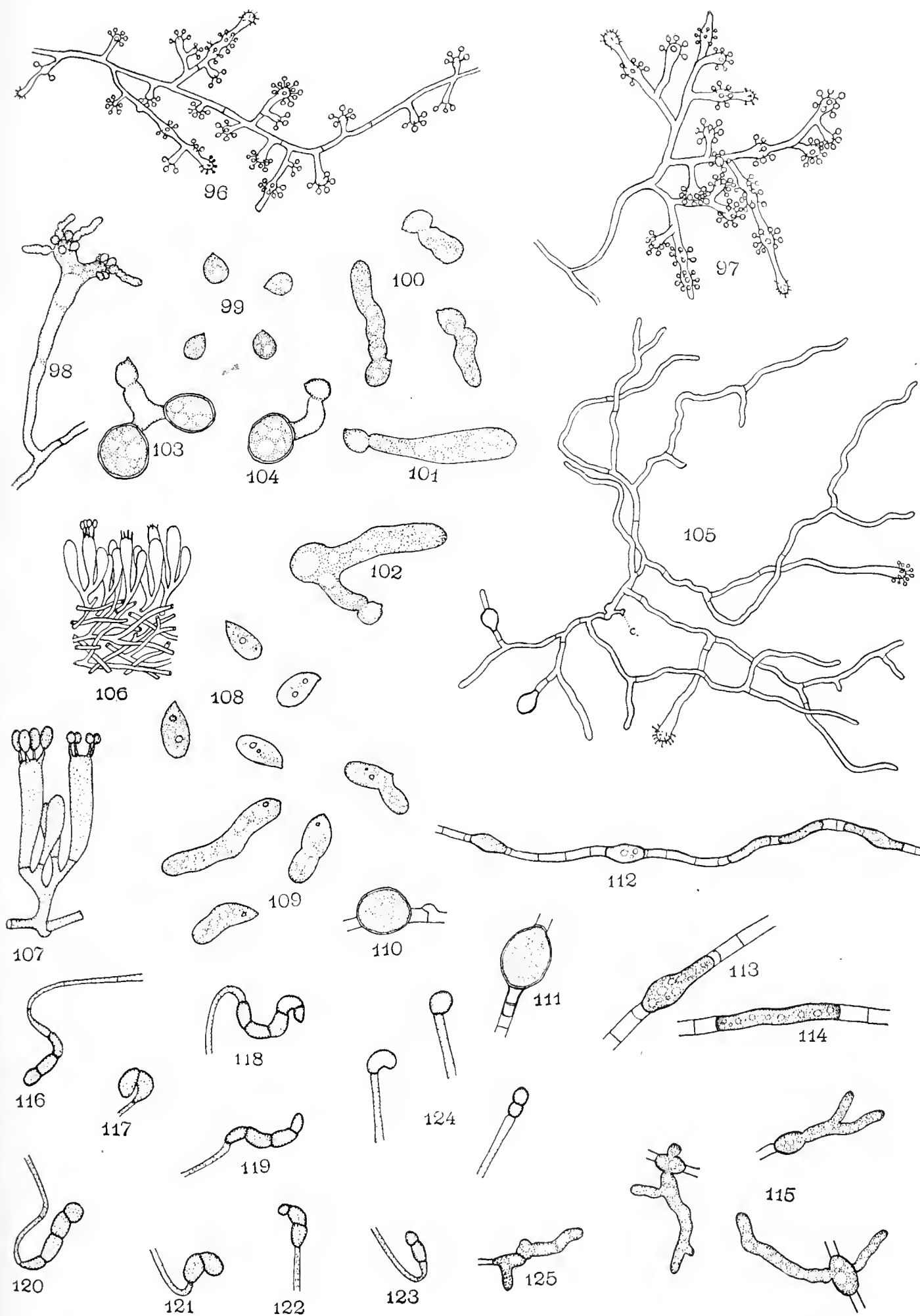
PLATE 22.

Corticium effusatum.

- Fig. 96. Hypha from which arise numerous conidiophores. $\times 315$.
Fig. 97. Compound conidiophore. $\times 315$.
Fig. 98. Conidia germinating *in situ* on conidiophore. $\times 550$.
Fig. 99. Conidia. $\times 1300$.
Fig. 100. Germinating conidia. $\times 1300$.
Fig. 101–102. Germinating conidia showing the enlargement of the small germ tubes to the size of normal hyphae. This takes place in figure 101 by gradual increase in size, and in figure 102 by a bulbous enlargement from which a normal-sized hypha arises. $\times 1300$.
Fig. 103–104. Chlamydospores forming in germ tubes from conidia. $\times 1300$.
Fig. 105. Young mycelium from germination of conidium (*c.*), showing production of chlamydospores and conidia. $\times 220$.

Lentodium squamulosum.

- Fig. 106. Section of hymenium. $\times 220$.
Fig. 107. Basidia. $\times 550$.
Fig. 108. Basidiospores. $\times 1300$.
Fig. 109. Germinating basidiospores. $\times 1300$.
Fig. 110–111. Normal chlamydospores. $\times 1000$.
Fig. 112. Developing chlamydospores. $\times 625$.
Fig. 113–114. Chlamydospores of abnormal shape. $\times 1300$.
Fig. 115. Germinating chlamydospores. $\times 625$.
Fig. 116–123. Conidia produced upon the young veil. $\times 930$.
Fig. 124. Conidia produced upon the margin of the young pileus. $\times 930$.
Fig. 125. Germinating conidium. $\times 930$.



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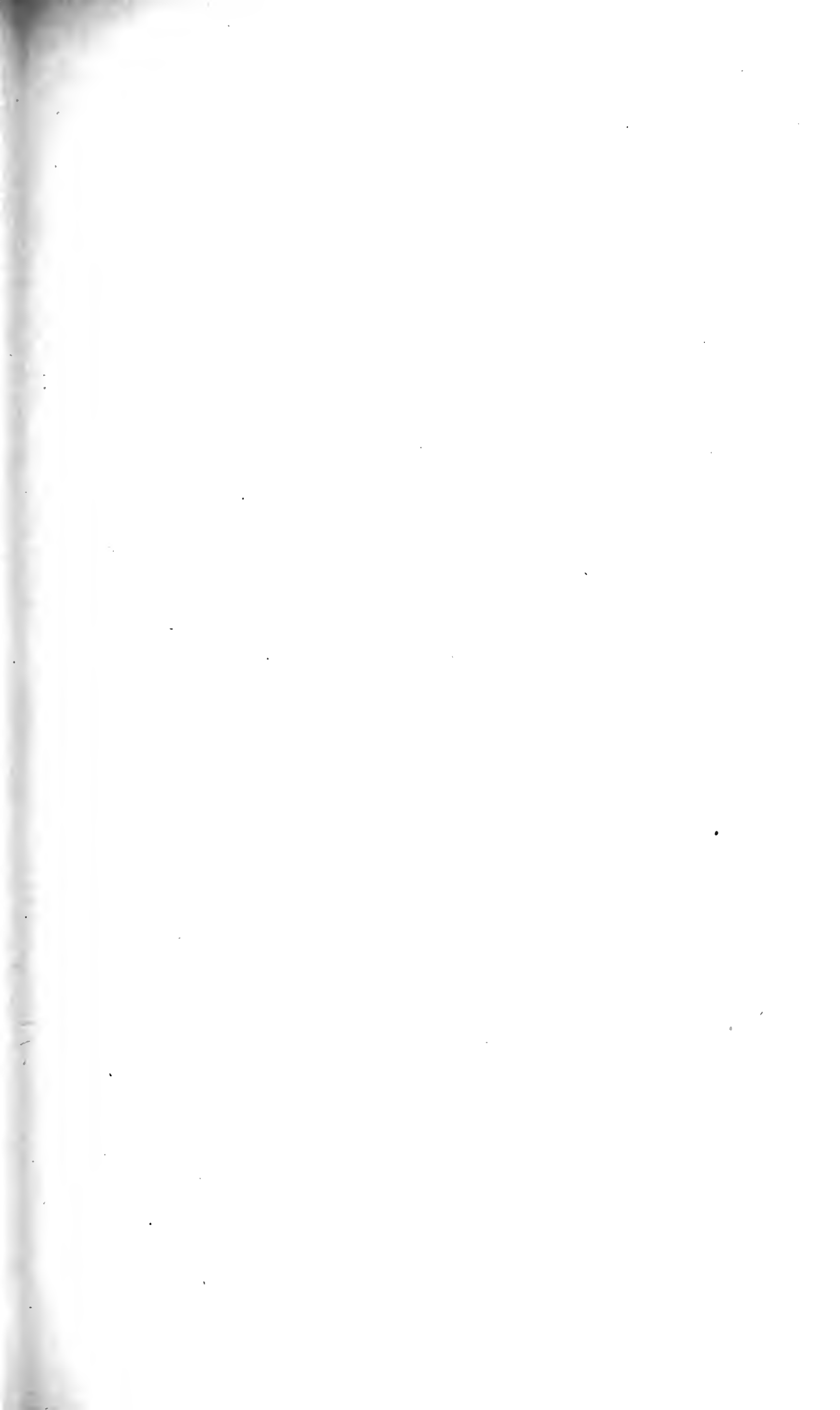


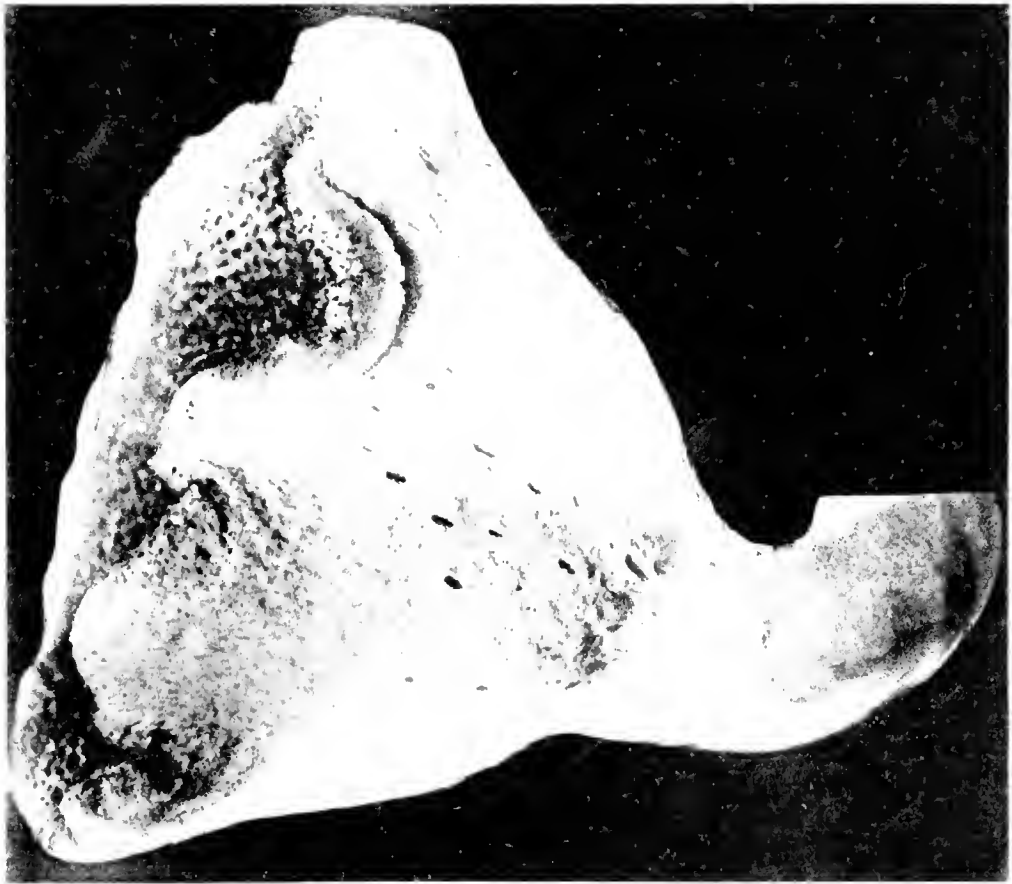
PLATE 23.

Lentodium squamulosum.

- Fig. 126. Two normal specimens with inrolled margin of pileus raised in pure culture in jar. $\times \frac{3}{4}$.
- Fig. 127. A single specimen from the jar in figure 128, showing the hymenial surface, the tendency toward radial arrangement of the chambers of the hymenial stratum showing through the cottony veil. $\times 4$.
- Fig. 128. Pure culture in jar upon stick of *Cephalanthus* wood, showing several fructifications, all with upturned pilei. $\times \frac{1}{3}$.



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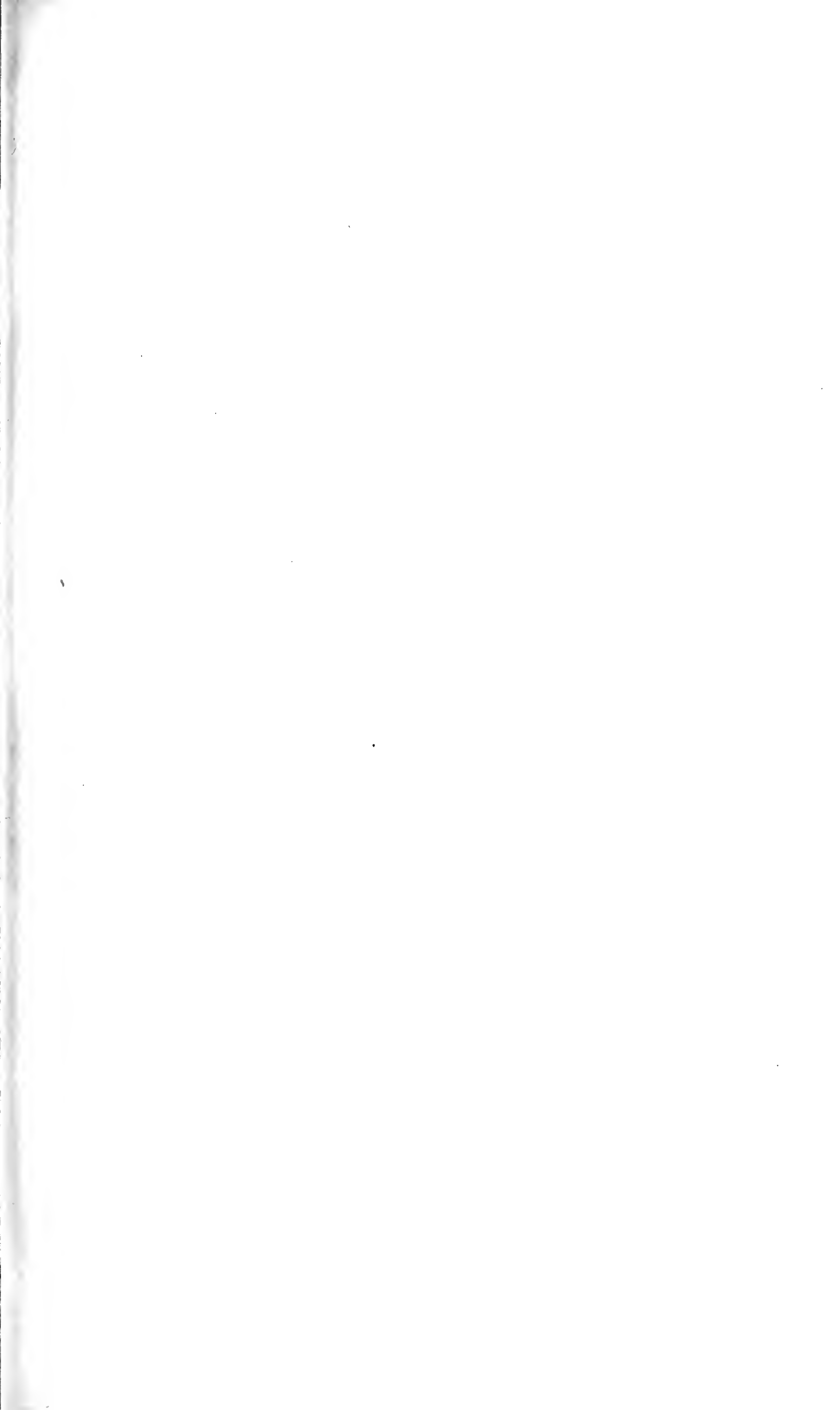
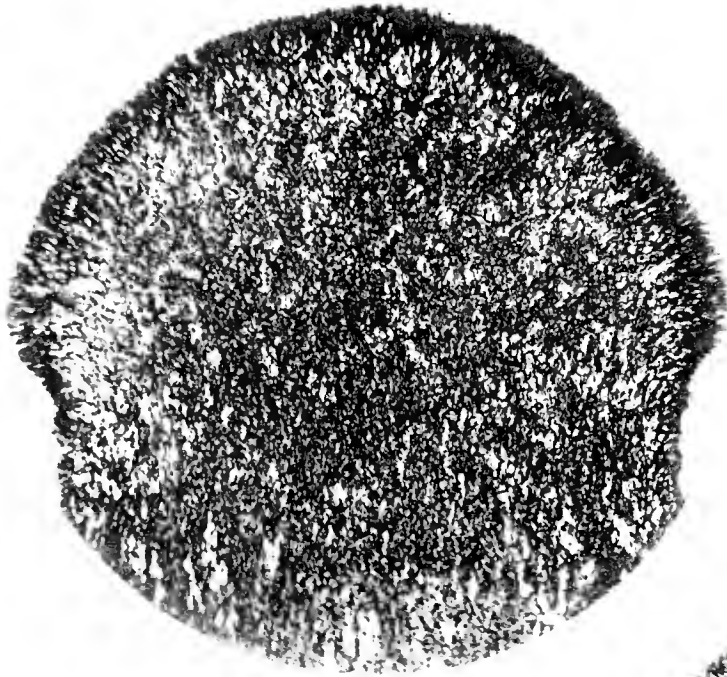


PLATE 24.

Lentodium squamulosum.

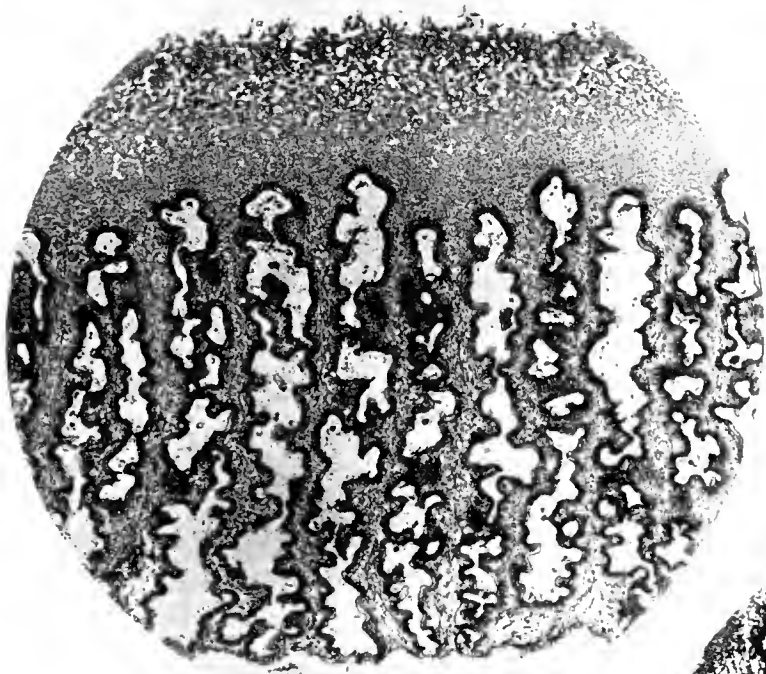
- Fig. 129. Section through the end of the stipe as it is beginning to expand to form the pileus. $\times 20$.
- Fig. 130. Section of young fructification showing the developing hymenium on the ventral surface of the growing pileus. $\times 15$
- Fig. 131. A vertical tangential section through the pileus showing the nature of the porose-cellular hymenial layer. $\times 30$.
- Fig. 132. A section similar to figure 131, showing the course of the hyphae and the nature of the veil. $\times 55$.



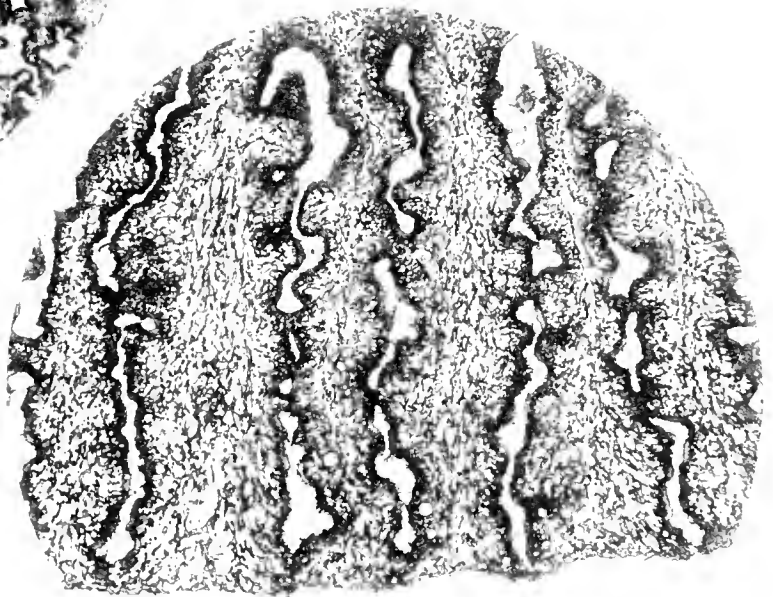
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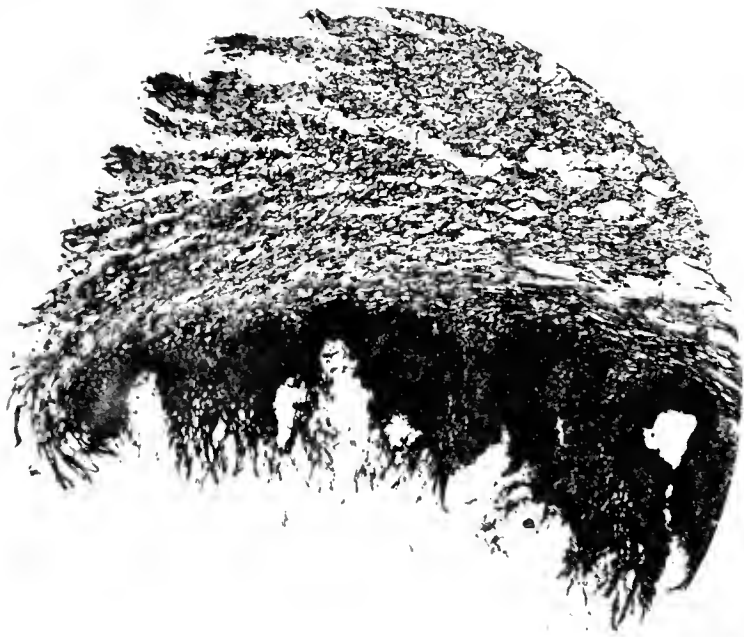
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PLATE 25.

Lentodium squamulosum.

- Fig. 133. Radial section through a young specimen showing hymenial region and margin of pileus. $\times 50$.
- Fig. 134. Edge of young hymenial plates showing the diffusely radiating conidiophores each bearing a single conidium. $\times 200$.
- Fig. 135. Section of specimen with upturned pileus. $\times 10$.
- Fig. 136. Section of abnormal specimen with no pileus, the globose head being entirely covered by the hymenial layer. $\times 6$.



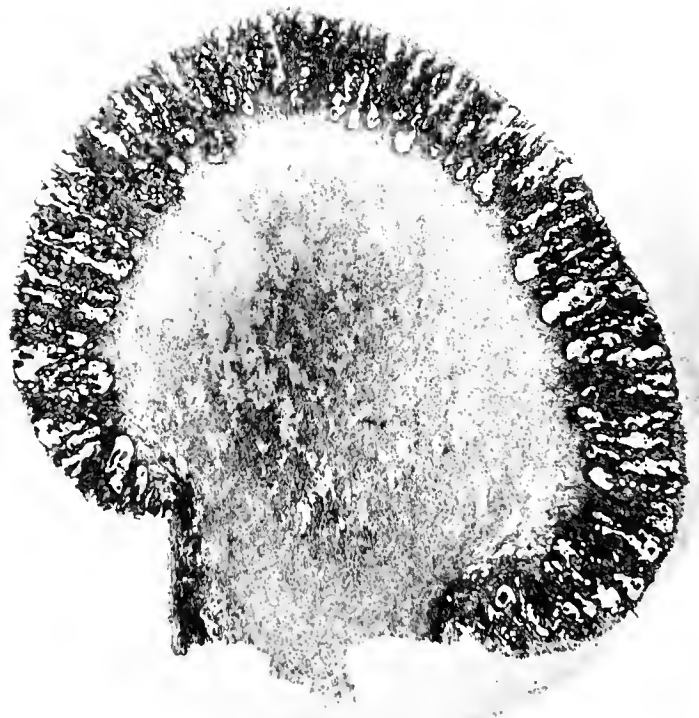
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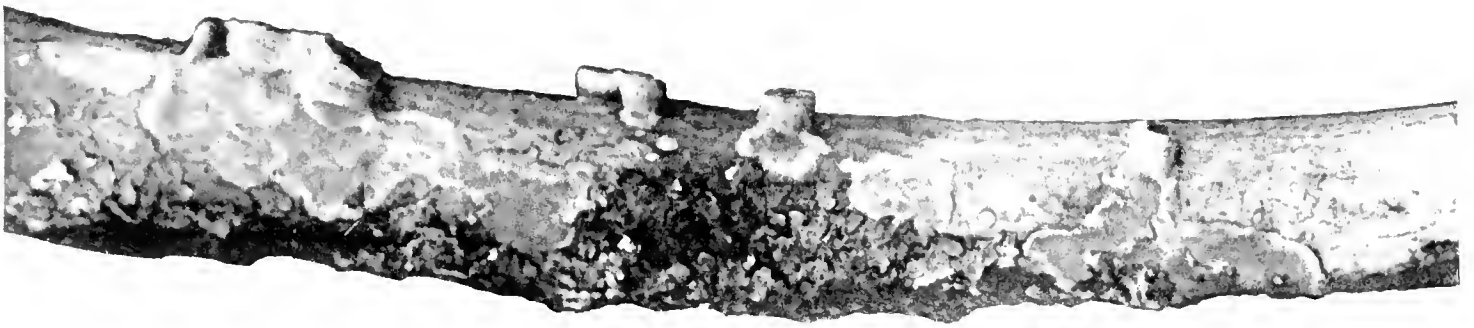
PLATE 26.

Corticium subgiganteum.

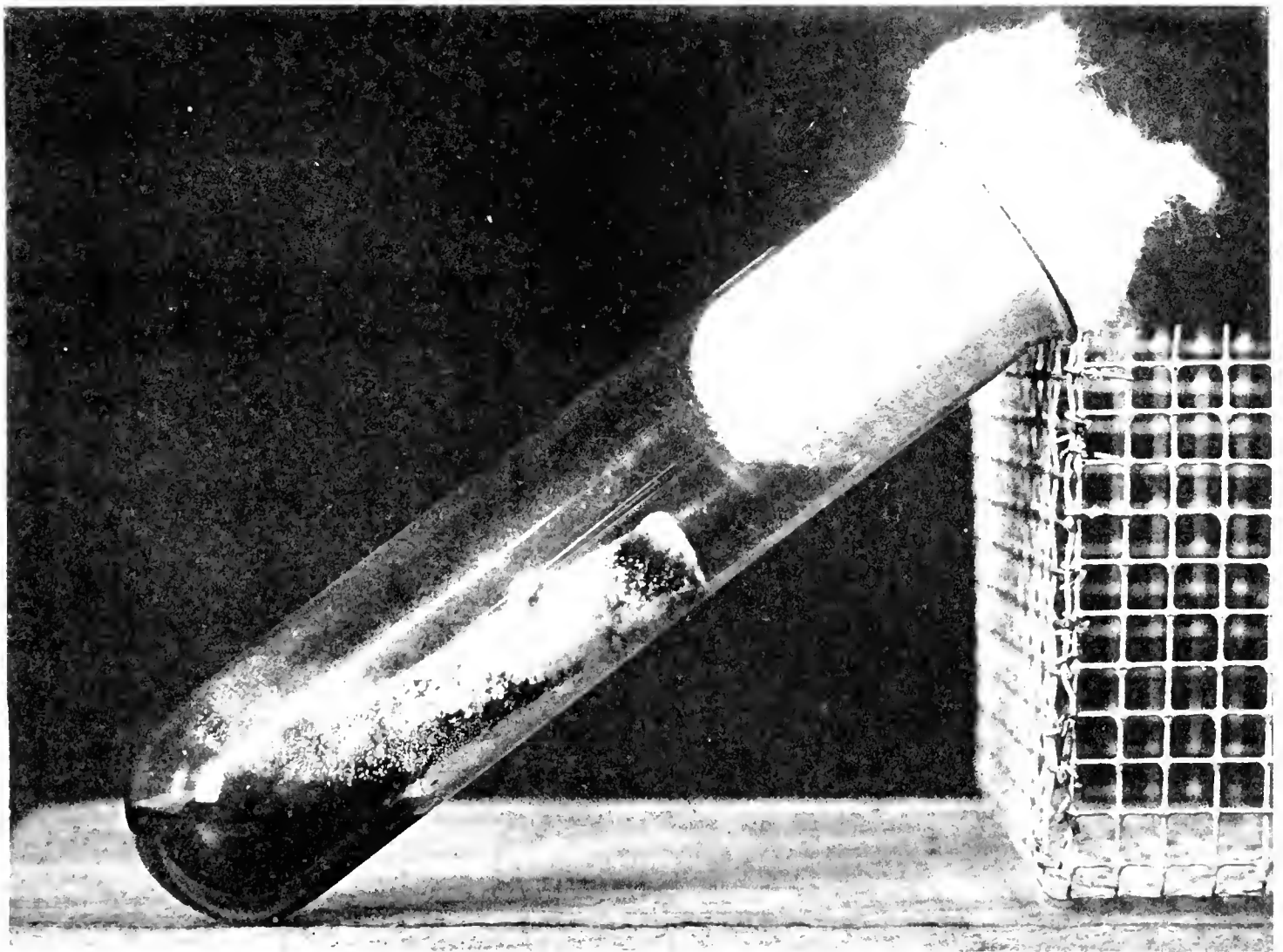
- Fig. 137. In normal specimens the fructifications of *Michenera artocreas* come on the upper side of the stick, and the hymenium of *Corticium subgiganteum* on the lower side. The figure shows two maple sticks which at first bore no trace of *Michenera* cups. They were then turned over so as to bring the *Corticium* hymenium uppermost, and after a time fructifications of *Michenera* developed, arising directly from the *Corticium* hymenium. The lower stick gives a vertical view and the upper stick a lateral view of the *Michenera* with the *Corticium* running over the bases and up the sides of the cups.

Peniophora candida.

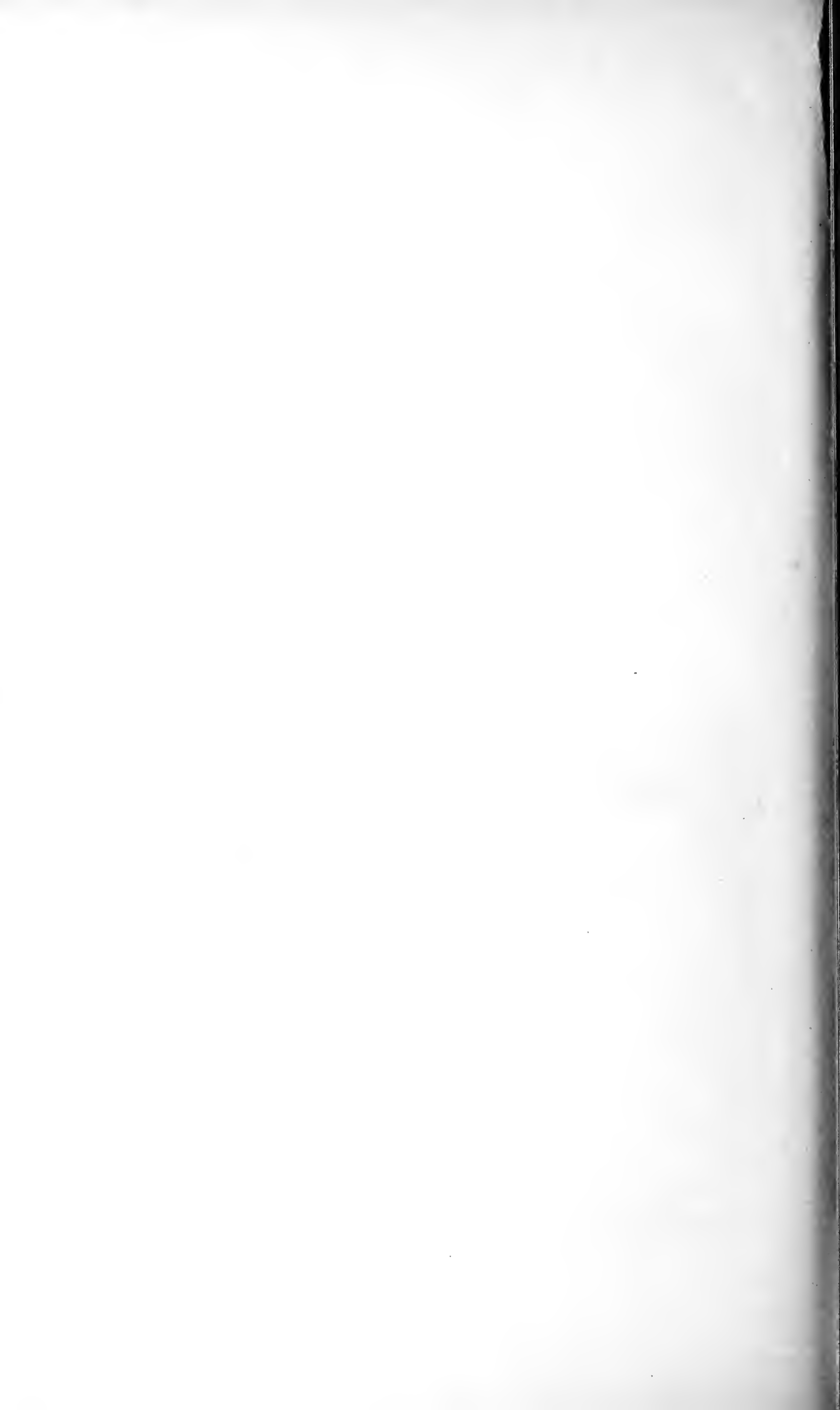
- Fig. 138. Large testtube in which is growing a pure culture of the basidiospores on a willow stick. A basidiosporic hymenium has developed on the stick, while *Aegerita* sporodochia have formed all over the surface of the stick and on the walls of the tube. $\times \frac{1}{2}$.



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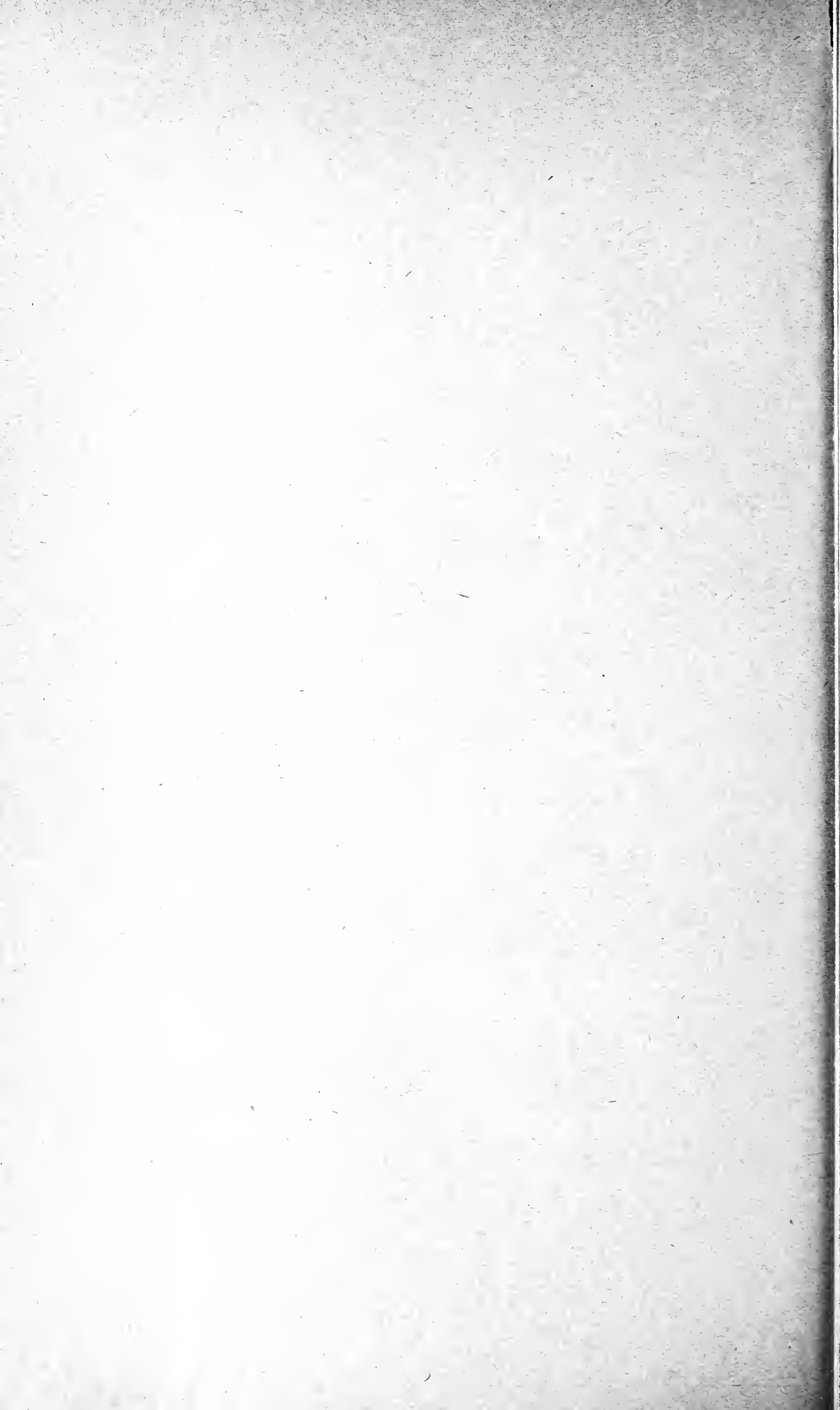
Proceedings of the Boston Society of Natural History.

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DRAINAGE MODIFICATIONS IN THE TALLULAH DISTRICT.

BY DOUGLAS WILSON JOHNSON.

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No. 5.— DRAINAGE MODIFICATIONS IN THE TALLULAH DISTRICT.¹

BY DOUGLAS WILSON JOHNSON.

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INTRODUCTION.

IN connection with the study of drainage modifications, the headwaters of the Savannah River have been frequently referred to as an example of drainage transferred from the Gulf system to the Atlantic, through the process of stream capture. The upper Savannah, known locally as the Chattooga River, flows directly southwest between Georgia and South Carolina to the westernmost point in South Carolina, there receiving the Tallulah River as a tributary from the northwest; it then turns abruptly southeast and continues, first under the name of the Tugaloo River and then of the Savannah River, to the Atlantic Ocean. Near the point where the river makes its peculiar bend to the southeast, there rises one of the headwater

¹ A Walker-prize essay, 1906.

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branches of the Chattahoochee system, which, under the local names of Deep Creek and Soque River, continues the southwesterly course started by the Chattooga. It has been considered that the Chattooga River formerly continued southwest by way of Deep Creek, Soque River, and the Chattahoochee River into the Gulf of Mexico; that it was diverted into the Savannah River by a process of stream capture; and that the sharp bend in the course of the stream and the falls and gorge on the Tallulah River are due to this capture.

In the spring of 1905 the writer visited the region in question, and spent several weeks in studying the geologic and physiographic

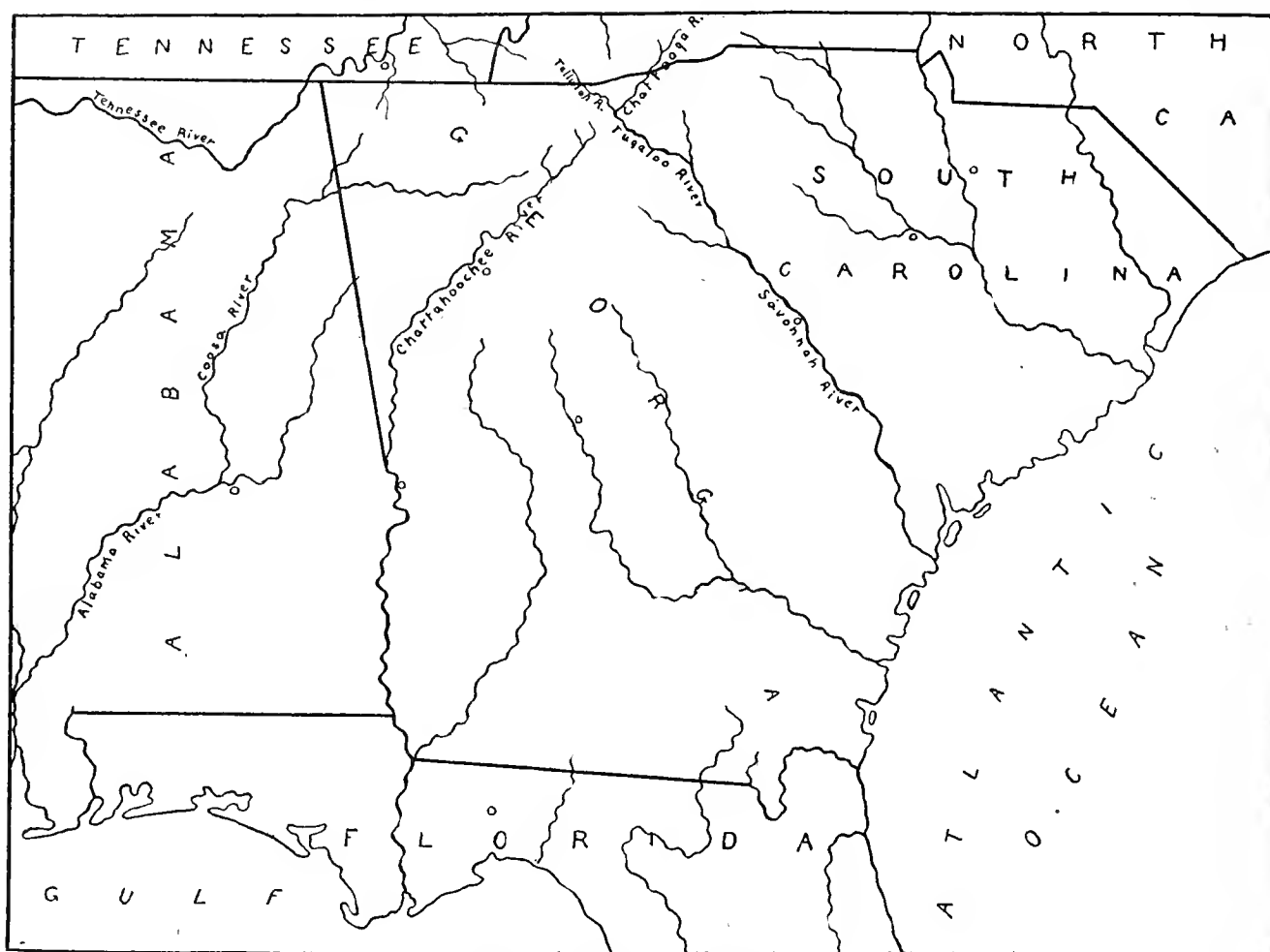


FIG. 1.— Location map.

features, with special reference to the supposed changes in drainage. The area examined is in western South Carolina and northeastern Georgia, and for the most part lies within the limits of the Walhalla (South Carolina) sheet of the United States topographic atlas. This sheet, however, is marked "reconnaissance map," and contains many inaccuracies, and hence is of little aid in our study because it does not show such critically important points as the great contrast between the deep gorges of Little Panther Creek and the broad open valley

of Deep Creek; the relations of a higher and lower peneplain surface to a prominent eastward-facing escarpment; certain well marked hanging valleys that exist in the area, and other points of special topographic significance. The greater part of the field work was confined to a rectangular area of 175 square miles, having Clarkesville at its southwest corner, Toccoa at the southeast, and the Tallulah Falls and Gorge a little north of the center. This area may be designated the "Tallulah district." Within its limits are located all of the critically important features, and the field study upon which this report is based, was made by traversing the railroads, wagon roads, and mountain trails of the district, as well as the wild stream gorges where trails were seldom found. The results of this study appear to justify the following conclusions:—

(1) The upper Savannah (Chattooga) River formerly flowed southwest through the Chattahoochee River into the Gulf of Mexico, but was diverted to the Atlantic drainage by a process of stream capture as has been previously announced by Hayes and Campbell.

(2) This capture furnishes an example of what may be termed "remote capture," having occurred so long ago that much of the direct evidence has been obliterated.

(3) The capture resulted from the advantage gained by the Atlantic drainage over the Gulf drainage, owing to the shorter course to the sea which streams of the former system enjoyed and possibly to favorable crustal warping.

(4) The place of the capture was near the junction of the Tallulah River with the Chattooga, and probably just below that junction.

(5) The falls of the Tallulah River, while initially caused by the capture, exist to-day because of a hard rock barrier crossed by the river, but not yet worn down by it.

(6) The similar falls which must have existed on the Chattooga River have been obliterated by that stream because the great lapse of time since the capture has been ample for it to grade its course in the less resistant rock over which it runs.

Acknowledgements are due to Professor W. M. Davis for valuable advice and criticism, and to the Massachusetts Institute of Technology for a grant of money for field expenses.

LITERATURE.

So far as the writer is aware no previous detailed study of the Tallulah district has been made; but a number of references to the region occur in both geologic and physiographic literature, and one short paper on the geology of the Tallulah Gorge has appeared. Only those accounts which are of interest in connection with the present problem are specially reviewed here.

Brief descriptions of the Tugaloo, Chattooga, and Tallulah Rivers are contained in a "Report on the water-power of the southern Atlantic water-shed," by Professor George F. Swain, published in the 10th Census reports, 1885.

About 1892 there was published in the Atlanta journal an article on the Tallulah Gorge, written by Dr. W. L. Jones, formerly professor of geology at the University of Georgia. This article is said to have been rather general in character (S. P. Jones, '01, p. 67) but has not been seen by the writer.

In a report on the "Corundum deposits of Georgia," published in 1894, Francis P. King devotes a chapter to the geology of the crystalline belt which crosses the northern half of the State, and in which the Tallulah region is located. Concerning the gorge King writes: "Before leaving this subject, an individual topographical feature, showing the wonderful erosive power of a river, is worthy of mention—the Tallulah Gorge in the southern part of Rabun county. Its superb grandeur people have traveled far to see; as a geological feature, its fame is world-wide. This narrow gorge is several miles long, and nearly a thousand feet deep."

In 1895, a paper by Dr. C. Willard Hayes on "The southern Appalachians" was published as a National geographic monograph. On page 327 of that report occurs the following paragraph: "The divide between the Atlantic and Gulf drainage follows the crest of the Blue Ridge, as already described, from the Roanoke southward. The eastward-flowing streams are pressing this divide gradually westward by the capture of territory from less favorably situated streams west of the divide. Cases of recent capture are seen at the head of the Linden and Tallulah Rivers, the falls on those streams showing that the newly acquired territory has not yet been in their possession sufficiently long to be completely subdued."

The following year, 1896, Marius R. Campbell, in discussing

“remote changes shown in the streams of the Atlantic slope,” in a paper entitled “Drainage modifications,” wrote as follows: “These minor streams have not only arranged themselves parallel with the line of greatest slope, but they have also extended their courses headwards, until at one point they are within a mile of the Chattahoochee River and at least 100 feet below it. At this point, which is in the vicinity of Gainesville, Georgia, the capture of the Chattahoochee is imminent, and if conditions remain unchanged, will doubtless be accomplished in the near geologic future. In the vicinity of Tallulah Falls the same process has been carried on, but in this case it has reached completion, and the Savannah River has cut through the divide and captured the portion which formerly constituted the headwaters of the Chattahoochee.”

In the report of the Division of hydrography of the United States geological survey, relative to “Operations at river stations in 1899,” there occurs a brief reference to the rivers of the Tallulah region including a short account of the Tallulah Falls.

Science for July, 1900, contains a short paper by Dr. C. Willard Hayes and Marius R. Campbell, entitled “The relation of biology to physiography,” and another paper by Charles T. Simpson, “On the evidence of the Unionidae regarding the former courses of the Tennessee and other southern rivers.” The former paper serves as an introduction to the latter, and while both are concerned chiefly with the supposed capture of the upper Tennessee River near Chattanooga, both contain references to the capture in the Tallulah district. In previous papers, Hayes and Campbell had advocated the theory that the upper Tennessee formerly flowed southward from Chattanooga into the Gulf by way of the Coosa and Alabama Rivers, but was diverted to the western drainage at a point near Chattanooga; that the headwaters of the Etowah River, a tributary to the Coosa, had in a similar manner been diverted to the Chattahoochee drainage; and that the upper Chattahoochee had likewise been diverted to the Savannah system, in the vicinity of Tallulah Falls. Simpson found molluscs very similar to the Tennessee River forms in the Coosa system, and molluscs similar to both Tennessee and Coosa forms in the Chattahoochee and Savannah Rivers, as well as molluscs of the Savannah drainage in the Chattahoochee River. From this he was led to support the theory of the captures, as the diversion of the streams referred to would effect the transference of their molluscan faunas

from one to another. Even the relative order of the successive captures was believed to be established, since "the migration of Coosa-Tennessee fauna from west to east shows conclusively that the changes in drainage must have followed a similar order."

In 1905, the writer published a paper on "The distribution of freshwater faunas as an evidence of drainage modifications," in which the biological evidence of river capture presented by Simpson was reviewed in some detail. It was shown that many means for the dispersal of molluscan faunas exist in addition to that of river capture; that the forms discussed by Simpson are found in other streams besides those which had been involved in the supposed captures; and that there was evidence tending to show that the reported capture of the Tennessee River, to which the biological evidence principally referred, had not taken place. From this it was concluded that the evidence brought forward by Simpson was not a valid proof of river capture, and that the captures referred to, including that in the Tallulah district, would have to be established, if at all, on some other lines of evidence.

In the February number of the *American geologist*, 1901, there appeared a paper by S. P. Jones, entitled "The geology of the Tallulah Gorge." Mr. Jones discussed the geology of the region, recognizing three main types of rock, only one of which, a quartz schist, occurred in the immediate vicinity of the gorge and falls. The possibility of capture already suggested by Hayes and Campbell, was considered, but no conclusion reached. The probable former course for the original southwest continuation of the Chattooga River, (supposing the capture did occur), was suggested, although nothing like river gravels could be found along that course. As an alternative theory, it was suggested that the steepness of the gorge might be due to "differential movements that . . . in some way caused particular activity in stream erosion at this locality." The necessity of some explanation for the absence of a gorge along the Chattooga similar to that below the falls of the Tallulah was stated, but no such explanation was offered. Further reference to the details of this paper will be found in subsequent pages.

In reviewing the paper by S. P. Jones on "The geology of the Tallulah Gorge," Professor W. M. Davis, in *Science* for 1901, writes as follows: "The precise order of events in the development of the gorge does not appear to have been made out; indeed the author

here cited does not seem entirely convinced of the process of capture as an efficient cause for the new order of things. Yet it is certainly significant that the gorge, unusual if not unique in sharpness of form among the southern Appalachians, should occur in immediate association with a group of features whose systematic relations would seem to point unequivocally to the invasion of one river basin by the head branches of another. In view of the open form and gradual descent of the Chattooga valley in contrast to the narrowness of the Tallulah Gorge and the rapid descent of the river throughout it, one may reasonably conclude that the first was captured much earlier than the second. This makes it seem probable that the Tallulah formerly followed a course near the railroad line, and that its entrance into the Chattooga is the result of diversion by the headward growth of a creek on the line of the gorge; although a somewhat different opinion is expressed in the article here abstracted."

In the March number of the *American geologist*, for 1901, is a brief paper by S. W. McCallie on the "Trap dikes of Georgia," accompanied by a map which shows one such dike crossing the railroad a short distance south of Tallulah Falls. The dikes are described as generally having a vertical dip, and northwest-southeast trend, thus cutting across the crystallines which have a northeast-southwest trend. They are believed to be of the Jura-Triassic age.

Professor T. L. Watson ('02, p. 63), in a report on the granites and gneisses of Georgia, published in 1902, gives a brief account of the geology and physiography of the Piedmont plateau of Georgia, and briefly refers to the reported capture in the Tallulah district.

In a report on "River surveys and profiles made during 1903," arranged by W. Carvel Hall and John C. Hoyt, and published in 1905, a brief account of the Tallulah, Chattooga, and Tugaloo Rivers is given, together with lists of elevations and figures of profiles. The statement that "the Tallulah River crosses the fall line at Tallulah Falls" is erroneous, for the fall line is about one hundred and twenty-five miles farther southeast.

In order to appreciate properly what follows, it is desirable to have clearly before us the general geologic and physiographic features of the Georgia-South Carolina region. To this end a brief review of the general geology and general physiography is first presented, after which the local details more intimately related to the problem of river capture will be discussed.

GENERAL GEOLOGY.

Three distinct geological provinces (see fig. 2) are represented in the Georgia-South Carolina region: (1) the coastal-plain belt; (2) the crystalline belt; (3) the paleozoic area.

The coastal-plain belt.—The southern three fifths of Georgia and the eastern half of South Carolina lie within the coastal-plain belt, which extends from New Jersey around the Atlantic and Gulf coasts and into Mexico. Composed of nearly horizontal Cretaceous and later sediments, unmetamorphosed and but little consolidated, these

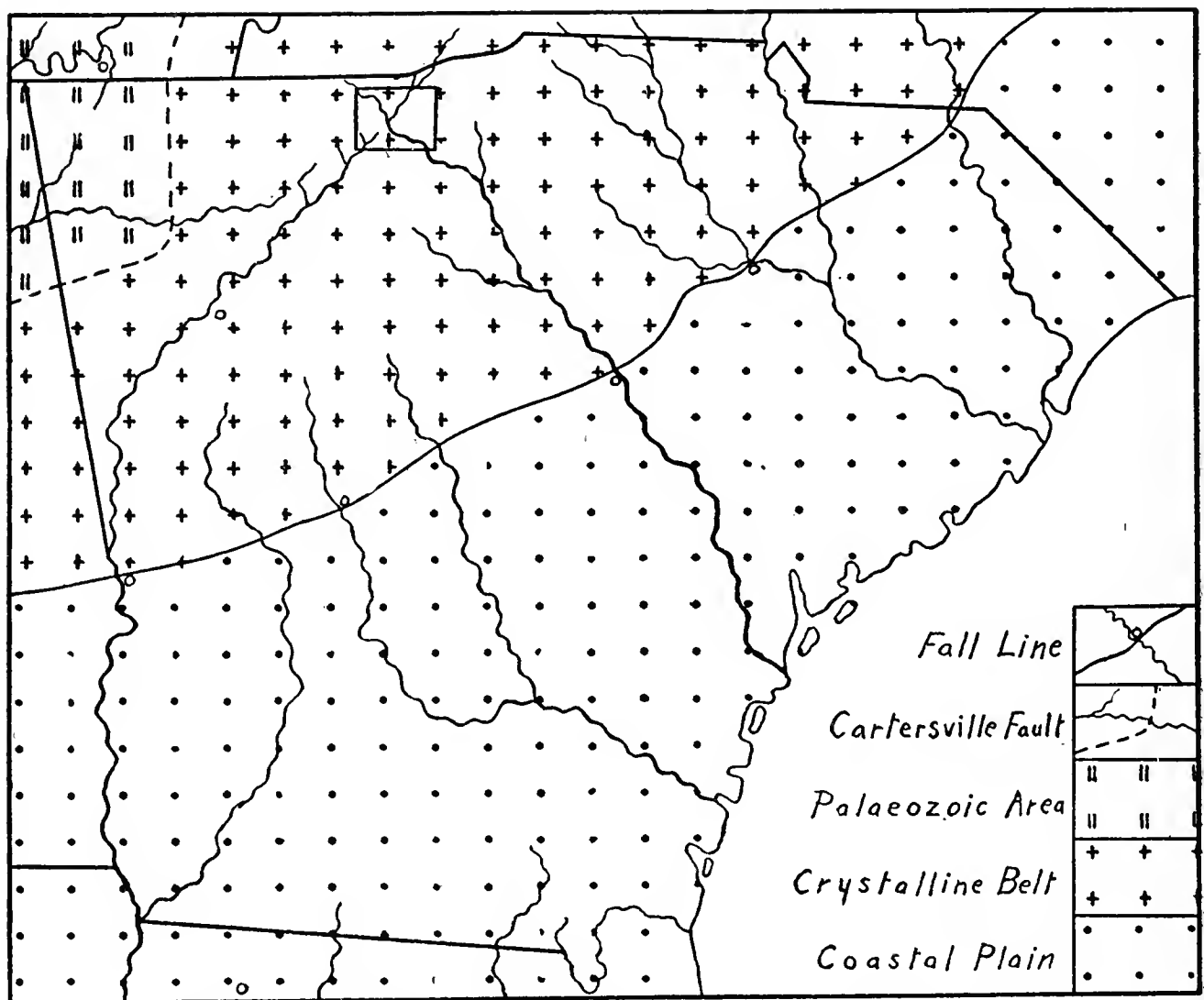


FIG. 2.— Geologic provinces, showing location of Tallulah district.

coastal-plain deposits contrast strongly with the rocks of the crystalline belt, which they overlap on the northwest.

The crystalline belt.— Crossing western South Carolina and northern Georgia is the southern extension of the crystalline belt, composed chiefly of much crumpled gneisses and schists, the strike of whose foliation is northeast-southwest. Associated with these rocks

are numerous bosses of granite and dykes of diabase and diorite, the latter having a prevailing northwest-southeast strike, across the trend of the crystallines. Professor T. L. Watson ('01) has shown that the granites of this region are intrusive in character, and that many of the gneisses are simply foliated igneous granites. On the other hand, occasional beds of limestone and quartzite, of undoubted sedimentary origin, are found interfoliated with the gneisses and schists. The rocks of this belt have generally been considered of pre-Cambrian age, with the exception of the basic dykes, a part of which, at least, probably belong to the Jura-Triassic (McCallie, '01). The presence of undoubted sediments shows that if the crystallines are correctly classed as pre-Cambrian, a part of them must be referred to the Algonkian.

The paleozoic area.—The northwestern corner of Georgia is crossed by paleozoic sediments,—limestones, shales, sandstones, etc.,—which have been compressed into northeast-southwest folds and eroded to produce the “ridge and valley” type of Appalachian topography. This area, which is the southeastern portion of a great extent of paleozoic rocks, is the smallest of the three geological provinces, and while it has been described in some detail by J. W. Spencer ('93), and by others, it is not of special importance in connection with the present paper.

These three geological provinces, described above, are separated from each other by rather sharp, well defined boundaries. Between the coastal plain and the crystalline belt is located the “fall line,” which passes through Camden and Columbia, South Carolina; Augusta, Milledgeville, Macon, and Columbus, Georgia. It marks the somewhat irregular contact of the nearly horizontal coastal-plain deposits with the highly tilted crystallines which they overlap on the northwest. The crystalline belt is separated from the paleozoic area by a great physical break, the “Cartersville fault,” which passes south to Cartersville, Georgia, and then a little south of west into Alabama.

GENERAL PHYSIOGRAPHY.

The studies of Hayes, Campbell, and others have made the general physiographic features of the southeastern United States so familiar that only a brief review is necessary in the present connection. In

general it is to be noted that the three geological provinces above referred to may be divided, according to the origin and evolution of their surface features, into five distinct physiographic provinces, (see fig. 3) as follows: (1) the coastal plain; (2) the Piedmont plateau; (3) the Appalachian mountains; (4) the Appalachian valley; (5) the Cumberland plateau. Since the two last provinces are not of special interest in connection with the present problem, only the first three will be here considered.

The coastal plain.—Passing inland from the Atlantic coastline, one crosses first the gently sloping surface of the coastal plain, rising from sea level at the coast, to an altitude of 250 or 300 feet a hundred miles or more farther west. Near the ocean this plain is not so maturely dissected as farther west, and the monotonous stretch of nearly level country is very striking. As the traveler nears the inner border of the plain, however, he is impressed with the greater degree of stream dissection, which is due in part at least to the longer time the land has here been subjected to erosion, it having been the first portion of the plain to rise above the waters of the ocean.

The Piedmont plateau.—Continuing westward, the same gentle slope is maintained by the surface of the Piedmont plateau, a peneplain developed on folded crystallines. As noted for the inner border of the coastal plain, stream dissection has destroyed much of the original surface, but the gently rolling uplands between the main streams preserve the characteristic features of the peneplain, and give a remarkably even skyline. Near the junction of the Piedmont plateau with the Appalachian mountain belt is encountered a feature of special significance in the present discussion. The west-bound traveler notes in places an escarpment which seems to mark the western limit of the plateau,—an escarpment which rises abruptly from the peneplain level to an altitude of from a few hundred to two thousand feet. In places this feature may be destroyed by erosion, or so complicated with mountain masses as to be indistinguishable, but where well developed, it forms a striking element of the topography. Leaving the level of the Piedmont plateau and ascending to the top of this escarpment, the observer looks westward out over another peneplain surface similar to the one just traversed, except that it slopes to the west, away from the top of the escarpment. Standing thus at the eastern edge of the upper level, he seems to be at the junction of two peneplains, which incline away from him in opposite

directions. But the two fail to "match" properly, the western edge of the one being some hundreds of feet below the eastern edge of the other. The steep slope joining the edges of the discordant levels forms the escarpment, in northeastern Georgia called the Chattahoochee Ridge, in western South Carolina the Chattooga Ridge. Farther northeast the same feature is known as the Blue Ridge, or Blue Ridge escarpment, where a discordance between the two levels

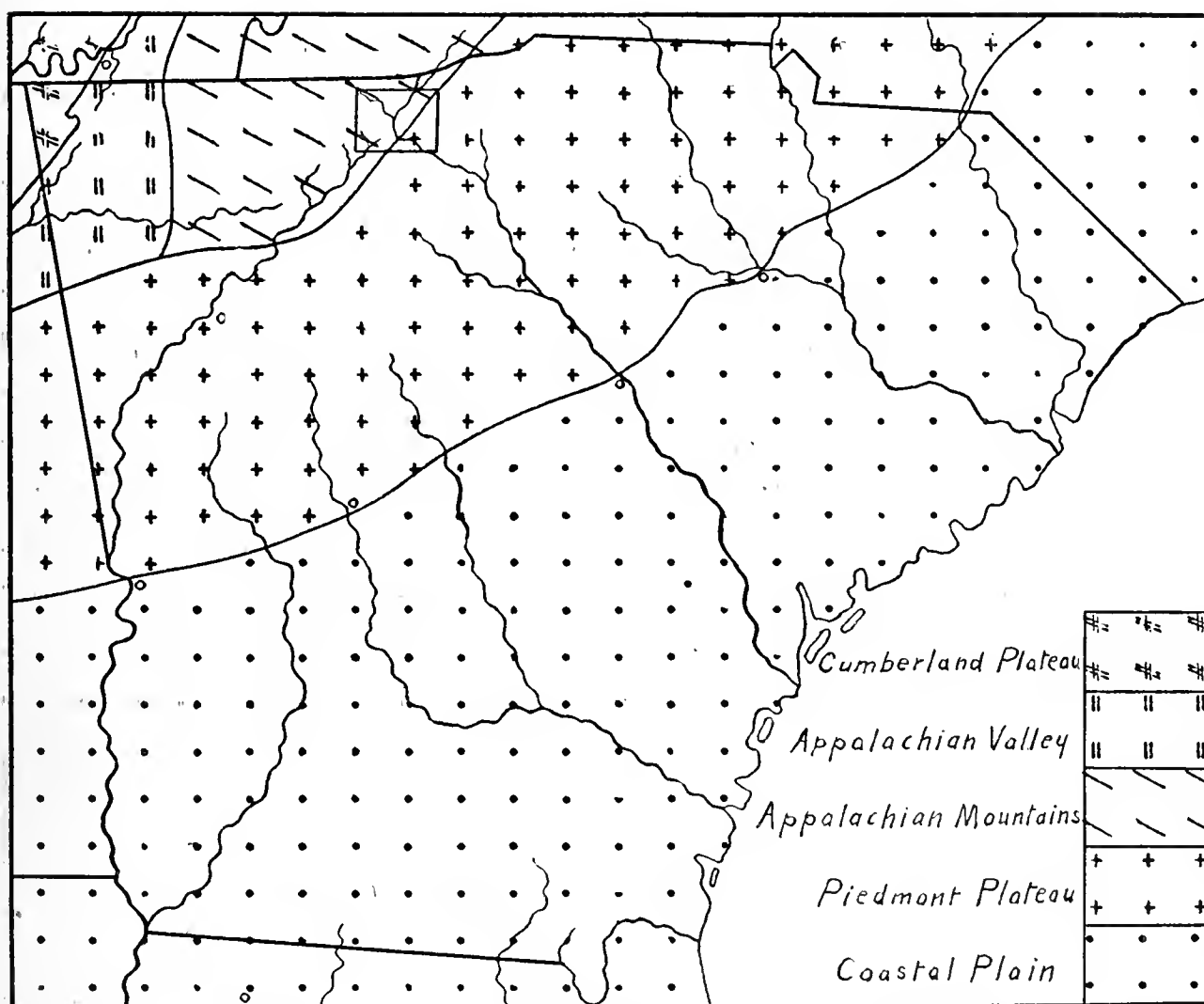


FIG. 3.— Physiographic provinces, showing location of Tallulah district.

of from fifteen hundred to two thousand feet, or more, exists. Farther southwest the discordance in levels diminishes, until the two peneplains seem to merge into one.

The simplicity of the relations detailed above is somewhat destroyed in northeastern Georgia and western South Carolina, by erosion and by the presence of higher mountain masses.

The origin and significance of the escarpment are considered in another portion of this paper.

The Appalachian mountains.—The Tallulah and adjacent ranges

are outlying members of the numerous mountain groups in the Appalachian mountain province. As the Blue Ridge escarpment and its equivalents in South Carolina and Georgia are generally taken as the boundary between the Piedmont plateau and the Appalachian mountains as far southwest as Gainesville, Georgia, it will be seen that much of the higher peneplain is thus included in the latter province.

The Appalachian mountains consist of the folded gneisses, schists, and granites of the crystalline belt which were not reduced to base level by the erosion which formed the Piedmont plateau, and contain the highest peaks of the southern States.

Summary.—The more important of the foregoing physiographic features, in relation to the present problem, may be summed up as follows. The region of the supposed river capture lies on the western border of the Piedmont plateau and the eastern border of the Appalachian mountain belt, in western South Carolina and northeastern Georgia. Through the region passes the southwestern continuation of the Blue Ridge escarpment, which joins the discordant levels of an upper and a lower peneplain surface. It was a stream (the Chattooga-Chattahoochee River) formerly flowing on the upper surface, which is believed to have been captured by a stream (the Tugaloo-Savannah River) undermining it from the vantage ground of the lower level.

GEOLOGY OF THE TALLULAH DISTRICT.

Having now considered the general relations of the Tallulah district to the broader geologic and physiographic provinces of the southeastern United States, I desire to present a short account of the more detailed geology of the immediate area under discussion. It is not necessary to burden this paper with a long account of all the features observed in the field, nor with much that is of interest from a strictly geological point of view. But an understanding of the general lithologic and structural features of the area is absolutely essential to a proper interpretation of many points involved in the problem before us. I shall therefore describe briefly the different rock types represented in the district, and outline their general areal distribution and structural relations.

Rock Types.

Mica schist.—By far the greater portion of the Tallulah region consists of rocks belonging to the mica-schist series. These rocks are extremely variable, presenting phases consisting largely of black biotite, others in which biotite and muscovite mingle with abundant quartz, and still others containing muscovite and quartz alone. In texture every gradation from very fine to coarse grained is represented. The schistosity may be very marked or scarcely perceptible in the hand specimen. Alteration often changes the surface portions of these rocks to beds of red and yellow sands.

With decrease in mica these schists grade toward the fairly pure quartzites, described below. Coarse-grained, feldspathic varieties give transition members between the more typical mica schists and the bands of gneiss. Both the quartzites and the bands of gneiss, as well as the slate and limestone belts, occur within the far more extensive mica-schist series, and seem to be parallel with the foliation of the schists. This foliation is variable, but has a general north-east-southwest strike, and a southeast dip.

The mica-schist series has not strongly resisted the actions of weathering and erosion, and we now find these rocks covered with red soil over a large part of the area, while even the smaller streams find it an easy matter to carve out deep valleys in them.

Quartz gneiss.—Within the mica-schist series, described above, are bands of somewhat more resistant rock, containing a large percentage of quartz, but with sufficient feldspar or mica (or both) to constitute a source of weakness as compared with the true quartzites. These rocks are coarser-grained and have a coarser type of foliation than the true schists to which they are closely related, and may be called quartz gneisses.

In the process of weathering, the gneisses prove a little more resistant than the schists, and stand out as layers of harder rock in the railroad cuts and valley sides. Stream erosion is not seriously retarded by the bands, however, although minor falls on the smaller streams are often located on them. The same is true of the more resistant phases of the mica schists.

Quartzite.—This rock is of prime interest to the student of the Tallulah district because of its close relation to the most striking

topographic features in the area. Careful study of a large number of representative specimens shows the occurrence of certain variations in texture and composition, but the typical examples contain little else than grains of quartz cemented into a firm, resistant, bluish-gray quartzite. Occasional grains of pyrite, muscovite, biotite, and feldspar occur. Crushing and shearing may be observed in some of the specimens, while in others the rock seems to have suffered but little from those forces which produced strong foliation in neighboring beds.

With increase of mica the quartzite grades into the mica schists, giving all stages between the two types of rocks. With increase of feldspar and more marked effects of shearing, transition to the gneisses takes place. It should be noted, however, that these changes involve changes in original composition and texture, and are not due to weathering.

The distribution of the quartzite is of peculiar interest. It forms occasional thin beds in the mica-schist series, but has its typical and extensive development in the vicinity of the Tallulah Falls and Gorge. Examples of its occurrence as thin beds are found in the gorge of Panther Creek below the juncture of the north and south forks, and on the north fork below the railroad. Falls occur at both places.

The quartzite beds conform to the general northeast-southwest strike and southeast dip of enclosing gneisses and schists.

Pegmatite veins.—The mica-schist series is cut by a number of pegmatite veins which may run parallel with or cut across the foliation. These veins are generally badly decomposed wherever exposed, consisting mainly of quartz in profoundly kaolinized feldspar.

Limestone.—At several localities in the gorge of Little Panther Creek are found exposures of a compact, fine-grained, bluish-gray limestone. This rock has been quarried on a small scale for the production of lime. From the distribution of the limited exposures it appears that the limestone belt strikes northeast-southwest, parallel with the general trend of the foliation in the gneisses and schists.

Slate.—In the gorge of Little Panther Creek near its junction with the main Panther Creek, and near the junction of the latter with the Tugaloo River, are exposures of an impure carbonaceous slate which weathers to a black soil. What appears to be a more micaceous variety of this same rock is found farther southwest on Little Panther Creek. These three exposures are in a northeast-

southwest line, parallel to the general trend of the foliation in the gneisses and schists of this region.

Both the slate and the limestone appear to form narrow bands enclosed on either side by the mica-schist series.

Diabase.—There is good evidence that the metamorphic series is cut by a number of diabase dykes. In the gorge of Little Panther Creek just below where it is joined by Devil Den Creek, large rounded boulders of diabase are found where the narrow strip of floodplain at this point meets the foot of the southeast wall of the gorge. These boulders show marked concentric weathering on the outside, but are quite fresh within. The ophitic texture is well developed, and is plainly visible on weathered surfaces. Similar boulders are found in the bed of the main Panther Creek below the junction of its north and south forks; while the presence of a west and east line of boulders on the lower slope of a ridge just east of the junction, indicates a dyke at that point. Between these two same forks of Panther Creek, but northwest of the railroad a mile and a half, a wide dyke of diabase is found near the Clayton road.

Diorite.—In a railroad cut two miles south of Turnerville there is a good exposure of a dyke of diorite cutting the mica-schist series. The hornblende seems quite fresh, although the dyke has been sheared to produce a marked gneissoid texture. The foliation in the dyke is not always parallel with that of the surrounding schists, and may even be perpendicular to it. The dip of the schists increases noticeably near the dyke.

General Structural Relations.

The rocks in the Tallulah region consist largely of the mica schists, as already noted, and as shown on the accompanying geological sketch map. From the description of the rocks given above, it is clear that they consist in part, at least, of altered sediments. No evidence regarding their geological age was secured in this region, but it is inferred that it is Algonkian. The dykes of diabase and diorite are probably of much more recent age, presumably Triassic as suggested by McCallie.

In general, the strike of the schist is northeast-southwest, with a dip about twenty degrees southeast. Both strike and dip are variable, however, the latter changing to a marked westerly inclination.

in cases. The most suggestive variations occur north of the gorge, where a number of readings show northeast dips over considerable areas, whereas the dip south of the gorge is rather more uniformly southeast. This indicates the possibility of an eastward-pitching anticline, the axis of which would cross the lower course of the Tallulah River, bringing to the surface at that point rocks which might lie buried far beneath the surface to the north, south, and east of the gorge. As a matter of fact, massive beds of easterly dipping quartzite

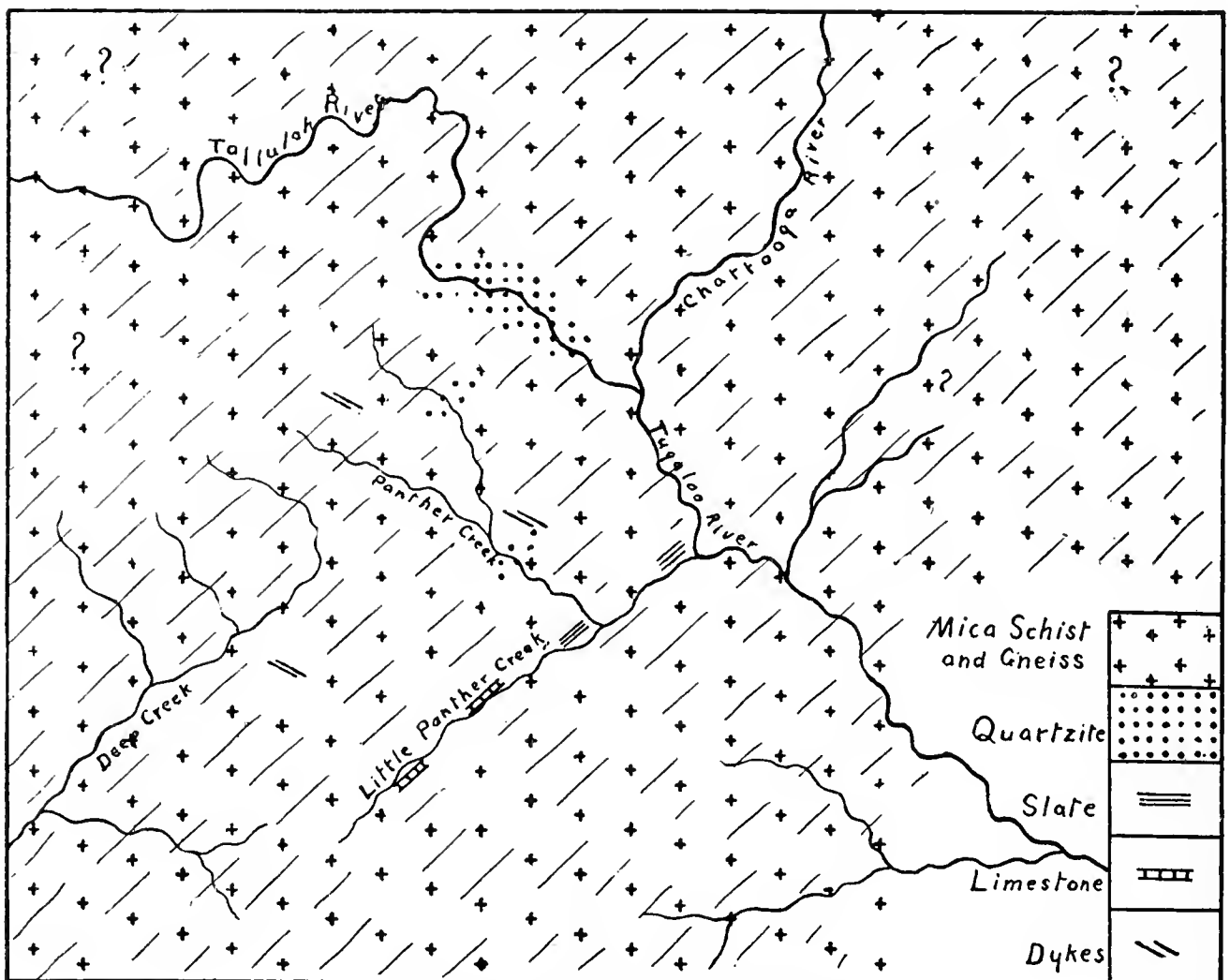


FIG. 4.— Geological sketch map of Tallulah district.

are found in the gorge,— a series of rocks which are absent in the streams of the rest of the area. Further field work will be necessary before the suggested structure can be proven responsible for the position of the quartzite extensively developed in that one locality. Small bands of quartzite at two points on Panther Creek are most likely due to more limited local changes in the quartz-mica schist.

In the preceding paragraph I have spoken of the strike and dip of the schistosity as giving possible clue to the structural relations of

the quartzite beds. This seems justifiable inasmuch as the beds of quartzite, slate, and limestone are apparently parallel to the foliation of the schists, as are also the included bands of gneiss. In his report Mr. Jones speaks of the foliation as making a marked angle with the limestone belt, but he has since informed me that this conclusion was not based on his own observation. The evidence of numerous sections seen in all parts of the field leads me to believe that the foliation has not obliterated all traces of the former bedding, but that foliation and bedding are approximately parallel.

In connection with the local geology it remains to emphasize the fact that the quartzite of the Tallulah Gorge is wholly distinct from the mica schist. Mr. Jones has considered the two rocks as practically identical, one being merely a weathered phase of the other, and has represented them by one pattern on his geological sketch map. It is true that the quartzite and mica schist grade into each other, just as a sandstone may grade into a limestone by gradual change in composition. But the mica schist is no more a weathered phase of the Tallulah quartzite than is the limestone a weathered phase of sandstone. Fresh quartzite is found from the bottom to the top of the gorge below the falls, and mica schist is found from the surface railroad cuts to the bottom of the various gorges. Gradations from quartzite to mica schist may be found in the same ledge in certain cases, but the change is independent of weathering. The weathering of the quartzite is distinctly different from that of the schist, and has seldom penetrated far into the rock, even on the upland surface, unless the quartzite has been strongly sheared. Where the latter is the case, the effect of the shearing is plainly visible in the fresh rock, giving a parallel gneissoid texture, which does not become much more prominent with discoloration and weathering. The very prominent foliation of the mica schists can in no case be correlated with the weathered phases of the quartzite.

This point requires special emphasis, since the fact that the Tallulah River has its lower course across a dense, resistant quartzite, while all the other streams are located almost entirely on weak mica schists, furnishes the key to the development of certain topographic features in the district. The failure to recognize this point has heretofore made it impossible to solve certain of the problems presented, and has led to unnecessarily complicated interpretations of the method of capture.

TOPOGRAPHIC FEATURES OF THE TALLULAH DISTRICT.

The accompanying diagram (fig. 5) will serve to illustrate the more salient topographic features of the Tallulah district. It is at once apparent that those features may be grouped under the following heads:—

(1) The lower peneplain level upon which the Tugaloo River has its open valley, and which may for convenience be called the Tugaloo level.

(2) The upper peneplain level, upon which the headwaters of the Chattahoochee River have their open valleys, and which may be called the Chattahoochee level.

(3) The marked escarpment, about 500 feet in height, joining the

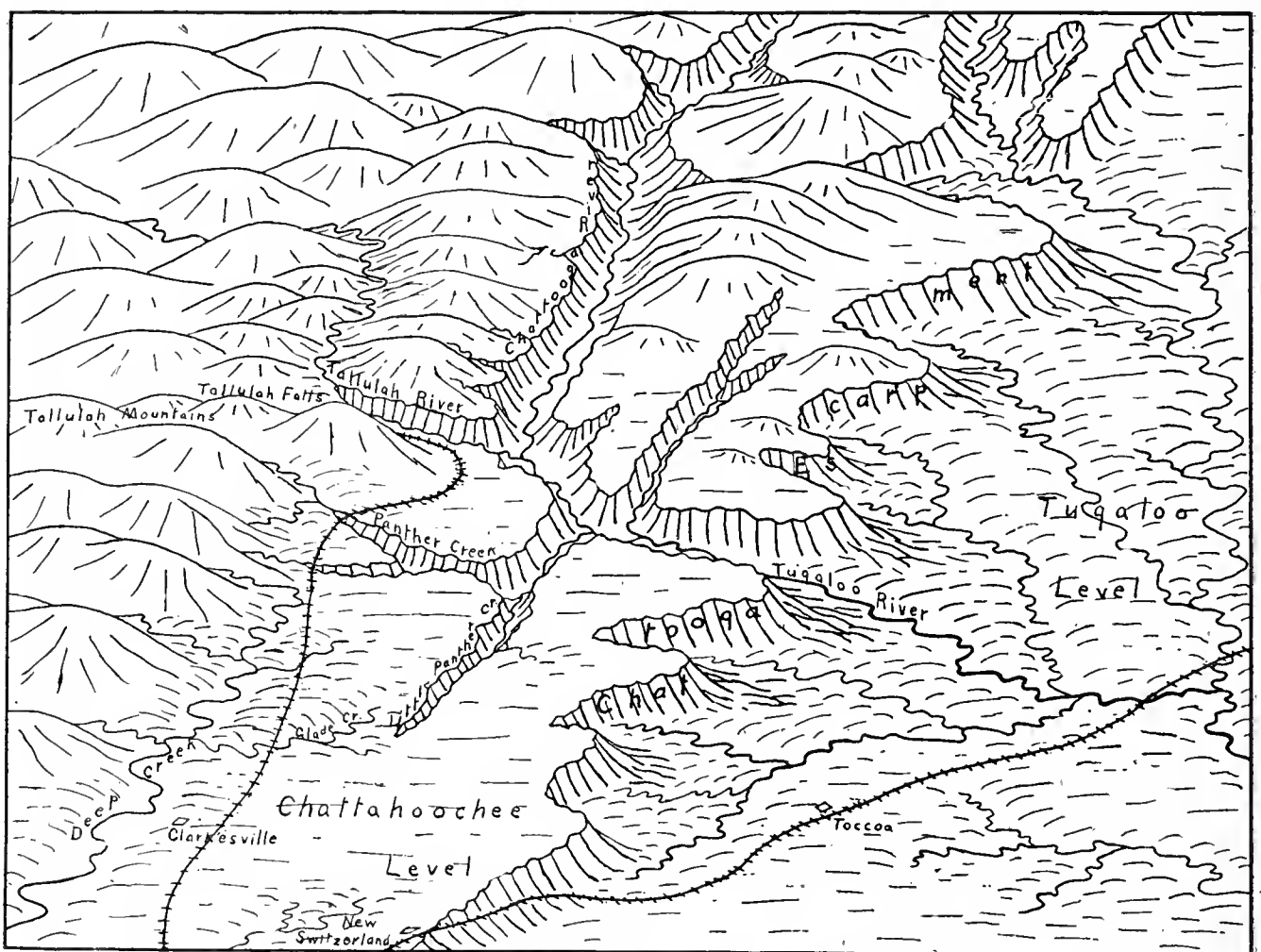


FIG. 5.— Topographic features of the Tallulah district.

western edge of the lower, Tugaloo level, to the eastern edge of the higher, Chattahoochee level, and locally known as the Chattahoochee or Chattooga Ridge. As this topographic feature was originally an escarpment rather than a ridge, and has only assumed the appearance

of a ridge because of subsequent erosion of gorges just back of its face, we may best term it the Chattooga escarpment.

(4) The Tallulah and other mountain groups, rising sharply above the Chattahoochee peneplain level.

(5) The broad open valleys of the tributaries to the Chattahoochee River, located on the Chattahoochee peneplain level, and known locally as Deep Creek, Big Hazel Creek, Glade Creek, etc.

(6) The fairly open valleys of that portion of the Tugaloo River and its main branches located on the Tugaloo level, southeast of the Chattooga escarpment.

(7) The deep narrow gorges of the upper Tugaloo headwaters, cut down into the Chattooga level to a depth of 500 feet in places, and known locally as the Tallulah River, Chattooga River, Panther, and Little Panther Creeks, etc. In the bottoms of these gorges are numerous falls and rapids, the most noted of which are the Tallulah Falls in the gorge of the lower Tallulah River.

(8) The fairly open valleys of several small streams on the Chattahoochee level, which end abruptly on the brinks of the deep gorges above referred to, the streams plunging down 400 or 500 feet to the bottom of the gorge below. The upland valleys of these streams may properly be termed "hanging valleys."

(9) In a more general way, we may note the abrupt right-angled bend which the Chattooga-Tugaloo River makes near where the Tallulah River empties into it, and the fact that a tributary to the Chattahoochee River (Deep Creek) continues the southwesterly course followed by the Chattooga before it made its sharp turn to the southeast.

The features just enumerated will be described more fully, in the order named.

(1) *The Tugaloo level.*—This appears to be the normal development of the extensive peneplain known as the Piedmont plateau, whose farther extent was outlined in the paragraphs on "General physiographic relations." In this region the peneplain has an elevation of from 800 to 1000 feet above sea level, and slopes gently to the southeast. In general, the upland surface is remarkably even, although stream erosion has dissected it to some extent since its uplift. Breaking from its gorge in the higher level to the northwest, the Tugaloo River flows out across this upland surface, cutting a

fairly open valley for itself, which is in strong contrast to the deep gorge from which it just escaped. The numerous branches of the Tugaloo are busy draining and dissecting the adjacent upland surface, and even gnawing headward into the higher Chattahoochee level, gradually pushing the ragged Chattooga escarpment farther back to the northwest.

(2) *The Chattahoochee level.*—That this represents a peneplain surface some 500 or 600 feet higher than the Tugaloo level, there can be no doubt. The surface is remarkably even, bevels across inclined crystallines in the same manner as does the lower level, but slopes gently down to the west instead of to the southeast.

The Chattahoochee level is by no means so continuous in the Tallulah district as is the lower level, but is interrupted by such notable elevations as the Tallulah Mountains and other mountain masses to the north and west, while the streams on the lower level have eaten back into its southeastern border, rendering this border very ragged. The Tugaloo River even heads within this level, and several of its branches have cut deep gorges into it. Farther southwest this level is more continuous and more readily discerned.

(3) *The Chattooga escarpment.*—As already indicated, this escarpment marks the place where the two peneplain levels “break joint,” its summit marking the eastern edge of the upper level, its base the western limit of the lower level. Headward erosion of many streams located on the lower level has made this escarpment extremely irregular, and there is every reason to believe that the continued work of these streams is pushing the escarpment gradually backward to the northwest, robbing the upper level of more and more of its area, and adding to the area of the lower level. To the southeast, in front of the present escarpment, are occasional hills, some of them flat-topped, which appear to be erosion remnants marking a former southeastward extension of the Chattahoochee level. How much farther southeast this level once extended I am unable to say, but there can be little doubt that it was a considerable number of miles.

A traveler on the railroad, leaving Toccoa, which is situated on the Tugaloo level, soon begins to pass up the heavy grade to the west, by which the train climbs slowly to the higher level of the Chattahoochee peneplain. At New Switzerland this level is first fairly reached, while near Mt. Airy the important features of the topography are especially plain. Here the Chattooga escarpment (locally called

the Chattahoochee Ridge), is finely developed, and one may look down some 500 feet upon the low rolling plain from which he has just ascended, or out across the upper level to where the Tallulah Mountains and other peaks rise sharply from the surface of this higher peneplain. In considering this escarpment in its broadest relations, we have already seen that it is a marked feature of southern Appalachian topography, with a height of from 1500 to over 2000 feet in northwestern North Carolina and southwestern Virginia, decreasing to 500 or 600 feet in the Tallulah district, becoming less distinct and having a height of but 200 or 300 feet in the vicinity of Gainesville, while it seems to disappear entirely before one reaches Atlanta. A good description of the northern portion of the escarpment is given by Davis ('03) in his paper on "The stream contest along the Blue Ridge."

The origin of this escarpment is a problem of great interest; but while it bears a close relation to the history of drainage modifications in the Tallulah district, it does not constitute an essential part of the problem of river capture now under consideration. I shall therefore content myself with a brief statement of two hypotheses which have been advanced in explanation of this striking feature.

According to Hayes and Campbell an erosion level known as the Cretaceous peneplain has been unsymmetrically warped along a northeast-southwest axis in such a manner as greatly to accelerate the activity of the stream flowing down the steeper slope of the uplift toward the Atlantic Ocean. As a result of their great activity the streams of the Atlantic drainage have eaten headward into the arch all along its length, developing a new erosion level, the Tertiary peneplain, at a lower altitude than the remaining portion of the Cretaceous peneplain which suffered warping and erosion (Hayes and Campbell, '94, pp. 75, 76; Davis, '03, p. 222).

Professor Davis has suggested that since the erosion level developed near the headwaters of a stream which has a long distance to traverse before reaching the sea, must be at a higher elevation than a similar level about the headwaters of a stream having a short course to the sea, we should expect to find the peneplain about the headwaters of the Gulf drainage distinctly higher than that about the headwaters of the Atlantic drainage. Where these two peneplains "break joint" we have an escarpment facing the lower level. Such an escarpment is the Blue Ridge. Under this interpretation, it seems to me that we

ought to expect the escarpment to increase in height as one goes northeast, since in this direction the distance from the Gulf increases while the distance from the Atlantic remains fairly constant. To the southwest the escarpment should decrease in height until a point equidistant from both Gulf and Atlantic drainage is reached, when the two peneplains should merge and the escarpment disappear. This agrees fairly well with the facts as noted above, the Blue Ridge escarpment increasing in height as one goes northeast from the Tallulah district until it reaches its maximum in North Carolina and Virginia; whereas it decreases to the southwest to a point near Atlanta, Georgia, where it seems to disappear entirely.

(4) *The Tallulah and other mountain groups.*—These constitute outliers of the Appalachian mountains, and as already noted are residual masses left unreduced by the erosion which formed the surrounding peneplain. They rise distinctly above the Chattahoochee level, and come so far eastward north of the Tallulah River that the level referred to is much obscured or wholly undeveloped in portions of that region. Having no critical bearing on the problem of river capture, they may be dismissed without further discussion.

(5) *Streams of the Chattahoochee drainage.*—The main tributary to the Chattahoochee system in the Tallulah district is Deep Creek. The name is curiously inappropriate, since many other creeks in the region are located in deep gorges, while this one and its tributaries flow in fairly open valleys on the upland surface of the Chattahoochee level. I followed along this creek from near its source west of Turnerville, to its junction with the Soque River, and was impressed with the maturity of its development, the absence of falls or rapids throughout most of its course, the open character of its valley, and the relatively sluggish water. One of its tributaries, Glade Creek, was likewise traversed from its source to its mouth, and even this small branch showed a degree of maturity in striking contrast with other streams close by, to be described later.

(6) *Streams of the Lower Tugaloo drainage.*—That portion of the Tugaloo River which flows over the lower level east of the Chattooga escarpment has a fairly open valley, as have also its main tributaries. Where these streams are actively cutting headward into the higher level and pushing back the escarpment, narrow valleys and extensive falls are common. Even as far east as near Toccoa a splendid fall is encountered on a branch of Toccoa Creek.

(7) *Streams of the Upper Tugaloo drainage.*—The Tallulah and Chattooga Rivers unite to form the Tugaloo; the other important tributary in the immediate vicinity is Panther Creek with its branch, Little Panther Creek. All of these streams are located in deep gorges, in general about 500 feet below the upland surface of the Chattahoochee level. Falls and rapids are abundant, the water swift and treacherous, the gorges wild and picturesque. In traversing Panther Creek from near its source to its mouth I found it impossible to make any progress along the precipitous walls of the gorge and was compelled to walk in its narrow bottom, climbing over giant boulders, wading pools waist deep, clambering down around falls from 30 to over 100 feet in height, while only occasional narrow strips of floodplain were found which afforded a rest from most strenuous exercise. In Little Panther Creek the same youthful characters of the stream were observed. The Tugaloo for several miles below the junction of the Tallulah and the Chattooga, has a very youthful gorge, but was traversed with less difficulty. Along the lower Chattooga a similar youthful gorge was found; the bed of the stream was full of large boulders of mica schist, but no falls of consequence were seen. Passing up the Tallulah from its mouth, the gorge became narrower and steeper-sided, while the waters churned madly among thousands of quartzite boulders. Rapids and little falls were abundant, and the swiftness of the water was not fully appreciated until one of the party in crossing from one side to the other, had his feet swept from under him, but was saved by a rope with which he was tied to another. The portion of the gorge immediately below the Falls is known as the Grand Chasm, and is wonderfully picturesque (plate 27). The walls of the gorge come down in sheer cliffs to the water's edge, and the stream rushes through the narrow chasm at a furious rate. Where the swift waters flow over hidden boulders a deceptive appearance of shallowness is produced, tempting one to risk wading across, sometimes with fatal results.

At the head of the Grand Chasm is found a series of magnificent cataracts, known collectively as the Tallulah Falls. Beginning with the swift rush through Indian Arrow Rapids at the top, the waters next drop 37 feet at the fall of L'Eau d'Or (pl. 28, fig. a), and a short distance below plunge almost vertically downward 76 feet in the splendid Tempestia Falls. Making a little turn to the right another sudden drop of 89 feet gives the Hurricane Falls (pl. 28, fig.

b) perhaps the most magnificent cataract of the series. Next comes Oceana Falls, a sort of double cataract having a fall of 41 feet. The Bridal Veil, a fall of 17 feet, is the last, its water flowing in a broad sheet down the sloping surface of the smooth rock floor.

This series of falls is famous throughout the South for its beauty, and has made the locality a well known summer resort. Trails have been built along the steep walls wherever possible, so that one may get down into the gorge near the falls without much trouble. The views up and down the gorge from the cliffs on either side are as wild and picturesque as one could desire.

Above the falls, the Tallulah River flows through a fairly young gorge between spurs of the Tallulah and other mountain groups. It is true that the features are not as youthful as in the Grand Chasm, and narrow strips of floodplain are found, now on one side of the river, now on the other. But the water is fairly swift, rapids occur, and the valley walls are steep-sided. The stream here has its path through the mountains, however, and not on the Chattahoochee level.

Surely nothing could be more striking than the contrast between these streams of the Tugaloo drainage with their deep gorges, swift waters, numerous falls and rapids, and boulder strewn channels and the streams of the Chattahoochee drainage flowing through shallow upland valleys with sandy floodplains and quiet waters.

(8) *Hanging valleys of minor tributary streams.*— There are certain streams in the Tallulah district which are tributary to the Tugaloo system, but which do not occupy deep gorges after the manner usually characteristic of the streams belonging to that system. These are very small streams or brooks, and flow through open upland valleys almost to the edge of the gorge occupied by the main stream into which they empty, when they plunge down by a series of cascades to the lower level. This drop of some hundreds of feet is not by a sheer fall on the very face of the gorge wall, but rather by a succession of leaps, some of which may be 50 or 75 feet vertically, and it generally takes place in a little notch cut slightly back into the wall of the main gorge. Nevertheless, this notch is so slightly developed in some cases, that it does not seem amiss to speak of the valleys as hanging valleys. One may drive for several miles along one of these streams, as the wagon road and stream channel are near the same level, but when the main gorge is approached he is surprised to find that without warning the stream has suddenly parted company with him; and he hears it

roaring among the trees far below him, and wonders how it got there. The wagon road winds tediously back and forth around the sides of the hills before it finds its way down to the level so suddenly reached by the stream. Here, in an unglaciated region, we find tributaries which do not join their mains at accordant levels, as we should expect under normal conditions.

(9) *The right-angled bend made by the Chattooga-Tugaloo River.*—This curious “elbow” is a striking feature on the map, and becomes even more suggestive when we note that the southwest course pursued by the Chattooga until it joins with the Tallulah to make the Tugaloo, is apparently continued by Deep Creek and the Soque River into the Chattahoochee. We are led to wonder if there may not be some rational explanation for this peculiar drainage pattern.

Résumé.

We have a whole series of interesting topographic features grouped together in this area for which we seek a rational explanation. It is not sufficient to say that they “happen” to be so. All the tributaries of one drainage system, be they large or small, have open upland valleys, while all the larger tributaries of another system close by and in the same upland, have deep gorges. The smaller tributaries of this latter system first flow through open upland valleys, and then all have falls at their mouths by which they reach the bottoms of the gorges. Falls or rapids are abundant in all the streams of one system, but are practically unknown in the streams of the other system. A peculiar elbow bend occurs in the main line of one drainage system, which seems to bear some relation to the course of the main line of the other system. Associated with these features are two peneplain levels, separated by a marked escarpment. The systematic grouping of features is certainly very notable, and if we can find a single reasonable explanation which will bring them all into a systematic relationship, there will be a good reason for accepting such an explanation as valid. When found, however, it must account for certain minor lack of agreement in cases, such as the presence of extensive falls in the Tallulah River, and the absence of any such falls in its neighbor the Chattooga, where only shallow falls and rapids occur, although the stream is of about the same size as the Tallulah.

DEDUCTIVE STUDY OF RIVER CAPTURE.

As pointed out in the introduction to this paper, a process of river capture has been supposed by some to account for certain of the topographic features of the Tallulah region, although others have not been able to explain all of the features on the basis of this theory, and have been led to suggest an alternative theory. It will be well for us to examine into the process of river capture, therefore, and determine what features should be produced as a result of such capture. We may then compare the results of our deductive scheme with the actual facts observed in the field, and see whether or not

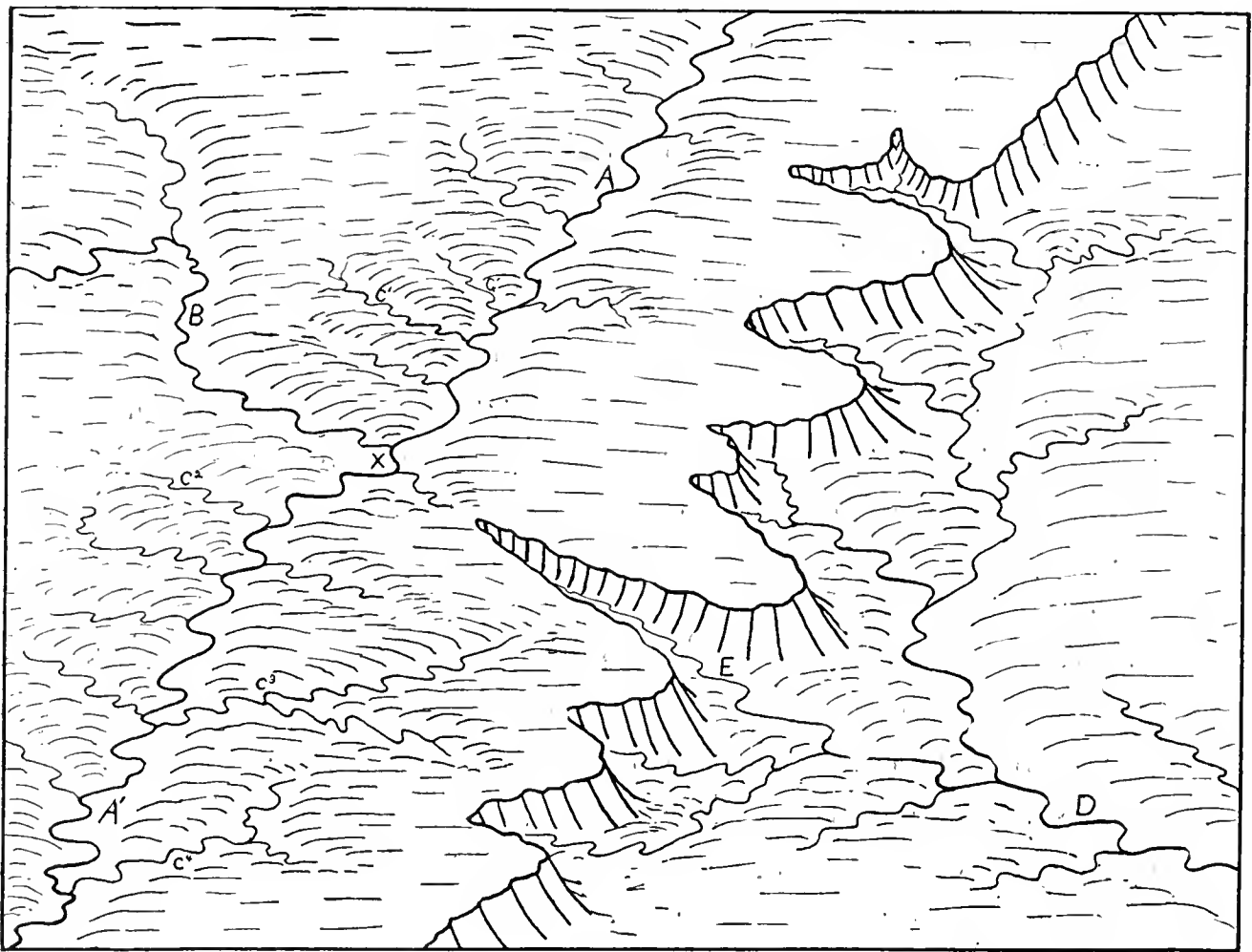


FIG. 6.

there is sufficient agreement to justify the acceptance of the capture theory.

Let us imagine that because of the warping of a peneplain and accelerated erosion along one side of the axis of uplift, or because of unequal lengths of rivers producing two parts of the same peneplain at different elevations, we have two erosion levels breaking joint along a marked escarpment, as shown in figure 6. On the

upper level let there be a stream, AA^1 , flowing from northeast to southwest, with one large tributary, B , coming down out of the mountains from the northwest, while many smaller tributaries, CC , come in from either side. We may imagine the larger streams to have fairly open valleys. On the lower level let there be a stream, D , whose tributaries are eating headward into the upper level, gradually pushing the escarpment back toward the northwest. The escarpment will be more or less irregular, due to the varying activity of the different tributaries. Let us suppose that E is that one of the tributaries

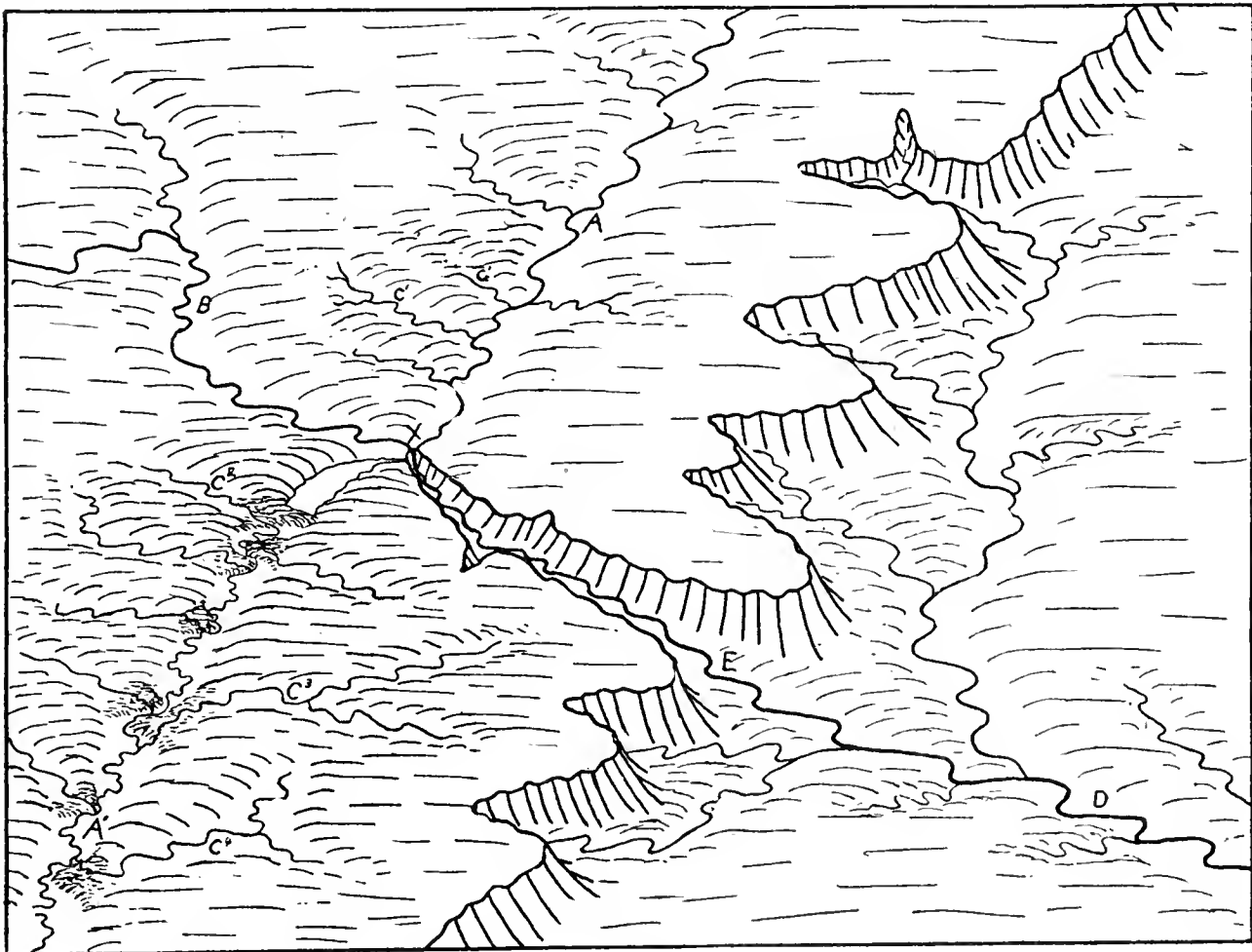


FIG. 7.

which has succeeded in pushing the escarpment back the farthest, and that it is about to undermine the stream AA^1 at the point X , and so capture its upper waters. Such are the conditions immediately preceding capture.

Figure 7 represents the conditions immediately after capture. At the point X , the captured stream, A , now falls down to the lower level of the captor, E , and turns abruptly from its former course to the southeast, making what we might call the elbow of capture. The stream E is greatly increased in volume, and will rapidly wear its

channel down nearer to grade, increasing the height of the fall at *X*. The beheaded stream, *A*¹, robbed of most of its water by the capture, now meanders aimlessly about in a valley wholly inappropriate to its diminished size. The tributaries, *C*², *C*³, *C*⁴, etc., continue to bring in an amount of sediment appropriate to the transporting power of the former large stream, but finding only a shrunken remnant of that stream, wholly unable to remove the sediment, they deposit much of it in the form of alluvial fans. It is possible that

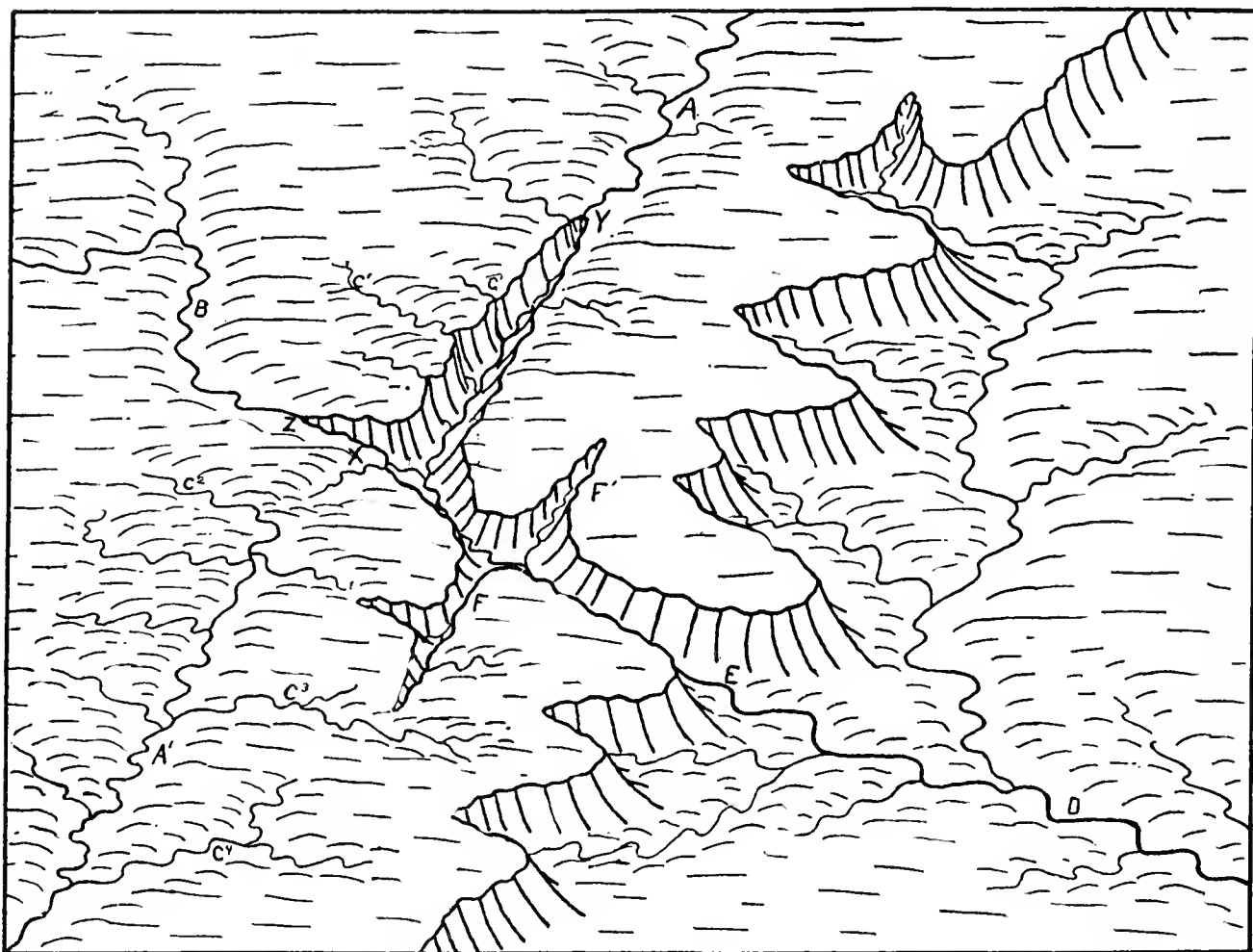


FIG. 8.

such a fan may spread across the valley and so obstruct the stream course as to cause a lake to form, as at *C*²; this lake finally overflows into the rapidly forming gorge at *X*, thus shifting the divide between the two drainage basins to the fan at *C*², and developing a small north-east-flowing tributary, which we may call the inverted stream.

A somewhat later stage is shown in figure 8. The falls have been pushed far up the main stream, and are being worn back along the tributary *B*, as well. In the latter case, however, we may imagine some harder rock to be encountered, so that the process of fall recession goes on much more slowly. Hence, while the falls on the main

stream, *A*, which runs over softer rock, have been worn back as far as *Y*, the falls on the tributary *B* have been worn back a much shorter distance in the hard rock, to the point *Z*; the retreat of the falls on the main stream past the mouths of smaller tributaries, as *C*, leaves the valleys of those streams hanging well above the bottom of the main gorge. These streams being small and weak, have not yet worn down to the new level, but are beginning that process, as shown by

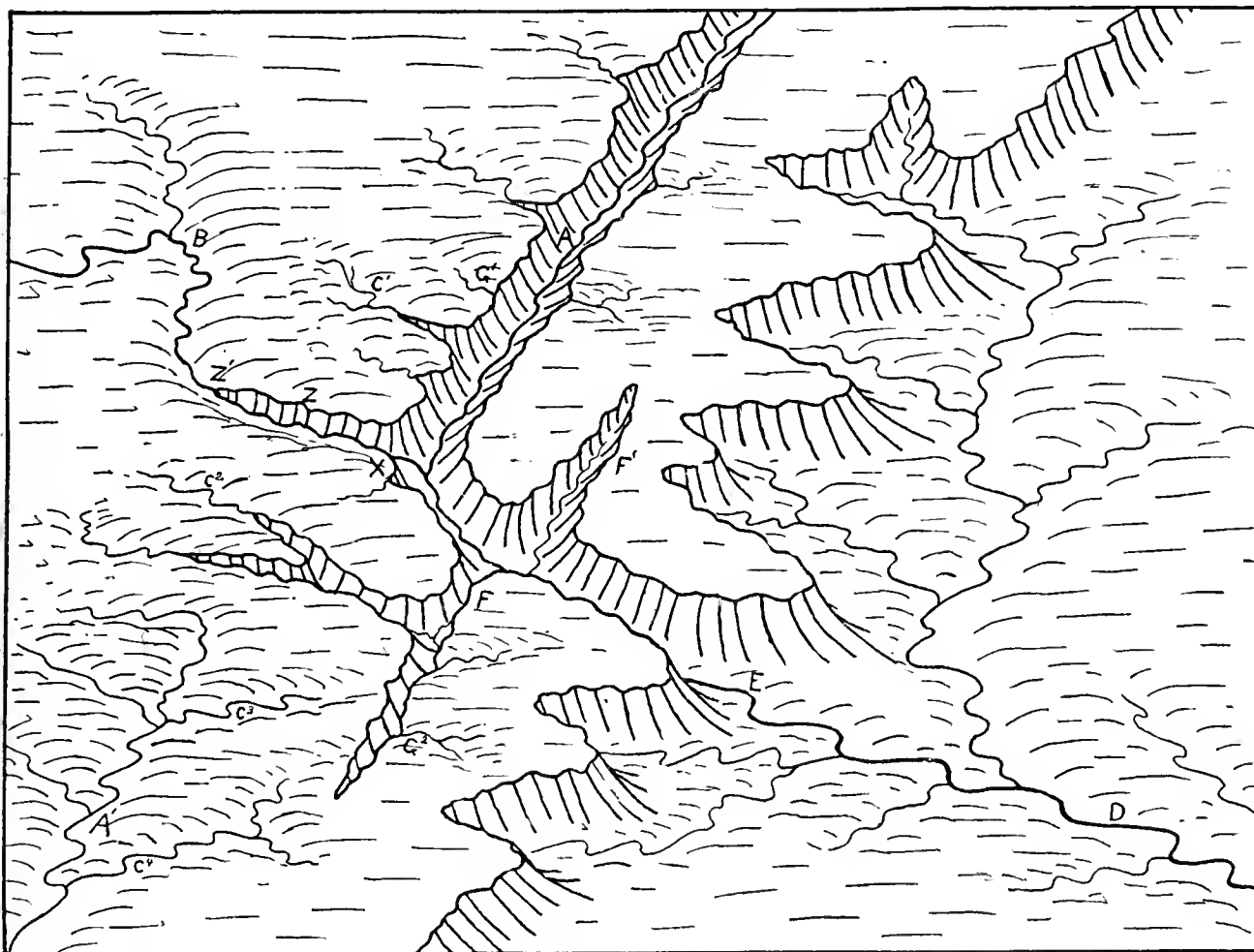


FIG. 9.

the slight notches in the walls of the gorge. The incision of the gorge in the bottom of the former more open valley leaves a series of benches or terraces marking the remnants of that former valley floor, except where the gorge has widened sufficiently to consume such terraces. The beheaded stream, A^1 , and its tributaries, C^2 , C^4 , etc., have become somewhat better adjusted to the new conditions; the alluvial fans are dissected and removed as the stream A^1 cuts down to a slightly lower level, and the tributaries bring in only such sediment as the main stream is able to remove. Branches F , F^1 , from the main stream in the gorge, possibly working back along a belt of weak rocks, or a crushed zone, begin to appear, the one at F

finally capturing the headwaters of C^3 . The inverted stream is beginning to notch the wall of the gorge at X .

The last figure, (fig. 9), represents the conditions a long time after capture. The falls on the main stream A have been so thoroughly graded that only minor rapids are to be found.

In the hard rocks across which it runs, B has not yet been able to grade its course, and the falls still persist, being worn back only to Z^1 . For the same reason the gorge below the falls remains deep and narrow, whereas A has widened its valley to a greater extent in the softer rocks, entirely consuming all evidence of the former valley floor, such as the terraces or benches seen in figure 8. Even the smaller tributaries on the soft rocks, C^1 , have worn their falls back to a considerable extent, but the very smallest ones, G^1 , G^2 , have only been able to notch the valley walls slightly, and still exist as hanging valleys. The tributary F has grown so extensively as to have robbed much of the drainage area of A^1 , and prevented further growth of the inverted stream south of X , while all streams have dissected the upland surface to a much greater extent than before. So great a lapse of time has resulted in perfect adjustment in the drainage of A^1 , and we no longer find alluvial fans, or pronounced meandering in an inappropriate valley. Maturity of development characterizes the streams of this upland area, but more youthful features still mark the streams of the other system. In the younger portions of F there may even be numerous falls not yet worn down to grade, while rapids are to be found along all the streams of this system. The conditions are typical of what might be termed "remote capture."

Much later even than this period, at a time when the capture might be termed "extremely ancient," the falls on all the streams will be graded, the gorges widened out to mature valleys, the interstream areas much dissected and subdued; even the smallest tributaries will enter their mains at accordant levels, and practically all the evidence of the capture will have disappeared, except the peculiar elbow bend in the main stream, produced by that capture. The drainage pattern alone will remain to suggest an important chapter in the history of the stream's development, and even that evidence may suffer extensive modification in time.

COMPARISON WITH FACTS AS OBSERVED IN THE TALLULAH DISTRICT.

It is at once apparent that the topographic features of the Tallulah district correspond most closely with the expectable results of remote river capture under the conditions outlined above. Referring to figure 5, and comparing it with figure 9, we see that the Chattooga escarpment is very ragged as a result of dissection by the headward-growing Atlantic streams; and that it separates a higher and a lower peneplain level, rendering the conditions favorable to capture; that the Chattooga River corresponds to the captured stream *A*; Deep Creek to the beheaded stream *A*¹; Tallulah River to the large tributary *B*, coming down out of the mountains; Panther Creek to the tributary *F*, and the Tugaloo to the captor *ED*. We note that Deep Creek occupies the upland surface, and is a fairly mature stream, whereas the streams of the other system are engorged, as we should expect on the basis of the capture theory. We find the gorge of the lower Tallulah River unusually narrow and steep-sided, the river plunging down into that gorge by a succession of magnificent falls, whereas the gorge of the Chattooga River is more open and no falls of consequence are found. Referring to the geological sketch map (fig. 4), we have a complete explanation of this discrepancy, in the hard rock encountered by the Tallulah River, which is not exposed in the Chattooga. I have traversed both stream beds for a number of miles, finding abundant ledges of quartzite and quartzite boulders in the lower Tallulah, but no such rock in the Chattooga, where the boulders and ledges were of mica schist. Nothing could be more striking than the difference in the rocks encountered by the two streams. As a result of this difference the Chattooga has been able more nearly to grade its course on the weak rocks, whereas the Tallulah has only been able to wear its falls back a short distance in the hard rocks.

Panther Creek and Little Panther Creek, while located for the most part on mica schist, are smaller, weaker streams than the Tallulah or the Tugaloo, and for that reason still have falls along their courses, although they have cut deep gorges, as we found expectable in the case of the theoretical stream *F*. Still smaller tributaries along the Chattooga and other main streams, have worn down their valleys

less perfectly, after the manner of the theoretical streams, C^1 , etc., while hanging valleys already described, are found on the smallest branches, corresponding to G^1 , G^2 .

No satisfactory evidence of terraces was found along the Chattooga, and it is presumed that the widening of the gorge has been sufficient to obliterate all traces of the former upland valley floor, as the conditions are similar to those imagined in figure 9, where the former terraces are consumed by valley widening.

The "elbow of capture," which we were led to expect under the conditions of capture outlined, is beautifully shown where the Chattooga-Tugaloo turns abruptly from its southwest course toward the Gulf, to a southeast course into the Atlantic. A State boundary has been determined by this drainage modification. The continuation of the former southwest course pursued by the upland stream before capture, is indicated by Deep Creek. No valley or channel remains to mark the former course of the upland stream across the present divide northeast of Deep Creek, since the inverted stream was hindered in its development by the rapid growth of Panther Creek.

Certainly the agreement between the expectable results of river capture and the features found to exist in the Tallulah district is most striking, and we are justified in accepting the theory of capture as well substantiated. The conditions for capture were highly favorable; indeed, it seems inevitable that capture must have occurred; and on the basis of capture all the observed facts are grouped systematically together and receive a rational explanation. We conclude, therefore, that the Chattooga formerly flowed southwest by way of Deep Creek, Soque River, and the Chattahoochee into the Gulf of Mexico, but was captured by the Tugaloo at a point below the junction of the Chattooga and the Tallulah, so that the waters of both these streams were diverted to the Atlantic drainage by way of the Savannah River.

The ultimate cause of the capture seems to have been the advantage gained by the Savannah River, the length of whose course to the Atlantic Ocean in the earlier geological periods, as now, was much shorter than that of the Chattahoochee, so that it was enabled to deepen its headwaters to a lower level than that occupied by the Chattahoochee, and finally to undermine it. There is no evidence of any advantage of rock structure, or stream volume, in favor of the Savannah, and the advantage of shorter length is wholly competent

to produce the capture. Acceleration of stream activity in the upper Savannah, due to warping, may have aided the capture, after the manner pointed out by Hayes and Campbell, but it is evident that the capture must have occurred in any case. The shorter streams of the Atlantic drainage are pushing the Blue Ridge escarpment westward all along its length, robbing the headwater areas of the Gulf drainage.

EVIDENCE OF THE GRAVELS.

Thus far we have considered topographic evidence alone. It remains to examine other lines of evidence, the first of which is that furnished by waterworn river gravels. If the Chattooga River deposited gravels along its course, and was then diverted, the abandoned portion of its valley should be marked by the occurrence of these gravels. Were the capture recent, we should expect to find these gravels on the well preserved upland surface, but if the capture occurred long ago, the great lapse of time would be sufficient for stream erosion to dissect the upland surface, wash the gravels down to lower levels, and transport them from the area. Under these conditions we might find occasional scattered gravels over the hills or along the valleys, or even larger deposits of them in unusually favored places. They should be sought, not along the main streams where erosion is greatest, but on the divides, or near the little brooks which have been too weak to remove them.

South of Tallulah Falls, where the headwaters of Panther Creek have greatly dissected the divide across which the Chattooga formerly had its course, waterworn gravels were found in a number of places. As a rule only scattered pebbles were found, but in one place a considerable deposit was encountered forming an indistinct terrace above one of the little brooks. There can be no mistaking these gravels. They are beautifully rounded and waterworn, whereas the material found in the present streams is all angular, and shows its local origin. In size they vary from small pebbles to large cobbles. Those found at the surface are broken and pitted as the result of long exposure to the influence of the weather, but those dug up from a little depth are smooth and fresh. Large numbers of them have been thrown up in piles where the farmers attempted to clear a field along the brook near the largest deposit.

I can account for the occurrence of these gravels on no other basis than the theory of capture so strongly supported by the topographic evidence. It seems certain that the gravels along the former course of the Chattooga have been removed from their initial position by the extensive erosion since the remote date of the capture, and were carried down into the present valleys where they are occasionally found in favorable localities.

On the supposition that these gravels would not be found northwest of the former course of the Chattooga (although they might be carried down-stream to the southeast any distance) the distribution of the gravels leads me to believe that the point of capture was just below the mouth of the Tallulah and that the former course was from that point strongly west and then southwest to the head of Deep Creek.

EVIDENCE OF THE SHELLS.

As noted in the review of the literature, the theory of capture has been supported on the basis of certain facts in the distribution of freshwater faunas. It appears that a few shells from the Chattahoochee and more western drainage basins are found in the Savannah River, while a number of forms from the Savannah system are found in the Chattahoochee system. It is argued that these forms must have passed between the two systems at the time of capture.

That the fauna of the upper Chattahoochee (the Chattooga River), might be transferred into the Savannah River by the capture would appear quite clear. It is much more difficult to account for the transfer in the opposite direction, however, if we limit ourselves to river capture as the means. Yet the main transfer is supposed to have been in that direction. That shells could have passed from the lower level of the Tugaloo up 500 or 600 feet over falls and rapids to the higher level of the Chattahoochee, does not seem probable. It is possible, of course, that the headwater portion of the capturing stream may have been a gradual slope instead of a series of falls, but the evidence of other streams working headward into the Chattooga escarpment suggests that the capture most probably was initiated by a series of more or less prominent cataracts. These would effectually prevent transfer through the water itself. Furthermore, there is good reason to believe that the transfer of water may have been

nearly or quite completed before an actual surface-valley connection was formed, since, as Lane ('99, p. 12) has pointed out, leakage through the rocks from the higher to the lower level will go on for a long time, possibly increasing until all of the water from the higher level passes underground to the lower stream, leaving a dry channel below the point of capture to the first water found in the shrunken, beheaded stream. Under these circumstances there could be no possible transfer of faunas dependent on direct freshwater communication.

On the other hand, there are so many other means for the dispersal of freshwater shells, and the evidence in other localities is so conclusive that they have been dispersed by such means, that we may reasonably suppose shells from either of the two systems might be transferred to the other independently of the capture. For this reason I do not believe the distribution of the shells can be urged as proof of capture, although the fact of capture is well attested by other lines of evidence.

ALTERNATIVE THEORIES.

Instead of capture of the upper Chattahoochee by the upper Savannah, we may suppose that the streams have always had their present relations. On the basis of this supposition it is difficult to account for the systematic relation of the topographic features, or the presence of river gravels in the area between the peculiar elbow bend and the head of Deep Creek. That one branch of the Tugaloo system should have eaten headward through the escarpment and developed a large tributary running well up into the mountains to the northwest, and another running northeast well into North Carolina, together with a large series of other tributaries, while in the same time similar branches, apparently little less favored, should only be able to make small notches in the face of the escarpment, seems quite unreasonable. Neither should we expect a considerable river system such as the Tallulah, to be developed by gradual headward erosion and branching and still preserve extensive falls on its lower course. Such falls might be the result of rejuvenation due to general uplift, but while all the streams of this district are cutting down to a lower level in an uplifted peneplain, the falls on the Tallulah cannot be correlated with other features due to that uplift, and evidently have an independent origin. Mr. Jones has suggested some local earth movements, affecting the lower Tallu-

lah alone, but does not make clear what they could be. It is difficult to imagine movements so profound as to produce a splendid series of cataracts in a deep, narrow gorge, and yet so limited areally as to have no effect on any of the other streams close by, and so obscure as to defy detection.

Finally, it may be noted that the distribution of the river gravels is inexplicable on the basis of any other theory than that of capture; and that this latter theory affords full and reasonable explanation for all the features noted in the district.

SUMMARY.

After a brief review of the literature on the Tallulah district, and a statement of the problem of river capture there presented, we have considered the relations of the region to the greater geologic and physiographic provinces of the southeastern United States. It was shown that the region lies wholly within the crystalline belt, on the western edge of the Piedmont plateau and the eastern edge of the southern extension of the Appalachian mountain belt. In the more detailed study of the local geology we found a series of mica schists and gneisses, striking northeast-southwest and dipping southeast, containing occasional beds of slate, limestone, and quartzite, and cut by pegmatite veins and dykes of diabase and diorite. The most striking features of the local topography were found to be the two peneplain levels separated by a marked escarpment, the open valleys on the upper level and the deep gorges cut far below that level, the hanging valleys of minor branch streams, the extensive falls on the Tallulah River, and the elbow bend of the Chattooga-Tugaloo. The process of river capture was then analyzed, and a series of expectable results deduced. When compared with the actual features in the Tallulah district the theoretical results of remote capture were seen to have a close correspondence to the observed facts, which furnishes a strong presumption in favor of the correctness of the capture theory. The distribution of river gravels completes the evidence in favor of capture, whereas the alternative theories advanced, fail to account for this and other features observed. While the distribution of freshwater shells does not appear valid evidence of capture, the other evidence is so convincing that we conclude the former headwaters of the Chattahoochee have been diverted to the Savannah

drainage by a capture which occurred at some remote period. The point of capture was a short distance below the junction of the Chattooga and Tallulah Rivers; the falls due to capture have been reduced nearly to grade in the weaker rock over which the Chattooga runs, while they still persist in the hard rocks crossed by the lower Tallulah. The cause of the capture was probably the advantage of a shorter course to the sea which the Savannah enjoyed, and by virtue of which it was able to reduce even its headwaters to a lower level than the upper Chattahoochee, and so to undermine and capture the latter.

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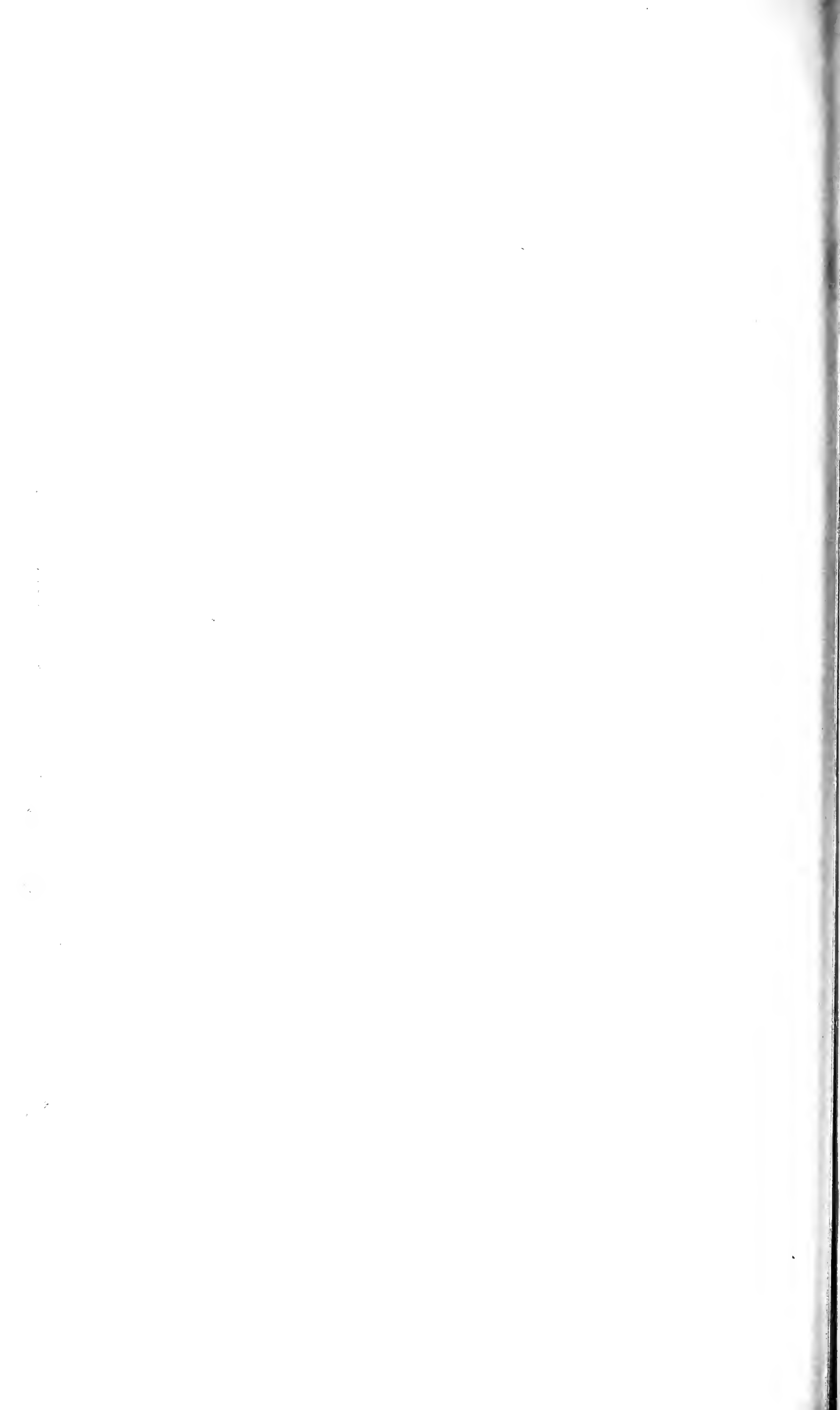
JOHNSON.— Tallulah district.

EXPLANATION OF PLATES.

PLATE 27.

The Tallulah Gorge, looking up the "Grand Chasm" toward the falls.







JOHNSON.— Tallulah district

PLATE 28.

Fig. a. Falls of L'Eau d'Or showing quartzite.

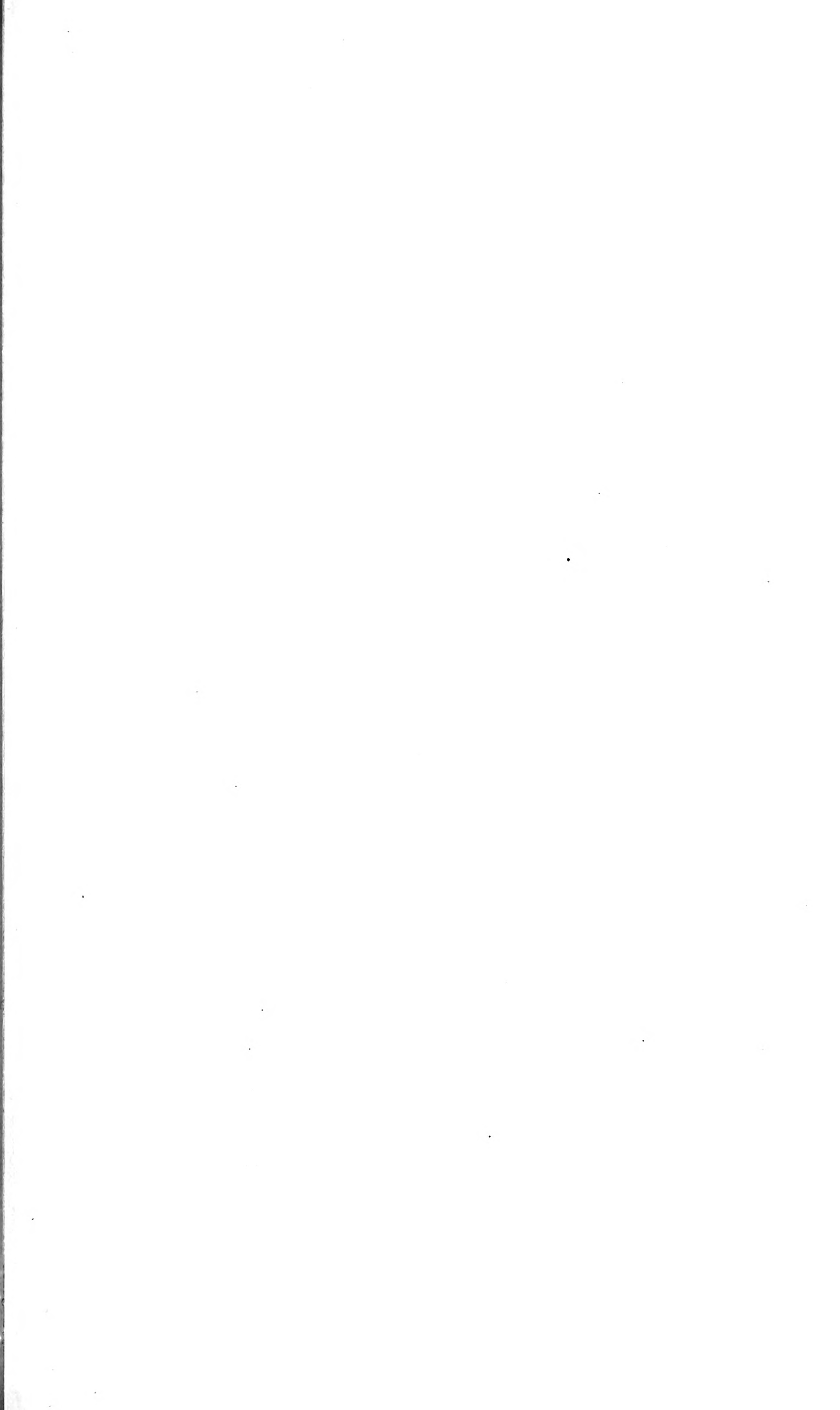
Fig. b. Hurricane Falls.

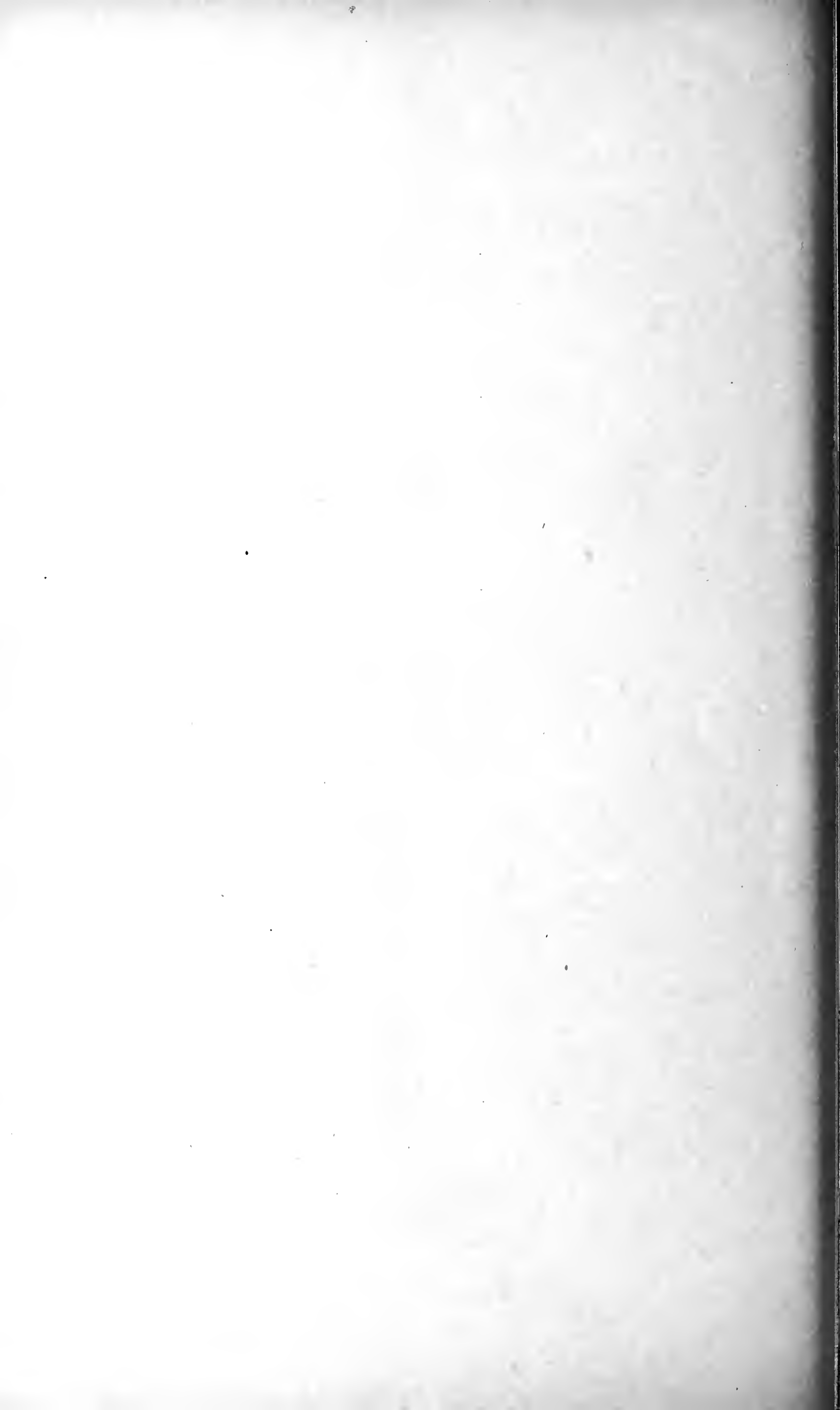


a



b





Proceedings of the Boston Society of Natural History.

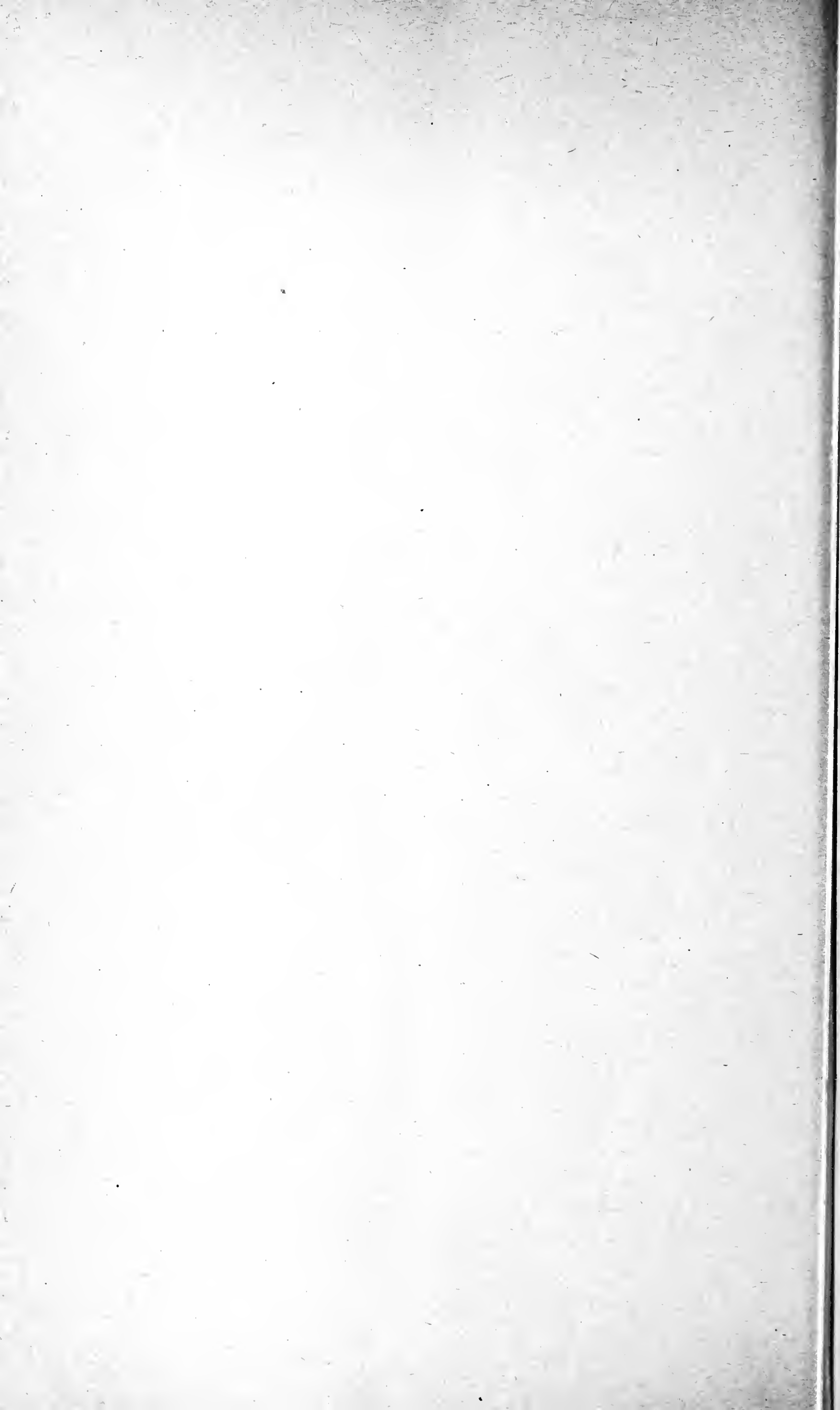
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p. 249-275.

TYPES IN THE PALEONTOLOGICAL COLLECTIONS OF THE
BOSTON SOCIETY OF NATURAL HISTORY.

BY JOSEPH A. CUSHMAN.

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MAY, 1907.



No. 6.—TYPES IN THE PALEONTOLOGICAL COLLEC-
TIONS OF THE BOSTON SOCIETY OF
NATURAL HISTORY.

BY JOSEPH A. CUSHMAN.

THIS catalogue is a list of the type fossils in the collections of the Boston society of natural history. The collections in the Museum are divided into two sections, American and European. The list is arranged so as to be as convenient as possible for a systematist in search of type material. The various groups are here separated and under these the species are arranged alphabetically. The data in regard to the species are given in the following order: (1) catalogue number, (2) name of species as it appears in the place given in the reference, (3) kind of type, (4) formation, (5) locality, (6) author and place of publication, and (7) a cross reference where there is more than one entry or the present accepted name of the species where it is different from the name under which the specimens appear in the catalogue. This latter reference has been given only in the case of the American species. A full list of the references to certain specimens has not been attempted but simply the more important ones are given.

The type specimens listed in this catalogue are divided into four groups, as follows:—

Holotype — either a particular specimen selected by the author from a series or the only specimen known to the author at the time of his publication of the species.

Paratype — any specimen of the original series left after the holotype has been selected.

Cotype — any specimen of the original series where no holotype was selected by the author.

Plesiotype — any specimen used in subsequent description or illustration of the species but not used in the original description of the species. This is here used to include specimens referred to by number as in the collection.

In cases where the specimen is represented by counterparts, the figured half is known as the *obverse*, its counterpart as the *reverse*.

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Among the American fossils the largest number of types occurs in the Rogers collection, especially Carboniferous plants and Tertiary molluscs; the Newell collection of Niagara cephalopods; a collection of Cretaceous plants containing many of Lesquereux's types; Cretaceous cephalopods described by Professor Hyatt; Triassic footprints described by Hitchcock and figured by Deane; and Cambrian material from local formations described by Dr. A. W. Grabau. Besides these there are many types scattered through the collection described or figured by various authors.

The European collection was in a large measure the result of the purchase of the collection of Herr Finanzrath Eser of Stuttgart, Germany. At the time of its purchase this collection was known to contain some types, but upon working over the material lately, many more type specimens were found than at first were thought to be there. Further study may add to the present number. These types are mostly those described by Hermann von Meyer in the various volumes of *Palaeontographica*. There are also types described by Heer and Plieninger. The listing of the types of this part of the collection is especially important as one would hardly look for the types of European species in an American museum.

In marking the type specimens a uniform method has been adopted. For the original types of a species (holotype, paratypes, or cotypes) a red diamond-shaped card has been glued to the specimen. In the case of subsequent types (plesiotypes) a green card of the same shape has been used. This is of a size to conform to the size of the specimen but has been placed on all specimens even when later placed in glass tubes or glass-covered boxes. All types have been placed with the exhibition series as they are there less apt to be overlooked than when packed away.

Some types which should be in the collection have not been located. These are here omitted entirely.

Plants.

CRYPTOGAMA.

- 8174 **Alethopteris distans** Lesq. Cotype.
Carboniferous. Muddy Creek, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 423.
" in Rogers, Geol. of Penn., 1858, p. 865,
pl. 12, fig. 2.
= *Pecopteris distans* Lesq.
- 8115 **Alethopteris serrula** Lesq. Cotype.
Carboniferous. Gate Vein, Port Carbon, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 423.
" in Rogers, Geol. of Penn., 1858, p. 865,
pl. 12, fig. 1.
= *Pecopteris serrula* Lesq.
- 6688 **Cyclopteris Browniana** Dawson. Plesiotype.
Devonian. Perry, Maine.
Dawson, Proc. Portland soc. nat. hist., vol. 1, pt. 2, 1863,
p. 100, pl. 2, fig. 5.
Dawson, Second ann. rept. nat. hist. & geol. Maine,
1862 [1863], p. 403.
= *Platyphyllum Brownianum* Dawson.
- 6688 **Cyclopteris Brownii** Dawson. Plesiotype.
Devonian. Perry, Maine.
Dawson, Quart. journ. geol. soc. London, vol. 19, 1863,
p. 463, pl. 17, fig. 6.
= *Platyphyllum Brownianum* Dawson.
- 8257 **Cyclopteris fimbriata** Lesq. Cotype.
Carboniferous. Pottsville, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 416.
" in Rogers, Geol. of Penn., 1858, p. 855,
pl. 4, fig. 18.
= *Neuropteris fimbriata* Lesq.

- 7618 **Lepidodendron** sp.? Lesq. Cotype.
Subcarboniferous. Mauch Chunk, Pennsylvania.
Lesquereux in Rogers, Geol. of Penn., 1858, p. 884, pl. 21,
fig. 2.
- 8284 **Neuropteris hirsuta** Lesq. Cotype.
Carboniferous. Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 417.
" in Rogers, Geol. of Penn., 1858, p. 857, pl. 4,
fig. 3.
= *Neuropteris Scheuchzeri* Hoffm.
- 8319 **Neuropteris hirsuta** Lesq. Cotype.
Carboniferous. Kenawha, West Virginia.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 417.
" in Rogers, Geol. of Penn., 1858, p. 857, pl. 4,
fig. 4.
= *Neuropteris Scheuchzeri* Hoffm.
- 8139 **Neuropteris Rogersi** Lesq. Cotype.
Carboniferous. Port Carbon, Pennsylvania.
Lesquereux in Rogers, Geol. of Penn., 1858, p. 856, pl. 7,
fig. 2.
= *Neuropteris speciosa* Lesq.
- 8139 **Neuropteris speciosa** Lesq. Cotype.
Carboniferous. Port Carbon, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1875, p. 417.
- 8239 **Odontopteris Schlotheimii** Brgt. Plesiotype.
Carboniferous. Pottsville, Pennsylvania.
Lesquereux in Rogers, Geol. of Penn., 1858, p. 860, pl. 7,
fig. 1.
- 8244 **Pachyphyllum Lactuca** (Presl.). Plesiotype.
Carboniferous. Gate Vein, New Philadelphia, Pennsyl-
vania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 422.
" in Rogers, Geol. of Penn., 1858, p. 863, pl. 8,
fig. 4.
= *Aphlebia germari* Zeill.

- 6688 **Platyphyllum Brownianum** Dawson. Plesiotype.
Devonian. Perry, Maine.
White, Professional paper no. 35, U. S. geol. surv., 1905,
p. 37, pl. 2, fig. 1.
- 8229 **Pseudopecopteris glandulosa** Lesq. Holotype.
Carboniferous. Shamokin, Pennsylvania.
Lesquereux, Coal flora, 1880, p. 210.
See *Sphenopteris glandulosa* Lesq.
- 8244 **Rhacophyllum Lactuca** (Presl.). Plesiotype.
Carboniferous. Gate Vein, New Philadelphia, Pennsylv-
vania.
Lesquereux, Coal flora, 1880, p. 315.
= *Aphlebia germari* Zeill.
- 8085 **Sigillaria cortei** Brgt. Plesiotype.
Carboniferous. Trevorton, Pennsylvania.
Lesquereux, Coal flora, 1880, p. 495.
- 8076 **Sigillaria discoidea** Lesq. Holotype.
Carboniferous. Lehigh Summit, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 427.
" in Rogers, Geol. of Penn., 1858, p. 873,
pl. 14, fig. 5.
- 8065 **Sigillaria dubia** Lesq. Holotype.
Carboniferous. Trevorton, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 427.
" in Rogers, Geol. of Penn., 1858, p. 872.
- 8076 **Sigillaria Lacoëii** Lesq. Cotype.
Carboniferous. Lehigh Summit, Pennsylvania.
Lesquereux, Coal flora, 1880, p. 499.
- 8229 **Sphenopteris glandulosa** Lesq. Holotype.
Carboniferous. Shamokin, Pennsylvania.
Lesquereux, Boston journ. nat. hist., vol. 6, 1857, p. 420.
" in Rogers, Geol. of Penn., 1858, p. 862, pl. 9,
fig. 2.
= *Pseudopecopteris glandulosa* Lesq.

- 8225 **Sphenopteris Lesquereuxii** Newb. Plesiotype.
Carboniferous. Room Run Mines, near Mauch Chunk,
Pennsylvania.
Lesquereux in Rogers, Geol. of Penn., 1858, p. 862,
pl. 10, fig. 1.

- 6687 **Sporangites Jacksoni** D. White. Holotype.
Devonian. Perry, Maine.
Professional paper no. 35, U. S. geol. surv., 1905, p. 76,
pl. 6, figs. 6, 6a.

PHAENOGAMA.

- 11063 **Andromeda Snowii** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892,
p. 117.
- 11056 **Betulites Snowii** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 64.
- 11041 **Betulites Westii cuneatus** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 62.
- 11042 **Betulites Westii latifolius** Lesq. Cotypes.
11043 Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 61.
- 11052 **Betulites Westii oblongus** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 61.
- 11049 **Betulites Westii obtusa** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 61.
- 11051 **Betulites Westii quadratifolius** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 62.

- 11050 **Betulites Westii reniformis** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 62.
- 11045 **Betulites Westii rotundatus** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 61.
- 11047 **Betulites Westii subintegrifolius** Lesq. Cotypes.
11048 Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 61.
- 11070 **Diospyros primaeva** Heer. Plesiotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892,
p. 109.
- 11057 **Diospyros rotundifolia** Lesq. Plesiotypes.
11059 Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892,
p. 112.
- 11084 **Galla quercina** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 58.
- 11067 **Ilex Dakotensis** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892,
p. 178.
- 11093 **Lindera venusta** Lesq. Cotype.
Dakota group (Cretaceous). Ellsworth County, Kansas.
Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 95.
- 11064 **Populus Kansaseana** Lesq. Cotypes.
11065 Dakota group (Cretaceous). Ellsworth County, Kansas.
11066 Lesquereux, Monograph 17, U. S. geol. surv., 1892, p. 42.
- 3341 **Potamogeton Eseri** Heer. Cotype.
Molasse (Miocene). Unterkirchberg, Germany.
Heer, Flora Tertiaria Helvetiae, vol. 1, 1855, p. 102.

- 11060 **Rhamnus inaequilateralis** Lesq. Cotypes.
 11061 Dakota group (Cretaceous). Ellsworth County, Kansas.
 Lesquereux, Monograph 17, U. S. geol. surv., 1892,
 p. 170.
- 11071 **Viburnum robustum** Lesq. Cotypes.
 11072 Dakota group (Cretaceous). Ellsworth County, Kansas.
 Lesquereux, Monograph 17, U. S. geol. surv., 1892,
 p. 120.

Animals.

PROTOZOA.

- 12710 **Eozoon canadense** Dawson? Plesiotypes.
 12712 Laurentian. Chelmsford, Massachusetts.
 Burbank, Proc. Bost. soc. nat. hist., vol. 14, p. 190-198,
 pl. 2. fig. 1-4.

The figures were printed directly from the etched specimens.

COELENTERATA.

- 8809 **Balanophyllia haleana** Milne-Edwards & Haime. Plesiotype.
 Eocene. Mississippi.
 Vaughn, Monograph 39, U. S. geol. surv., 1900, p. 178,
 pl. 21, fig. 2.
- 13338 **Ceratopora dichotoma** Grabau. Cotypes.
 Hamilton. Eighteen-mile Creek, New York.
 Grabau, Proc. Boston soc. nat. hist., vol. 28, 1899, p. 418.
- 1554 **Endopachys maclurii** (Lea). Plesiotype.
 Claibornian (Eocene). Claiborne, Alabama.
 Vaughn, Monograph 39, U. S. geol. surv., 1900, p. 186,
 pl. 21, fig. 15.

According to Schuchert's Catalogue of type specimens in the U. S. national museum, the original of fig. 15 is in that collection. This is undoubtedly an error as our specimen was returned by Dr. Vaughn, marked as the one figured and it agrees in all the individual irregularities with the figure.

- 8864 **Endopachys shaleri** Vaughn. Cotypes.
Eocene? Alabama?
Vaughn, Monograph 39, U. S. geol. surv., 1900, p. 190,
pl. 22, fig. 11-14.
- 8861 **Oculina vicksburgensis** (Conrad). Plesiotype.
Oligocene. Locality unknown.
Vaughn, Monograph 39, U. S. geol. surv., 1900, p. 116.

ECHINODERMATA.

- 13327 **Gennaeocrinus carinatus** Wood. Holotype.
Hamilton (Devonian). Charlestown, Indiana.
Wood, Am. journ. sci., ser. 4, vol. 12, 1901, p. 297.
- 11601 **Lepidesthes wortheni** Jackson. Holotype.
Keokuk group (Subcarboniferous). Crawfordsville?, In-
diana?
Jackson, Bull. geol. soc. Am., vol. 7, 1896, p. 207, pl. 9,
fig. 53.
- 11696 **Melonites multiporus** Norwood & Owen. Plesiotypes.
11569 St. Louis group (Subcarboniferous). St. Louis, Missouri.
Jackson, Bull. geol. soc. Am., vol. 7, 1896, pp. 143, 155.
- 11603 **Platycrinus hemisphericus** Meek & Worthen. Plesiotypes.
11604 Keokuk group (Subcarboniferous). Crawfordsville?, In-
diana?
Jackson, Bull. geol. soc. Am., vol. 7, 1896, p. 207.
- 11602 **Scaphiocrinus depressus** Meek & Worthen. Plesiotype.
Keokuk group (Subcarboniferous). Crawfordsville?, In-
diana?
Jackson, Bull. geol. soc. Am., vol. 7, 1896, p. 207.

VERMES.

- 12833 **Scolithus linearis** Hall. Plesiotypes.
to Lower Cambrian. L'Anse au Loup, Straits of Belle Isle,
12836 Labrador.
Walcott, Tenth ann. rept. U. S. geol. surv., 1890, p. 603,
pl. 63, figs. 1, 1a-c.

- 11976 **Scolithus**, cf. **S. linearis** Hall. Plesiotype.
 Upper Cambrian or Lower Ordovician occurring as a pebble in Carboniferous conglomerate. Newport, Rhode Island.
 Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, p. 614.

BRACHIOPODA.

- 20 **Lingula antiqua** Rogers (not Hall). Plesiotype.
 Upper Cambrian or Lower Ordovician. Newport, Rhode Island.
 Rogers, Proc. Boston soc. nat. hist., vol. 7, 1861, p. 389.
 = *Lingulella rogersi* Walcott.
- 20 **Lingulella rogersi** Walcott. Plesiotype.
 Upper Cambrian or Lower Ordovician. Newport, Rhode Island.
 Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, p. 625.
- 2750 **Lingulella rogersi** Walcott. Plesiotype.
 Upper Cambrian or Lower Ordovician. Fall River, Massachusetts.
 Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, p. 624, pl. 31, fig. 4.
- 11970 **Obolella crassa?** Hall. Plesiotype.
 Lower Cambrian. East Point, Nahant, Massachusetts.
 Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, p. 619, pl. 31, fig. 3.

CRUSTACEA.

- 11975 **Agraulos quadrangularis** (Whitfield). Plesiotypes.
 11976 Middle Cambrian. Hayward Creek, Braintree, Massachusetts.
 23
 Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, pp. 674, 677, pl. 34, fig. 10.

- 12940 **Archaeoplax signifera** Stimpson. Plesiotypes.
to Miocene. Gay Head, Martha's Vineyard, Massachusetts.
12947 Cushman, Am. nat., vol. 39, 1905, p. 383, pl. 2, figs. 1,
12969 2, 4-8, 10-12.
- 13328 **Balanus concavus** Bronn. Plesiotypes.
to Miocene. Gay Head, Martha's Vineyard, Massachusetts.
13330 Cushman, Am. geol., vol. 39, 1904, p. 294, fig. 1-3.
- 3216 **Beyrichia maccoyiana** Jones. Plesiotype.
Salina (Silurian). Penn's Valley, Pennsylvania.
Jones, Ann. mag. nat. hist., ser. 3, vol. 1, 1858, p. 252,
pl. 10, fig. 15.
Rogers, Geol. of Penn., 1858, p. 834, fig. 695.
- 3215 **Beyrichia pennsylvanica** Jones. Cotypes.
3217 Salina (Silurian). Penn's Valley, Pennsylvania.
Jones, Ann. mag. nat. hist., ser. 3, vol. 1, 1858, p. 253,
pl. 10, fig. 16-18.
Rogers, Geol. of Penn., 1858, p. 834, fig. 696.
- 4919 **Cancer kressenbergensis** Meyer. Holotype.
Nummulitic (Eocene). Kressenberg, Germany.
Meyer, Jahrb. für mineral., 1846, p. 463.
= *Xanthopsis kressenbergensis* Meyer.
- 13333 **Cancer proavitus** Packard. Holotype.
Miocene. Gay Head, Martha's Vineyard, Massachusetts.
Packard, Proc. Am. acad. arts and sci., vol. 36, 1900,
p. 3, pl. 1, fig. 1-3.
- 12970 **Cancer proavitus** Packard. Plesiotype.
Miocene. Gay Head, Martha's Vineyard, Massachusetts.
Cushman, Am. nat., vol. 39, 1905, p. 386, pl. 2, fig. 14.
- 4840 **Cancer sonthofensis** Meyer. Holotype.
Nummulitic (Eocene). Sonthofen, Germany.
Meyer, Jahrb. für mineral., 1846, p. 463.
= *Xanthopsis sonthofensis* Meyer.

- 11388 **Ceratiocaris acuminatus** Hall. Plesiotype.
Waterlime (Silurian). Buffalo, New York.
Stose, Proc. Boston soc. nat. hist., vol. 26, 1894, p. 369,
2 figs. in text.
- 12981 **Dalmanites lunatus** Lambert. Cotypes.
12982 Niagara (Silurian). Littleton, New Hampshire.
Lambert, Bull. geol. soc. Am., vol. 15, 1904, p. 480, pl. 44,
fig. 2.
Lambert, History of Littleton, 1905, (sep.) "The geology
of Littleton, N. H.," p. 36, pl. 2, fig. 2.
- 5074 **Illaenus ambiguus** Foerste. Plesiotype.
Niagara. Mifflintown, Pennsylvania.
Foerste, Fifteenth ann. rept. geol. & nat. hist. surv.
Minnesota, 1886, p. 480, fig. 3.
- 3164 **Leperditia gibbera scalaris** Jones. Cotypes.
12878 Lower Helderberg (Silurian). Pennsylvania.
Jones, Ann. mag. nat. hist., ser. 3, vol. 1, 1858, p. 250,
pl. 10, figs. 8, 9.
Rogers, Geol. of Penn., 1858, p. 834, fig. 698.
- 12879 **Leperditia ovata** Jones. Holotype.
Trenton (Ordovician). Potter's Fort, Penn's Valley,
Pennsylvania.
Jones, Ann. mag. nat. hist., ser. 3, vol. 1, 1858, p. 252,
pl. 10, fig. 14.
Rogers, Geol. of Penn., 1858, p. 834, fig. 697.
- 3166 **Leperditia pennsylvanica** Jones. Cotypes.
12875 Clinton. Barre Forge, Pennsylvania.
12877 Jones, Ann. mag. nat. hist., ser. 3, vol. 1, 1858, p. 251,
pl. 10, figs. 12, 13.
Rogers, Geol. of Penn., 1858, p. 834, fig. 699.
- 6264 **Paradoxides harlani** Green. Holotype.
Middle Cambrian. Hayward Creek, Braintree, Massa-
chusetts.
Green, Am. journ sci., ser. 1, vol. 25, 1834, p. 336.

Jackson, Proc. Boston soc. nat. hist., vol. 7, 1859, p. 54.

Walcott, Bull. no. 10, U. S. geol. surv., 1884, p. 46.

Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, p. 681, pl. 36.

- 1 **Paradoxides harlani** Green. Plesiotype.
Middle Cambrian. Hayward Creek, Braintree, Massachusetts.

Walcott, Bull. no. 10, U. S. geol. surv., 1884, p. 45, pl. 7, fig. 3.

Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, pp. 681, 693, pl. 35, fig. 3.

- 2754 **Paradoxides harlani** Green. Plesiotypes.
6265 Middle Cambrian. Hayward Creek, Braintree, Massachusetts.
Counter- parts Walcott, Bull. no. 10, U. S. geol. surv., 1884, p. 45, pl. 9, fig. 1.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, pp. 681, 692, pl. 39.

- 4573 **Paradoxides harlani** Green. Plesiotypes.
2753 Middle Cambrian. Hayward Creek, Braintree, Massachusetts.
2756
12040 Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, pp. 692, 693.

- 6263 **Selenisca gratiosa** Meyer. Holotype.
Oxford clay, Middle Oolite. Würmlingen near Tuttlingen, Würtemberg, Germany.
Meyer, Palaeontographica, vol. 1, pt. 3, July, 1847, p. 141, pl. 19, fig. 1.

- 11968 **Strenuella strenua** Billings. Plesiotype.
Lower Cambrian. Nahant, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4, 1900, p. 672, pl. 34, fig. 8.

- 12978 **Strenuella strenua** Billings. Plesiotype.
Lower Cambrian. Mill Cove, Weymouth, Massachusetts.
Shimer, Am. journ. sci., ser. 4, vol. 23, March, 1907, p. 199, fig. a-c.

- 4838 **Xanthopsis bruckmanni** Meyer. Plesiotypes.
Nummulitic (Eocene). Sonthofen, Germany.
Meyer, *Palaeontographica*, vol. 10, pt. 3, July, 1862,
p. 152, pl. 16, fig. 5-11.
- 4919 **Xanthopsis kressenbergensis** Meyer. Holotype.
Nummulitic (Eocene). Kressenberg, Germany.
Meyer, *Palaeontographica*, vol. 10, pt. 3, July, 1862,
p. 156, pl. 16, fig. 12-14.
- 4840 **Xanthopsis sonthofensis** Meyer. Holotype.
Nummulitic (Eocene). Sonthofen, Germany.
Meyer, *Palaeontographica*, vol. 10, pt. 3, July, 1862,
p. 159, pl. 18, fig. 7-9.

ARACHNIDA.

- 4101 **Clubiona eseri** Heer. Holotype.
Molasse (Miocene). Oeningen, Switzerland.
Heer, *Urwelt der Schweiz*, 1865, p. 356, fig. 213.

INSECTA.

- 8497 **Gerephemera simplex** Scudder. Holotype.
Devonian. "Fern Ledges," Lancaster, New Brunswick.
Scudder, *Geol. mag.*, vol. 5, 1868, p. 174; *Anniv. mem.*
Boston soc. nat. hist., 1880, p. 12, pl. 1, figs. 8, 8a
(reverse); *Foss. ins. No. Am.*, 1890, pp. 164, 276, pl. 7,
figs. 8, 8a (reverse).
- 8495 **Lithentomum harttii** Scudder. Holotype.
Devonian. "Fern Ledges," Lancaster, New Brunswick.
Scudder, *Can. nat.*, ser. 2, vol. 3, 1867, p. 206, fig. 4;
Geol. mag., vol. 4, 1867, p. 387, pl. 17, fig. 4; *Anniv.*
mem. Boston soc. nat. hist., 1880, p. 22, pl. 1, fig. 3;
Foss. ins. No. Am., 1890, pp. 174, 278, 305, pl. 7, fig. 3.
- 8496 **Platephemera antiqua** Scudder. Holotype (reverse)
Devonian. "Fern Ledges," Lancaster, New Brunswick.
Scudder, *Can. nat.*, ser. 2, vol. 3, 1867, p. 205, fig. 2

(reverse); Geol. mag., vol. 4, 1867, p. 387, pl. 17, fig. 2 (reverse); Anniv. mem. Boston soc. nat. hist., 1880, p. 7, pl. 1, fig. 9 (obverse); Foss. ins. No. Am., 1890, pp. 159, 277, 287, pl. 7, fig. 9 (obverse).

- 8498 **Xenoneura antiquorum** Scudder. Holotype.
Devonian. "Fern Ledges," Lancaster, New Brunswick.
Scudder, Can. nat., ser. 2, vol. 3, 1867, p. 206, fig. 5;
Geol. mag., vol. 4, 1867, p. 387, pl. 17, fig. 5; Anniv.
mem. Boston soc. nat. hist., 1880, p. 24, pl. 1, figs.
5, 7; Foss. ins. No. Am., 1890, pp. 176, 280, 302,
pl. 7, figs. 5, 7.

PTEROPODA.

- 11966 **Hyalithellus micans** Billings. Plesiotype.
Lower Cambrian. Nahant, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 658, pl. 32, fig. 12.
- 11974 **Hyalithes** (?) **haywardensis** Grabau. Holotype.
Middle Cambrian. Hayward Creek, Braintree, Massa-
chusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 653, pl. 32, fig. 11.
- 11967 **Hyalithes searsi** Grabau. Cotype.
Lower Cambrian. Nahant, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 649, pl. 32, fig. 5b.
- 11963 **Orthotheca cylindrica** Grabau. Cotype.
Lower Cambrian. Sandy Cove, Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 654, pl. 32, fig. 8a.
- 13337 **Orthotheca cylindrica** Grabau. Cotype.
Lower Cambrian. Pleasant Beach, Cohasset, Massa-
chusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 654, pl. 32, fig. 8d.

- 11959 **Orthotheca cylindrica** Grabau. Cotype.
Lower Cambrian. Nahant, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 654, pl. 32, fig. 8c-f.
- 11969 **Orthotheca emmonsi** (Ford). Plesiotype.
Lower Cambrian. Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 655, pl. 32, fig. 9a-d.
- 11973 **Orthotheca** (?) **foerstei** Grabau. Cotype.
Lower Cambrian. Pleasant Beach, Cohasset, Massachu-
setts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 657, pl. 32, fig. 10.

PELECYPODA.

- 9499 **Arca protracta** Rogers. Holotype.
Miocene. Prince George's County, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 5, 1835, p. 332;
vol. 6, 1839, pl. 26, fig. 5.
- 9492 **Cucullaea onochela** Rogers. Holotype.
Eocene. Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 6, 1839, p. 372,
pl. 28, fig. 2.
= *Cucullaea gigantea* Conrad.
- 12985 **Cucullaea transversa** Rogers. Holotype.
Eocene. King George's County, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 6, 1839, p. 373,
pl. 29, fig. 1.
- 9510 **Lucina speciosa** Rogers. Holotype and paratypes.
Miocene. James River region, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 5, 1835, p. 333;
vol. 6, 1839, pl. 26, fig. 6.
= *Codakia speciosa* (Rogers).

- 9582 **Teredina fistula** H. C. Lea. Plesiotypes.
Miocene. Virginia.
Johnson, Nautilus, vol. 18, 1904, p. 13, 2 figs. in text.
- 3583 **Unio eseri** Krauss. Cotypes.
to Molasse (Miocene). Oberkirchberg, Germany.
3585 Krauss, Jahreshefte d. vereins f. naturkunde in Württemberg, vol. 8, 1852, p. 153.
- 12986 **Venericardia ascia** Rogers. Holotype.
Eocene. King George's County, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 6, 1839, p. 374,
pl. 29, fig. 2.
= *Venericardia planicosta* Lam.
- 9576 **Venus cortinaria** Rogers. Holotype.
Miocene. King's Mill, James River, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 5, 1835, p. 333;
vol. 6, 1839, pl. 26, fig. 7.
= *Chione cortinaria* (Rogers).

GASTROPODA.

- 9604 **Fasciolaria rhomboidea** Rogers. Holotype.
Miocene. James River, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 6, 1839, p.
376, pl. 33, fig. 3.
- 9601 **Natica perspectiva** Rogers. Holotype and paratypes.
12983 Miocene. Williamsburg, Virginia.
Rogers, Trans. Am. phil. soc., ser. 2, vol. 5, 1835, p. 332
vol. 6, 1839, pl. 26, fig. 3.
= *Polinices perspectiva* (Rogers).
- **Planorbis.** Plesiotypes.
Tertiary. Steinheim, Germany.
Hyatt, Anniv. mem. Boston soc. nat. hist., 1880, 114 pp.,
9 pls.

The numerous specimens illustrating the paper by Hyatt on "Tertiary species of Planorbis at Steinheim" were arranged on tablets and photographed for the plates published with the paper as cited above. These tablets with the specimens are preserved in the collection as originally prepared.

- 11965 **Platyceras deflectum** Grabau. Holotype.
Lower Cambrian. Sandy Cove, Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 630, pl. 31, fig. 8a-b.
- 11960 **Platyceras primaevum** Billings. Plesiotype.
Lower Cambrian. Sandy Cove, Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 628, pl. 31, fig. 7a-b.
- 11955 **Raphistoma attleborensis** Shaler & Foerste. Plesiotypes.
11957 Lower Cambrian. Sandy Cove, Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 633, pl. 31, figs. 10a-c.
- 11971 **Scenella** (?) sp. Holotype.
Lower Cambrian. Pleasant Beach, Cohasset, Massa-
chusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 637, pl. 31, fig. 6a-c.
- 11962 **Stenotheca abrupta** Shaler & Foerste. Plesiotype.
Lower Cambrian. Nahant, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 637, pl. 31, fig. 12b-c.
- 11964 **Stenotheca curvirostra** Shaler & Foerste. Plesiotype.
Lower Cambrian. Sandy Cove, Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 638, pl. 31, fig. 13.
- 11961 **Stenotheca levis** Walcott. Plesiotype.
Lower Cambrian. Pleasant Beach, Cohasset, Massachu-
setts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 641, pl. 31, fig. 15.
- 11963 **Stenotheca pauper** Billings. Plesiotype.
Lower Cambrian. Sandy Cove, Cohasset, Massachusetts.
Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
1900, p. 639, pl. 31, fig. 14.

- 11958 **Straparollina remota** Billings. Plesiotypes.
 11959 Lower Cambrian. Pleasant Beach, Cohasset, Massachusetts.
 Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
 1900, p. 635.
- 9626 **Turritella quadristriata** Rogers. Holotype and paratypes.
 12984 Miocene. Williamsburg, Virginia.
 Rogers, Trans. Am. phil. soc., ser. 2, vol. 5, 1835, p. 331;
 vol. 6, 1839, pl. 26, fig. 2.
- 9627 **Turritella terstriata** Rogers. Holotype and paratypes.
 Miocene. Burwell's Mill, James River, Virginia.
 Rogers, Trans. Am. phil. soc., ser. 2, vol. 5, 1835, p. 331;
 vol. 6, 1839, pl. 26, fig. 1.
- 11951 **Watsonella crosbyi** Grabau. Cotypes.
 to Lower Cambrian. Cohasset, Massachusetts.
 11954 Grabau, Occasional papers Boston soc. nat. hist., vol. 4,
 1900, p. 632, pl. 31, fig. 9a-f.

CEPHALOPODA.

- 11189 **Ascoceras indianensis** Newell. Holotype.
 Niagara (Silurian). Delphi, Indiana.
 Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 484,
 4 figs. in text.
- 11188 **Ascoceras newberryi** Billings. Plesiotype.
 Niagara (Silurian). Delphi, Indiana.
 Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 484.
- 10855 **Buchiceras syriaciforme** Hyatt. Cotype.
 Cretaceous. Cajamarca, Peru.
 Hyatt, Proc. Boston soc. nat. hist., vol. 17, 1875, p. 371.
 = *Roemeroceras syriaciforme* Hyatt.
- 11176 **Gomphoceras angustatum** Newell. Holotype.
 Niagara (Silurian). Wabash, Indiana.
 Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 475,
 2 figs. in text.

- 11177 **Gomphoceras angustatum** Newell. Paratypes.
to Niagara (Silurian). Wabash, Indiana.
11180 Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 475.
- 11175 **Gomphoceras linearis** Newell. Holotype.
Niagara (Silurian). Bridge's Quarry, Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 473,
2 figs. in text.
- 11181 **Gomphoceras projectum** Newell. Holotype.
Niagara (Silurian). Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 476,
4 figs. in text.
- 11174 **Gomphoceras wabashensis** Newell. Holotype.
Niagara (Silurian). Harley Bros. Quarry, Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 470,
3 figs. in text.
- 11173 **Gomphoceras wabashensis** Newell. Paratype.
Niagara (Silurian). Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 470,
1 fig. in text.
- 11174a **Gomphoceras wabashensis** Newell. Paratypes.
Niagara (Silurian). Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 470.
- 11173a **Gomphoceras wabashensis** Newell. Paratypes.
Niagara (Silurian). Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 470.
- 11184 **Hexameroceras cacabiformis** Newell. Holotype.
Niagara (Silurian). Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 481,
3 figs. in text.
- 11184a **Hexameroceras cacabiformis** Newell. Paratypes.
Niagara (Silurian). Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 481.

- 11185 **Hexameroceras cacabiformis** Newell. Paratypes.
11186 Niagara (Silurian). Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 481.
- 11182 **Hexameroceras delphicum** Newell. Holotype.
Niagara (Silurian). Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 479,
4 figs. in text.
- 11168 **Kionoceras angulatum** Wahl. Plesiotypes.
to Niagara (Silurian). Wabash, Decatur, Huntingdon, and
11172 Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 470.
- 11162 **Kionoceras columnare** Hall. Plesiotypes.
to Niagara (Silurian). Wabash and Huntingdon, Indiana.
11165 Newell, Proc. Boston soc. nat. hist., vol. 23, p. 469.
- 11166 **Kionoceras strix** Hall & Whitfield. Plesiotypes.
11167 Niagara (Silurian). Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, p. 469.
- 11149 **Orthoceras crebescens** Hall. Plesiotypes.
to Niagara (Silurian). Wabash, Indiana.
11156 Newell, Proc. Boston soc. nat. hist., vol. 23, p. 466.
- 11160 **Orthoceras obstructum** Newell. Holotype.
Niagara (Silurian). Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, p. 467, 2
figs. in text.
- 11159 **Orthoceras rigidum** Hall. Plesiotype.
Niagara (Silurian). Peru, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 467.
- 11157 **Orthoceras unionensis** Worthen. Plesiotypes.
11158 Niagara (Silurian). Wabash, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 467.
- 11187 **Pentameroceras mirum** Barrande. Plesiotype.
Niagara (Silurian). Delphi, Indiana.
Newell, Proc. Boston soc. nat. hist., vol. 23, 1888, p. 483.

- 12932 **Placenticerus placenta** DeKay. Plesiotypes.
Eutaw beds (Upper Cretaceous). Green County?, Ala-
bama.
Hyatt, Monograph 44, U. S. geol. surv., 1903, p. 211.
- 8577a **Placenticerus syrtale halei** Hyatt. Holotype.
Eutaw beds (Upper Cretaceous). Green County?, Ala-
bama.
Hyatt, Monograph 44, U. S. geol. surv., 1903, p. 206,
pl. 28, figs. 3, 4.
- 8577 **Placenticerus syrtale halei** Hyatt. Paratypes.
8577b Eutaw beds (Upper Cretaceous). Green County?, Ala-
bama.
Hyatt, Monograph 44, U. S. geol. surv., 1903, p. 206,
pl. 27, figs. 16, 17; pl. 28, figs. 5, 6.
- 12928 **Placenticerus whitfieldi** Hyatt. Cotype.
Upper Cretaceous. Black Hills, South Dakota.
Hyatt, Monograph 44, U. S. geol. surv., 1903, p. 221,
pl. 46, figs. 1, 2.
- 8614 **Placenticerus whitfieldi** Hyatt. Cotypes.
8615 Upper Cretaceous. El Paso County, and 7 miles E. of
12931 Fort Collins, Colorado; Cheyenne River and Black
8529 Hills, South Dakota.
12923 Hyatt, Monograph 44, U. S. geol. surv., 1903, p. 221.
12926
12927
12929
12930

PISCES.

- 3476 **Clupea gracilis** Meyer. Holotype.
Molasse (Miocene). Unterkirchberg, Germany.
Meyer, Jahrb. für mineral., 1848, p. 780.
= *Clupea humilis* Meyer.
- 3476 **Clupea humilis** Meyer. Plesiotype.
3472 Molasse (Miocene). Unterkirchberg, Germany.
Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851,
p. 87, pl. 16, figs. 12, 13.

- 3420 **Clupea lanceolata** Meyer. Cotypes.
 3442 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Jahrb. für mineral., 1848, p. 780; Palaeontographica, vol. 2, pt. 3, Oct., 1851, pp. 87, 89, 93, pl. 14, figs. 2, 4.
- 3444 **Clupea ventricosa** Meyer. Cotypes.
 to Molasse (Miocene). Unterkirchberg, Germany.
 3446 Meyer, Jahrb. für mineral., 1848, p. 780; Palaeontographica, vol. 2, pt. 3, Oct., 1851, pp. 87, 90, 93, pl. 14, figs. 1 a, b, 5.
- 3491 **Cottus brevis** Agassiz. Plesiotypes.
 3492 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 107, pl. 16, figs. 7, 9.
- 3493 **Cottus (?) multipinnatus** Meyer. Holotype.
 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 106, pl. 17, fig. 1
- 3449 **Cyprinus priscus** Meyer. Cotypes.
 to Molasse (Miocene). Unterkirchberg, Germany.
 3451 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 95
 3480 pl. 15, figs. 1-3, 5; vol. 6, pt. 1, Sept., 1856, p. 22, pl. 1, fig. 1.
- 3478 **Leuciscus gibbus** Meyer. Holotype.
 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 98, pl. 15, fig. 6.
- 3465 **Smerdis elongatus** Meyer. Holotype.
 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 110, pl. 16, fig. 6.
- 3453 **Smerdis formosus** Meyer. Holotype.
 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 110, pl. 16, fig. 5.

- 3454 **Smerdis minutus** Agassiz. Plesiotypes.
 3455 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851,
 p. 109, pl. 16, figs. 2, 3.
- 3484 **Solea antiqua** Meyer. Cotypes and plesiotype.
 3486 Molasse (Miocene). Unterkirchberg, Germany.
 3487 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851,
 p. 103, pl. 17, figs. 4, 5; vol. 6, pt. 1, Sept., 1856, p. 26,
 pl. 1, fig. 5.
- 3485 **Solea kirchbergana** Meyer. Cotypes.
 3488 Molasse (Miocene). Unterkirchberg, Germany.
 Meyer, Palaeontographica, vol. 2, pt. 3, Oct., 1851, p. 102,
 pl. 17, figs. 2 3.

BATRACHIA

- 2765 **Rana jager** Meyer. Holotype.
 Süßwasserkalk (Miocene). R. R. cut at Haslach, near
 Ulm, Württemberg Germany.
 Meyer, Jahrb. für mineral., 1851, p. 78; Palaeonto-
 graphica, vol. 7, pt. 3, July, 1860, p. 144, pl. 22, fig. 5.

REPTILIA.

- 7512 **Belodon planirostris** Meyer. Cotypes.
 7513 Keuper-Steuben Sandstone (Triassic). Aixheim, Germany.
 7515 Meyer, Palaeontographica, vol. 10, pt. 5, Jan., 1863,
 7516 p. 241, pl. 41, fig. 1-11.
 7518
 7520

MAMMALIA.

- 3466 **Amphicyon eseri** Plien. Holotype.
 Molasse (Miocene). Unterkirchberg, Germany.
 Plieninger, Jahreshefte für naturk. in Württemberg,
 vol. 5, 1850, p. 216, pl. 1, fig. 9.

- 2710 **Tapirus helveticus** Meyer. Plesiotypes.
 2720 Süßwasserkalk (Miocene). Eggingen and Haslach, near
 to Ulm, Württemberg, Germany.
 2724 Meyer, *Palaeontographica*, vol. 15, pt. 4, Feb., 1867,
 p. 191, pl. 26, fig. 5-13; pl. 28, fig. 10-13.

VERTEBRATE FOOTPRINTS.

- 11000 **Amblonyx giganteus** E. Hitchcock. Cotype (reverse).
 Triassic. Turner's Falls, Massachusetts.
 Hitchcock, *Ichnology of New England*, 1858, p. 71,
 pl. 38, fig. 1.
 = *Eubrontes platypus* Lull.
- 8492 **Anisopus gracilis** E. Hitchcock. Plesiotype (reverse).
 Triassic. Turner's Falls, Massachusetts.
 Hitchcock, *Ichnology of New England*, 1858, p. 61,
 pl. 58, fig. 9.
 = *Batrachopus gracilis* (E. Hitchcock).
- 8490 **Brontozoum giganteum** E. Hitchcock. Plesiotype.
 Triassic. Turner's Falls, Massachusetts.
 Hitchcock, *Ichnology of New England*, 1858, p. 64.
 = *Eubrontes giganteus* E. Hitchcock.
- 11000 **Brontozoum validum** E. Hitchcock. Plesiotype (reverse).
 Triassic. Turner's Falls, Massachusetts.
 Hitchcock, *Ichnology of New England*, 1858, p. 67, pl. 38,
 fig. 1.
 = *Anchisauripus tuberosus* (E. Hitchcock).
- 8476 **Brontozoum validum** E. Hitchcock. Plesiotype.
 Triassic. Connecticut River, Massachusetts.
 Deane, *Ichnographs from the sandstone of the Conn.
 River*, 1861, p. 39, pl. 12.
 = *Anchisauripus tuberosus* (E. Hitchcock).
- 8483 **Macropterna divaricans** E. Hitchcock. Plesiotype.
 Triassic. Connecticut River, Massachusetts.
 Deane, *Journ. acad. nat. sci. Phila.*, ser. 2, vol. 3, 1856,
 p. 175, pl. 20, diag. B, fig. b; *Ichnographs from the*

sandstone of the Conn. River, 1861, p. 45, pl. 24,
fig. 1.

= *Palamopus divaricans* (E. Hitchcock).

- 13339 **Macropterna gracilipes** E. Hitchcock. Cotype (reverse).
Triassic. Lily Pond, Turner's Falls, Massachusetts.
Hitchcock, Ichnology of New England, 1858, p. 129,
pl. 34, fig. 1.
= *Palamopus gracilipes* (E. Hitchcock).

- 12857 **Otouphepus magnificus** Cushman. Holotype.
Triassic. Gill, Massachusetts.
Cushman, Am. geol., vol. 33, 1904, p. 154, pl. 6.

- 13340 **Plesiornis quadrupes** E. Hitchcock. Cotypes.
Triassic. Turner's Falls, Massachusetts.
Hitchcock, Ichnology of New England, 1858, p. 102,
pl. 35, figs. 1, 2.
= *Anomoepus intermedius* E. Hitchcock.

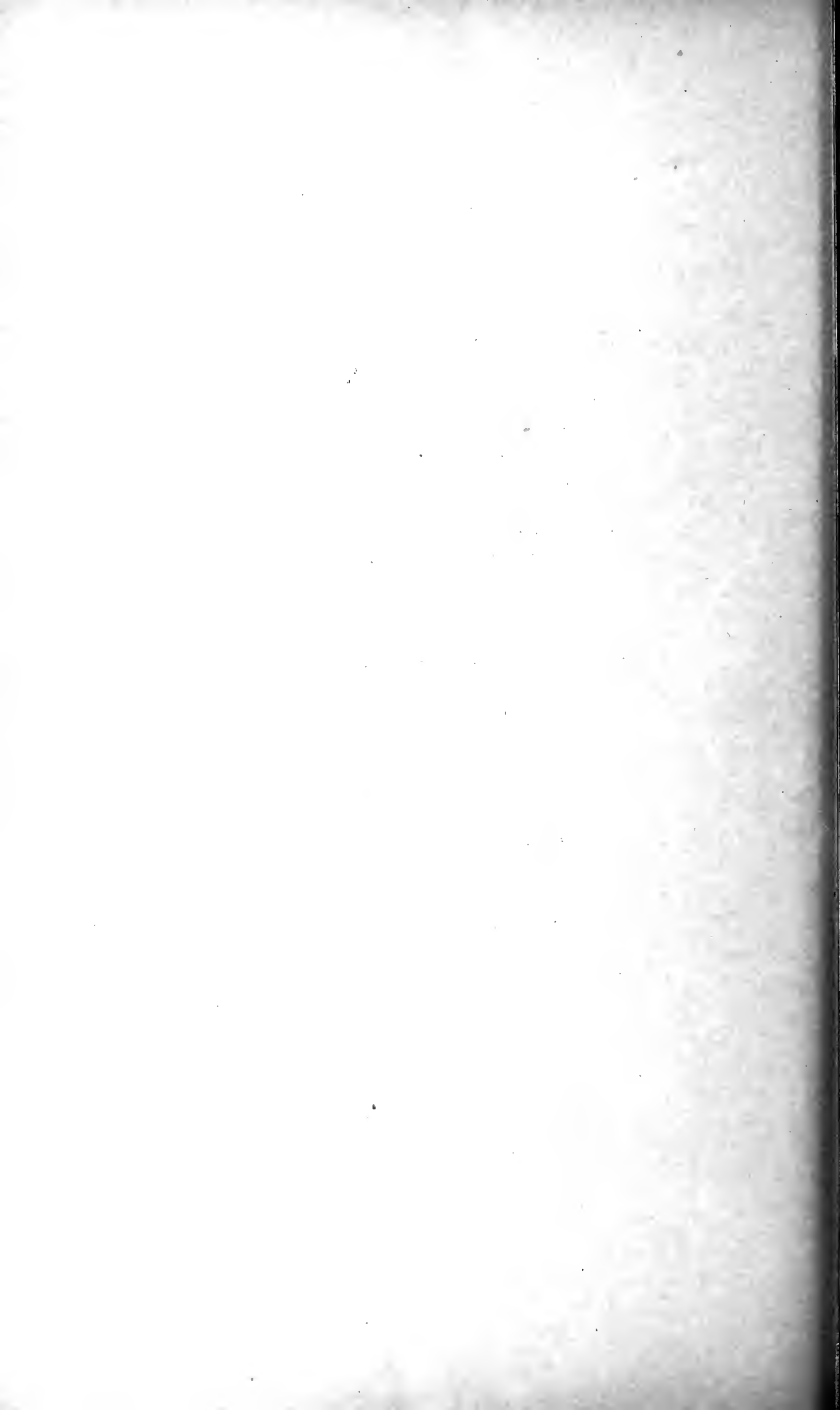
FOOTPRINTS OF UNCERTAIN CHARACTER.

- 8462 **Acanthichnus saltatorius** E. Hitchcock. Plesiotype.
Triassic. Connecticut Valley, Massachusetts.
Deane, Ichnographs from the sandstone of the Conn.
River, 1861, p. 57, pl. 40, fig. 1.

- 8482 **Bifurculapes elachistotatus** E. Hitchcock. Cotypes.
Triassic. Mr. Field's farm, Turner's Falls, Massachusetts.
Hitchcock, Ichnology of New England, 1858, p. 154,
pl. 30, fig. 3 [in part].
Deane, Ichnographs from the sandstone of the Conn.
River, 1861, p. 58, pl. 41, fig. 6.

- 8482 **Bifurculapes laqueatus** E. Hitchcock. Cotype.
Triassic. Mr. Field's farm, Turner's Falls, Massachusetts.
Hitchcock, Ichnology of New England, 1858, p. 153,
pl. 30, fig. 3 [in part].
Deane, Ichnographs from the sandstone of the Conn.
River, 1861, p. 58, pl. 41, fig. 5 [in part].

- 8481 **Bifurculapes tuberculatus** E. Hitchcock. Cotype.
Triassic. Mr. Field's farm, Turner's Falls, Massachusetts.
Hitchcock, *Ichnology of New England*, 1858, p. 153,
pl. 30, fig. 4 [in part].
Deane, *Ichnographs from the sandstone of the Conn.
River*, 1861, p. 58, pl. 41, fig. 2.
- 8481 **Conopsoides larvalis** E. Hitchcock. Cotype.
Triassic. Mr. Field's farm, Turner's Falls, Massachusetts,
Hitchcock, *Ichnology of New England*, 1858, p. 152,
pl. 30, fig. 4 [in part].
Deane, *Ichnographs from the sandstone of the Conn.
River*, 1861, p. 58, pl. 41, fig. 3.
- 13336 **Halysichnus tardigradus** E. Hitchcock. Holotype.
Triassic. Mr. Field's farm, Turner's Falls, Massachusetts.
Hitchcock, *Ichnology of New England*, 1858, p. 163,
pl. 26, fig. 8.
- 8482 **Lithographus cruscularis** E. Hitchcock. Cotype.
Triassic. Mr. Field's farm, Turner's Falls, Massachusetts.
Hitchcock, *Ichnology of New England*, 1858, p. 157,
pl. 30, fig. 3 [in part].
Deane, *Ichnographs from the sandstone of the Conn.
River*, 1861, p. 58, pl. 41, fig. 5 [in part].
- 8464 **Lithographus hieroglyphicus** E. Hitchcock. Plesiotype.
Triassic. Connecticut Valley, Massachusetts.
Deane, *Ichnographs from the sandstone of the Conn.
River*, 1861, p. 58, pl. 42, fig. 2.



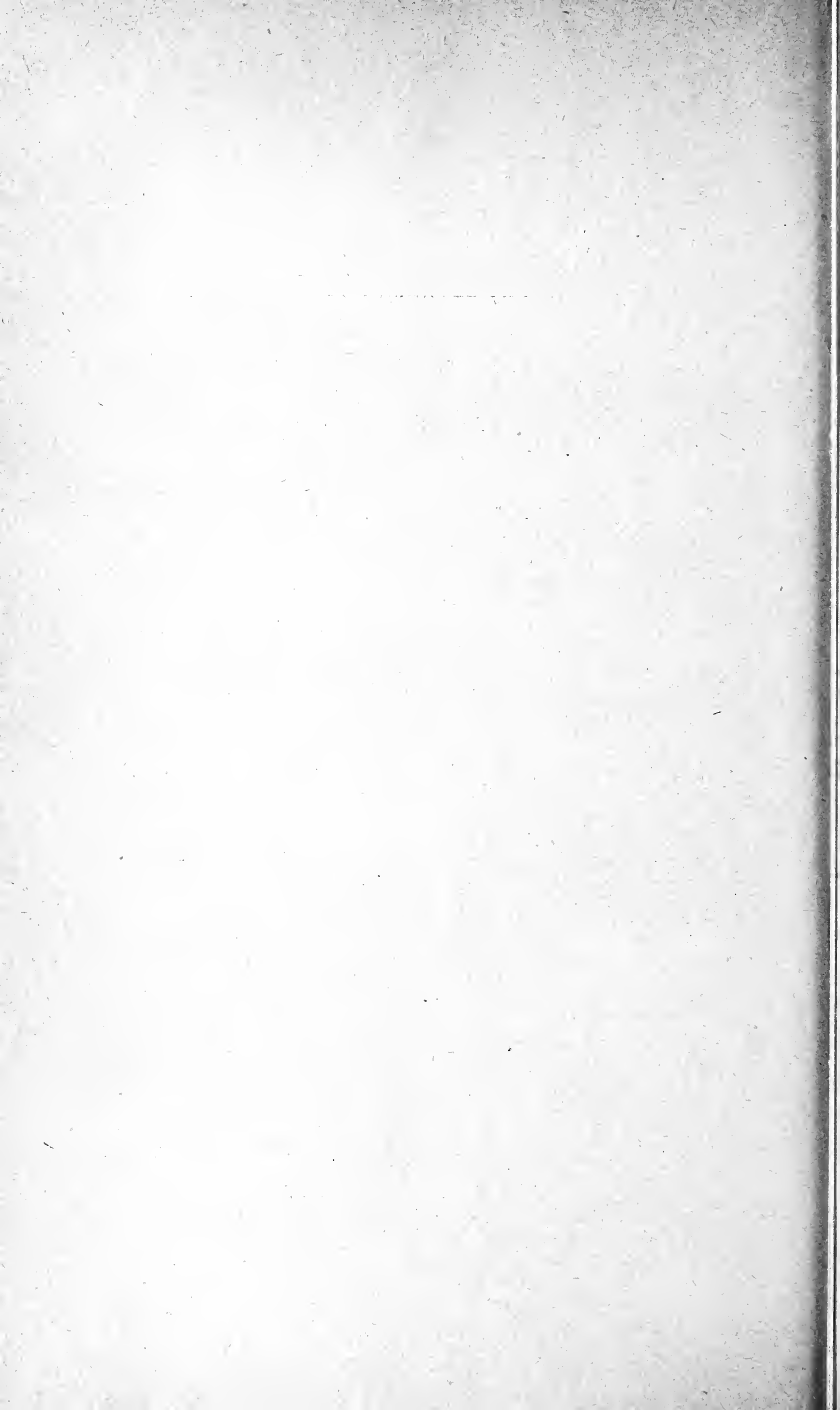
Proceedings of the Boston Society of Natural History.

VOL. 33, No. 7,
p. 277-428, pl. 29.

BIRDS OF LABRADOR.

BY CHARLES W. TOWNSEND, M. D., AND GLOVER M. ALLEN.

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No. 7.— BIRDS OF LABRADOR.

BY CHARLES W. TOWNSEND, M. D., AND GLOVER M. ALLEN.

INTRODUCTION.

THE birds of Labrador have been studied by a number of observers and several lists, mostly partial, have been published. The most extensive of these appeared in 1891, published by Professor A. S. Packard. This list of 208 species was originally prepared by L. M. Turner in 1885 and was brought down to date by Dr. J. A. Allen.

Our own studies of the avifauna of this interesting region include a review of all the literature on the subject we have been able to find, and a visit to the Labrador coast in the summer of 1906. Although this visit was brief, we feel that we have obtained an idea of this region which our previous reading was unable to supply, and also that we have settled the status of the Horned Lark in Labrador, and cleared up the erroneous ideas that previously prevailed owing to the lack of definite information and extreme paucity of specimens. The study of this question was one of the chief objects of our trip. We were also fortunate in being able to make detailed observations on the interesting flight song of the American Pipit and the Horned Lark.

Our itinerary was as follows: crossing the Straits of Belle Isle from the Newfoundland coast in the mail steamship *Home* on July 10, 1906, we skirted the southern coast of Labrador from Blanc Sablon eastward, stopping at a few places and reaching Battle Harbor on the next day. Here we spent four days and explored Battle and Great Caribou Islands and also sailed in a small boat up St. Lewis Inlet to Mary Harbor where we spent a day and a night. From Battle Harbor we sailed on the *Virginia Lake* on July 15th to Nain which we reached on July 21st, and returned to Battle Harbor on July 26th. On the way north we dropped anchor at forty-five different ports of call and at about the same number on the return. We went ashore at as many of these places as possible, spending from fifteen minutes to three quarters of an hour at most of them, but having over an hour at Cartwright, and a whole day at Rigolet and again at Long Tickle. Even during the short stays we endeavored

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to cover as much ground as possible, made notes on the birds observed, and shot specimens from time to time. On both steamers except when we were eating or sleeping we were always on deck either on the bridge or in the bow, making note of all the birds seen, using constantly strong binoculars, and occasionally having resort to a telescope. On the return trip we pursued the same tactics.

From July 26th to August 2d, we waited for the *Home* to take us south, but employed the time in a careful exploration of the bird life of Great Caribou Island, and the region about Cape Charles. At the latter place we stayed three days, and extended our trips from Indian Cove to The Lodge and some miles inland. On our return trip on the *Home* we went a little farther west than before, as we had a short time ashore at Bradore, the most easterly point reached by Audubon on the Labrador coast. We steamed away from there on our return by way of Newfoundland on August 3d.

We brought back 58 skins we had prepared and 20 skins we obtained from the Eskimos.

We gathered as much information as possible about the bird life from the natives, from Dr. Grenfell's assistants, and from the Moravians. Through the latter at Hopedale we obtained most of the skins made by the Eskimos. To Brother Schmitt at Nain we are greatly indebted for many interesting notes of arrival of birds and nesting dates. Although we were so unfortunate as to miss meeting Dr. W. T. Grenfell in Labrador, we are greatly indebted to him for his kind offers of assistance and hospitality, and for valuable information he has since given us in Boston.

We are also indebted to Mr. William Brewster and to Mr. Outram Bangs for the privilege of examining specimens in their collections and for other kind help; to Bowdoin college for the loan of a specimen of Horned Lark; and particularly to Mr. Harry C. Oberholser of the Biological survey at Washington for his study of our specimens of Horned Lark and Savanna Sparrows as well as other kind assistance. To Dr. Malcolm Storer we are indebted for the loan of his father's manuscript journal written in Labrador in 1849.

We are also indebted to Dr. B. L. Robinson, of the Gray herbarium, for the identification of our specimens of flowering plants and grasses, and to Dr. W. G. Farlow for the identification of lichens brought back by us from Labrador.

In the following pages will be found first a description of the topog-

raphy and faunal areas of Labrador, followed by an ornithological history, including an account of the expeditions of the ornithologists who have visited Labrador, and of the destruction of bird life and eggs there, and lastly an annotated list of the birds of this region as well as a bibliography.

Many of the ornithological records for Labrador are imperfect and of doubtful value and we have often found considerable difficulty in deciding on their merits. It is therefore possible that some of the species that are condemned to the doubtful or erroneous list (in small type) may be worthy of a higher position, and that some of the species in the regular list do not deserve that honor. We have, however, presented all the evidence we can find in all cases, so that readers can draw their own conclusions.

We have considered in all 259 species and subspecies, two of which are now extinct. Of the remainder we have put 44 species in the doubtful or erroneous list, leaving 213 species and subspecies whose status for Labrador we have considered certain. Of these, however, some 15 are of accidental occurrence only. The nomenclature and order followed, are those of the Check-List of the American ornithologists' union as corrected up to 1906, except in the case of the Horned Owl. Here we have adopted the name given by H. C. Oberholser.

TOPOGRAPHY.

Geography.—Labrador is a peninsula on the northeast coast of North America lying north of the Gulf of St. Lawrence. Its eastern coast, washed by the North Atlantic Ocean and the Arctic current, is some seven hundred miles in length, extending from Cape Charles at the entrance to the Straits of Belle Isle in north latitude 52° , north-northwest to Cape Chidley in latitude $60^{\circ} 30'$. On the north the peninsula is bounded by Hudson Strait and its offshoot, Ungava Bay. From Cape Chidley at the eastern to Cape Wolstenholme at the western extremity of this boundary the distance in a straight line, which runs about west-northwest, is nearly five hundred miles. The actual coast line is nearly twice as long. The western boundary is formed by the shores of Hudson Bay, and its prolongation southward into James Bay. This boundary runs nearly north and south for about eight hundred miles. The southern boundary is arbitrary, but is generally taken, and is so considered in this paper, as a line

drawn from the south end of James Bay near latitude 51° easterly to the Gulf of St. Lawrence near Seven Islands in latitude 50° , and from there along the shore of the Gulf of St. Lawrence and the Straits of Belle Isle to our starting point at Cape Charles. This southern shore boundary is something over five hundred miles in length and the line from James Bay to the shore is nearly six hundred miles long.

As will be seen by the map, records from Moose Factory, Godbout, Point des Monts, and Anticosti Island are excluded as these places are outside of the limits of Labrador.

The most southern point in Labrador is at the fiftieth degree of north latitude on the southern coast near Seven Islands. The most northern station is Cape Wolstenholme at about latitude 63° N. The most eastern point is Battle Harbor at $55^{\circ} 32'$ west longitude, and the most western point is Cape Jones on Hudson Bay at longitude $79^{\circ} 50'$ W.

The total area embraced within the boundaries given above, according to Low, is approximately 511,000 square miles.

Much of this area is practically unexplored. The region lying north of Clearwater Lake, the Larch and Koksoak Rivers at Fort Chimo, has never been visited by white men. It extends from the boundary just mentioned in latitude 57° and 58° to the northern extremity of Labrador at Cape Wolstenholme, about latitude 63° . In this northern region it is probable that certain gulls, ducks, and shore birds may be found breeding that are as yet unrecorded for Labrador, except as transient visitors.

Geology.—To A. P. Low we are chiefly indebted for an account of the geology of this region. More than nine tenths of the rocks of the Labrador peninsula are highly metamorphosed Laurentian rocks, gneiss, and schists. The remainder belong in the Huronian and Cambrian horizons and occur in scattered areas. "Under the name Huronian are included several widely separated areas of clastic and volcanic rocks, together with many basic eruptives; these are represented by various schists, conglomerates, breccias, diorites and other rocks more or less interfolded with the Laurentian.

"The Cambrian rocks rest unconformably upon the Laurentian and Huronian, and are made up of bedded sandstones, argillites, shales and limestones, along with bedded traps and other basic intrusive or volcanic rocks" (Low, '96, p. 196).

Along the southern coast fronting the Straits of Belle Isle extend

red sandstone hills and cliffs, showing horizontal strata. The underlying Laurentian rocks appear at the eastern end of the Straits. Narrow strata of light-colored limestone appear in places. The cliffs at The Battery near Forteau reach a height of 350 feet; the small mountains immediately behind are 1100 feet high. The sandstone is soft and, as at Paroquet Island, makes excellent burrowing material for the nests of Puffins.

The exposed rocks of the eastern coast are largely Laurentian, cut by numerous basaltic dikes. Immediately back of the coast the land rises gradually from insignificant hills in the south to mountains of 6000 feet near Cape Chidley.

The coast line itself, although showing in many places evidence of recent elevation in the form of raised beaches, is characteristic of a depressed or drowned region. This is shown by the numerous islands and the deep fiords, called here "tickles," with which the coast is beset. These features furnish excellent nesting sites for many water birds. The largest of the fiords is Hamilton Inlet, which stretches back into the land one hundred and fifty miles, with an average width of fourteen miles. Evidences of recent glaciation are shown everywhere, in the *roches moutonnées*, the glacial grooves and scratches, and the numerous erratics.

In the interior, much of which is unexplored, are high tablelands, numerous hills, a few mountains, and a network of rivers, lakes, and ponds. The most noticeable of these features are the Mealy Mountains, the Hamilton or Grand, Nauscaupée, George, Koksoak, East Main, Whale, Eskimo, and Natashquan Rivers, and Mistassini, Nichicun, Petitskapau, Michikamau, Clearwater, and Indian House Lakes.

During the long winter from October to June the lakes and rivers are covered with ice and the ice along the seacoast forms a solid highway upon which the inhabitants travel on dog-sledges. Dr. W. T. Grenfell tells us that the breadth of this strip of solid ice along the eastern coast every winter is from twenty to twenty-five miles, while outside of this is the loose "slob" ice, which drifts back and forth with the winds and tides, varies greatly in thickness and density, and may extend fifty or more miles out to sea. In the Straits of Belle Isle, with their strong tides, there are generally a few open places even in mid-winter, and Cartwright speaks of open places near some of the outer islands even on the eastern coast. Even in the northern parts of Hudson Bay open water is to be found in places in winter.

Low in "The cruise of the *Neptune*" speaks of finding Brännich's Murres, Dovekies, and Old-squaws in the open water at Fullerton, northwest of Cape Wolstenholme throughout the winter. The presence or absence in winter of such water birds as Glaucous Gulls, Eiders, Razor-billed Auks, and Dovekies is of course dependent on the presence or absence of these open spaces.

Mention will be made of the tree growth and other flora under the following head.

FAUNAL AREAS.

Three life zones may be recognized with more or less clearness, in the peninsula of Labrador. These are the Arctic, the Hudsonian, and the Canadian zones.

Arctic zone.—This is the most clearly defined of the three areas. It includes the barren grounds of the northern portion of Labrador south to the upper limit of tree growth on a parallel nearly coinciding with that of the southern shores of Ungava Bay in about latitude 58° N. Thence the Arctic area extends in a narrowing strip along the entire east coast and on the south coast as far west as Mingan. On the Hudson Bay side, according to the observations of Low, the barren coastal strip extends southward about as far as the mouth of the Great Whale River (lat. 55° N.).

Elsewhere, in the interior of the peninsula, the Arctic zone includes the barren tops of the mountains and higher hills, but the precise level at which the tree growth ends and the barren area commences, varies from near sea level at a short distance from the coast in southern Labrador to several hundred feet in the latitude of the Mealy Mountains, as determined by the factors of slope and exposure.

In the vicinity of Battle Harbor at the easternmost point of the country, the Arctic strip extends from the exposed coasts of the outer islands, in onto the mainland for from one to three or four miles as a practically unbroken "barren," sprinkled with lichen-covered ledges and carpeted with turf of reindeer lichen, sphagnum, *Empetrum*, sedges, creeping willows, and various other species of herbaceous plants, including the following, kindly determined for us by Dr. B. L. Robinson of the Gray herbarium, from specimens collected at various points along the coast: *Betula pumila*, *Salix argyrocarpa*, *S. uva-ursi*, *S. anglorum*, *S. glauca*, *Polygonum viviparum*, *Saxifraga caespitosa*, *S. rivularis*, *Cerastium alpinum*, *Rubus chamaemorus* ("bake-apple"), *R. arcticus*, *Vaccinium uliginosum*, *Sedum roseum*,

Silene acaulis, *Menyanthes trifoliata*, *Loiseleuria procumbens*, *Smilacina trifolia*, *Phyllodoce caerulea*, *Kalmia polifolia*, *Cornus suecica*, *Luzula parvifolia*, *Pinguicula vulgaris*, *Linnaea borealis*, var. *americana*, *Festuca ovina*, *Calamagrostis Langsdorffii*, *Plantago borealis*, *Epilobium palustre*, *Potentilla palustris*, *Elymus mollis*, *Poa laxa*, *Poa pratensis*, var. *domestica*, *Carex atrata*, *C. rariflora*, *C. rigida*, var. *Bigelovii*, *Eriophorum Scheuchzeri*, *E. polystachion*, *Cochlearia officinalis*, *Scirpus caespitosus*.

In addition to these the common plants of which we did not bring back specimens were: *Empetrum nigrum*, *Ledum palustre*, *Lathyrus maritimus*; also much dwarfed and procumbent specimens of *Abies balsamea*, *Picea Canadensis*, *Picea Mariana*, and *Larix laricina*. As proof of the Arctic difficulties with which these trees labored, we found 54 rings in the cross section of the trunk of a fir 2 inches in diameter whose topmost twig was only thirteen inches from the ground.

The following lichens we collected, were kindly identified by Dr. W. G. Farlow: *Nephroma arcticum*, *Buellia geographica*, *B. petraea*, *Parmelia saxatilis*, *Alectaria ochroleuca*, var. *nigricans*, *A. jubata*, *Umbilicaria cylindrica*, *Placodium elegans*, *Pannaria brunnea*, *Peritularia* sp.?, *Stereocaulon coralloides*, *S. paschale*, *Cladonia rangiferina*, *C. deformis*, *Lecanora bodia*, *Trentepoplia aurea*.

In the latitude of Nain (57° N.) the Arctic area extends considerably farther in from the sea than at points more to the south. Moreover, since the land rises gradually with the increase of latitude, this life zone has a greater extent, inasmuch as the upper limit of the stunted tree growth is reached at a lower level than farther south.

The avifauna of the Arctic zone in Labrador is limited as to both species and individuals. Of characteristic Arctic land birds that breed in Labrador may be mentioned: Rock Ptarmigan, Reinhardt's Ptarmigan (in northern portion), American Rough-legged Hawk, White Gyrfalcon, Black Gyrfalcon, Snowy Owl, Horned Lark, Snow Bunting, Lapland Longspur, American Pipit, and Wheatear. Possibly the White Wagtail may be added to this list, although the presence of this species and of the Wheatear as breeding birds in the area under consideration is probably sporadic. In the marshy pools grown up to rushes and sedges Northern Phalaropes are to be found breeding. The Semipalmated, Least, and Spotted Sandpipers, and Semipalmated Plover also breed on and near the coast. Along the

rocky shores are numbers of seafoal whose breeding area does not of course closely coincide with that of land birds.

The few species of characteristic Arctic land birds are not evenly distributed over the barren area. They are most numerous, at least in point of species, in the more northern part. Thus in the region about Ungava, Ptarmigan, Rough-legged Hawks, Gyrfalcons, Snowy Owls, Horned Larks, Snow Buntings, Lapland Longspurs, Pipits, and Wheatears are all breeding birds, but as we follow the Arctic coastal strip south, the Ptarmigans, Snow Buntings, and Lapland Longspurs soon become less common, and over most of the southern portion of this area, the Rough-legged Hawks, Horned Larks, and Pipits are the only Arctic birds that seem to be of general distribution. In addition to these species, however, should be mentioned the Savanna Sparrow, which, with the Horned Larks and the Pipits, is one of the most characteristic of the barren-ground birds of Labrador. To us who are accustomed to seeing this bird in the grassy meadows of the eastern United States, it seems strangely out of place on the wind-swept moors of this bleak coast.

Hudsonian and Canadian zones.—These two zones, inasmuch as they are separated by no sharp line of demarcation, may best be considered together. Although the upper limit of the Hudsonian fauna coincides closely with that of the stunted tree growth, the transition from the Hudsonian to the Canadian is so gradual that no definite boundary can be traced between them. At the upper limit of the Hudsonian, where it borders upon the Arctic zone, the trees become greatly dwarfed and exceedingly dense and scrubby. White and black spruces, balsam firs, and larches grow in matted thickets from three to six feet high with outlying clumps of even less height occurring in sheltered spots as “islands” within the Arctic area. Back from the barren coastal strip in the sheltered valleys, ravines, and river bottoms these trees attain a more vigorous growth so that along the shores of Hamilton Inlet and southward they reach here and there the height of twenty-five or thirty feet. In addition to the conifers, there are occasional clumps of stunted paper birch and aspen, while along the streams there are thickets of alder and willow. Inland, “the forest is continuous over the southern part of the peninsula to between latitudes 52° and 54° To the northward of latitude 53°, the higher hills are treeless and the size and number of the barren areas rapidly increase. In latitude 55°, more than half the

surface of the country is treeless, woods being only found about the margins of small lakes and in the valleys of the rivers. Trees also decrease in size until, on the southern shores of Ungava Bay, they disappear altogether. The Leaf River, which empties into the bay a few miles north of the mouth of the Koksoak River, is the northern limit of forest trees on the west side of Ungava Bay. Along the east coast of Hudson Bay, Dr. Bell found trees growing a few miles beyond the north end of Richmond Gulf. . . . So that a line drawn a little south of west, from the mouth of the Leaf River to the mouth of the Nastapoka River on Hudson Bay, would give a close approximation to the northern tree limit [and thus to the Hudsonian zone] of western Labrador" (Low, '96, p. 31). In eastern Labrador, Low states that the tree line "skirts the southern shore of Ungava Bay and comes close to the mouth of the George River, from which it turns south-southeast, skirting the western foothills" of the treeless Atlantic coast range, southward at a short distance from the coast, until at the latitude of Battle Harbor, small trees are found in sheltered places at a distance of a mile or less from the open sea.

There are comparatively few species of birds in the stunted growth at the upper edge of the Hudsonian zone. Most characteristic, however, is the White-crowned Sparrow which is everywhere common in the small trees and continues to be met with as the trees diminish in size and abundance even until they finally become mere scattered clumps or islands reaching into the lower edge of the Arctic zone. Thus the outpost colonies of one or more pairs of these birds were often found in barren situations where a few small dwarfed clumps of fir and spruce gave a little shelter. Such birds of course found it necessary to extend their feeding grounds into the surrounding Arctic zone, and it seemed evident that at the upper limit of their range they should be considered as inhabitants of that area, although clearly invaders from the Hudsonian zone. In common with the White-crowned Sparrows, the Tree Sparrows also inhabit the stunted growth at the upper edge of the Hudsonian area which they appear to choose in preference to the thickets of taller trees in less exposed situations.

The more extensive tracts of small trees up to fifteen feet in height are the home of numerous other characteristic Hudsonian birds. White-winged Crossbills in small flocks pass occasionally overhead, or make a brief pause among the tops of the evergreens; Redpolls

are common among the low scraggly firs and spruces, or fly about overhead singing. Lincoln's Sparrows occur in small numbers along the edges of open barrens or near swamps, and Fox Sparrows and Alice's Thrushes sing from the fir thickets. Along the courses of streams in the tangles of alder and willow, an occasional pair of Tennessee Warblers is established and Wilson's Warblers delight in similar situations as well as in the low second growth of bushes and young evergreens that follows a clearing of the original forest.

The following fifteen species, found breeding in Labrador, may fairly be considered as typical Hudsonian birds: Willow Ptarmigan, Pigeon Hawk, Richardson's Owl, American Hawk Owl, Hoary Redpoll, Common Redpoll, White-crowned Sparrow, Tree Sparrow, Lincoln's Sparrow, Fox Sparrow, Northern Shrike, Tennessee Warbler, Wilson's Warbler, Ruby-crowned Kinglet, Alice's Thrush.

The northern limits of the so called Canadian zone are difficult to fix in Labrador. A number of land birds that are most common in the Canadian zone extend their range northward (often more or less sporadically as in favored valleys or sheltered places) so that they occur in territory whose inhabitants are for the greater part typical Hudsonian species. The following 22 species represent this class of birds whose range includes both the Canadian zone and more or less, as the case may be, of the Hudsonian: Spruce Grouse, Canadian Ruffed Grouse, Goshawk, Labrador Great Horned Owl, Arctic and American Three-toed Woodpeckers, Labrador Jay, Rusty Grackle, Canadian Pine Grosbeak, Pine Siskin, White-throated Sparrow, Slate-colored Junco, Myrtle Warbler, Bay-breasted Warbler, Black-poll Warbler, Yellow Palm Warbler, Northern Water-Thrush, Winter Wren, Red-breasted Nuthatch, Hudsonian Chickadee, Golden-crowned Kinglet, Olive-backed Thrush. Of these the White-throated Sparrow, Junco, Myrtle, Bay-breasted, and Yellow Palm Warblers, Water-Thrush, Winter Wren, Red-breasted Nuthatch, Golden-crowned Kinglet, and Olive-backed Thrush are more Canadian in their tendency and do not appear to go much farther north than the southernmost part of the Labrador peninsula, while others, as the Spruce Grouse, Goshawk, Labrador Jay, Rusty Grackle, Canadian Pine Grosbeak, and Black-poll Warbler extend more into the Hudsonian zone and occur over much more of the small tree growth.

The following 11 species are more typically Canadian, and barely reach the southern portion of Labrador, where they occur in favor-

able localities more especially toward the southwestern portion of the peninsula, and the region about Lake Mistassini: Saw-whet Owl, Northern Hairy Woodpecker, Olive-sided Flycatcher, Yellow-bellied Flycatcher, Purple Finch, American Red Crossbill, Magnolia Warbler, Black-throated Green Warbler, Canadian Warbler, Black-capped Chickadee, Hermit Thrush.

In a very general way, the latitude of Hamilton Inlet may probably be taken as the northern limit for the Canadian species of birds, though a few such as the Rusty Grackle and Pine Grosbeak extend their ranges much beyond this. On the other hand, most of the species that are strictly limited to the Canadian zone do not come quite so far as this.

The intermingling of these species of the Hudsonian and Canadian zones was well shown by our experience at St. Lewis Inlet near Battle Harbor. Here we found Redpolls, White-crowned Sparrows, Lincoln's Sparrows, Black-poll, Wilson's, and Tennessee Warblers, and Alice's Thrush, as well as White-throated Sparrows, and Hermit Thrushes. The strong-flying, wide-ranging American Robin was also a common bird here.

In addition to these land birds that are characteristic breeding species, there are others that occur occasionally as stragglers in the southern part of Labrador, having come from still farther south, and whose general northern range is limited by the Transition zone. Such are the Marsh Hawk, Belted Kingfisher, Northern Flicker, Nighthawk, American Crow, Song Sparrow, and Cedar-bird. The presence of these birds, however, is more or less irregular or accidental.

MIGRATION.

The coastwise migration of many of the waterfowl of Labrador is of interest. Dr. Grenfell has described the "ceaseless stream of birds" passing south during the last of October near Battle Harbor. "Long solemn streams of eider ducks, leisurely, and more graceful clouds of gulls, more bustling companies of auks and guillemots, and all the while fringes of fussy murrelets" (Dovekies). These birds appear to follow along the coast to the southern shores of Labrador and the Gulf of St. Lawrence, or even farther, to the Nova Scotia waters. The amount of ice along shore determines largely whether the ducks, gulls, guillemots, and auks stay during the winter in south-

ern Labrador. As long as there are stretches of open water near shore they can obtain food, but when the bays and inlets are frozen and the ice floes become more or less solid for miles from land, the birds are forced to keep farther south.

Bell ('83, p. 54) describes the fall migration to the west of Labrador in the following words: "On Hudson's Bay in autumn, the geese, ducks, plover, etc., come from the north, and also gather from either side, and fly southward along each line of shore, congregating in large numbers where these two meet at the head of James' Bay, from which they fly so as to pass eastward of Lake Superior." Doubtless many of the water birds that reach the St. Lawrence River basin in Ontario, during the fall migration, come by this route, overland from James Bay.

The immense numbers of Eskimo Curlew that formerly migrated to the south and east shores of Labrador before departing over sea for the Antilles and South America are elsewhere mentioned, as well as the migrations of the ptarmigan from the interior to the southern coast of Labrador.

Regarding the spring migrations there is comparatively little known. Audubon mentions the arrival of the Loons on the south coast, that had apparently come directly across the Gulf of St. Lawrence. The passage of the Brant from the southern shores overland to the polar seas is said to be accomplished at a single flight. Cartwright speaks of the flights of ducks in early spring looking for water and the great flocks of eiders in the spring migrations are described by him and by Stearns.

An interesting wanderer is the Snow Bunting that passes south in great numbers from the far north during fall. This is a bird of strong flight but appears often to be carried out to sea by the northwesterly gales and is known to reach even the Azores. That many of the smaller land birds do cross the full breadth of the Gulf of St. Lawrence in their spring and fall migrations seems to be indicated by the observations recorded by Trumbull ('05). It is not clear, however, to what extent the presence of small birds crossing this wide stretch of water is accidental.

In addition to the migration of many of the land birds to more southern climes in winter, there is some evidence of a more restricted movement on the part of the hardier species, from the interior or northern part to the coast of southern Labrador. Thus the Labra-

dor Jay and the Hudsonian Chickadee, perhaps also the Pine Grosbeak, have been observed moving in fall in a definite migratory way, but the extent of these movements is quite unknown.

ORNITHOLOGICAL HISTORY — ORNITHOLOGISTS.

Although Audubon was the first ornithologist to study the birds of Labrador, there is much of ornithological interest to be found in the writings of an earlier explorer of this region. George Cartwright, Esq., published in Newark, England, in 1792, three quarto volumes entitled: "A journal of transactions and events during a residence of nearly sixteen years on the coast of Labrador, containing many interesting particulars both of the country and its inhabitants not hitherto known. Illustrated with proper charts." The abundant bird life of his times is vividly portrayed in the accounts of the flights of Curlew in the fall, the great numbers of ducks and geese, murre, and gulls crowding the islands and furnishing the polar bears and Cartwright's company with many feasts of eggs. Some of these notes will be entered later in the annotated list, but it is of interest to mention here that Cartwright describes the capture of a Great Auk. He also speaks several times of shooting *pie'd* ducks, but there is of course considerable doubt as to whether the now extinct *Camptolaimus labradorius* is referred to, although there are reasons to believe that this is the case. The names he uses for other wild fowl, as Whabby for Red-throated Diver, Hound for the Oldsquaw, Tinker for the Razor-billed Auk, and Bull for Dovekie are still employed on the coast.

Cartwright's chief places of residence in Labrador were at Cape Charles at the eastern end of the Straits of Belle Isle, and at Sandwich Bay the present site of the Hudson's Bay company's post of Cartwright. He arrived at Labrador in July, 1770, and left it for the last time in the summer of 1786.

The earliest definite ornithological investigation of the Labrador fauna was made by the illustrious Audubon.¹ He departed on a long-contemplated trip to this region from Eastport, Maine, on June 6, 1833, on the schooner *Ripley*, commanded by Captain Emery. His party, all young men under twenty-four years of age, consisted

¹ The observations made by Sir John Richardson and recorded in his "Fauna Boreali-Americana" (1829-1837) were all made in the regions to the north and west of Hudson Bay. They are therefore outside of the Labrador region.

of his son, John Woodhouse Audubon, Dr. George C. Shattuck and William Ingalls of Boston, Thomas Lincoln of Dennisville, Maine, and Joseph Coolidge. They sailed through the Strait of Canso, visited the Magdalen Islands, and passed Bird Rock, white as snow with Gannets. The *Ripley* came to anchor in American Harbor, Labrador, near the mouth of the Natashquan River, on June 17th. From this point they cruised easterly along the southern coast of Labrador, touching at Little Mecatine, Baie de Portage, and Bras d' Or. They spent nearly two months in Labrador and sailed for home on August 11, 1833.

Audubon's southern blood was chilled by the rough climate, and his spirits were depressed by the ruggedness and desolation of the scenery. He accomplished an immense amount of work, however, rising at three o'clock, and drawing often for seventeen hours almost continuously in the crowded, wet, and usually very unsteady cabin. Here he was obliged to protect his work from the water which dropped from the rigging, as there was no window to the cabin and the only light was admitted through the hatches. He was often wet to the skin, chilled by the cold, pestered by the innumerable flies and mosquitoes, frequently seasick and worn by the long hours without sleep. He attributes his fatigue to none of these, but exclaims: "No! No! It is that I am no longer young." He found the sea birds breeding in great numbers on the islands, observed the actions of the piratical "egggers," and witnessed the great flight of Eskimo Curlew. He added a new species to science in the Lincoln's Sparrow, named by him after his young companion, Tom Lincoln.

His "Journal" states that "twenty-three drawings have been executed, or commenced and nearly completed." Among these are the drawings of the Loon, Puffin, Pomarine Jaeger, Arctic Tern, Gannet, Common Cormorant, Eskimo Curlew, Willow Ptarmigan, Labrador Gyrfalcon, Horned Lark, White-winged Crossbill, Redpoll, Lincoln's Sparrow, Pipit, Hudsonian Chickadee, and Ruby-crowned Kinglet. Seventy-three bird skins were prepared, mostly by his son John. Besides the plates, the results of this Labrador trip are given in frequent references in Audubon's written works.

Audubon recorded many birds for southern Labrador that are unknown there today. Some of these are now more northern, others more southern in their distribution. In the case of some of the fly-catchers and other poorly marked birds it is probable that he was

mistaken in his identification, but we cannot believe that he made an error in the case of other birds such as the Oyster-catcher, Least Tern, or Black-throated Loon. It seems probable that some of these birds were on the frontiers of their breeding grounds in southern Labrador and that as the numbers of birds were diminished by the agency of man, the species as a whole withdrew its outposts and the more favorable central portions of its range were alone utilized. For example the Least Tern which Audubon found breeding in Labrador, also formerly bred on the Massachusetts coast north of Cape Ann but is not found now north of Cape Cod. In a similar way the Black-throated Loon is not now known to breed in southern Labrador, but Audubon found it preparing to breed in that part of the peninsula.

In the summer of 1849, Dr. Horatio R. Storer with his brother F. H. Storer, and Dr. Jeffries Wyman, explored the southern coast of Labrador from American Harbor to Red Bay. They were there from July 20th to September 25th. Dr. Storer published in the *Journal of the Boston society of natural history* the results of his studies on the Labrador fishes. His manuscript journal, kindly lent us through his son Dr. Malcolm Storer, contains several interesting observations on birds which are noted elsewhere in this paper. Dr. Storer's bird skins were unfortunately largely destroyed by the dampness of the climate.

Dr. Henry Bryant studied the birds of the Bay of St. Lawrence in the summer of 1860, visiting Bird Rock and the southern coast of Labrador from the Romaine River on the west to Chateau on the east.

Dr. Elliott Coues visited Labrador in the summer of 1860 in order to procure specimens of birds and eggs for the Smithsonian institution. He arrived at Sloop Harbor on the southern coast about the 3d of July. Leaving there on the 6th, he proceeded directly to Esquimaux Bay, where the greater part of the summer was spent. He was at Rigolet for a few days. On August 15th, he sailed to Henley Harbor on the Straits of Belle Isle and remained there two weeks before sailing for home.

A. E. Verrill, in 1861, studied the natural history of the Bay of St. Lawrence, particularly the island of Anticosti. He extended his observations, however, to the limits of Labrador, visiting the Mingan Islands from July 4th to July 11th.

In the summer of 1862 the late N. Vickary, of Lynn, went to Labrador, but published nothing on the subject.

Dr. A. S. Packard visited Labrador in 1860 and in 1864, as will be noted later.

W. A. Stearns spent two summers and one whole year in Labrador, his explorations being confined to the southern coast. The two summer months of 1875 were spent within a radius of 60 miles southwest and 10 miles northeast of Bonne Esperance. He stayed from September, 1880, to September, 1881, at Bonne Esperance and explored the coast from Mingan to Red Bay; in July and August, 1882, he again visited the Labrador coast sailing from Boston in a sloop. He touched at various points between Bonne Esperance in the Straits of Belle Isle and Triangle Harbor a few miles south of Hamilton Inlet.

Ludwig Kumlien did not actually visit Labrador, but he has recorded some interesting observations made while skirting its coast on his voyage to and from Greenland. He sailed north from Newfoundland in 1877, going through the Straits of Belle Isle on August 18th. On August 22d he was off Cape Mugford. His return trip was made in October, 1878, along the northern coast of Labrador and the eastern coast of Newfoundland.

William Brewster, in 1881, while exploring the Bay of St. Lawrence and Anticosti, reached the southern coast of Labrador at the Mingan Islands. He was at these islands from July 17th to July 22d.

Lucien M. Turner appears to have been the first ornithologist to reach northern Labrador. He was in Labrador from June 15, 1882, to October 3, 1884, and he stayed at Fort Chimo on the shores of Ungava Bay from August 6, 1882, to September 4, 1884. His ornithological notes, including a list of the birds, were first published in 1885.

In 1891, A. S. Packard republished this list bringing it up to date by notes written by Dr. J. A. Allen. Professor Packard spent the summer of 1860 on the southern Labrador coast near the mouth of the Esquimaux River. In the summer of 1864 he joined the party of William Bradford, the marine artist, and explored the coast in a schooner from Henley Harbor to Hopedale. On the return trip he sailed along the Straits of Belle Isle as far west as Caribou Island. Although he devoted himself chiefly to the geology and marine invertebrates, he has recorded many interesting observations on the birds.

M. Abbott Frazar spent the summer of 1884 on the southern Labrador coast, arriving at Esquimaux Point on May 15th. From here he went to Wolf Bay near Cape Whittle, reaching this place June 10th. He devoted himself to the collection and study of the sea birds and their eggs. He returned to Esquimaux Point the first week in September and left there for home a week later.

Dr. Robert Bell in the summer of 1884, in the course of the Canadian geological survey, skirted the coast of Labrador from the Straits of Belle Isle to Cape Chidley. The expedition entered Hudson Bay and proceeded as far as York Factory, returning by the same route. He gives a nominal list of the birds observed.

William Palmer and Frederic A. Lucas, in July and August, 1887, visited the southern coast of Labrador between Black Bay and Mingan Islands in the United States fish commission schooner *Grampus*.

In the summer of 1891, between July 13th and September 7th, an expedition organized by Bowdoin college explored the coast from Red Bay to Hopedale. Two of the party pushed up Hamilton Inlet about 300 miles. The expedition brought back ninety-five specimens representing thirty-two species. These were studied and the results published in a paper by Arthur H. Norton, in May, 1901.

Between 1892 and 1895, the interior of Labrador was explored by the Canadian geological survey under the leadership of A. P. Low and the birds were studied and reported on.

In 1892 and in 1897, J. D. Sornborger spent some months at Nachvak. He has not yet published the results of his studies there.

In the summer of 1900, July 13th to September 26th, Henry B. Bigelow accompanied the Brown-Harvard expedition which studied the Labrador coast from Belle Isle to Nachvak. He spent a month from August 13th to September 11th at Port Manvers.

The latest published ornithological report referring to Labrador is by the Rev. C. W. G. Eifrig entitled: "Ornithological results of the Canadian '*Neptune*' expedition to Hudson Bay and northward, 1903-1904." This report is based on specimens and notes furnished by A. P. Low and A. Halkelt of the expedition. Still more recently the Rev. Mr. Eifrig has published a few more notes on the same subject and Low's report on the *Neptune* expedition has just appeared (Low, '06).

BIRD AND EGG DESTRUCTION.

Before the arrival of the white man, the Indian, the Eskimo, the fox, and the polar bear levied contributions on the multitudes of birds nesting along the coast. These contributions of eggs and young were comparatively small in amount and probably had little effect on the numbers of the birds. In the day of Cartwright more systematic efforts were made, yet the number of eggs taken was still comparatively small. Thus on June 16, 1776, he records: "After breakfast I went in a skiff with two of the people to Swallow and Middle Islands; we killed nine eider ducks, one black-duck, and a gull, and gathered five hundred and six eggs. Five hands went after dinner to Beaver and Speckled Islands; they killed nine ducks and gathered five hundred eggs; and the skiff which I sent out yesterday returned this morning with twelve ducks, a lord [*♂ Histrionicus histrionicus*], and seven hundred and twenty-six eggs."

On July 6, 1776: "Proceeded to Egg Rock where they killed six ducks and two pigeons, and gathered two hundred and fifty eggs. This is the fourth time that this rock has been robbed this year, and we have taken in all, about a thousand eggs off it, although it is not above a hundred and fifty yards long, and fifteen broad." And again on June 18, 1786, he took from the Duck Islands "eighteen eider ducks and above a thousand eggs." On June 17, 1777, a female polar bear and cub were shot on Ledge Island and he says: "On examining the paunches of the bears they found them well filled with eggs. I had often heretofore observed that all the nests upon an island had been robbed, and the down pulled out; but I did not know till now how those things had happened."

Audubon, in 1833, was filled with horror and disgust at the destruction that was then going on. The following is from his Labrador "Journal" for June 21, 1833, written at American Harbor:

"We ascertained to-day that a party of four men from Halifax took last spring nearly forty thousand eggs, which they sold at Halifax and other towns at twenty-five cents per dozen, making over \$800; this was done in about two months. Last year upwards of twenty sail were engaged in 'egging'; so some idea may be formed of the birds that are destroyed in this rascally way. The eggers destroy all the eggs that are set upon, to force the birds to lay again, and by robbing them regularly they lay till nature is exhausted, and few young are

raised. In less than half a century these wonderful nurseries will be entirely destroyed, unless some kind government will interfere to stop the shameful destruction." And again at an island near Cape Whittle on June 28, 1833, Audubon found two eggers gathering the eggs of Murres. "They had collected eight hundred dozen, and expected to get two thousand dozen. The number of broken eggs created a fetid smell on this island, scarcely to be borne."

Among the episodes, published in his "Ornithological biographies," Audubon wrote a highly dramatic one on this subject, entitled, "The eggers of Labrador," parts of which are here quoted. He describes a shallop with a crew of eight men. "There rides the filthy thing! The afternoon is half over. Her crew have thrown their boat overboard; they enter and seat themselves, each with a rusty gun. One of them skulls the skiff towards an island for a century past the breeding place of myriads of Guillemots, which are now to be laid under contribution. At the approach of the vile thieves, clouds of birds rise from the rock and fill the air around, wheeling and screaming over their enemies. Yet thousands remain in an erect posture, each covering its single egg, the hope of both parents. The reports of several muskets loaded with heavy shot are now heard, while several dead and wounded birds fall heavily on the rock or into the water. Instantly all the sitting birds rise and fly off affrighted to their companions above, and hover in dismay over their assassins, who walk forward exultingly, and with their shouts mingling oaths and execrations. Look at them! See how they crush the chick within its shell, how they trample on every egg in their way with their huge and clumsy boots. Onward they go, and when they leave the isle, not an egg that they can find is left entire. The dead birds they collect and carry to their boat. Now they have regained their filthy shallop; they strip the birds by a single jerk of their feathery apparel, while the flesh is yet warm, and throw them on some coals, where in a short time they are broiled. The rum is produced when the guillemots are fit for eating, and after stuffing themselves with this oily fare, and enjoying the pleasure of beastly intoxication, over they tumble on the deck of their crazed craft, where they pass the short hours of night in turbid slumber. . . . The light breeze enables them to reach another harbour a few miles distant, one which, like the last, lies concealed from the ocean by some other rocky isle. Arrived there, they re-act the scene of yesterday, crushing every egg they can find. For a week

each night is passed in drunkenness and brawls, until, having reached the last breeding place on the coast, they return, touch at every isle in succession, shoot as many birds as they need, collect the fresh eggs, and lay in a cargo. . . .

“With a bark nearly half filled with fresh eggs they proceed to the principal rock, that on which they first landed. But what is their surprise when they find others there helping themselves as industriously as they can! In boiling rage they charge their guns, and ply their oars. Landing on the rock, they run up to the Eggers, who, like themselves, are desperadoes. The first question is a discharge of musketry, the answer another. . . .

“The Eggers of Labrador not only rob the birds in this cruel manner, but also the fishermen, whenever they can find an opportunity; and the quarrels they excite are numberless. . . . These people gather all the eider down they can find; yet so inconsiderate are they, that they kill every bird that comes in their way. The eggs of Gulls, Guillemots, and Ducks are searched for with care; and the Puffins and some other birds they massacre in vast numbers for the sake of their feathers. So constant and persevering are their depredations that these species, which, according to the accounts of the few settlers I saw in the country, were exceedingly abundant twenty years ago, have abandoned their ancient breeding places, and removed much farther north in search of peaceful security. Scarcely, in fact, could I procure a young Guillemot before the Eggers had left the coast, nor was it until late in July that I succeeded, after the birds had laid three or four eggs each, instead of one, and when nature having been exhausted, and the season nearly spent, thousands of these birds left the country without having accomplished the purpose for which they had visited it. This war of extermination cannot last many years more. The Eggers themselves will be the first to repent the entire disappearance of the myriads of birds that made the coast of Labrador their summer residence, and unless they follow the persecuted tribes to the northward, they must renounce their trade.”

Dr. H. R. Storer entered in his journal on July 23, 1849, the following interesting note: “In the afternoon I started in the Englishman’s whaleboat with part of his crew for the Egg Islands [near American Harbor] . . . It was very rough and we had some difficulty in landing. When we did, however, I was amazed at the immense number of birds here breeding — we found in places the eggs so thickly

strewn that some care was necessary to avoid treading upon them — and to procure birds it was only necessary to knock them upon the head as they stumbled past. Tiger [the dog] dug out many Puffins, whose eggs I speedily appropriated, and after I had filled my collecting box I was glad to leave a place where such wholesale murder is daily committed. Although such great quantities of eggs are carried away or destroyed by the eggers, it seems as if the number of birds could hardly have been larger than at present.” He refers to these birds as Murres, Razor-billed Auks, and Puffins.

Again on July 23, 1849, at the Island of Great Mecatine, he says: “In the harbor we had now entered we found one of the Labrador eggers so much talked off — a small schooner from St. John’s, Newfoundland, with a piratical-looking crew. She had just completed her cargo, only twenty hundred dozen eggs! and was to return home the next day.”

In 1884, Mr. M. Abbott Frazar found the sea birds much diminished in numbers owing largely to the “eggers.” To the Halifax eggers he attributed the decrease of only one species, namely, the Murre, and he describes at some length their proceedings. “But,” he goes on to say, “the fishermen should be held responsible for the greatest general destruction. During the fishing season every bay and sheltered place will have its proportion of from one to twenty fishing schooners anchored there for protection. During the week the men are all busy out in their dories fishing, but their Sundays are their own and are generally spent on the islands gathering eggs and shooting birds, and they stop at nothing but shoot everything which flies whether eatable or not, and shoot just for the sport they find in destruction; and as they keep it up during the whole season the poor birds have but a slim show.”

Barnston, writing in 1861, recounts the slaughter of geese of several species by the natives of Hudson and James Bay. Canada, Snow, and Blue Geese gathered in vast numbers at the southern shores of Hudson Bay in both spring and fall; and upon these birds the inhabitants, Indians, whites, and Eskimos, depended for much of their sustenance. Barnston estimated the total yearly kill of geese in southern Hudson Bay at from 74,000 to 80,000, of which about three quarters were taken in the fall of the year. He “would place the Moose Indians as killing, at all seasons, 10,000; Rupert’s River natives, 8,000; Eastmain and to the north, including Esquimaux, 6,000”

which represent roughly the numbers killed by the Labrador natives. Brant are less molested, as they keep farther out from shore.

In Canadian Labrador the laws against shooting the nesting birds and egging are now fairly well enforced, we were told. Our own brief observations on the small piece of Canadian Labrador we saw, would seem to bear this out. On Newfoundland Labrador, which includes a coastal strip extending from Blanc Sablon on the southern coast easterly to Cape Charles, and thence north along the eastern coast, there seems to be no pretence of bird or egg protection.

It is perhaps natural that the fishermen should consider the eggs and young and even the breeding parents as godsend to eke out their scanty larder. Knowing every rock as they do, along the entire coast, they can easily keep in touch with the birds and rob them of their treasures. At Windsor Harbor we saw six young Great Black-backed Gulls cooped in an ancient wreck, for the purpose of fattening for the pan. Unless some penalty can be imposed one cannot expect a man to pass by a nest full of Eider Duck's eggs, or even leave the fat mother unmolested if he can shoot her. Young or molting ducks are easily caught and make very good eating, and are no doubt a delightful change from the usual course of fish. One of the Moravian brethren at Hopedale spoke to us with great gusto of the delights of an omelette made of Eider's eggs. The Eskimos procure, he said, from two to three hundred eggs of all kinds for them every spring.

There is no doubt but that the Eskimo dogs destroy a quantity of eggs and young birds yearly. The dogs are not fed in the summer and must forage for themselves. We judged by their tracks and signs that the dogs explored great regions of the coast and some distance back from it. The eggs and young of Eider Ducks or even of Pipits and other ground-nesting birds must have but little chance to escape detection. The manner in which Pipits and Spotted Sandpipers flew anxiously about when dogs appeared on the scene, seemed to point to the truth of this theory. We saw them fly at the dogs fiercely, almost hitting them in their desire to drive off the intruders. On going ashore from the steamer for a hasty reconnaissance of the bird inhabitants, we soon learned to expect a dearth of ground-nesting birds if Eskimo dogs were about. On this account, at least, the substitution of the reindeer for the Eskimo dog would be of great advantage.

During the migrations, both spring and fall, the "liveyers" take

large toll of the ducks and other water birds. Even gulls are shot for their flesh as well as their feathers. Ptarmigan are sometimes killed in great numbers and are barrelled for winter use. The Eskimo Curlew, that formerly came in vast flocks every autumn to the coast-wise hills of Labrador, is now all but exterminated there. In the annotated list a full discussion of the diminution in numbers of the Eskimo Curlew is given. (See also under Eider for a suggestion as to the preservation of this species as is now done in Norway and Iceland.)

Single-barrel, muzzle-loading guns are the common weapons used and large charges of powder and shot are the custom. We were told that one hundred and twenty-five ducks chiefly Eiders were picked up at one place near Cape Charles last spring after a volley of five guns. Twenty-five more were picked up the next morning. The fishermen, with whom we talked, made no concealment of the fact that they took all the eggs and killed all the birds that they could. They often took their guns with them when they visited their fish traps.

What is to be the result of all this if nothing be done to stop the destruction? There can be only one result, and this is already shown in places. For example, near Battle Harbor where fishermen are plenty sea birds are very scarce and the same holds good for much of the coast, especially in the vicinity of settlements. It is true that in the deep bays and inlets which are deserted in summer by man, and given over to the flies and mosquitoes, a number of water birds breed comparatively unmolested. Many of the water birds, however, such as Murres, Razor-billed Auks, and Puffins will not resort there but prefer the islands.

It is sincerely to be hoped that the wonderful nursery for water birds in Labrador will not be entirely depopulated, but that sufficient protection for the breeding birds will be given and that speedily, lest it be too late.

ANNOTATED LIST.

Colymbus holboellii (Reinh.).

HOLBOELL'S GREBE.

Rare transient visitor.

According to Stearns ('83, p. 17) this grebe is "not rare in spring and fall" on the southern Labrador coast. He also states that it occasionally breeds, but this may be considered somewhat doubtful. He refers to it in one place as the "Whabby" a name given on the Labrador coast to the Red-throated Diver, as he himself recognizes.

Colymbus auritus Linn.

HORNED GREBE.

Rare transient visitor; possibly breeds.

The only definite record for this bird in Labrador is of a specimen taken at Fort George, James Bay, by R. Bell ('83). Turner speaks of having seen a single grebe "in a tidepool at the mouth of the Koksoak River, September 15, 1882" but he was unable to determine whether it was this species or *C. holboellii*.

Gavia imber (Gunn.).

LOON; "LOO."

Common summer resident.

The Loon is well distributed throughout Labrador, although nowhere very abundant. It is found among the lakes of the interior and along the entire coast of the peninsula, north into Hudson Strait, especially in the deeper fiords and inlets.

Cartwright, on his arrival at Cape³⁷ Charles on July 30, 1770, says: "As none of these people, who were employed in the boats, had ever been in this part of the world before, they were greatly terrified with the continual crying of the loons, believing them to be Indians."

Cartwright records the first Loons in 1775 on April 14th; Audubon speaks of having "witnessed the arrival of some on the coast of Labrador, after they had crossed the Gulf of St. Lawrence, as late as the 20th of June." Various observers agree that they nest exclusively on the borders of the freshwater lakes, large and small, that are so numerous on the mainland. Low and others who have traversed the

peninsula, report the Loon as breeding commonly in the interior, and Macoun records a nest July 25th at Clearwater Lake.

Along the east coast, in the latter part of July we saw Loons frequently flying about in pairs, and on some occasions they were gathered in small flocks of three or four. On July 23, 1906, we saw a flock of six flying past near Makkovik. Mr. Schmitt, one of the Moravian brothers at Nain, told us that the Loon bred in that vicinity early in July.

***Gavia arcticus* (Linn.).**

BLACK-THROATED LOON.

Summer resident, not uncommon in the north, very rare in the south.

Audubon says: "Whilst in Labrador, I saw a few pairs courting on wing, much in the manner of the Red-throated Diver." No nests were found. Stearns says: "Two . . . obtained . . . off the Labrador coast by one of the French priests at Bersimis, one in 1880."

Macoun regards the Black-throated Loon as "occasional on the coast of Labrador but apparently common on the shores of Hudson Bay, where they breed. Male and female and young, nearly full grown, shot on Nottingham Island, Hudson Strait, August 28th, 1884. (*R. Bell*)."
Low ('06) found it very common in the northern parts of Hudson Bay where it nests "on islands or along the swampy edges of ponds not far from the coast." Bell also found them on the East Main coast of Hudson Bay. The record by J. M. Macoun that a few breed at Lake Mistassini may be open to question.

***Gavia lumme* (Gunn.).**

RED-THROATED LOON; "WHABBY."

Common summer resident.

Cartwright describes the "Whabby," as "a water-fowl of the diving genus" and he occasionally shot one with his rifle. He probably referred to this species, for it was so called by Stearns, and the name is used at the present day by the natives to designate it.

The Red-throated Diver is a common bird throughout Labrador. Audubon, Verrill, Stearns, Frazar, and Brewster found it breeding in southern Labrador. Low found it breeding commonly on the upper Hamilton and Koksoak Rivers, and it was common along the

shores and islands of Hudson Bay and Hudson Strait. Turner found it breeding plentifully at Ungava. Eifrig found it at Cape Chidley. It nests in tussocks along ponds or on islets and lays two eggs. Bigelow states that it nests by small ponds inland and that it appears on the coast after the young are able to fly. Some individuals may, however, be found there throughout the summer. It begins to breed in southern Labrador early in June and leaves the country when the ice begins to form. At Nain, according to the Rev. Mr. Schmitt it breeds early in July.

We saw only four of these birds in the Straits of Belle Isle near Battle Harbor on the 10th and 12th of July, and five between Double Island and Nain on July 21st. All of these appeared to be adults.

***Fratercula arctica* (Linn.).**

PUFFIN; "PAROQUEET."

Abundant summer resident along the southern and eastern coast.

The Puffin or "Paroqueet" as it is universally called in Labrador breeds in colonies on islands along the southern and eastern coasts. Turner says it is not known to enter Hudson Strait. Audubon found fresh eggs on June 28th and young in the nest at Paroqueet Island near Bradore on August 12th.

H. R. Storer visited Paroqueet Island (near Bradore) on August 18, 1849. He says in his journal: "We found the island completely undermined by the Puffins, every inch of soil and every cranny in the rocks taken possession of. Audubon says that more Puffins breed here than on all the rest of the coast — however that may be we found an immense number as well as of the Razor-bills. Got some birds and a few eggs."

Coues in 1860 met with many thousands of Puffins breeding on the Paroqueet Islands in Esquimaux Bay, and found eggs nearly ready to hatch on July 25th. Brewster observed a large colony of many thousands on Paroqueet Island near Mingan Harbor.

Stearns says of Puffin at Greenery Island near Blanc Sablon: "There could easily have been a multiple, and not a small one of ten thousand. . . . They make a harsh, rasping sound, not unlike the filing of a saw. . . . Though they appear in large numbers at stated times, they disappear, or rather disperse after breeding, almost as suddenly as they came, yet stragglers do not leave until the harbors are blocked up with ice."

Palmer says: "At the Mingan group these birds breed only on an islet near Mingan or Bald Island, and on the little group of islets to the westward called Perroquet Islands."

Frazar records a large colony—about 1000—nesting at Wolf Island near Cape Whittle. Of the thousand nests, he found twelve with two eggs. Macoun says they breed at Gannet Island.

Norton ('01, p. 142) from an examination of specimens brought back by the Bowdoin college expedition, finds that the Labrador birds "differ perceptibly from the European birds in having the outline of the culmen less convex—descending directly from the base of the culmen to its tip—and in having the eminentia symphysis in relation to the base of the tomia farther back. The bill is heavier in appearance, being relatively shorter and deeper. The mandible is in the average deeper, and the keel of the gonys much thicker." Temminck described the American bird under the name of *Mormon glacialis*. Norton concludes therefore that "it is evident that *glacialis* of Temminck is the American subspecies which if not worthy of recognition, must make his *glacialis* a synonym of *arctica*."

As will be seen by the table, we met with Puffins all along the Labrador coast but especially in the Straits of Belle Isle near Bradore. Here on August 3d, between 5 and 6.30 A. M., we passed within a mile of Paroquet Island going in and out from Bradore. The island is somewhat over an acre in extent, composed of soft red Cambrian sandstone, which is elevated to the height of 20 or 30 feet with a small cliff on the seaward side. Puffins were to be seen flying about the island in large numbers. Many were sitting on the rocks of the shore below the cliffs, others occupied the flat top of the island. The surface of the water all about was dotted with them. Singly and in groups of two or three,—very often the latter number,—and in larger flocks of seven or eight these birds were flying straight away from the island, generally close to the water. Others were returning close to the water or at an elevation of 50 or 60 feet each with a capelin hanging from its bill. There were at least 500 of them, perhaps many more.

As observed from the steamer all along the coast, Puffins generally allowed of close approach. After dipping its head nervously into the water several times, a bird would either fly away with difficulty, splashing along the water some distance in its endeavor to rise above it, or it would flop out its wings and dive, using its wings under water for subaqueous flight. Occasionally the two actions were combined

in rapid succession. Thus a bird would dive to reappear in a few seconds flying, only to flop down and fly below the water again. The red bill and red feet show conspicuously both in flight and in swimming. The gray patches like spectacles about the eyes, the dark ring about the neck, the stout chubby build, small black wings, and black backs are all good field marks.

Cepphus grylle (Linn.).

BLACK GUILLEMOT; "SEA PIGEON"; "PIGEON"; "PITSULAK" (Eskimo).

Abundant summer resident along the entire coast.

The Black Guillemot breeds on rocky islands in deep clefts in the rock where it lays one or two eggs, well protected by their position from the hand of man or the jaws of Eskimo dogs. It apparently prefers the clefts in the ancient metamorphic rocks of the eastern coast to those in the softer sedimentary rocks of the southern coast, although it is common there in localities.

Macoun has eggs from Big Island collected on June 20th, and from Ungava Bay on July 9th. Robert Bell found it everywhere on the Hudson Bay coast.

Cartwright (1792, vol. 1, p. 233) speaking of an Indian fishing for salmon says: "He had the skin of the leg of a sea-pigeon, which is scarlet, fastened on the shank of a cod-hook, tied to a cod-line. This he threw by hand down the stream, and played it in the same manner as we do a fly."

The Eskimo women are said formerly to have cut off the red feet of this bird, withdrawn the leg bones, and then filled the inflated skins with reindeer tallow, to provide a confection.

We found the Black Guillemot one of the commonest and most universally distributed of the waterfowl along the eastern coast, but with the exception of a few near Battle Harbor, we saw only one in the Straits of Belle Isle. On our trip north from Battle Harbor to Nain we counted 464 birds of this species and 563 on the return.

Mr. Schmitt at Nain has found their eggs in the middle of July.

Cepphus mandtii (Licht.).

MANDT'S GUILLEMOT.

Summer resident.

The exact status of this species and its relation to the abundant *C. grylle* are somewhat doubtful. It is generally supposed to be

more northern in its distribution than *grylle* but Frazar ('87, p. 2) obtained a specimen taken on its nest near Cape Whittle in southern Labrador. Turner says it "occurs in Hudson's Strait occasionally only, according to my own observation. Plentiful on the eastern coast of Labrador. Specimens procured at Fort George by Drexler, July 17, 1861." Low ('06) found it "common everywhere in Hudson Bay and in smaller numbers northward."

As there seems to be no way of distinguishing this species from *grylle* in life, we considered all the Black Guillemots we saw as belonging to the latter species.

Uria troile (Linn.).

MURRE; "TURRE."

Common summer resident in southern part, a few winter.

The Murre is still common locally on the south and east coasts of Labrador where it nests in colonies on certain islands. When Audubon visited the southern coast of the peninsula in 1833 he found an immense colony breeding on the Murre Rocks near Great Mecatina Harbor, and he gives an account of the destructive work of the Nova Scotian "egggers" at whose hands the birds were under constant persecution. In 1884, William Brewster recorded a colony at Paroquet Island, near Mingan Harbor, and Stearns speaks of the bird as then abundant and breeding in vast colonies on the islands, especially to the south of Esquimaux River. Frazar, in 1887, found them "common but rapidly diminishing" along the southeast coast. Bigelow, in 1900, found them "fairly common to Hamilton Inlet" and was told of a colony at Eclipse Harbor, slightly farther north.

The form of this species known as *U. ringvia* occurs with the other murre in the Labrador colonies. Audubon in his "Journal" (p. 372) speaks of drawing a female at American Harbor on June 20, 1833; Norton ('01, p. 146) records two taken at Herring Islands on August 22, 1891; and there is a male in the Bangs collection taken at L'Anse au Loup, on July 1, 1899. Verrill ('62, p. 143) in writing of the birds of Anticosti, estimated that about one half of the Murres breeding there represented this phase. It is interesting to recall in connection with the supposed specific distinctness of the *ringvia* birds, the statement of S. H. C. Müller ('62) that it "is certainly only a variety of *Uria troile*. I have been an eye-witness that a Ringed and a Common Guillemot have paired themselves together, and besides have seen a *ringvia* feed a young one which a *troile* had under its wing."

Although most of the Murres retire farther south in winter, a moderate number remain in the patches of open water off the southern coast and Low records that in the open water of Hamilton Inlet they were common until January 20th in 1894.

We saw but very few Murres on the Labrador coast, namely, one near Hawke's Harbor on July 16th, and ten near Indian Tickle on July 17th.

***Uria lomvia* (Linn.).**

BRÜNNICH'S MURRE.

Common summer resident, a few winter.

This species occurs with the preceding species in colonies on the south and southeast coasts, but continues farther north into Hudson Strait, where Turner obtained breeding birds. Eifrig ('05, p. 235) also found it common all through this strait and Low ('06) adds that it breeds in great numbers at Cape Wolstenholme, and remains in the open water of Hudson Bay throughout the winter. Coues, in 1860, recorded that great numbers were breeding in early July at Murre Rocks, a few miles north of the harbor of Little Mecattina. He says: "The birds at this date [July 6, 1860] were breeding on the islands by tens of thousands; their number was truly incredible, and yet I was informed that these were rather fewer than usual."

Mr. Schmitt at Nain stated that they bred there early and in the middle of July.

***Alca torda* Linn.**

RAZOR-BILLED AUK; "TINKER"; "TURRE"; "GUDDS" (Stearns).

Common summer resident; a few winter.

The Razor-billed Auk still breeds, in much diminished numbers, however, on the numerous rocky islands that line the southern and eastern Labrador coast. Turner states that it was not observed in Hudson Straits, and we have no records for it on the western coast. Kumlien says it "was seen on many occasions and often in close proximity to the ship from the outer islands of the middle Labrador coast to Frobisher Straits."

Audubon in his "Journal" records the first of this species out of the egg about July 4th. Cartwright records, on February 11, 1779, that "during the whole of the winter season, small holes, like ponds, are kept open on one side or other of most of the outer islands (by the set of the wind) to which these birds resort for food." He occasionally

found them frozen inland or on the ice. Cartwright's definition of "Tinker" is: "A sea fowl. 'Razorbill'—Pennant."

The immense numbers of these birds on the southern coast in Audubon's time are attested in his accounts and have been already referred to under "Bird and egg destruction." Stearns says: "At the Fox Islands, off Kecarpin River they are very abundant....I noticed them in thousands about several other small islands also, and am informed by the inhabitants that this species was always very abundant about this locality." Unfortunately at the present day the rapacious fishermen have played havoc in their ranks. We saw about two dozen only along the southern coast, but in the vicinity of Battle Harbor not a bird of this species, and scarcely a gull was to be seen. Only the cautious Black Guillemots that hide their eggs in rocky clefts and keep themselves out of gunshot flourished. Between Battle Harbor and Nain fiord north we saw about 84 Razor-billed Auks, and about 47 on our return south. We saw about 25 flying around an island between Holton and Cape Harrison, and about 40 near a high rocky island a little south of Nain. The "thousands" of bygone years are no more!

In flight the birds sway from side to side like all the Alcidae and they generally fly thirty feet or so above the water, not skimming close to it like the Black Guillemot and Puffin. They are distinguished from Murres in flight by their short neck, and from Puffins by their larger size and the absence of the gray patch on the side of the head. As they fly away, they show white on either side of a black median line, while the Puffin shows a continuous black back. Swimming on the water, they sometimes cock their tails at an angle of about 45°. On the rocky ledges they sit bolt upright displaying their white breasts.

Mr. Schmitt at Nain told us they laid their eggs there early and in the middle of July.

[*Plautus impennis* (Linn.). GREAT AUK; "PENGUIN."—Extinct. The last Great Auk seen alive was in 1852. In 1853, the dead body of one was found floating in the waters of Trinity Bay, Newfoundland. Like the Gannet at the present day, it is probable that the Great Auk bred in only a few chosen places, chief of which was Funk Island, lying 32 miles off the north-east coast of Newfoundland, and although the bird may have bred on the Labrador coast we have no evidence of it, either from history or from the presence of egg shells or bones, such as have been found in numbers at Funk Island. However, there is no doubt but that the bird, if not a resident, was formerly a frequent visitor to the Labrador coast.

An erroneous Labrador record was published on the authority of Alfred Lechevallier by Ruthven Deane (*Amer. nat.*, vol. 6, 1872, p. 369) viz: that one was found dead near St. Augustine on the coast of Labrador, in 1870. This was discredited by J. E. Harting (*Zoologist*, ser. 3, vol. 8, 1884, pp. 141, 142).

As all contemporary references to this extinct bird are of great interest, we quote the following from Cartwright's Labrador "Journal," although all the records are at some distance from the Labrador coast (Cartwright, 1792, vol. 1, p. 155). "We were about four leagues from Groais Island [Newfoundland] at sun-set, [August 5, 1771] when we saw a snow standing in for Croque. During a calm in the afternoon, Shuglawina went off in his kyack in pursuit of a penguin; he presently came within a proper distance of the bird, and struck his dart into it; but, as the weapon did not enter a mortal part, the penguin swam and dived so well, that he would have lost both the bird and the dart, had he not driven it near enough the vessel for me to shoot it." "This day [June 10, 1774] we saw the first penguin and several bulls [Dovekies]." This latter was in long. 48°, 42' W., and lat. 51° 45' N., during a voyage from England (Cartwright, 1792, vol. 2, p. 7). His account of Funk Island is classical and prophetic, and was written on July 5, 1785 (Cartwright, 1792, vol. 3, p. 55). "Funk Island is a small flat island-rock about 20 leagues east of the island of Fogo, in the latitude of 50° north. Innumerable flocks of sea-fowl breed upon it every summer; which are of great service to the poor inhabitants of Fogo; who make voyages there to load with birds and eggs. When the water is smooth, they make their shallop fast to the shore, lay their gang-boards from the gunwale of the boat to the rocks, and then drive as many penguins on board, as she will hold; for, the wings of those birds being remarkably short, they cannot fly. But it has been customary of late years, for several crews of men to live all the summer on that island, for the sole purpose of killing birds for the sake of their feathers, the destruction which they have made is incredible. If a stop is not soon put to that practice, the whole breed will be diminished to almost nothing, particularly the penguins; for this is now the only island they have left to breed upon; all others lying so near the shores of Newfoundland, they are continually robbed. The birds which the people bring from thence, they salt and eat, in lieu of salted pork."

It is to be noted that Cartwright says that Funk Island is the only place where the "Penguins" bred. It seems hardly probable that they would have been driven off their breeding places on the Labrador coast in his day if any such existed, and it is equally improbable that he would have failed to find any such or to record them in his valuable "Journal."]

Alle alle (Linn.).

DOVEKIE; "TURRE"; "LITTLE BULL"; "BULL-BIRD"; "ICE-BIRD."

Abundant transient and winter visitor.

Cartwright in his "Journal" (1792, vol. 2, p. iii) says: "Bull. A small sea bird. I believe it is called the ice-bird." This bird breeds north

of Labrador and Audubon was probably misinformed when he states: "The cod-fishers assured me that they frequently breed there." He himself did not see any. Stearns says they are "abundant certain seasons. Occasional all along the coast," and ("Bird life in Labrador"): "From October 15 until the ice sets in, I found these little fellows common." Turner found them "common in Hudson Strait" and on December 19, 1882, a specimen was taken 100 miles up the Koksoak River. "Occurs in myriads along the eastern shore of Labrador. Breeds plentifully in certain localities not visited by me." Low reports that they were very common in Hamilton Inlet till January 20, 1894. Numbers were found frozen in bushes along the edge of open water. More recently, Low ('06) found them not common during winter in Hudson Bay, but rare in the summer. Bigelow saw one on September 18th off Cape Harrison. Mr. Schmitt, the Moravian brother at Nain told us that he not uncommonly saw this species in summer.

We saw none on the Labrador coast, but at Flower's Cove, Newfoundland, across the Straits of Belle Isle, on July 9th, a bird that was crippled by the loss of one foot swam up to the steamer's side and was captured by the mate with a bucket. The specimen (coll. C. W. Townsend, no. 1204) is a female in much worn summer plumage. Its crippled condition undoubtedly accounted for its presence so far south at this season. Its occurrence on the coast in winter is of course determined by the ice or rather by the presence of open water. If there is no open water, water birds are not found.

Megalestris skua (Brünn.).

SKUA; "SEA-HEN."

Accidental visitor.

There is but one record for this species on the Labrador coast. Turner (in Packard, '91, p. 438) states that one was "seen near the vessel, sitting in the water off the north side of the Strait of Belle Isle, June 22, 1882." Low ('06) speaks of having seen this bird in the eastern part of Hudson Strait.

Stercorarius pomarinus (Temm.).

POMARINE JAEGER; "BO'S'N."

Common summer visitor; probably breeds in northern part.

Audubon saw some Pomarine Jaegers "not far from shore" at

about forty miles from Little Mecattina, and in early August noted twenty or thirty in Bradore Harbor during a heavy gale. Stearns records a specimen from near the mouth of the Esquimaux River, Palmer saw a few in the Straits of Belle Isle, and Kumlien found them abundant from this point to Hudson Strait. It is not unlikely that this and the following species will be found to breed in northern Labrador.

Jaegers occur off shore in some numbers along the Labrador coast in summer. More often we found them in pairs or less frequently in small scattered groups of from four to seven or ten. The first birds seen on our trip were off Cape Harrison on July 19, 1906, and after that we noted them almost daily until our return south to Battle Harbor at the end of July. A number were in the black phase. We saw none in the Straits of Belle Isle.

The Jaegers were readily distinguished by their easy gull-like flight with frequently a short sail on set wings which curved sharply down. They were constantly chasing one another, as well as the gulls and even the shearwaters.

***Stercorarius parasiticus* (Linn.).**

PARASITIC JAEGER.

Common summer visitor; perhaps breeds in northern part.

This species occurs along the coast with the preceding in summer and like it, is not known to breed in Labrador. It appears to be less common, however, than the Pomarine Jaeger. We saw several birds whose smaller size seemed to indicate that they were *parasiticus* while on our way along the east coast, and Coues, Brewster, and Bigelow also mention it as observed by them off the southern and eastern shores.

***Stercorarius longicaudus* Vieill.**

LONG-TAILED JAEGER.

Rare summer resident.

Off the Labrador coast this bird appears to be less common than the preceding two species in summer, but is known to breed in the northern part of the peninsula. Coues ('61) noted a few at sea on the south coast in July, and Brewster saw one July 20, 1881, near Min-

gan Harbor. In Ungava Bay, in the northern part of the peninsula, Turner ('85, p. 252) obtained a specimen in the early part of July and saw several other birds, and Macoun ('00, p. 30) records an egg of this species from George River, Ungava, taken by J. Ford, in 1896. Two other eggs, thought to be those of the Long-tailed Jaeger, were obtained from the Eskimo at Cape Chidley, Ungava, in 1903, by Eifrig ('05, p. 235). We saw nothing of this bird during our stay on the coast.

Pagophila alba (Gunn.).

IVORY GULL; "ICE PARTRIDGE."

Common winter visitor.

Audubon says: "Old and young [Kittiwakes] leave the coast of Labrador at the first appearance of winter, or when the Ivory Gull reaches that country. This, however, I know only from hearsay, having received the information from a settler at Bras d'Or, who has lived here many years, and . . . was in the habit of . . . shooting the Ivory Gull when it arrived over his harbour in the month of December." Low reports that one was shot at Rigolet in winter, and that the bird was seen in late December at Northwest River. Macoun says that it was seen by Low on Hudson Bay near Great Whale River in the spring and winter and Low ('06) adds that "occasional birds of this species are seen in the early summer among the heavy ice on the Atlantic coast of Labrador and in Hudson Strait."

Dr. Mumford, Mr. Frank Lewis, and others at Battle Harbor told us of shooting "Ice Partridges" which came with the ice and seals in November or December. They stay for about two weeks or a month and then depart, not to be seen again for a year. At times they are very abundant and even fly about the houses. These birds are shot for food and are often obtained in the following manner: about a gallon of seals' blood is poured on the ice near the rocks, and as the birds hover about they are easily shot. Some of the birds in their eagerness to obtain the blood dash themselves with such force against the ice as to kill themselves.

We obtained from the Eskimos at Hopedale the skin of an immature Ivory Gull shot the previous winter at that place. On showing the skin to our informants at Battle Harbor, they all agreed it was their "Ice Partridge."

***Rissa tridactyla* (Linn.).**

KITTIWAKE; "TICKLER."

Abundant summer resident.

The Kittiwake is abundant during the summer all along the southern and eastern coasts of Labrador. Turner says it is rare in Hudson Strait but records one seen over 100 miles up the Koksoak River on October 13, 1883. He says it "breeds plentifully on northern portions of the Atlantic coast of Labrador." The birds seen in the Straits of Belle Isle and along the southern coast probably come from Anticosti for Verrill and Brewster found them breeding there in great numbers. A. P. Low found them common on the edge of the ice at Great Whale Bay but "not very common in the northern part of Hudson Bay."

We saw Kittiwakes in large numbers along the coast, but saw no breeding places. It seems probable that most of the birds on the eastern coast breed on the lofty cliffs to the north of Nain. On July 10th we saw a flock of 200 near Blanc Sablon; on July 16th, 6 birds near Frenchman's Isle; on July 17th, 5 near Pack's Harbor; on July 18th, a flock of 5000 at the mouth of Hamilton Inlet; on July 19th to 21st from Holton to Nain we saw 466 Kittiwakes. On the return we saw between 2000 and 3000 Kittiwakes between Nain and Pack's Harbor; none between Pack's Harbor and Battle Harbor; about 2500 in the Straits of Belle Isle. The large flocks were of exceeding grace and beauty. At Hamilton Inlet thousands of Kittiwakes covered the water, and, as we steamed on, they rose in bodies of five hundred or more and whirled about like gusts of snow driven by the wind, their pure white plumage lit up by the rays of the setting sun. Silent for the most part, they occasionally emitted cries of *kae kae*, or *ka-ake* and at times one could imagine the syllables of *kittiwake*. On our return trip we ran into a flock of nearly the same size near Cape Harrison. The appearance of a snowstorm here was more perfect, for there was a thick fog bank on the edge of which the Kittiwakes played. The sun shining on the birds before the fog shut them out was very striking. They were occasionally plunging for capelins, at times disappearing entirely under water with a splash. One could often be seen flying with a fish hanging by one end from its bill. A Jaeger suddenly appeared on the scene and the twisting and turning of pursuer and pursued was interesting to see. The Kittiwake finally dropped his prey, and the Jaeger settled on the water to pick it up.

Larus glaucus Brünn.

GLAUCOUS GULL; BURGOMASTER; "WHITE WINTER GULL."

Common summer resident in northern Labrador, rare in southern Labrador; a few winter.

Audubon speaking of the southern coast says: "I found this species on the coast of Labrador in very small numbers, all paired, in the month of July." They were very shy and he found no nests. Coues saw but few though he was told there was a colony at Esquimaux Bay. Packard stated that the bird "breeds plentifully on the eastern and southern coast of Labrador." Frazar said: "Occasionally up to the last of May, I would see one of this species, but saw none later than that. Doubt if it ever breeds where I was" (Cape Whittle). Bigelow found the bird common north of Cape Harrison, and particularly abundant at Port Manvers. Young birds appeared in numbers about the end of August. Macoun says that large numbers bred on the cliffs at Richmond Gulf in July, 1898. Low found it "common throughout the interior; seen May 19th; eggs June 14th."

We first met with the Glaucous Gull several miles up St. Lewis Inlet on July 12th. Here we saw two or three with a flock of about 40 Herring Gulls and 15 Great Black-backed Gulls. When first seen they were standing on a ledge of rocks near the water. On our way north from this point we saw a dozen or more of these birds, and the same number on the return trip. We saw none on the southern coast. A pair appeared to be breeding on Sloop Island off Hopedale. On one high crag rising for some hundreds of feet from the sea, near Nain, we saw at least four pairs of these snowy birds, evidently nesting. In each case, one of the pair seemed to be sitting on the nest where a slight ledge made possible a growth of green plants, while near by stood the mate, basking in the afternoon sunlight. Several times we saw them flying about the ice floes or perched on the shelf of an iceberg. Most of them showed the pearl gray mantle of the adult, while several, presumably immature birds, were of a uniform white with a slight but distinct buffy tint and the plumage showed dirty brownish patches in places. They gave the impression of slightly soiled white birds. Their call note which we heard only on one occasion was a sharp *kūk kūk*. Mr. Schmitt at Nain had found the eggs of this species from the end of June to the middle of July.

Larus leucopterus Faber.

ICELAND GULL.

Rare transient or winter visitor.

No definite record of the presence of this species in Labrador has been found, but it is doubtless of general occurrence coastwise in the colder months of the year. Reeks states that it is common in autumn and winter from Greenland to Newfoundland. We found on Great Caribou Island the wing feathers of a white gull, the measurements of which correspond closely to those of the Iceland Gull. The bird had evidently been killed during the previous winter (1905-6).

Audubon, in 1833, "was surprised to find but very few on the coast of Labrador, and these did not seem to be breeding," but it is open to considerable doubt whether Audubon was right in identifying the birds that he saw, with this species.

[**Larus kumlieni** Brewst. KUMLIEN'S GULL.— We have no record for this gull but as it is believed to breed in Cumberland Gulf it doubtless is found as a transient visitor along the Labrador shores.]

Larus marinus Linn.

GREAT BLACK-BACKED GULL; "SADDLE-BACK."

Common summer resident.

These fine birds are found breeding along the entire southern and eastern Labrador coasts; on the Hudson Bay side we have no record of them, and the only interior record is that given by Macoun of an egg taken by A. P. Low on the Hamilton River in 1894.

Cartwright refers to the "Saddle-back," and so long ago as 1833, Audubon found that "the parents were so shy and so wary that none could be shot," and the constant persecution of the fishermen has not served to lessen this wariness during the intervening years. Audubon also adds that they "suck other birds' eggs like Crows, Jays, and Ravens." Audubon caught some young as early as June 18th but according to Coues these gulls are said to arrive in the latter part of May, and eggs are found on the south coast in the middle of June. He speaks of finding young birds on July 4th. Stearns, Coues, and Verrill found this gull common along the southern coast and among the Mingan Islands. Frazar was served at breakfast with the eggs of this species by the people with whom he was staying.

We saw about 43 Great Black-backed Gulls on our trip north, generally scattered pairs or single birds about the rocky islands, but on July 12th we saw a flock of about 15 in St. Lewis Inlet. On the return trip from Nain we counted only 25 until we neared Bradore when as many as 200 were seen flying about our vessel. Mr. Schmitt at Nain had found eggs of this species from the end of June to mid-July. At Winsor Harbor on July 22d we saw four young birds about the size of large pigeons caged in the hull of an old stranded boat, where, as we were informed by the fishermen, they were being fattened for the table. They were fed with capelin, which they swallowed whole.

***Larus argentatus* Brünn.**

HERRING GULL.

Common summer resident.

This is the most abundant gull in Labrador and it is more or less common along the entire coast, and about the large lakes and ponds. Verrill and Palmer record it as abundant at the Mingan Islands, nesting on the ground; Turner states that it is "excessively abundant in Hudson Strait," and Macoun says it breeds along the shores of Hudson Bay.

Audubon relates that at the time of his visit, the young birds were caught by the Labrador fishermen and salted down for winter use. The depredations of the fishermen on this and on other seabirds still continue with the result that these birds are much diminished in numbers at the present day.

We saw only single birds and scattered pairs or small flocks on the Labrador coast except on one occasion when we observed about a thousand Herring Gulls on July 18th at the mouth of Hamilton Inlet. Aside from this we counted only 42 Herring Gulls on our trip north along the southern and eastern coasts of Labrador and about 60 on our return trip.

***Larus delawarensis* Ord.**

RING-BILLED GULL.

Uncommon summer resident locally in southern Labrador.

Colonies of this gull have been found breeding in southern Labrador, but very little has been ascertained in a definite way, concerning the distribution of the species on these coasts. Audubon records

that in a large colony of Herring Gulls that were breeding on a rocky island on the southern coast, a small number had the bill marked with a black ring. Presumably these may have been Ring-billed Gulls. Frazar found a few moderate-sized colonies in the vicinity of Cape Whittle, and refers to their frequently changing location owing to their being so often disturbed. Three eggs was the largest number he found in a nest. According to A. P. Low, these gulls nest at Lake Mistassini and in the vicinity of Hamilton Inlet. Coues records three young of the year shot at Henley Harbor, on August 21, 1860, from a flock of gulls. The most northern record is of a young specimen taken by H. B. Bigelow at Port Manvers (lat. 57° N.) on September 6th.

[**Larus canus** Linn. MEW GULL.— The following is from Audubon's Labrador "Journal" under date of June 18, 1833. "John and Co. found an island [near Little Mecattina] with upwards of two hundred nests of the *Larus canus*, all with eggs, but not a young one hatched. The nests were placed on the bare rock; formed of sea-weed, about six inches in diameter within, and a foot without; some were much thicker and larger than others; in many instances only a foot apart, in others a greater distance was found. The eggs are much smaller than those of *Larus marinus*." Elliott Coues adds the following note after *Larus canus*: "Common Gull. This record raises an interesting question, which can hardly be settled satisfactorily. *Larus canus*, the Common Gull of Europe, is given by various authors in Audubon's time, besides himself, as a bird of the Atlantic Coast of North America, from Labrador southward. But it is not known as such to ornithologists of the present day. The American Ornithologists' Union catalogues *L. canus* as merely a straggler in North America, with the query, 'accidental in Labrador?' In his Notes on the Ornithology of Labrador, in Proc. Acad. Nat. Sci. Phila., 1861, p. 246, Dr. Coues gives *L. delawarensis*, the Ring-billed Gull, three specimens of which he procured at Henley Harbor, Aug. 21, 1860. These were birds of the year, and one of them, afterwards sent to England, was identified by Mr. Howard Saunders as *L. canus* (P. Z. S., 1877, p. 178; Cat. B. Brit. Mus., XXV, 1896, p. 281). This would seem to bear out Audubon's Journal; but the 'Common American Gull' of his published works is the one he calls *L. zonorhynchus* (*i. e.*, *L. delawarensis*), and on p. 155 of the Birds of Am., 8vo ed., he gives the very incident here narrated in his Journal, as pertaining to the latter species. The probabilities are that, notwithstanding Dr. Coues' finding of the supposed *L. canus* in Labrador, the whole Audubonian record really belongs to *L. delawarensis*.— E. C."]

Larus philadelphia (Ord).

BONAPARTE'S GULL.

Common transient autumnal visitor in south.

There is no evidence to show that this species breeds in the Labrador peninsula. The migrants appear to come from the westward of Hudson Bay and in the fall of the year are found in large flocks along the south coast and the east coast south of Hamilton Inlet (Bigelow, '02). Palmer in 1887 found the immature birds "abundant at the mouth of Mingan River, together with a limited number of old birds."

Xema sabinii (Sab.).

SABINE'S GULL.

Rare transient visitor.

Kumlien says: "On the 6th of October, 1877, on the passage from the Kikkerton Islands northward, a pair of these birds kept close to the stern of the schooner for many miles." Turner reports that "a single male was obtained in the middle of July, 1884, near the mouth of George's River, flowing into the eastern side of Ungava Bay." Robert Bell records that one was shot at Port Burwell in September, 1884. In the Bang's collection is a specimen (no. 9740) taken at Okkak in 1894.

Sterna caspia Pallas.

CASPIAN TERN.

Very rare summer resident in southern Labrador.

Audubon in his Labrador "Journal" mentions finding on an island near Little Mecattina on July 18, 1833, the eggs of the Cayenne Tern, and "a single pair of these remarkable birds, which could not be approached." Later, on August 16th, in St. George's Bay, Newfoundland, he notes "several pairs of Cayenne Terns on their way south. The Cayenne or Royal Tern, *Sterna maxima*, is more southern in its distribution than the Caspian Tern, which was unknown to Audubon and could easily have been mistaken by him for the Cayenne Tern. Coues states under this latter bird: "Audubon's Labrador record belongs to *S. caspia*."

More recently Frazar has found this bird in Labrador and he reports as follows: "This majestic Tern is but a sparing resident along the Labrador Coast, as I met with but one colony, which was located about twenty miles to the westward of Cape Whittle, where I found a colony of some two hundred pair mixed with a larger settlement of Ring-billed, and a few Herring Gulls. Their nests were built upon

the ground, and generally contained two eggs, never more." One of Frazar's specimens from Cape Whittle, dated June 24, 1884, is no. 1164, Bangs collection.

[*Sterna forsteri* Nutt. FORSTER'S TERN.—There is an erroneous record by Low ('96, p. 323) who says it is "common throughout the interior; seen June 13, Hamilton River, June 1st Mistassini." We are informed in a letter from Macoun under date of March 13, 1906, that Low referred to the Common Tern.]

***Sterna hirundo* Linn.**

COMMON TERN; WILSON'S TERN; "STEERINE."

Common summer resident in southern Labrador.

Audubon observed it in the "Straits of Belle Isle, May 18, 1833, in great abundance about American Harbor, Labrador. Breeds here." Coues says: "A good many seen at Rigolet but not elsewhere." Macoun records it "common from Moose Factory to Richmond Gulf, Hudson Bay (*Spreadborough*)."

It must of course be remembered that careful scrutiny is necessary to distinguish this bird from the Arctic Tern and it is possible some of the records, especially the northern ones, refer to the latter bird.

***Sterna paradisaea* Brünn.**

ARCTIC TERN.

Common summer resident locally.

Audubon found this bird breeding at American Harbor in June, 1833, and old and young about Bras d'Or harbor on August 5th. Frazar found a few colonies on the small grassy islands near Cape Whittle. Stearns speaks of them as only a spring and fall migrant. Turner says they "breed plentifully on islets in Ungava Bay," and Eifrig says they were taken at Cape Chidley in June, 1903. Macoun records eggs from Green Island, Sandwich Bay. Weiz says they breed at Okkak.

We saw but one tern while we were in Labrador and this was at Bradore on August 3d.

***Sterna antillarum* (Less.).**

LEAST TERN.

Extirpated.

The only record for this tern whose breeding range has rapidly

retreated southward, is that of Audubon ('38, p. 175) who says: "It is to be supposed that it is not met with beyond the western shores of Labrador, where, however, I found it in abundance and breeding, in the beginning of June, 1833," and he obtained specimens.

Fulmarus glacialis (Linn.).

FULMAR.

Common visitor.

Fulmars are very abundant along the north and east coasts of Labrador at times. They are usually met with off the Straits of Belle Isle, northward, in summer, and according to Audubon are "regularly observed in spring moving northward in files" opposite the entrance of these Straits. They appear to enter the Straits rarely, if at all, but keep out to sea, and approach land during storms only. In our voyage along the east coast, we observed them but once, when on July 19th, during a violent northeast storm, a few came about the vessel off Cape Harrison. In all about eight birds were seen, of which but two were in the light phase. The species is not known to breed in Labrador.

Puffinus gravis (O'Reilly).

GREATER SHEARWATER; "HAG"; "HAGDON."

Abundant summer visitor.

This bird, breeding in the Antarctic summer, avoids winter altogether by spending the non-breeding season in the summer of the northern seas. It is found at sea off the southern and eastern coasts of Labrador, rarely approaching very close to land except in storms and fog. In one of the frequent storms of this coast we were so fortunate as to run into a great flock of these birds on July 15th not far from Spear Harbor. As we steamed along we first passed single birds, then groups of from 50 to 300, and later great flocks of 1000. It was impossible to count them but we roughly estimated from five to ten thousand shearwaters. Among them were only three Sooty Shearwaters. It was a rare sight and had a fitting setting in a background of rough and broken granitic rocks, a stormy sea, and scudding drifts of fog. With outstretched and almost motionless wings slightly decurved, the shearwaters glided over the waves, following them so closely, that we momentarily expected to see the birds disappear in the foam. Again they swing about in graceful curves,

turning from side to side, so that sometimes one, sometimes the other wing almost touches the great surges. All their motions on the wing are graceful in the extreme and devoid of any appearance of effort. Again they ride the water lightly in companies of a hundred, or swim rapidly over the surface to seize some delectable morsel, holding their heads up, their wings partly spread. In rising from the water, the birds show less grace, and a large flock makes the water foam as they try to push away the surface, paddling vigorously with alternate feet.

[**Puffinus puffinus** (Brünn.). MANX SHEARWATER.—As this European bird is exceedingly rare on the North Atlantic coast, and as Kumlien makes no mention of the abundant Greater Shearwater, this author's note that the Manx Shearwater is "abundant from Belle Isle to Resolution Island" can be disregarded. There is no other mention of this bird for Labrador.]

Puffinus fuliginosus (Strick.).

SOOTY SHEARWATER; "BLACK HAG" OR "HAGDON."

Common summer visitor.

This shearwater generally accompanies the Greater Shearwater but in much smaller numbers. Palmer found them common in the Straits of Belle Isle, and saw a few as far west as the Mingan Islands. Coues and Bigelow note them on the eastern coast in company with the other species.

We saw one in the Straits of Belle Isle and three in an immense flock of over 5000 of the greater species not far from Spear Harbor.

[**Puffinus tenuirostris** (Temm.). SLENDER-BILLED SHEARWATER.—R. Bell records the capture of one at Port Burwell on September 28, 1884. This was an error. The bird was in fact a Fulmar (J. Macoun *in litteris*, March 13, 1906)].

[**Puffinus kuhlii** (Boie). MEDITERRANEAN SHEARWATER.—Kumlien records this as "common from Belle Isle to Grinnell Bay," evidently a mistake. See note under *P. puffinus*.]

Procellaria pelagica Linn.

STORMY PETREL.

Rare summer visitor.

It is possible that after the breeding season, this species wanders to the American shores more often than is supposed. It is well known to occur off the Newfoundland coasts, but the statement of Reeks

(see Macoun, '00, p. 62) that it breeds on the islands about Newfoundland seems quite without foundation. The only specific record for the Stormy Petrel in Labrador is that of Turner who obtained one in the "middle of July, 1882," twenty miles up the Koksoak River, in Ungava, and saw another seventy miles up that river, October 9, 1882. Possibly these birds had been blown inland by a storm and become lost.

***Oceanodroma leucorhoa* (Vieill.).**

LEACH'S PETREL.

Common summer resident in south.

Bryant saw this species frequently off the southern coast but found it breeding only on Gull Island near Romaine, and on a small island between Mecattina and Bradore. Bigelow speaks of finding it commonly. He says: "We visited several islets where the turf was riddled with their holes and the air reeked with their sharp musky odor." North of Hamilton Inlet Bigelow says it is very rare.

We saw none on the Labrador coast, although a petrel (possibly of this species) was described to us, that flew aboard the vessel one night in southern Labrador, and was captured but afterwards released. Dr. Grenfell told us it breeds at Peter's Island near Henley Harbor.

***Oceanites oceanicus* (Kuhl).**

WILSON'S PETREL.

Common summer visitor.

Apparently this species does not often reach the offshore waters of Labrador in its summer wanderings from the southern hemisphere. Coues and Brewster both observed it in fair numbers in the Gulf of St. Lawrence in July, but the former states that he saw none off the Labrador coast. Turner records that he saw it off the "Atlantic coast of Labrador, . . . mostly in spring and fall," but it is not clear that he distinguished carefully between this and Leach's Petrel. No other observers report it. On Battle Island, we found the wings of a Wilson's Petrel, August 1st, but saw no living birds.

***Sula bassana* (Linn).**

GANNET.

Uncommon summer resident, locally, on southern coast.

Formerly the Gannet was a common bird on the southern coast of

Labrador, although its breeding area appears to have been confined to one locality. Constant persecution has greatly diminished its ranks, although it still breeds in the same places.

Audubon said that the Gannet arrived at Chateau Bay about the middle of May, but he did not find any breeding birds. Bryant, in 1860, said that the Gannet was known to breed at only three places in the Gulf of St. Lawrence, namely, at Bird Rock, at an island near Gaspé,¹ "and at Gannet Rocks near Mingan, which will soon be deserted by those birds in consequence of the depredations of the fishermen."

Coues, in 1860, refers to Gannet Rocks as follows: "On the first of July our proximity to the celebrated Gannet Rocks was clearly indicated by the numbers of these birds seen flying in every direction, engaged in seeking for food, which consists principally or wholly of fish. . . . Again, on the 11th of September, on our return we saw many Gannets; but though on both these occasions we passed within fifty miles or less of the rocks, I was denied the pleasure of observing the birds at their great breeding place."

Brewster, in 1881, visited this same colony near Mingan which he states bred on Paroquet Island. He says it "was despoiled the day before we landed by Indians, who did their work so thoroughly that only empty nests and occasional broken eggs remained to mark the spot where less than a week before we had seen hundreds of birds sitting in fancied security."

Frazar, in 1884, states that with the exception of this colony, there were "no other colonies at least as far as the Straits of Belle Isle." Lucas, in 1887, visited this colony and found "a few Gannets. . . . in spite of the incessant persecution of the Indians who regularly make a clean sweep there."

Near Indian Tickle just south of Hamilton Inlet, is an island which bears the name of Gannet Island. Neither Cartwright nor Coues who were familiar with this region, mentions any Gannets there. We saw a few Gannets on the southern side of the Straits of Belle Isle, but none on the Labrador coast.

Phalacrocorax carbo (Linn.).

CORMORANT.

Common summer resident locally in south.

¹ Byrant inadvertently located this colony at Percé Rock instead of the nearby Bonaventure Island.

On the south coast, colonies of Cormorants still breed, but we find no definite evidence that they do so north of Belle Isle. Audubon, in 1833, found a large colony on the cliffs near Wapatigun, and on the nearby Shag Rocks, off the St. Mary Islands, thousands of both species nested.

In 1860, Bryant visited this colony and estimated the number of breeding cormorants to be from four to five thousand. He thought there were about four Common Cormorants to one of the Double-crested species.

In May, 1881, Stearns visited these Shag Rocks. He speaks of thousands of cormorants. The two species were equally represented. "At a distance these rocks present the appearance of being covered with snow, but a nearer approach shows that this is a covering of guano from the continual droppings of the birds."

What was probably the remnant of this colony is described by Frazar who visited Labrador in 1884. He found about 200 pairs of both species together, and states that many nests contained large young on June 19th, "which went to prove what the natives said, that they commenced to build long before the snows of winter had disappeared." He also mentions finding a set of six eggs in one nest. Another colony was recorded by Stearns at the Mecattina Islands. Weiz ('66) lists the Cormorant as found at Okkak, but no evidence is adduced to prove this. It is certainly rare or even accidental on the northeast coast.

***Phalacrocorax dilophus* (Swains.).**

DOUBLE-CRESTED CORMORANT; "WAPATIGUN."

Common summer resident locally in south.

In general the remarks under the preceding species apply also to this. Both are found nesting together in colonies at certain chosen spots on the southern coast of Labrador. Audubon found large colonies on islands near Great Mecattina and at Cormorant Island, near Cape Whittle. Wapatigun Island, near the latter point, appears to be named after this bird. Frazar who visited this same region in 1884 speaks of the Cape Whittle colony as consisting of but 200 or so pairs of birds, of both species; he also mentions a colony found June 2d, about 75 miles east of Esquimaux Point. We have been unable to find any good evidence to show that this species breeds on

the east coast, but Coues, in 1860, was informed of a colony at Sloop Harbor, just north of Hamilton Inlet. After the breeding season the birds scatter and may be found in small numbers along the southern coast.

Merganser americanus (Cass.).

AMERICAN MERGANSER; GOOSANDER.

Rare summer resident in the interior.

This merganser is not so fond of salt water as its red-breasted cousin, and is rarely seen on the coast. Stearns, however, says that he has "seen one. . . taken near Fort Island" and Palmer says that "one was seen at Mingan." Low says: "Common throughout the interior; seen May 28th; eggs June 25th." He gives precisely the same record for *M. serrator*. Macoun says that "Mr. A. P. Low found it breeding on the shores of small lakes in Labrador; eggs were taken with the bird from under small spruces on the upper part of the Hamilton River, in the summer of 1896." As the habit of the American Merganser is to nest in a hole in a tree or cliff it seems reasonable to suppose that *M. serrator* was confused with this species.

Merganser serrator (Linn.).

RED-BREASTED MERGANSER; "SHELLDRAKE"; "SHELL-BIRD,"

Common summer resident along the coast and in the interior; more common transient visitor.

Cartwright and Stearns both speak of this bird as the "Shell-bird." It is widely distributed both in the interior and along the seacoast. It breeds preferably on the shores of freshwater ponds and rivers. Coues found nearly fresh eggs on July 4th, and Low records eggs for June 25th.

At Mary Harbor on St. Lewis Inlet we observed several of these birds on July 12th and 13th flying back and forth from the salt water to the pond-like expansions of the Mary River. It is probable that they were breeding in the latter locality. They emitted a harsh quacking croak as they flew. These were the only birds of this species we saw in Labrador except one near Cartwright.

Lophodytes cucullatus (Linn.).

HOODED MERGANSER.

Rare summer resident.

Stearns says it is "rather rare but occasional." Macoun says that a pair was seen by Spreadborough in the interior of Labrador on July 16, 1896.

Anas boschas Linn.

MALLARD.

Rare transient visitor.

According to Cooke the Mallard breeds west of Hudson Bay and also in Greenland. In Labrador it is found only as a migrant. Packard mentions specimens from Davis Inlet and from the mouth of the Koksoak River and says it is "rare at Fort Chimo. Common on eastern and more plentiful on southeast coast." Coues saw a pair offered for sale by one of the natives.

Anas obscura Gmel.

BLACK DUCK.

Common summer resident.

It is of course impossible to separate most of the records of *obscura* from those of *rubripes*, a subspecies established by Brewster in 1902. Examples of both forms have been obtained from Labrador. Here a general account of the species in Labrador will be given without attempting to subdivide it.

The Black Duck breeds throughout Labrador, more commonly away from the coast, on the shores of inland ponds. Cartwright shot one in Sandwich Bay, containing a hard egg on May 28, 1778. Mr. Schmitt at Nain told us they bred in that vicinity from the end of June to mid-July.

Audubon found them incubating in Labrador June 17, 1833, and with young on July 5th. Brewster said they bred along the coast near Mingan. Frazar found a few breeding on the islands near Cape Whittle. Palmer found them abundant at Mingan. Coues says it "breeds very plentifully" but is more common away from the coast. Half-grown young were seen with parents on August 1st. Low found them not common throughout the interior. They were seen May 1st on the upper Hamilton River and eggs found on May 23d. Spreadborough found them breeding in northern Labrador on July 7, 1896, but not commonly. Packard says it is "not common in Hudson Strait. Doubtless breeds there." Wallace in the "Lure of the Labrador Wild" speaks of seeing Black Ducks as late as October

2d north of Hamilton Inlet. Again he says ('07, p. 434): "From the day we entered the George River [Sept. 14, 1905] until we were well down the stream they were plentiful. . . . This is apparently a breeding ground for them."

We obtained the skin of a typical *obscura* from the Eskimos at Hopedale. The bird was undoubtedly killed in that vicinity. We have presented the skin to Mr. Brewster in whose collection it now is. Brewster ('02, p. 187) says that a female in the Bangs collection taken in the Straits of Belle Isle on April 25, 1900, must be referred to *obscura*. "Another, belonging to Mr. J. D. Sornborger, which, with her brood of ducklings, was captured on July 8, 1896, at Okkak, on the north-eastern coast of Labrador, is intermediate in certain respects between *obscura* and *rubripes*, but on the whole perhaps nearer the former."

Anas obscura rubripes Brewst.

RED-LEGGED BLACK DUCK.

Common summer resident.

See remarks under *obscura*. There is only one specimen of this form from Labrador, namely, one taken at Ungava by Turner on July 1, 1884. One from Okkak is intermediate as already noted. A good deal can be said in favor of the view that Red-legged Black Ducks are merely old Black Ducks (see Townsend, "Birds of Essex County," pp. 127, 128).

Mareca americana (Gmel.).

BALDPATE; AMERICAN WIDGEON.

Rare transient visitor in southern Labrador.

Stearns says it occurs "as far as Natashquan; said to occur inland at Esquimaux River" and, "a single female of this species was shot in Old Fort Bay on November 27, 1880. . . . Said to breed." Packard says: "Mr. John Ford assures me it is common in Hamilton Inlet and on the southeast shore of Labrador." "Widgeon" is a name so loosely applied to various species of ducks that the last record at least is of very doubtful value.

Nettion crecca (Linn.).

EUROPEAN TEAL.

Accidental visitor.

This is a straggler from the Old World, for which there are two Labrador records. The first is that of Coues ('61, p. 238) who states that he "was so fortunate as to procure a well characterized specimen" on July 23, 1860. He does not mention the locality. Norton ('01) records the skin of a male which was obtained in 1891 by the Bowdoin college expedition, near Eskimo Island, Hamilton Inlet. It was purchased of a half-breed Eskimo woman by whom it had been prepared.

***Nettion carolinensis* (Gmel.).**

GREEN-WINGED TEAL.

Rare summer resident.

Cooke states that the "regular breeding range extends from New Brunswick, through northeastern Quebec and Newfoundland, to Ungava Bay, Labrador, latitude 58°". Turner records that "fully-fledged young females were obtained at Fort Chimo late in July." Coues saw a skin in a collection at Rigolet. Frazar mentions two specimens which had been killed "early in September" from a bunch of six, near Esquimaux Point. Further than these there are no exact records for Labrador.

***Querquedula discors* (Linn.).**

BLUE-WINGED TEAL.

Very rare summer resident in northern Labrador.

The only record is that of Macoun ('00, p. 83) who states that a pair, evidently breeding, was found July 11, 1896, by Spreadborough, at Clearwater Lake in latitude 56° N. The principal summer home of this teal is the interior of North America between the Rocky Mountains and the Great Lakes (Cooke).

***Spatula clypeata* (Linn.).**

SHOVELER.

Accidental visitor.

We are enabled to add this species to the list of Labrador birds on the evidence of Dr. W. T. Grenfell who stated that he shot two specimens near Cartwright in September, 1901.

Dafila acuta (Linn.).

PINTAIL.

Very rare transient visitor.

The only records are the following. Turner records a female young of the year taken at the mouth of the Koksoak River and an adult at Davis Inlet. Presumably both are fall records. Stearns records the capture of one specimen of a pair seen at Old Fort Island, and adds that another was taken near the same place a short time before.

We obtained the skin of a young male prepared by the Eskimos at Hopedale and saw the skin of another. Both birds were believed to have been taken the previous autumn.

[**Aix sponsa** (Linn.). WOOD DUCK.—Stearns ('83) states that this duck is "not rare in the interior" of Labrador, but it seems doubtful if this report is based on good evidence.]

Aythya americana (Eyt.).

REDHEAD.

Very rare transient visitor.

This duck is probably a rare fall migrant to the coast of Labrador. None have been reported by those who have penetrated to the interior of the peninsula. The only definite record is that of Stearns who saw one on September 23, 1880, at Baie des Roches on the southern coast. Cooke ('06, p. 42) says: "An individual was taken in the fall in southeastern Labrador." He perhaps refers to this record.

Aythya marila (Linn.).

GREATER SCAUP DUCK.

Rare summer resident in northwestern Labrador.

According to Macoun ('00), a few were observed by Spreadborough in James Bay and in the interior of Labrador in 1896, and a set of six eggs was taken June 16, 1896, near Whale River on James Bay. The only record for the east coast is that of a specimen shot near Nain in October, 1899 (Bigelow, '02). Dr. R. Bell gives the Lesser Scaup Duck as breeding in large numbers on Nottingham Isle in Hudson Strait and at Churchill and York Factory in Hudson Bay, but as Macoun says, it is more probable that the birds were *A. marila*.

[*Aythya affinis* (Eyt.). LESSER SCAUP DUCK.— Dr. Robert Bell's ('83) record of the breeding of this species in Hudson Strait probably refers to *A. marila*.]

***Clangula clangula americana* (Bonap.).**

AMERICAN GOLDEN-EYE; "WHISTLER"; "WHISTLE-DIVER."

Common summer resident in central and southern parts.

The Golden-eye breeds along the large streams and lakes of the interior of Labrador from the upper Hamilton River, southward. Farther north, Spreadborough saw none in the barren regions of the upper part of the peninsula in crossing from Whale River to Fort Chimo. Doubtless the birds are confined in summer to the timbered portions of stream beds owing to their choice of hollow trees as nesting sites. Low saw them at Lake Mistassini on May 3d, and found a few flocks in June on the upper Hamilton River. Brewster saw a large brood of young accompanied by what was probably a female of this species, near the mouth of Mingan River, July 20th. The Bowdoin college expedition, on August 9, 1891, came upon a female and brood of young supposed to be of this species, some 200 miles up Grand River, Hamilton Inlet. They were originally reported as Labrador Ducks! In autumn the Golden-eye is common on the coast and doubtless remains until driven south by the closing of the bays.

***Clangula islandica* (Gmel.).**

BARROW'S GOLDEN-EYE.

Rare transient visitor and summer resident.

According to Turner who obtained specimens from Davis Inlet, it is "plentiful" in fall on the coast. Stearns records it from the south coast where it is said to occur in Esquimaux River in mild winters. Cooke states that "a few breed in eastern Canada from the Gulf of Saint Lawrence (Point des Monts) to northern Labrador (Davis Inlet)." Merriam states that it breeds at Point des Monts (outside of Labrador) but we have not found any record of breeding birds in Labrador except this record of Cooke.

***Charitonetta albeola* (Linn.).**

BUFFLE-HEAD; "SLEEPY DIVER."

Rare transient visitor.

Stearns says this duck is a common migrant in the fall on the south

coast. No other observers have recorded it. Cooke says: "Undoubtedly some pairs breed in Quebec and southern Labrador, though it is as yet unrecorded from there. . . . except as a rather rare visitant."

Harelda hyemalis (Linn.).

OLD-SQUAW; "HOUNDS"; "COC-CAW-WEE."

Common summer resident.

Besides spending the summer commonly, especially in the northern parts, the Old-squaw is an abundant transient visitor, and a few winter in patches of open water off the southern coast, if such occur.

Cartwright, in 1770, describes this species as follows: "HOUND. A water-fowl rather larger than a teal. These birds migrate to the north in large flocks in the spring, and as they fly, make a continual noise, than which nothing can more resemble the cry of a pack of beagles when in chase. When, and how they return to the south again I am unacquainted." Gurdon Trumbull in "Names and portraits of Birds" published in 1888, gives as one of the synonyms of this bird, "HOUND, a name applied in Newfoundland (the musical gabble of a flock being likened to the cry of hounds)." We found the name "Hound" still in common use along the Labrador coast.

Cartwright gives May 16th at Sandwich Bay for the date of arrival of Old-squaws in 1776, which means simply that open water appeared about that time.

On July 28, 1833, Audubon found several broods of Old-squaws on a large freshwater lake at Bradore, but it is doubtful if many breed there at the present day owing to constant persecution by the natives. Frazar ('87) observed it at Cape Whittle as a migrant only, and saw none after the first week of June. In Ungava, Turner found it breeding, Weiz ('66) gives it as breeding at Okkak, and a pair was seen in June, 1896, by Spreadborough, at Cape Jones, Hudson Bay. Low ('06) found it very common in the northern parts of Hudson Bay; it breeds "on the islands of the ponds."

Mr. Schmitt at Nain told us that the Old-squaw breeds in that vicinity early in July.

Histrionicus histrionicus (Linn.).

HARLEQUIN DUCK; "LORD AND LADY."

Common summer resident in northern, common transient visitor in southern Labrador.

The quaint definitions of Cartwright are worth quoting: "LADY, A water-fowl of the duck genus, and the hen of the lord." "LORD. A water-fowl of the teal kind." These names are still used on the coast for this species.

On July 29, 1770, he enters in his journal: "I shot four eider ducks and seven lords and ladies; the latter being in full moult could not fly, but they were very fat." This was at St. Peter's Islands in the Straits of Belle Isle.

According to Turner, the Harlequin Duck is abundant in Hudson Strait and "certainly breeds at Ungava." It is uncommon on the southern coast and its presence there in winter is probably dependent upon the extent of open water, for Brewster ('84) says that it occurs at Anticosti in winter only, where "hundreds sometimes collect in the tide openings." Stearns found it "rather rare" on the south coast in spring and autumn, but a few immature birds and an occasional adult were found in summer by Frazar about the outer islands and exposed ledges near Cape Whittle. These, however, were not breeding birds. We saw but a single bird on our trip, an immature specimen swimming among the cakes of pack ice near Makkovik. As the vessel passed, it dove several times opening its wings at it went under. In swimming it cocked its tail slightly up.

Mr. Schmitt at Nain said that some were to be seen in that vicinity all summer while Mr. Frank Lewis at Battle Harbor was familiar with the bird during the spring and fall migrations only.

[*Camptolaimus labradorius* (Gmel.). LABRADOR DUCK; PIED DUCK.—Extinct. Very little has come down to us concerning the former presence of this now extinct species in Labrador. Cartwright in his journal probably refers to it when he speaks of having killed "only a pied-duck" on October 26, 1770, at Charles Harbor; and again, under date of July 16, 1771, when he writes: "Killed a whabby [Red-throated Loon] with my rifle, and a pied duck with shot." Again on October 6, 1773: "One of my people killed a pair of pied-birds." Audubon, when he visited southern Labrador in 1833, did not see the Pied Duck, but in his "Journal," writing from Bras d' Or, July 28, 1833, speaks of it as breeding "on the top of low bushes, but the season is so far advanced we have not found its nest." In his "Ornithological Biography" he also states that nests, said to be those of Labrador Ducks, were pointed out to his son on this same date, at Blanc Sablon. When Coues visited southern Labrador in 1860 he was "informed that, though it was very rarely seen in the summer, it [was] not an uncommon bird in Labrador during the fall." This statement is thought by Dutcher (*Auk*, vol. 11, p. 10) to indicate a fall migration northward, though it may quite as well mean

that birds from the interior or even from the heads of inlets moved to the coast in the fall migration southward. Probably, however, the birds were nearly extirpated by the time of Coues' visit, and his testimony is based merely on hearsay. Dutcher also corrects the statement that a female with a brood of young was observed by members of the Bowdoin college expedition in 1891, 200 miles up the Grand River, Hamilton Inlet. The birds were probably Golden-eyes.

There appear to be but three Labrador specimens of this duck extant, according to Dutcher; one in the American museum of natural history, an adult male (no. 3739) from the Wied collection; and a pair formerly in the possession of Sir Joseph Banks that came from Labrador (Latham, Gen. hist. birds, 1804, vol. 10, p. 318).]

***Somateria mollissima borealis* (Brehm).**

GREENLAND EIDER.

Abundant summer resident on the eastern coast and on the west coast of Richmond Gulf, north of Hamilton Inlet; transient visitor in the southern part.

Packard says: "Abundant in Hudson Strait. Eggs, young,.... adults procured in Ungava Bay." It is probably the common breeding Eider on the Hudson Bay coast north of latitude 56°. Bigelow says it is abundant north of Hamilton Inlet on the east coast, breeding near most of the fiords.

At Nain, Mr. Schmitt told us that the eiders bred during the latter part of June and early in July.

Dr. Grenfell tells us that north of Nain, where the summer or "green" fishermen rarely penetrate on account of the ice, the Eider, undoubtedly the Greenland Eider, still breeds in great numbers. On the Metik Islands between three and four thousand Eider's eggs were taken off by a man in 1905. He stated that the man could hardly find a place large enough, free from eggs, to place his sleeping bag. Dr. Grenfell is anxious to employ a keeper for these islands, and says that the down alone would pay his salary. He fears, and with reason, that the advent of steam trawlers would allow the fishermen to penetrate to these regions, and that the birds would be doomed.

***Somateria dresseri* Sharpe.**

AMERICAN EIDER; "SEA DUCK"; "LAYING DUCK"; "SHOREYER";
"ESKIMO DUCK"; "MORGAC" (Indian); "METIK" (Eskimo).

Common summer resident along the south coast and south of Hamil-

ton Inlet on the east coast and of Richmond Gulf on the west coast (Macoun, '00).

The northward range of this species is not fully known. Low ('06) found it "common everywhere in Hudson Bay and to the northward." He speaks of shooting a number of this species and the Greenland Eider at Cape Fullerton at the northwest part of Hudson Bay.

The American Eider has been much more persecuted than the Greenland Eider as its home country is visited every summer by the large fishing fleet, bearing 30,000 egg-loving individuals, from Newfoundland. Besides these most of the 3,000 permanent inhabitants of Labrador live in its breeding range.

The presence of Eider Ducks or indeed of any water bird in winter is dependent upon the presence of open water. This is clearly shown by Cartwright in his "Journal." Stearns also speaks of it. In the Straits of Belle Isle with its strong tides, there are generally a few open places even in midwinter and here Eider Ducks are almost always to be found.

The date of arrival of the Eider Duck in the spring depends on the season. Cartwright, at Cape Charles, notes March 7, 1771, two pairs of ducks; March 23d, "a flock of ducks looking for water"; April 26th, "thousands of ducks flying north." In 1775 he notes that the spring is about three weeks late and he saw the first ducks (King Eiders) at Cape Charles on April 7th.

Stearns says of the American Eiders: "They remain in this region [near Red Bay] until the last waters of the bay freeze over, and are then seen no more until spring returns and thaws the ice, when they appear in company with the King Eider....which are also found in immense flocks, but distinct from, that is not mingling with the others." Again he says: "The King Eider came first, then the Common Eider....The birds at first fly in large flocks often thousands in a flock, and generally the different species do not mingle." (This was about the first week in April.) In another place Stearns speaks of shooting Eiders in the spring from the edge of the ice first on April 12th. The birds are called by whistling and there are often thousands in a flock. Early in October snow and ice appear on the eastern coast. Thus Cartwright, writing at Sandwich Bay on October 11, 1778, says: "Winter begins to appear; the Mealy Mountains have put on their new liveries, and every downfall whitens the heads of the high hills. The deer [caribou] are beating out to the barren

headlands on the sea coast; the Eider, and King-ducks are hastening southward; and the grouse [Ptarmigan] are chattering in great flocks upon the hills,"—a vivid picture, truly! At the same place on October 8, 1783, he writes: "The first flight of Eiders went up the river this evening. As those birds trim the shore along in the flight-times, great numbers of flocks go up this river as high as Friend's Point, and sometimes higher, but on finding their mistake, they commonly return again along the opposite side, . . . in general they keep over salt water."

On May 10, 1771, near Chateau Bay, he records the following interesting observation: "I measured the flight of the eider ducks by the following method: viz. on arriving off Duck Island, six miles distant from Henley Tickle, I caused the people to lie on their oars; and when I saw the flash of the guns, which were fired at a flock of ducks as they passed through, I observed by my watch how long they were in flying abreast of us. The result of above a dozen observations ascertained the rate to be ninety miles an hour." Bryant in 1860 says of the Eider: "Though constantly harassed by the fishermen and inhabitants, [it] still breeds in great abundance along the whole extent of the north shore." On Greenlet Island in the Straits of Belle Isle he found over 60 nests. On this island was a stone hut used "for the purpose of concealing the hunters in the spring, at which time they shoot immense numbers of the Eider or Sea Ducks, as they call them."

We have already given in a previous chapter, accounts of the taking of Eider's eggs on the Labrador coast. The earliest date given by Cartwright for the eggs of this duck is June 3, 1778. On June 12, 1779, he writes: "But the ducks had only scraped out their nests yet." This was in Sandwich Bay. Some of his men, however, found a few duck's eggs the same day.

Eiders are shot in great numbers by the "liveyers" as the ducks pour along the coast both spring and fall. They are less wary than the King Eider and their tameness or stupidity leads to their destruction.

Our experience with Eiders in Labrador was as follows. In the Straits of Belle Isle we saw none on the Labrador side except near Battle Harbor, and about 30 on the Newfoundland coast. In three days, July 11th to 13th, about Battle Harbor and St. Lewis Sound we saw 71 Eiders, some of which we may have counted twice. We saw one in Hamilton Inlet, 38 near Hopedale, and 32 between Double

Island and Nain. On the return we saw much fewer birds, but in the same localities. It is evident that the constant persecution of these birds by the liveyers, summer fishermen, and Eskimo dogs has sadly thinned their ranks. It is also apparent that many of them when driven off from the exposed coast and outer islands continue to breed in lessened numbers in the deep bays and inlets which are shunned by man in summer on account of the flies and mosquitoes.

The Eiders we saw were generally in small flocks, some in male others in female plumage, although once or twice we saw single birds, and occasionally we saw small flocks all in one plumage. Thus we saw a flock of 4 adult males on July 9th; a flock of 18 adult males and 6 brown birds on July 11th; a flock of 7 adult males and 4 brown birds on July 13th; a flock of 11 adult males and 11 brown birds on July 21st. On July 21st off Nain we saw 2 adult males, one apparently adult female and five young, three of whom fluttered along the water seemingly unable to fly. These were probably the Greenland species. The next day we saw four Eiders fly by, the first two brown birds, the third an adult male, and the fourth was evidently an immature male showing white only in the middle of the back and part of the wings. These observations are interesting as it is generally stated that as soon as the eggs are laid the male Eiders flock by themselves at sea. We discovered a field mark of considerable value in recognizing these birds, and with its help we could distinguish this species even when the light was so poor we could not make out the colors. We refer to the characteristic manner during flight in which the bill is held, pointing obliquely downward at a considerable angle, instead of straight out in front as is the case with most ducks.

The Eiders generally flew in Indian file close to the water. The strikingly marked adult males with their black bellies and white breasts, necks, and backs are easily recognized. The female is a great brownish bird, looking very dark in some lights, and entirely lacks distinctive markings. In the sunlight the back of the female looks a lighter brown than the belly. The wings are of the same color as the back. The young looked a lighter brown than their mothers.

In Norway and Iceland the very similar European Eider is thoroughly protected and has become very tame, nesting freely close to the houses. The eggs and down are taken under careful supervision and are the source of considerable profit. The birds are

allowed to rear a few young so that their numbers are not diminished. If the people of Labrador could be made to understand this, a new industry would arise and the Eider instead of being a vanishing race, would again populate the numerous islands along the southern coasts of the peninsula. At present the people are actively engaged in killing "the goose that lays the golden egg."

[*Somateria v-nigra* Gray. PACIFIC EIDER.—Stearns referred to this species as abundant in large flocks. It is of course conceivable that a few western birds may have strayed to the eastern coast and that Stearns shot one or two out of a flock of Common Eiders. The following note on the subject by Leonhard Stejneger ('85) is interesting: "Mr. W. A. Stearns, in a paper entitled 'Notes on the Natural History of Labrador,' published in the 'Proceedings of the U. S. National Museum,' Vol. VI, 1883, says (p. 121) that the *Somateria v-nigra*, the Pacific Eider, is 'abundant in large flocks in spring,' and that he himself 'obtained specimens that had the decided 'V-shaped black mark' on the chin.' The statement has been doubted, and critics have considered it a mild expression when saying that it 'seems to require confirmation.' It is not my intention to defend Mr. Stearns' identification, but having found a notice which seems to point in the same direction, I think it safer to postpone a final decision in the matter. The notice to which I allude is found in Degland and Gerbe's 'Ornithologie Européenne (Paris, 1867), II, p. 557, where, under the head of *Somateria mollissima*, Mr. Gerbe writes: 'Three or four specimens received from Newfoundland had under the throat two black lines similar to those of *Somateria spectabilis*, but of a color less deep. May they not be mules between the latter and the female Eider? Mr. de Sélys-Longchamps, in his second note on the hybrids of the Anatidae, in quoting this example, remarks that Prince Ch. Bonaparte and Mr. W. Jardine consider these specimens as a distinct species, which they name *Somateria v-nigrum*, but that there is occasion to wait for new observations before deciding.'"]

Somateria spectabilis (Linn.).

KING EIDER; "KING DUCK"; "KING-BIRD"; "PASSING DUCK."

Abundant transient visitor; not uncommon summer resident in the north.

The King Eider breeds from Nachvak north. The greater portion breed on the west coast of Greenland. Stearns refers to a breeding record of this species on an island opposite Mingan, an exceptional and rather doubtful southern instance. Macoun records the taking of a set of three eggs of this species at Nachvak by G. Ford in 1897. Low mentions the shooting of one in the interior at Lake Mistassini.

The King Eider is generally an earlier arrival in the spring than the

American Eider. They both fly in flocks, and as a rule the two species do not mingle (Stearns). Under date of April 7, 1775, at Charles Harbor, Cartwright records: "Also one flock of King-ducks, which are the first I have heard of this year." It is found in winter if there is any open water.

We saw only two King Eiders on the Labrador coast. The first was an adult male on the shore at the mouth of St. Louis Inlet on July 13th. As we approached in a sail-boat he waddled down to the water and swam off. His light color and cocked up tail suggested a gull, but with glasses we could make out the characteristic spectacle side-face markings and projection over the bill. In flight he showed dark on his back posteriorly and light wings. In diving he opened his wings for subaqueous flight. The second bird, apparently in immature plumage, was seen between Fanny's Harbor and Nain.

***Oidemia americana* Swains.**

AMERICAN SCOTER; "BUTTER-BILL COOT."

Common transient visitor, rare summer resident.

As all the Scoters are frequently found in summer sometimes in considerable numbers far south of their breeding grounds even to the Massachusetts and Rhode Island coast, it is never safe to record the breeding range of these birds except by the discovery of their nests, eggs, or ducklings. Cooke ('06, p. 59) says of this bird: "The lack of information in regard to the breeding of this species in northeastern North America is surprising. The species was described from the west shore of Hudson Bay, and occurs on the coasts of Labrador and the Gulf of St. Lawrence, but there seems to be no record of the discovery of the nest in this region. Nonbreeding birds are known to occur far south of the breeding grounds. The species is unknown from the whole vast interior of North America, between Hudson Bay on the east and the Yukon Valley on the west, and south almost to the United States boundary; it ranges north to Ungava Bay, Hudson Strait, and Fort Churchill, Hudson Bay, and apparently does not breed south of Newfoundland, nor in Labrador south of about latitude 52°; so that it follows by exclusion that the multitudes of these ducks that winter from the Gulf of St. Lawrence south along the Atlantic coast must breed in northern Ungava.

"The American scoter is much more abundant on the Pacific coast,

and breeds from the Aleutians and Near Island north to Kotzebue Sound and northeastern Asia."

The breeding records of this species that we have been able to obtain for Labrador are few and only one is positive. This is Audubon's record of a nest and eight eggs nearly ready to hatch found a mile inland from the southern coast on July 11, 1833. He says: "A few pairs breed on the shores of Labrador, but the great body of these birds proceed further north." Stearns says it is "abundant. Breeds by inland ponds"; but he gives no evidence of finding the nests. Frazar found a few, apparently not breeding, in summer about Cape Whittle. Coues did not meet with it. Low says it is common as a migrant on the Hamilton River from May 26th into June. Packard records that it is "obtained at the mouth of the Koksoak River. Abundant in Hudson Strait and eastern shore of Labrador, where it is reported to breed sparingly."

The absence of more records of the breeding of this scoter in Labrador would lead one to think that the majority of the migrants on the eastern North American coast nest farther north. The bird is common during the migrations along the Massachusetts coast but less common than the other scoters.

Our experience with the three species of scoters in Labrador was as follows: we saw a flock of 82 scoters of all three species in St. Lewis Inlet near Mary Harbor on July 12th. Of these the White-winged species was by far the most abundant, the American appeared to be next in abundance, the Surf Scoter least. On the same day we saw a flock of 14 American Scoters, and another flock of 30 White-winged Scoters. Near Francis Harbor on July 15th we saw 4 scoters, apparently Surf Scoters. On July 16th near Hawke's Harbor we saw 31 White-winged Scoters, 1 American Scoter, and 8 scoters whose species we could not determine. On July 17th near Cartwright we saw 4 White-winged Scoters and 2 doubtful American Scoters. On the 18th at the mouth of Hamilton Inlet we saw 42 White-winged and 8 apparently Surf Scoters. On the 21st near Hopedale we saw a flock of over 500 mostly White-winged Scoters, although the other species were represented. Near Fanny's Harbor on the same day we saw two flocks of White-winged Scoters each containing about 30 birds. On the return trip we saw very few scoters.

***Oidemia deglandi* Bonap.**

WHITE-WINGED SCOTER; "BRASS-WING DIVER."

Abundant summer resident.

This scoter is abundant in summer as well as in the migrations along the Labrador coast. Audubon found great numbers on the southern Labrador coast in mid-June, but he says that few stay to breed. He found nests June 1st to 10th and young several days old on July 28th. Stearns on the other hand, who found them common in the fall and rare in the spring, says they are not known to breed. Frazar says they are common in summer about Cape Whittle but apparently none breed. Palmer saw several flocks at the Mingan Islands. Coues and Bigelow report them as abundant on the eastern coast and Spreadborough found them abundant from Moose Factory to Richmond Gulf in June, 1896. Audubon's record is the only definite one we can find of the breeding of this scoter.

Cooke ('06, p. 61) says: "This scoter breeds along the north shore of the Gulf of St. Lawrence and north to Nachvak Bay, Labrador, about latitude 59°." Like most sea birds the scoters are not found in Labrador in winter owing to the absence of open water, except occasionally on the southern coast and near the outer islands.

We found this the most abundant of the three scoters as already recorded.

***Oidemia perspicillata* (Linn.).**

SURF SCOTER; "BOTTLE-NOSED DIVER."

Abundant summer resident.

From the time of Cartwright to the present day this bird has been called "Bottle-nosed Diver" by the Labrador men. It is an abundant migrant all along the Labrador coast. It is common there in summer and breeds. Audubon saw "millions" in southern Labrador passing north. A few stayed and he found one nest near Little Mecattina. Neither Stearns nor Frazar found it breeding. Coues found it abundant along the eastern coast "where many breed." Packard says it is "rare in Hudson Strait. Abundant on the eastern coast of Labrador, where it breeds sparingly." Spreadborough found it common from Cape Jones to Richmond Gulf in June, 1896.

Our experience with this bird is related under *O. americana*.

Erismatura jamaicensis (Gmel.).

RUDDY DUCK.

Uncommon summer resident on eastern shore of Hudson Bay.

Macoun states that it breeds "sparingly from Richmond Gulf to Ungava." A female with four young about a week old was taken on June 21, 1896, in northern Labrador by Spreadborough.

[**Chen hyperborea** (Pall.). LESSER SNOW GOOSE.—The record of Eifrig ('05, p. 237): "They breed mostly on islands along the eastern shores of Hudson Bay," refers probably to *nivalis*; *hyperborea* is more western in its distribution than *nivalis*.]

Chen hyperborea nivalis (Forst.).

GREATER SNOW GOOSE; "WAVY"; "KANGOK" (Eskimo).

Very rare summer resident, but common transient visitor on the eastern shores of Hudson Bay.

Packard says: "Occasionally a straggler is seen in the western portion and along the western end of Hudson Strait. Eskimo from the eastern shore of Hudson Bay reported it to be very plentiful during the migration." Macoun records a set of 3 eggs from one of the Twin Islands, James Bay, in 1898, from A. P. Low. Weiz records it from Okkak, but the record is to be doubted. Cooke says that the Greater Snow Goose "is enormously abundant on both the eastern and western shores of Hudson Bay during spring migration."

Chen caerulescens (Linn.).

BLUE GOOSE; "BLUE WAVY."

Common transient visitor on east coast of Hudson Bay; said to breed in northern Labrador.

Nothing is known in a definite way of the breeding of this species in Labrador. George Barnston ('61), formerly of the Hudson's Bay company, has given an account of the geese as observed by him in the southern portion of Hudson Bay. He states that the Blue Geese are found mostly on the east (Labrador) side of Hudson Bay in both spring and fall migrations, and comparatively few are to be observed on the southwest shores. Rae (Can. rec. sci., vol. 3, 1888, p. 136) corroborates this statement.

In regard to the breeding of this goose, he adds that "according to Indian report, a great breeding-ground for the blue wavy is the country lying in the interior of the north-east point of Labrador, Cape Dudley Digges. Extensive swamps and impassable bogs prevail there; and the geese incubate on the more solid and the driest tufts dispersed over the morass, safe from the approach of man. . . . In May it frequents only James's Bay and the Eastmain of Labrador, and it is probably the case that its hatching-ground is on the north-west extremity of that peninsula, and the opposite and scarcely-known coast of Hudson's Straits. In the autumn their bands, increased six or sevenfold by the young, return by the same route."

The region indicated as the breeding ground of the Blue Goose is still, as then, a *terra incognita*. The slaughter of geese of this and other species by the natives of the Hudson Bay shores is mentioned under the heading "Bird and egg destruction."

Anser albifrons gambeli (Hartl.).

AMERICAN WHITE-FRONTED GOOSE.

Accidental visitor.

The only record is that of Bigelow ('02, p. 28): an adult male received from Dr. Heltasche, shot near Hopedale, May, 1900.

Branta canadensis (Linn.).

CANADA GOOSE; "NEKLEK" (Eskimo).

Common summer resident; April 30 to November 25.

The Canada Goose once bred abundantly throughout the length and breadth of Labrador but the depredations of the fishermen along the seacoast have caused it to desert this vulnerable region, and it is now found breeding in the interior only or in the remote north and west. Along the southern and the southern part of the eastern coast it occurs now only as a migrant, but in Cartwright's day it was a common summer resident in these regions. Cartwright has a good deal to say about this species, and we have obtained from his journal a number of interesting records. As to date of arrival he records on May 4, 1775, at Charles Harbor: "I saw a goose this afternoon for the first time. The spring is about three weeks later than usual." In 1776, he records the first geese on April 30th. In 1779, the first geese flew over on May 1st, and in 1786, on May 8th.

As to nesting, the following records are of interest: "Found [May 28, 1771, near Cape Charles] the trap which was lost on Saturday last, with a good, fat goose in it, full of hard eggs." On July 10, 1771, he found a nest of this species with seven eggs in it at Mary Harbor off St. Lewis Inlet. On May 30, 1776, in Sandwich Bay he found two eggs. On June 25, 1774, he caught five young but a few days old. On July 24, 1774, at Cutter Harbor he caught a young goose alive, and saw three broods. He speaks of two geese *in full molt* being killed on July 20, 1775. At Sandwich Bay on July 8, 1776, he records: "The geese are beginning to moult," and again on July 25, 1776: "In the course of our walk to Dove Point, we gathered above a hundred excellent goose quills, which were lately shed, this being the moulting season." On August 26, 1777, he says: "Great numbers of geese have appeared lately, as they are getting the use of their wings very fast now." On November 15, 1775, he saw several geese and on November 21, 1774. On November 25, 1777, he says: "I had an opportunity of shooting at a goose today, although it is very late in the year for those birds to be seen."

Over half a century later Audubon found the Canada Goose still a common summer resident in southern Labrador, breeding in every suitable marshy place. He speaks of seeing several hundred young geese at Great Mecattina killed before they were able to fly and salted for winter use. Their gizzards contained fir leaves. In 1860, Coues did not see any until the second week in August, when several small flocks appeared flying southward. Stearns ('83, p. 13) observed it only as a migrant. Frazar ('87, p. 20) found none breeding in southern Labrador, but heard that one or two pairs bred on a large island off Wolf Bay. Low noted it at Mistassini on May 2d. Weiz ('66, p. 268) records that it breeds at Okkak. Bigelow ('02, p. 28) says it is abundant in the spring and common in fall after August 1st. Palmer ('90, p. 259) records: "A small flock was seen flying southward on August 11 at Mingan." Packard states it breeds along Hudson Strait near the mouth of the George River. Low says it breeds in the marshes throughout the northern interior and he gives the average date of arrival for the Northwest River as May 10th. Macoun says that two eggs were taken on Whale River, Ungava Bay, on June 11, 1896. On July 27, 1905, Wallace came upon two adult and three young geese near Lake Nippisish. The "old ones had just passed through molting, and their new wing feathers were not long enough

to bear them, and the young ones though nearly full grown, had not yet learned to fly."

On August 18, 1902, Hubbard and Wallace, on their unsuccessful attempt to find Lake Michikamau observed two young geese unable to fly. On September 24th, they saw geese flying south.

Mr. Goldsby, one of the Moravians at Hopedale, told us that this goose breeds in the inlets near the Mission and lays its eggs about the first week in June, or even during the last of May. At this time the men go on dog sledges to obtain the eggs. In the middle and latter part of July the Moravians catch the young geese and fatten them for Christmas.

***Branta bernicla glaucogastra* (Brehm).**

WHITE-BELLIED BRANT.

Rare transient visitor.

The Brant breeds far to the north of Labrador and is apparently but rarely seen there during the migrations. Stearns observed it on the southern coast. Turner saw it only in the spring at Fort Chimo. Low says it is very rare in the interior; a sick bird was killed at Lake Mistassini on July 2d. Bigelow says it is reported as very rare. He obtained a specimen from Dr. Grenfell that was shot at Nain in October, 1899. In Hudson Bay also Bell states that it is very rare.

[***Branta leucopsis*** (Bechst.). BARNACLE GOOSE.— This is recorded by Weiz at Okkak, but the record is open to doubt for Weiz reported many Old World birds there, perhaps because he was more familiar with their names. There is no reason, however, why a straggler should not be taken there, and Cooke ('06, p. 82) accepts the record.]

***Olor columbianus* (Ord).**

WHISTLING SWAN.

Very rare summer resident in the northwest part.

Packard says it is "an occasional straggler over the southern portions only of Labrador." Weiz records it from Okkak. Robert Bell says: "The Whistling Swan breeds near Churchill and on the islands towards the eastern side of Hudson's Bay. Their skins constitute an article of trade, but only a small number of them are collected annually."

Cooke states that "a few nest on Southampton and Nottingham Islands in Hudson Bay." The latter island is not far from the north-west coast of Labrador.

[*Olor buccinator* (Rich.). TRUMPETER SWAN.—The statement of Robert Bell ('83) that this species breeds on the islands off the East Main coast of Hudson Bay, doubtless applies instead to *O. columbianus*.]

***Botaurus lentiginosus* (Montag.).**

AMERICAN BITTERN.

Very rare summer visitor.

In all probability the Bittern occasionally breeds on the southwest shores of Labrador as it is well known to do on Anticosti, but no positive evidence on this point has as yet been obtained. Coues found a wing in the possession of a hunter in southern Labrador, and Bigelow speaks of seeing two or three birds at Cape St. Francis, north of St. Lewis Sound. Robert Bell states that this species "is found on both sides of Hudson's Bay."

***Ardea herodias* Linn.**

GREAT BLUE HERON.

Accidental visitor.

This species is a straggler in Labrador, for which we have found but a single record, *viz.*, that of one seen near Whitefish Lake, Fort Chimo, Ungava, by John Saunders of the Hudson's Bay company, in the summer of 1880 (Turner, '85).

***Florida caerulea* (Linn.).**

LITTLE BLUE HERON.

Accidental visitor.

"On May 23, 1900, a Little Blue Heron was brought to Mr. Ernest Doane at Lance au Loup, Labrador, by a man who had shot it there a day or two before. . . . The specimen (No. 4433, Coll. of E. A. & O. Bangs) is a young male just emerging from the white plum-

age, having some blue feathers in the wings, a few long blue black plumes, and the back, neck and head much intermixed with grayish" (Bangs, '00a).

Nycticorax nycticorax naevius (Bodd.).

BLACK-CROWNED NIGHT HERON.

Accidental visitor.

This heron is also a straggler to southern Labrador and has been once recorded from Lake Mistassini, August 6, 1885 (Macoun, '00).

Rallus virginianus Linn.

VIRGINIA RAIL.

Accidental visitor.

The claim of this species to a place among the birds of Labrador rests on none too substantial a basis. The only record is that of Turner ('85) who writes that "a single specimen was taken in Hamilton Inlet a few years ago and submitted to M. Fortesque, esq. (of the Hudson Bay Company), who identified it beyond question."

Porzana carolina (Linn.).

SORA.

Accidental visitor.

Dr. W. T. Grenfell has added this species to the list of Labrador birds, as he secured a specimen in Sandwich Bay in 1898. The skin was sent to Cambridge, England.

Fulica americana Gmel.

AMERICAN COOT.

Accidental visitor.

That this species occasionally strays north into Labrador is attested by Turner who records that a specimen was shot about 1880 on a lake near Nain, and was described so accurately to him by several persons who saw the stuffed bird that he was enabled to identify it "beyond

possibility of doubt." Dr. W. T. Grenfell informed us that he took a specimen of this species at Longstretch, Sandwich Bay, in August, 1899.

Crymophilus fulicarius (Linn.).

RED PHALAROPE.

Common transient visitor off the coast; rare summer resident.

Packard says that this bird is abundant north of Davis Inlet, and that it breeds sparingly in Hudson Strait. One specimen was obtained in Ungava Bay. Coues shot three at sea off Belle Isle from a flock of six. Frazar obtained a fine adult male killed at Cape Whittle on June 25th. Bigelow saw it several times in small flocks off shore.

We saw three on July 20th off Long Tickle. We also obtained the skin of a fine bird in full adult plumage at Hopedale from the Eskimos. Mr. Schmitt at Nain told us that this species as well as the Northern Phalarope breeds in that vicinity.

Phalaropus lobatus (Linn.).

NORTHERN PHALAROPE; "GALE-BIRD."

Common summer resident.

The Northern Phalarope breeds along the entire Labrador coast in freshwater marshes on the borders of ponds and lakes. Audubon found them and their nests on the southern coast. Low saw some on the upper Hamilton River on June 13th. Bigelow states that they breed "in almost all the suitable marshes; occasionally very abundant off shore." Turner found them common and breeding on the islets in Ungava Bay, and Spreadborough found about a dozen on a small pond on an island in James Bay on June 16, 1896.

We had an interesting experience with this species at Great Caribou Island, on July 27th. At the small freshwater pools only a few yards in extent, partly grown up with sphagnum and sedges we saw four of these birds and shot two, both males. It was evident from their actions that young were concealed in the sedges, as they flew about us uttering a harsh scolding twitter, shortened occasionally to a *quip*. This twitter sounded at times sweet like that of a Barn Swallow. At

times a gentle little note like *ee-ep* was emitted. The birds frequently swam about gracefully, nodding their heads like doves. Once or twice they stopped to scratch their heads with a foot, again they would circle about quickly on the water, or they would swim forward and continue their progression by walking up onto a rock. Among the reeds they skilfully threaded their way, bending low their heads.

[**Philohela minor** (Gmel.). AMERICAN WOODCOCK.—Turner ('85) was assured by several persons "that they had killed Woodcocks on the eastern portions of the Labrador shore" but we know of no more positive evidence that the bird actually occurs there.]

Gallinago delicata (Ord).

WILSON'S SNIPE.

Rare summer resident.

Wilson's Snipe probably breeds sparingly in suitable localities throughout Labrador. Turner "heard and saw a male making the peculiar noise with its wings, in early June, over a swamp to the north of Davidson's Lake, a few miles from Fort Chimo," Ungava. Low also saw and heard a male performing its flight song at Lake Petisikapau, on the Hamilton River, on June 28th; Macoun records a bird with a young brood in July, 1896, seen at Great Whale River, Hudson Bay, by Spreadborough. Turner also says that specimens were procured at Rupert House on June 15, 1860. Coues met with the bird but once on the southeast coast and Bigelow saw three or four near Cape St. Francis.

Cartwright records seeing on September 10, 1772, a snipe "which is the first I have seen in this country"; again on September 19, 1775, he says: "Saw a snipe; which is the second that I have seen in the country." This was in Sandwich Bay; the first near Cape Charles.

[**Gallinago major** (Gmel.). GREATER SNIPE.—Coues called attention to the specimen of this species from Hudson Bay in the collection of the British museum but there is nothing to show whether or not it came from the Labrador side of Hudson Bay.]

Macrorhamphus griseus (Gmel.).

DOWITCHER.

Rare transient visitor.

This species may breed in Ungava but the evidence at hand does not prove that it is more than an uncommon migrant on the Labrador coasts. Turner speaks of it as rare at Fort Chimo, and mentions specimens from that place and from Davis Inlet. Coues also obtained an immature bird in southern Labrador on August 23, 1860.

The coast of Labrador is largely rocky, and in most places bold and precipitous. Salt marshes, sand beaches, and even pebbly beaches are few and far between; most of the shore birds, therefore, are not tempted to tarry long on the coast during the migrations.

Tringa canutus Linn.

KNOT.

Uncommon transient visitor.

Stearns found it an uncommon migrant on the southern coast and in his account of "Bird-life in Labrador" records having obtained a specimen on September 30th. Coues also shot a few immature birds after August 21st on the south coast (Henley Harbor) and Palmer secured two females from flocks of White-rumped Sandpipers on the Mingan Islands.

Arquatella maritima (Brünn.).

PURPLE SANDPIPER.

Rare transient and winter visitor.

The only positive record we have for this species is that of Audubon who speaks of shooting specimens at Bradore on August 4, 1833. Turner did not observe them. As they breed in Greenland and remain off the coast in winter if the sea be open, it is probable that they occur more commonly in Labrador than our records would admit. It is possible that they may yet be found breeding in northern Ungava.

***Actodromas maculata* (Vieill.).**

PECTORAL SANDPIPER.

Common autumnal transient visitor.

This species is a common migrant on the east and south coasts of Labrador after the middle of August. It is not known to breed in the peninsula. We obtained the skin of one from the Eskimos at Hopedale.

***Actodromas fuscicollis* (Vieill.).**

WHITE-RUMPED SANDPIPER.

Common transient visitor.

Stearns was probably mistaken in supposing that "a few breed" in southern Labrador, as this species is not known to nest even in Ungava (Turner). The fall migration is under way early in July. Stearns notes a specimen as late as October 8th, on the south shore. We saw two flocks of these birds of twenty or thirty each at Battle Harbor on August 1st and 2d. One of the flocks was waiting quietly for the fall of tide on the weed-grown ledges.

***Actodromas minutilla* (Vieill.).**

LEAST SANDPIPER.

Common summer resident and abundant transient visitor.

Low found the Least Sandpiper nesting commonly on the upper Hamilton River, and Turner supposed that a few might breed about the mouth of the Koksoak River. Audubon found a nest and four eggs in southern Labrador on July 20, 1833, but as he says, this is probably a late date for eggs, since full-grown young in flocks are seen already moving south in the first week of August. Frazar found small flocks "all through the summer" in southern Labrador. Coues states that they were still abundant on the south coast on September 1st. At Battle Harbor, where no birds were found breeding, we saw the first migrant on July 26th, a single bird feeding on the edge of a little pool.

***Pelidna alpina sakhalina* (Vieill.).**

RED-BACKED SANDPIPER; AMERICAN DUNLIN.

Uncommon transient visitor.

Bigelow records "a few at Port Manvers in early September." Weiz ('66) includes it as breeding at Okkak, but this is probably an error.

***Ereunetes pusillus* (Linn.).**

SEMIPALMATED SANDPIPER.

Common summer resident locally; abundant transient visitor.

Audubon found this species nesting in early June in southern Labrador. He also adds this note ('42, vol. 5, 277): "About the period when these birds prepare to return southward, they congregate in large flocks, the young separate from the old. In Labrador this takes place from the beginning to the middle of August." Bigelow found them breeding locally and describes the downy young. Turner notes their breeding at the mouth of the Koksoak River.

We saw only a few migrants on July 27th at Great Caribou Island.

***Calidris arenaria* (Linn.).**

SANDERLING.

Common transient visitor.

The Sanderling has been noted by several observers during the migrations in various parts of the peninsula. Audubon says: "Some young birds were seen at Bras d' Or, in little parties of four or five individuals early in August, and they were already on their way southward"; and Packard says: "Three seen (2 taken) at mouth of Koksoak River." Macoun reports that a pair was seen by Spreadborough on a small island in James Bay, June 16, 1896, and adds, "doubtless breeding." As shore birds occasionally linger on the New England coast on their way north as late as this, and as non-breeding birds sometimes spend the summer considerably south of their breeding range this note should be received with caution.

***Limosa haemastica* (Linn.).**

HUDSONIAN GODWIT.

Very rare transient visitor; July 30 to September 30.

There are only three records of this bird. "Drexler obtained a specimen near Rupert House, July 30, 1860" (Packard, '91, p. 430). Stearns ('90) says that one was shot at Bonne Esperance on September 30, 1880. He states that this was the only one taken on the coast. Again he refers in this same publication to a single specimen taken on September 10th, at Old Fort Island.

***Totanus melanoleucus* (Gmel.).**

GREATER YELLOW-LEGS; WINTER YELLOW-LEGS; "AUNTSARY."

Common summer resident; May 7 to October 19.

Cartwright defines "Auntsary" as "a bird of the wading genus, resembling a redshanks." He shot one on the late date of October 19, 1770, near Cape Charles.

Audubon found it breeding in Labrador in June. Frazar found a pair breeding at Esquimaux Point. Palmer reported it as "very abundant at Mingan." Low says it is "occasional throughout the interior, breeds"; he saw a pair at Lake Mistassini, May 1st. Coues found it "very common along the coast during summer and early fall." Bigelow saw a few late in September at Port Manvers. Turner says: "Not common in Ungava district. Specimens in fall only at mouth of Koksoak River."

We heard the note of one of these birds at Battle Island on August 2d.

***Totanus flavipes* (Gmel.).**

YELLOW-LEGS; SUMMER YELLOW-LEGS.

Uncommon transient visitor.

There are but few records of this bird for Labrador. The fact that it is so extremely rare on the New England coast in the spring while abundant in the autumn, and the fact that it goes north by a more inland route would lead one to infer its absence or great rarity on the

eastern and southern coast of Labrador in the spring. Audubon says he found "a few on the coast of Labrador." Packard reports "one seen Oct. 8, about 50 miles above Fort Chimo on the Koksoak River." Low says: "Seen only after August 1st, on Hamilton River and at Mistassini." On the west coast, however, it is reported in the spring by Spreadborough who saw a number on the shore of James Bay, June 15, 1896.

Helodromas solitarius (Wils.).

SOLITARY SANDPIPER.

Uncommon summer resident.

Packard reports that "one was obtained near Fort Chimo in July whose actions indicated breeding." Spreadborough shot one from the top of a spruce at Seal Lake, northern Labrador, on July 24, 1896. Low says: "Common throughout the interior, especially south of latitude 54°. Breeds. Seen May 27th. Eggs, June 19th."

[**Heteractitis incanus** (Gmel.). WANDERING TATLER.—An erroneous record of this western bird was made by Bell ('83, p. 51): "I obtained a specimen of the Wandering Tatler (*Heterocelus brevipes* Vieill.) supposed to be a western species, on the East Main coast."

In reference to this Dr. J. Macoun writes us under date of March 13, 1906: "We are all satisfied that it is a mistake to consider the Wandering Tatler as having been taken on the Labrador peninsula."]

Tryngites subruficollis (Vieill.).

BUFF-BREASTED SANDPIPER.

Very rare transient visitor.

Coues records the capture of a specimen near Henley Harbor on August 20, 1860, and Robert Bell records one at Port Burwell on September 28th.

Actitis macularia (Linn.).

SPOTTED SANDPIPER.

Common summer resident.

This familiar bird finds suitable nesting places all along the rocky

shores of Labrador from Ungava to Mingan, and along the courses of the numerous rivers and the shores of lakes in the interior. The eggs are laid during the latter part of June or early in July and the young appear in July.

Audubon in his Labrador journal speaks of finding a nest "made of a quantity of dried grass, forming a very decided nest, at least much more so than in our middle states."

We observed this bird only at Battle and Great Caribou Islands and at Cape Charles, four or five birds in all. At Battle Island on July 13th, we watched the manoeuvres of a pair of these birds in their efforts to drive a couple of Eskimo dogs away from the vicinity of their young which were probably hidden in the grass. The birds alternately attacked the dogs and then allowed themselves to be chased by them. In the first instance the birds flew furiously at the dogs, almost striking them and whistling loudly. In the second instance, the birds flew away slowly close to the ground so that the dogs were tempted to chase them. The incident illustrated the dangers of Eskimo dogs as destroyers of eggs and young birds.

[**Numenius longirostris** Wils. LONG-BILLED CURLEW.—Coues was assured of the occurrence of this bird in Labrador by hunters, but Audubon and Turner both state that they could obtain no evidence of its presence. As old female Hudsonian Curlews, with their long bills are often mistaken by gunners for this species, we have placed this bird in the doubtful list. It is western in its distribution.]

Numenius hudsonicus Lath.

HUDSONIAN CURLEW.

Uncommon autumn transient visitor.

Coues saw a few and states that they were shy and were most numerous at the time *N. borealis* was taking its departure. Turner saw three at the mouth of the Koksoak River in September, 1882. Weiz records it at Okkak, and Stearns and Frazar both state that it is not a rare migrant in the autumn. Audubon, on the other hand, says: "Entirely unknown. Even Mr. Jones and his sons, who had probably killed thousands [of *N. borealis*] . . . had never seen it in the course of their long residence at Bras d' Or." On September 3, 1776, Cartwright says that a curlew he had shot "weighed 15 oz. (the common

sort but nine and a half) and the wings extended are longer by five inches." It is very possible that this may have been a Hudsonian Curlew.

Numenius borealis (Forst.).

ESKIMO CURLEW; "THE CURLEW"; "THE C'LEW."

Formerly an abundant but now a very rare autumn transient visitor; July 28 to October 24.

The Eskimo Curlew was formerly the most characteristic bird of Labrador, where it was found in great multitudes during the autumn migrations.

Cartwright makes frequent reference to them in his journal, and recorded their arrival and departure for many years. Thus on August 26, 1770, at Charles Harbor, he writes: "On some low hills, partly barren, and the rest covered with small bad spruce-bushes were many large flocks of curlews feeding on the berries, which were very plentiful there; but could kill only one. The berries of the *Empetrum Nigrum*, and likewise some delicious blue berries which grow on a small shrubby plant, called Ground Whortle, both of which are now ripe, are what the curlews delight to feed on. These not only make them uncommonly fat, but also give their flesh a most delicious flavor." In another place he indulges in rhyme:

"When August comes if on the Coast you be,
Thousands of fine Curlews, you'll daily see."

The dates he gives of arrival and departure are as follows: August 4 to September 10, 1770; August 3, 1771; August 5 to October 2, 1772, and one which he shot near Chateau on October 24, 1772; August 4, 1774, at Mary Harbor; August 6 to September 18, 1776; July 28, 1777, this date he notes as being a few days earlier than usual; October 3, 1778; August 3, 1779; September 9, 1783; August 1, 1785; August 2, 1786. He gives no record of their appearance in the spring, and as he was constantly in the field with gun in hand it is probable that he would have noticed them if they were ever to be seen at that season. It is well known that these curlews go north by the Mississippi valley route. As Cartwright generally killed single birds with his rifle, by knocking their heads off, his influence on their numbers could not have been very great.

Chappell in the beginning of the nineteenth century, while on his voyage in the ship *Rosamond* notes "a sort of *Curlew* makes its appearance here about the middle of *August*, and as suddenly takes its departure towards the end of September; they move in flights containing many thousands; and when gorged with food, it is not unusual to kill ten or twelve at a shot; at such times they are found to be exceedingly plump and delicate, and far surpassing any of our *English Game* in richness and flavour."

Audubon first met with this bird at Bras d' Or on August 3, 1833, when it arrived from the north. His description in his Labrador journal is as follows: "This afternoon we all went ashore, through a high and frightful sea which drenched us to the skin, and went to the table-lands; there we found the true Esquimau Curlew, *Numenius borealis*, so carelessly described in Bonaparte's Synopsis. This species here takes the place of the Migratory Pigeon; it has now arrived; I have seen many hundreds this afternoon, and shot seven. They fly in compact bodies with beautiful evolutions, overlooking a great extent of country ere they make choice of a spot on which to alight; this is done wherever a certain berry, called here 'Curlew berry' proves to be abundant. Here they balance themselves, call, whistle, and of common accord come to the ground, as the top of the country here must be called. They devour every berry, and if pursued squat in the manner of partridges. A single shot starts the whole flock; off they fly, ramble overhead for a great distance ere they again alight. This rambling is caused by the scarcity of berries." And again on August 4th: "This species of Curlew, the smallest I ever saw, feeds on the berries it procures, with a rapidity equalled only by that of the Passenger Pigeon; in an instant all the ripe berries on the plant are plucked and swallowed, and the whole country is cleared of these berries as our western woods are of the mast. In their evolutions they resemble Pigeons also, sweeping over the ground, cutting backward and forward in the most interesting manner, and now and then poising in the air like a Hawk in sight of quarry."

On August 10th he notes: "Curlews have increased in numbers, but during two fair days we had they could not be approached; indeed they appear to be so intent on their passage south that whenever the weather permits they are seen to strike high in the air across the harbor."

Tucker, who visited Labrador in 1838, says: "The curlews are

extremely abundant. They appear on the coast in the beginning of autumn in vast flocks."

Dr. J. H. Storer records in his manuscript journal that he saw the first curlews on August 3, 1849, at Red Bay. On August 7th he makes the following entry: "The Curlews began to come and in immense flocks though very shy."

Packard writes of the Curlew as follows: "On the 10th of August [1860] the curlews appeared in great numbers. On that day we saw a flock which may have been a mile long and nearly as broad; there must have been in that flock four or five thousand! The sum total of their notes sounded at times like the wind whistling through the ropes of a thousand-ton vessel; at others the sound seemed like the jingling of multitudes of sleigh-bells. The flock soon after appearing would subdivide into squadrons and smaller assemblies scattering over the island [Caribou Island] and feeding on the curlew-berries now ripe."

Coues, who was in Labrador in 1860, says that the Curlew "arrived on the Labrador coast from its more northern breeding grounds in immense numbers, flying very swiftly in flocks of great extent. These immediately broke up into smaller companies, and proceeded at once in search of food. They remained but a very short time. . . . For two or three days before their final departure, we had noticed them all moving directly southward, flying very high in the air in loose straggling flocks, with a broad extended front."

Stearns says the Eskimo Curlew were "formerly abundant; now common in the interior in the fall." Turner, whose investigations extended from June 15, 1882, to October 3, 1884, states that they are "plentiful in the fall in the southern portions and as far north as Davis Inlet; they do not halt above this latter place while on their way southward."

The Bowdoin college expedition brought back the skins of two males and one female from Holton Harbor taken on August 20, 1891.

Bigelow in 1900 "heard of only about a dozen, which were seen on the coast this fall." Of these he saw five. He states that he "made careful inquiries among the settlers and obtained the following rather interesting information: (1) the Curlew remained in their former numbers in spite of the persecution to which they were subjected until eight years ago [this would be 1892]. (2) They then appeared no more."

Dr. Wilfred T. Grenfell wrote us under date of March 10, 1906: "Eskimo Curlew (*borealis*) are getting *very* scarce. I hear only of a few dozen a year being killed. I didn't *see* one last year." Again in September, 1906, in answer to further inquiries he wrote: "There were Labrador Curlew this year on the coast about Hare Islands, Sandwich Bay, in small numbers. . . . The Curlew became scarce in the end of the eighties. In 1892 when I came on the coast I saw only a few flocks of any size. Of late years I never saw more than five or six." In a conversation with Dr. Grenfell during his visit to Boston in January, 1907, he stated that in 1892 he saw two flocks each containing two or three hundred, but he had not seen any numbers since.

We met with none during our visit to the coast. We talked with many natives and summer residents on the coast and they all agreed that the Curlew though formerly very abundant, suddenly fell off in numbers, so that now only two or three or none at all might be seen in a season. Capt. Parsons of the mailboat *Virginia Lake* said that they were very abundant up to thirty years ago. So abundant were they that he often shot a hundred before breakfast during the season, often killing twenty at a single discharge. The fishermen killed them by the thousands. He thought that they diminished in numbers rather rapidly between twenty and thirty years ago, and at the latter date [1886] there was a great and sudden falling off. Now he saw from six to twenty only during a season. Mr. William Pye at Indian Cove, Cape Charles, told the same story, except that he put the sudden diminution in numbers about 15 years ago or about 1891. He said, and this was confirmed all along the coast, that the fishermen kept loaded guns at their fish stages and shot into the flying masses of these birds often bringing down twenty or twenty-five at a discharge. The birds frequented the beaches and hillsides. On the hills they ate the "black-berry" (*Empetrum nigrum*). They were exceedingly fat and good eating. He advanced the theory, which we heard commonly along the coast, that the shooting had nothing to do with the diminution in the numbers of the Curlew, but that they had troubled the farmers in the "States" by eating their corn, and hence had been poisoned by the wholesale. One fisherman even went so far as to back up this statement by saying he had seen corn in their stomachs!

To sum up the evidence, we can state that the natives of Labrador persistently harassed the Eskimo Curlew but did not realize that there was any diminution in their numbers until about 1888 to 1890. After

1892, but a small remnant of this formerly abundant bird has visited the shores.

It is possible that the sudden falling off in the numbers of this Curlew may have been because they were overwhelmed by a storm in their long ocean trip to the Antilles, but it is evident that the constant persecution to which they were subject was largely responsible for their decrease. It is apparent that they are now a vanishing race — on the way to extinction.

***Squatarola squatarola* (Linn.).**

BLACK-BELLIED PLOVER; "GREY PLOVER" (Cartwright).

Common transient visitor.

Audubon found some young birds in southern Labrador in the beginning of August; Stearns reported it as "common in spring and fall." It was not observed in the Ungava district by Turner, but Weiz reported it from Okkak.

***Charadrius dominicus* Müll.**

AMERICAN GOLDEN PLOVER.

Uncommon autumn transient visitor.

Packard says it "occurs in fall only, at Koksoak. Common on south and west coasts." Weiz observed it at Okkak. Coues says it appeared in small flocks the last of August, and Bigelow found it "not common. Several flocks, mostly young birds, after August 22."

***Aegialitis semipalmata* Bonap.**

SEMIPALMATED PLOVER; RING-NECK.

Common summer resident; May to September.

The Ring-neck is found throughout the length and breadth of Labrador, breeding all along the coastline and on the outlying islands, as well as on the shores of lakes in the interior. Audubon, Coues, Stearns, Brewster, and Palmer found it on the southern coast. Coues, Weiz, and Bigelow found it on the eastern coast. Turner found it

breeding abundantly at Ungava and Davis Inlet. Low found it common on the upper Hamilton River and Spreadborough saw it throughout the interior wherever there were large lakes with sandy shores.

We found a pair at Battle Island, three pairs at Great Caribou Island, and a pair each at Long Tickle and Hopedale. Their actions suggested the presence of young.

***Arenaria morinella* (Linn.).**

RUDDY TURNSTONE.

Common transient visitor.

Stearns found it along the southern coast in small flocks; Frazar saw one flock late in May at Esquimaux Point; Palmer found a few at Mingan; Coues saw it "commonly from August 20 to September 1 at Henley Harbor." Packard records it as "occasional at Ungava. Not rare on east coast."

***Haematopus palliatus* Temm.**

AMERICAN OYSTER-CATCHER.

Extirpated; formerly summer resident.

There is no question but that this interesting bird formerly extended its breeding range much farther north than at the present day when it is found breeding only as far north as New Jersey while stragglers are occasionally taken on the coast as far north as Grand Manan.

As recently as Audubon's day, however, the Oyster-catcher occurred on the southern coast of Labrador, as the following extracts from his writings clearly show. In his Labrador journal under date of July 6, 1833, when he was near Cape Whittle, he writes: "Coolidge and party shot two Oyster Catchers; these are becoming plentiful." Again ('35a, p. 181): "It occurs all the way to Labrador, in which country I found that several were breeding in the month of July In Labrador, I met with it farther from the open sea than in any other part, yet always near salt-water I have seen it knock off limpets from the rocks on the coast of Labrador, using its weapon [bill] sideways and insinuating it between the rock and the shell like

a chisel. . . . I saw them at Labrador until the 11th of August." Again ('42, vol. 5, p. 237) he says: "On the coast of Labrador, and in the Bay of Fundy, it lays its eggs on the bare rock." He also states that he procured a specimen.

Canachites canadensis (Linn.).

HUDSONIAN SPRUCE GROUSE; "SPRUCE GAME"; "SPRUCE PARTRIDGE."

Common permanent resident.

Low says this species is common throughout the wooded and semi-barren areas and he found eggs on June 1st. Coues found several broods on July 24th; Stearns says they are common in southern Labrador all the year round; Turner describes them as abundant throughout the wooded tracts and says they breed at Fort Chimo. Palmer, who visited the south coast in 1887, says: "We were informed that they were generally very abundant, but that great numbers had been destroyed by the severity of the previous winter."

Audubon ('35, p. 439) says: "The females of the Canada Grouse differ materially in their colour in different latitudes. In Maine, for instance, they are more richly coloured than in Labrador, where I observed that all the individuals procured by me were of a much grayer hue than those shot near Dennisville."

The subspecific difference indicated by Audubon and previously by Brisson was not formally recognized, however, until 1899 when Bangs described as a new subspecies some birds obtained at Rigolet. Norton ('01) has shown, however, that the Labrador bird is the true *canadensis*.

At Indian Cove, Cape Charles, we saw a pair of this species that had been caught near there and were confined in the upper story of a boat house.

Bonasa umbellus togata (Linn.).

CANADIAN RUFFED GROUSE; "BIRCH PARTRIDGE"; "FRENCH HEN."

Not uncommon permanent resident in southern half.

Brewster records that this bird was reported from Mingan Harbor and to the northward. Packard says it is rare at Hamilton Inlet and only on the south side; rather common at Paradise River, Sandwich

Bay; abundant in valleys to southward where white birch is plentiful. Low states that it is common at Mistassini and not rare at the mouth of Hamilton River, but that it is not found on the upper Hamilton River.

Lagopus lagopus (Linn.).

WILLOW PTARMIGAN; "BROWSE PARTRIDGE"; "GROUSE" (Cartwright).

It is often difficult to separate in the records of travelers and even in those of ornithologists the three species of ptarmigan found in Labrador. In general the Willow Ptarmigan is an abundant resident throughout Labrador south of the tree line. The Rock Ptarmigan is found on the barren treeless areas of the Arctic zone especially from Hamilton Inlet northward, while Reinhardt's Ptarmigan is found in the extreme northern parts of Labrador.

The Willow Ptarmigan breeds in the interior of Labrador in the forested region and migrates in great flocks to the barren seacoast in winter. Cartwright's observations on this bird, which he calls "Grouse," are so acute and interesting that we quote some of them in full here. He entered in his journal at Cape Charles on September 28, 1773, the following: "This morning I took a walk upon the hills to the westward, and killed seven brace of grouse. These birds are exactly the same with those of the same name in Europe, save only in the colour of their feathers, which are speckled with white in summer, and perfectly white in winter, (fourteen black ones in the tail excepted which always remain the same). When I was in England, Mr. Banks, (now Sir Joseph Banks) Doctor Solander and several other naturalists having enquired of me respecting the manner of these birds changing colour, I took particular notice of those I killed, and can aver, for a fact, that they get at this time of the year a very large addition of feathers, all of which are white; and that the coloured feathers at the same time change to white. In spring most of the white feathers drop off, and are succeeded by coloured ones; or, I rather believe, all the white ones drop off, and that they get an entire new set. At the two seasons they change very differently; in the spring, beginning at the neck, and spreading from thence; now, they begin on the belly, and end at the neck. There are also ptharmagans in this country, which are in all respects, the same as those I have killed on some high

mountains in Scotland." On April 19, 1776, he enters that the ptarmigan on the hills are "beginning to change colour now."

Audubon says that they are abundant at Bras d'Or in winter, congregating "in flocks of immense numbers, now and then mixed with the smaller species. . . . (*Lagopus rupestris*). Their flesh is then salted for summer use." He found the bird with young just out of the shell on July 5, 1833. Frazar says that this ptarmigan visits the southern coast regularly in winter, but retreats into the interior in summer. It was unusually abundant in the winter of 1886-7. In February, 1885, two or three invoices of ptarmigan from Labrador were offered in the Boston markets (*Ornith. and oologist*, vol. 10, 1885, p. 32). Low found eggs on the upper Hamilton River on June 25th.

Lagopus rupestris (Gmel.).

ROCK PTARMIGAN; "MOUNTAIN PARTRIDGE"; "ROCKER";
"AKKIGIK" (Eskimo).

Common permanent resident in the treeless region except in the extreme north.

The Rock Ptarmigan is found in summer in the treeless region and on the hilltops except in the extreme north where it is replaced by Reinhardt's Ptarmigan. In winter it migrates to the southern parts of the peninsula. Low says it is common in the valley of the Hamilton River during the winter, and that it leaves for the northward about April 15th. Audubon was informed by Mr. Jones that when the last of the Wild Geese had passed, the Rock Ptarmigan came in numbers about Bras d'Or and spent the winter on the wind-swept hilltops, repairing in the beginning of summer to the open grounds of the interior to breed. In another place he says: "They keep in great packs [in winter], and when disturbed are apt to fly to a considerable distance, shifting from one hill to another, often half a mile off." Frazar says: "Mr. Jones, with whom I lived at Cape Whittle, and who was a very reliable man, told me that several years before he was on the shore of the Straits one day in early winter, and that flock after flock of these birds were flying in from across the water and that they lit upon the first land they could reach, evidently being greatly fatigued."

Dr. Grenfell told us that ptarmigan sometimes alight on vessels in the Straits of Belle Isle. Ptarmigan are easily killed and form an important food supply for the fur trappers in winter.

Lagopus rupestris reinhardi (Brehm).

REINHARDT'S PTARMIGAN.

Common permanent resident in the extreme north.

Bigelow says that it is probably this race that is found north of Okkak. They migrate back and forth across Davis Strait in spring and fall.

Dr. Grenfell told us that they gather at Cape Chidley in multitudes in the spring just before their annual migration across the Hudson Straits. They are killed by the Moravians and Eskimos in great numbers and barrelled. He illustrated the abundance of this bird in winter as well as its tameness and the skill of the Eskimos with the whip by the following anecdote. During a three-day sledge trip made in winter by the Rev. S. M. Stewart from the George River to Fort Chimo his Eskimo driver succeeded in killing 500 ptarmigan by cutting off their heads with his long whip.

Pedioecetes phasianellus (Linn.).

SHARP-TAILED GROUSE.

Uncommon permanent resident in southwestern Labrador.

Low says that it has been killed in winter at Great Whale River, and states that its northern limit in Labrador is at lat. 57°. He took a set of eggs on May 20, 1889, at Fort George, on James Bay. Spreadborough states that it is said to be common at Fort George in winter, and one was shot on June 18, 1896, a short distance south of Fort George, James Bay. Fleming ('06) records, that according to Bishop Newnham, there is a fall migration of these birds from the northeast, to be observed at Moose Factory, "usually when the marsh hay is being gathered."

Ectopistes migratorius (Linn.).

PASSENGER PIGEON.

Formerly very rare, now extirpated.

"Baird, Brewer, and Ridgway say of this bird: "On the coast of Hudson's Bay it reaches no farther than the 58th parallel, and only in

fine summers, but in the interior or in the warmer central districts it attains to the 62d degree. Mr. Hutchins mentions, as a remarkable occurrence, that a flock of these Pigeons visited York Factory and remained two days." Low's record is: "Very rare. Eggs obtained at Fort George, 1887."

Cartwright on August 22, 1775, in Sandwich Bay enters in his journal this note: "Near the mouth of the brook we saw a pair of doves, and I killed one with my rifle; it was much like a turtle dove and fed on the berries of the *Empetrum nigrum*. I never heard of such a bird in the country before, and I believe they are very scarce." These may have been either Passenger Pigeons or Mourning Doves.

***Zenaidura macroura* (Linn.).**

MOURNING DOVE.

Accidental visitor.

There is only one record, that of Norton: "A badly mutilated specimen. . . . taken at Red Bay, Labrador, September 7," 1898, by the Bowdoin college expedition.

***Cathartes aura* (Linn.).**

TURKEY VULTURE.

Accidental visitor.

We are enabled to add this species to the list of Labrador birds, having received a letter under date of November 18, 1906, from Mr. Ernest Doane of West St. Modest to the effect that a Turkey Vulture was caught in a fox trap at that place on November 10, 1906.

***Circus hudsonius* (Linn.).**

MARSH HAWK.

Very rare summer visitor in southern Labrador.

Audubon says: "I have met with it in Newfoundland and Labrador." Stearns obtained one specimen at Dead Island Harbor.

***Accipiter velox* (Wils.).**

SHARP-SHINNED HAWK.

Very rare summer resident in southern Labrador.

Verrill said that one was seen "evidently nesting" near Salmon River on July 3, 1861. Macoun says that Spreadborough saw only one in northern Labrador and this on July 8, 1896.

***Accipiter cooperii* (Bonap.).**

COOPER'S HAWK; "PARTRIDGE HAWK" (Stearns).

Rare summer resident in southern Labrador.

Stearns is our only authority for this species. He says that he saw the bird "several times"; and again: "I saw the tail of a Cooper's Hawk in the possession of one of the natives, a few miles in the interior up Esquimaux River. . . . He did not regard it as at all rare."

***Accipiter atricapillus* (Wils.).**

AMERICAN GOSHAWK; "PARTRIDGE HAWK."

Uncommon permanent resident.

Packard states that this hawk is resident in Ungava, breeding near Fort Chimo. A specimen was obtained in early December, 1882. Coues obtained an immature bird from the natives. Low says that a specimen was killed near Cambrian Lake, Koksoak River; also on the lower Hamilton River, "not common." Spreadborough noted one at Seal Lake, Ungava, on July 24, 1896; another a short distance above Ungava Bay on August 23, 1896. He took a set of two eggs of this species at Great Whale River on June 18, 1896.

***Buteo borealis* (Gmel.).**

RED-TAILED HAWK.

Very rare summer visitor.

Audubon in his journal under date of July 11, 1833, near Cape

Whittle says: "A tail feather of the Red-tailed Hawk, young, was found; therefore that species exists here." Palmer records that "two were seen at the Mingan Islands."

[*Buteo platypterus* (Vieill.). BROAD-WINGED HAWK. — One was obtained at Moose Factory in 1862, but there is no record for Labrador.]

***Archibuteo lagopus sancti-johannis* (Gmel.).**

AMERICAN ROUGH-LEGGED HAWK.

Very common summer resident.

Macoun says this is the common hawk of Ungava and the barren-grounds. It was observed by Spreadborough at the mouth of Great Whale River. It breeds on the high cliffs from James Bay to Ungava Bay and also on the east coast. Three incubated eggs were found July 13th, and a nest with half-grown young at Seal Lake, Ungava, on August 3d. Macoun also reports a set of eggs from Hamilton Inlet on May 17th, and from Fort Chimo on June 20th. Bigelow found it very common on the east coast where it nests on cliffs some distance from the sea. Packard says that both light and dark phases breed at Fort Chimo, and that it is more abundant on the east and north, than on the south shores. Norton mentions two specimens brought back by the Bowdoin college expedition from the south coast, one from Chateau the other from Red Bay, taken in mid-July. Dr. H. R. Storer records in his journal that on August 15, 1849, he found the nest and young of this species at Red Bay. On August 16th he found a nest, egg, and fledged young at Bras d'Or. The account of this last nest is given in detail by Baird, Brewer, and Ridgway ('74, vol. 3, p. 309).

We saw one of these birds at Long Tickle on July 20th, one at Pack's Harbor on July 24th, one at Great Caribou Island on July 27th, and one near Battle Island on August 1st. They were all in the black plumage. We also obtained the skin of one from the Eskimos at Hopedale. This was very black including the rump, which was no lighter than the rest of the back. The bird seen at Pack's Harbor poised motionless for several minutes about a hundred feet above a high hill over which a strong wind was sweeping. He was suspended like a kite in the strong air currents, heading into the wind.

He seemed to be looking down, but occasionally turned his head from side to side. Once he dropped momentarily his heavily feathered legs.

***Aquila chrysaetos* (Linn.).**

GOLDEN EAGLE.

Very rare permanent resident.

Audubon records one of these birds for southern Labrador in these words: "At Labrador, we saw an individual sailing, at the height of a few yards, over the moss-covered surface of the dreary rocks." Packard says that specimens of the Golden Eagle have been procured in the Ungava district, and that it breeds in the northeastern portions among the hills. A pair also bred at the "Forks" in the Ungava district. Low states that it "breeds at head of Lake Michikamau. Seen in several places along upper Hamilton River." Spreadborough thought he saw one near the "Forks" above Ungava, and, at Fort Chimo, in September, 1896, he saw a skin of one shot a few days before on the river. Bryant saw a single Golden Eagle at Bradore in 1860.

[***Haliaeetus albicilla* (Linn.).** GRAY SEA EAGLE.—Weiz stated that this bird breeds at Okkak, but he was probably in error and confused this species with the Bald Eagle.]

***Haliaeetus leucocephalus alascanus* C. H. Townsend.**

NORTHERN BALD EAGLE.

Rare summer resident.

Frazar saw one at Cape Whittle on the southern coast and states that it is "not a rare summer resident, as I heard of about six pair that bred at different places along the coast and always in trees." Low saw a pair on the Hamilton River below Grand Falls on April 28th. Cartwright obtained three eagle's eggs on April 30, 1775, near Cape Charles. On May 30, 1776, in Sandwich Bay he records two eggs of eagles, and again on June 11, 1773, three eggs. The species is not mentioned. A pair of this species was seen on August 17, 1896, by A. P. Low near Ungava Bay.

Falco islandus Brünn.

WHITE OR ICELAND GYRFALCON.

Common permanent resident.

There is great confusion as to the specific status of the gyrfalcons, and it is thought by some that there may be only one species with various color phases. The four forms have all been observed and specimens taken in Labrador. Two, the white and the black forms, have been found breeding. Our own observations of this class of falcons in Labrador were very meager. They will be referred to later. We have entered here all the records for Labrador we could obtain.

Audubon describes a pair of adults of this species shot on August 6, 1833, eight or ten miles from Bradore on the south coast of Labrador. Their full-grown young escaped. The nest was on a cliff and was surrounded by remains of Puffins, Murres, and Ptarmigan.

Packard says it is "common at Fort Chimo and east coast of Labrador. Resident in northern portions, breeds at Fort Chimo." Weiz says it breeds at Okkak. Harvie-Brown says a specimen was shot at Ungava Bay by Thomas Mackenzie in 1890. Robert Bell says that two were killed at Port Burwell in August and September. The following specimens of *islandus* are in the Bangs collection: no. 9742, Hopedale, 1898; no. 9743, Okkak, 1895; no. 9744, Okkak, October, 1896; no. 9741, Makkovik, late autumn, 1900.

At Henley Harbor on August 2d, we saw a bird evidently of this species circling about some high cliffs half a mile distant. It sailed up to a deep cleft into which it disappeared, soon to re-appear and alight on a shelf. Here it hopped and fluttered a few paces before again taking flight. The bird was noticeably white, somewhat mottled with darker color, especially on the wings whose primaries appeared white at the ends.

Falco rusticolus Linn.

GRAY GYRFALCON.

Rare winter visitor.

The only record is that of Packard ('91, p. 423): "Winter specimens only obtained at Fort Chimo. Not known to breed in the Ungava district."

Falco rusticolus gyrfalco (Linn.).

GYRFALCON.

Rare visitor.

The A. O. U. check-list for 1895 records this form for "Arctic America, from Northern Labrador and Hudson Bay to Alaska." There is a specimen in the Bangs' collection, no. 9745, from Okkak, taken September, 1896. We obtained a good skin of this form of gyrfalcon taken by the Eskimos at Hopedale in the winter of 1905-06. It was identified by Mr. William Brewster. Of considerable interest in this specimen is the presence of a white and mottled tail feather, the first to the left of the center. This feather is entirely different from the others being nearly white with considerable mottling and spotting of dark brown on the outer web, and eight fairly distinct half bars on the inner web. The markings are more distinct in the distal half of the feather and are fainter on the lower surface. Feathers similar to this occur in the tails of some specimens of *islandus* and suggest that the bird may have been changing from one to the other color phase. Both the white feather and the dark ones appear to be of the same age, however, all being slightly brown. The case may have been one of partial albinism only. The observations of Hagerup ("The Birds of Greenland," edited by Montague Chamberlain, Boston, 1891) are of interest in this connection. He obtained specimens of the white form with dark spots on the thighs and ventral regions, that resembled in this respect specimens of *rusticolus*. He says: "As Holböll and Flucker repeatedly observed mated pairs, one of which was white (*F. islandicus*), and the other dark (*F. rusticolus*), and as Holböll also found light and dark-colored young in the same nest, I conclude with these observers that there is but one species of Gyrfalcon found in Greenland."

Falco rusticolus obsoletus (Gmel.).

BLACK GYRFALCON; LABRADOR GYRFALCON.

Common permanent resident.

This is the variety *labradorius* of Audubon. He found a pair of these birds with two young on August 6, 1833, eight or ten miles from Bradore. Stearns found the Black Gyrfalcon in southern Labrador

and thought it was nesting. It was reported to Coues and said to be commoner in winter. Turner found it abundant at Fort Chimo in summer, but very rare in winter. He found eggs on May 24th. Low shot a specimen at Cape Chidley. Spreadborough found it common below Fort Chimo on September 18, 1896. A set containing three eggs was taken at Fort Chimo in June, 1897. Bigelow states that the Black Gyrfalcon is "rare. One at Port Manvers, September 4." Eifrig in a recent note ('05, p. 239) says that this species is "reported by Mr. [A. P.] Low as common near Cape Chidley and over the whole of Ungava, where they also breed in numbers."

There are two specimens in the Bangs collection from Labrador: no. 9747, Hopedale, November 4, 1898, and no. 9746, Hopedale, August 9, 1898. Baird, Brewer, and Ridgway mention a female from Rigolet, and two females from Fort Nescopec [= Nascopee].

***Falco peregrinus anatum* (Bonap.).**

DUCK HAWK.

Common summer resident.

The Duck Hawk has been reported as breeding from Cape Whittle to Cape Chidley. Audubon found a nest and young about one week old near the former cape on July 5, 1833. Turner says it is abundant at Fort Chimo and he found eggs on May 24th. Macoun records two sets of three eggs each from Fort Chimo taken in June, 1898. Weiz says it breeds at Okkak. Low found it "not uncommon throughout the interior," and Bigelow says: "Fairly common, especially wherever the sandpipers were flocking."

***Falco columbarius* Linn.**

PIGEON HAWK.

Common summer resident.

Audubon found three sets of five eggs each of this hawk in southern Labrador. They were all laid about June 1st. On July 1, 1833, he found a nest containing three eggs and two young just out of the shell. Coues, Stearns, Frazar, and Palmer also report it for the southern coast. Weiz says they breed at Okkak, and Spreadborough reports

them off Cape Chidley, and across Ungava from Great Whale River almost to Fort Chimo.

We saw one bird of this species near Long Tickle on July 20th.

Falco sparverius Linn.

AMERICAN SPARROW HAWK.

Rare summer visitor.

The only record we have is that of Coues ('61, p. 216): "A single individual. . . . was observed during my stay in Labrador."

Pandion haliaëtus carolinensis (Gmel.).

AMERICAN OSPREY; FISH-HAWK.

Common summer resident in the southern parts of Labrador.

Audubon records: "Many Fish-Hawks are found here, and I saw several of their nests, placed on the low fir trees." Frazar found them "common and breeding all along the coast as far east as Cape Whittle." Palmer saw several pairs at the Mingan River. Low states they are "common throughout southern interior, to lat. 54°. Seen May 27th. Eggs June 12th." Spreadborough did not see any of these birds in Labrador north of Moose Factory. Macoun records eggs found by Low on the upper Hamilton River on June 10, 1894. Turner was assured by John Ford that four or five pairs bred some four miles above the Hudson's Bay company's post on the Northwest River. Dr. Grenfell noted a Fish-hawk at Nachvak in the spring of 1900.

While we were in Labrador we saw two hawks of this species, one on July 12th near St. Lewis Sound, the other on July 18th at Rigolet.

Asio accipitrinus (Pall.).

SHORT-EARED OWL.

Common summer resident.

One specimen was taken in southern Labrador on October 16th by Stearns. Brewster saw two on July 22d on one of the Mingan Islands.

Low saw the birds on the upper Hamilton and Romaine Rivers. Bigelow reported it "rather common at Port Manvers and Nachvak in September." Weiz says it breeds at Okkak and Packard states that it is "common and breeds at Fort Chimo. Plentiful on east shore of Hudson Bay. Not known to winter." Mr. Schmitt of Nain told us that he had found this species breeding near that mission, and we obtained a specimen from the Eskimos at Hopedale.

***Syrnium varium* (Barton).**

BARRÉD OWL.

Very rare summer visitor in the south.

The only record is that of Audubon ('39, p. 386): "A few were seen by myself and my party in Labrador."

[***Scotiaptex nebulosa* (Forst.).** GREAT GRAY OWL.—A specimen of this species was taken by James McKenzie at Moose Factory close to, but just outside of the western boundary of the Labrador peninsula. Its occurrence in Labrador is doubtful, notwithstanding Weiz's assertion that it breeds in Okkak, and Audubon's poetic mention of this bird in his journal written evidently during a state of depression brought on by the hard work and arctic environment. He does not mention the occurrence of this owl in Labrador in his ornithological writings. In his journal, however, under date of July 10, 1833, written near Cape Whittle, he describes "one of these dismal gales which blow ever and anon over this desolate country . . . the Great Gray Owl is perched on the southern declivity of some stupendous rock, and the gale continues as if it would never stop."

In Cartwright's "Journal" under date of October 29, 1773, the following record occurs: "Walked upon Lyon Neck, and there broke both the legs of a large grey owl." This he did with his rifle. Lyon Neck is a rocky neck devoid of trees, at the northern entrance to The Lodge. It is not a place where one would expect to find a Great Horned Owl, hence it is possible that Cartwright refers to the Great Grey Owl.]

***Cryptoglaux tengmalmi richardsoni* (Bonap.).**

RICHARDSON'S OWL.

Rare permanent resident.

The only record we have for this owl is a specimen in the Bangs collection taken by Doane at Lance au Loup on March 1, 1899. It will probably be found breeding.

Cryptoglaux acadica (Gmel.).

SAW-WHET OWL.

Rare summer resident.

The only record is that of a specimen reported by Low as shot near Lake Mistassini. It probably breeds.

Megascops asio (Linn.).

SCREECH OWL.

Audubon ('39, p. 392) states explicitly that this species "is . . . met with abundantly in . . . Labrador, where I procured it." It does not seem possible that he could have mistaken the Hawk Owl or any other small owl for this species especially as he "procured it." No other ornithologist has met with it in Labrador, yet we cannot disregard this record of Audubon which apparently points, as in the case of the Oyster-catcher to a wider range in former times for this species, as it is now rarely found north of New Brunswick on the eastern American coast although it is reported as a summer migrant to Newfoundland.

Asio magellanicus heterocnemis Oberholser.

LABRADOR HORNED OWL.

Common permanent resident.

Oberholser's Labrador form of the Horned Owl seems to be so distinct that we have recognized it here. Previously considerable confusion existed as to the status of this bird in Labrador, and it has been reported under the head of *Bubo virginianus*, *B. virginianus saturatus*, and *B. virginianus pacificus*.

Stearns states that it is not rare about the Esquimaux River in southern Labrador; Macoun reports a skin and two eggs taken on May 1, 1896, at Sandwich Bay by W. Raine. Coues reports a single bird seen at Rigolet. Low says it is "common about Northwest River during winter. Common in the interior." Norton records a bird in juvenal plumage taken at Cullingham's Cove, Hamilton Inlet, on August 1st. Spreadborough saw none while crossing Ungava. Packard says it is a resident and not rare at Fort Chimo. Downy young were obtained there on June 20, 1884.

Oberholser describes this form as considerably larger than *virginianus* and darker; grayish and blackish tints predominate over rufous ones. It differs from *saturatus* in having a larger bill; posterior lower parts paler; feet lighter colored and less heavily spotted; upper parts with usually less ochraceous. He gives the distribution as "Labrador, including at least the north coast of the Territory of Ungava." He has examined specimens from Okkak, Makkovik, Hopedale, Turnavik, Lance au Loup, Fort Nascopee, Fort Chimo, and near Forks.

We obtained a very good skin from the Eskimos at Hopedale. The Moravians said it must have been shot near there sometime during the previous winter. The measurements are: wing, 380 mm.; tail, 225 mm.; exposed culmen, 43 mm.; culmen without the cere, 31 mm. The measurements are those of a female of this race and the coloring is characteristic.

[*Bubo virginianus*, *B. v. saturatus*, *B. v. pacificus*. See *Asio magellanicus heterocnemis*.]

Nyctea nyctea (Linn.).

SNOWY OWL.

Not common permanent resident.

The Snowy Owl occurs apparently only in winter on the southern coast but breeds in the northern parts. Stearns found it not rare in winter all along the southern coast "to Red Bay, at least." He speaks of a single bird that stayed about Old Fort Island all winter and could not be stalked. He says that the Indians hunt this owl in pairs, one Indian going in one direction and attracting the bird's attention, while the other crawls up to shoot it. Packard says it is common and breeds at Fort Chimo. Bendire mentions eggs in the National museum from Labrador.

Mr. W. B. Cabot, who has made a number of trips into the interior of Labrador, tells us he has only once seen this bird. Mr. Schmitt of Nain told us that the Snowy Owl breeds in that vicinity. Low ('06) records that "at Cape Dufferin on the east side of Hudson Bay, upwards of thirty of these birds were caught by placing fox traps on the top of short poles, at intervals along the coast, during the southern migration of the birds in October, 1901." At Dead Island on July 26th, we found the dried and disintegrated body of a Snowy Owl.

***Surnia ulula caparoch* (Müll.).**

AMERICAN HAWK OWL.

Uncommon permanent resident.

Turner found the Hawk Owl rare at Fort Chimo, and he took its eggs on June 8, 1884. The young were ready to leave the nest on June 20th. Low saw the bird several times on the upper Hamilton River and Macoun reports a set of five eggs from Hamilton Inlet taken on May 24, 1896, by Raine. Macoun says it is rare at Lake Mistassini where it is found in winter. In the Bangs collection is a specimen from Black Bay on the Straits of Belle Isle taken on November 18, 1898, by Doane.

We saw three or four skins of this bird in Dr. Grenfell's hospital at Battle Harbor and obtained one. The bird had been killed at Fox Harbor. We also saw the skin of one at Hopedale.

[***Coccyzus americanus*** (Linn.). YELLOW-BILLED CUCKOO.—Although Audubon says: "Even in Labrador . . . I saw a few," we think he must have confused this species in his memory with the Black-billed Cuckoo of which he gives a more definite record.]

***Coccyzus erythrophthalmus* (Wils.).**

BLACK-BILLED CUCKOO.

Very rare summer visitor in the southern part.

Audubon's is the only record; he says ('39, p. 524): "We saw a few in Labrador, amid the clumps of low trees a few miles from the shore of the Gulf in secluded and pleasant valleys."

***Ceryle alcyon* (Linn.).**

BELTED KINGFISHER.

Common summer resident in the southern part of Labrador.

Audubon, Stearns, Brewster, Frazar, and Palmer found this bird on the southern coast of Labrador. Low says it is "not found north of the vicinity of the Grand Falls, Hamilton River. Common on Romaine River and at Lake Mistassini." He records its arrival at

Lake Mistassini on May 14th. Frazar reports its arrival at Esquimaux Point on May 22d. Packard says it breeds at Northwest River.

***Dryobates villosus leucomelas* (Bodd.).**

NORTHERN HAIRY WOODPECKER.

Uncommon resident in southern Labrador.

Stearns found it "common inland in winter at least about Esquimaux River." Packard says it is "resident in southern portions. Probably absent north of 'Height of Land.'" Low, however, "shot [it] in valley of Hamilton River in March," where it was "not rare." Spreadborough found none farther north in Labrador than the foot of James Bay.

We saw no Hairy Woodpeckers in Labrador and were unable to obtain any specimens.

***Dryobates pubescens medianus* (Swains.).**

NORTHERN DOWNY WOODPECKER.

Common permanent resident in southern half of Labrador.

Audubon and Stearns found this woodpecker in southern Labrador. Packard states that it is a "common resident in southern portions; probably does not range north of 56°." Low states that it is common on Hamilton River throughout the year and that it is seen at Lake Mistassini throughout the winter.

***Picoides arcticus* (Swains.).**

ARCTIC THREE-TOED WOODPECKER.

Common resident north to tree limit.

Frazar found a pair at Esquimaux Point in early September and Brewster heard one at the mouth of the Mingan River in southern Labrador. Packard states that it is a common resident throughout the wooded portions, and Low found it common along the lower Hamilton River. Bangs lists a specimen from Bechoine and one from Makkovik.

Picoides americanus Brehm.

AMERICAN THREE-TOED WOODPECKER.

Common permanent resident north to tree limit.

Packard says it is "common and resident throughout the wooded portions" and Norton records a bird in juvenal plumage from the Northwest River.

Bangs ('00, pp. 138, 142) characterizes the Labrador bird as *Picoides americanus labradorius*, type from Okkak; range, Labrador peninsula north to tree limit; intergrades in Quebec. He bases this on 24 specimens as follows: from Okkak, 8; Nain, 4; Hopedale, 3; northern Labrador, 1; Black Bay, 2; Lance au Loup, 2. We obtained the skins of two from the Eskimos at Hopedale which Mr. Bangs recognizes as of the same type. In the article referred to above, he characterizes *labradorius* as "the blackest of the American black-and-white-backed three-toed woodpeckers." "Crown patch of ♂ darker yellow, about ochre yellow." This form has not, however, been recognized by the American ornithologist's union.

Colaptes auratus luteus Bangs.

NORTHERN FLICKER.

Uncommon summer resident in southern half of Labrador, occasional as far as Hudson Strait.

Stearns on the southern coast found it "not rare, at least as far as L'Anse Claire." Low says a single specimen was seen near the Grand Falls of the Hamilton River on May 30th. Spreadborough reported a few as far north as Fort George, James Bay, in June, 1896, and Packard states that a "straggler was procured from the mainland near Akpatok Island, Hudson Strait, October, 1882. Reported common summer resident to Northwest River."

Chordeiles virginianus (Gmel.).

NIGHTHAWK.

Common summer resident in southern Labrador locally.

Stearns says it is "common at Natashquan." Low reported:

“Very rare on upper Hamilton River. Single specimen seen near the Grand Falls, May 31st. Common at Mistassini and along Romaine River.” He records its arrival at Lake Mistassini the last of May.

Trochilus colubris Linn.

RUBY-THROATED HUMMINGBIRD.

Very rare summer visitor.

Audubon states that “a few were seen by me in Labrador.” Turner records that a male was seen on July 17, 1882, on the hill-top (825 feet elevation) back of the station at Davis Inlet.

Tyrannus tyrannus (Linn.).

KINGBIRD.

Rare summer resident in southern Labrador.

The only record we have of this bird for Labrador is Audubon’s statement ('39, p. 420): “I have found it breeding in . . . Labrador.” As this species is common locally in Newfoundland and Cape Breton it might be expected in southern Labrador.

Sayornis phoebe (Lath.).

PHOEBE.

Very rare summer resident in southern Labrador.

The only record we have for this bird is Audubon’s statement ('39, p. 424): “I have found it in Labrador [where] it breeds.” There is no reason why this species should not occur in southern Labrador as Macoun records it for Newfoundland and Quebec.

Nuttallornis borealis (Swains.).

OLIVE-SIDED FLYCATCHER.

Very rare summer resident in southwest portion.

Audubon again is the only authority for this species. He says,

('35, p. 425): "I found this species. . . . on the Magdalen Islands, and on the coast of Labrador." We should expect to find this species in southwestern Labrador where the trees were of any size. Spreadborough observed one near Moose Factory just outside the limits of Labrador.

[**Contopus virens** (Linn.). WOOD PEWEE. — Audubon states ('40, p. 232): "I have seen them in Labrador," but in his Labrador journal his only mention of this bird is on June 22, 1833, at American Harbor, where he enters: "I heard a Wood Pewee." As he was not familiar with the Yellow-bellied Flycatcher some of whose notes suggest those of the Wood Pewee, and as the latter bird is more southern in its distribution, we have omitted it from the list.]

[**Contopus richardsonii** (Swains.). WESTERN WOOD PEWEE. — Audubon's account of flycatchers in Labrador is considerably confused. He speaks ('35, p. 93) of a species smaller than *Muscicapa acadica* as abundant in Labrador and described in the "Fauna Boreali-Americana" as *Tyrannula richardsonii*. And again ('39, p. 300): "Whilst in Labrador, I examined several nests of the Short-legged Pewee." It is reasonable to suppose that these were either the Alder or the Yellow-bellied Flycatchers.]

Empidonax flaviventris Baird.

YELLOW-BELLIED FLYCATCHER.

Common summer resident in southwestern Labrador.

Frazar picked up one dead at Cape Whittle in early July. Low states that it is "common at Lake Mistassini. Not seen at Hamilton Inlet." At Lake Mistassini Low noted their arrival between the 1st and 15th of June. Macoun records it as breeding. It is probable, as already stated, that Audubon found this species but gave it another name.

Empidonax traillii alnorum Brewst.

ALDER FLYCATCHER.

Not common summer resident in southwestern Labrador.

We have ventured to include this species on the strength of Audubon's statement ('39, p. 289) that he found *Muscicapa pusilla* "on the coast of Labrador in considerable numbers." One nest was found

in July in a bush. It contained five speckled eggs. Since the nest of the Yellow-bellied Flycatcher is usually built on the ground, the presumption is that Audubon's nest was that of the Alder Flycatcher.

Otocoris alpestris (Linn.).

SHORE LARK; HORNED LARK; "SKYLARK"; "MUD LARK."

Abundant summer resident throughout the Arctic zone, especially on the coast.

This race of Horned Lark is found breeding wherever there is barren ground in Labrador. Thus it is found on the southern coast from its eastern extremity to the point where the forest growth comes down to the shore near the Mingan Islands; and on the entire eastern, northern, and western coasts. Low states that it is common on the barrens of the upper Hamilton River, where he obtained eggs on June 19th. Macoun says it is common and breeds on the rocky islands of James Bay from Moose Factory to Richmond Gulf. Breeding birds have been examined from Fort Chimo and Davis Inlet. A set of three eggs was taken at Great Whale River, James Bay, in June, 1899, by A. P. Low; another of three eggs on an island in James Bay on June 18, 1896, by Spreadborough. The latter explorer failed to find it, however, between Richmond Gulf and Ungava Bay.

Audubon records in his Labrador journal the drawing of three young Shore Larks "the first ever portrayed by man" at Bras d'Or on July 29, 1833. He adds: "I saw one beautiful male in full summer dress which I secured and have drawn with a portion of moss. I intend to add two drawn in winter plumage."

We found Horned Larks common in the Arctic coastal region all along the Labrador shore, and we obtained ten specimens from Cape Charles on the south to Fanny's Harbor, between Hopedale and Nain, on the north. We observed them on the southern coast near Cape Charles and also at Flower's Cove in Newfoundland on the southern side of the Straits of Belle Isle, where we obtained two more specimens. All our specimens and all the birds observed were of the same type, with nearly pure white superciliary lines and pale yellow throats. The superciliary lines although nearly pure white, all show on close scrutiny a very faint tinge of yellow, especially just above the eye. This tinge of yellow varies in amount in our specimens and

is never pronounced. In some it is nearly absent. On the throat the yellow tinge is present although faint in all the specimens and is most marked medially and close to the bill. The edges of this patch below and behind the black markings and therefore well on the side of the head, are in all the specimens nearly pure white. In the color of these markings, therefore, the birds resembled *praticola*, not *alpestris*.

Two specimens in the Bangs collection from Lance au Loup on the southern Labrador coast taken on May 3 and May 14, 1899, although both females, have a more pronounced yellow tint in both the throat and the superciliary markings. Examination of specimens in Mr. Brewster's collection shows a fainter yellow in the specimens taken in April in Massachusetts than in those taken in October.

As to measurements it will be seen from those given below that the birds are large and correspond in size to the northern race, *alpestris*, and not to *praticola*.

All our specimens show considerable wear in the feathers, for all were taken just before the annual August moult.

Measurements in millimeters of Otocoris alpestris.

| No. ¹ | Sex. | Locality. | Date. | Wing. | Tail. | Tarsus. | Bill from nostril. | Exposed culmen. |
|-------------------------------|-------|---------------------|---------------|-------|-------|---------|--------------------------|--------------------|
| 1164 | ♂ | Cape Charles, Lab. | July 30, 1906 | 111.3 | 72 | 22.5 | 11.8 | 13.9 |
| 1162 | ♂ | Battle Harbor, Lab. | July 14, 1906 | 109 | 73 | 23 | 11.5 | 12.8 |
| 1165 | ♂ | " | July 14, 1906 | 111.2 | 69.2 | 21.8 | 10.5 | 12 |
| 1167 | ♂ | " | July 11, 1906 | 109 | 71 | 23.4 | 11.5 | 13 |
| 1166 | ♂ | Pack's Harbor, Lab. | July 24, 1906 | 112.8 | 76 | 22.5 | 10 | 12 |
| 1163 | ♂ | Fanny's Harbor, Lab | July 21, 1906 | 111.5 | 74 | 20 | 10 | 12 |
| Average of six adult males | | | | 110.8 | 72.5 | 22.2 | 10.9 | 12.6 |
| 1161 | ♀ | Flower's Cove, NF. | July 9, 1906 | 104 | 65 | 19.6 | 11 | 13 |
| 1168 | ♀ | Battle Harbor, Lab. | July 27, 1906 | 105 | 64.2 | 20.5 | 10.8 | 12.2 |
| 1169 | ♀ | Holton, Lab. | July 19, 1906 | 101 | 60.4 | 20.8 | 10 | 11.8 |
| 1170 | ♀ | Long Tickle, Lab. | July 20, 1906 | 102 | 61 | 20 | 10.5 | 12 |
| Average of four adult females | | | | 103 | 62.6 | 20.2 | 10.5 | 12.2 |
| 1160 | ♂juv. | Flower's Cove, NF. | July 9, 1906 | 96 | 51.8 | 18 | 9.5 | 10.2 |
| 1171 | ♂juv. | Cape Charles, Lab. | July 30, 1906 | 104 | 64 | 21 | 9.9 | 12 |
| Average of two young males | | | | 100 | 57.9 | 19.5 | 9.7 | 11.1 |

From these considerations we have concluded that the Horned

¹Collection of Dr. C. W. Townsend.

Lark of the Labrador coast, both eastern and southern, is the northern race, *Otocoris alpestris alpestris*, and that the difference observed in the tint of the yellow in the plumage is due largely to fading, and to some extent to wear as the bases of the yellow feathers are white. The fading is least where the feathers are most shaded under the chin.

We have measured ten worn feathers taken from the throats of our July birds and ten unworn feathers taken as nearly as may be from the same region of birds shot on the Massachusetts coast in October and December. The average length of the first set is 5.95 mm., of the second set 8.25 mm. showing a loss of 26 percent in the length of the feathers by wear.

It is evident that besides changing the color of the plumage of the bird, a fact which is well known, wear must make a great difference in the warmth of the plumage. The Horned Lark wears its thinnest clothes during the time when its love passions are at their summit and when the thermometer is highest. As its love cools and the days begin to grow shorter and cooler it dons its thick winter clothes which do not begin to show much wear until the days are growing warmer and love begins to stir the blood with its old heat.

Although part of the southern coast of Labrador is of a different geological formation from the eastern coast it belongs in the same life zone, namely, the Arctic, as shown by the same flora and by the presence of the American Pipit as on the eastern coast. To the west of Mingan the Hudsonian region as shown by the forest growth reaches the coast, and the country beyond is not suitable for either of these birds except possibly in limited areas. Thus Merriam (Bull. Nuttall orn. club, vol. 7, 1882, p. 234) says of the Pipit at Point des Monts, near Godbout on the Gulf of St. Lawrence (about 50 miles southwest of the Labrador boundary): "Tolerably common summer resident and doubtless breeds." Of the Horned Lark he says: "First seen April 21, 1882, after which they were common for about three weeks and then disappeared. I found a young one, dead, at Godbout in July, 1881." With the exception of this record no larks have been found breeding west of Mingan. Between Montreal and Quebec the Prairie Horned Lark is found breeding, and as far as we can discover this is the most eastern breeding place on the north side of the St. Lawrence for this bird.

Macoun says of the Prairie Horned Lark: "A common summer resident in the Montreal district. They have been found breeding

here before the winter's snow has melted off the ground; they arrive in February and leave in November. (Wintle.) Occasional at Quebec. (Dionne)."

Our brief examination at Flower's Cove on the Newfoundland side showed an Arctic flora and the presence of the same Horned Larks as on the opposite side of the Straits, some fifteen miles distant.

We have discussed this subject at some length for H. C. Oberholser ('02, p. 828 and map) has extended the breeding range of the Prairie form (*praticola*) along the whole south coast of Labrador to the entrance of the Straits of Belle Isle. This he has done on the strength of one specimen obtained by the Bowdoin college expedition to Labrador in 1891, which certainly seemed to belong to this race (*praticola*). This view was fortified by Audubon's description and by his plates of a bird taken at Bras d'Or, southern Labrador, in 1833. Here the throat and frontal band are white. These facts were noted by Mr. A. H. Norton in his report on the birds collected by the Bowdoin college expedition. The one specimen on which so much was made to depend, was taken on July 14, 1891, at Chateau Bay, but a few miles to the westward of Cape Charles where we obtained specimens and considerably to the east of Lance au Loup, the locality of the Bangs specimens. Mr. Norton says: "It is a female in somewhat worn nuptial dress and is quite typical [of *praticola*], though nearly reaching the maximum measurements of its sex. The wing measures 99 mm.; bill from nostril 9.9 mm. . . . Though the characteristics of this specimen are so well marked that its identity is not questionable, yet on account of the interest attached to it, it was forwarded to the United States National Museum for verification. Mr. Richard Rathbun, Assistant Secretary, informed me that it had been determined by Mr. H. C. Oberholser as being of this form [*praticola*]."

We forwarded all our specimens, together with the two from the Bangs collection from southern Labrador, to Mr. Oberholser and he identified them all as *alpestris*. We have also examined the Bowdoin college specimen and find that it corresponds to ours. In fact although it is rather a small specimen of a female *alpestris* its markings are no whiter than those of our female specimens. We find it to measure: wing, 99 mm.; tail, 62 mm.; tarsus, 19 mm.; bill, 13 mm.; from nostril, 10 mm.

Mr. Oberholser under date of January 8, 1907, writes us as regards our specimens: "They prove to be *alpestris* as I have indicated on

the labels. This is simply another proof of the difficulty and danger of attempting to identify specimens of *Otocoris* from new localities! As I remember, Mr. Norton's female was rather small and unusually grayish; but your good series leaves no room for doubt."

Of the Bowdoin college specimen he writes (February 4, 1907): "It is certainly only a specimen of *alpestris*, probably somewhat aberrant."

In this connection we wish to speak of the recent extension of the breeding range of *praticola* to the east. This was a subject about which one of us wrote in "The birds of Essex County" (Townsend 1905, p. 235) and the *Auk* (vol. 21, 1904, p. 81). In the *Auk* (vol. 23, 1906, p. 225) Mr. Norton controverted this view basing his argument primarily on what he believed to be evidence of the existence of this form even in Audubon's time on the southern Labrador coast as well as its occurrence there today. As we have just shown, Mr. Norton was in error as regards this. He also refers to Maynard's record for eastern Massachusetts in July, 1869. A single case is of course of trifling value and when we consider that the numerous ornithologists in the well studied part of eastern Massachusetts have only within recent years found this bird breeding, it seems probable that some recent change in its range has occurred. The evidence in New Hampshire and Vermont is also strongly suggestive.

We observed the flight song of the Horned Lark at various places along the coast, and made an especial study of it at Great Caribou Island, Battle Harbor. The bird suddenly mounts high into the air, going up silently in irregular circles, at times climbing nearly vertically, to such a height that he appears but a little speck in the sky, several hundred feet up. Arrived at this eminence he spreads his wings and soars, emitting meanwhile his song, such as it is — one or two preliminary notes and then a series of squeaks and high notes with a bit of a fine trill. The whole has a jingling metallic sound like distant sleigh bells, although the squeaks remind one strongly of an old gate. The whole effect, however, is not unpleasant,— even melodious. Having finished one bar of his song, he flaps his wings a few times, closes them and sails again, repeating the song. One bird repeated his song twenty-four times and remained in the air one and a half minutes; another remained in the air three minutes, during which he repeated his song thirty-two times. During all this time the bird is flying in curves or irregular circles, sometimes in straight

lines, or if the wind be strong, he heads up into it and remains in the same place. The performance ended, he plunges head foremost down to the earth, reaching it in a marvelously short space of time. The descent is as silent as the ascent.

Several times we heard the birds singing above us out of sight in the fog, and occasionally they sang from a rock the same song, but with less energy and abandon. In one case the bird appeared to be singing as he went up, and he disappeared into the fog but it is possible he had already attained the summit of his flight.

The familiar sibilant squeaking call note was commonly used, and also a note which we do not remember to have heard during the migration in Massachusetts. This sounded like *zzurrit* and was often preceded by another note thus, *whit-zzurrit*. These notes were occasionally so soft and sweet that they recalled the trilling whistle of the Least Sandpiper.

At Frenchman's Isle on July 16th, we found the nest of a Horned Lark composed of dried grass and a few large feathers, deeply sunk into the reindeer lichen and moss in a level piece of ground. There was no shelter or covering of any sort. It contained three dark-skinned young, clothed sparingly in sulphur-yellow down. Their eyes were not yet open. There was also one egg containing a large embryo. The egg was gray in color, thickly spotted with fine dots, especially at the circumference of the larger end, where they formed a distinct brown ring. Birds in juvenal plumage, of which we saw a number, with their spotted backs were difficult to distinguish among the lichen-covered rocks. In the adults the "horns" of the males could be seen at a considerable distance and distinguished them from the females. The Horned Lark is not so confiding as its arctic companion the Pipit, and unlike that bird it was never seen among the tilts and fish stages.

[*Otocoris alpestris praticola* Hensh. PRAIRIE HORNED LARK.—Erroneously recorded for southern Labrador by Norton (see *O. alpestris*).]

***Perisoreus canadensis nigricapillus* (Ridgw.).**

LABRADOR JAY.

Abundant permanent resident in forested regions.

Wherever there is tree growth there this jay is found in Labrador.

Its tameness and thieving qualities are noted by Cartwright. He makes frequent complaint of its robbing his traps of bait and occasionally he catches one in a trap. On November 5, 1770, he caught two with bird lime. On November 7, 1770, he notes: "The two jays which I caught on the fifth instant, I have hitherto kept confined in a cage; but they now have the liberty of the room; and I was greatly surprised to see them fly to me for food, and familiarly perch upon my hand; they even suffered me to stroke them with one hand, while they were eating some pork fat out of the other."

In another place (vol. 2, p. 151) on March 12, 1776, he speaks of the jay "which chants its short coarse tune every mild day through the whole winter." And he says this is the only song he had heard that winter until the day when the "cross-beaked linnets" sang. It is probable that the song of the Labrador Jay is very similar to that of the Canada Jay which is thus described by O. B. Warren (Auk, vol. 16, 1899, p. 14): "On pleasant days the male trilled from a spruce top a song of sweetly modulated notes wholly new to my ears. He always sang in *sotto voce*, and it required an acquaintance with the songster to realize that he, though so near, was the origin of those notes which seemed to come from somewhere up in the towering pines which surrounded this strip of swamp, so lost was the melody in the whispering, murmuring voices of the pines."

Seebohm ("Birds of Siberia," 1901, p. 33) speaking of the Siberian Jay (*Perisoreus infaustus*) says: "Their song was by no means unmusical, a low warble like that of the starling, but not so harsh."

Spreadborough found the Labrador Jay throughout Ungava to Ungava Bay. Turner says it is a resident and breeds at Fort Chimo; Weiz says it breeds at Okkak; Low found it very common throughout the interior and he records a nest with four eggs at Rigolet, March 24, 1894, and one with three eggs from the Northwest River about the same date. The young were able to fly from the nest at Grand Falls on May 18th. Audubon says he found the young following their parents on June 27, 1833, in southern Labrador.

Frazar noted in the second week of September an "immense migration" of jays. Flocks of a dozen to fifty were constantly passing. The direction of flight is not stated but it was apparently to the south.

Bendire ('95, p. 392-393) gives an interesting account of this bird copied from the manuscript notes of L. M. Turner from which we extract the following:

“This Jay is an abundant resident throughout the entire region wherever timber is to be found. I observed this bird at Rigolet, Davis Inlet, George’s River, Whale River, Fort Chimo, and far in the interior. At certain seasons it is more plentiful than at other times; after August it is very abundant until the next May, and is then very scarce until the following September. . . . The Indians will not be tempted to procure the eggs of this bird under any circumstances. They believe that if a person sees the eggs in the nest, and especially if he counts them, some great misfortune will befall him. Repeated inquiry among them elicited the statement that they had never seen the eggs, and knew nothing about the number laid.

“Its general habits are similar to those of the other members of this family. It is one of the greatest nuisances the trappers have to contend against, and one of these assured me that he had taken fifteen of these birds from a line of less than forty traps in a single day, and with good reason he called this bird a ‘wolverine’ with feathers on!

“I have never found the Labrador Jays in flocks, although several may be in the neighborhood, and on a single occasion only I saw five perched in one tree. If a gun be fired it is certain to cause a Jay to investigate it, and I think experience has taught him that food may be procured at such times.”

We saw the Labrador Jay only at Rigolet on July 18th, about six individuals in all, and we procured an adult male and one immature bird. The habits and notes appeared to be the same as in *canadensis*. We heard them emit a considerable variety of squeaks, whistles, and groans. The young are dark plumbeous in color, and look very much like a large Cat-bird; and they frequently acted in a similar manner, hopping about with their tails cocked up between their wings.

A young ♀ taken by us at Rigolet on July 18th, appeared blacker below than a young ♀ *canadensis* taken at Hawke’s Bay, Newfoundland on July 8th. In the young *canadensis* the white cheek line was noticeable, while in *nigricapillus* it was confined almost entirely to one point at the base of the bill. In *canadensis* there was a faint white mark on the forehead close to the bill. This was absent and the region almost black in our immature specimen of *nigricapillus*.

[*Perisoreus canadensis* (Linn.). CANADA JAY.—The earlier records of the Labrador Jay were entered under this heading and Macoun refers the bird of interior and western Labrador to this form, but in the absence of specimens we have placed it in the doubtful list.]

Corvus corax principalis Ridgw.

NORTHERN RAVEN; "CROW."

Common permanent resident.

While the American Crow is rare and limited to the southern part of Labrador the Raven is a common resident everywhere. It breeds along the entire coastline and in the interior. Cartwright complained that Ravens stole the bait from his traps, but occasionally were caught. Audubon found a nest at Little Mecattina Harbor in July, 1833, with full-fledged young on July 29th. He speaks of seeing flocks of 40 or 50 or more after the breeding season. Coues found a nest at Henley Harbor and Turner found them breeding at Fort Chimo. Low says they are a common resident throughout the interior and Spreadborough found them in pairs throughout the country. He shot one at Lake Mistassini on May 30, 1885.

We saw two Ravens at West St. Modest, one at Henley Harbor, one at Snug Harbor, three at Great Caribou Island, and two or three at Cape Charles. At Great Caribou Island on July 27th, we found the nest of a pair of these birds on a cliff on the westerly side of the island. The nest was in an inaccessible recess about 80 feet above the base of the cliff and 20 or 30 feet from the top. It was as large as a great clothes-basket and made of twisted and weather-bleached branches of fir and spruce. The rocks about were painted white with excrements. A full-fledged young was clinging to the rocks near, fluttering its wings to be fed, while the old ones which at first flew about croaking at our intrusion, carefully kept out of gunshot and disappeared. The old birds were everywhere very wary.

Mr. Schmitt has recorded the breeding of Ravens at Nain in mid-April.

Corvus brachyrhynchos C. L. Brehm.

AMERICAN CROW.

Uncommon summer resident on the southern coast.

Audubon noted a few Crows on the southern coast. Stearns said a few were occasionally to be seen as far north and east as Esquimaux River. Frazar said Crows were not rare along the southern coast and that none wintered. Palmer considered them "quite common"

at the Mingan Islands. Unlike the Raven, the Crow in these northern regions where no corn is grown, is very tame. Both Verrill and Brewster noted this in Anticosti, and it is a marked characteristic at Cape Breton.

[**Dolichonyx oryzivorus** (Linn.). BOBOLINK.—It is erroneously stated by Nuttall that this bird is found “from Labrador to Mexico.”]

[**Molothrus ater** (Bodd.). COWBIRD.—An erroneous record was made by Low ('96, p. 326) that the Cowbird is “common at Lake Mistassini.” Dr. J. Macoun states in a letter to us, dated March 13, 1906, that this record referred to the Rusty Grackle.]

Xanthocephalus xanthocephalus (Bonap.).

YELLOW-HEADED BLACKBIRD.

Accidental visitor.

We are able to add this species to the list of Labrador birds on the strength of the following note sent us on November 18, 1906, by Mr. Ernest Doane of West St. Modest: “About the 15th of September this year I saw a female Yellow-headed Blackbird. About the same date eight years ago I shot one, they being the only two I have ever seen here.”

Euphagus carolinus (Müll.).

RUSTY BLACKBIRD.

Common summer resident except in the Arctic zone.

Audubon says that many breed in Labrador, beginning to lay eggs about the middle of June. Frazar recorded that “five, evidently just arrived, were seen in a swamp at Esquimaux Point the latter part of May. They did not remain.” Coues found the young just from the nest on July 24th. Turner says: “Common. Breeds at Fort Chimo.” Young, July 10 1884. Low says: “Common throughout the interior.” Macoun adds: “Tolerably common in marshes from Richmond Gulf to Ungava; seen in flocks in the interior, July 24th. (*Spreadborough*); . . . Common and breeding at Lake Mistassini. (*J. M. Macoun.*)” Low gives the date of arrival at Lake Mistassini as May 14th. Frazar mentions that this species occasionally builds its nests in the tall wigwam-shaped woodpiles.

We did not see any Rusty Grackles in Labrador, but obtained the skin of a bird from the Eskimos at Hopedale.

***Pinicola enucleator leucura* (Müll.).**

CANADIAN PINE GROSBEAK; "MOPE"; "SPRUCE-BIRD"; "BULLFINCH."

Common summer resident, wintering in southern forested portions. Coues, Weiz, and Bigelow speak of this bird as common in summer back of the coast where there are woods. Packard records it as "abundant in summer only at Fort Chimo, where it breeds; resident south of 'Height of Land'." Stearns found it common in fall and winter on the southern coast. Low found it common on the upper Hamilton River and records one seen on May 1st. Macoun says: "One seen at Richmond Gulf, July 1st, 1896; not again observed in Labrador. (*Spreadborough*.) . . . Common in the winter at Lake Mistassini, Que. (*J. M. Macoun*.)"

Cartwright on March 20, 1776, says in his journal: "I shot an American bullfinch, which is as large as an English thrush. They come here in spring to breed and leave us at the latter end of the summer; this bird was full of partridge-berries." Also on March 30, 1778: "I saw a bullfinch for the first time this year."

We saw the skin of a Pine Grosbeak taken near Hopedale by an Eskimo, and Mr. Schmitt at Nain told us it bred there.

***Carpodacus purpureus* (Gmel.).**

PURPLE FINCH.

Common summer resident in southern Labrador.

Audubon "found this species from Labrador to Texas." Kumlien observed it off Resolution Island. Packard says it is "plentiful in southern portions."

***Loxia curvirostra minor* (Brehm).**

AMERICAN CROSSBILL.

Uncommon summer resident; may winter.

This species is more southern in its distribution than *leucoptera*.

Audubon says: "While in Labrador I was much disappointed at not finding a single bird of this species, although the White-winged Crossbill was tolerably abundant there." Macoun says that a set of 4 eggs was taken by L. Dicks at Cartwright on April 20, 1895, and that a bird of this species that had flown on board ship was taken in Hudson Strait.

***Loxia leucoptera* Gmel.**

WHITE-WINGED CROSSBILL.

Common permanent resident.

Weiz found it breeding at Okkak. Packard states that it is "resident and breeds in central portions; seen at Fort Chimo in winter only." Low found it "common on Hamilton River in March and April." Macoun says it is found in winter at Lake Mistassini and that a set of 4 eggs was found at Sandwich Bay on April 9, 1894.

On March 12, 1776, Cartwright records in his journal: "I was pleasingly entertained with the melodious singing of the cross-beaked linnets; they remain all winter with us, and feed on the seeds of the black spruces. What made their music more agreeable, was the novelty; this being the first time that I have heard the note of any bird this year, except the jay." Again on March 29, 1778, he says: "I heard some crossbeak linnets sing for the first time this year." He probably referred to the White-winged Crossbill. The full song of this bird is certainly very "melodious," and one of the most delightful of bird songs.

***Acanthis hornemanni* (Holb.).**

GREENLAND REDPOLL.

Abundant winter visitor in the northern portions.

Turner found this species "very abundant in winter," in Ungava occurring from September 1st to May 15th.

***Acanthis hornemanni exilipes* (Coues).**

HOARY REDPOLL; "PEOGWAK" (Eskimo).

Abundant permanent resident in northern Labrador.

Turner found it breeding plentifully at Fort Chimo and obtained

nests and eggs. Macoun says that a large series of eggs of this species was taken at Nachvak in 1895. Also one set of five eggs and nest were taken there by G. Ford in 1897, and two eggs at Fort Chimo on June 13, 1896.

***Acanthis linaria* (Linn.).**

REDPOLL; "ALDER-BIRD" (Stearns).

Abundant permanent resident.

The Redpoll is found and has been noted breeding throughout the length and breadth of the Labrador peninsula. During the fall and winter it collects in large flocks. During the summer it is not so gregarious.

Macoun says: "During the last week of May and early in June, 1899, Mr. A. P. Low found this bird breeding abundantly at the mouth of the Great Whale River, Hudson Bay, and I secured close upon 150 eggs of this species that were then collected. The nests were built low down in stunted willows, not more than two or three feet from the ground and contained five or six eggs each. I have also several sets that were taken at Cartwright, Labrador, by the late Lambert Dicks during June, 1895. . . . (*W. Raine*)." Kumlien says that "off Kikkertarsoak Islands, on the Labrador coast, as much as one hundred miles from land, these birds came aboard of the schooner in a gale. They were all young birds." Mr. Schmitt at Nain told us that two kinds of Redpolls nested there.

We noted 57 Redpolls on our trip north and 77 on our return, most of them at Great Caribou Island, Cape Charles, St. Lewis Inlet, and Rigolet. They were seen singly or in pairs, and occasionally in small loose flocks up to 8 or 10. Their most frequent call note was a rough *chug* or *chee* resembling very closely the call note of the White-winged Crossbill. They also frequently emitted a sweet Goldfinch-like note *deé-ar*. They were constantly singing either from the top of a spruce or fir or in the air, flying in irregular circles, flitting about from place to place, and frequently dropping suddenly into a tree where they continued their song. The song recalls the song of the White-winged Crossbill but is much inferior in quality. It is a succession of *chugs* interspersed with *deé-ars* and *chee-chee-chees*, with every now and then a fine rattling trill.

They were difficult birds to observe not because they were shy, for the reverse was the case, but because they were so restless. We saw several full-fledged young on July 28th at Cape Charles.

[*Aegiothus fuscescens*.— This “new species” described by Coues ('61, p. 222-223) from Labrador specimens was evidently *Acanthis linaria*.]

***Acanthis linaria rostrata* (Coues).**

GREATER REDPOLL.

Common winter visitor; rare summer resident in north.

Macoun gives this note: “A few pairs breed in northern Labrador, though its summer home is in Greenland. I have three sets of eggs of this bird that were collected by Mr. Ford at Ungava Bay, northern Labrador, June 15th, 1894. The nests were built in willows two or three feet from the ground and contained five eggs each, which are easily distinguished from [those of] the common redpoll by their larger size. . . . (*W. Raine*).”

Eifrig ('05, p. 240) says: “A specimen of what seems to be this species was taken on the vessel off the Labrador coast, Sept. 4, 1903.”

***Astragalinus tristis* (Linn.).**

AMERICAN GOLDFINCH.

Accidental visitor in southern Labrador.

The only definite record is by Kumlien of “an adult male caught on shipboard, August 22, 1877, off Cape Mugford, Labrador.”

***Spinus pinus* (Wils.).**

PINE SISKIN.

Uncommon summer resident in southern Labrador.

Audubon found the Pine Siskin abundant in Labrador. He says: “At the Harbour of Bras d'Or, on the coast of Labrador, in the end of July, we met with a great number of these birds. They were then accompanied by their young, and moved in flocks composed of a single

family, or at most of two." Bigelow saw a few south of the tree line. Macoun records several nests with sets of eggs taken at Hamilton Inlet; one set was taken on June 17, 1895.

We saw only one Pine Siskin in Labrador, a single bird that flew over Battle Island on July 15th.

***Passerina nivalis* (Linn.).**

SNOWFLAKE; SNOW BUNTING.

Abundant summer resident in the north; winter visitor in the south.

Packard says that the Snow Bunting is abundant at Fort Chimo and breeds on the islands in Ungava Bay, occasionally on the mainland. Weiz says it breeds at Okkak. Macoun records a large series of eggs from Nachvak taken by Mr. Gray, in 1897. Bigelow says it appeared at Port Manvers on August 10th, after which it was abundant. J. M. Macoun noted that it left Lake Mistassini for the north about May 10th. Between August 10th and May 10th would then be the season when the Snow Bunting is found wintering in the southern half of the peninsula.

We saw no Snow Buntings although we were told by Mr. Schmitt at Nain that a few spent the summer and bred there. Most if not all of this species go farther south in winter. He said they arrived from the south early in March and were abundant until the end of May. A few remained and bred in mid-June.

***Calcarius lapponicus* (Linn.).**

LAPLAND LONGSPUR.

Abundant summer resident in the north; winter visitor in the south.

Packard says of this species: "Abundant at Fort Chimo. Breeds near the mouth of the Koksoak River and on the larger islands in Ungava Bay." Weiz found it breeding at Okkak. Bigelow says it breeds from Nachvak, northward. Macoun records three sets of eggs from Nachvak. Stearns found it rather common in winter in southern Labrador, and Low says it is common on the Hamilton River in early spring. Spreadborough saw one on an island in James Bay on June 15, 1896, and not again until September. He found it in large numbers on the barren-grounds below Fort Chimo.

We saw a pair of these birds evidently breeding at Holton, just north of Hamilton Inlet, on July 19th. Mr. Schmitt at Nain told us that the Lapland Longspur arrived at that place early in May and bred in mid-June.

[**Passerculus princeps** Mayn. IPSWICH SPARROW.—The only known breeding place for the Ipswich Sparrow is Sable Island. We were unable to visit the sand dunes at Blanc Sablon and near Bradore Bay where it seems possible this bird may be found. We have learned that there are dunes at L'Anse aux Dunes, sand banks at the mouth of the Mingan River, a sand beach six miles long from Mingan west to Long Point; also a sand beach at Cape Porcupine south of Hamilton Inlet, but as yet there is no evidence of the presence of this species at such places on the Labrador coast.]

Passerculus sandwichensis savanna (Wils.).

SAVANNA SPARROW; "CHIP-BIRD."

Very common summer resident.

The Savanna Sparrow breeds everywhere in the open treeless regions of Labrador especially near the coast. Frazar speaks of it as the commonest land bird in southern Labrador. Low found it "very common" on the upper Hamilton River and obtained eggs on June 24th. Audubon found a nest with two eggs near Cape Whittle, on June 30th. Packard says it is "common throughout the region. Breeds at the mouth of the Koksoak River and at Davis Inlet." Coues says it is abundant in meadows and near the seashore, and it was still in Labrador on September 1st. Bigelow says it leaves Labrador the last of August and first of September. Audubon says it leaves early in September. Spreadborough found it common on the shores of James Bay to Richmond Gulf, but no more were seen in crossing northern Labrador till Fort Chimo was approached.

We found this sparrow common all along the southern and eastern coasts. At Battle Island there were two pairs with their young. On Great Caribou Island we saw four or five pairs. In the forested region of Rigolet we saw none. We were struck by the dark, almost black backs of the Labrador bird and the dark and clear-cut spots on the pure white of their breasts. We shot half a dozen specimens. Stearns ('90) says of the Savanna Sparrow: "White very clear, the dark inverted arrowpoints quite distinct. . . . One specimen alone had the

buffy suffusion covering the breast." He mentions examining thirty specimens. He also speaks of a small tuft of white feathers at the base of the primary coverts.

Reginald Heber Howe, Jr., gave the Labrador bird a subspecific rank as *Passerculus sandwichensis labradorius* but this form was not recognized by the American ornithologists' union. His description is as follows:

"*Type*, from Lance au Loup, Labrador, No. 4479, adult male. Collection E. A. & O. Bangs. Collected May 17, 1899, by Ernest Doane.

"*Geographical Range*: Labrador.

"*Subspecific Characters*: The largest of the *Passerculus sandwichensis* races. Wings, tail and tarsi longer than in *savanna*. Bill shorter and thicker. Upper parts uniform grayish black, with but little trace of rufous. Distinct white median line on crown, and with a great deal of bright yellow about the head. The eye line and ring, forehead, lores and auriculars being strongly tinged.

"*Remarks*: There is no difficulty in separating the two races *savanna* and *labradorius* on account of the greater size of the latter, their wing measurements showing no overlapping."

He had at this time two adult birds from Labrador.

We sent our specimens to Mr. Oberholser, at Washington, who kindly examined them and wrote us as follows, under date of February 4, 1907: "The Savanna Sparrows I have compared carefully with a large series in the collections here in Washington, and I cannot find any substantial difference worth recognizing by name. It is true they *average* very slightly darker and very slightly larger than more southern birds, but the differences are altogether *too slight* and too inconstant, in my opinion, to warrant their subspecific separation. Their dark color is due in part to their worn condition, and in both this respect and in size I can match them with southern breeding birds. I am somewhat surprised myself, for I have always entertained a suspicion that *labradorius* was a good race, though I have never before made any actual comparison."

Zonotrichia leucophrys (Forst.).

WHITE-CROWNED SPARROW.

Abundant summer resident.

This is probably the most common sparrow in Labrador, as, although it is a bird of the Hudsonian zone it encroaches on the Arctic zone, breeding contentedly among the stunted fir and spruce bushes in sheltered ravines along the entire wind-swept coast as well as in the forested region of the interior. Audubon, Stearns, Frazar, and Palmer speak of it on the southern coast. Coues, Weiz, Packard, and Bigelow found it along the eastern coast. Turner found it "very plentiful" and "breeding abundantly at Fort Chimo." Low says it is "very common" on the upper Hamilton River and Spreadborough found it "very abundant from Richmond Gulf across Ungava to Fort Chimo."

Audubon says they reach Labrador about June 1st. Frazar observed them first at Esquimaux Point on May 18th, and Low noted them on May 16th on the upper Hamilton River. Audubon found a nest and five eggs on July 6th at American Harbor. Low obtained eggs on June 25th on the upper Hamilton River. Macoun records eggs from Whale River in June, four sets of four eggs each; one set of four taken at Fort Chimo in June; one set of four taken at Nachvak in June, and one set of three from an island in James Bay on June 23d.

We found the White-crowned Sparrow everywhere in Labrador not only on the bleak coast, wherever there were sheltering ravines but also in the forested region at Cape Charles, St. Lewis Inlet, Cartwright, and Rigolet. It was the common dooryard bird and was frequently to be seen hopping about the fish stages and tilts, where, without their shelter, we should not have expected to have found this bird of the Hudsonian zone. We even saw one singing from the cross-stay at the main-mast head of a schooner anchored close to the shore at White Bear Island, one of the bleakest outer islands. Mr. W. B. Cabot told us of seeing one hopping along the body of a sleeping Eskimo dog, picking at the flies that surrounded him. The call note of this bird as we heard it in Labrador was characteristic and easily recognized, a metallic *chink*. Its alarm note was a sharp *chip*. Its song we often heard even in foggy and wet weather. When singing in a tree the bird generally sat concealed near the trunk several feet from the top. We also heard the song from the sod-covered roofs of the houses and, as just mentioned, from the rigging of a schooner.

There is a long and somewhat mournful stress laid on the first note of the song and a buzz, not easily expressed in words, comes in near the end. We wrote the song down in various ways to memorize it as *more, wet-wetter-wet chézee*, or *wheéa, sorg a lét-zee* or *whee whit, whittle-wee-déwhee*, all of course very unsatisfactory. We saw full-fledged young on July 28th. They are very plain, spotted birds with but a faint grayish streak to suggest the glorious white crown of the adult.

Mr. Schmitt at Nain told us that this species arrived there on May 18th and laid eggs by the middle or end of June.

Zonotrichia albicollis (Gmel.).

WHITE-THROATED SPARROW.

Common summer resident in southern part.

Frazar thought this species arrived at Esquimaux Point on the southern coast about May 20th. Stearns found them everywhere common on the southern coast. Low reported them common at Lake Mistassini where they arrived on May 20th, and on the Romaine River. He heard them at Grand Falls, Hamilton River, which is the farthest north of which we have record.

We found four of these birds in the shelter of the woods at and near Mary Harbor, St. Lewis Inlet, on July 12th, and three in the woods near White Bear Bay, Cape Charles. In the woods of Cartwright and Rigolet we did not find them. The birds we observed were in full song.

Spizella monticola (Gmel.).

TREE SPARROW.

Common summer resident.

Audubon failed to find the Tree Sparrow in Labrador and Stearns speaks of it as occurring on the southern coast only in spring and fall. He records the latest date as October 12th. Packard says it is "common throughout the entire country. Breeds plentifully at Fort Chimo." Coues says it is "common in all wooded districts." Low states that it is "common everywhere. Breeds in great numbers on

upper Hamilton River. Seen May 31st, eggs June 21st." He records its arrival at Lake Mistassini on May 15th. Macoun says that none were seen on James Bay till reaching Fort George when they became common, across Ungava (Spreadborough). Quite common at Lake Mistassini (J. M. Macoun). Eggs in June, 1898, at Whale River. Bigelow records "a good many at Port Manvers." Mr. Schmitt told us that this species bred at Nain early in July.

Our experience with this bird in Labrador was rather peculiar. Although we were constantly on the lookout for it we failed to find it in such favorable localities as St. Lewis Inlet, Cartwright, and Rigolet, and we met with the bird only at Great Caribou Island near Battle Harbor, and at Cape Charles. On July 27th at Great Caribou Island which is almost entirely arctic in its characteristics we found some three pairs of these birds in small thickets of balsam fir and black spruce which in sheltered localities managed to reach a height of three or four feet. At and near Cape Charles on July 28th we saw 4; on July 29th, 10; on July 30th, 8; and on July 31st, 1. On Great Caribou Island the males were in full song and we saw no young birds. At Cape Charles the males were singing less frequently and we saw several immature but fully grown birds, one of which we took. The chestnut caps of the adults appeared to be very bright and the spot on the breast a deep black. The song was a simple one and easily expressed in words, and unlike, it seemed to us, the song of these birds heard in Massachusetts in the spring. We noted the song as *seet-seet*, *seetiter-sweet-sweet*, the last two notes lower than the first two. The birds were unsuspecting and allowed of close approach.

[**Spizella socialis** (Wils.). CHIPPING SPARROW.— This bird is not found in Labrador, although Nuttall makes the loose statement that it is found "from Labrador to the tableland of Mexico."]

Junco hyemalis (Linn.).

JUNCO; BLACK SNOW-BIRD.

Generally uncommon summer resident throughout the peninsula; but common in some localities.

Palmer records "but one at Mingan." Stearns found it not rare

in southern Labrador in spring and fall but did not find it in numbers. Coues says: "Not as abundant as might be expected." Low says it is "common at Lake Mistassini, and upper Hamilton River. Seen May 29th. Eggs June 27th." Packard recorded that it is not seen in the Ungava district, but is common in eastern and southern portions of Labrador and breeds at Davis Inlet and Rigolet. Macoun records a "pair breeding at Fort George; only seen twice in crossing Ungava from Richmond Gulf to Fort Chimo (*Spreadborough*). . . . Abundant in summer at Lake Mistassini." Bigelow says it is "locally common as far as the tree line, particularly at Aillik," and Kumlien records "one obtained on shipboard off Belle Isle, October, 1878." Mr. Schmitt told us that a few bred at Nain the end of June.

We saw very few Juncos in Labrador and only at Cartwright and Rigolet. At the former place on July 17th, we saw two, at the latter on July 18th, we saw about eight, one of which, an adult male, we procured. We submitted this bird to Dr. J. Dwight, Jr., who found it a typical *hyemalis*.

Melospiza cinerea melodia (Wils.).

SONG SPARROW.

Uncommon summer resident in southwestern part.

The only locality recorded for this bird in Labrador is Lake Mistassini. Low states it is "common at Lake Mistassini" and that it arrives there the last of May. Thinking that Lincoln's Sparrow might have been mistaken for the Song Sparrow, we wrote to Dr. J. Macoun who replied under date of March 13, 1906, as follows: "My son who was at Lake Mistassini . . . says that the Song Sparrow was a common bird there and not Lincoln's Sparrow."

The Song Sparrow probably occurs elsewhere in southwestern Labrador as Merriam lists it as "a rather common summer resident" at Point des Monts.

Melospiza lincolni (Aud.).

LINCOLN'S SPARROW.

Common summer resident in southern part.

The discovery of this sparrow is recorded by Audubon in his Labra-

dor journal for June 27, 1833. The locality was American Harbor near the mouth of the Natashquan River. He says: "We shot a new species of Finch, which I have named *Fringilla lincolni*; it is allied to the Swamp Sparrow in general appearance, but is considerably smaller, and may be known at once from all others thus far described, by the light buff streak which runs from the base of the lower mandibles, until it melts into the duller buff of the breast, and by the bright ash-streak over the eye. The note of this bird attracted me at once; it was loud and sonorous; the bird flew low and forward, perching on the firs, very shy, and cunningly eluding our pursuit; we, however, shot three, but lost one. I shall draw it to-morrow." He named the bird after one of his party, Thomas Lincoln, of Dennisville, Maine.

Bigelow says the Lincoln's Sparrow is common as far north as Hamilton Inlet on the wooded parts of the coast. Turner, however, found it as far north as Fort Chimo where he states it is rare. He obtained a male there on June 10, 1883. This is the only record we have for the north of Hamilton Inlet. The bird does not seem to be found in the interior. Dr. John Macoun writes us, under date of March 16, 1906, that it is not found at Lake Mistassini, and that he has no record of its occurrence in the interior of northern (Labrador) Quebec.

We found Lincoln's Sparrow only at Mary Harbor on July 12th where we saw four; and at Cape Charles where on the 28th, 29th, and 30th of July we saw 4, 10, and 4, respectively. We had previously found it common at Bay of Islands, Newfoundland. It was everywhere very retiring, skulking among the thick growths of evergreens and only a few times did we hear it sing in Labrador. It sang as late at the 29th and 30th of July. In singing it keeps concealed so that it is very difficult to see the performer. The song that we heard was a wild, hurried warble, somewhat like that of the Purple Finch but quicker, ending at times with a fainter trill suggestive of a House Wren. Its call note was a sharp *chip* and it also occasionally emitted a *smack*, probably an alarm note.

Melospiza georgiana (Lath.).

SWAMP SPARROW.

Common summer resident in southwestern Labrador.

Audubon "found it plentiful in Labrador." In Anticosti just south of the Labrador region it was found in abundance by Brewster.

Passerella iliaca (Merr.).

FOX SPARROW; "RUSSINGEL"; "RED SINGER";
"RED THRUSH" (Stearns).

Common summer resident in southern Labrador; May 20 to September 1.

Audubon says: "They leave Labrador about the 1st of September in small groups, formed each of a single family. When in that country I frequently observed them searching along the shores for minute shell-fish, on which they feed abundantly." Frazar says they "arrived at Esquimaux Point on May 20th, soon becoming common and rare again, evidently passing farther north to nest; but at Hegaska, on my return in August, I saw a pair with their young." Packard says: "Common along southern portions; young at Rigolet in June." Bigelow found a few at Aillik. Macoun says it is common from Moose River to Richmond Gulf; not seen crossing to Ungava; July 1, 1896, young able to fly (Spreadborough).

We found the Fox Sparrow common at Forteau, Cartwright, Rigolet, and Cape Charles. At Forteau we found them directly on the coast. The other three localities are all farther inland and Hudsonian in character. The bird was everywhere in full song even as late as July 30th at Cape Charles. The song seemed richer and fuller than the best song given by this species during the spring migration in Massachusetts. Its clear flute-like notes are somewhat ventriloquial in character, and as the bird sings generally from a concealed perch inside of a spruce or fir tree a foot or two from the top, it is often difficult to find the performer. We have written down the song very inadequately in words thus: *cher-ee, hear-her, hear-her, tellit*. Or *to-whip, to whee, oh-whee buzz tellit*, the last note short and faint and the main stress on the second and third bars.

The long drawn call note *stssp* so commonly heard in Massachusetts during the migrations, was rarely heard in Labrador. A short *chip chip* was occasionally emitted, and the bird when disturbed sometimes gave the usual alarm note, a loud *smack*, richer than that of the Junco and more like that of the Brown Thrasher. One individual who was *smacking* in a fir tree emitted faint sneezy notes with motions of swallowing between the *smacks*.

[**Pipilo erythrophthalmus** (Linn.). TOWHEE. — Audubon states that this bird occurs northward to Labrador, but gives no further note of it for Labrador. J. A. Allen's note in Packard ('91, p. 419) is: "Doubtless an error." We shall let it stand as doubtful.]

[**Zamelodia ludoviciana** (Linn.). ROSE-BREADED GROSBEAK. — Nuttall says: "On the dreary and desolate coast of Labrador Mr. Audubon found this species breeding commonly." This must be a mistake for Audubon ('35, vol. 2, p. 167) says: "I saw none in Labrador" although he found them in Newfoundland.]

[**Petrochelidon lunifrons** (Say). CLIFF SWALLOW. — Verrill found this species breeding in large numbers at Cape Eagle, Anticosti, in July, 1861. We have no records, however, for Labrador although it has doubtless visited that country.]

Hirundo erythrogaster Bodd.

BARN SWALLOW.

Very rare summer resident.

The only record is that of Packard ('91, p. 416): "Breeds at Northwest River at the head of Hamilton Inlet." The absence of barns and farms in Labrador perhaps accounts for the rarity of this bird. The locality mentioned above is the only one where cattle are kept.

Iridoprocne bicolor (Vieill.).

TREE SWALLOW.

Common summer resident locally.

Packard says it is "abundant throughout northern portions"; breeds at Fort Chimo. Low states that it is "common throughout the interior. Seen May 25th." He records it on May 10th at Mistassini.

Frazar says he saw two when he arrived on the coast on May 22d. Later in July, several passed his house at Cape Whittle. Palmer states they were "seen at . . . Mingan Islands though not abundant." Kumlien wrote that two followed the schooner for two days in succession off Belle Isle in August, 1877, and adds the query: "Where were they during the night?"

Cartwright records the arrival of two swallows on May 18, 1778.

We saw not a swallow of any kind in Labrador.

Riparia riparia (Linn.).

BANK SWALLOW; SAND MARTIN.

Common summer resident in a few localities.

Audubon ('35) says that "many Sand Martins" were seen in Labrador and "it rarely begins to breed before the beginning of June." Weiz reported that it bred at Okkak. Mr. Goldsby, one of the Moravians, told us of finding a Sand Martin's hole with two eggs in a sand bank at Ogjuktok Inlet near Hopedale.

Ampelis cedrorum (Vieill.).

CEDAR WAXWING.

The only record for Labrador we have is that of Low: "Rare at Lake Mistassini." He found it there after the middle of June.

Lanius borealis Vieill.

NORTHERN SHRIKE; "BUTCHER-BIRD."

Not uncommon summer resident.

Packard says that it is not common at Fort Chimo, where it breeds; young out of nest June 30, 1884. It is said to be common in more southern parts. Low records that it is "common on Hamilton River; seen April 16th." Norton records a young female from Lake Melville, July 29th, in faded juvenal plumage. Cartwright records that on May 14, 1779, at Sandwich Bay he took "an egg out of a butcher bird's nest, which is in the top of a spruce tree." On May 20th he

took six more eggs and shot and stuffed both the male and female birds.

[*Vireo olivaceus* (Linn.). RED-EYED VIREO.— We have no exact record of this bird for Labrador although Verrill found it common at Anticosti. Nuttall says it “appears to inhabit every part of the American continent from Labrador to . . . Jamaica.”]

[*Vireo philadelphicus* (Cass.). PHILADELPHIA VIREO.— One was obtained at Moose Factory in 1860, but there is no record for Labrador.]

[*Vireo noveboracensis* (Gmel.). WHITE-EYED VIREO.— The only record of this bird for Labrador is that of Audubon ('39, p. 431): “A few were seen by me in Labrador.” As this is a bird of the Upper Austral zone, the record has been discredited by J. A. Allen (Packard, '91, p. 415), yet it breeds regularly as far north as Essex County, Massachusetts, and stragglers have been recorded from New Brunswick, Cape Breton, Ontario, and Newfoundland. It would perhaps be no more remarkable than the record of the Little Blue Heron. It is possible, however, that Audubon confused the Philadelphia Vireo with this species.]

[*Mniotilta varia* (Linn.). BLACK AND WHITE CREEPER.— Drexler took this bird at Moose Factory and Brewster found it at Anticosti, but we have no records for Labrador.]

Helminthophila rubricapilla (Wils.).

NASHVILLE WARBLER.

Very rare summer visitor in the southern part.

The only record is that of Audubon ('39, p. 461): “A few were procured by us in Labrador.” Cooke ('04, p. 37) does not record this bird northeast of Gaspé Bay. Audubon's record is unique, but can hardly be doubted.

Helminthophila peregrina (Wils.).

TENNESSEE WARBLER.

Not uncommon summer resident in Hudsonian zone.

Packard states that it was obtained by Drexler at Fort George, James Bay, in June and July, 1860. Low says it is “not rare at Lake Mistassini” where it arrived between the 1st and 15th of June.

Our experience with this bird was interesting but decidedly tantalizing. At Mary Harbor, St. Lewis Inlet, on July 12th, at Rigolet on July 18th, and at Cape Charles on July 28th and 29th, we heard the song of a warbler which we are convinced was of this species, although we were unable to catch a glimpse of the performer except on July 28th. This was but a glimpse only of a small neat warbler, nearly white below and darker above. We were unable to procure the bird. The song was similar at all three places, and we had heard it on July 8th at Lark Harbor, Newfoundland, but were unable to see the shy performer. Any attempt to discover the bird resulted always in the cessation of the song. At Cape Charles when the song ceased on one occasion the bird began emitting a sharp chipping alarm note which it kept up almost constantly. We followed the bird about for nearly three quarters of an hour in a thicket of spruces, fir, alders, and willows but only twice did we catch momentary glimpses of him. Finally the bird became silent and we were obliged to give up our quest. On the 29th we did not once see the bird in a two-hour search.

The song appeared to be the same in all cases and to consist of three parts, although the last part was occasionally omitted. The middle part suggested the song of the Nashville Warbler. We have written the song thus: *tsit, tsit, tsit — wot, wot, wot — tsee, tsee, tsee.*

[**Compothlypis americana usneae** Brewst. NORTHERN PARULA WARBLER. — Brewster saw this bird at Anticosti but we have no records for Labrador.]

[**Dendroica tigrina** (Gmel.). CAPE MAY WARBLER. — Drexler obtained this bird at Moose Factory but we have no record for Labrador.]

Dendroica aestiva (Gmel.).

YELLOW WARBLER.

Common summer resident locally in southern parts.

Drexler obtained one July 12, 1860, at Fort George, James Bay. One was seen by Frazar on June 4th and another in August at Kegaska on the southern coast. Low states that it is "common at Lake Mistassini; seen near Grand Falls, Hamilton River, May 31st." Macoun states that it is common up James Bay to Richmond Gulf; nest June 26, 1896, on an island in James Bay; none seen crossing Ungava (Spreadborough).

***Dendroica caerulescens* (Gmel.).**

BLACK-THROATED BLUE WARBLER.

The only record is that of the finding of a dead bird by Audubon ('35, p. 309): "In Newfoundland I saw none, and in Labrador only a dead one, dry and shrivelled, deposited like a mummy in the fissure of a rock, where the poor bird had fallen a victim to the severity of the climate."

***Dendroica coronata* (Linn.).**

YELLOW-RUMPED WARBLER; MYRTLE WARBLER.

Common summer resident, chiefly in the Canadian zone.

Audubon states that this was among the first birds observed by him in southern Labrador. Stearns says it is "common in interior. Breeds." Frazar saw four on one day in July at Cape Whittle, and Low records a "specimen from Grand Falls, Hamilton River, May 31st."

***Dendroica maculosa* (Gmel.).**

MAGNOLIA WARBLER.

Common summer resident in the Canadian zone.

Audubon found a nest with five eggs of this species in southern Labrador in the beginning of July, and in the first days of August he saw many young following their parents. Low says it is "not rare at Lake Mistassini," where it arrives the last of May.

***Dendroica castanea* (Wils.).**

BAY-BREASTED WARBLER.

Very rare summer resident.

Turner records that "three individuals were seen at Black Island, Hamilton Inlet, by me July 9, 1882. Two were shot, but lost in the thick undergrowth; one of the birds was actually in my hand, but escaped." It is a bird of the Canadian zone and has been taken just outside of the limits of Labrador at Moose Factory.

***Dendroica striata* (Forst.).**

BLACK-POLL WARBLER.

Very common summer resident.

The Black-poll Warbler frequents all the wooded region of Labrador in summer and advances well to the borders of the Arctic zone taking advantage of islands of the Hudsonian zone in the form of dwarfed firs and spruces. Audubon says it arrives in southern Labrador from the 1st to the 10th of June. Low found it on the upper Hamilton River on May 31st. Spreadborough saw it at Fort George, James Bay, on June 20th and he found it common throughout Ungava, where he noted the last one at Fort Chimo on August 23d. Turner found it breeding at Fort Chimo and Macoun notes two sets of eggs from this point.

We found the Black-poll Warbler common at Mary Harbor, St. Lewis Inlet, also at Cartwright and Rigolet, and at Cape Charles; that is, wherever we came in contact with the Hudsonian fauna. The males were singing commonly.

***Dendroica blackburniae* (Gmel.).**

BLACKBURNIAN WARBLER.

Very rare summer resident in the southern part.

The only record of this bird of the sub-Canadian and Transition zone for Labrador is that of Audubon ('35, p. 208): "In Labrador we saw several individuals of both sexes."

***Dendroica virens* (Gmel.).**

BLACK-THROATED GREEN WARBLER.

Very rare summer resident in southern Labrador.

Frazar records: "A bird of the year, which I killed at Esquimaux Point on September the 4th, was all I saw of this species." Palmer referring to this species says: "Two birds were taken at the Mingan Islands."

***Dendroica vigorsii* (Aud.).**

PINE WARBLER.

Very rare summer resident.

Coues obtained on August 1st in dense fir woods, a young bird just able to fly. This was apparently at Esquimaux Bay and constitutes the only record of this species we have for Labrador.

***Dendroica palmarum hypochrysea* Ridgw.**

YELLOW PALM WARBLER.

Rare summer resident in southern Labrador.

Audubon says: "I found it abundant in Newfoundland and Labrador, where I seldom passed a day without searching for its nest, although I am sorry to say, in vain."

According to Cooke ('04, p. 95), Hudson Bay is supposed to be the dividing line between the summer home of the western Palm Warbler and *hypochrysea*. He adds: "The northern limit of its range is not yet clearly determined, but is probably in Quebec, southern Labrador, and Newfoundland."

***Seiurus aurocapillus* (Linn.).**

OVEN-BIRD.

Rare summer resident in southern portions.

The only record we have for this bird is from Stearns who said it was "not uncommon in the interior. Breeds." Verrill and Brewster observed it at Anticosti.

***Seiurus noveboracensis* (Gmel.).**

WATER-THRUSH.

Not uncommon summer resident in wooded portions.

The Water-Thrush is generally distributed throughout the wooded portions of Labrador. It has been seen even at Fort Chimo and at

Koksoak according to Macoun, who also says it is common at Fort George, James Bay, and that one was seen a short distance inland from Richmond Gulf. It breeds commonly at Lake Mistassini where Low notes its arrival on May 20th. Turner took several, including young of the year, at Davis Inlet in August, 1884. Bigelow says it is locally common as far north as Aillik. Low says it is common about the Grand Falls, Hamilton River.

We did not find the bird in Labrador even in the places where the Black-poll Warbler was common.

***Geothlypis trichas brachidactyla* (Swains.).**

NORTHERN YELLOW-THROAT.

Common summer resident in southern Labrador.

Stearns found it common at Natashquan and records it at this point on May 26, 1881. Packard states that it is "common in southern portions." These are the only records.

***Wilsonia pusilla* (Wils.).**

WILSON'S WARBLER.

Not uncommon summer resident in southern Labrador.

Audubon in his Labrador journal speaks of finding the nest and four eggs of this species at Little Mecattina Harbor on July 14, 1833. Stearns noted it near the Esquimaux River. Low saw it near the Grand Falls of the Hamilton River on May 31st and states that it is not rare at Lake Mistassini. Spreadborough saw one at Fort George, James Bay, on June 20th.

We saw two Wilson's Warblers among the alder and fir thickets at Mary Harbor, St. Lewis Inlet, on July 12th, and three at Cape Charles on July 29th and 30th. They were in song at this time.

***Wilsonia canadensis* (Linn.).**

CANADIAN WARBLER.

Rare summer resident in southern Labrador.

Audubon says: "I have traced it from Pennsylvania to Labrador";

and again: "Nor did I see any in Labrador after the first of August." Bigelow noticed it in the extreme south of Labrador.

***Setophaga ruticilla* (Linn.).**

REDSTART.

Rare summer resident.

One was obtained by James McKenzie at Rupert House, September 3, 1860; Brewster ('84, p. 372) reported that "several [were] seen at Fox Bay [Anticosti] and others near Mingan." Eifrig says that "a poor skin of one was shown to Mr. Halkett at Port Burwell by the factor of the station, showing that this species occasionally reaches the north of Labrador."

***Motacilla alba* Linn.**

WHITE WAGTAIL.

The only record for this bird is by Turner: "Four individuals of this species were seen by Alex. Brown and James Lyall (of the Hudson Bay Company), August 29, 1883, at Hunting Bay, 4 miles south of Fort Chimo. These persons described the bird accurately, and declared they were the two parents and two young of the year. I must add that I place the fullest reliance in their assertion."

***Anthus pensilvanicus* (Lath.).**

AMERICAN PIPIT; TITLARK; "WAGTAIL."

Abundant summer resident throughout the Arctic zone.

Everywhere in Labrador within the limits of the Arctic zone this bird is found breeding. Stearns reported it as common along the southern coast as far west as Mingan. Beyond this the forest region of the Hudsonian zone comes down to the shore. Audubon met with them abundantly, and found a nest with a set of five eggs near Cape Whittle on June 29, 1833. On the eastern coast this species is everywhere to be found in summer and it has been reported there by Coues, Packard, Weiz, and Bigelow. Macoun records a set of eggs taken at Hamilton Inlet on June 30, 1895, and another on June 15th

at Nachvak. Turner found them breeding plentifully at Fort Chimo in the extreme north, and Spreadborough found them common on the rocky islands in James Bay, and on all the hills between Richmond Gulf and Ungava Bay. He took a nest with five eggs on June 18, 1896.

We found Pipits commonly wherever we landed on the Labrador coast, and we frequently saw or heard them as we steamed along the shores. We noted 49 individuals on our way north, and 103 on our return trip. Their slim graceful forms and quaker-gray and brown plumage make them very attractive birds. We frequently saw them walking on the roofs of the tilts and fish houses as well as on the rocks close to the dwellings of the inhabitants. There were about eight pairs on Battle Island. They frequented commonly the rocky and pebbly shores of the sea. During our visit they appeared to be busy feeding their young, and could frequently be seen with their bills full of insects. We found a full-fledged young at Battle Harbor on July 15th.

The habit of wagging the tail up and down is shared even by the young that are able to fly but a short distance, birds whose tails are only half grown. In walking, Pipits thrust their feet well out in front and nod their heads gracefully in a dove-like manner.

Their call note *tseé-ket*, so familiar on the Massachusetts coast in the autumn migrations was occasionally heard, but the common note at this season, and one constantly repeated by reason of the solicitude for their young was a loud whistling *tswit*, resembling at times very closely the alarm note of the Spotted Sandpiper. Once or twice we heard a *churr* like that of a Red-poll.

The flight song of the American Pipit is an interesting performance. One was observed at Great Caribou Island on July 11th under especially favorable circumstances. He was standing on a rock in a valley about 150 feet nearly vertically below us. He suddenly sprang into the air, mounting nearly vertically, but circling slightly. As he went up he sang repeatedly a simple refrain, *che-whée, che-whée* with a vibratory resonance on the *whée*. Attaining an eminence of some 50 feet obliquely above us, perhaps 200 feet from the ground, he checked himself and at once began the descent. He went down faster and faster, repeating his song at the same time faster and faster. Long before he reached the ground he set his wings and tipped from side to side to break his descent. After remaining quiet on the ground

for a few moments he repeated the performance and we watched him go up four or five times. On one occasion he was twenty seconds going up, emitting his refrain forty-eight times. In the descent he was quicker, accomplishing it in ten seconds and singing thirty-two bars of his song. Most of the birds had stopped singing by the middle of July, but we occasionally heard a rapid repetition of the call notes *tsée-ket*, suggestive of a Barn Swallow and almost forming a song.

[**Troglodytes aëdon** Vieill. HOUSE WREN.— There is no record for this bird in Labrador except this sentence of Nuttall: "Its northern migrations extend to Labrador." For this there is no real foundation.]

Olbiorchilus hiemalis (Vieill.).

WINTER WREN.

Uncommon summer resident in southern Labrador.

Macoun says it is not rare at Lake Mistassini. Audubon saw the bird in southern Labrador on July 20th. "They leave Labrador by the middle of August at the latest." Frazar said it was "not common, though regularly heard in the thick woods about Esquimaux Point."

Sitta canadensis Linn.

RED-BREASTED NUTHATCH.

Uncommon summer resident in southern Labrador.

Audubon "saw . . . only one in Labrador, which had probably been blown thither by a gale." Frazar "saw several broods with their parents at Esquimaux Point the first week of September." Palmer says: "I captured a young bird with a dip-net, on board, when about 12 miles south of Natashquan Point, Labrador, on August 9."

We heard one in a small grove of spruces near Indian Cove at Cape Charles on July 30th.

Parus atricapillus Linn.

CHICKADEE.

Not uncommon summer resident in southern Labrador.

The records for this species are very few. J. M. Macoun found it

rather common at Lake Mistassini. Turner says: "I am informed by credible persons, long resident in the country, that two species of Chickadees occur at Northwest River [Hamilton Inlet]." Bigelow ('02) says: "Locally abundant in timbered regions." This note is probably intended for *P. hudsonicus*, as the latter bird is not mentioned in this first paper but is listed in his second paper (Bigelow, '02a) on the ornithology of the Brown-Harvard expedition, which omits mention of *atricapillus*.

***Parus hudsonicus* Forst.**

HUDSONIAN CHICKADEE.

Abundant permanent resident.

Audubon found a nest of this species with young in southern Labrador on July 18th. Frazar says he saw two in the spring at Esquimaux Point but "none others until my return in September, when they were migrating in abundance along with the Labrador Jays. . . . They passed in fifties and hundreds, and the two mornings that I was out I must have seen as many as twenty such bunches." Stearns said they were abundant along the coast all the year. Low says they are abundant on Hamilton River from April 1st. Spreadborough observed them about 75 miles inland from Richmond Gulf and at the George River. Turner says they are abundant in the wooded tracts; young of the year were seen at Davis Inlet on July 19th and at Fort Chimo in early August.

Rhoads ('93, p. 328-330) quotes Forster that the type locality of *P. hudsonicus* is Fort Severn at the mouth of the Severn River, and describes *Parus hudsonicus unгава* on the basis of specimens from Fort Chimo collected by Turner. Another specimen from Rigolet is referred to this form, and one from southern Labrador is intermediate.

We saw only three Hudsonian Chickadees in Labrador and these were in the woods near Rigolet.

As there has been some discussion of the song of this bird, the present status of the question is given here. The Hudsonian Chickadee was not known to have any song, and no mention seems to have been made of it until 1905 when H. W. Wright (*Auk*, vol. 22, 1905, p. 87) in speaking of a Hudsonian Chickadee he had seen at Ipswich, Massachusetts, on November 12, 1904, stated that "[he] was very finely seen

while he gave a sweet warbling song." Of another bird, seen on November 25th, he said: "The Belmont bird was also well seen and gave a few notes of the warbling song." At Cape Breton Island in August, 1905, Dr. Townsend heard in four different places a pleasant warbling song emitted by this species. "It was a low, bubbling, warbling song, which I vainly attempted to describe in my notes. It began with a *pset* or *tsee*; followed by a sweet but short warble" (Auk, vol. 23, 1906, p. 178). While this was in press, C. H. Clark wrote as follows in the Journal of the Maine ornithological society (vol. 8, 1906, p. 27): "I ran into a flock of Hudsonian Chickadees (ten or twelve), and these, too, were exercising their voices, and mingled with the 'dee, dee, dees,' and 'chick-a-dee dees' was a sweet little song of three or four notes and new to me, but I was not long in doubt as to what it was, for soon a Hudsonian came out on a limb not over three feet from my face and sang it right at me." This was at Lubec, Maine, on February 11, 1906. Again in the same Journal (vol. 8, 1906, p. 83) Dana W. Sweet records a pair of Hudsonian Chickadees on Mt. Abraham, near Phillips, Maine, on June 22, 1906. He says: "Twice I heard the song of the Hudsonian Chickadee." Dr. Townsend wrote to Mr. Sweet asking for fuller particulars. Mr. Sweet kindly replied as follows under date of December 8, 1906: "I have never read anything about the notes of the Hudsonian Chickadee. . . . January 19, 1905, I heard what I am very sure is the warbling song that you mention. At the time I was unable to describe it in my notes. . . . It was, however, entirely different from any other notes of either species. As I remember, it was a clear, sweet soprano, and was quite a remarkable performance from a musical standpoint."

Although we did not hear the song in Labrador, we heard at Bay of Islands, Newfoundland, on July 6, 1906, a song which Dr. Townsend recognized as the warbling song of this species he had heard the previous summer in Cape Breton. We are both agreed that it should be classed as "a warbling song" of considerable merit. We had been watching a pair of Hudsonian Chickadees with the hope of hearing them sing, but as the birds were concealed in the spruces at the time the song was heard, we could not be absolutely sure that one of these was the author. In speaking of the song Mr. Brewster ("Birds of the Cambridge region," 1906, p. 379) says: "I have never heard anything of the kind from the Hudsonian Chickadee, although I am reasonably familiar with that species, having had abundant

opportunities for studying its notes and habits in the forests of northern New England where I have met with it on many different occasions and during every month of the year excepting April.”

Regulus satrapa Licht.

GOLDEN-CROWNED KINGLET.

Common summer resident in southern portions.

Low found this bird “common on Hamilton River between Grand Falls and Sandy Lake; rare to northward; seen May 19th.” Bigelow says it is “fairly common in patches of spruce timber as far as Aillik.” Macoun records a set of seven eggs from Cartwright taken on June 15, 1895. “Nest suspended from a branch of a spruce tree 15 feet from the ground (W. Raine).”

Regulus calendula (Linn.).

RUBY-CROWNED KINGLET.

Common summer resident in southern portion; May 11 to October 11.

Audubon and Stearns found this bird on the southern coast; Coues found it at Rigolet; Low says it is “very common along Hamilton River between Grand Falls and Sandy Lake.” J. M. Macoun says it breeds commonly at Lake Mistassini where Low noted its arrival on May 11th; Spreadborough found it at Fort George, James Bay, and it was common at Richmond Gulf.

[**Polioptila caerulea** (Linn.). BLUE-GRAY GNATCATCHER.— Audubon ('39, p. 551) says: “A pair were observed in one of the valleys of Labrador.” It seems improbable that this bird of the Austral zones should have wandered thus widely. As Audubon does not state that he saw the bird himself it is possible that a kinglet was confused with this species.]

[**Hylocichla mustelina** Gmel. WOOD THRUSH.— Stearns ('83, p. 9) reported that this species was “heard” by him ten miles up the Esquimaux River in late July. This record was discredited by Ridgway and by J. A. Allen, and was omitted by Stearns from his “Bird life in Labrador.” It is probable that the song heard was that of the Hermit Thrush.]

***Hylocichla fuscescens* (Steph.).**

WILSON'S THRUSH.

Rare summer resident in southern part.

The only record of this species for Labrador is by Audubon ('35, p. 362). He says: "On the 20th of July, while in the latter country [Labrador], I saw the young of this species following their mother. They were then almost full grown, and could fly a hundred yards or so at a time. By the 12th of August none were seen, although during my stay they were as common as any other bird."

Brewster ('84, p. 368) closely observed a pair at Ellis Bay on the island of Anticosti, a few miles south of the Labrador region.

***Hylocichla aliciae* (Baird).**

ALICE'S THRUSH.

Common summer resident; rare in the northern portions.

Stearns says this bird is everywhere abundant in the interior. Coues found it breeding abundantly, the young flying on July 24th. Bigelow saw it as far north as Aillik. Macoun records a set of three eggs from James Bay taken in June, 1896. Turner found it "rare in Ungava, common in southeastern and southern portions. Breeds wherever found in summer." He records a nest and eggs taken at Fort Chimo on June 28, 1884.

We saw and heard Alice's Thrush at various places in Labrador as follows: 1 singing at Forteau on July 10th; 3 at Mary Harbor on July 12th and 2 on July 13th; at Cape Charles on July 28th, 7 were seen or heard, 12 on July 29th, 16 on July 30th, and 2 on July 31st at the same place. Some of these were of course the same birds counted more than once on successive days. They were still in song the last of July. The call note is a *phéu*, at times faint and at times loud, often resembling closely the call note of the Veery. What appears to be an alarm note is a loud *speé-a* with a vibratory character, resembling at times closely the note of the Night-Hawk and at times that of a Veery.

The song when heard at close range is sometimes introduced by faint and curious sounds as if the bird were breathing through its

nose. Then there is a single or double first note followed by a long Veery-like vibration, sweet yet mournful. As would be expected, the song is not noticeably different from that of Bicknell's Thrush as heard in the White Mountains of New England and does not, as has been stated, resemble that of the Hermit Thrush.

We obtained only one specimen of this species, a worn female at Cape Charles in July. The measurements of this specimen which are as follows: wing 92 mm., tail 64 mm., bill 14 mm., tarsus 24 mm., correspond to those of a large Bicknell's Thrush or a small Alice's Thrush. A series of specimens from Labrador might throw interesting light on the standing of Bicknell's Thrush.

***Hylocichla ustulata swainsoni* (Cab.).**

OLIVE-BACKED THRUSH.

Common summer resident in the interior and on the southwestern coast.

Specimens were obtained by Drexler at Rupert House on June 13th and in July, 1860. Low says that it was very common along the upper Hamilton River; it was seen May 16th and eggs were found on June 30th. A set of four eggs was taken on the Hamilton River on July 3, 1894. Spreadborough observed it as far north as Fort George, James Bay, in June, 1896.

We did not observe the bird but our observations extended but a short way from the Arctic coastal zone. It is a bird of the Canadian zone pushing its way in places into the Hudsonian zone.

***Hylocichla guttata pallasii* (Cab.).**

HERMIT THRUSH.

Common summer resident in southern part.

The Bowdoin college expedition brought back a specimen of this thrush from Chateau Bay taken July 14th and there is another in the Bangs collection from Lance au Loup taken June 1, 1899. Low says it is "not rare at Lake Mistassini." Spreadborough says he observed it only twice, on July 4th and 24th, 1896, in the interior of the peninsula.

We found the Hermit Thrush only at Mary Harbor, St. Lewis Inlet. Here we heard two or three singing in the afternoon and evening of July 12th and the morning of July 13th.

Merula migratoria (Linn.).

AMERICAN ROBIN.

Abundant summer resident throughout Labrador; April 26 to October 10.

The strong-flying Robin disregards the boundaries of faunal zones and is found breeding everywhere in Labrador. It was the first land bird seen by Audubon on reaching Labrador. Cartwright notes the finding of a Robin's nest with three eggs on June 29, 1779. He states that they seldom lay more than three eggs in Labrador. He records the first arrivals in 1786 on May 8th.

All writers describe the Robin as common or abundant and it is unnecessary to give all the records. Stearns says they are never seen in winter and gives the earliest and latest dates as above. Spreadborough found them common across Ungava from Moose Factory to Fort Chimo. Eggs were taken at Fort Chimo on June 13th, and on the upper Hamilton River on July 5th.

We found 1 Robin at Lance au Loup, 6 or more at Mary Harbor, 4 at Cartwright, 4 at Rigolet, 2 at Hopedale, 12 or more at Cape Charles, and 1 at Henley Harbor. We found a nest containing three eggs at Rigolet on July 18th. It was placed about seven feet up in a spruce, near the houses of the Hudson's Bay company's post, and was constructed of twigs, lichens, and mud, lined with finer material.

At Hopedale the birds were seen in the Eskimo village and they were said to have a nest there. We were told that a pair of Robins had nested at Battle Island the previous year. Mr. Schmitt records the arrival of the Robin at Nain on May 10. It was interesting to see this familiar bird in such wild and arctic surroundings, and to hear its beautiful morning hymn in the wilderness at Mary Harbor. As far as we could see, specimens of Labrador Robins in the Bangs collection did not differ from those from Massachusetts; we did not shoot any specimens.

***Saxicola oenanthe leucorhoa* (Gmel.).**

GREENLAND WHEATEAR.

Rare summer resident.

Baird, Brewer, and Ridgway say of the Wheatear: "Dr. H. R. Storer of Boston found them breeding in Labrador in the summer of 1848, and procured specimens of the young birds which were fully identified by Dr. Samuel Cabot as belonging to this species. In the following year Andrew Downs, of Halifax, gave me the specimen described and figured by Mr. Cassin. This was secured late in the summer near Cape Harrison, Labrador, where it had evidently just reared its brood. . . . Its occurrence in considerable numbers on the coast of Labrador is further confirmed by a writer ('W. C.') in the 'Field' for June 10, 1871."

A specimen was brought to Coues by a sailor at Henley Harbor on August 25, 1860. It was said to be in company with two others. Coues thought it might be *S. oenanthoides* of Vigors, an incorrect view for Vigors' measurements showed that he referred to the small form *S. oenanthe*. Bigelow says that the Hudson's Bay company's factor at Nachvak had three nests.

This Wheatear that breeds in Labrador reaches its summer home from Africa by way of England, Iceland, and Greenland. It is a larger race than *oenanthe* which is found in Alaska.

Stejneger's ('01, p. 477) remarks on the wheatears in North America are here worth quoting. He says: "We have, consequently, in America both forms, *Saxicola oenanthe* in Alaska and *Saxicola leucorhoa* in Greenland and adjacent parts of northeastern North America. As all the birds found in the latter part of the continent belong to the large race, it is settled beyond the shadow of a doubt that the Wheatears which breed in Alaska do not migrate by way of Greenland or Labrador, but that they retrace their steps into the Tchuktchi Peninsula and farther south into Asia, as indicated by me fifteen years ago.

"The Wheatear, the most widely distributed species of the genus *Saxicola*, thus extends its range across the entire palaeartic continent from the Atlantic to the Pacific Ocean. At both extremities of its home continent, however, it has expanded its range into the New World, and no one who follows on the map the route of the retreating

winter migrants can for a moment be in doubt that these routes really represent the way by which the species originally invaded America. It would be difficult to find a more beautiful example to illustrate that now well-known law which was first formulated by Prof. Johan Axel Palmén, of Helsingfors. Moreover, no better example could be found for demonstrating the necessity of minute discrimination in ascertaining the characters by which these 'migration route races,' as Palmén calls them, are characterized.

"It seems that one more lesson can fairly be drawn from the differentiation of the Greenland race, viz, that the Greenland-Iceland-England route must be considerably older than the Alaska-Tchuktchi-Udski route, since it has resulted in the establishment of a separable race. A consideration of the further fact that no regular migration route could have been effected between Greenland, Iceland, and Great Britain during the present distribution of land and water in that part of the world also leads us back to a period when the stretches of ocean now separating those islands were more or less bridged over by land. For such a condition of affairs we shall have to look toward the beginning of the glacial period. At that time it must, therefore, be assumed that the Wheatear extended its range into Greenland. The advent of the typical form into Alaska, on the other hand, is probably one of very recent time, an assumption corroborated by the somewhat uncertain and erratic distribution of the species in that northwestern corner of our continent."

SUMMARY.

| | | | | |
|--------------------------------------|---|---|--------|------------|
| Authenticated species and subspecies | . | . | . | 213 |
| Extinct species | . | . | . | 2 |
| Doubtful and erroneous species | . | . | . | 44 |
| | | | Total, | <u>259</u> |

The following table presents in the form of a summary, the approximate numbers of the different species of birds observed by us during our journey along the coast, and is of interest as showing what species are most likely to be met with on these shores, and at what points we found them in greater or less abundance.

APPROXIMATE NUMBERS OF BIRDS SEEN IN LABRADOR, JULY 10 TO AUGUST 3, 1906.

| Species. | Southern coast: Blanc Sablon to Battle Harbor July 10-11. | Battle Harbor to Hamilton Inlet including Gt. Caribou Isl. and St. Lewis Inlet July 12-17. | Hamilton Inlet to Nain including Rigolet July 18-21. | Nain to Hamilton Inlet July 22-24. | Hamilton Inlet to Battle Harbor including Gt. Caribou Isl. and Cape Charles July 25-Aug. 1. | Southern coast: Battle Harbor to Bradore Aug. 2-3. |
|-------------------------|--|---|--|--|--|--|
| Red-throated Diver | | 7 | 28 | 24 | | |
| Loon | 1 | 3 | 3 | 2 | | |
| Puffin | 177 | 12 | 1 | 33 | 10 | 1007 |
| Black Guillemot | 1 | 193 | 261 | 412 | 137 | 4 |
| Murre sp? | | 11 | 0 | | | |
| Razor-billed Auk | 7 | 15 | 69 | 45 | 2 | 20 |
| Pomarine Jaeger | | | 23 | 57 | | |
| Parasitic Jaeger | | | | 4 | | |
| Kittiwake | 200 | 11 | 5465 | 1261 | 50 | 2360 |
| Glaucous Gull | | 4 | 10 | 18 | 1 | |
| Great Black-backed Gull | 6 | 29 | 8 | 6 | 10 | 209 |
| Herring Gull | 20 | 34 | 1013 | 22 | 13 | 25 |
| Arctic Tern | | | | | | 1 |
| Fulmar | | | 8 | | | |
| Greater Shearwater | 19 | 5027 | | 2 | 7 | |
| Sooty Shearwater | 1 | 3 | | 2 | 1 | |
| Wilson's Petrel | | | | | 1 | |
| Red-breasted Merganser | | 5 | | | | |
| Harlequin Duck | | | | 1 | | |
| American Eider | 35 | 37 | 70 | 20 | 1 | |
| King Eider | | 1 | 1 | | | |
| American Scoter | | 45 | 12 | | | |
| White-winged Scoter | | 115 | 652 | | | |
| Surf Scoter | | 8 | 8 | 5 | | |
| Red Phalarope | | | 3 | | | |

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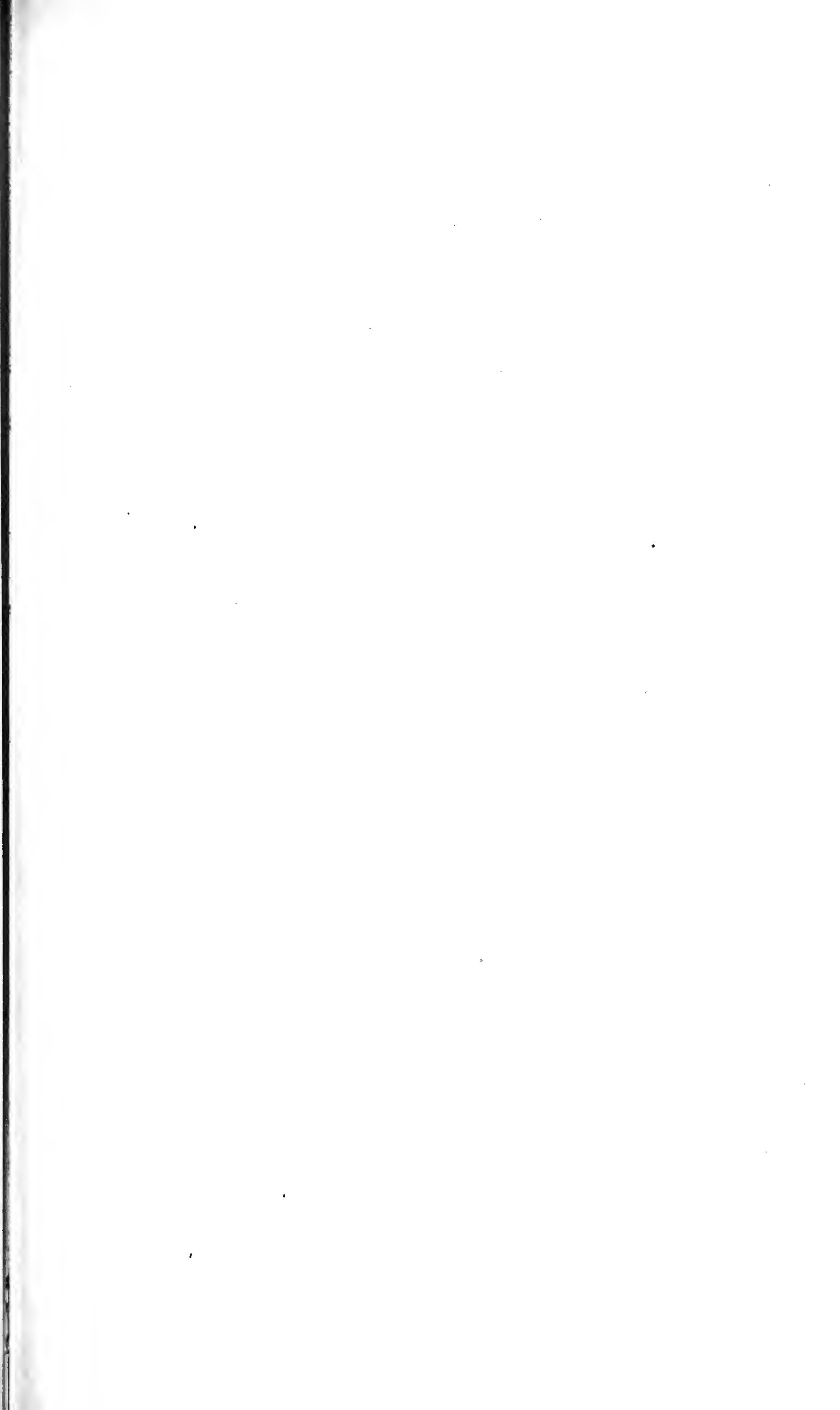
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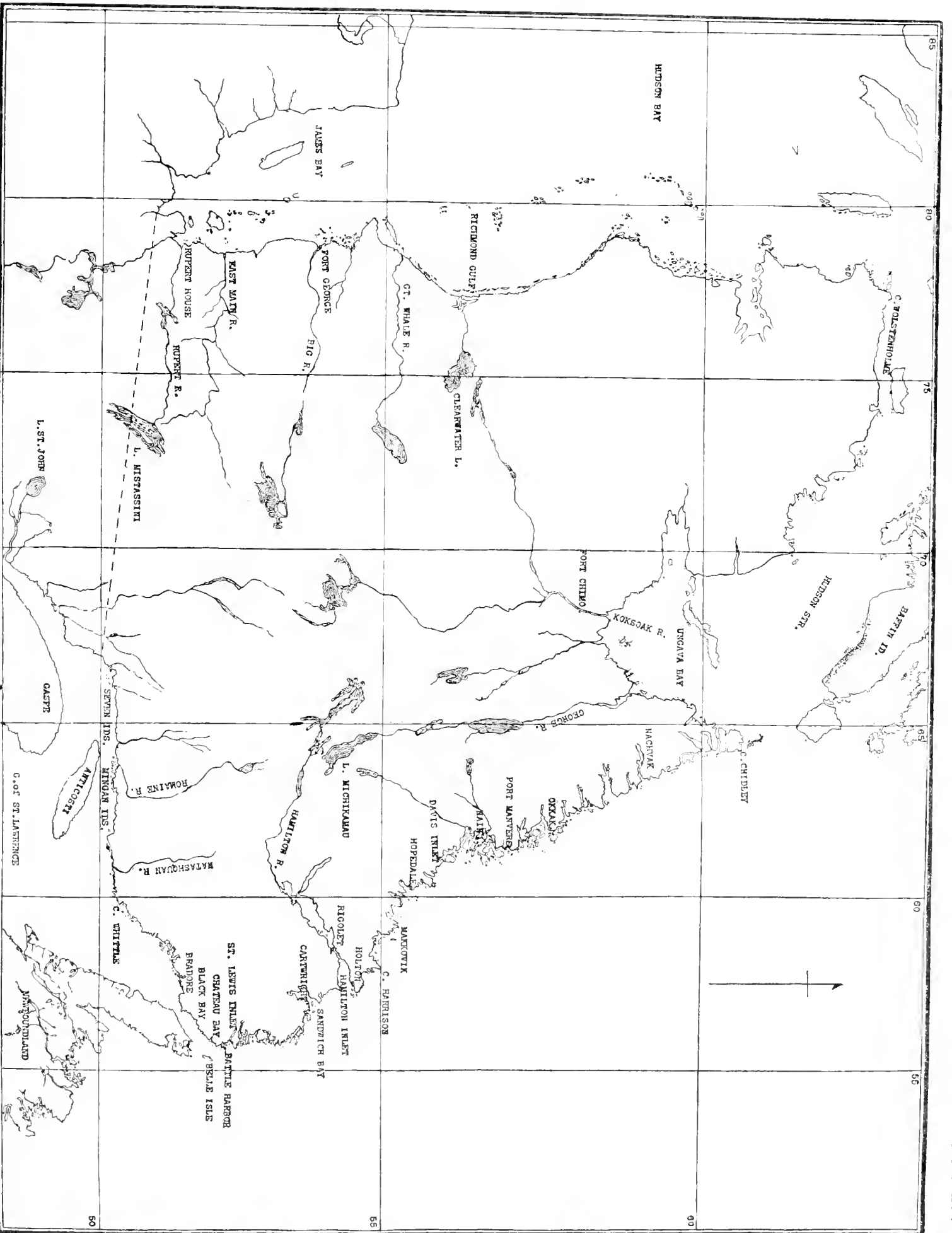
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TOWNSEND AND ALLEN. — Labrador Birds.

PLATE 29.

Map of the Labrador peninsula.





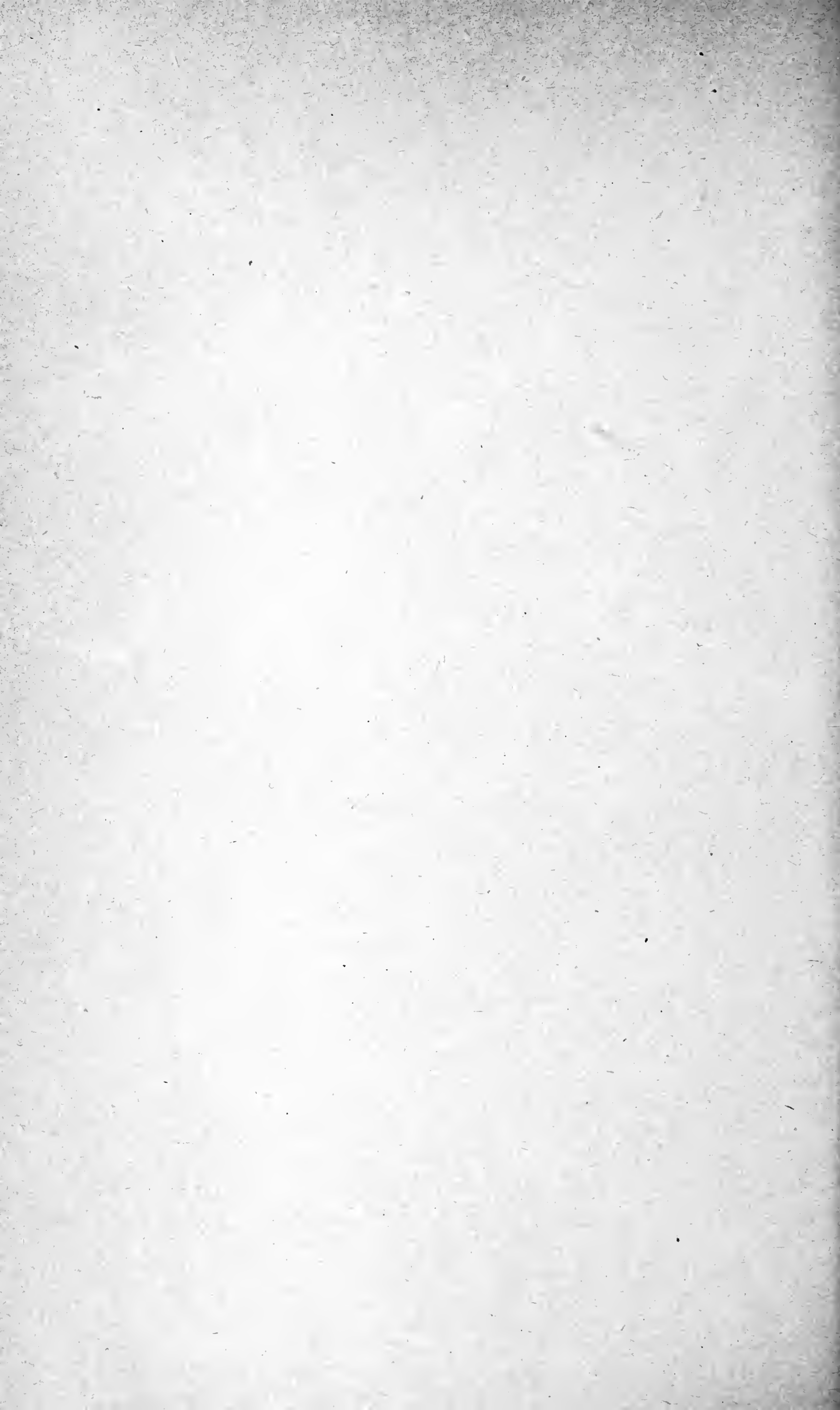
Proceedings of the Boston Society of Natural History.

VOL. 33, No. 8,
p. 429-460, pl. 30-35.

ON *TURRITOPSIS NUTRICULA* (McCRA DY).

BY WILLIAM KEITH BROOKS AND SAMUEL RITTENHOUSE.

BOSTON:
PRINTED FOR THE SOCIETY.
SEPTEMBER, 1907.



No. 8.— ON *TURRITOPSIS NUTRICULA* (McCRADY).

BY WILLIAM KEITH BROOKS AND SAMUEL RITTENHOUSE.

PART 1. THE METAMORPHOSIS OF *TURRITOPSIS*.

BY WILLIAM KEITH BROOKS.

(The references in Part 1 are to the illustrations in a memoir on the life-history of the Hydromedusae, which was published by the Boston society of natural history in 1886, as volume 3, no. 12, of the Memoirs of the Society.)

IN a memoir that was written in September, 1885, and published more than twenty-two years ago, I gave a figure, plate 37, of a hydroid cormus of *Turritopsis* with medusa buds in many stages of development as well as free medusae at successive stages of growth up to the mature sexual adult. From this memoir I have compiled the following account, in order to point out the more prominent features in the life history (Brooks, '86, p. 391–393). While I have made a few verbal changes and abridgments, the extracts are practically as they were printed in 1886.

“The only colony of the hydroid which I obtained was scraped from the piles of the steamboat wharf at Morehead City, seven or eight feet below low tide mark. The tips of two of its branches are shown in *H*, in Pl. 37. It lived for two weeks in the house, and set free great numbers of hardy medusae which were reared until they had acquired the characteristics of the genus.”

The upright stems of the hydra, from 8 mm. to 12 mm. high, bear large terminal hydranths, as well as smaller ones which are scattered irregularly along the stem on short stalks. The long fusiform body of the hydranth carries from eighteen to twenty thick, short, filiform tentacles, which are arranged in three or more indefinite whorls. The medusa-buds, *B*, *B*, originate around the stem just below the hydranths, and they are themselves carried on short stems. The perisarc is not annulated, and it forms a loose cylindrical sheath around the main stem and the short branches which carry the lateral hydranths and the young medusae, while the latter are closely invested by a much thinner and more transparent capsule of perisarc. The sheath on the stems is thick and crusted with foreign matter. It terminates abruptly by a sharp collar just below each hydranth.

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The young hydranths and the medusae are budded off above the collar, but they soon become entirely sheathed in perisarc by the growth of the stem. The pale yellowish-red hydranths, are very similar to those of *Tubularia* (Allman) and the hydroid is so similar to *Dendroclava Dohrnii* recently described by Weismann, that they undoubtedly belong in the same genus.

“The little medusa remains attached to the stem, as shown in Pl. 37, *C*, for some time after the rupture of its capsule of perisarc. At this time it is nearly spherical and covered with large conspicuous ectoderm cells. Its eight short tentacles are thrown backwards in contact with the outer surface of the bell, and their tips are hooked or bent upon themselves in a very characteristic manner, which is shown in the figure. This position of the tentacles renders the bulb at the base, with its ocellus, very prominent.

“The medusa when set free, Pl. 37, figs. *D* and *E*, has eight tentacles, a thin globular bell, and a short simple proboscis. When the animal is in active motion the tentacles are contracted, bent into hooks and thrown back against the umbrella, as shown in fig. *D*.” When it is relaxed after a pulsation the bell is nearly globular, but it is lengthened and emarginated at each pulsation, so that it exhibits rhythmical changes of outline. Figure *D* shows a young medusa in the shape which it assumes while swimming, at each period of contraction, while *E* shows a medusa of the same age floating in a relaxed condition. When the medusa is at rest the height of the umbrella is about equal to its diameter, and the shape is that of a spherical segment almost equal to a sphere. The tentacles are capable of extension to a length equal to about twice the diameter of the bell, and when the animal is at rest they are stretched out almost horizontally, and the distal half is bent downward at an acute angle near the middle of the tentacle. The four interradial tentacles, when thus extended, lie nearly in the plane of the velum, while the four perradial tentacles are carried a little lower. This peculiar bending and alternation of the tentacles, which is very characteristic, is well shown in figure *E*, which, like all the other figures, is a careful study from life. Many hydroids carry their tentacles bent so as to form two cycles, and the resemblance to these hydroids, which *Turritopsis* exhibits, seems to be a larval, or hydroid characteristic, for I have failed to observe anything of the sort in older medusae. The tips of the extended tentacles are slightly clavate, each with a spot of dark orange pigment.

The length of the proboscis of the young medusa is about two thirds the height of the umbrella, and its upper and lower ends are smaller than the middle. The mouth when the medusa is first set free, and for several days afterwards, is simple and circular, and the endoderm of the oral end of the proboscis is thin; but, just below the aboral constriction, it becomes very thick and cartilage-like, and the thickened area arches out into the subumbrella in the course of the radial canals, as is shown in figure 7. This thickening of the endoderm of the proximal ends of the radiating tubes, where they join and open into the stomach, is characteristic of *Turritopsis*, and, in specimens a week old, (fig. *J*) the peduncle that is thus formed is about equal in length to the proboscis proper, which is suspended at the lower end of a peduncle consisting of four great masses of cartilage-like endoderm cells. These four hollow tubes of cartilage are the endodermal portions of the proximal regions of the radial canals, which meet each other in the central axis. The singular structure which is thus formed is quite unlike anything that has been described in other genera. Some authors have regarded it as an ordinary gastrostyle or gelatinous prolongation of the subumbrella. It is not a gastrostyle but a peduncle formed of endoderm cells. As the young medusa grows, the proximal ends of the radiating tubes are drawn down into the cavity of the umbrella, as is shown in figure *H*, until in specimens two weeks old the stomach is suspended some distance below the sub-umbrella by a transparent mass of large cells meeting in the central axis, and perforated by the cavities of the four tubes. In the adult, figures *I*, *J*, *K*, this body almost entirely fills the upper half of the cavity of the bell.

In a medusa a week old, figure *H*, the four oral lobes or lips are present, and are covered by the stalked bunches of lasso-cells that have been described in the adult by McCrady and others.

At about this time traces of the reproductive organs make their appearance in the walls of the proboscis just below the lower ends of the masses of endoderm cells. The tentacles, at the stage shown in figure *H*, are still carried in two cycles, the interradials being higher than the perradials. There are only eight, and no more were developed in the medusae which I reared from the hydra, although I captured many specimens in the same stage, and at all the following stages up to maturity.

In specimens from one to two weeks old the lower surface of the

very wide velum, figure G, is pushed out to form eight hemispherical pouches, four of them radial and four interradial, in the planes of the eight tentacles. They project so much that they are prominent in profile view, as shown in figure H. May they not be homologous with the pouches that become converted into marginal vesicles in the vesiculated medusae?

“The adult medusa is shown in figs. *I*, *J* and *K*. When it is swimming up from the bottom the tentacles are carried tightly curled up close to the edge of the bell. When it reaches the surface they are suddenly extended on all sides, shown in fig. *K*. They are nearly straight, but their tips are a little bent and sometimes coiled. This attitude is preserved only for a few seconds and the medusa at once begins to sink towards the bottom, while the tentacles coil up at their tips and assume the position shown in fig. *I*. The bell also becomes flattened and nearly hemispherical, and before the animal reaches the bottom of the aquarium it usually assumes the appearance which is shown in fig. *J*. As it nears the bottom it suddenly draws in its tentacles and rises to the surface, and again extends them, as shown in fig. *K*. . . . The figures of the adult medusae, *I*, *J*, *K*, are much less magnified than the others, which are all drawn to the same scale.”

The memoir of 1886 also contains an account, (p. 391), of a planula that was reared from the egg of *Turritopsis*, and of the larval or first hydranth which arises from the planula and forms the basis of a new hydroid cormus. These stages are shown in figures 2 and 3 of plate 42. A record is also made (p. 391) of the fact that the planula does not become converted into a hydranth, but becomes a root, from which the first hydranth is formed as a bud.

Dr. S. Rittenhouse has recently reared a number of planulae of *Turritopsis* from the egg, and he has verified the observation that the planula becomes a root, from which the first hydranth arises as a bud, and he has traced the further development of the hydranth. When joined to the memoir of 1886, his observations, which are contained in Part 3 of this paper, give us all the prominent facts in the life history of *Turritopsis*.

PART 2. NOTES ON THE ANATOMY AND SYSTEMATIC AFFINITY
OF TURRITOPSIS.

BY WILLIAM KEITH BROOKS AND SAMUEL RITTENHOUSE.

(With plates 30-32. The references in Part 2 and Part 3 are to the illustrations that accompany this paper. Of these, plate 30, figure 4, and plate 31, figure 8, were drawn by W. K. Brooks, and the remaining figures by Samuel Rittenhouse.)

The illustrations of the adult *Turritopsis* in the memoir of 1886 are too small to show the anatomical details, and they are now supplemented by an enlarged figure of the adult (pl. 30, fig. 4), which was drawn from a living specimen by W. K. Brooks at Beaufort, North Carolina, in 1885; and by the illustrations of sections by Samuel Rittenhouse in plates 30 and 31.

As figure 4 of plate 30 shows, the radiating canal is bent upon itself twice, at right angles, and consists of four sharply defined regions: an ascending region which arises from the stomach, a horizontal region, a descending region which ends in the circular marginal canal, and a blind diverticulum which is a continuation of the ascending region.

Plate 30, figure 1, is a section through the plane of the middle of the reproductive organs in figure 4. It shows that the radial canal arises from the stomach as a groove or channel that consists of prismatic transparent endoderm cells with conspicuous cell walls. As figure 4 shows, the channel arises from the stomach in the plane of the oral ends of the reproductive organs and remains an open groove as far as the plane of the aboral border of these organs, gradually deepening and infolding until it becomes converted into a tube as is shown in plate 30, figure 2. This is a section through a plane that is just above the reproductive organs. The endoderm cells are now chorda cells with conspicuous cell walls and transparent contents. The four radiating tubes meet each other and are flattened by pressure over the areas of contact, where the ectoderm is absent, so that the endoderm of one tube is separated from that of adjacent ones by the supporting layer only. In the center is a square area lined with the ectoderm of the subumbrella, and occupied by the jelly of the umbrella. The convex peripheral portion of each tube is covered with ectoderm. The distribution of the ectoderm will be understood by reference to

figure 9 of plate 31, which is part of a cross section in the plane which, in figure 4, is just below that in which the radiating tubes become horizontal. The endoderm cells are here very much elongated, and their transparency and the sharpness of the walls between the cells, and the other chorda-like characters, are most marked at this level. The change from the highly specialized endoderm of the ascending region of the canal to the ordinary endoderm of the descending region takes place in the horizontal region, as plate 30, figure 4, illustrates, in such a way that the aboral surface of the canal is covered with ordinary endoderm where its side walls still consist of the elongated and specialized endoderm. This results in the formation, on the top or aboral surface of each canal, of a groove, which is narrow and shallow at its axial end, while it is very broad and deep peripherally, as figure 4 shows. The floor of the groove consists of ordinary endoderm covered by the ectoderm of the subumbrella, and its cavity is occupied by the jelly of the bell. The sides of the groove are high walls of the modified endoderm covered by ordinary ectoderm. These walls are nearly vertical on their inner surfaces, and rounded on their outer surfaces.

The descending regions of the radiating canals are shown at *a* in plate 30, figures 1 and 2, and more enlarged in plate 31, figure 6. In this figure, *a* is the cavity of the canal; *b* the flattened ectoderm of the exumbrella; *c* the jelly; *d* the endodermal lamella, which consists of flattened and rudimentary endoderm, and joins each radial canal to the adjacent ones; *f* is the ectoderm of the subumbrella, with a well marked layer of longitudinal muscles, and a thick supporting layer, *e*; *g* is the endoderm of the outer or peripheral surface of the canal, consisting of cells that are nearly cubical, and so crowded with small granules that they are nearly opaque in preserved material; *h* is the endoderm of the central or internal side of the canal. The cells are columnar, and they contain numerous granules that are much larger than those in the external endoderm. The endodermal lamella is continuous with the internal endoderm.

Plate 31, figure 7, is a section through the circular marginal canal, *a*. Its wall consists of two sorts of endoderm: flattened and cubical, and long and prismatic; but their relative positions are the reverse of those in the radiating canals, as the cubical endoderm is on the internal side and adjacent to the ectoderm of the subumbrella, and the elongated endoderm adjacent to the exumbrella. This figure

illustrates a section through the base of a tentacle, *t*, and shows that the tentacular chorda-like endoderm, which is so common in the tentacles of hydroids and hydroid jellyfishes, is of the same character as that of the radiating canals of *Turritopsis*. The velum is shown in this figure at *v*; the velar nerve ring at *n 1*; the tentacular nerve ring, which innervates the visual organs, at *n 2*; *f* is the ectoderm of the subumbrella; *b* that of the exumbrella; and *d* the endodermal lamella.

Figures 1, 2, 3, and 5 (pl. 30), are a series of successive sections through the stomach and proboscis. The reproductive organs are shown in cross section in plate 30, figure 1, and in side view in plate 30, figure 4. They are, no doubt, fundamentally radial, but the halves are pushed apart by the channels through which the radiating canals open into the stomach, so that each half joins the half of the adjacent reproductive organ in the interradial plane. There are, in effect, four interradial gonads, although each is to be regarded as the halves of two perradial gonads. Four vertical interradial furrows, shown at *e* in the section, and shown much more plainly in the older medusa that is represented in figure 4 (pl. 30), indicate the planes in which this secondary union is to be regarded as having taken place.

Haeckel recognizes four species of *Turritopsis*: *T. armata* from the Mediterranean; *T. polynema* from the Atlantic coast of France; *T. nutricula* from the Atlantic coast of North America; and *T. pleurostoma* from the coast of Australia.

A number of medusae, from various parts of the world, which are very similar to *Turritopsis*, have been described, and placed together in the genus *Modeeria*. They exhibit most of the distinctive characteristics of *Turritopsis*, in a much less pronounced condition, and they, no doubt, present these characteristics in their more primitive form. One of them is represented in plate 31, figure 8, which is from drawings made at Nassau in 1886. It closely resembles *Turritopsis* in habits and form, and the account of the habits and form of *Turritopsis* in the memoir of 1886 applies to it without any changes. It resembles *Turritopsis* in the way that the tentacles are carried; in the position of the ocelli, and in the suspension of the proboscis by a stalk of modified, chorda-like, endoderm cells. The radiating canals communicate with the stomach by vertical grooves, as in *Turritopsis*, and the perradial gonads are divided into halves by these grooves, but not so completely as in *Turritopsis*. The peduncle consists of the endoderm of the radial canals, as in *Turritopsis*, but the enlargements are not so

great, and they do not meet in the central axis. The lips, which are simple in *Turritopsis*, are bifurcated.

Haeckel has described, from the Canary Islands, and figured in his "System der medusae," a medusa, *Callitiara polyophthalma*, for which he has established the genus *Callitiara*. It is very close to *Turritopsis*, as Haeckel points out, differing from it in little except the presence of a second ocellus on the exumbrel side of the bulb of each tentacle, in addition to the one that is situated on the velar side in *Turritopsis* and its allies. Its endodermal peduncle is less developed than it is in *Turritopsis*. Its lips are simple as in *Turritopsis*.

The genus *Modeeria* was established by Forbes for a medusa, *Modeeria formosa*, with four tentacles, without a peduncle, and with the gonads simple and perradial; and it is so treated by Haeckel in his "System der medusae." It seems, therefore, to be a most inappropriate name for a *Turritopsis*-like medusa; and it should be restricted to *Modeeria formosa* of Forbes and its natural allies; while the *Turritopsis*-like medusae, which have no affinity with *Modeeria* of Forbes, form a natural genus which should be closely associated, in the system of the medusae, with *Turritopsis* and *Callitiara*. Haeckel, who puts *Turritopsis* and *Callitiara* together in his "System" while he puts the genus *Modeeria* of Forbes in another family, thus exhibits a sound insight into the question that is here at issue.

We take this occasion to call to the attention of those who may undertake the systematic revision of these medusae to the fact that allies of *Turritopsis*, which have nothing in common with *Modeeria* of Forbes, except so far as they are hydroid jelly-fishes, have been wrongly referred to this genus, while they constitute another natural genus.

We suggest, to those who may revise the subject, the propriety of establishing a genus for these medusae, to which the name, *Mocradia*, might well be given in honor of John McCrady, the discoverer of *Turritopsis*.

If this suggestion be accepted, three genera of *Turritopsis*-like medusae should be recognized. The three genera are characterized as follows:

TURRITOPSIS: Tentacles numerous, in two alternating rows in young medusae, in one row in adults, with a single ocellus on the velar side of each tentacular bulb; oral lips four, simple; perradial gonads split on perradii, and fused on interradii; endodermal peduncle nearly solid.

CALLITIARA: Tentacles numerous, in two alternating rows, one row without ocelli, and the other with two ocelli on each tentacular bulb; lips simple; gonads slightly split in perradii; proximal regions of radiating canals with chorda-like endodermal cells.

MCCRADIA gen. nov. (*Modeeria* in part). Tentacles numerous, in one row, with a single ocellus on velar side of each tentacular bulb; oral lips branched once dichotomously, perradial gonads slightly split in perradii; proximal regions of radial canals with chorda-like endoderm.

PART 3. EMBRYOLOGY OF *Turritopsis nutricula*.

BY SAMUEL RITTENHOUSE

INTRODUCTION.

Work on the embryology of *Turritopsis nutricula* was begun at the suggestion of Professor Brooks. The material was collected and the observations on the living specimens were made during the summers of 1903 and 1904, while I occupied a table at the United States fisheries laboratory at Beaufort, North Carolina. *Turritopsis* is one of the most common medusae in the harbor during the summer. In the two years that I was there they became abundant in the beginning of July and remained more or less plentiful until I left Beaufort September 13th. While the medusae could be collected in fairly large numbers, many of them were immature. They lay only a limited number of eggs. Material was preserved and sectioned, however, for the study of such facts as could not be made out from the living forms. The work was finished in the Biological laboratory of the Johns Hopkins university.

DEVELOPMENT OF THE OVARIAN EGG.

The ova develop in the ectodermal layer of the manubrium. The epithelium becomes very much thickened in four regions; these enlarged areas form the ovaries. The primitive ovarian cells when first differentiated are larger than the ectodermal cells of other parts. Their protoplasm becomes homogeneous and of a finely granular character. The nuclei are less hyaline in appearance; and the

nucleolus stains deeply. The primitive ova are first distinguished from the rest of the ovarian cells by the increase in the density of the cytoplasm and the enlarging of the nucleus. The latter becomes very large in proportion to the size of the cell, and acquires a vesicular character. The nucleolus is conspicuous, and a network of chromatin is scattered throughout the germinal vesicle.

The primitive ova grow by the absorption of the ovarian cells around them. As growth takes place there is a change in the character of the cytoplasm. It loses its homogeneous and finely granular nature and develops a supply of deuteroplasm in the form of yolk granules. These are large and stain very darkly. They first appear around the germinal vesicle. As they become more numerous by the continual formation of new ones, they are pushed out through the cytoplasm toward the periphery. The formation of the yolk spheres goes on until the ovum is densely crowded with them except for a narrow peripheral zone, in which the protoplasm retains its homogeneous and finely granular character and forms the ectoplasm of the mature egg. Figures 10 to 15 of plate 32 show different stages in the development of the ovarian egg and the formation and migration of the yolk granules. Some idea of the extent to which the protoplasm becomes crowded with spheres of deuteroplasm can be formed from figure 15 (pl. 32) which is drawn from a nearly mature ovum. In the fully developed egg the layer of ectoplasm is narrower than represented in this figure.

The yolk granules first appear around the nucleus of the ovum; and it is not improbable that they are, in part at least, the result of nuclear activity. During the formation of these bodies, the nucleolus shows signs of being in an active condition and it may also be connected with their manufacture. In some stages the nucleolus is dense and homogeneous; in others it has one or two clearer globules in its interior. These facts seem to show that it is not in a dormant state; and it is possible that it may be associated in some way with the transformation of the absorbed protoplasm into deuteroplasm. That the yolk spheres arise directly through the activity of the cytoplasm, independently of any nuclear or nucleolar function, is doubtful at least. If this were the case we should expect the yolk bodies to arise in other parts of the ovum than around the germinal vesicle. There is no evidence from the study of many eggs that this occurs. The primitive ovarian cells are all, or nearly all, absorbed and used in the

manufacture of the yolk granules by the growing ova, except a layer at the outside which is transformed into the epithelium of the ovary. The cells of the ovarian wall are small and somewhat flattened. Their nuclei are of about the same size as the nuclei of the primitive germ cells, but are less dense. The nucleoli are conspicuous and stain deeply. In general the cells of the epithelium of the ovary are similar to the cells in other parts of the ectodermal layer of the subumbrella except that they are not as much flattened. The eggs in the ovary lie next to the mesogloea, that is, there is no ectodermal tissue between them and the supporting layer. The ovarian eggs are irregular in shape due to their being crowded together; but when liberated they become spherical.

DEHISCENCE.

The eggs are imbedded in the ectodermal layer of the manubrium. As the ova grow and increase in size the epithelium of the ovary becomes more and more distended. When they have reached maturity the outer ectodermal tissue of the ovary is under considerable tension. Finally, when the time for dehiscence arrives, the outer wall of the ovary is ruptured by the aid of the muscular contractions of the manubrium and bell, and the eggs escape into the cavity of the umbrella. The process of egg laying is very similar to that described for *Stomotoeca*.

The number of eggs deposited by a single female medusa varies considerably. It is usually between twenty and thirty-five. On one occasion an exceptionally large female was taken in the tow; her ovaries were seen to be crowded with eggs. She was put into a separate dish of seawater for the purpose of counting the number of eggs that she would lay. The next morning at the regular hour the eggs were deposited and the number was found to be fifty-six, which is unusually large. I made many other counts, but this was the only time that the number exceeded fifty. As a rule it is from twenty to thirty-five; only rarely is it as high as fifty. These numbers seem remarkably small when we consider the enormous quantities of eggs that are laid by many of the other animals of the ocean, the numbers often reaching many millions, as among some of the Echinodermata and Mollusca.

It is a rather curious fact that these animals are always so very

regular in the time for depositing their eggs, which is from 5 to 6 A. M. During the two summers that I studied *Turritopsis* at the seashore, great numbers were collected and kept in aquaria. On many occasions I arose early in the morning to observe the act of spawning,—one time they were watched through the entire night,—and always the act of egg laying was seen to commence at about 5 o'clock or a few minutes after. Very rarely did it take place as late as 6 o'clock; and on no occasion was the phenomenon observed more than a few minutes before 5 A. M.

This precise periodicity is not confined to *Turritopsis*, but seems to be very prevalent among the medusae in general. In *Stomotoca apicata*, *Stomotoca rugosa*, and a species of *Eucheilota*, I find that the eggs are deposited also at a fixed hour, namely, 5 to 5.30 A. M. Professor Brooks found that *Liriope* and *Eutima* spawn at about 8 P. M. In *Gonionema* Perkins found the time to be from 7 to 8 P. M. Bunting found the period of dehiscence for *Hydractinia* to be at about 10 P. M. Mérejkowsky says that the eggs of *Obelia* are laid early in the morning. Metschnikoff also gives the time of spawning of 14 species.

Regular breeding habits have also been found to exist among other marine animals, and may be more general than has been suspected. Wilson, in his work on the development of *Renilla*, found that the eggs of that form were always laid at about 6 A. M. In a single case only, he says, the spawning took place as early as 5.30 and it was never observed to occur later than 7 o'clock. The pelagic crustacean *Lucifer*, Professor Brooks observed to deposit its eggs at from 9 to 10 P. M.

Bunting found that by packing *Hydractinia* in ice and keeping it at a lower temperature she was able to delay the time of egg laying. On restoring the animals to the normal temperature, the eggs were laid after a short period of time. Perkins found that the periodicity of spawning in *Gonionema* is definitely affected by changes in light. By placing his medusae in a dark place for an hour and then putting them in the daylight, apparently normal egg laying again took place.

While I did not try experiments on *Turritopsis* with regard to either temperature or light, yet the changes of temperature from day to day had no noticeable effect on the time at which they discharged their eggs, that is, it occurred at the same hour on warm days and cool days. In like manner the fact that the aquarium in which the medusae were contained, was kept before a lighted lamp all night had no effect on

the time of spawning the next morning, which took place at the fixed period.

THE EGG.

The egg of *Turritopsis* is spherical and devoid of a membrane when first laid, and none is subsequently formed. In size it is very small and may easily be overlooked. If the water is free from sediment and the dish containing the eggs is placed upon a piece of black paper, the eggs are visible to the naked eye. They measure 0.116 of a millimeter in diameter. They are among the smaller of the medusan eggs. Metschnikoff gives the measurements of the ova of 19 species of medusae. The sizes range from 0.024 mm. to 1.5 mm. *Cunina proboscidea* has the smallest and *Polyxenia albescens* the largest egg of the species included in his list. The egg of *Turritopsis* is just slightly larger than that of *Rathkea fasciculata* according to the measurement of Metschnikoff.

In the substance of the egg two parts are distinguishable: an outer layer of clearer ectoplasm which consists of viscid formative yolk composed of protoplasm with very fine granules; and a central mass of entoplasm which is dense and opaque and filled with large, dark granules of nutritive yolk. From the fact that the entoplasm is crowded with these coarse dense granules of nutritive material, the egg is very opaque and the germinal vesicle is not to be seen from the exterior. Thus the changes which take place during maturation and fertilization, and the nuclear phenomena of segmentation, as well as the formation of the entoderm cannot be followed in the living egg. For this reason the egg of *Turritopsis* is not as suitable for study during life as are the beautifully transparent eggs of *Liriope* and *Eutima* for instance, which allow all the changes that take place within the egg during development to be followed easily.

The specific gravity of the eggs is greater than that of seawater and consequently they sink to the bottom of the aquarium as soon as they are discharged from the cavity of the umbrella. In opacity the egg of *Turritopsis* is intermediate between the egg of *Stomotoca rugosa*, which is extremely dense and of a chalky white color, and the egg of *Stomotoca apicata* which is semi-transparent and appears bluish white by reflected light. In color the egg of *Turritopsis* is yellowish white.

MATURATION AND FERTILIZATION.

Because of the opacity of the egg, satisfactory observations on the phenomena of maturation and fertilization are impossible during life, except for those changes which take place on the outside. A few minutes after the egg is laid the first polar body is given off at the upper pole of the egg. The second polar globule follows after a very short interval. These structures are of an ephemeral nature and soon disintegrate or pass out into the water and are lost. Nothing can be made out of their internal structure or of the arrangement of the chromatin with the low magnification which one is obliged to use in the study of the living egg. However, I was fortunate enough to get sections of the early stages of preserved eggs which show the polar bodies in the process of being extruded. The germinal vesicle moves to the periphery of the egg, then a part of its substance is divided off and extruded as the first polar body. In plate 32, figure 16, which is a section of an egg that was preserved a few minutes after it had been laid, the second polar body is just being given off. It contains several granules of chromatin scattered through its clear hyaline substance. In the first polar body, which has moved a little distance from the egg, but is still held in connection with it by some means of attachment, the chromatin has come together and forms a single mass in the center of the polar globule. The means of attachment of the polar bodies to the surface of the egg is not quite clear, as the egg is destitute of a membrane. It is possible that some of the clear liquid part of the protoplasm may exude from the substance of the egg as the polar bodies are extruded, and be the means of holding them to the surface of the egg even during fixation.

As can be seen in the figure, the germinal vesicle during the extrusion of the polar bodies is situated at the very edge of the egg; about half of its bulk even extends beyond the general contour of the surface. The yolk granules are crowded around the nucleus with the same density as in other parts of the egg. After the second polar body has been given off, the female pronucleus moves back from the periphery some distance. Here it is met by the sperm nucleus and fusion of the two takes place. Whether there is any definite spot for the entrance of the spermatozoon or not, could not be decided. But I am inclined to think that the sperm is capable of penetrating the egg at any part;

and that when it has once entered the substance of the egg, the male and female pronuclei are brought together by the attraction existing between the two.

It was impossible to see the discharge of the spermatozoa from the males; neither did I see the spermatozoa enter the eggs. Moreover, as stated before, the eggs are so opaque that the internal phenomena of fertilization could not be followed in the living specimens. There is reason to believe that the sperms are discharged at about the same time that the females lay their eggs. Fertilization takes place in the water immediately following maturation, and segmentation begins in a very short time.

SEGMENTATION.

Segmentation is total and approximately equal. While there is a slight difference in the size of the blastomeres at times, yet this difference is not constant and they all have the same value in development, that is, they are not divided into macromeres and micromeres. There is no evidence either from observations of the living eggs, or from the study of sections of preserved material that any of the blastomeres can be localized as forming distinct parts of the future embryo. During the first two or three cleavages the process is usually quite regular, but beyond the eight-cell stage the segmentation becomes very irregular and erratic; almost if not fully as remarkable as that described and figured by Hargitt for *Pennaria tiarella* and of which he says: "Between the extremes of the embryonic history from the early cleavage to the formation of the morula are to be found the most erratic and anomalous exhibitions of developmental phenomena which have ever come to my knowledge, if indeed its counterpart has hitherto been known. It is not strange that with the mental pictures of such steady-going exhibitions as are found in the development of annelids, molluscs, etc., one should regard such monstrosities as are very inadequately represented in the various figures illustrating this paper as abnormal to the degree of being pathologic! And thus it seemed to me when first observed; and as pointed out in the earlier paper, the first batch of eggs were discarded as having 'gone bad.'"

When I first began the study of the development of *Turritopsis*, the irregularities of segmentation struck me as very peculiar and I was at first inclined to think that they were abnormal. After I allowed

the eggs time to progress I discovered that they developed into normal planulae and thus was forced to conclude that this strange and irregular cleavage must after all be normal for the species. On several occasions the attention of a number of other observers, who were working in the same marine laboratory, was called to this phenomenon, and they also expressed surprise and remarked that they had never seen segmentation presenting such anomalous and irregular features.

Metschnikoff describes and gives a few figures of a very similar condition of segmentation in *Oceania armata*. He says: "Wenn bei den beschriebenen Medusen verschiedene Abweichungen in dem Zustandekommen des vierten Furchungsstadiums constatirt werden mussten, so konnte man doch bei allen eine gewisse Regelmässigkeit auffinden. Ganz abweichend in dieser Beziehung verhält sich *Oceania armata*, da bei dieser Meduse die kaum mit einander vereinigten Blastomeren durchaus unregelmässig und ordnungslos neben einander liegen. . . . Das Abweichende in der Embryonalentwicklung der *Oceania armata* hört noch nicht so bald auf. Die Furchung setzt sich in unregelmässigster Weise fort und führt zur Bildung unförmlicher Zellenhaufen, in deren Innern Mann eine Furchungshöhle durchschimmern sieht. Oft nehmen solche Embryonen eine ganz abenteuerliche Gestalt an, deren Ursache zum Theil darin liegt, dass sie sich durch Theilung vermehren. Diesen Process habe ich an mehreren isolirten Blastula-Stadien beobachtet, so dass ich an dessen Existenz nicht zweifle." In *Turritopsis*, likewise, the later cleavages take place in a most irregular manner and lead to the formation of a shapeless and grotesque mass of blastomeres in which the cells are frequently held together very loosely. The accompanying drawings unfortunately represent only the most regular forms. This is due in part to the fact that the very irregular forms were at first thought, as stated before, to be abnormal; and partly because it was difficult to make accurate camera sketches of these shapeless masses during life while cleavages were taking place rather rapidly.

Whether these embryos multiply by division, as Metschnikoff states to be the case with *Oceania armata* and to which he attributes in part the cause of their peculiar shapes, I have no direct evidence; but think that it is very probable that such may be the case. Frequently the blastomeres are separated into two distinct masses held together by a small isthmus of cells. If they do not divide by an internal activity, they must, occasionally at least, be broken apart by the action of the

tides when in the open ocean. Several times the experiment of dividing the egg during the comparatively early cleavages was tried and the parts were found to continue their development without any hindrance. These experiments will be described more in detail later.

Another point in which the segmenting egg of *Turritopsis* differs from that of *Oceania armata* is that it does not form a true cleavage cavity. The blastomeres always form a more or less solid embryo, as shown in the sections of these stages. Occasionally there are small spaces left between the cells; but a true segmentation cavity that later forms a blastocoele is never formed. In this respect also it is similar to the development of *Pennaria tiarella* as described by Hargitt. As the completion of segmentation approaches, these irregular masses of cells gradually take on a more symmetrical form and, finally, there is formed an oval embryo composed of a solid mass of cells constituting a morula.

The first cleavage takes place about twenty to thirty minutes after the polar bodies have been given off. It begins at the upper pole of the egg and passes down to the lower pole. Thus the egg is divided meridionally into two cells of approximately equal size. When division is complete the blastomeres do not remain in close union, but move apart so that the two spheres are connected by only small arcs of their circumference. The protoplasmic bridge, which frequently occurs in hydroid eggs at the lower pole just previous to the completion of the two-celled stage, is usually to be seen in the egg of this species; but it is much less conspicuous than is the case in *Stomotoca*. When it occurs, it is less definite and clearly defined than in *Hydractinia*, as described and figured by Bunting. Metschnikoff, also, figures a very beautiful example of this protoplasmic connection in the egg of *Nausithoe marginata*. In *Turritopsis* the condition is much like that of *Rathkea fasciculata*, as shown by the last-mentioned observer, in which the connections instead of becoming a very definite bridge remain for a time as a less clearly outlined portion of the ectosarcal material. Protoplasmic currents may be seen at times in these connecting filaments. Their function does not seem to be clearly known; but it very probably is connected with a readjustment of the cytoplasm and the establishment of an equilibrium between the different blastomeres.

Hargitt in his paper on "The early development of *Pennaria tiarella*" discusses the occurrence of papillae, threads, and bridges; and reviews

briefly the observations of a number of other investigators in regard to these phenomena and the cytoplasmic activities which have been seen to take place in the eggs of a number of animals widely separated morphologically. No definite conclusions are reached as to the functions of these various phenomena, but it is generally thought that they are concerned with fundamental intrinsic changes within the cytoplasm.

These protoplasmic connections are usually composed of the ectosarc only. They are present not only in the two-celled stage, but in several of the following stages as well. As the number of cells increases, the connecting films become less easily recognized.

The second cleavage occurs about twenty-five or thirty minutes after the first. The plane of division is also meridional and at right angles to the first segmentation. It begins at the center of the egg next to the furrow of the first cleavage and slowly extends out toward the periphery. When the division is completed the four blastomeres undergo a slight rotation from right to left; and in the center of the egg between the cells there is at times to be seen a small open space or segmentation cavity which may extend through the entire egg as shown in figure 21, plate 32.

After a lapse of time equal to that which occurs between the first and second divisions, the third cleavage furrow appears. This plane of division is equatorial and divides the egg into eight blastomeres. When the segmentation is first completed the two quartets of cells are situated one upon the other and form a more or less spherical whole, as is the usual arrangement in eggs in which segmentation is equal and regular. This arrangement of the blastomeres is, however, of very short duration, for soon a separation takes place between the cells of the lower quartet and two of them roll away from the plane of separation in one direction; the other two move out in the opposite direction. In this migration the blastomeres move through an angle of 45 degrees or more, and finally come to lie in such a position as to form a semicircular plate as shown in figures 22 and 23 of plate 32. The separation and rotation of the cells of one quartet seem to be constant in their occurrence; but the final arrangement of the blastomeres is not always as regular and definite as that shown in the figure. At times they are more loosely and irregularly connected, and may assume relative positions similar to that shown by Metschnikoff for *Oceania armata* in figure 34, plate 1, of his "Embryologische studien."

In the case referred to, the blastomeres are spread out so that the individuals, with three exceptions, touch only one of their fellows, thus resembling a string of beads somewhat coiled.

With this separation and rolling apart, the regularity of arrangement of the cells in the segmenting egg is lost, and the stages from this point on become more and more irregular with each successive division up to the time when the readjustment takes place which is the beginning of the formation of the free-swimming embryo.

It is possible to distinguish, during these early cleavage stages, a layer of ectosarc around each individual blastomere. Later as the cells increase in number and become smaller, the ectosarc covering becomes less conspicuous and finally is lost from sight entirely.

After an interval of about one half an hour, the fourth segmentation begins. The divisions of the different cells no longer take place simultaneously; some occur a few minutes before others, but all are completed within a comparatively short time. So far as the cleavage itself is concerned, it is still equal and regular, but the arrangement of the blastomeres is no longer regular nor definite. They apparently follow no law of symmetry, and may come to lie in any position. Figures 24-26 (pl. 33) show three different forms which the cells of the sixteen-cell stage acquire, and various other arrangements of the blastomeres which could not be figured for want of space, were seen while studying the living eggs. However, the three figures are sufficient to show that the general form of the egg in this stage may be inconstant. In figure 24 of plate 33, it is possible to imagine a direct relationship to a preceding form just a little more irregular than is shown in figure 23 (pl. 32). In a form represented in figure 25 (pl. 33) the descent of the different cells from the individual blastomeres of the eight-cell stage is less easily recognized. Figure 26 (pl. 33) shows an egg in which all sixteen blastomeres are spread out to form a flat plate one cell thick in the form of a quadrangle. One can easily conceive how this arrangement can have resulted from a regular eight-cell stage in which the rotation of the cells of the one quartet was greater than that shown in figure 22 (pl. 32). The flat, spread-out position of the cells at once suggests the idea that the egg may have been subjected to pressure. This might have been the case if the eggs had been studied on a slide under a cover glass; but there is no evidence that pressure was the cause of this plate-like arrangement, for these forms were occasionally found among a variety of other

forms while studying the living eggs in a small preparation dish in seawater with a two-thirds objective. As the eggs present a number of different forms when subjected to the same external conditions, it seems that the cause of these differences must be sought in the nature of the egg itself rather than in any surrounding influences.

The later cleavages follow at intervals of about the same duration as in the preceding stages. The irregularities of arrangement of the blastomeres increase as the cells become more numerous. On account of the smallness of the blastomeres and the extreme opacity of the egg, it becomes impossible to follow the segmentation in detail any farther. Figures 27-30 of plate 33 show a few of the later stages of comparatively very regular forms. Figure 29 (pl. 33) represents an egg in which the blastomeres are arranged in two main groups held together by a narrow isthmus of only one cell in thickness. Some eggs were separated into three or four thickened clusters that were joined together by smaller masses of connecting cells. In others there were smaller groups of blastomeres projecting out from the general mass of cells, thus giving the whole somewhat of an amoeboid appearance. The term amoeba-like seems most clearly to represent the shape which some of these late segmentation stages assume, for if a simple outline of these remarkable and grotesque forms is drawn, it has a general resemblance to an amoeba with thick, blunt pseudopodia. Whether these irregularities in the shape of the egg during late segmentation, and the tendency of the cells to arrange themselves into more or less distinct lobes are due to an amoeboid property of the cytoplasm of the egg, or to a tendency to multiply by division during cleavage, as was suggested by Metschnikoff for *Oceania armata*, there is not sufficient evidence to decide. It may be possible that both these factors act in determining the shape of the segmenting mass of cells. Doubtless the membraneless character of the egg plays a part in these phenomena.

PLANULA.

When segmentation is complete a solid embryo is formed which may at first be called a morula. Small spaces occur sometimes between the blastomeres during the different cleavage stages, but they are sooner or later obliterated by the crowding together of the cells. A central cleavage cavity which is later transformed into a blastocoele

is not formed; consequently a true blastula does not exist in the development of *Turritopsis*. In this respect it differs very markedly from *Stomotoca* and the majority of hydromedusae whose development has been studied, in which a definite blastocoele is formed that becomes filled finally with the migrating endoderm cells. When the developing egg is about six to eight hours old, the very irregular shape which the segmenting mass has assumed, becomes less marked. Gradually the cells become rearranged; the lobes and processes which previously were so conspicuous are now drawn into the main mass of cells, and the egg is transformed into an oval embryo. This process of rounding up lasts from two to four hours. The cells of the embryo now develop cilia, and the larva begins to move. At first the movements are feeble, but soon the larva is able to leave the bottom of the aquarium and swim free in the water. Eggs that are laid at from 5 to 6 o'clock in the morning develop to the free-swimming stage by 4 in the afternoon. The larva swims with its broad end forward, and has a spiral or corkscrew motion, which propels it onward. This method of swimming is common to hydroid larvae. When the embryo reaches this stage the cells become very numerous and small. Before the cilia are developed and movement begins, it resembles an unsegmented egg very much, except that instead of being spherical it is now oval. In size it is about the same as the unsegmented egg, if anything rather smaller. The decrease in size must be accounted for by the fact that some of the yolk has been digested; and the larva evidently has not yet acquired any means of receiving food from the external world.

The larva remains in this oval condition for some hours, after which it elongates to form a typical planula. When the embryo is twenty-four hours old it lengthens out and becomes more slender and assumes the general appearance shown in figure 32 (pl. 33). As it becomes older it grows still longer. Figure 33 (pl. 33) shows a larva of thirty hours. It has now the power of contraction, and is sensitive to stimuli. When the cilia are first developed and for some time during the oval condition of the larva, it swims near the bottom of the aquarium. As it grows older and elongates it rises in the water and swims at or near the surface. The length of time during which the embryo remains in the free-swimming planula stage is variable; but, as a rule, by the time it is about forty-eight hours old, it begins to sink toward the bottom of the aquarium, and to swim less rapidly. After the spiral

swimming movements are lost, the planula is capable of gliding along the bottom of the dish for some time. Finally motion ceases altogether and the larva loses its cilia and is ready for attachment. This stage of development is reached under favorable conditions from about forty-eight to fifty hours after the eggs have been laid.

The planula is very opaque, and thus it is impossible to make out anything about its internal structure in studying the living forms. Specimens in various stages of development were preserved and sectioned for the study of cellular structure. The description of this structure will be given in connection with the formation of the germ layers.

Brooks describes and figures an ectodermal invagination at the posterior end of the planula. He says: "In a living planula it is easy to make out the posterior end, an ectodermal invagination, which looks very much like the mouth of an invaginate gastrula, but this resemblance is misleading, for the careful study of a similar structure in the planula of *Eutima* shows that the invagination has no connection with the digestive cavity, but is an ectodermal gland for the attachment of the planula." From my observations I am forced to regard this structure, which he describes, as a variation rather than a normal feature. It seems to be an abnormal occurrence which is found only rarely. Among the many specimens which I studied both in life and from preserved material, such an invagination was met with only on one occasion. Then it was at the anterior end of the planula instead of the posterior. These structures are clearly abnormal features of the developing *Turritopsis* planula.

EXPERIMENTAL.

The very irregular character of the segmenting egg and the loose connection of the blastomeres, and their tendency to separate into more or less definite lobes and protuberances, as has been described in the section on segmentation, suggested the problem: what would be the effect of dividing the eggs during the comparatively early stages of cleavage? With this question in mind a few experiments were tried. The eggs were divided during several stages of segmentation. The best method for separating the cells was found to be by placing them on a clean glass plate moistened with seawater. Then with a

finely pointed needle or with a very delicate scalpel the blastomeres could be cut or torn apart without being crushed. After they were divided, they were flooded from the glass plate by water from a pipette into a dish of seawater, and watched in their development. The advantage of separating the eggs on a glass plate is that they are held slightly by surface tension, and do not rotate as readily while being cut apart. Eggs were divided during different stages of cleavage from two to six hours old. They were then placed under conditions as nearly as possible like those under which the undivided eggs developed. Unfortunately, as these experiments were incidental and incomplete, no eggs were divided during the two-cell stage and their cleavage followed in detail. Some eggs that were laid between 5 and 6 in the morning were divided at 10.45 A. M. More than one half of the fragments continued to develop and by 6 o'clock in the evening had reached the free-swimming stage. They were retarded a little in their development; whole eggs usually arrive at this stage at about 4 to 4.30 P. M. They were slightly smaller than embryos from whole eggs, but apparently just as active and normal. By the next morning they had reached the elongated planula stage and were in good condition, swimming at the surface of the water.

At another time some younger eggs were divided. These showed practically the same results in development. The opacity of these embryos made the study of their minute structure impossible during life; and because of scarcity of material none could be preserved to study their histology from sections. However, these few incomplete experiments show that fragments of the egg of *Turritopsis* are capable of developing into apparently entire and normal embryos of slightly smaller size.

Hargitt artificially divided some *Pennaria* eggs during the first cleavage and figures a number of resulting segmentation stages, which are very similar to those of whole eggs. He says: "As will be seen, each of the resulting halves behaved in a manner indistinguishable from that of normal eggs. These half embryos were followed through the entire process of cleavage and through the later metamorphoses into planula and polyp, and in every respect, size alone excepted, the processes were perfectly normal."

To my knowledge Haeckel was the first to publish the statement that halves of hydromedusa eggs would develop into normal embryos. For some time naturalists in general were inclined to doubt the fact;

but since the work of Boveri, Hertwig brothers, Roux, Driesch, Wilson, Morgan, Loeb, and others on the fragments of eggs, the development of embryos, abnormal and normal, from portions of eggs is a question no longer to be doubted.

FORMATION OF THE ECTODERM.

In the development of the egg of *Turritopsis* the germinal layers are not differentiated by the process of epibole, delamination, or cellular ingression. During segmentation the blastomeres do not separate and arrange themselves around a segmentation cavity which later is transformed into a blastocoele. Thus instead of having formed a coeloblastula, we find that cleavage results in the formation of a solid oval embryo destitute of a blastocoele, which may be called a morula stage. The cells of the segmenting egg are all alike in structure and nearly equal in size; so that they are not distinguishable into primitive ectoderm and primitive endoderm, which is the case in forms where a definite delamination takes place, as is so beautifully shown in *Liriope* and *Geryonia*, and in species where cellular ingression occurs as in *Stomotoca* and *Clytia* for example. Figures 34 (pl. 33) to 39 (pl. 34) illustrate the uniformity of the cells, and the solid character of the egg during segmentation. In figure 36 (pl. 34) a space exists between the blastomeres near one end of the egg, but this is not to be regarded as a true cleavage cavity. The next figure shows three of these false cleavage cavities. They occur only occasionally. As stated before most of the eggs are entirely solid.

About the time the irregular mass of segmenting blastomeres is metamorphosed into the oval embryo, the cell boundaries are lost for a short time and a syncytium is formed. This syncytial structure is crowded with yolk granules and nuclei are scattered throughout the protoplasm. The nuclei soon become more numerous near the periphery; and then cell walls begin to appear as shown in plate 34, figure 47. These cells are to become the ectoderm, which is soon separated from the inner structureless mass by the development of the mesogloea. Now the ectoderm forms a distinct layer, composed of columnar cells all of which are at first similar in structure and lie parallel to each other as shown in figure 48 (pl. 34). The differentiation of the ectoderm cells takes place later.

The formation of the germinal layers in *Turritopsis* is different from that which has generally been described for the development of hydromedusae. In the majority of forms previously studied the differentiation took place either by delamination or by cellular ingression, unipolar or multipolar. These methods have been well described and figured by Metschnikoff.

In *Aglaura* and *Rhopalonema* there is found according to Metschnikoff a solid so called morula stage destitute of cleavage cavity, the superficial cells of which are converted into the ectodermal layer, while those within represent the endoderm. Here the two layers are formed directly without the formation of a syncytial structure.

In *Eudendrium* and *Pennaria* according to Hargitt's description, a condition somewhat similar to that of *Turritopsis* is found. He says: "Indeed in both *Eudendrium* and *Pennaria*, not to mention other cases, cleavage would seem to result primarily in the formation of a more or less characteristic syncytium, the subsequent development of the germ layers taking place by a gradual differentiation of the syncytial elements, first and naturally the ectoderm, and later, often very much later, the endoderm."

The syncytial character in *Turritopsis* is acquired under favorable conditions, when the embryo is about six hours old, at the time that the irregular mass of segmenting cells is metamorphosed into the oval embryo. I am inclined to think that the formation of the syncytium and the change of shape of the developing embryo are connected phenomena. The length of time during which this condition lasts is evidently comparatively short, for soon cilia develop and the larva begins to swim; but meanwhile the peripheral region of the syncytium has been transformed into a distinct layer of ectoderm cells, separated from the inner mass of tissue, still structureless in character, by the development of the mesogloea.

From the fact that a syncytium or plasmodium-like structure is formed, it is impossible to localize any of the blastomeres of the segmenting egg which will form special parts of the future embryo. Even those cells which are at the surface at the completion of segmentation cannot be regarded as primitive ectoderm, for in the breaking down of the cell boundaries, the formation of the syncytium, and the recasting of the cells, it is quite impossible to say what changes of the protoplasm may take place.

FORMATION OF THE ENDODERM.

The formation of the endoderm in *Turritopsis* cannot be adapted to any of the schemes of the development of the hydromedusae that have been sketched by Metschnikoff. He distinguishes three principal methods for the development of the inner germ layer: first, delamination, a process in which the segmenting blastomeres divide in a plane nearly parallel to the surface, and the inner parts or cells become primitive endoderm, while the outer parts remain as primitive ectoderm. Second, multipolar ingression, in which cells migrate into the blastocoele from different regions of the peripheral cell layer, and are transformed into endodermal tissue directly. Of this mode he describes several subordinate types. Third, unipolar migration, similar to the preceding except that the primitive endoderm cells are given off at one pole only, at the posterior end of the larva.

In *Turritopsis* the endoderm is derived from the syncytial mass of tissue left in the center of the embryo after the ectoderm has been formed and separated off by the development of the mesogloea. The inner germ layer as a rule is formed much later than the ectoderm. Soon after the supporting membrane is developed, cell boundaries begin to appear in the syncytium in the interior of the larva. The cells thus formed are primitive endodermal cells, and are crowded together without any definite arrangement for a number of hours. Stages in which the cell walls are reappearing are shown in figures 48, 49 (pl. 34) and 50 (pl. 35). When the embryo is about forty-eight to sixty hours old, the time at which attachment takes place, a fissure appears in the middle of the mass of endodermal tissue. This is the beginning of the coelenteric cavity. This separation begins near the anterior part and grows toward the posterior end. The coelenteron gradually increases in size, and at the same time the endodermal cells begin to be rearranged, and finally become situated parallel to each other with their bases against the mesogloea and form a definite inner germ layer.

Gerd has observed in *Bougainvillia* that during the course of cell multiplication the boundaries of the cells become indistinct and that the peripheral and central nuclei are altogether identical. But this species differs from *Turritopsis*, according to his description, in the formation of the compact morula stage, in that it is brought about by a multipolar migration of cells into the interior of the coeloblastula;

while in *Turritopsis* the morula stage results directly from segmentation without any recognizable migration of cells.

The formation of the endoderm in *Turritopsis* therefore differs from nearly all the methods which have previously been described, and which in the main conform to one or another of the stereotyped methods as established by Metschnikoff. The nearest approach is that briefly described by Hargitt for *Eudendrium* and *Pennaria*, in which there is also more or less of a syncytium formed prior to the differentiation of the germ layers.

CELL MULTIPLICATION.

During the early cleavage phases the cells multiply entirely by the process of mitosis. In the later phases, especially when the egg is approaching that stage in which the cell boundaries are lost, there is good evidence that direct cell division is also of frequent occurrence. In this period of development mitosis and amitosis take place simultaneously in the different cells of the segmenting egg. Figure 40 (pl. 34) shows a karyokinetic spindle in the metaphase; and figure 41, (pl. 34) one in the anaphase. The chromosomes are large and prominent, but are too closely crowded together to be counted with accuracy.

The nuclei, which divide amitotically, vary in size considerably, and have a reticular appearance. Figure 42 of plate 34 shows a large nucleus of this reticular character with the chromatin scattered about in the linin meshwork. Figures 43-46 (pl. 34) illustrate nuclei in various stages of amitotic division. Frequently in cells where amitosis takes place, many of the yolk granules have been digested and consequently are fewer than in cells where digestion is less active. It may be that the more active functions of digestion and the phenomena of direct cell division are associated with each other; or it may be that the view of Flemming and Ziegler, that amitosis is connected with a high specialization of the cell or is the forerunner of degeneration, applies in this case. This latter conception seems plausible, for we find amitosis to be most abundant shortly before the cell boundaries disappear and the embryo is transformed into the syncytium.

For a number of years it has been known that amitosis is common in follicle cells, digestive epithelial cells, supporting cells, etc.; but generally it was not supposed to take place in early embryonic develop-

ment. Within the last few years, however, a number of observers have discovered this phenomenon in the developmental stages of various forms.

ATTACHMENT.

Under favorable conditions when the larva is about fifty hours old it reaches that stage of development at which attachment takes place. In preparation for this process the planula settles to the bottom, loses its cilia, and consequently its movements cease. The manner of attachment in *Turritopsis* like that in *Stomotoca* differs from that usually described in hydroid development. Instead of settling down on the anterior end of the planula according to the method which occurs in *Eudendrium*, and which has been regarded as typical and used in descriptions of the embryology of the hydromedusae in textbooks, the planula becomes attached on its side by nearly its whole length and is transformed into a root. The hydranth instead of growing up from the posterior end of the planula as in forms which attach themselves by the anterior end, develops from a bud that is given off from the root, usually at about the middle.

Professor Brooks observed the fact that the planula is transformed into a root in *Turritopsis*, *Eutima*, and *Hydractinia*, and gives a brief account of the same in his paper on "The life history of *Eutima*" (Brooks, '84). Metschnikoff ('86) describes and figures for *Mitrocoma* the fact that the larva becomes attached by its side and is almost wholly employed in the formation of the hydrorhiza, while the first hydranth grows out of it by a kind of budding.

In general the attachment of the planula is similar in *Turritopsis* to the method which is followed by *Stomotoca*, but the former does not commonly produce secondary hydrorhiza. In *Stomotoca* at about the time the hydranth bud appears, or even before, the root branches, giving rise usually to one or two secondary roots. In *Turritopsis* this branching rarely takes place, at least during the first few days of the development of the hydranth.

Professor Brooks describes and figures in the planula of *Eutima* an ectodermal adhesive gland. It occurs after the endoderm and the digestive cavity are formed, and before the appearance of the mouth as an ectodermal invagination at the small end of the planula. In *Turritopsis* no such special organ of attachment is found. The larva

probably becomes fixed by a secretion extruded from the ectoderm cells along the whole length of its body.

DEVELOPMENT OF THE HYDRANTH.

Shortly after the larva becomes attached, a bud develops, usually at about the center of the root, which is the beginning of the first hydranth. Four small projections appear early around the distal part of the bud; these will later form the first circle of tentacles. At this time no mouth has yet developed. A young polyp in this stage of development is shown in figure 51 of plate 35. The hydranth bud continues to grow taller and after a few hours a second whorl of tentacular buds is formed some distance below the first circle of tentacles. When the polyp is from twenty to twenty-four hours old, or at about seventy-two hours after the egg is laid, it is ready to develop the third whorl of tentacles. Thus the tentacles nearest the apex of the hydranth are the oldest and largest. The circles are indefinite, that is, the tentacles of a whorl do not all arise from the same level, so that in the advanced hydroid they have rather the appearance of being scattered than arranged in circles. The tentacles when fully developed are stout and filiform; and are capable of much extension and contraction. Figures 51 to 55 of plate 35 illustrate various stages in the early development of the hydranth; the youngest being about fifty hours and the most matured some seventy hours old. Figure 53 (pl. 35) shows a form in which the polyp arises from near the end of the hydrorhiza. This is exceptional. A hydranth with the third circle of tentacles is shown in figure 55 (pl. 35); the tentacles of the first whorl have become considerably elongated. The hydrocaulus now becomes longer and more slender and the hydranth assumes a fusiform body.

The polyps that I reared from eggs were at the age of three days like the hydranths of the adult colony found and figured by Professor Brooks in the main features, except that they had not yet developed as many tentacles. In his description he says: "The upright stems of the hydra, from 8 mm. to 12 mm. high, bore large terminal hydranths, as well as smaller ones which were scattered irregularly along the stem on short stalks. The long fusiform body of the hydranth carries from eighteen to twenty thick, short, filiform tentacles, which are arranged in three or more indefinite whorls. The medusa buds

originate around the stem just below the hydranths, and they are themselves carried on short stems. The perisarc is not annulated, and it forms a loose cylindrical sheath around the main stem and the short branches which carry the lateral hydranths and the young medusae, while the latter are invested by a much thinner and more transparent capsule of perisarc. The sheath on the stem is thick and crusted with foreign matter. It terminates abruptly by a sharp collar just below each hydranth. The young hydranths and the medusae are budded off above the collar, but they soon become entirely sheathed in perisarc by the growth of the stem. The pale yellowish-red hydranths are very similar to those of *Tubularia* (Allman) and the hydroid is so similar to *Dendroclava dohrnii* recently described by Weismann, that they undoubtedly belong to the same genus."

SUMMARY.

1. The ova of *Turritopsis* arise in the ectoderm of the manubrium. They grow by the absorption of the primitive ovarian cells and when mature are densely crowded with large yolk granules.
2. Dehiscence takes place at a definite time, from 5 to 6 o'clock in the morning.
3. The egg is spherical and membraneless. It is composed of an outer layer of clearer ectoplasm and a central mass of endoplasm which is dense and opaque and filled with large, dark yolk spheres.
4. Maturation and fertilization take place in the water after the eggs are deposited. It is impossible to make out details in the living eggs because of their opacity.
5. Cleavage is total and nearly equal. The first three divisions are fairly regular; but during the later segmentation the arrangement of the blastomeres becomes very irregular and erratic. At the completion of segmentation a solid morula stage is formed, in which the cell boundaries are lost for a time, giving rise to a syncytium.
6. Parts of eggs which are divided during the cleavage stages continue to develop and form larvae which are normal in every respect except size.
7. The ectoderm is formed by the reappearance of cell walls in the periphery of the syncytium mass, and is separated from the anterior part by the formation of the mesogloea.

8. The formation of the endoderm follows none of the typical methods described by Metschnikoff. It arises late in the larval life from the syncytial mass of tissue left in the interior of the embryo after the separation of the ectoderm by the mesogloea. When the cells first reappear they are crowded together without any definite arrangement; finally they come to form the distinct endodermal layer.

9. During the late segmentation there is evidence that some of the nuclei divide amitotically.

10. The planula becomes attached on the side by nearly its entire length, and is transformed into a root.

11. The first hydranth develops from a bud which is given off at about the middle of the root soon after attachment.

12. The tentacles develop in indefinite whorls. Each whorl has four tentacles. The oldest are nearest the distal end. In the fully developed hydranth they have the appearance of being scattered rather than of being arranged in circles.

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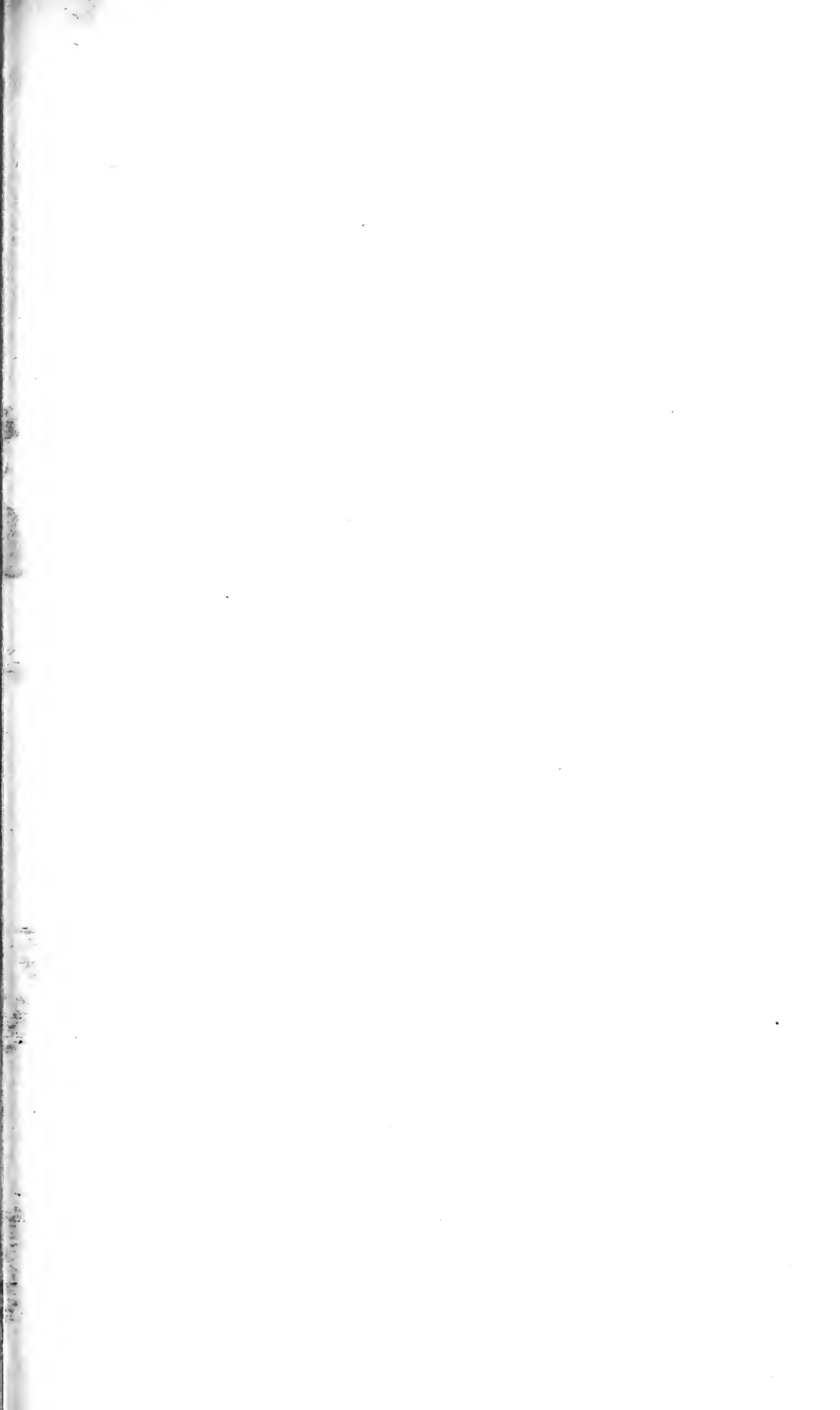
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EXPLANATION OF PLATES.

PLATE 30.

The anatomy of *Turritopsis*.

Letters of reference; *a*, peripheral region of radial canal; *b*, central region of radial canal; *c*, groove through which the radial canal communicates with the stomach; *d*, cavity of stomach; *e*, reproductive organ; *f*, ectodermal epithelium of subumbrella.

- Fig. 1. Transverse section in the plane of the reproductive organs.
- Fig. 2. Transverse section a little above the reproductive organs.
- Fig. 3. Transverse section through the proboscis.
- Fig. 4. The adult *Turritopsis* in side view, enlarged about twelve diameters.
- Fig. 5. Transverse section through the oral lobes.

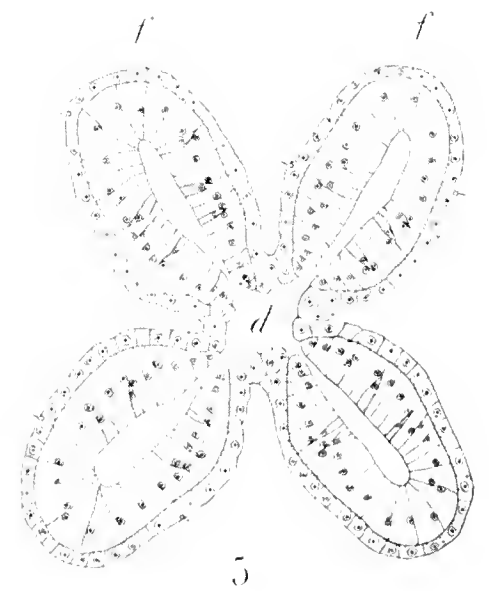
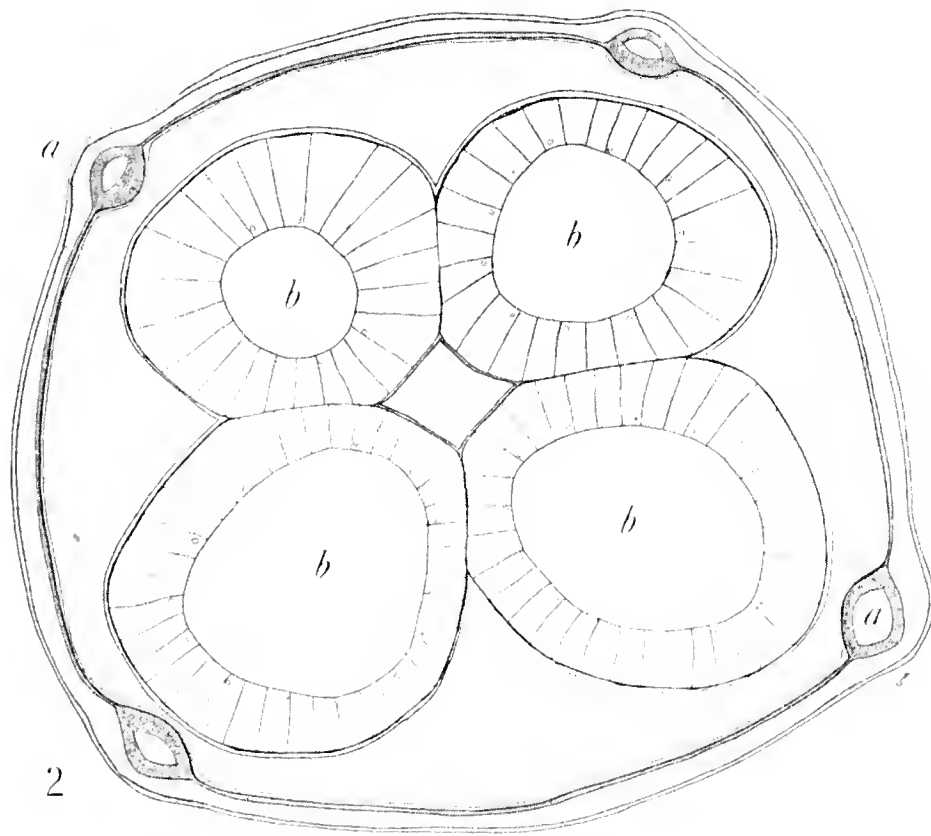
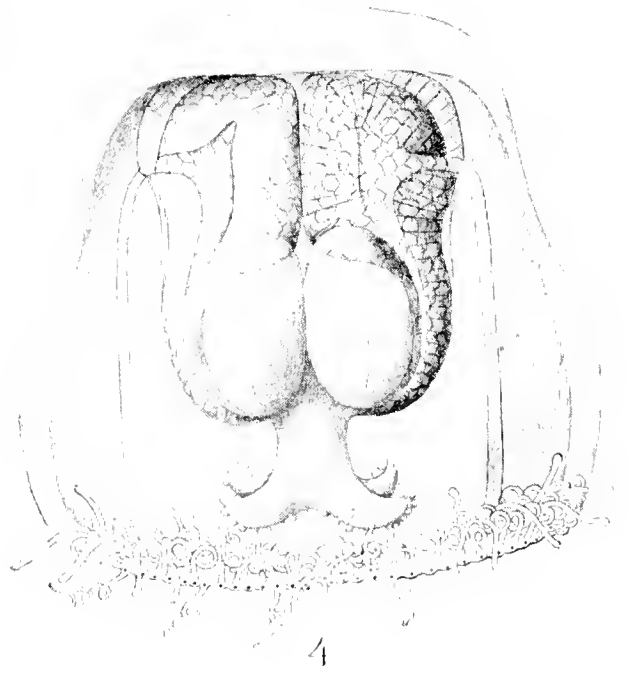
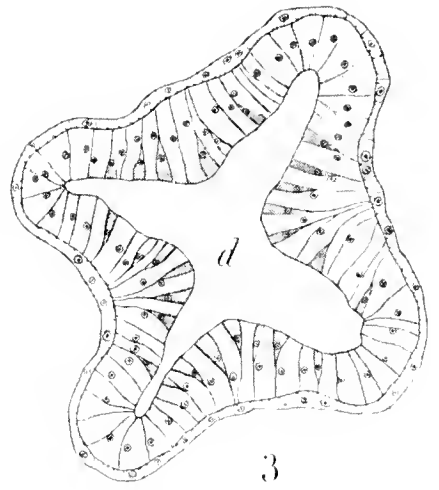
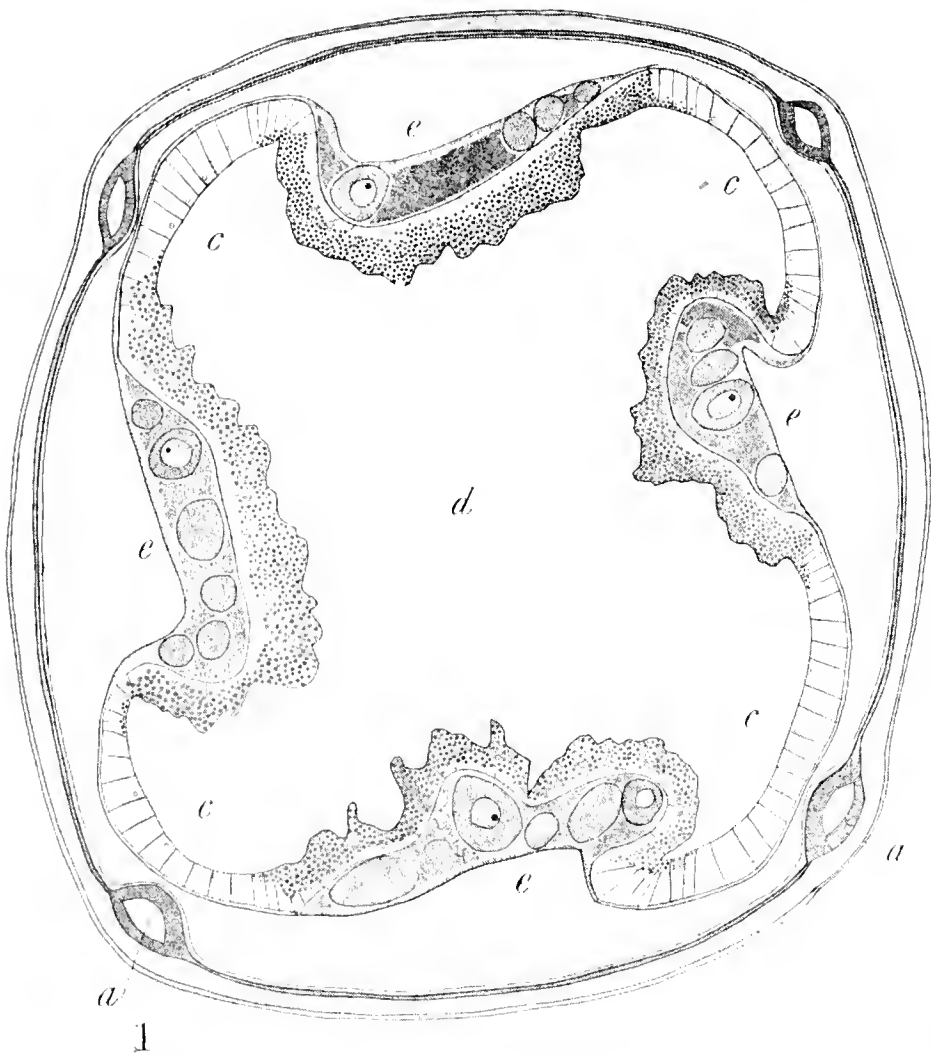


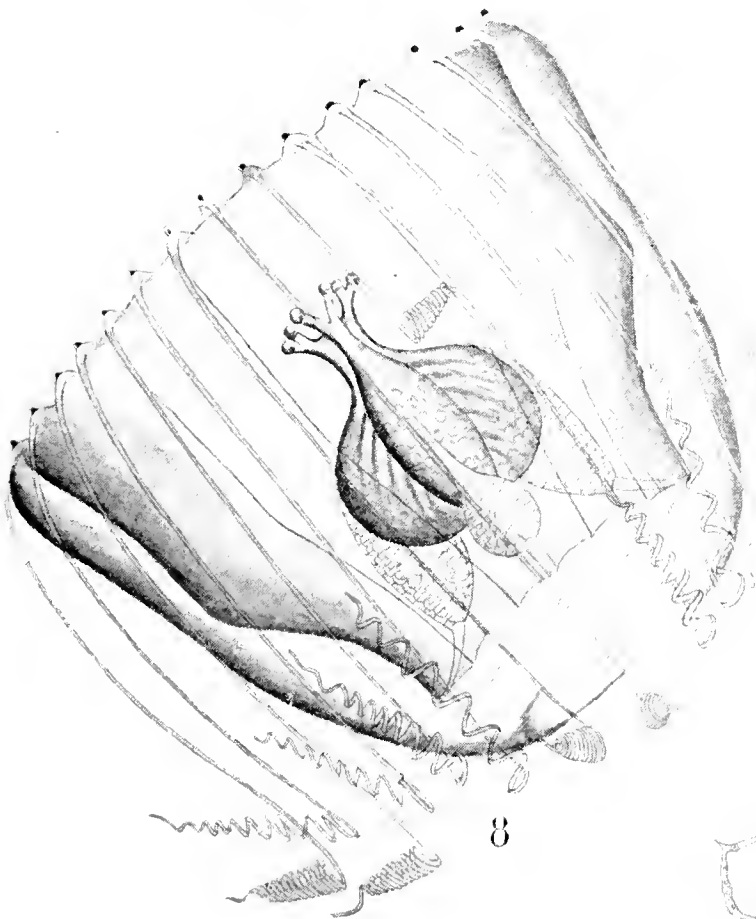
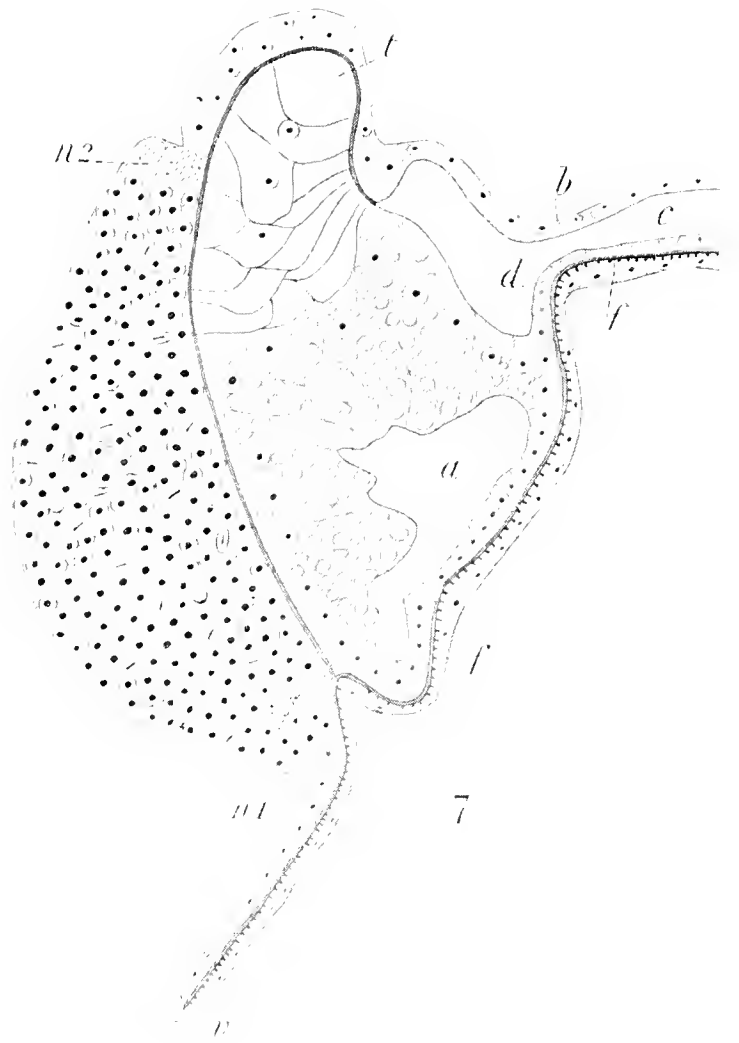
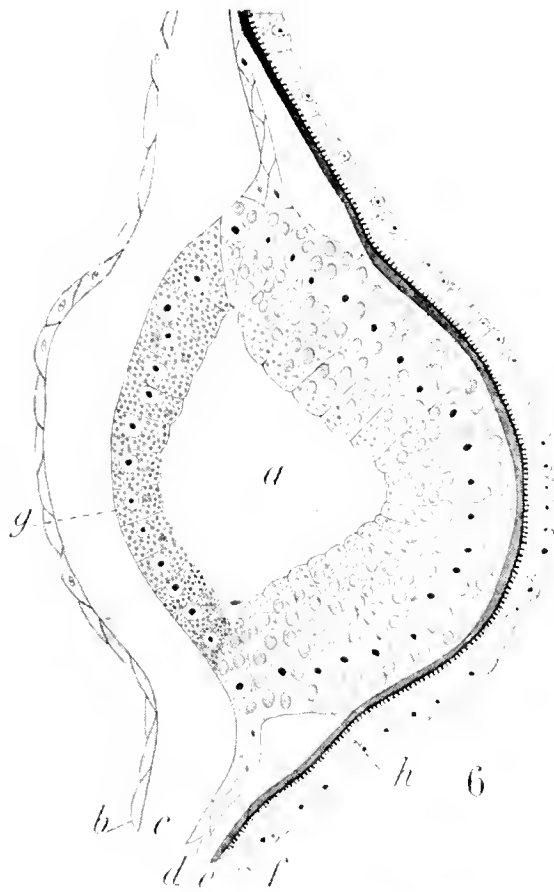


PLATE 31.

The anatomy of *Turritopsis*.

Letters of reference; *a*, cavity of radial canal; *b*, ectoderm of exumbrella; *c*, jelly of umbrella; *d*, endodermal lamella; *e*, muscular layer of subumbrella; *f*, ectoderm of subumbrella; *g*, endoderm on external surface of chymiferous tube; *h*, endoderm on internal surface of chymiferous tube; *n 1*, velar nerve-ring; *n 2*, sensory nerve-ring; *t*, tentacle with ocellus; *v*, velum.

- Fig. 6. Section through a radial canal close to its junction with the circular canal.
- Fig. 7. Section through the circular canal and the base of a tentacle.
- Fig. 8. A drawing, made at Nassau, New Providence, in 1886, of a medusa, which has recently been included in the genus, *Modeeria*. It is here figured in order to show that it has nothing in common with the genus *Modeeria* of Forbes, and is closely related to *Turritopsis*.
- Fig. 9. A cross section of the ascending region of the radial canal of *Turritopsis*, above its union with the horizontal region.



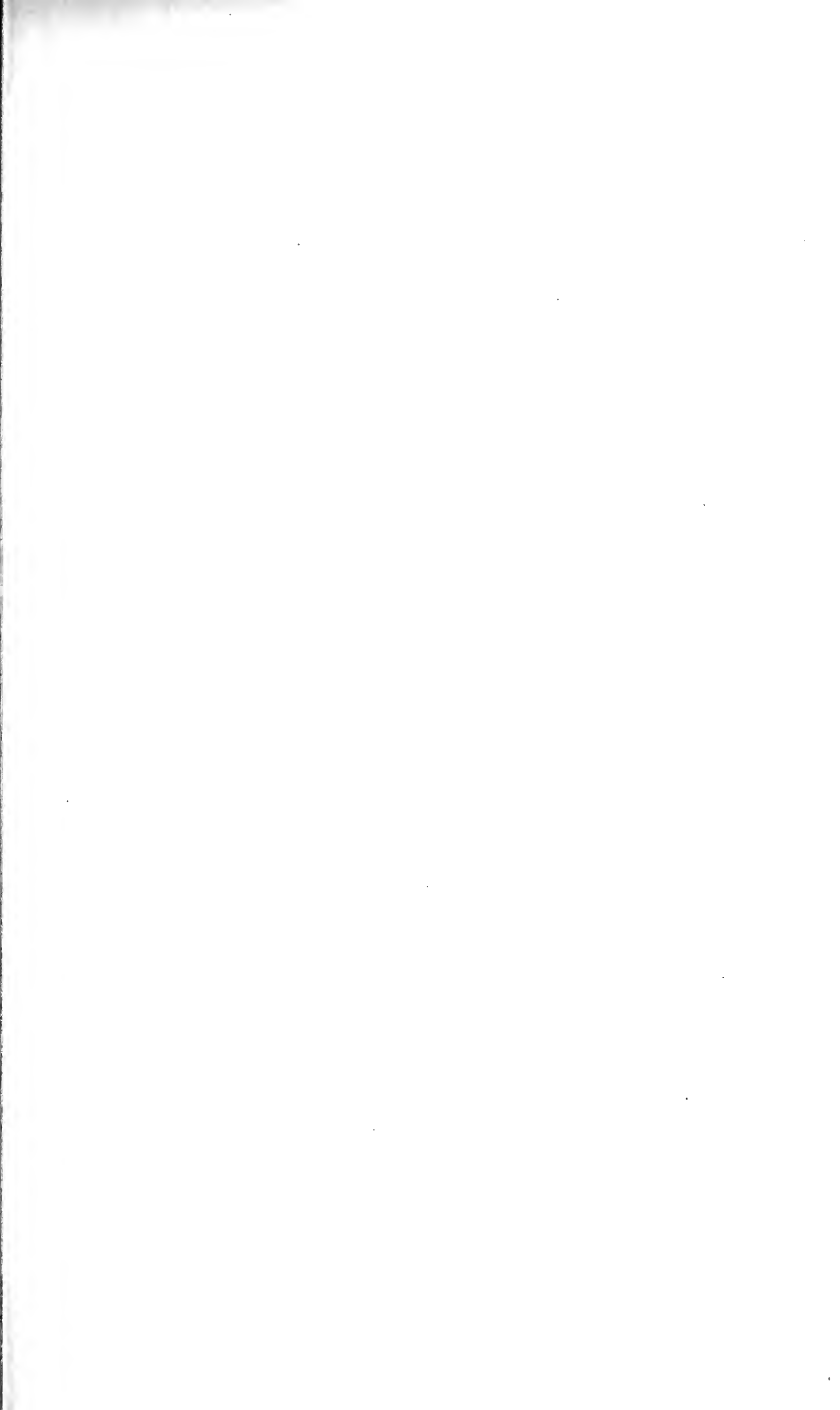


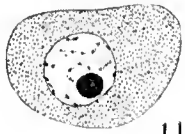
PLATE 32.

The embryology of Turritopsis.

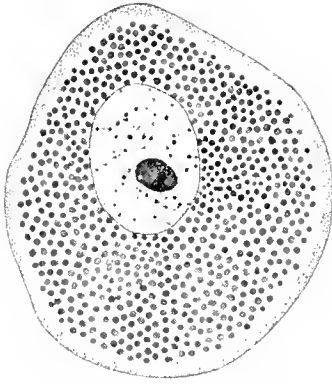
- Fig. 10-15. Stages in the growth and maturation of the ovarian eggs of Turritopsis.
- Fig. 16-18. Stages in the formation of the pole cells.
- Fig. 19. A fertilized egg.
- Fig. 20. The two-celled stage of segmentation.
- Fig. 21. The four-celled stage.
- Fig. 22. The eight-celled stage.
- Fig. 23. Another view of same.



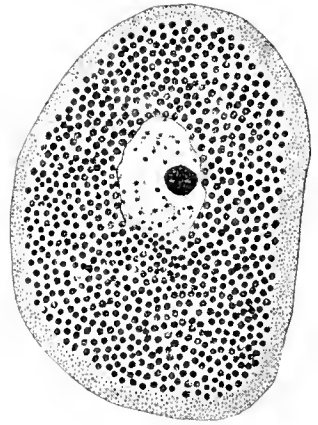
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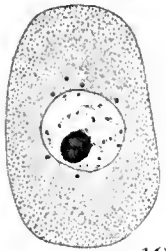
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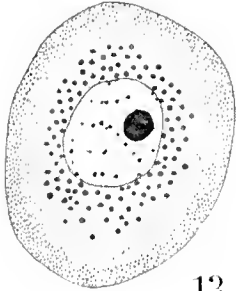
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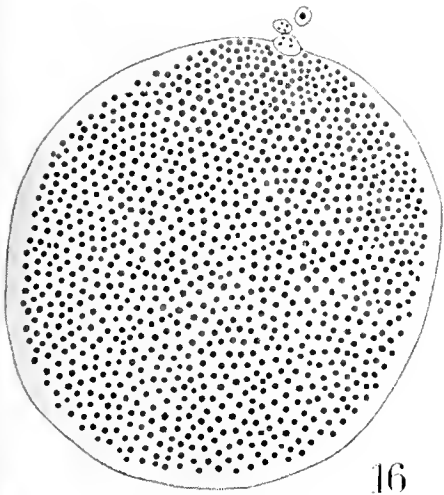
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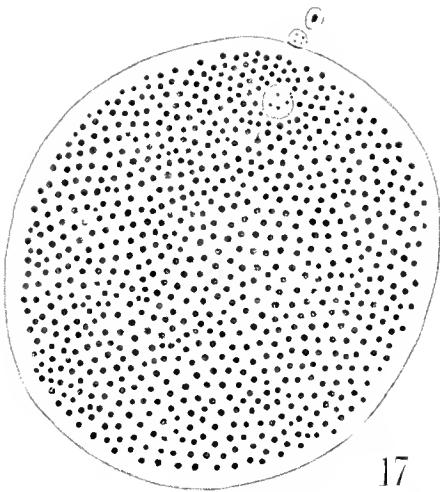
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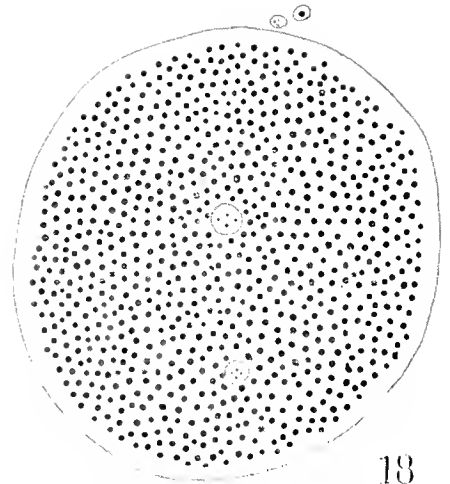
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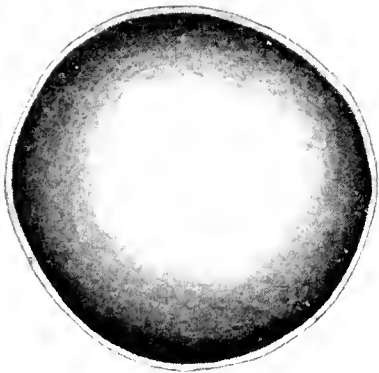
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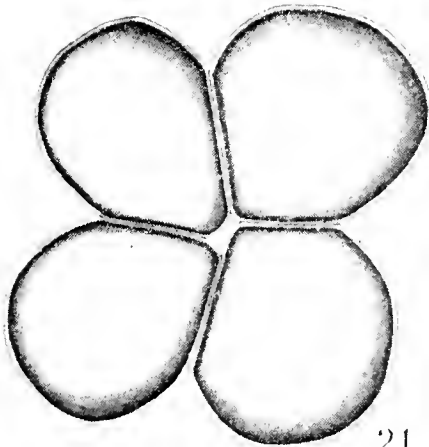
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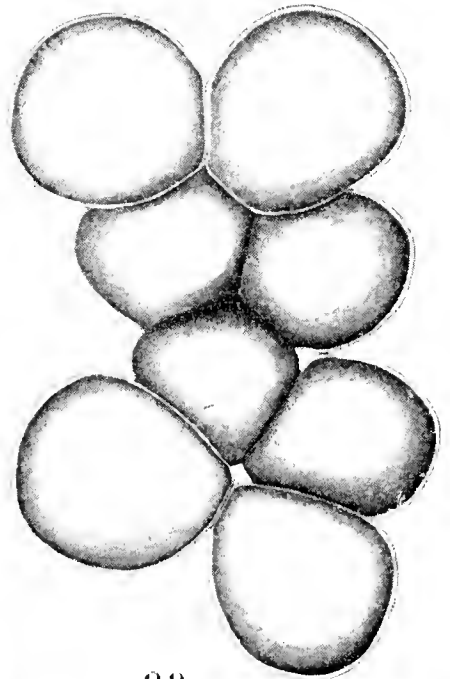
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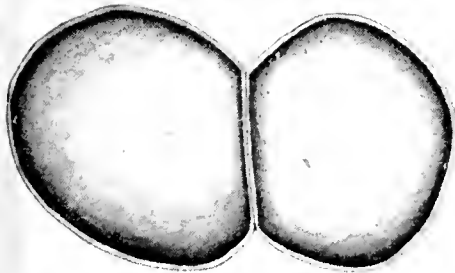
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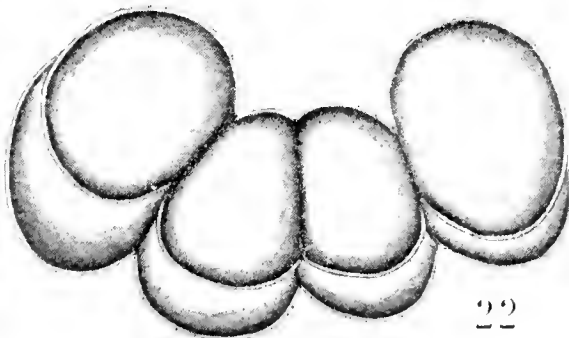
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PLATE 33.

The later stages of segmentation, and the planula.

- Fig. 24. The sixteen-celled stage.
Fig. 25-26. Two more embryos in the same stage, to illustrate the irregularity of the segmentation.
Fig. 27. A more advanced stage of segmentation.
Fig. 28. An embryo, still more advanced, with an indication of division into two.
Fig. 29. The division into two is still more marked, only a single cell joining them together. When the two portions are separated artificially at this stage a normal planula arises from each, and it is probable that the embryos multiply by fission in a state of nature.
Fig. 30. Another embryo exhibiting division into two parts.
Fig. 31. The young planula.
Fig. 32. An older planula beginning to elongate.
Fig. 33. An older planula, more elongated.
Fig. 34. A section through the embryo shown in figure 28.

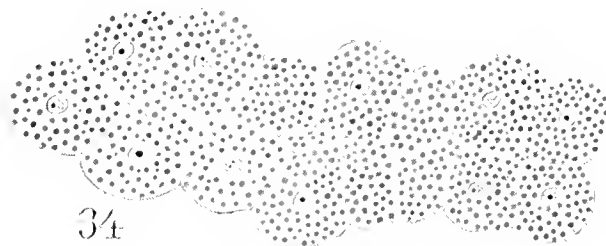
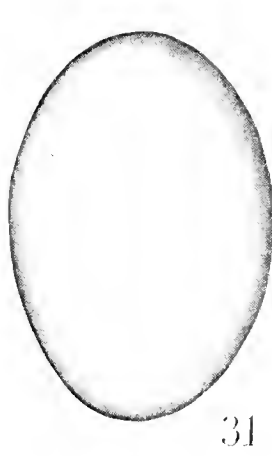
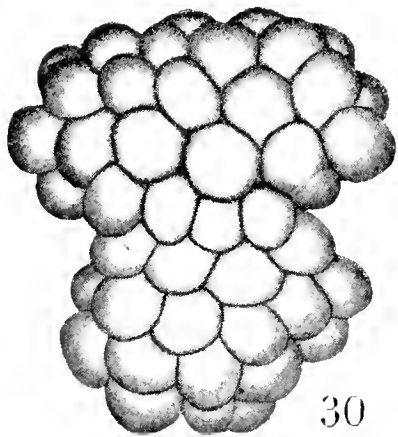
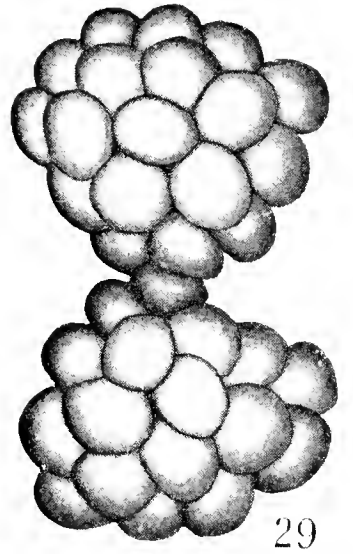
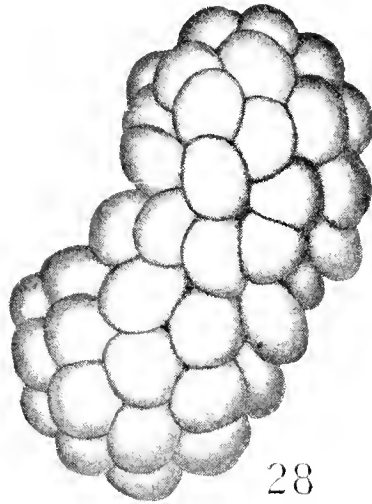
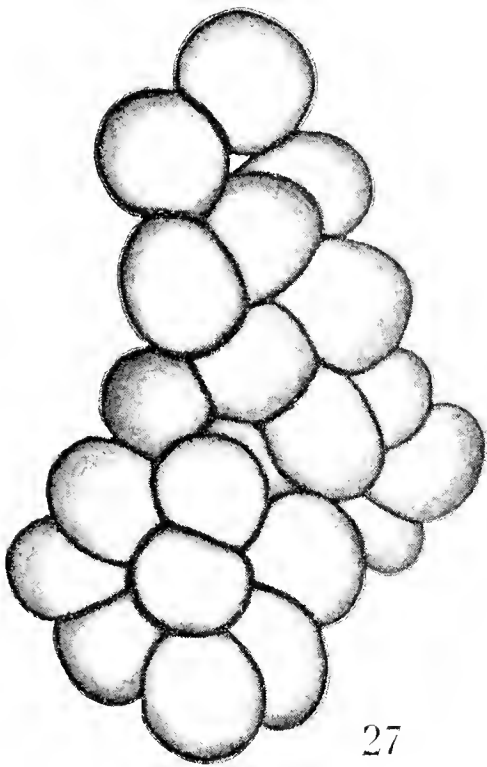
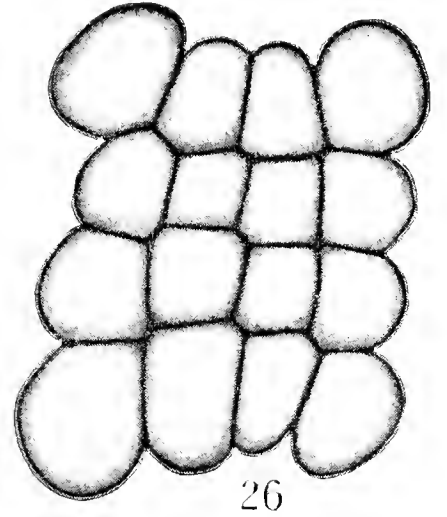
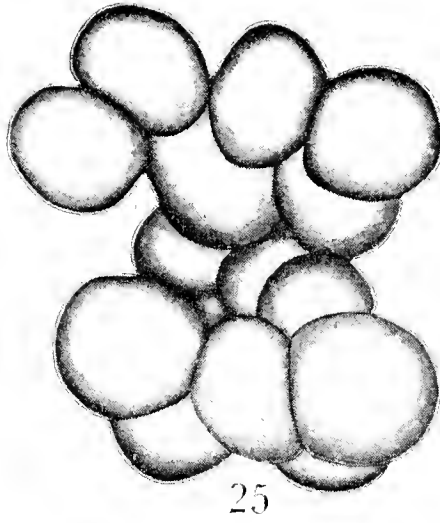
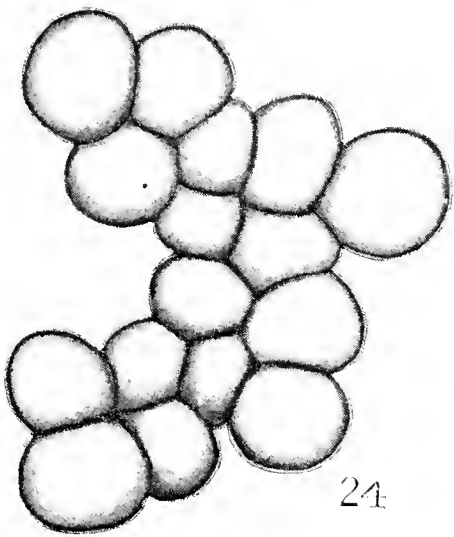


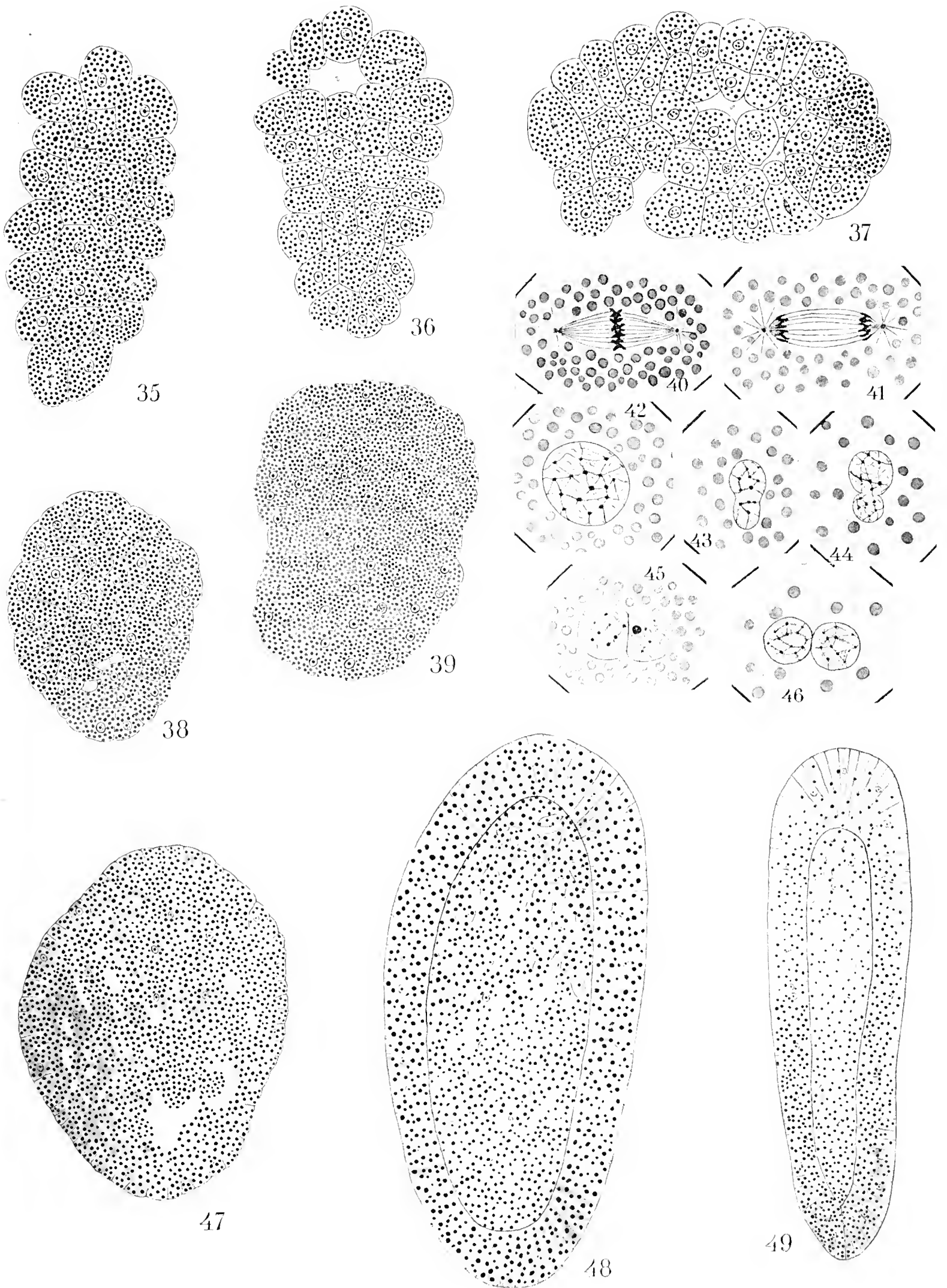




PLATE 34.

The older stages of the development of the embryo.

- Fig. 35-39. Sections of successive stages of development to show the way in which the outlines of the cells gradually disappear until, in the stage that is shown in figure 39, they are converted into a syncytium with no traces of cell boundaries. Mitosis of the cells of the blastoderm in the early stages of segmentation.
- Fig. 40-41. Mitosis of the cells of the blastoderm during the early stages of segmentation.
- Fig. 42-46. Amitotic division of the cells of the blastoderm during the later stages of segmentation.
- Fig. 47. The first traces of the differentiation of the ectoderm.
- Fig. 48. The ectoderm is well defined and there are traces of the differentiation of the cells of the endoderm.
- Fig. 49. Section of a planula a little older than the one shown in figure 48.



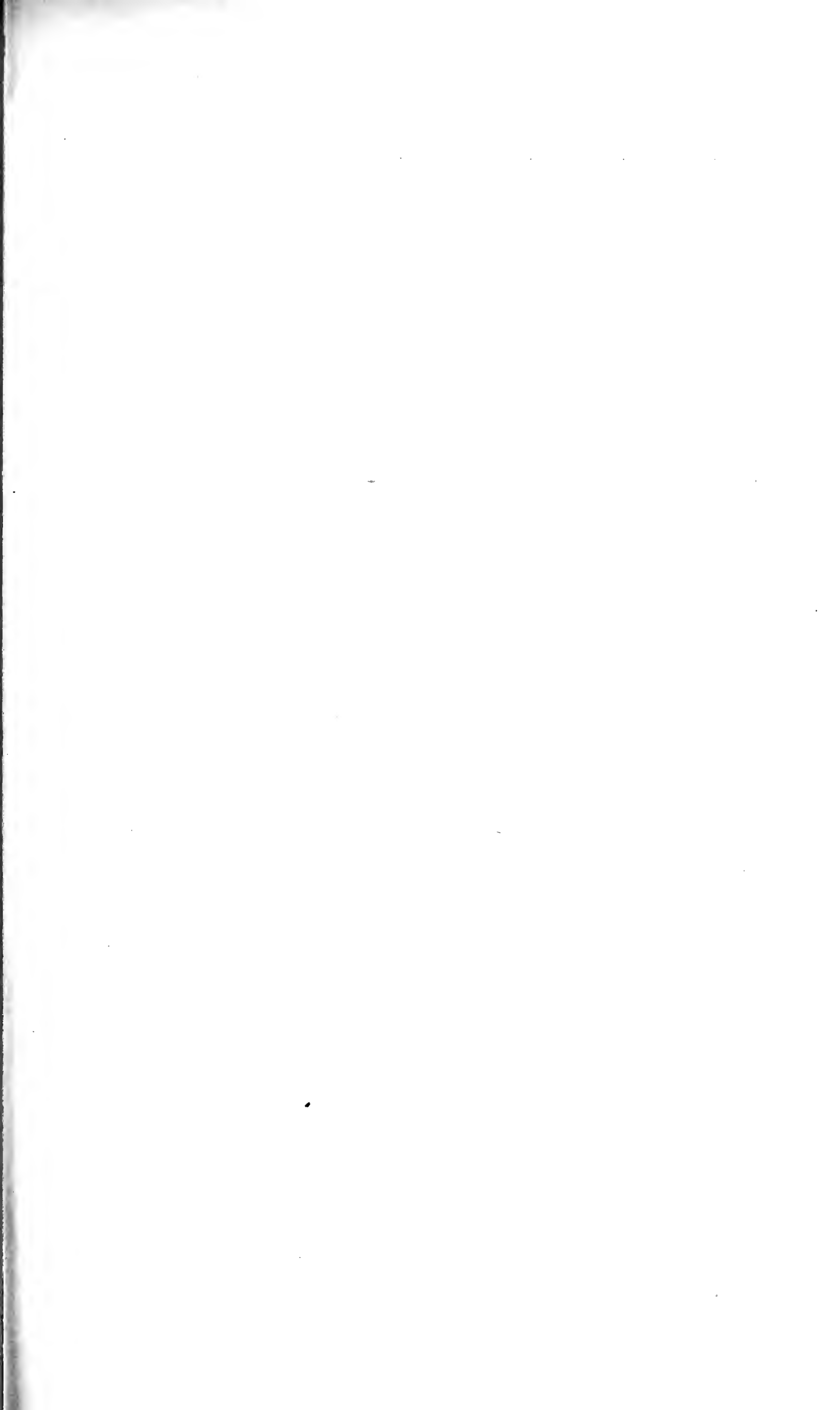
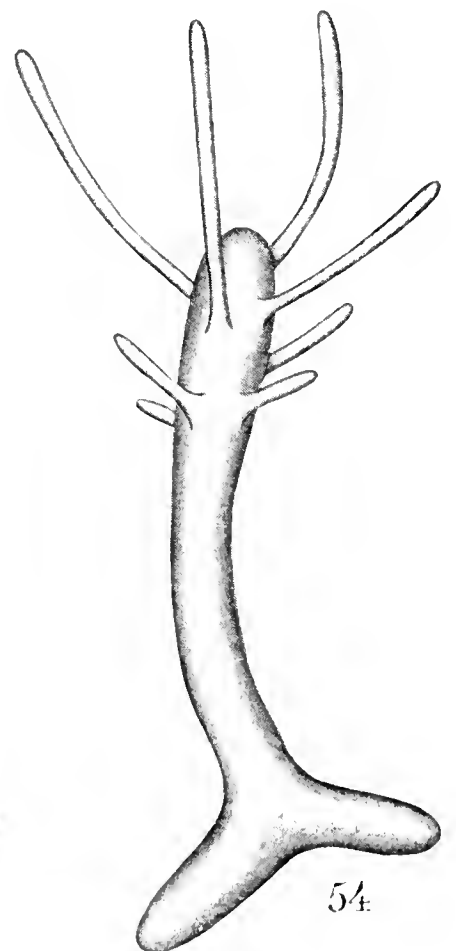
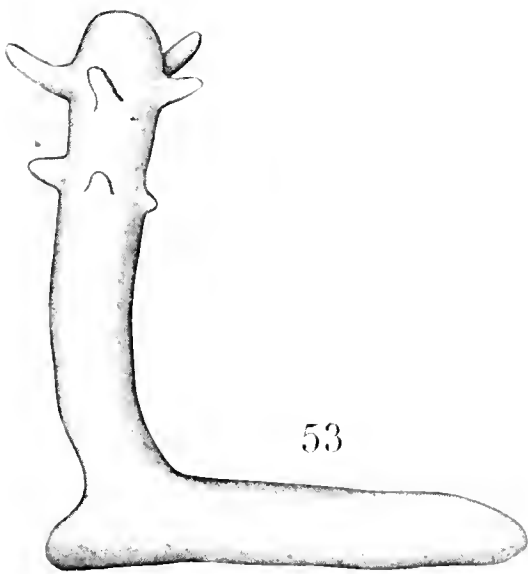
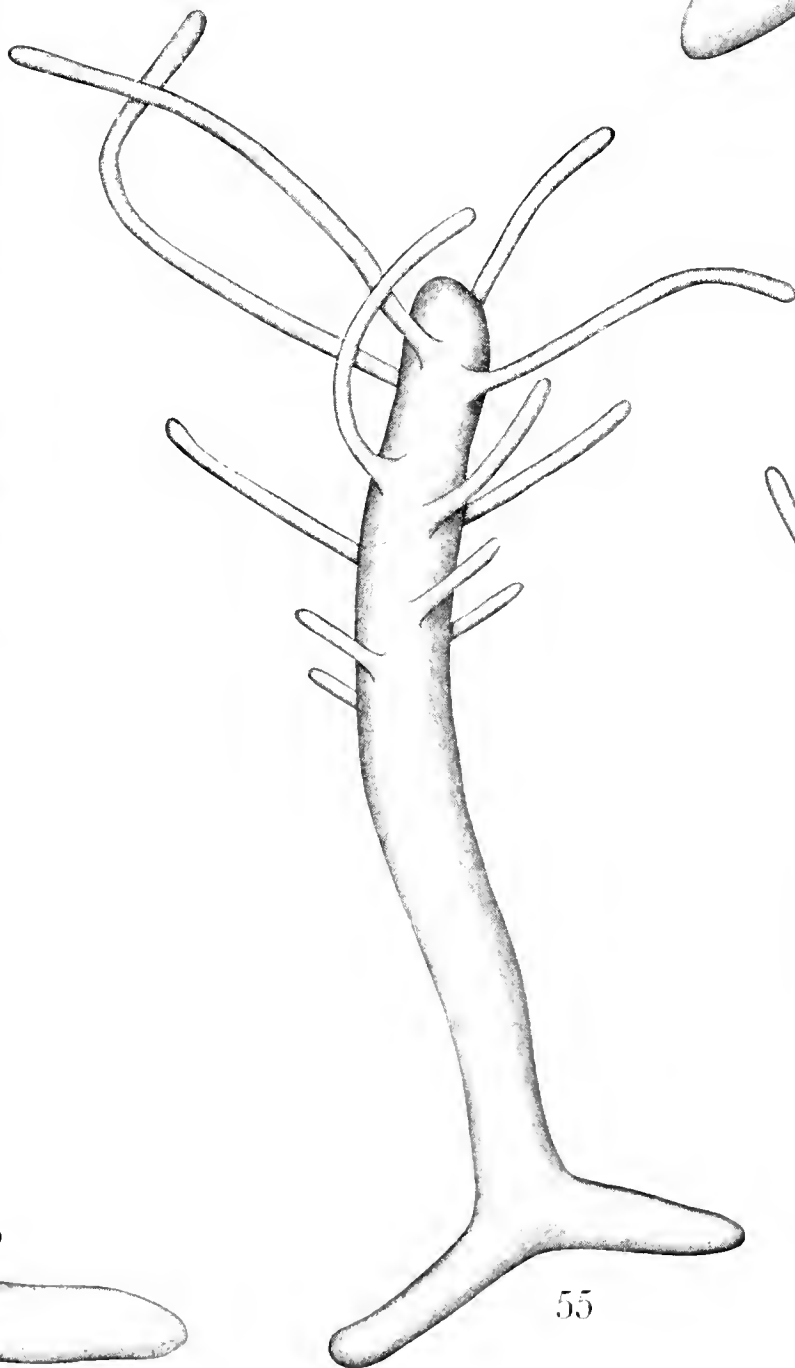
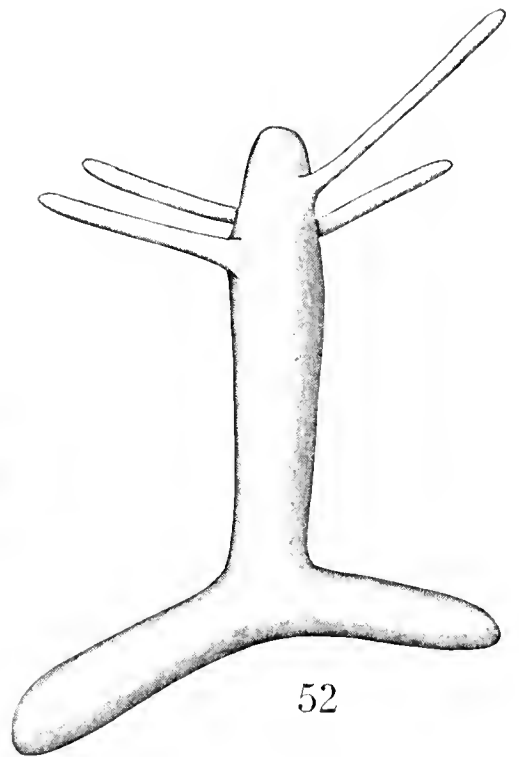
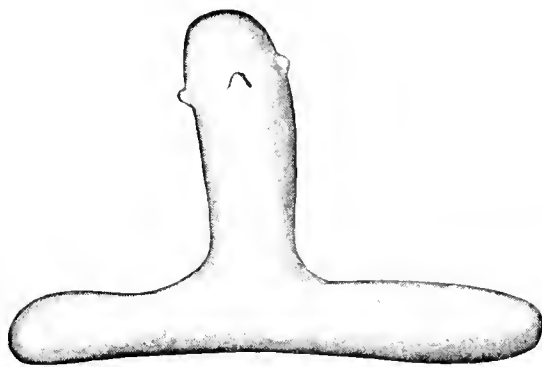
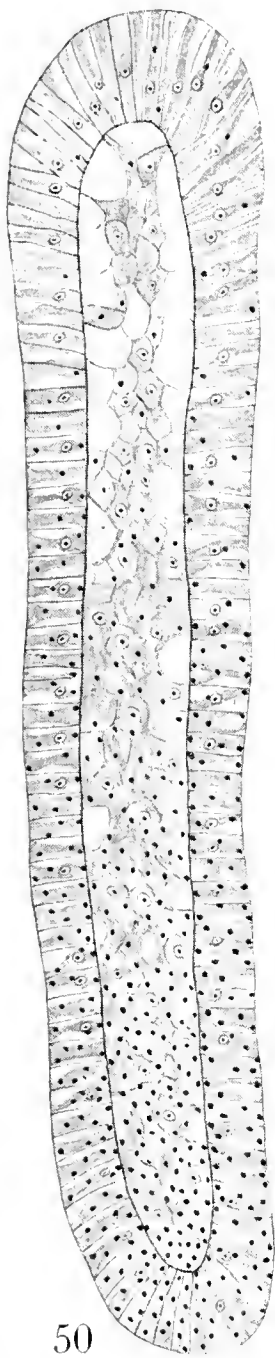
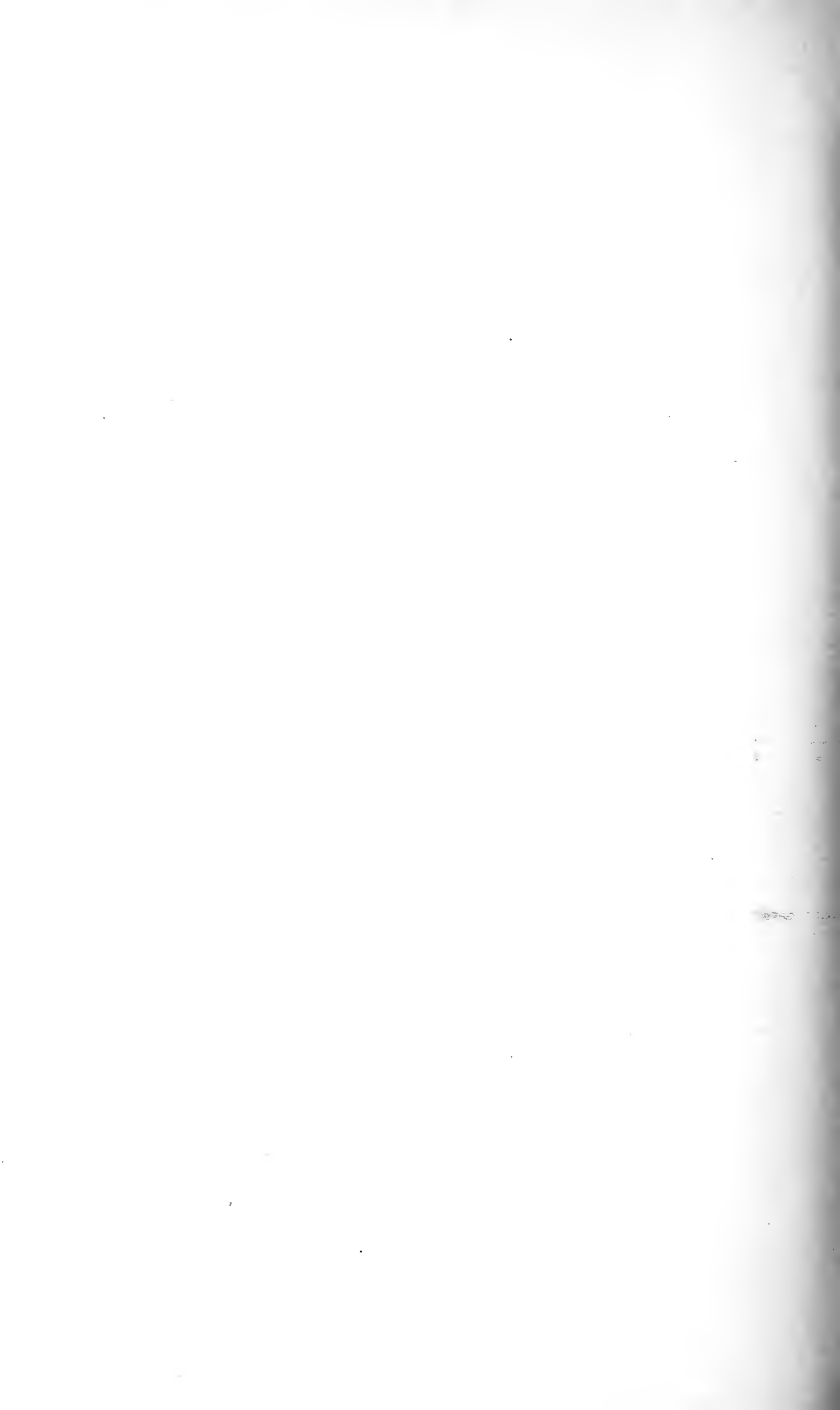


PLATE 35.

The conversion of the planula into a hydrorhiza; and the origin of the first hydranth as a bud.

- Fig. 50. A section of a fully grown planula, with both ectoderm and endoderm well defined.
- Fig. 51. The planula has become a hydrorhiza, and the bud that is to become the first hydranth shows traces of the first cycle of tentacles.
- Fig. 52. The tentacles of the first cycle are well developed.
- Fig. 53. The rudiments of the tentacles of the second cycle are present as buds.
- Fig. 54. Two cycles of well developed tentacles are present.
- Fig. 55. All three cycles of tentacles are present.





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HABITS AND STRUCTURE OF *SCUTIGERELLA IMMACULATA*
(NEWPORT).

BY S. R. WILLIAMS.

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OCTOBER, 1907.

No. 9.—HABITS AND STRUCTURE OF *SCUTIGERELLA*
IMMACULATA (NEWPORT).

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INTRODUCTION.

THE present age is the age of insects. No other animals so abound, few have such intimate relationship for good or evil with mankind. Since the group is of such importance, those naturalists who have investigated the origin and ancestral history of the Hexapoda have become interested in the Symphyla, that group of arthropods which seems to partake to a certain extent of the characters of the millepedes, the centipedes, and the thysanuran division of the insects. To quote from Packard ('73): "It [Scolopendrella or the Symphyla] may be regarded as a connecting link between the Thysanura and Myriapoda and shows the intimate relation of the myriapods and the hexapods, perhaps not sufficiently appreciated by many zoologists." Again Packard ('98, p. 24) says: "The embryology [of the Symphyla] is entirely unknown and it need not be said that a knowledge of it is a very great desideratum."

Any points which can be added to those already known of the life history of the Symphyla seem therefore well worth while and it is the purpose of this paper to give the results of a study of one of the Symphyla, *Scutigereilla immaculata*, and especially the observations concerning its eggs and newly hatched larval form.

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HISTORICAL REVIEW.

It will be more convenient to review the literature that has been accessible to me in two parts: first, those papers which deal with the systematic position of *Scutigere*lla, and second, those treating of the anatomical details.

Systematic.—According to Latzel ('84), the first of these forms known to science (*Scutigere*lla *nivea*) was described by Scopoli in 1763 as a *Scolopendra*.

The second, called by Gervais *Geophilus junior* in 1836, he recognized as a distinct genus in 1839, and named it *Scolopendrella notacantha*.

In 1884, Newport described *Scolopendrella immaculata*, now *Scutigere*lla *immaculata*, which is the most common and most widely distributed form of the group.

Ryder ('80) instituted a new order for these animals, the Symphyla, indicating by the name the combination of myriapodean and thysanuran characters which characterizes the group.

In 1882, Ryder separated the species of the order into two genera, *Scutigere*lla and *Scolopendrella*, on the character of the dorsal scutes. Ryder ('80) also described a species of *Scolopendrella* — *S. gratiae* — which was withdrawn by Latzel ('84) as a synonym for *Scutigere*lla *nivea* Scop.

Scudder ('83) published a species, *Scolopendrella latipes*, which was not included by Latzel ('84) in his list and is cancelled by Hansen ('03) as incompletely described from imperfect material.

Latzel ('84) gave full descriptions of the three species then known to science, *Scutigere*lla *immaculata*, *S. nivea*, and *Scolopendrella notacantha*. His description of the larval forms as far as known and the habits of the animals is very complete.

Grassi ('86) described a fourth species, *Scolopendrella isabellae*, which as an adult has but eleven pairs of legs instead of the twelve pairs more usually found.

Hansen ('03) reviewed the whole order and described ten new *Scutigere*llas and nine new *Scolopendrella*s. He also re-established *Scolopendrella microcolpa* published by Muhr ('81) and withdrawn by that author as a synonym of *S. notacantha* Ger. in the following year.

Hansen's new species are as follows:

| | |
|---------------------------|-------------------------------|
| <i>ScutigereUa armata</i> | <i>Scolopendrella subnuda</i> |
| “ <i>unguiculata</i> | “ <i>silvestrii</i> |
| “ <i>caldaria</i> | “ <i>texana</i> |
| “ <i>orientalis</i> | “ <i>vulgaris</i> |
| “ <i>plebeia</i> | “ <i>neotropica</i> |
| “ <i>chilensis</i> | “ <i>simplex</i> |
| “ <i>capensis</i> | “ <i>pusilla</i> |
| “ <i>angulosa</i> | “ <i>brevipes</i> |
| “ <i>crassicornis</i> | “ <i>antennata</i> |
| “ <i>pauperata</i> | |

Hansen's paper enumerates, then, twenty-four published species of the Symphyla, twelve of these belonging to the genus *ScutigereUa* and twelve to the genus *Scolopendrella*. It is his expectation that many more species of both genera are yet to be found.

Anatomical.—The first author to treat of the anatomy of the Symphyla in any detail was Menge ('51), whose observations were rather complete, and considering his lack of the later methods of work, surprisingly accurate. He saw the dorsal blood vessel or heart, the ovary, the intestine, tracheae, the spinning glands ending in the cerci, and the movable paired “parapods” accompanying the pairs of legs. He reported four Malpighian tubules instead of two, the correct number, and made the mistake of finding a sexual opening behind and dorsal to the posterior opening of the intestine. Menge considered the parapods as prominences to which eggs were to be fastened.

Packard ('81), in discussing *Scolopendrella*, put the Symphyla among the Thysanura as a suborder with the Cinura and Collembola. This was based on certain very evident outward resemblances which *Scolopendrella* has to the thysanuran *Campodea*, but was at once seen to be an untenable grouping. The numerous large differences, such as the differences in the number of legs, the presence of spinning glands, and cerci on the posterior end of the Symphyla, and the anterior genital opening in the Symphyla render such a relationship impossible.

Wood-Mason ('83) described in detail the appendages of the Symphyla. “*Scolopendrella* has very remarkable antennae; they may be compared each to a series of glass cups strung upon a delicate, hyaline and very extensible rod of uniform thickness throughout.” He described the ventral sacs or abdominal vesicles (on the 2d to 10th segments inclusive) as “a pair of huge two-lipped apertures surrounded by a circular wall, the summit of which is defended by a circlet of movable spines.” He also concluded from his observations that

the addition of new segments "therefore takes place in this animal by the intercalation of two at each moult between the antepenultimate and penultimate sterna as in the Chilognatha and as also in some of the Chilopoda."

Haase ('83) corroborated the statements of Menge in regard to the tracheae and demonstrated two stigmata on the head. He corrected Ryder and Wood-Mason, who had interpreted as tracheae the endoskeletal bars of each segment.

Latzel ('84) gives a most valuable description of the external anatomy. In repeating the description of the order Symphyla given by Ryder ('80), he says (p. 1): "Orificium genitale in segmento ultimo corporis situm." In the body of the text, however (p. 5), he speaks of the pore "den Mann bei grosser Anstrengung auf dem Bauchschilde des vierten Segments der Scolopendrellen bemerkt. Lange Zeit habe ich an der Existenz dieser Oeffnung gezweifelt." This opening of which he speaks is, of course, the anterior genital opening.

Latzel also discussed the variability of these forms and described on page 14 a young *Scutigereilla nivea* which I conclude by comparison with young *S. immaculata* hatched in the laboratory, must have just escaped from its egg envelope.

The first paper to cover at all fully the finer anatomy of one of the Symphyla is that of Grassi ('86) on *Scolopendrella (Scutigereilla) immaculata*. He discusses with much detail the cuticula, nervous system and sense organs, the respiratory and digestive systems, the dorsal blood vessel, the silk or spinning glands, the ventral vesicles, the sex organs, the mouthparts, and finally, the relationship of the Symphyla to the Pauropods, the Diplopods, Peripatus, and Campodea and Japyx among the Thysanura.

Haase ('89) modified and extended somewhat Grassi's descriptions of the coxal sacs or ventral vesicles. With regard to the abdominal appendages known as "Huft-griffeln" or parapods he maintains (p. 432) that these are not rudimentary legs but that they are secondary paired sense organs developed from hairs which have been modified to become locomotor instead of purely sensory. In this interpretation he is not supported by other writers.

Schmidt ('95) corroborated Haase in his interpretation of the coxal sacs as organs of respiration. He, however, opposes the theory put forward by Haase with reference to the parapods and maintains that these are rudimentary abdominal appendages or legs and each with

its own rudimentary coxal gland as well. He further considers the pair of cerci, which carry the ducts of the spinning glands, as homologous with a pair of legs. The paired stylets by the cerci, considered sensory by all authors, would then probably be the modified parapods of the segment on which the cerci represented the legs.

Hansen ('03) in his paper adds a description of a peculiar type of sense organ, the striped sense organ, of which he finds one or more examples on the terminal segments of the antennae and which are also found, but less abundantly, on other antennal segments. "An organ of this kind consists of a stalk, which is either short or rather long, often gradually increasing in thickness outward and from its end originate four fine branches which are slightly convex outward, subparallel or slightly diverging and certainly always united by a very thin clear membrane." These organs are exceedingly small. He used a magnification of 600 diameters in their study. Hansen also described the mouthparts in the following order: (1) two-jointed mandibles, (2) maxillae with palps, (3) labium, (4) maxillulae (paraglossae of Grassi) which he considers homologous with the first maxillae in Crustacea and lower insects.

Carpenter ('05) emphasizes the presence of three pairs of mouthparts behind the mandibles in the Symphyla. His description of the mouthparts differs in its order from that of Hansen. He describes (1) mandibles, (2) maxillulae, (3) 1st maxillae, (4) labium.

He finds in the Symphyla the same number of trunk segments as in insects and the same total number of segments (22) in this group of the Symphyla as in the widely separated arthropod forms, the lobster, the cockroach, and the scorpion.

DISTRIBUTION.

Till 1903 there had been but four accepted species of the Symphyla described in the 138 years that had elapsed since Scopoli described the form now known as *ScutigereUa nivea*. These were known only from Europe and the United States of America.

The paper by Hansen ('03) on the genera and species of Symphyla describes a total of twenty-four species all but five of which are new. Twelve of these belong to the genus *ScutigereUa* and twelve to the genus *Scolopendrella*.

These animals have thus far been found in Europe, Algeria, Cape

Colony, many localities in the United States, Mexico, Venezuela, Chile, southern Brazil, Patagonia, Java, Sumatra, Siam, and India. To quote from Hansen: "I venture to state that species of this group can be captured in all countries of the world with the exception of the Arctic and Antarctic regions." "I am convinced that nearly one hundred species and perhaps a considerably higher number are still undiscovered."

Hansen finds that *Scutigere* seems to be distributed a little nearer to the polar regions than *Scolopendrella* and he thinks that there will be more *Scolopendrellas* than *Scutigere*s found in the warmer regions. He also states that with the exception of *Scutigere* *immaculata* all the species are moderately limited in range. This one species seems to have a rather general distribution from 60° N. lat. in Sweden throughout Europe, in Algeria, in South America, in Mexico, and in several localities in the United States.

SURROUNDING FAUNA.

The group of animals found with *Scutigere* in southwestern Ohio is a somewhat definite one, comprising as it does those animals that live in non-cultivated and protected localities under stones, or between the decaying layers of forest leaves or in the loose loam beneath these leaves.

The particular forms found in the same general habitat with *Scutigere* *immaculata* are as follows:

MYRIAPODA.

Scolopendrella sp. unidentified, very infrequently found.

Pauropus sp., abundant.

Scolopocryptops sexspinosus.

Lithobiidae — several species, common, including *Lithobius multidentatus*.

Mecistocephalus sp.

Polydesmus sp. (probably *serratus*), common.

Fontaria sp.

Iulidae, several species.

COLLEMBOLA (kindly identified by Dr. J. W. Folsom).

Isotoma viridis.

Aphoura ambulans.

Tomocerus sp.

Pseudosinella sp.

THYSANURA.

Campodea sp.

Nicoletia sp. (?)

ACARINA.

Unidentified but abundant. A young tick of an undetermined species was found on a *Scutigere*lla.

PSEUDOSCORPIONIDAE, possibly *Atemnus elongatus* Banks.

MOLLUSCA (kindly identified through Mr. C. C. Adams).

Bifidaria armingeria Say.

Bifidaria pentodon Say.

Polygyra sp.

A species of Ponerine ant is fairly common in the *Scutigere*lla habitat. It is probably *Ponera coarctata*.

The spiders, flies, beetles, and ants are all unworked and those who are familiar with faunal lists from similar habitats perceive that this list is far from complete. Enough, however, is given to show something of the character of the fauna.

LIGHT AND WATER RELATIONS.

*Scutigere*lla is a cave animal as is seen by its white color and the slight development of eyes. According to Grassi ('86) they prefer rocky soil in the shaded regions for their habitations and where there are no stones the animals are not to be found. Williams ('04) reported that they are to be found isolated beneath flat stones in the drier portions of a stream bed and in a restricted area along the body of the stream.

Neither of these authors is absolutely correct. During parts of the year here in Ohio at least, the *Scutigere*llas are to be found in the spaces between the decaying leaves of the forest floor, quite far from either soil or stones. Moist wood that is sufficiently decayed to be burrowed in by insects is likely to contain them in its passageways.

The chief factors determining their distribution seem to be an atmosphere of great humidity, a moderate temperature, comparative darkness, and an undisturbed — at least uncultivated — soil.

In April, when *Scutigere*lla is fairly abundant, the temperature of the air is low and it is usually well laden with moisture. Several experiments with a wet-bulb thermometer indicated a relative humidity of the air above the ground of 60%. In the leaves on the ground where the animals were found, water always deposited at once on the sides of the glass vessel in which the captured animals were placed indicating a still higher relative humidity of the atmosphere, essentially saturation.

In August on the other hand, *Scutigereellas* are found only beneath heavy stones in the moist bed of the stream or deep in the earth in shady places, and it is only in such localities that, at that time of the year, there is any quantity of moisture in the air.

One can also prove experimentally their need of a humid atmosphere by placing, during a warm day, some specimens in an open vessel and others in a closed vessel, the air of which contains water vapor. Those exposed to the circulation of the air even though at the bottom of a bottle will be likely to die within a short time, while those in the humid and unchanging atmosphere can be brought into the laboratory unharmed. Too great moisture is disastrous. Specimens after capture were kept in Petri dishes with a little earth. When, as sometimes happened, the earth was kept too moist the animals in the wet dish died more rapidly than those in drier dishes. They can, however, live for some time immersed in clear water without drowning. A record for May 9, 1906, states that "an individual has been immersed in water under a glass slide for the last three days and is still active."

The surface film of water is something that they seem hardly able to break through, either from the outside into a drop of water or from the inside of the drop to the air. When submerged in water, they wander back and forth, stopping each time as the antennae or front of head as the case may be, reach the outer film and rarely if ever breaking through unaided. It is evident that any animal living in the narrow bed of a small water course must often be submerged for a time in air spaces beneath small stones at least, if not directly in the water itself, so that this endurance of immersion is not entirely unexpected.

According to the "Cambridge natural history," Plateau records two Chilopods, *Geophilus maritimus* and *Geophilus submarinus* which live between tide marks and are able to withstand a submergence of from 12 to 70 hours in sea water and of from 6 to 10 days in fresh water.

Though *Scutigereella* is found in darkness it becomes perfectly acclimated to diffuse light and gives no indication of disturbance when a covering cloth is removed from the Petri dish. Specimens have been kept in saturated air in a tightly corked homoeopathic vial for some months with no protection from the light whatever and no evil effects were seen.

EXPERIMENTAL EVIDENCE CONCERNING FOOD.

To quote from Latzel ('84): "Welche (Nahrung) wahrscheinlich in noch kleineren Arthropoden besteht. Auf animalische Nahrung weist nicht bloss der Bau ihrer Mundtheile und in gerader Erstreckung verlaufende Darmcanal hin, sondern auch die ziemlich bedeutende Agilität dieser Thierchen." The ease with which *Scutigere*lla can be kept in captivity would indicate, however, a notable ability for resisting starvation if they are carnivorous. After being kept for six months in the laboratory under conditions which would promise very little sustenance of any sort, animal or vegetable, some individuals still survived. Though the animals are at all times very busy with their mouthparts, it is impossible to prove that they are eating. A specimen which had been isolated in an air bubble for some time, when freed, acted as if it were licking the surface of a cast skin on which it happened to stumble. Their diet is to be determined definitely only by microscopic examination of the contents of the digestive tract. The sections which have thus far been examined offer no conclusive arguments for or against Dr. Latzel's theory as stated above. There is no question but that vegetable material of one kind or another is among the contents of the intestine, nor that it makes up the greater portion of the oval masses of faecal matter which are to be found wherever *Scutigere*lla inhabits decaying wood. These masses vary in length from 0.12 mm. to 0.2 mm., and in breadth from 0.1 mm. to 0.16 mm.

The contents of the mid-gut are bounded by a membrane-like line such as Folsom and Welles ('06) indicate about the contents of the gut of a *Collembolan* (see fig. 7, pl. 38). This peritrophic membrane they found was secreted by the epithelium of the intestine.

The material in the mid-intestine shows by its reaction to stains that it is composed of material much more like protoplasm than like cellulose in its appearance. Especially is this true in the anterior part of the mid-intestine where the food has not yet been sufficiently digested to concentrate foreign bodies like bast fibers, wood fibers, and fungus threads, as these would be concentrated in the posterior end of the mid-gut.

Those specimens in which the intestinal contents were plainest indicated that Protozoa which swarm over the decaying materials

of a forest floor probably made the major portion of the animal's food. Round or oval masses which appear like infusorian nuclei make up a large part of the intestinal contents. (The paper of Folsom and Welles would suggest by analogy that some of these at least might be intestinal parasites.) If *Scutigерella* lives on the organisms (and perhaps on certain fungi) which it can secure from decaying leaves and other plant remains the fibrous material in its intestine would simply be that taken in incidentally while securing its regular food.

A further indication of carnivorous habit is the sudden disappearance from a Petri dish containing other adults of the young individuals after the mother ceased guarding them, as reported by Williams ('06).

The empty shells of young *Bifidaria* are found in great abundance among the leaves which are the habitat of *Scutigерella* and are always found cleaned very thoroughly, but the agency, of course, is in doubt.

Certainly *Scutigерella* does not pursue its prey in the way Chilopods do. It is a most timid creature, fleeing instantly from other animals or from its own kind when informed either by the anal stylets or by the ever-moving antennae of a foreign presence. They are usually alone and rarely to be found in places accessible to other creatures. This is evidently a wise precaution as a small spider not so large as a *Scutigерella*, that was accidentally introduced into a collecting bottle, entangled and killed all the *Scutigерellas* in the bottle while they were being brought to the laboratory.

I give the results of certain experiments with different sorts of surroundings which might influence the food supply. The animals were brought in late in the fall and kept under fairly uniform heat conditions.

TABLE 1.

| Days | Initial no. of animals | 1-5 | 5-10 | 10-15 | 15-20 | 20-25 | 25-30 | 30-35 | 35-40 | 40-45 | 45-50 |
|---|------------------------------|-----|------|-------|-------|-------|-------|-------|-------|-------|-------|
| Petri dish <i>No. 1.</i> Clean sand with several large lumps of decaying wood. | 12 | 12 | 12 | 12 | 10 | 10 | 8 | 8 | 3 | 3 | 3 |
| <i>No. 2.</i> Soil baked in oven. | 9 | 8 | 6 | 4 | 4 | 3 | 3 | 3 | 2 | none | — |

TABLE 1. *Continued.*

| Days | Initial no. of animals | 1-5 | 5-10 | 10-15 | 15-20 | 20-25 | 25-30 | 30-35 | 35-40 | 40-45 | 45-50 |
|---|------------------------------|-----|------|-------|-------|-------|-------|----------------|-------|-------|----------------|
| <i>No. 3.</i> Soil had been in laboratory for two years. Had been used for <i>Scutigere</i> lla the previous year. | 11 | 11 | 11 | 11 | 11 | 11 | 10 | 8 | 4 | 3 | 2 |
| <i>No. 4.</i> Like no. 3. | 7 | 7 | 7 | 7 | 7 | 5 | 5 | 5 | 4 | 2 | record stopped |
| <i>No. 5.</i> Common loam from out-doors. | 8 | 8 | 8 | 6 | 6 | 6 | 4 | record stopped | | | |
| <i>No. 6.</i> Baked soil and common soil mixed. | 11 | 4 | 3 | 3 | 2 | 2 | 2 | 2 | 2 | none | |
| <i>No. 7.</i> Common soil kept rather wet. | 8 | 7 | 7 | 7 | 7 | 6 | 6 | 6 | 6 | 6 | 3 |
| <i>No. 8.</i> Common soil like no. 5. | 12 | 12 | 12 | 12 | 12 | 12 | 12 | 9 | 8 | 4 | 3 |
| <i>No. 9.</i> Baked soil like no. 2. | 8 | 4 | 4 | 2 | 1 | 1 | 1 | none | | | |

This table may indicate, however, that none of the dishes contained any food for *Scutigere*lla and that at the end of 50 days most of the individuals had starved to death in each dish.

In dish no. 1, a specimen survived for 112 days. The table indicates without a doubt that those dishes in which the soil was either wholly (nos. 2 and 9) or partially (no. 6) sterilized were more unfavorable for the animals than the unsterilized soils. At the end of 15 days but three animals had died out of 58 individuals in the other six dishes, while 19 out of 28 individuals had died in the three dishes sterilized wholly or in part. Moreover, all the 28 animals died by the fortieth day while those of the other dishes whose record was kept, still contained some *Scutigere*llas at the end of 50 days.

Those animals in dishes with little organic matter soon became very translucent and the mid-gut appeared dark, due to the amount of earth introduced into the intestine.

The animals survive much better if instead of a thin layer of earth the bottom of the dish contains moist leaves. For the sake of keeping

the *Scutigere*llas in sight these leaves should be partly decayed, an open network of mid-rib, veins, and veinlets. If then the microscope be focussed on the water around these leaves it will be found to be full of Protozoa (chiefly Ciliata), rotifers, and worms.

Since the colonies live better in such an environment, as *Scutigere*llas are to be found most abundantly in similar environments in nature and judging from the contents of the mid-intestine already referred to in figure 7 (pl. 38), one would conclude that the microscopic animals just mentioned form some part and perhaps a great part of the food of *Scutigere*lla.

GENERAL ANATOMICAL RELATIONS.

There are twelve pairs of legs in the adult, the first leg on each side having four segments while the other legs are made up of five segments each. Hansen says that the true coxa is firmly fused to the ventral plate and that the first movable joint is the trochanter. This necessitates his naming the segment after the tibia a metatarsus. It will accord better with the nomenclature of most authors if in this paper the first freely movable joint be still known as the coxa.

At the side of the coxae of the legs behind the second pair there are found small movable organs, the rudimentary legs. If these are added to the twelve pairs of walking legs they will make 22 pairs, and if with Schmidt we include the cerci and the special sense bristle at the hinder end of the body there would be 24 pairs of legs in all.

There are fourteen large plates or scutes on the dorsal body wall of *Scutigere*lla. Latzel says there may be 15 or 16 dorsal scutes, but this must be meant to include an incomplete scute just behind the head and a variation which *Scolopendrella* shows at the hinder end of the body.

There are then not quite two pairs of legs to one dorsal plate, which is the relationship in other families of millepedes. Sinclair ('95, p. 71), shows that a dorsal scute of a millepede should represent two plates, one fused behind the other. His argument is based on fossil forms. In *Palaeocampa anthrax* each dorsal plate covers but one somite whereas in later fossil species, though consolidation of two plates into one has begun, the line of fusion is plainly visible. Hansen ('03) states that a transverse suture is to be seen in each dorsal scute of *Scutigere*lla which separates it into unequal anterior and posterior parts.

The alimentary canal is a non-coiled tube running through the body with a median enlargement, the stomach, or better the mid-gut. This is separated from esophagus and intestine by valve-like folds as the diagram (text fig. A) shows (also see fig. 7, pl. 38).

Above the alimentary canal lie the dorsal longitudinal muscles and the dorsal blood vessel. The location of the dorsal muscles is shown in figure 6 (pl. 37).

On the sides of the intestines in the posterior part of the body lie the paired ovaries or the testes. The testes are said to be connected by one or more commissures. From the sex organ a duct passes forward on either side, at last uniting with its fellow from the opposite side in an unpaired sexual opening between the coxae of the fourth pair of legs. No author has yet demonstrated any secondary sexual differences between the male and female though Grassi would seem to indi-

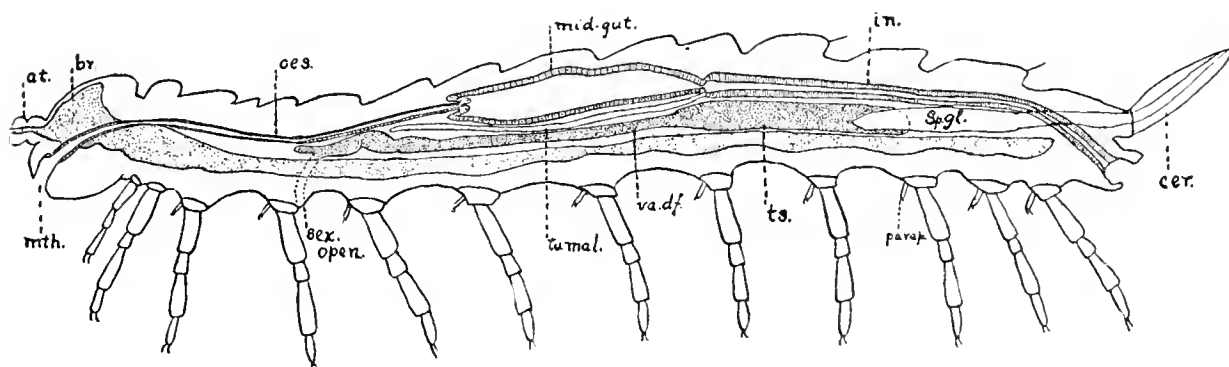


FIG. A.

cate, when he says that males were taken for females with undeveloped eggs, that the males are smaller than the females. The male organs are active in animals taken in October in this region. This has been shown by sections.

A pair of Malpighian tubules branches off from the intestine just back of the mid-gut, one on either side, and passes forward. The fact that there is but one pair shows that the Symphyla are Diplopod-like and not like the Chilopods which have four Malpighian tubes, two on each side of the intestine.

The spinning glands extend forward from the cerci to about the third segment from the last. They are modified dermal glands whose secretions unite to form the thread which *Scutigerebella* spins so freely. In the diagram (text fig. A) the gland is shown as transparent in order not to obscure the intestine just behind it.

The nervous system lies in the mid-line of the body and beneath the

other internal organs previously mentioned. It shows little trace of the longitudinal division into two parallel cords so evident in the Chilopods and also shows a very indefinite segmentation. There are two problematic appearances to be seen (not in all cases) on the outside of the body on the anterior part of the head. They are well drawn by Grassi. He considers them to be a pair of eyes even though they are not subtended by optic lobes of the brain.

The animal breathes by means of two tracheal systems which are found in the head and possibly the first two somites. Behind these somites the conjecture that the coxal sacs serve as respiratory organs by allowing the passage of oxygen through their exceedingly thin walls is a very happy one. There seems to be an imperfect sac at the base of the second coxa and thereafter there are ten perfect pairs near the third to the twelfth pair of legs inclusive.

MUSCULATURE.

The dorsal and ventral musculature is made up of small muscle bundles which originate on and are inserted on the tergites or sternites. On the dorsal side the distance between the origin and the insertion of these muscle bundles is usually the width of one, two, and even three dorsal scutes.

The ventral longitudinal muscle band is double, being parted in the mid-line by the nerve cord and its surrounding tissue.

The musculature of any two adjacent somites is quite similar. According to Gegenbaur ('78): "Where metameres are similar the muscles are similar." This similarity is especially well shown in the case of the leg musculature. There are five principal sets of muscles which are inserted on the coxa (trochanter, Hansen) of each leg except at the extreme anterior or posterior ends. These five different muscles can be seen on legs 4 to 10 inclusive (pl. 37, fig. 6).

Two of these originate anteriorly, two posteriorly, and one is nearly vertical as seen from a side view. One of these muscles comes from the opposite side of the dorsal scute, crossing the body diagonally. Muscles were not seen to run forward from the coxae of the first or second pair of legs and but a single one forward from the third coxa. The eleventh coxa shows but three muscles and the twelfth but one and that originates anteriorly. The hinder legs seem to drag rather than to step as the animal moves forward. These muscle bundles

in any particular somite originate on the under side of the dorsal plates and are inserted on the inner surface of the coxa to move it in the different directions. In some cases fibers originate on the lower surface of the third scute in front of or behind the scute most nearly over the leg. These may unite with fibers whose origin is on scutes nearer the leg.

ECDYSIS.

(Methods of ecdysis as derived from a study of the cast skins of adults.)

Since Grassi ('86, p. 597) stated that he had never found specimens of *ScutigereUa immaculata* in ecdysis a number of the ecdyses of adults cast in the laboratory were studied to determine the general method of shedding.

No. 1. Torn laterally on the left side along and just above the coxae of the posterior legs.

No. 2. Torn ventrally between posterior legs.

No. 3. Opened at dorsal suture of next to last somite. Not torn, cerci flexed downward.

No. 4. Slit lengthwise on ventral side for last 7 somites.

No. 5. Head broken off, ventral wall partly torn.

No. 6. Top of head gone, ventral wall torn, and the posterior segments turned downward.

No. 7. Torn on the ventral side between the legs of the last five somites. The anterior end all crowded.

No. 8. Torn on the ventral side between the legs of the last six somites. The anterior end all crowded.

No. 9. Torn from the fourth to the ninth segment on the ventral side. Segments 10 and 11 open on the dorsal side. Possibly the top of the head gone.

No. 10. Torn all along one side above the coxae of the legs. Legs fastened firmly to the soil.

No. 11. Cast broken in half at the 8th somite. Not torn.

No. 12. Torn on the right side just below the coxae of the legs. Head much earth-stained and somewhat concentrated. Posterior end perfect.

From these examples it is plain that the animal may escape from its cast skin either by tearing between the legs or just above the attachment of the legs on either side or by tearing the dorsal covering longi-

tudinally or by disarticulating the cast somewhere on the dorsal side and extricating the body. The most common method is to disarticulate the cast at the junction of head and first segment and to creep out forward thus causing the anterior end of the cast to crowd together as seen in four out of these twelve examples. I have seen one individual in the process of casting its cuticle and it proceeded according to this method. Healthy individuals cast at intervals of a few weeks in the laboratory.

LOCOMOTION.

In a species of the millepedes according to Sinclair ('95) the wave-like motion seemed to pass along the legs moving them in sets of five.

Lankester ('03) calls this a "swing group," including in this term all those legs in different stages of taking a step between any two legs in the same stage. He finds that the change of phase appears from behind and passes forward and that the smallest possible "swing group" (two) was shown in *Peripatus*, one of six was shown in a Chilopod *Scolopendra subspinipes*, and one of sixteen in the millepede *Archispirostreptus pyrocephalus*.

Its method of locomotion goes to prove that *Scutigereilla* is Chilognath-like rather than like a Chilopod. Lankester states that in the Diplopods there are symmetrical and identical movements on the two sides of the body whereas in the Chilopods, correlated with the lateral

undulation of the body, the legs on the opposite sides of the body act in alternating groups.

Now the "swing group" of *Scutigereilla* seems to be three, that is, every fourth leg on the one side of the body is in the same relative position and the two sides correspond. The three in the swing group have their

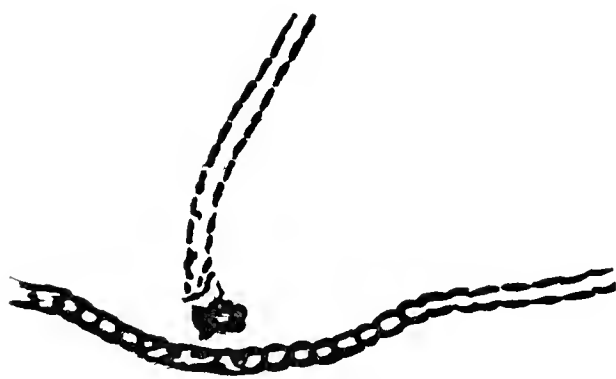


FIG. B.

tarsi closely approximated at times so that the threefold mark made by the feet looks nearly like one. As the feet are not usually raised much but are dragged through the arc when changing position, the trail of a *Scutigereilla* is made up of two parallel lines separated by the space between the claws (a little greater than the width of the body) and marked by opposite three-parted dots, the claw marks.

This is difficult to reproduce satisfactorily. The best results obtained are shown in text figure B which is drawn from a photograph.

Scutigерella when jarred or when chilled takes a very characteristic attitude. It contracts one side of the body till its shape is that of a crescent and is quiet. Then if further disturbed by taking up the stone or leaf on which it is, it may loosen its foothold and roll or drop to the ground and thus usually escapes. If no opportunity is given for dropping it will straighten itself and busily search with its antennae for some crevice in which to hide.

EGGS AND LARVAE.

Nothing definite concerning the embryology of this form had been reported until a note in Science by Williams ('06, p. 527) entitled "The young of Scutigерella." Latzel ('84) described a *Scutigерella nivea* 1.13 mm. long with 6-jointed antennae, ten dorsal scutes, six pairs of well developed legs, and a seventh pair budding. Packard ('98, p. 24) after stating that Henshaw reports finding a hexapodous young one (said to be *Scolopendrella latipes* Scudder), says that it is most probable that the young is hexapodous since the first pair of limbs is 4-jointed, all the rest 5-jointed.

On April 15, 1902, six or eight Scutigерellas were taken beneath flat stones in the bed of a small rivulet flowing through a piece of woodland. These were placed in a Petri dish with earth which was kept moist. By May 20th, they were reduced to four individuals and these had spun their webs around on the surface of the earth in the dish. By this time at least three of the animals had shed their cuticular coverings. One of these skins was cast May 1st, one May 3d, and the third May 20th. The time of this casting is significant for the egg laying.

On May 23d, while inspecting the dish with a hand lens two very minute individuals, each of which seemed to have but six pairs of legs, were seen in the part of the dish where the earth was deepest. On account of the amount of earth it was impossible at first to determine with certainty the number of pairs of legs. On May 27th when the animals were seen under more favorable conditions and with a compound microscope, each young animal showed conclusively that it had seven pairs of legs. On June 3d buds for the eighth pair of

legs were seen and, with some question, traces of a ninth pair behind these. These young cast their skins at least once each as a small cast was found on May 28th and another June 5th. The animals, both young and adults, died during the summer.

In 1903, taught by the experience of the previous year, only enough earth was provided to shelter the animals so that a more satisfactory view could be obtained with the microscope. A number of individuals were brought in at different times from April 10th to April 23d. About ten survived.

On May 12th, a number of white bodies slightly less than 0.5 mm. in diameter were found lying on the surface of the earth in the Petri dish. There were five of the bodies and their surfaces were not smooth but as if covered with an irregular network. On gently moving the earth these bodies were found to be fastened to the earth particles by fine fibers. These fibers (*Scutigere*lla web) were likely attached to the surface network of the problematic bodies but this was not certainly to be determined. The bodies were of a glistening pearly white when first seen but the next day the elevated network showed a pinkish tinge. One of the bodies showed a shallow depression on its surface also but this was probably not a normal phenomenon but an evidence of shrinkage, because by May 19th, seven days after the bodies were first seen, they were dry and shrunken.

In 1904, other individuals were brought in from April 18th to May 5th. The earth in the Petri dishes was kept very moist and several glass slides were provided for the *Scutigere*llas to rest beneath. As the most usual place to find them in their habitat is on the lower surface of stones or leaves, they take very kindly to the lower surface of glass which rests on the earth in which they are. Whenever water was added to the dishes to moisten the soil, air bubbles of some size were formed beneath the glass slides. On May 9th an individual was seen in an air bubble entirely isolated from its companions. It was freed artificially May 11th and seemed in all ways lively and healthy. Another 3 mm. in length which was found in an air space on May 10th remained in that space until freed on May 21st. On the next day the same animal went into a new air space 10 mm. in diameter and there on May 25th was found to have laid 8 eggs (text fig. C). These were smaller than the glistening bodies of the preceding year but otherwise were not different. The mother stayed for 13 days in the air space with the eggs, moving about slowly from time

to time but usually remaining quiet. On the 6th of June it could be seen by the motion of the bodies that they were in the process of hatching. It seems to be a matter of difficulty to escape from the eggshell and whether the anterior end or the posterior end freed itself from the shell first, the free end waved and writhed frantically for some hours at least in the efforts of the animal to extricate itself. As a matter of fact some specimens in this nest freed the anterior end of the body first and others freed the posterior end first.

I do not know how many of the 8 eggs hatched. On the next day, June 7th, four larvae were to be seen with the mother, moving about near the empty egg envelopes and others may have wandered into crevices in the earth. On this day one young one was taken for

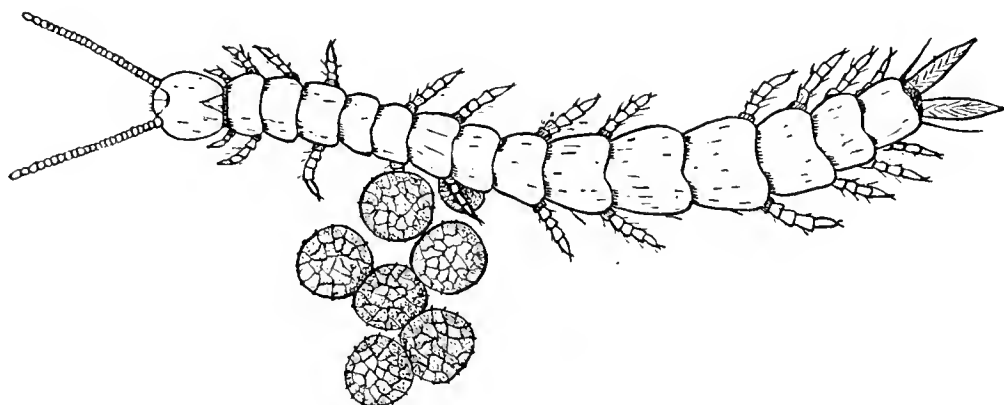


FIG. C.

purposes of preservation and on moving the glass the mother fled. By June 8th all the rest of the young had disappeared and nothing further was ever seen of them.

Again, in 1905, many individuals were brought in during the last week of April. On April 28th one was found asphyxiated in a bubble of air not as long as the animal itself. On May 9th an egg was found isolated on the wall of a dish, on May 11th another egg, and on May 18th a group of 4 eggs unlike in size and a separate single egg were found in this same dish. On May 28th two separate eggs were found in another dish and by the following day three more were found scattered about that dish. By this time both the group of eggs and the single egg in the first dish were covered with fungus and two or three days thereafter those in the second dish were also moldy. On June 2d an egg was found in a third dish but it came to nothing. These dishes with their 24 occupants were inspected at short intervals from this time on until August 12th when the last one died. All this time there had been no more eggs laid. Sections of the adults made in

October show the testes especially filled with ripe products and fertilization (which has never yet been observed) may take place in the fall. Oviposition certainly takes place in May and is preceded by ecdysis.

In 1906, 75 individuals were brought in at different times, the first on April 3d. These were kept in a basement room with a rather low but uniform temperature. No eggs were laid by these animals until the month of June when several masses of them were found. No mass was guarded by the adult and as a result the eggs were attacked by fungi and disappeared.

Having gained confidence in my ability to recognize the eggs of the *Symphyla* at sight, much time was spent during the season of 1906 in looking for these eggs in their natural surroundings. On May 30th while carefully looking over a much decayed log which had an unusual number of casts of the *Symphyla* in its crevices, there were found three nests of eggs, two with 8 each and one with 9 eggs. These nests were brought in with extreme care and the next day two sets of eggs were beginning to hatch. The three views of the larvae in plate 36 were made from specimens of these broods.

EGGS.

Myriapod eggs according to Korschelt and Heider ('99, vol. 3, p. 219) are "surrounded by a vitelline membrane and another structureless but firmer envelop, the chorion, which is apparently secreted by the genital ducts." This description is applicable to the eggs of *Scutigereilla*. In figures 4 and 5, plate 37, and figure 9, plate 38, the roughened appearance of the outer envelope or chorion may be seen. The vitelline membrane envelops closely the egg itself and the egg is seen as the dark central portion in both figures. Sections show the vitelline membrane to be very thin.

The surface of the chorion is rendered very irregular by a number of large or primary ridges connecting with each other and between these are smaller or secondary elevations. The primary ridges project about 20μ above the general level of the chorion. The whole surface of the chorion is made up of irregular polygonal depressions bounded by these primary ridges. Their largest dimension is rarely more than 0.1 mm. and usually it is much less. The floor of one of these depressions is again roughened by the slight secondary ridges

shown in plate 38, figures 10 and 11. - These are respectively a surface view of a small portion of the chorion and a profile view of a section through the chorion. The section indicates that the chorion is non-cellular in its structure.

The egg envelope is opaque, or at least only slightly translucent, and of a special pearly whiteness so that the eggs are exceedingly beautiful objects.

Incidentally figures 4 and 5 of plate 37 show the egg envelope while they illustrate the larvae during the time of freeing themselves from the envelope.

In handling the eggs, a few were accidentally injured and these exuded drops or spheres of perfectly clear liquid and left the membrane of the egg much shrunken. Such eggs never hatched.

LARVAE.

The young of the *S. immaculata* when entirely freed from the egg envelope, varies from 0.75 mm. to 1.5 mm. in length and is about 0.5 mm. wide. After the severe struggles to escape from the eggshell the animal is quiescent. It will, however, move if disturbed and seek a more protected crevice in the wood or earth on which it is resting.

The young has usually six joints in the antennae (pl. 36, fig. 1-3).

It has ten dorsal shields or scutes and seven pairs of legs. In some specimens the buds of the 8th pair are distinctly visible ventral to the tenth dorsal scute. The legs (shown in pl. 36, fig. 1) are seen to arise from beneath dorsal scutes 1, 3, 4, 5, 7, 8, 9. In figure 3 (pl. 36) of the ventral view one cannot see the relationship the legs bear to the dorsal scutes, but in certain places the boundaries of the ventral plates are visible. The top view of a specimen (pl. 36, fig. 2) shows the scutes and shows that the trochanters of the legs point toward an origin from beneath the same scutes as were indicated in the side view. The varying positions of the animals change the relationship between the scutes and the legs somewhat so that these may not always correspond. As the dorsal scutes are not homologous to single tergites according to Sinclair ('95), it is possible that variation in their widths may aid different positions of the body in changing the seeming relationships of the legs and scutes.

The first leg on each side has but four joints while there are five joints in each of the other six pairs of legs. Excepting the first pair of legs again, the other pairs are all about the same length. All are used

in locomotion. The young animal (after the first day) is nearly as rapid in its movements as the adult with its twelve pairs of legs, but moves somewhat less often.

The pair of cerci, which are evident at the posterior end of the young *Scutigere*lla, is sufficient evidence that the addition of segments must be between the last leg-bearing segment and the last segment of the body as Wood-Mason ('83) has already shown.

The body of the immature *Scutigere*lla is provided with long setae or bristles. One bristle usually arises from each side of the body about midway between the coxae of successive legs. At the posterior end of the body there is a pair of especially long setae which are sensory in an especial sense. This sense organ, the anal stylet, has been called by Muhr "Tastorgan." If the cerci be considered homologous to the walking legs (Wood-Mason), then these organs are homologous either to the bristles between the successive walking legs previously spoken of or else to the parapodia to be described later.

The whole body of the animal is also covered over with shorter hairs. These are especially developed on the joints of the antennae and the mouthparts.

The ventral drawing (pl. 36, fig. 3) shows two series of the most interesting organs to be found on the animal, the parapodia and the ventral sacs. All indications are that the view of Schmidt ('95) is the correct one and that the so called "Pseudobeinen," "Huftgriffeln," "Exopoditen" or parapods are really rudimentary legs. *Scutigere*lla is hatched with at least four pairs of parapods and more probably with five pairs. The first two pairs of walking legs seem to have neither parapods nor ventral sacs though ventral sacs may be present in a greatly reduced form at the base of the coxae of the second pair of legs. Both these organs appear by the coxae of the third pair of legs and also with the fourth, fifth, and sixth pairs. The ventral sacs which are to be near the seventh pair of legs in the adult, are not visible in any of these recently hatched larvae. The small legs, however, can be seen in some cases, under favorable conditions of light, at the base of the seventh pair of legs.

The ventral sacs or "blood gills" are eversible organs and one can either assume that the fifth pair has been drawn in in all of these specimens or that they are not yet functional and will appear at a later ecdysis.

Williams ('06) stated that *Scutigere*lla larvae were hatched with six pairs of legs and not seven as has just been shown. These larvae

may have been Scolopendrellas. Herewith are given three drawings (pl. 38, fig. 12-14) of a recently hatched larva of undetermined species which may be a young Scolopendrella. There are adults of this genus which have but eleven pairs of legs (Grassi, Hansen). In the side view of this larva, one may notice a distinct elevation or papilla on the body in the place of the first pair of legs. Behind this there are six pairs of legs, which are free and a seventh, in an advanced stage of development. This animal hatched with ten antennal joints instead of six. It has the same ten dorsal scutes and is much like the *Scutigere* larva, except in being more delicate and slender.

SUMMARY AND CONCLUSIONS.

Scutigere *immaculata* has been found to lay eggs and hatch young in the latitude of southern Ohio during late May and early June. The time of laying is influenced by the temperature.

The adult *Scutigere* is needed (at least in the laboratory) to keep off destructive fungi from its eggs so that they may hatch.

The egg of *Scutigere* is covered by a vitelline membrane and a much ridged chorion.

In the pairs of legs (7) and number of dorsal scutes (10), the larva of *Scutigere* *immaculata* is hatched more nearly like the adult than any Diplopod of which I can ascertain the embryology and more like the adult *Scutigere* than the recently hatched *Lithobius* among the Chilopods is like its adult. It is, therefore, a highly specialized young rather than a generalized ancestral form such as the hexapod larva of other Diplopods is considered to be.

Scutigere is probably carnivorous. It appears to secrete a peritrophic membrane about the contents of its mid-gut as do some of the lower insects.

The first joint of a typical walking leg is moved by five slender muscles which originate on the dorsal scutes.

In its method of locomotion (but not the rate) *S. immaculata* resembles the Diplopods.

In *Scutigere* ecdysis probably precedes oviposition by a short space of time.

The most common method of escape from the cast skin is by freeing the head and then creeping forward out of the old shell. This is not the only method.

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EXPLANATION OF PLATES.

ABBREVIATIONS.

| | |
|--|--|
| <i>at.</i> , antenna. | <i>pr. r.</i> , primary ridge of chorion. |
| <i>br.</i> , brain. | <i>sac. vent.</i> , ventral sac or blood gill. |
| <i>cer.</i> , cercus. | <i>scut. d.</i> , dorsal shield or scute. |
| <i>dig. ep.</i> , digestive epithelium. | <i>sec. r.</i> , secondary ridge of chorion. |
| <i>in.</i> , intestine. | <i>set. tac.</i> , sense organ. |
| <i>m. b. p'troph.</i> , peritrophic membrane. | <i>sp. gl.</i> , spinning gland. |
| <i>mid-gut</i> , mid-gut. | <i>st.</i> , sternite. |
| <i>m'th</i> , mouth. | <i>ts.</i> , testes. |
| <i>mu.</i> , muscle. | <i>tu. mal.</i> , Malpighian tubule. |
| <i>oes.</i> , esophagus. | <i>va. d'f.</i> , vas deferens. |
| <i>parap.</i> , parapodia or rudimentary legs. | <i>vl.</i> , valve on mid-gut. |

PLATE 36.

- Fig. 1. Side view, young Scutigera. × 100.
Fig. 2. Dorsal view, young Scutigera. × 100.
Fig. 3. Ventral view, young Scutigera. × 100.

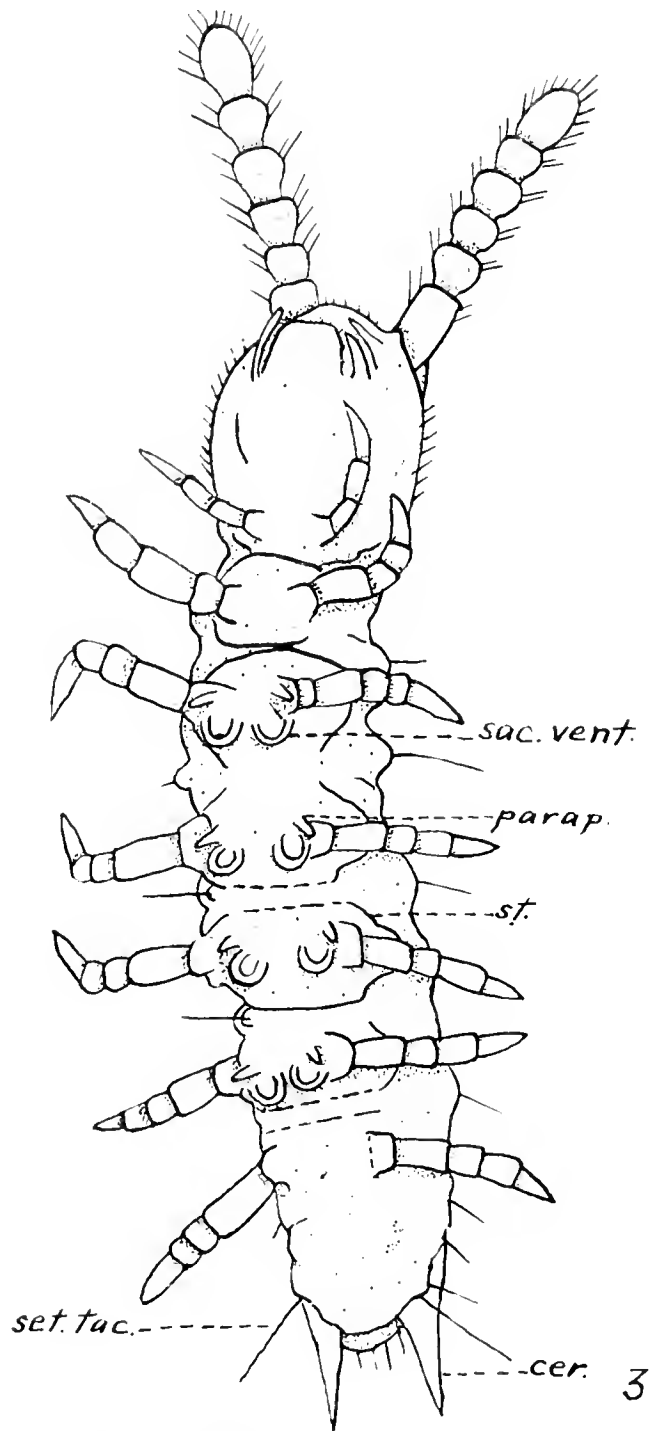
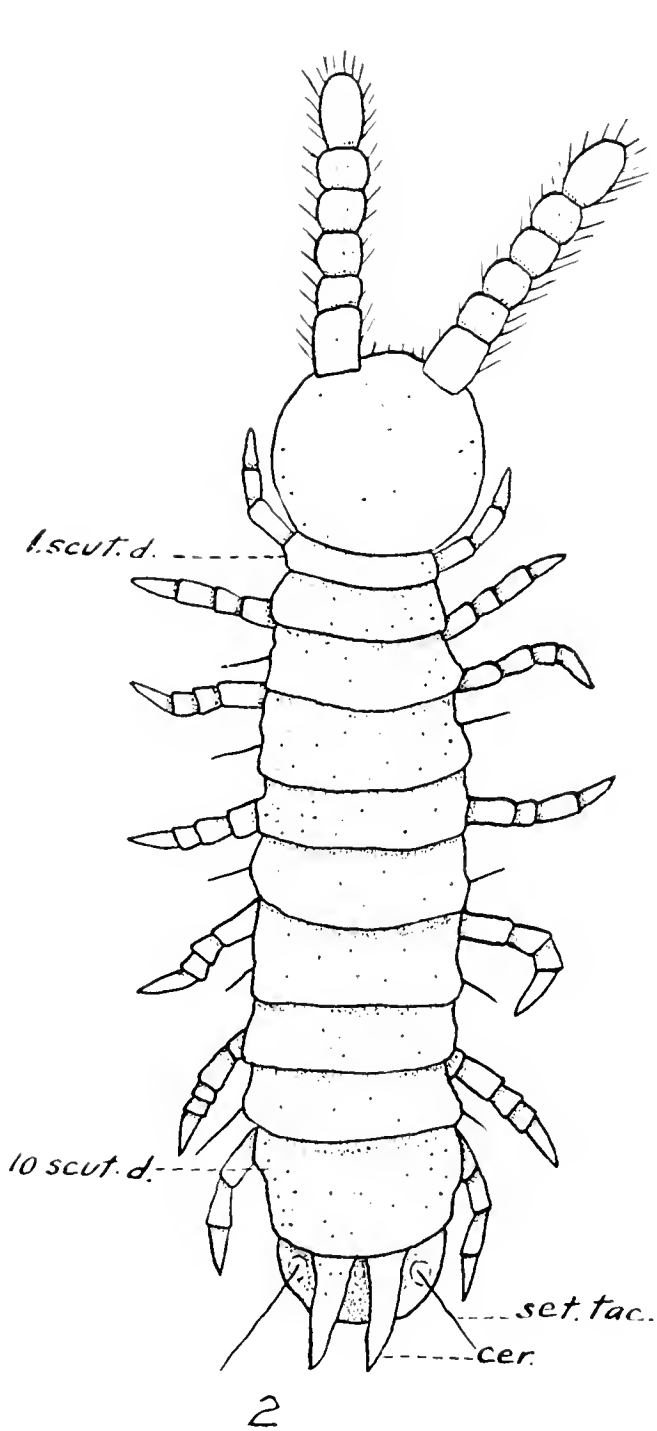
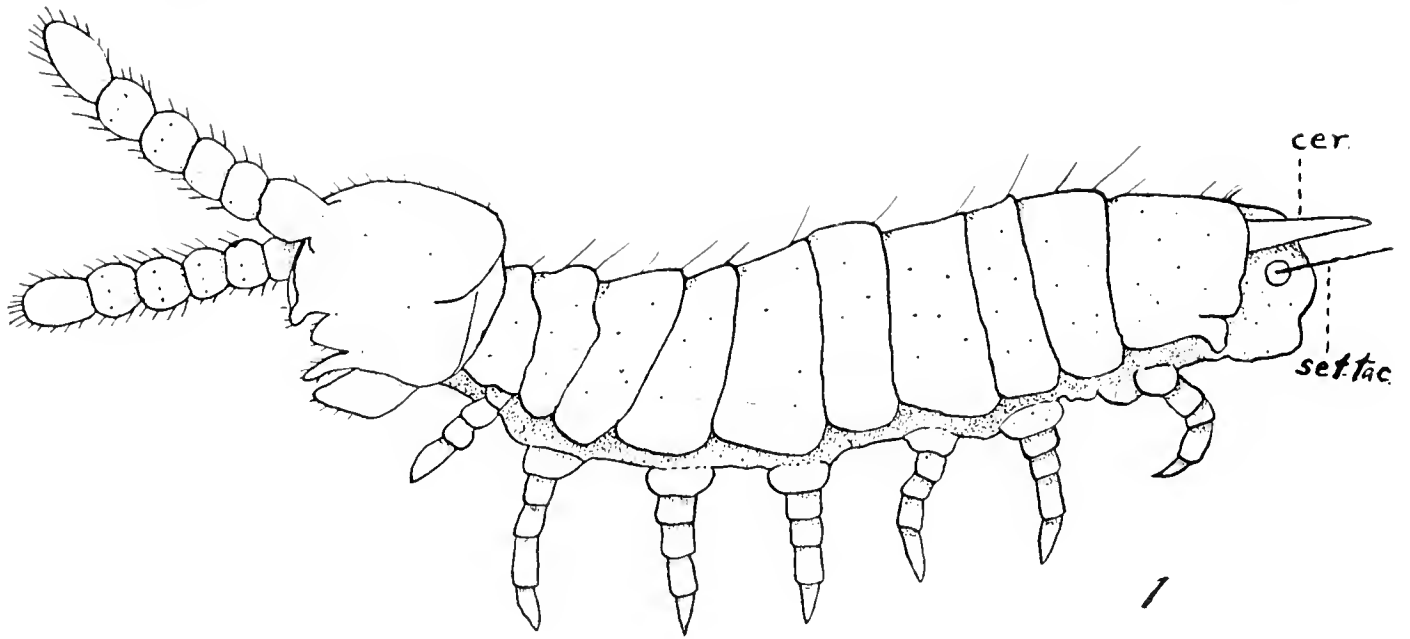
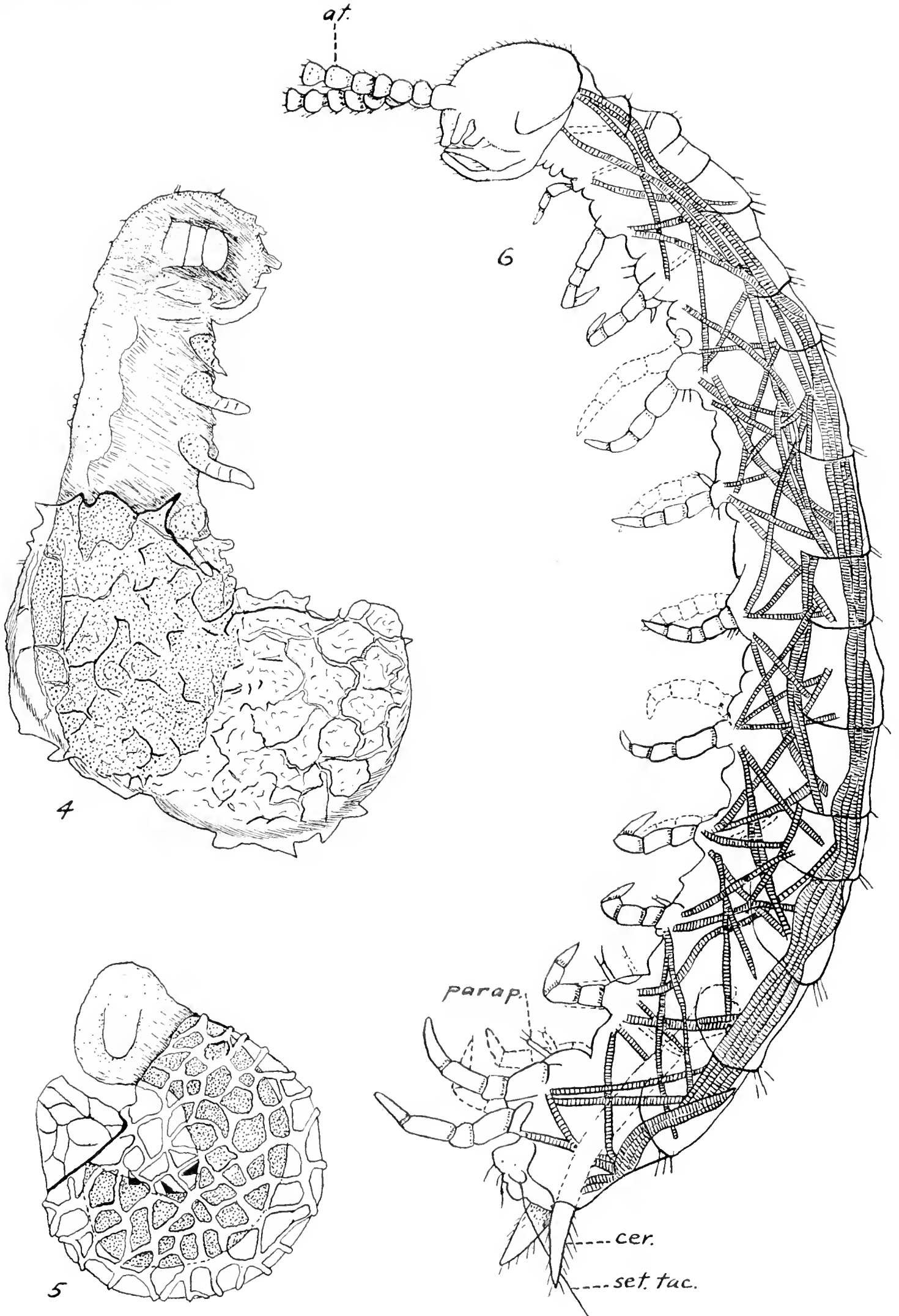






PLATE 37.

- Fig. 4. Young escaping from egg. × 100.
Fig. 5. Young, dead in chorion. × 100.
Fig. 6. Drawing of adult showing musculature. × 60.



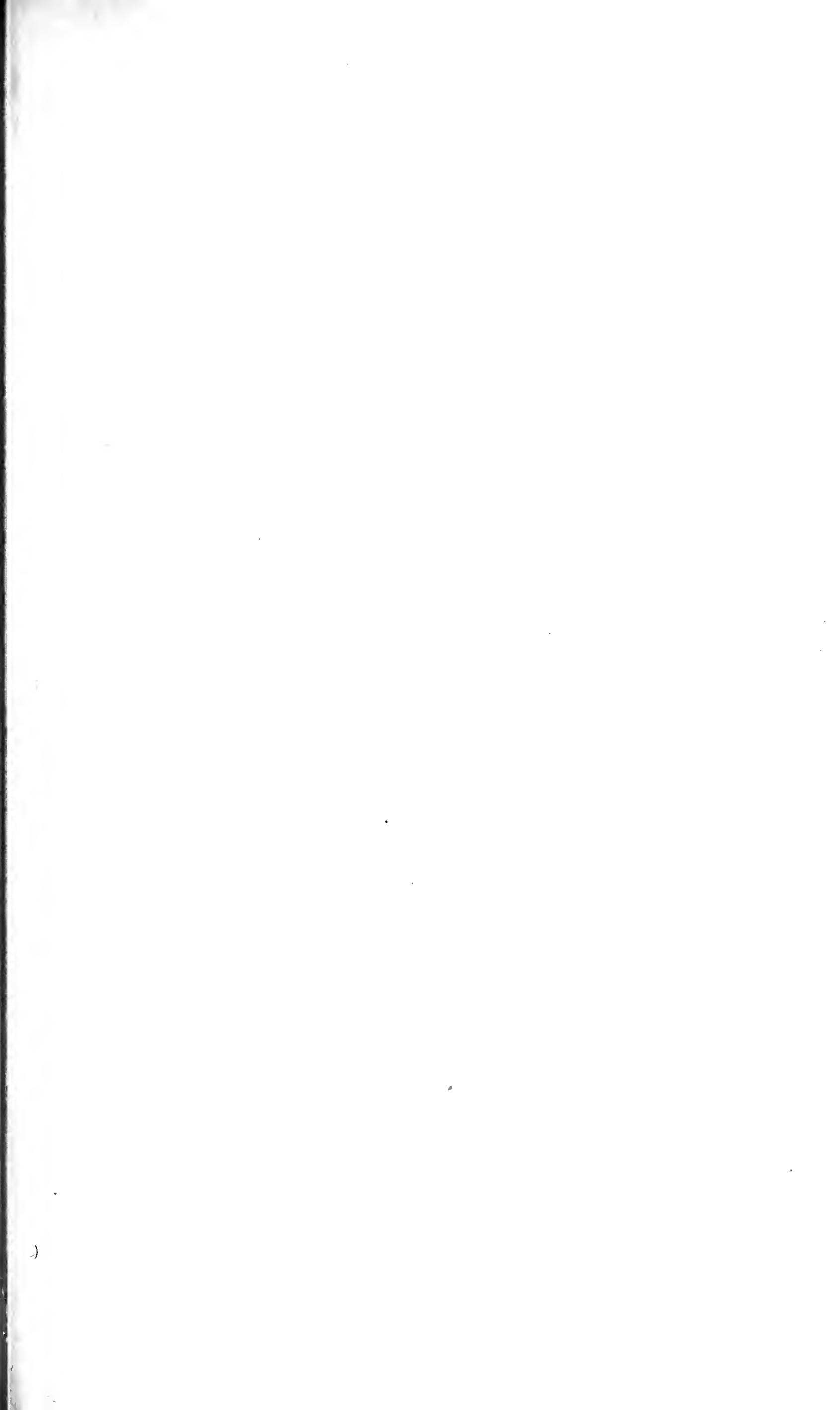
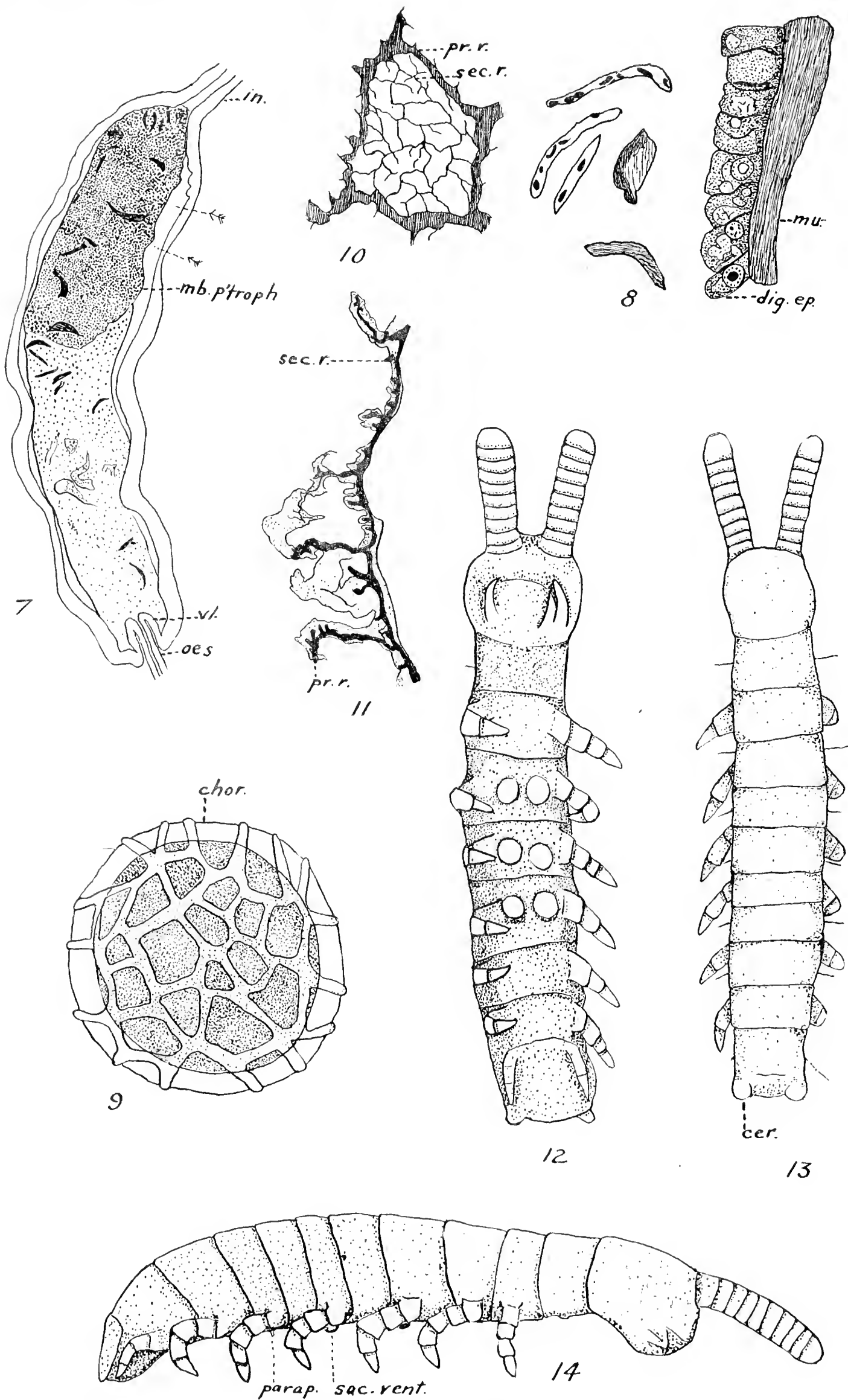


PLATE 38.

- Fig. 7. Drawing of mid-gut. $\times 125$.
Fig. 8. Small portion of wall of mid-gut. $\times 533$.
Fig. 9. Egg. $\times 100$.
Fig. 10. Surface of part of chorion. $\times 266$.
Fig. 11. Portion of section of chorion. $\times 533$.
Fig. 12. Ventral view, same specimen. $\times 100$.
Fig. 13. Dorsal view, *Scolopendrella* (?) sp. $\times 100$.
Fig. 14. Side view, same specimen. $\times 100$.







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