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A MORPHOLOGICAL STUDY OF NAIAS AND ZANNICHELLIA.

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SUMMARY AND CONCLUSIONS.

June 4, 1897.

IF ONE examines the enormous mass of literature bearing upon the great group of Angiosperms that has accumulated and that is being rapidly augmented, one must be impressed with the very great preponderance of work of an exclusively descriptive character. Whether one examines descriptive floras or monographs of special groups, the number where the descriptions extend beyond a mere enumeration of external characters is astonishingly small. While this is usually quite sufficient for the mere identification of a plant and for determining its relation to nearly allied forms, it is quite inadequate for settling questions of relationship between more remote groups, and especially those of obscure affinities. The constant addition of new forms to the already immense list of known species but adds to the confusion which exists, and out of which it seems hopeless to expect ever to bring order. What is needed is not so much additions to this great mass of undigested material, as some beginning of a more thorough study of the materials at hand. How greatly would the value of many an important monograph on a genus or family be enhanced did it but include a connected account of the whole life-history of one or two representative forms! Were this done, we should soon have a collection of data upon which to make a beginning, at least, of a classification of the Angiosperms, which would be something more than mere guess work. Such minute histological study of all the phases of development is of especial importance in those simpler groups of both Monocotyledons and Dicotyledons, where the floral parts are very simple, and where doubt arises whether we have to do with structures primitively simple or the result of degradation. The present chaotic condition of taxonomy is beyond question largely due to the superficial methods which are adopted in classification. An inheritance from a former scientific era, these primitive methods are held to with a persistency which does not augur especially well for the future.

The great advances made of late years in microscopical technique, both in regard to preserving and staining methods, and especially the use of the microtome, have been as yet but little utilized by the systematic botanists. While these cannot be expected to be the principal tools of the systematist, they should prove invaluable aids in his work. The improvement in technical methods also makes necessary a revision of much of the older histological work, which is often either inaccurate in detail or incomplete. Many of these older contributions, of course, are of the greatest importance, but all the more is it necessary to correct any inaccuracies which they may contain. Naturally, with the improvement in technique there has been an increasing number of accurate histological studies of the flowering plants, especially investigations bearing upon the development of the reproductive parts. It is these which must serve as the starting point for the accumulation of data for the final classification of the higher plants. It is true that the structure of the flower and fruit of the Angiosperms is of the greatest importance in their classification; but these alone are not sufficient for settling positively questions of affinity, except between nearly related groups. An accurate knowledge of the development and histology of the reproductive parts and embryo is also very important in this connection. Not until very much more is known than at present about the life-history of representatives of all the principal types of flowering plants, shall we be in a position to begin to build up a system of classification which we can hope to be even approximately accurate.

Among the interesting problems awaiting solution is the character of certain simple Monocotyledons. Indeed, the whole question of the relation of this group to the other flowering plants is one about which there is much disagreement. With the hope of perhaps being able to throw some light on this question, and at the same time to call attention to these problems, and perhaps interest other botanists in the same or similar work, the writer decided to begin a series of investigations upon the structure and development of some of the simpler Monocotyledons. The present paper is the first of a series which he hopes to publish from time to time, as the materials become available. While no very startling results have been brought out as yet, nevertheless, a number of interesting and more or less important structural details have been brought to light, which it is hoped will serve for the basis of more extended researches in the future.

How poorly the affinities of the simpler Monocotyledons are understood is at once evident from the extraordinary divergence of opinion among botanists in their arrangement of genera and families. Thus, *Naias* is sometimes included with *Potamogeton* and *Zannichellia* in the family of Naiadaceæ(Morong, 1893); while on the other hand, most botanists at present consider this family to contain only the single genus *Naias*, while *Zannichellia* is placed in the Potamogetonaceæ (Ascherson, 1889); and it has been recently suggested that it should stand as a type of a separate family, Zannichelliaceæ (Schumann, 1892). These instances will serve to show how urgent is the need of a thorough investigation of these doubtful forms, and as the two genera, *Naias* and *Zannichellia*, are structurally among the very simplest of the Monocotyledons, they were selected as the first forms for investigation. Both genera, especially *Naias*, have been examined carefully as to their gross morphology, but the histological details concerning them are very scanty. The most important work done of late years is that of Magnus and Schumann. The former confined his work mainly to *Naias*, although in his last paper (1894) he also gives some details for *Zannichellia;* Schumann (1892) has given a fairly full account of the general development of *Zannichellia;* but owing to his depending entirely upon a study of the external structure and not using sections at all, he has made some serious mistakes in his interpretations of the homologies of the floral structures. Most of the work of the earlier botanists was unfortunately inaccessible to the writer, but in Magnus' first paper (1870) there is a very full and clear résumé of the results of these observations, to which the reader is referred for further details.

The writer has confined himself mainly to a study of the development and histology of the reproductive parts of the plants, as the general structure and histology of the vegetative parts has already been, on the whole, accurately described; nevertheless, it has been found necessary to correct a few points, the most important being the structure of the vascular bundle of *Naias*. The absence of tracheary tissue, which has been supposed to be characteristic of this genus[1], it is found is only apparent, at least in *N. flexilis*, the only species studied. Here tracheids are always found in the young bundles, but are subsequently destroyed by the great elongation of the parts, so that in the fully developed bundle no trace of them is to be found. This will serve as one more instance of the importance of studying the development of the parts as well as their structure when fully formed.

Most of the results here given were obtained from the study of serial microtome-sections. The material was in most cases fixed with one per cent. aqueous solution of chromic acid, and after thoroughly washing was transferred gradually to alcohol, where it remained until wanted. No other reagent employed gave as good results as chromic acid, although material so fixed, unless very thoroughly washed, is apt to offer resistance to nuclear stains. The material was stained *in toto* with Czokor's alum-cochineal, and after dehydrating was imbedded in paraffin. The earlier preparations were passed through turpentine before imbedding, but later xylol was substituted with excellent results, the formula being that given by Zimmermann (1893, p. 33), except that a much shorter time than he gives was found to be sufficient. The series of sections was afterwards stained on the slide with a solution of Bismarck brown in 70 per cent. alcohol. In the study of the embryo-sac of *Naias*, the anilin-safranin method recommended by Schaffner (1896, p. 123) was used to some extent and with good results.

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[1] While Magnus denied the presence of tracheary tissue, he refers to the work of an Italian, Pollini, who claims to have seen it.

A.—Naias.

The most important contribution to our knowledge of the genus *Naias* we owe to the admirable monograph of the genus by Magnus (1870). In the introduction he has given a very clear and satisfactory résumé of the work done by earlier observers, from Vaillant's account in 1719, up to the time of the publication of his own memoir. He has also written the account of the Naiadaceæ in Engler and Prantl's "Die natürlichen Pflanzenfamilien" (1889), and still more recently a paper in the "Berichte der deutschen botanischen Gesellschaft" (1894). He clearly made out the relation of the floral parts and the anatomy and histology of the mature plant and fruit, as well as the general facts of germination; but he gives no account of the histology of the growing parts of the flowers. He also gives no account of the embryo, beyond a reference to the gross anatomy of the embryo in the ripe seed.

Schumann (1892) has also investigated the structure of *Naias*, but, like his predecessors, pays no attention to the minute structure of the floral parts. His results agree in the main with those of Magnus, but he does not agree with the latter in considering the envelope surrounding the ovule as a peculiar structure, but, in common with other botanists, regards it as a carpel, a view which Magnus vigorously opposes.

My own observations were based entirely upon *Naias flexilis* Willd., the only available species, and it will be necessary to examine critically other species before we can generalize as to results. It is true that all those so far examined agree closely in most of their details; but as in *N. flexilis* there is a considerable degree of variation in certain structures, especially in the embryo-sac, it is highly important that these should be compared with the corresponding ones in the other species.

The material used was collected in the Detroit river, but the species is of wide distribution in the United States and occurs in certain parts of California.

The genus *Naias* is of world-wide distribution, but owing to the great simplicity of the flowers and the variation in the habit of the same species, the limits of the species are very uncertain. There are probably about ten species known (Watson, 1880, p. 191; Morong, 1893, p. 60), of which four occur in the United States, two of these being found in California, (Watson, l. c.); i. e., *N. flexilis* and *N. major* (*N. marina* L.). They are all entirely submersed aquatics and remarkable for the extraordinary simplicity of the flowers, which consist respectively of a single carpel or stamen; and these are remarkably simple in structure and curiously similar both in their origin and early stages of development. It is generally considered that this extreme simplicity of structure is the result of the aquatic environment, but this is by no means certain, as the flowers cannot readily be considered as derived from any more perfect type, and the genus stands very much isolated.

Magnus (1870) has given a very complete and accurate account of the relation of the stem and leaves, and the position of the flowers. The slender stem has the leaves apparently in whorls of three, but a careful examination shows that in reality one of these three leaves is the basal leaf of a branch springing from the axil of one of the leaves. Except for this basal leaf on each branch, the leaves are in pairs, the lower of each pair always developing a branch from its axil, while the upper one is invariably sterile. A further examination shows that in place of the absent leaf at the base of the branch there is a flower, which may be either male or female in *N. flexilis*, but in *N. major*, which is diœcious, is always of the same kind on one plant. These flowers, as Magnus (l. c.) showed conclusively and as we shall see later, are morphologically the equivalents of axes, and the ovule and anther strictly terminal organs. Owing to this formation of a branch in the axil of one of each pair of leaves, the whole plant is bushy in form. Perhaps the most remarkable thing in regard to the flowers is their striking similarity, both in origin and structure, the male and female in the earlier stages being almost indistinguishable. The stamen is invested with envelopes which seem to correspond to the outer integuments of the ovule and possibly the carpel. A further discussion of these points, however, must be left for the present.

I. THE GROWING-POINT OF THE STEM.

The relation of the leaves, stems, and flowers has been carefully worked out by Magnus and confirmed by Schumann. The writer has nothing to add to their conclusions; but in order to follow out the histological details, a brief review of the facts may be useful.

If the terminal bud is carefully dissected out, it will be found that the shoot terminates in a conical tip, which projects considerably above the lateral organs (fig. 1). The leaves arise in pairs, mostly on opposite sides of the stem (fig. 5). The lower one is larger, and its base extends around the stem in the form of a sheath; almost as soon as it is visible, there is formed, just above it, a protuberance (fig. 5, *k*), which a careful examination shows to be considerably extended laterally. Very early this outgrowth shows a cleft in the middle, by which it is divided into two nearly equal parts; of these, one becomes the beginning of the branch found in the axil of the older leaf, and the other the rudiment of a flower. At first it is impossible to distinguish between them, but soon they undergo further changes which render their recognition easy.

If a section is made, cutting through the centre of the apex, it presents the appearance shown in fig. 5. The primary tissue-systems are clearly recognizable and show the arrangement typical of most angiospermous plants. There is, as usual, a well defined epidermis, all of whose cells are for some time capable of division, but the divisions are always radial, and this epidermis continues without break over the apex, and over the surface of the young appendicular organs. Below the epidermis is the periblem, also composed for the most part of a single layer of cells in the younger parts, but of course later undergoing periclinal divisions. The plerome is well marked, and in longitudinal section shows usually two rows of cells. A single large cell (fig. 5, *x*), which is sometimes conspicuous, may perhaps be the single initial cell for the plerome, but its position is such as to make it also possible that it belongs to the periblem, and that there are several initial cells for the plerome.

In regard to the form of the stem-apex, *N. flexilis* resembles more nearly *N. graminea*, to judge from Schumann's figure (fig. 1), than it does *N. major* (Magnus, 1870, Pl. IV, figs. 6–11), where the apex is shorter and thicker than in any of the other species. The apex of the stem is seldom perfectly straight, and the first indication of the formation of the lateral appendages is the appearance of two slightly projecting ridges, one immediately above the other and placed upon the convex side of the apical cone (figs. 3, 5, *k*, *l*). The lower one of these is the leaf and the upper the structure (primordium) which subsequently gives rise to a lateral branch and a flower. A little later there is found on the opposite side of the apical cone and a little higher up than the other leaf, another projecting ridge, which does not, however, show any structures above it. This is the second leaf of the pair (fig. 5, l^2). The tissues of the appendages show the same arrangement as those of the stem-apex and are continuous with them.

The tissues of the mature stem are very simple, but their origin is readily traceable to the primary tissues of the apex. As in all aquatics, large air-channels are developed, arising here between the two outer layers of the cortical cells. In the specimen of *N. flexilis* figured (fig. 6), there were six of these intercellular spaces (*i*), and the general structure is much the same as in *N. minor* (Magnus, 1870, Pl. VII, fig. 4). *N. major* (Magnus, 1870, Pl. VII, fig.2) has a more massive stem, a larger number of air-spaces, and a thicker cortex. There is in all cases a single axial, vascular bundle, with a well defined endodermis, showing, when mature, the characteristic radial foldings of the walls, and derived as usual from the innermost layer of the periblem.

The intercellular spaces are separated by a single layer of cells, and the general appearance of the section is much like that of such aquatic Pteridophytes as *Marsilia* or *Azolla*. Like these, the bundle is typically concentric. Magnus (1889, p. 215) states, and his statement has not been contradicted, that there is no tracheary tissue present. This is incorrect, at least for *N. flexilis*. In longitudinal sections of the younger parts of the stem, spiral or annular tracheids are always found, forming a single line in the axis of the bundle. The thickenings on the walls are formed at an early period, and with the rapid growth of the stem in the lower internodes, these primary tracheids are pulled apart and destroyed, leaving the central canal, which Magnus figures. It may be noted that Caspary (1858, p. 515) noted traces of these tracheæ in this same species, at the base of the funiculus, but apparently overlooked them in the other parts of the plant. It is evident from his account, however, that his investigations were not very extensive, and it is by no means unlikely that further investigation, using microtome-sections of the younger parts of the stem, will reveal the presence of tracheids with normal thickenings, in the other species as well as in *N. flexilis*. In common with other submersed aquatics, *Naias* has the epidermal cells containing chlorophyll, and not noticeably different in form or contents from the outer cells of the cortex.

II. THE LEAVES.

The structure and arrangement of the leaves is very similar in all species of *Naias* yet investigated. The base of the leaf is expanded and forms a sheath surrounding the stem more or less completely. In the case of the sterile leaves, i. e., those which develop no axillary products, the base of the leaf envelops the stem completely and one edge overlaps the other, much as is found in the case of the cotyledon (fig. 80). The marginal cells of the leaf are extended into the brown teeth, which gives the leaves a distinctly serrate outline. Cross-sections of the leaf show a structure similar to, but simpler than that of the stem. In *N. flexilis*, except in the middle, the leaf is composed of but two layers of cells. The center is traversed by a vascular bundle, much like that of the stem, but without a definite endodermis. In the younger stages, a single line of tracheids can be seen penetrating into the base of the leaf, but no trace of these is visible in sections of the fully developed leaf. The bundle is surrounded by a layer of large cells, which abut immediately upon the small intercellular space on either side of the bundle. *Naias major* (Magnus, 1870, p. 49) differs markedly from all the other species in having a well marked epidermis consisting of small cells. This is correlated with the thicker cortex of the stem[1]. Between the base of each leaf and the stem are two scale-like structures, the "squamulæ intravaginales," structures found very generally throughout the Naiadaceæ and Potamogetonaceæ.

III. The Roots.

The primary root of the *Naias flexilis* is remarkable for the absence of a root-cap, a fact which has apparently been hitherto overlooked. Unfortunately my material of the mature plants did not include the roots, and I am unable to say whether this condition is also found in the later roots, nor have I been able to find any reference to the subject elsewhere. As to the position of the roots in the fully developed plant, the writer cannot speak from his own observations, and the account given by Magnus (1870, p. 16) is not entirely clear. To judge from his figures, however, it would appear that the roots are produced in regular succession, one to each of the lower nodes of the stem, arising between the two leaves of the node on the side toward the leaf at the base of the branch.

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[1] For further details of the structure of the leaves, the reader is referred to Magnus' monograph.

IV. THE FLOWERS.

The flowers of *Naias* represent the simplest form which an angiospermous flower can assume, consisting simply of a single carpel with but one ovule, or of a single stamen, which in most species has but one pollen cavity. In origin and in their earlier phases of development, ovule and stamen present very marked similarity, and this is heightened by the development about the stamen of structures corresponding to the integument of the ovule, and of an envelope which imitates very closely the carpellary covering of the ovule; this even extending to the formation of similar teeth at the apex. The resemblance of both to the sporangia of certain Pteridophytes, especially *Azolla*, where the macrosporangium has a similar investment, is also noteworthy.

As we have seen, the rudiment of the flower is formed by the equal division of the primordium, which is formed above the lower of each pair of leaves. At first these are not distinguishable, but very soon one of them becomes somewhat larger than the other (fig. 11, *f*), and this, which is the young flower, soon develops about it a ring-shaped wall—the carpel or its equivalent—and thus is readily distinguishable from the other protuberance, which is also more pointed and becomes the apex of the lateral shoot. It is thus plain that the origin of the ovule or anther, as the case may be, is strictly terminal; i. e., that the flower and the lateral branch are due to the dichotomy of a common primordium and therefore are of equal morphological value. The male and female flowers are scarcely distinguishable at first, as the envelope about each is entirely similar; but as a rule the young ovule is somewhat more slender than the anther. The question of the homologies of the envelopes of the flowers will be better understood after considering the development of the latter.

1. THE MALE FLOWER.—Shortly after the separation of the primordium into the rudiments of the lateral branch and flower, the latter grows much more rapidly, and its real nature becomes evident. It begins to broaden at the base

(fig. 8), and this enlargement quickly assumes the form of a ridge running round it and growing up about the apex in the form of a cup-shaped envelope. A longitudinal section of the young male flower at this stage shows a structure very similar, as might be expected, to that of a vegetative shoot. A definite epidermis covers the apex, and the inner tissues show a separation into plerome and periblem, although not quite so definite as in the vegetative apex. There is next to be seen a second envelope growing up, separated from the first by a short interval and remaining closely applied to the body of the stamen, which latter is formed from the whole of the terminal part of the flower; i. e., the apex of the floral shoot is transformed directly into the anther. The resemblance to the young ovule invested with its single integument is very striking, and it is difficult to see why this inner envelope of the stamen should not be considered to be the homologue of an ovular integument. At this stage there can usually be made out a pretty definite central row of cells (fig. 9), corresponding to the plerome of the vegetative shoot, and from which, alone, the sporogenous tissue arises. The outer envelope grows more rapidly than the inner one and soon extends far beyond the apex of the anther. It consists throughout of two layers of cells. Whether this envelope is to be regarded as a perianth, or whether it is the homologue of the carpel, or finally whether it is to be considered merely as a bract, it is difficult to say. Its absolute similarity in origin to the outer envelope of the female flower is perfectly obvious, and Magnus (1870, p. 38) tries to solve the question by denying that this envelope in the female flower is really of carpellary nature, but states that it is rather of the nature of a bract or rudimentary perianth, comparable, perhaps, to the envelope about the pistillate flower of *Zannichellia.*

At the time when the archesporium is first recognizable, the anther (fig. 12) shows an epidermis, below which are two rows of cells surrounding the plerome cylinder. It is the upper cells of the latter which constitute the archesporium, but its exact limits are not easily determined. It is pretty certain, however, that its origin is not traceable to a single cell. As the anther grows, the archesporial cells rapidly divide in all directions and become distinguished by their denser contents and larger nuclei (fig. 13); but even in the later stages the boundary between the sporogenous cells and those lying outside is not always perfectly clear. In general, however, the two layers of cells lying within the epidermis do not divide any further by periclinal walls, and the inner one may be considered as a tapetum. The outer cells later become much compressed by the growth of the sporogenous tissue, and the inner layer almost absorbed before the final division of the spore-mother-cells. Before the spore-mother-cells separate, the inner envelope, or integument, has grown up beyond the apex of the anther, and the cells of the upper part become enlarged, so that two thickened lobes are formed, the whole, in section, closely resembling the micropyle of an ovule (figs. 14, 15). The flower has a short, thick stalk, and in the center is a vascular bundle, which, like the other parts of the plant, shows in its earlier stages a single row of short annular or spiral tracheids, which are later destroyed by the rapid elongation of the pedicel.

(*a*) *Development of the Pollen.*—The spore-mother-cells, previous to their separation (fig. 15), show the usual dense, granular contents. The nucleus is of moderate size, with a distinct but not specially large nucleolus. The individual cells are decidedly elongated, and even after they separate retain this form (figs. 17–21). Just before the first nuclear division takes place, the nucleus appears larger than in the cells which have not yet separated, and the protoplasm presents a more or less definitely vacuolar appearance. Probably the centrospheres are always present, but it must be admitted that the observations made were by no means conclusive. Owing to the granular nature of the cytoplasm and the difficulty in differentiating these very elusive bodies, the writer does not feel in a position to speak positively about the matter, and must pass over the behavior of these structures during the process of nuclear division.

The divisions of the spore-mother-cell are successive, and the resulting pollen-spores of the bilateral type common to most Monocotyledons. The successive stages in the division of the spores is shown in figs. 17–22.

It follows the usual form, and there were no remarkable variations from the common type of nuclear division. The number of nuclear segments could not be determined positively, but it is not very large, probably 8–12. During the earlier phases of division the nuclear spindle was distinct and relatively large, the nuclear segments not occupying the whole of the equatorial diameter. The formation of the connecting threads, the cell-plate, and finally the cellulose division wall, agree with other Monocotyledons, and the subsequent divisions of the cells, resulting in the tetrads of spores (fig. 22), show nothing peculiar. Unlike most Spermaphytes, both spore-mother-cells and spores have thin walls; this is probably simply an accompaniment of the aquatic habit, but it is interesting, as the spore-mother-cells in this respect are more like those of the Pteridophytes than those of the typical Spermaphytes. After the division is complete, the young spores separate and round themselves off, but do not develop the cuticularized exospore found in most plants. This is no doubt simply the result of their submersed condition, for, as they remain permanently under water, such a condition would naturally be expected. The young spore at this stage is a globular thin-walled cell, with nearly clear contents, and contains a single, large nucleus. It soon, however, divides into two cells of very unequal size, a large vegetative cell and a small antheridial one. These are separated by a distinct membrane (fig. 23), and are also distinguished by the very unequal size and different appearance of the nucleus. That of the vegetative cell is large, with a distinct nucleolus, but comparatively poor in chromatin. The nucleus of the generative or antheridial cell has a very inconspicuous nucleolus, but stains deeply with ordinary staining agents. After the division of the pollen-spore it rapidly grows, becoming much elongated, and before it is ripe there is a division of the generative cell into two. The two resulting cells separate, and it is not quite certain whether up to the time they pass into the pollen-tube they still retain the cell wall. The generative nuclei are extremely small and stain much more strongly than the vegetative nucleus, which remains permanently undivided. With the growth of the ripening pollen-spore, there is a great increase in the granular contents. Finally, a great amount of starch is developed, which renders the pollen-spores quite opaque (figs. 25, 26).

The fully developed male flower of *Naias flexilis* (figs. 27, 28) has a pedicel nearly equal in length to the flower itself. The mature anther, whose wall consists now of little more than a single layer of epidermal cells, is also surrounded by the integument, whose upper part is developed into swollen lobes, which open finally to allow the escape of the pollen (fig. 28). The lower part of the integument is very much compressed. The outer envelope is prolonged above the summit of the anther and its apex terminates in a number of brown teeth, very much like those of the carpellary envelope of the female flower. When the spores are to be shed, there is a rapid growth of the filament, by which the anther is carried up and breaks through the outer envelope laterally, and assumes a nearly horizontal position. This does not correspond with the description of this species given by Magnus (1870, p. 23, Pl. II, figs. 28, 29), who describes and figures it as having the anther pushing through the apex of the outer envelope. All the specimens examined by the writer, however, were of the type given. Of the species examined by Magnus (1870, p. 25), only one is mentioned as having this form of dehiscence, viz., *N. tenuifolia* R. Br. The pedicel of the flower, also, found by the writer regularly in *N. flexilis*, was not observed in this species by Magnus, who expressly states that the only species with stalked flowers is *N. podostemon* (Magnus, 1870, p. 24).

The anther in *N. flexilis* has, as we have seen, but a single loculus, corresponding in this respect to most of the other species. *N. major* (Magnus, 1870, p. 22), however, and several other species have normally four loculi. On page 24 of his memoir, Magnus states that he had earlier supposed that *N. tenuifolia* had two loculi, and that the same might possibly be the case in *N. indica* Willd. and *N. graminea* Del. He concluded, however, on the basis of later investigations, that he had been mistaken, and that there were really four loculi in these species. In one or two instances the writer found specimens of *N. flexilis* where the cavity of the anther was completely divided by a longitudinal partition (fig. 29), and several interesting intermediate conditions were met with, one of which is shown in fig. 16. This indicates that the uni-locular condition is the original one, and that the pluri-locular condition has arisen secondarily by the conversion of some of the originally sporogenous tissue into a septum, as Bower (1894) has pointed out in some other cases.

(*b*) *The Germination of the Pollen.*—The ripe pollen-spores are elongated and contain much starch in large granules, more or less obscuring the other contents. The pollen-tube is formed either at one end or laterally (figs. 30, 31); into it pass most of the granular contents and the two generative nuclei. The history of the vegetative nucleus was doubtful, but it probably may either pass into the tube or remain in the spore. In either case it appears to be finally disorganized. As the pollen-tube grows, the starch is gradually used up, the growth being apparently entirely at the expense of the reserve starch, and not at all from the cells of the pistil until the cavity of the ovary is reached. The plugs of cellulose so common in pollen-tubes are also found here. The growth of the pollen-tubes was quite as often upon the outside of the style as through its canal and seemed quite independent of any nutriment which the tube derived from the cells of the style.

2. THE FEMALE FLOWER.—The fully developed female flower in *Naias flexilis* consists of a single carpel, enclosing a solitary anatropous ovule (fig. 44). The ovary is but slightly enlarged and is prolonged above into a somewhat tapering style. At the apex are four lobes, two of which

terminate in dark brown teeth, like those upon the envelope of the staminate flower (fig. 46); the other two, which alternate with the tooth-bearing lobes, are more or less distinctly papillate, and may be called the stigmatic lobes (fig. 45). A narrow canal traverses the style, and surrounding the place where it enters the ovary, there are a number of projecting papillæ, much like those found in certain Aroids. A similar group of papillæ is found at the base of the funiculus, close to the micropyle (fig. 47). The ovule arises from the base of the ovary and is bent on itself, so that the micropyle is close to the insertion of the funiculus. The whole structure of the pistil corresponds to that of the typical Angiosperms, and it is difficult to see any valid reason for accepting Magnus' view that this envelope is not of the nature of a carpel.

The origin of the female flower is identical with that of the staminate one. Like the latter, the floral rudiment is formed by the dichotomy of a primordium, the other half of which develops into a branch; and as was the case with the anther, the ovule is the transformed apex of the floral shoot. In their earliest phases, the two sorts of flowers are scarcely distinguishable; but while still very young, the female flower can be recognized by the greater development of the envelope and the more slender form of the apex of the shoot. The structure of the young flower, seen in longitudinal section (fig. 34), is very much like that of the male flower; but the young ovule is distinctly narrower, and the outer envelope (carpel) has already reached beyond its apex before any trace of the ovular integuments is to be seen. The arrangment of the tissues is much the same as in the young anther, but the plerome consists of but a single row of cells, separated from the epidermis by a single-layered periblem (fig. 34). A noticeable difference in the two is the origin of the archesporium. This, instead of arising from the plerome, as in the anther, can be traced to a single hypodermal cell, which, however, is apparently continuous with the single axial row of plerome cells. This archesporial cell is the shaded cell in fig. 34.

The first integument becomes evident about the same time that the primary archesporial cell undergoes its first division. The basal part of the ovule enlarges and the integument appears in the form of a ring, in the ordinary way, and grows up about the upper part of the ovule, which becomes the nucellus (figs. 35, 36). The growth is stronger on one side, almost from the first, the nucellus begins to bend over, and the anatropous position of the mature ovule is thus indicated. The first integument, like the corresponding structure in the stamen, is two cells thick and closely resembles it in nearly every particular. It closes over the top of the ovule, leaving, however, the narrow micropyle open. The second integument, as usual, is developed just below the first one (figs. 38, 39), but is almost entirely suppressed on the side in contact with the funiculus (fig. 47). Even up to a late period the second integument remains behind the inner one, but finally extends to about the same level.

The funiculus has an axial vascular bundle which develops a single line of tracheids with spiral or annular thickenings, which, like those in other parts of the plant, are ultimately almost completely obliterated. From its basal part, close to the micropyle, a bunch of short secretory cells is found, probably concerned with the directing of the pollen-tube into the micropyle.

The further development of the archesporium shows considerable variation, but corresponds in its essential details with the typical form in most other Angiosperms. The primary archesporial cell very early divides by a transverse wall into an outer tapetal cell, and a larger inner one (fig. 36), and the former next divides into two by a second transverse wall (fig. 35). Usually the tapetal cell undergoes no further development, at least until a much later period. In one exceptional case observed (fig. 38), where the archesporium was divided into five cells, it was not possible to determine positively whether the third and fourth cells, which were obviously sister cells, had been derived from the division of the tapetum or from the inner of the two primary cells; but from comparison with other more typical cases (fig. 39), it seems more probable that the three lower cells were derivatives of the inner cell. Another exceptional case is shown in fig. 41, where the archesporial cell has formed vertical walls as well as transverse, and the whole archesporial complex is nearly globular, instead of the usual row of cells. In all cases, it is the lowest cell of the series which finally becomes the embryo-sac. The number of specimens examined was not sufficient to decide positively whether the inner of the two primary archesporial cells may be transformed directly into the embryo-sac, but it is certainly not the case generally. As a rule, the mother-cell divides into two, and the upper cell again into two (fig. 39). Of the three cells thus formed, the lower one is the larger, and its lower end more or less pointed. Soon, by its growth, it destroys the others, so that it finally occupies the whole space filled by them, and only traces of the latter can be seen between it and the tapetal cells (fig. 42). The further development of the normal embryo-sac differs in no wise from the familiar type of the Angiosperms. The primary nucleus divides into two, one going to either end of the young embryo-sac (fig. 42). Each of these divides again (fig. 43), and by a further division there result, as usual, four nuclei at each end. These nuclei stain strongly, and are embedded in granular protoplasm, which is absent from the central part of the embryo-sac.

Of the four nuclei at each end, which at first are much alike, one grows rapidly in size and forms the polar nucleus. The two polar nuclei then move toward the centre of the embryo-sac, or the lower one may remain nearly stationary. These polar nuclei (fig. 50) have a large and conspicuous nucleolus, but the writer was not successful in clearly demonstrating the centrospheres, which Schaffner (1896, p. 125) states are very easily seen in *Alisma*. The antipodal nuclei are small and stain strongly; they become surrounded by definite cell walls, in which respect they differ from *Alisma* (Schaffner, l. c.), but agree with most of the Monocotyledons (Goebel, 1887, p, 386). I could observe no noticeable difference in the size of the polar nuclei, such as Schaffner (l. c., p. 126) mentions for *Alisma*.

In the upper part of the embryo-sac the changes are more marked. Two of the nuclei enlarge but little and show but little chromatin and a small nucleolus. The third one, however, enlarges a good deal, and has a large nucleolus and much more chromatin than the others. The smaller nuclei are those of the synergidæ, the other the nucleus of the egg, which extends below the two synergidæ (figs. 50–52). All these cells are bounded by a clearly defined protoplasmic membrane, and the protoplasm within shows a somewhat vacuolate structure, especially in the egg. Here, too, the demonstration of the centrosphere was not satisfactory, but it may have been on account of defective methods.

The cells covering the apex of the embryo-sac divide but little, but are not encroached upon by its growth; while the lateral cells of the nucellus are much compressed and the inner layers completely destroyed, so that at the time of fertilization there is but a single complete layer of cells bounding the sides of the embryo-sac (fig. 57).

In the course of these investigations a number of striking departures from the normal type of embryo-sac were observed. In the one shown in fig. 54 there was apparently no absorption of the cells above the embryo-sac, and in the embryo-sac itself the usual course of development had not gone on in a normal way. There were three nuclei, one somewhat larger than the others, at the apex of the sac, and it looked as if there might be an imperfect septation by very thin walls; but the latter may have been simply sections of the walls of the nucellar cells surrounding the embryo-sac. The egg apparatus was not differentiated, but the polar nuclei were formed as usual. The antipodal cells were, however, six instead of three (fig. 55), presumably due to an extra division in each, subsequent to the formation of the polar nuclei. Another striking instance is shown in fig. 56. Here, apparently, fertilization had not been effected and the embryo-sac had become filled with parenchymatous tissue, composed of elongated, somewhat thick-walled cells. As this was the only instance of the kind found, it is not possible to say what the origin of this tissue was; but it probably may be considered as mainly due to the development of the endosperm. So far as I know, such a development of the prothallial tissue in Angiosperms, except as a result of fertilization, has not been recorded.

The general development of the carpel has been treated fully by Magnus, but he did not study some of the minute details herewith given. In *Naias flexilis* the carpel rapidly grows up beyond the enclosed ovule, and just above this point there is a marked thickening of the walls (fig. 37), so that the pistil is closed above except for a narrow canal in the middle, which communicates with the cavity of the ovary. Very early, too, the margin of the carpel shows unequal growth, resulting in the formation of four lobes (fig. 40), of which two are decidedly longer than the others (indeed, in the case figured, one of the smaller lobes is scarcely visible). The two longer lobes finally have the terminal cell transformed into a thick-walled brown spine (fig. 46). The two shorter lobes between the spiny ones are the stigmatic lobes; these have the terminal cells more or less papillate. In *N. major* there are three papillate lobes, and in *N. minor* and most other species, two; but none of these species has the spiny lobes (Magnus, 1870, p. 20, Pl. II). Two Brazilian species, according to Magnus (l. c., p. 21) have the same structure as *N. flexilis*. There are also several Mexican species which sometimes show a similar structure, but they are extremely variable, while in *N. flexilis* this structure is usually very constant.

Finally, there must be noted the occurrence of a second envelope in several species (Magnus, 1870, p. 22, Pl. III, figs. 1–3), among which may be mentioned *N. ancistrocarpa*. Here the outer envelope bears several spiny teeth, while the inner one (carpel) bears two stigmatic lobes. This outer envelope is perhaps to be considered as a floral envelope and the possible homologue of that surrounding the stamen. The case of *N. flexilis* suggests that the two envelopes are of the same nature and that this species is intermediate between those like *N. major*, where there are only stigmatic lobes found, and those like *N. ancistrocarpa*, where two distinct envelopes, perianth (?), and carpel are developed.

The wall of the ovary is composed for the most part of but two layers of cells (fig. 47); but the walls of the style, especially at the base, are thicker. The style in our species is longer than in most others and is traversed by a very evident canal (fig. 47). Schumann (1892, p. 183) failed to see this, but it was accurately described by Magnus. While still quite young the cells at the base of the canal, lining the ovarian cavity, enlarge and soon project into the cavity as conspicuous papillæ (figs. 48, 49). The contents of these cells are very dense, and the nuclei become very large and conspicuous. It is evident that they are secretory cells, and the presence of a structureless substance, often quite filling the cavity and staining strongly with Bismarck brown, suggests that the secretion is of a mucilaginous nature and is in all probability concerned with the direction of the growth of the pollen-tube. The bunch of similar papillæ at the base of the funiculus has already been referred to. The cells of the style next the canal are very narrow, but the outer ones are much broader, and those at the base of the style elongated radially, so that there is a distinct enlargement of the pistil just above the ovary. In the cells of the style were noticed numbers of crystals of calcium oxalate, mostly octahedral in form.

V. POLLINATION.

The pollen-grains probably are carried to the stigma by the movements of the water, although in the form of *Naias flexilis* studied by the writer, the position of the open anther would allow of their falling spontaneously upon any female flowers that might be situated below them. Jönsson (Magnus, 1889, p. 216) concludes that this is regularly the case, the pollen being heavier than the water and striking upon the female flowers which are placed lower down. Magnus' objection, that the male flowers stand upright and so prevent the pollen-spores falling out spontaneously, will not hold for *N. flexilis*, nor has the writer observed in this species the pollen germinating within the cavity of the open anther as Magnus (l. c.) found to be the case.

Germinating spores were found in abundance upon the stigmas of the mature flower. The pollen-grains were held between the stigmatic lobes and in some cases seemed to adhere to the style, possibly by a secretion of the stigmatic cells. The germination is probably entirely at the expense of the spore contents and no nutriment is apparently received from the stigmatic cells. The tube quite as often grows down on the outside of the style as between its lobes. Some of the pollen-tubes, however, penetrate into the canal of the style and make their way into the ovarian cavity. After reaching this, it is extremely likely that they are nourished by the secretion of the papillæ at the lower opening of the canal, which seems to fill the cavity of the ovary. The exact course of the tubes was not traced, as they are not easily seen in sections; but probably the course follows the inner wall of the ovary until the group of papillæ at the opening of the micropyle directs the growth of the tube into the micropyle itself. The end of the pollen-tube, where it was found on the outside of the style (figs. 32, 33), was usually slightly swollen and contained dense, finely granular protoplasm, in which, in favorable cases, could be seen the two, small, generative nuclei. In none of those examined could the vegetative nucleus be seen with any certainty. In the germinating spores the outline of the pollen-spore was retained, but all the granular contents had passed into the tube and mostly disappeared as the tube lengthened.

VI. FERTILIZATION.

The penetration of the pollen-tube into the embryo-sac was seen in several instances, but the nuclear elements are too small to make this a specially favorable subject for the study of the phenomena of fertilization and no very detailed investigation was made.

At the time that the pollen-tube enters the embryo-sac, the apical cells of the nucellus enlarge and their walls stain more strongly than before, as if there had been a change in their composition. Probably they become somewhat mucilaginous and thus are more easily forced apart by the growing pollen-tube. The latter, after it has entered the micropyle, pushes down between the cells of the nucellus (figs. 57, 58), forcing them apart and finally penetrating the wall of the embryo-sac. After it has entered, the end enlarges, sometimes very much (fig. 58), and this seems to be at the expense of the contents of the part of the tube lying outside of the embryo-sac, which in the specimens seen was much collapsed. The pollen-tube was not nearly so conspicuous as Schaffner figures it for *Alisma*, but the further history corresponds closely with his account. As in other cases that have been described, one of the synergidæ appears to be regularly destroyed by the growth of the pollen-tube close to it, and collapses completely, while the other remains intact for some time longer. For demonstrating the presence of the pollen-tube within the embryo-sac, the anilin-safranin method recommended by Schaffner (1896, p. 123) was found to give good results, although here, too, I failed to see the centrospheres, which he figures and describes in *Alisma*. One or both of the generative nuclei could be seen and, in some cases at least, had changed form, becoming somewhat elongated. The actual penetration of the generative nucleus into the egg and its fusion with the egg-nucleus, were not seen; but there is no reason to doubt that it takes place in the usual way.

VII. THE EMBRYO.

The embryogeny of *N. major* has been worked out by Hofmeister[1], but his paper was not accessible to me, so that I cannot say how his results compare with my own on *N. flexilis*, which are here given. Some important differences

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[1] Hofmeister—"Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen." Leipzig, 1861.

were noted between this species, however, and the generally accepted account of the early divisions in the monocotlydenous embryo, which tend to verify the recent account given by Schaffner for *Alisma*, and to indicate the necessity for a further revision of the older work on the embryogeny of other Angiosperms.

After fertilization is effected, the egg becomes invested with a cellulose membrane and elongates considerably before dividing. It is in contact, usually, with the wall of the embryo-sac, except at the apex. The nucleus at this stage (fig. 60) is large and very conspicuous, with large nucleolus and abundant chromatin. The cytoplasm is granular, especially at the apex, where the nucleus is placed. At this stage one of the synergidæ is still unchanged, but the other can no longer be made out, nor is the pollen-tube any longer visible.

The first division wall, as usual, is transverse, dividing the egg into a basal, or "suspensor," and a terminal, or "embryo," cell. The basal cell, which is applied to the wall of the embryo-sac, undergoes no further division, and all the subsequent growth of the embryo is due entirely to the divisions of the terminal cell. Hanstein (Sachs' Text-book of Botany, 1882, p. 589) states that in *Alisma* the terminal cell only produces the cotyledon, while the basal, or suspensor cell, undergoes further divisions by transverse walls, resulting in the formation of other parts of the embryo. Famintzin, to judge from the review of his paper in Just's Jahresbericht (Jahrg., VII, heft 1, p. 90), agrees in the main with Hanstein. According to his account, the first three divisions are transverse and occur in regular basipetal order, and these result at once in the establishment of the initials for cotyledon, stem, and root. The early stages of the embryo of *Alisma* have been investigated recently by Schaffner (1896, pp. 129, 130), and he states that the conclusions of Hanstein and Famintzin are either incorrect, or that there is remarkable variation in *Alisma*. According to his account, the basal cell undergoes no division, agreeing with my observations in *Naias*, and the next divisions are acropetal, the terminal cell dividing twice. He says that he has verified this repeatedly, having followed the stages of nuclear division, so that there was no doubt about the accuracy of his conclusions. Inasmuch as my own investigation of *Zannichellia* also shows that the basal cell remains permanently undivided, it seems quite probable that this is regularly the case and that this cell never takes any further part in the formation of embryo. Further investigations on the point are very much to be desired.

The second division takes place in *Naias flexilis* after the terminal cell has elongated, and results in the formation of two cells of unequal size. Whether the next division is due to a second segmentation of the terminal cell, as Schaffner describes for *Alisma*, or by division of the middle cell, could not be positively determined; but it certainly was not formed by a second division of the basal cell. The latter almost as soon as it is formed begins to enlarge, and its nucleus also increases very much in size, finally reaching enormous dimensions, but never showing any indication of division[1]. This, as Schaffner has shown, is also true for *Alisma;* and Scott (1894, pp. 187, 188) in a recent work has reached the same conclusion, although it is not clear from his statement whether he considers the middle of the three cells of the young embryo as arising from the division of the upper or lower of the two primary cells. Following these transverse walls in the young embryo, there is next formed a vertical wall in the terminal cell, which latter develops into the single terminal cotyledon of the older embryo. This is next followed by a similar wall in the cell below it, and about the same time, by a transverse wall in the cell next the enlarged basal cell. At this stage the embryo consists (fig. 64) of the very much enlarged basal cell, followed by two short secondary suspensor cells, and terminated by a nearly globular body composed of four cells arranged like the quadrants of a sphere. Each of these sphere-quadrants next divides by octant walls, and from the upper four arises the cotyle-

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[1] This appears to be much less marked in *N. major* (see Magnus, 1870, p. 31).

don; from the lower ones, the middle part of the embryo and stem-apex. There is now formed in each octant cell a periclinal wall, separating it into an inner and outer one, the latter constituting the dermatogen of the upper part of the embryo (fig. 65).

While these changes have been going on in the upper part of the embryo, the cell next below has enlarged laterally, and the one below this divided again. In the former there are then formed quadrant walls, and each of the quadrant cells next separates into a peripheral, or epidermal cell, and an inner one, exactly as was the case in the two upper divisions.

Up to this point all the secondary divisions, except the periclinal ones in the upper section of the embryo, have been vertical, and the limits of the primary segments are still very evident (fig. 66). The first transverse divisions appear in the middle segment, and this determines the separation of the stem from the root, the bulk of both of these organs being derived from this segment of the embryo. If the accounts of Hanstein and Famintzin are correct, *Alisma* differs very essentially from *Naias*, in that the root of the former is not the product of the middle cell, but of the one next the suspensor, and is derived from it by a secondary division. As the term hypophysis, used by Hanstein for this basal segment, implies a structure not belonging strictly to the embryo itself, but to the suspensor, it would seem best to discard this term, as Schaffner has shown that in *Alisma*, also, the primary suspensor cell undergoes no further divisions and all the parts of the embryo are derivatives of the primary embryo cell. In both Hanstein's and Famintzin's figures, transverse walls are shown in the terminal segment before any periclinal walls appear, but it is quite possible that we really have the same state of things as in *Naias*, and that the two lower cells of the four terminal sphere-quadrants really belong to the second of the primary segments of the embryo and not to the terminal one. However, as the cotyledon of *Alisma* is larger at this stage than that of *Naias*, and the whole embryo longer, it is quite possible that the four terminal quadrants may arise as stated by Hanstein and Famintzin, but further investigations are needed to settle this.

A study of the older embryos of *Naias* shows that the great bulk of the embryo is derived from the first two segments. The third one, as we have already seen, forms a series of transverse walls; and of the cells thus formed, the two upper ones divide by a series of longitudinal walls, but no secondary transverse walls are formed, at least for some time, so that they form single layers of cells, easily recognizable in exact median sections of the older embryos. The lower of the two has only a limited development and forms a small group of cells continuous with the epidermis of the rest of the embryo (fig. 70). The segment above it, like the terminal ones, has first two intersecting median walls, and next, by periclinal walls, the epidermis is separated.

The differentation of the primary tissue-systems is brought about very early and is especially evident in the middle region of the embryo (figs. 68, 70). The dermatogen, as we have seen, is determined by the first periclinal walls in the upper segments (fig. 65), and this is followed later by the somewhat similar division in the next lower one. The separation of plerome and periblem is determined in the upper segments by the subsequent divisions, which are longitudinal and divide each of these segments into a group of four central cells (two when seen in logitudinal section) and a single layer of cells between them and the epidermis—the periblem. The formation of these primary tissues is very regular in the central segment, from which the stem and root are formed, but in the cotyledon they are not quite so clearly defined. Famintzin states that in *Alisma* there is at first but a single plerome cell in each segment, but Hanstein's figures show an arrangement very similar to that in *Naias*, and as Famintzin studied this from optical sections, it is quite probable that he was mistaken. Even from a study of his own figures, it is difficult to understand how he can have reached this conclusion. In the basal segment of the embryo of *Naias* there is no formation of a plerome, but all the inner cells form the initial cells for the periblem of the root and are continuous with the periblem of the middle segment. Finally, the segment below this is simply a continuation of the epidermis of the rest of the embryo, which thus extends without interruption completely around it. About as soon as the tissue-systems are clearly defined, there begins the external differentiation of the embryo into the primary organs of the young plant.

VIII. THE COTYLEDON.

The cotyledon of *Naias*, as in other typical Monocotyledons, is strictly terminal and is the product of the whole of the terminal segment of the embryo. There is early a marked enlargement in the middle region of the embryo (figs. 69, 70), corresponding to the stem-segment, while the cotyledonary portion, although elongating, does not increase so rapidly in diameter. This enlargement of the stem-segment is largely on one side and results in the formation of a prominence at this point (figs. 70, 71, *st*)—the apex of the stem of the young plant. It is evident that this is here strictly lateral in origin. By the growth of the stem-apex, which is quite active from the first, the cotyledon is pushed somewhat to one side. The growth of the cotyledon, which is at first terminal and due largely to the growth of the tissues at the apex, is soon replaced by the formation of a zone of meristem at the base, which not only causes the subsequent growth in length, but by the active multiplication of the cells laterally forms a sheath-like stipular growth, surrounding the base of the cotyledon (fig. 69) and finally completely concealing the stem-apex, which comes to lie in a cavity completely enclosed by the overlapping edges of the leaf-base (figs. 72, 73). In median sections of the young cotyledon (fig. 70, *b*), the separation of the tissue-systems is evident, but the plerome is never so well developed as in the stem and root, and this corresponds with the slight development of the vascular bundle in the mature cotyledon. The fully grown cotyledon is about half the length of the whole embryo (fig. 73).

IX. THE STEM.

The origin of the stem is, as we have seen, lateral, and it can be readily traced to the upper half of the middle segment of the young embryo. The projection of the apex is brought about by an acceleration of the growth in the dermatogen and plerome at one point of the segment, which soon results in the development of an evident bluntly conical protuberance, which grows rapidly and assumes a more pointed form. A longitudinal section of the embryo at this time (fig. 70, *a*) shows that the plerome cylinders of the stem, leaf, and root are continuous, forming a single axial strand; but at the point where the stem-apex is forming there is an enlargement of the plerome, which is beginning to form a branch going into the stem. Very soon after this, the stem-apex shows the same arrangement of tissues as is found in the fully developed embryo.

X. THE ROOT.

The primary root of the *Naias* differs in several important points from that of the other Monocotyledons that have been described. In the first place, the bulk of the root, at least the whole of the plerome and part of the periblem and epidermis, are parts of the same segment of the embryo as the stem, while the plerome initials and terminal epidermis alone are formed from the lowest of the primary embryonic segments. Another very important difference is the complete absence of a root-cap. In none of the specimens examined was there the slightest trace of this structure, unless we can regard the cells at the apex of the root, which are continuous with the epidermis of the rest of the embryo, as such. Unfortunately Hofmeister's paper, where the embryogeny of *Naias major* is described, was not accessible, and so we cannot now make a comparison with that species; but no mention of the absence of a root-cap in *Naias major* is made in any of the references to Hofmeister's paper examined by me. The separation of the root from the stem does not occur until after the differentiation of the tissue-systems in the central part of the embryo (compare figs. 66 and 68). The tissues, therefore, are strictly continuous in the two. The first transverse walls, however, in the primary plerome and periblem cells of the middle segment, effect the separation of these tissues in the stem and root. At this period, and for a long time after, the two terminal cells of the plerome (seen in longitudinal section) abut against the central cells of the segment below, and the latter form at once the periblem initials of the root.

The differentiation of the tissues becomes very plain as the root grows, and the arrangement of the tissues at the apex is found to be quite constant. In a median section (figs. 75, 76) the tissues are arranged as follows: Bounding the section is a single layer of epidermal cells, which, at the apex, are continuous with the cells formed by the division of the lowest segment of the embryo. Between the latter and the primary suspensor are two or three short cells, formed by transverse division of the lowermost of the primary embryonic segments. These are usually considered as belonging to the suspensor, and may perhaps be called suspensor cells; but it must be borne in mind that they are not derived from the primary suspensor, but from the embryonic half of the young embryo.

Below the epidermis and separating it from the end of the plerome cylinder is the single layer of periblem initials. The plerome cylinder usually shows in a longitudinal section a single terminal cell, which is probably to be considered as the initial for the plerome. The latter shows in longitudinal section about three rows of cells, although this is not so evident in the younger embryo, where the apex often shows but two rows of cells, corresponding to the primary arrangement. Immediately back of the apex each periblem cell divides by a longitudinal wall, thus forming two layers of periblem cells, and the inner layer is soon divided again in the same way; but the hypodermal layer remains for the most part undivided and may be recognized as such in the older root, all the subsequent thickenings of the root being due to the divisions of the inner layers of the ground-tissue, which are all derivatives of the sister cells of the hypoderma, from which they are finally separated by a well marked air-space (fig. 77). From the innermost layer of the periblem there is finally cut off a layer of narrow cells, in direct contact with the plerome, forming the endodermis, or bundle-sheath.

A comparison of cross-sections of the root with a median longitudinal section of the older embryo (see figs. 76, 78, 79) shows that the plerome is composed of a single axial row of cells surrounded by a single layer of outer cells. The central row can be easily traced to the single terminal cell of the plerome, and in such sections as that shown in fig. 76 it looks as if the lateral rows of cells might also be traced to segments of the same initial cell. Whether this is always the case it is not possible to say, but it is quite likely. A cross-section of the root, a short distance back of the apex, shows the arrangement of the cells plainly (fig. 78). The plerome consists in this view of a single central cell surrounded by a row of quite similar cells, and the whole complex is bounded by the endodermis *(en)*. A section of the same root higher up (fig. 79) shows much the same arrangement of cells, but the central cell of the young vascular bundle is larger now, and in the ground-tissue of the root there have been developed numerous intercellular spaces *(i)*. The central row of cells represents a vessel, but in none of the embryos examined was there seen any trace of the usual thickenings on the walls. These cells early cease to divide by transverse walls, and increase very much in length with the growth of the root; but even in the oldest embryo examined there was no sign of a breaking down of the division walls, and the large elongated nucleus was conspicuous in each cell (fig. 74, *a*).

The embryo grows rapidly and at the time the seed is ripe fills up the embryo-sac completely. At maturity it shows besides the cotyledon three other leaves; the first two arranged almost opposite each other, the third forming a slight angle with them (fig. 80). Between the cotyledon and the enclosed bud there are two small scales (squamulæ) and similar ones are developed later in the axils of all the other leaves. The stem-apex at this time projects strongly and shows the same arrangement of cells as in the mature plant (fig. 74).

All the cells of the embryo contain starch in large quantities, and the nuclei are very distinct and rich in chromatin. The walls of the superficial cells are rather thick, and, perhaps, cuticularized, and it is quite possible that the embryo is mainly nourished through the enormously enlarged suspensor cell, where the thick, granular cytoplasm and large nucleus suggest that it is actively concerned in the elaboration of food for the growth of the embryo.

XI. THE ENDOSPERM.

The actual fusion of the two polar nuclei to form the primary endosperm nucleus was not seen, although in one or two instances they were found in close contact (fig. 50), apparently in process of fusion; and in only a few instances was a single endosperm nucleus observed. So generally were the polar nuclei separate, that the possibility of there being no fusion suggested itself. However, this latter is merely a suggestion which was not proved. A peculiarity noted, which was also observed in *Zannichellia*, was the presence of a single large nucleus close to the antipodals, which was conspicuous at an early period and behaved much like the nucleus of the suspensor. Whether this was the lower polar nucleus or one of the two endosperm nuclei resulting from the first division of the primary endosperm nucleus, could not be determined. Whichever is the case, it never divides, and all the endosperm nuclei arise from the division of the other primary endosperm (or polar?) nucleus. The development of the endosperm is limited, there being usually no trace of cell formation. The endosperm nuclei are distinct, with a well marked nucleolus, and are embedded in the granular cytoplasm lining the wall of the embryo-sac, and especially in that immediately about the young embryo (fig. 64, *k*). In the later stages they present quite a different appearance, having a less sharply defined contour, and they are much more granular. These later stages also often show more than one nucleolus, each being surrounded by a clear area. Some of these nuclei have the appearance of being formed by the fusion of two or three, but this could not be determined positively (fig. 59, *b*).

The lower nucleus (fig. 59, *a*) finally reaches an extraordinary size and becomes a very conspicuous feature of the embryo-sac. It lies close to the wall of the embryo-sac, above the antipodal cells, and is surrounded by granular cytoplasm. It has a very large nucleolus, which shows a distinctly vacuolar structure. The chromosomes are remarkably distinct and form thick sinuous threads, staining readily, and occasionally with still more deeply stained granules embedded in them. The close resemblance between this nucleus and that of the suspensor is noteworthy.

The development of the fruit was not followed, as Magnus (1870, p. 41) has given a full account of this in his monograph of the genus. For a time there is a growth of the outer cells of the nucellus, keeping pace with the developing embryo-sac; but, according to Magnus, the whole of the tissue of the nucellus and inner integument is destroyed by the growing embryo, and only the outer integument develops further to form the somewhat complicated seed-coat. The carpel itself remains membranaceous and forms simply a thin investment for the seed.

B.—Zannichellia.

The genus *Zannichellia* contains but one species, *Z. palustris*, a plant of almost world-wide distribution and not uncommon in California. While several species have been described, the more recent students of the genus have reduced them all to a single one (Ascherson, 1889, p. 213). Like *Naias*, the plant is an entirely submersed aquatic, growing either in stagnant or running water. While usually a fresh-water plant, it is also said to grow in brackish water. In general appearance the plant recalls *Naias*, but has longer and more slender leaves and stems, and on closer examination is found to resemble more some of the slender species of *Potamogeton*.

The flowering shoots arise from a creeping rhizome, and each node develops two slender, unbranched roots, which finally penetrate the mud and hold the plant firmly in position. The slender stems are abundantly branching, at least in the specimens examined by the writer. At each node there is an apparent whorl of three leaves, as in *Naias*, below which is a delicate, membranous, cylindrical sheath, which completely envelopes these in their younger stages; and an entirely similar sheath forms a bell-shaped involucre about the pistillate flower, or, more correctly, inflorescence. The male flower here, as in *Naias*, is reduced to a single stamen and is borne close to the female inflorescence at each node. Of the three grass-like leaves at each node, the two lower are opposite and have a membranous, closed, stipular sheath; the third leaf is above these and the sheath is either wanting or is incomplete. The plants from which the following account was made were collected at Stanford University, in a ditch in which the water is usually running swiftly. Most of the material was collected in the late winter and early spring, but during November and December of 1896 the plant was found with fruit and a few flowers. Ordinarily, however, the plant has been observed only in the early spring months.

There is much disagreement as to the systematic position of *Zannichellia*, as we have already intimated. In our American manuals the plant, in common with several other genera, is placed in the family, Naiadaceæ (Morong, 1893; Britton & Brown, 1896, p. 79). In Engler & Prantl's "Natürliche Pflanzenfamilien" the family Naiadaceæ is made to include only the single genus *Naias*, and *Zannichellia* is placed in the Potamogetonaceæ, but forming a special subfamily Zannichelliæ. Schumann (1892), who has made the most recent study of the genus, considers it to be sufficiently distinct from the other Potamogetonaceæ to rank as the type of a separate family, Zannichelliaceæ, in which is also included the genus *Althenia*, and this view is probably borne out by a study of the facts of structure and development.

In his careful study of the morphology of *Zannichellia*, Schumann has given a review of the literature bearing upon the subject and refers to the early work of Irmisch, who was the first to make a detailed account of this plant. Eichler, in his "Blüthendiagrammen" (1875, p. 1), also treats briefly of the morphology of this plant; and most recently of all, there are some brief references to the structure of the female flower in a paper by Magnus (1894, pp. 222, 223) called out by Schumann's work. Beyond those references the writer is not aware of any other accounts of the plant, beyond the ordinary ones in the descriptive manuals. Even in the work of Schumann, which is much the most complete so far as the flowers are concerned, no attention is given to the histology, which has apparently never been examined at all.

In studying the development of the tissues of the young vegetative organs and flowers, the same methods were used as in *Naias*, and the results given were mainly obtained from series of microtome-sections.

I. General Morphology.

Schumann (1892, p. 155) has made a very careful study of the arrangement of the stem, leaves, and flowers, and has shown that the only way to understand clearly their real relationship is to study the history of their development. While he succeeded in correcting some of the errors of the earlier observers, he himself failed to reach a clear understanding of the relation of the flowers to the main axis of the plant, from failure to study sections of the youngest stages. He showed conclusively that the anther was a truly terminal structure, as in *Naias*, but the group of carpels, which, in common with Magnus, he is inclined to consider as a single flower, he concludes to be the transformed apex of the main axis, a view which, as we shall see, is not borne out by a study of the youngest stages.

The general study of the apex of the stem and the origin of the lateral members is very much as in *Naias*. The stem-apex shows a conical form, and from it are produced the leaves in a quite similar manner. It differs from *Naias* in the formation of the sheath (fig. 81, *sh*) below each node. As in *Naias*, the lower of the two leaves alone develops axillary structures, the upper one being sterile. The products developed from the axil of the lower leaf of the pair are the stamen and a lateral branch. Schumann considers that the apex of the main axis develops into the female inflorescence and that the continuation of the axis, which is a sympodium, is due to the development of a lateral shoot in the axil of the second leaf. In reality the second leaf does not develop any axillary structure at all, but the apex of the stem divides into two equal parts, one of which develops into the female inflorescence, while the other continues as the main axis of the stem, which is therefore not such a sympodial structure as Schumann and Irmisch supposed. The stamen bears precisely the same relation to the lateral branches that the female inflorescence does to the main axis; i. e., there is a division of the axillary primordium into equal parts, one of which becomes the stamen, the other the lateral branch, which is, therefore, not to be considered as an axillary structure arising from the basal leaf of the staminal shoot.

II. THE STEM-APEX.

The apex of the shoot is occupied by a more or less conical growing point, whose tissues show the usual arrangement, but the appearance varies a good deal, depending upon the stage of development of the appendicular organs. The general arrangement of the latter is well shown in fig. 83. At the base of the apical complex is the sheath (*sh*) formed at the base of each node of the stem. Above this are the two leaves (l^1 and l^2), and in the axil of the lower one is the primordium (♂), which later gives rise to the stamen and lateral branch. The prominence (*x*) at the apex, on examining the neighboring sections of the series from which the figure was drawn, is seen to be one of two, lying side by side and apparently resulting from a true dichotomy of the stem-apex. A somewhat older stage is shown in fig. 85, cut nearly at right angles to this view. At first it is impossible to say which of these is to continue the growth of the stem and which is the young inflorescence; but this is soon determined by the rapid broadening of the floral rudiment.

A cross-section of the staminal primordium shows it to be very early much extended laterally (fig. 84), and it soon divides into two equal parts, one developing into the stamen, the other into the lateral branch, in precisely the same way as in *Naias*. The structure of the stem and arrangement of the vascular bundles is much like *Naias*, but those of the latter are better developed, especially as to the tracheary tissue, which is conspicuous in the younger parts of the bundles, but as in *Naias* becomes mostly destroyed by the subsequent lengthening of the internodes. A single strand passes from the single axial bundle of the stem into the lateral appendages, leaves, flowers, and lateral branches. The structure of the bundle is concentric throughout. In the stem the central strand of tracheary tissue is finally replaced by a large canal (fig. 125). The rest of the bundle is made up of thin-walled conducting tissue, and the whole shows a well marked endodermis. The air-spaces are more numerous than in *Naias flexilis* and not quite so symmetrically arranged.

The leaves show two rows of large intercellular spaces on either side of the mid-rib, and these spaces are separated from each other by diaphragms at pretty regular intervals. The whole structure of the stem and leaf is very similar to that of other submerged aquatics. The sheaths below the nodes are usually not symmetrical, one side being higher than the other (fig. 81, *sh*), and are usually regarded as leaves destitute of a proper lamina. They are of very delicate membranaceous texture and composed of two layers of cells. They show no trace of a vascular bundle or mesophyll.

The squamulæ are conspicuous in *Zannichellia;* their cells are filled with granular protoplasm and the nuclei are large. Their whole aspect is that of secretory cells, and the mucilaginous matter which is found about the younger parts of the plant probably arises from them.

III. THE ROOTS.

The roots occur in pairs at the nodes and are slender and unbranched. Their most remarkable peculiarity is the presence of a definite dermatogen extending over the apex, quite distinct from the periblem below it and the calyptrogen outside. In fig. 126 is shown a longitudinal section of the root-apex, in which the arrangement of the primary tissues can be easily followed. The periblem is referable to a single layer of cells, which divide rapidly by longitudinal walls back of the apex, so that the ground-tissue becomes many layered in the older parts of the root. The epidermis, as already stated, is continuous over the apex, outside of which lies the massive root-cap, whose growth is due to the rapid multiplication of the cells of its inner layer. This type of root is an unusual one, and according to De Bary (1884, p. 9) is known only in two other plants—*Pistia stratiotes* and *Hydrocharis.* Another unusual appearance observed in *Zannichellia* was the presence of what looked like secretory cells in the epidermis of the root. These are shown in fig. 127. They differ from the neighboring cells in their compressed form, dense contents, and large nuclei.

IV. THE MALE FLOWER.

Of the two parts into which the staminal primordium is divided, one lies nearer the main axis, and this one becomes the stamen. It is at first scarcely distinguishable in form from its twin structure, the young lateral shoot; but it very soon broadens above, while the base grows but little in diameter and forms the filament, the enlarged end being the young anther. At this stage it resembles curiously in form the young sporophyll of *Equisetum*. There is formed about the base of the whole complex, a rudimentary sheath, homologous with that about the stem-apex, but usually inconspicuous and easily overlooked. Schumann (1892, p. 160) denies the presence of such a sheath, although both Irmisch and Eichler have described it. In a number of the specimens examined by me, however, there was no question as to its presence, although, as usual with the sheaths in the main stem, one side (the inner) is usually higher than the other; so that here the outer margin may be almost or quite abortive. It is, however, extremely likely that Schumann (l. c., p. 161) really saw this but mistook it for anther structure. He describes what he calls a "Vorblatt," which, as he says, is never found in the "branch from the upper sheath-leaf." From a study of Schumann's figures and my own preparations, I am strongly inclined to believe that what Schumann supposed to be a special subtending leaf is in reality the inner margin of the sheath at the base of the staminal complex, which was not developed, or only slightly so, on the outer side.

The origin of the sporogenous tissue of the anther is not easy to trace, as the archesporial cells are at first hardly distinguishable either in form or contents from the adjacent cells. As soon as they are recognizable there is already a group of them whose relation to each other is not entirely clear. The archesporium is developed at four points, and in this respect, as well as in the general structure of the older anther, *Zannichellia* is very different from *Naias flexilis* and resembles more the typical Angiosperms, with their four loculi in the anther. Whether these four loculi are to be considered as each homologous with the single one in *Naias flexilis*, or whether the latter is to be considered as made up of four confluent loculi, is a question which it is not now possible to answer. It will first be necessary to study the development of the anther in some species of *Naias* which is normally quadri-locular.

The anther grows rapidly and becomes longer proportionately, and with this there is a rapid growth and division in the sporogenous tissue. The latter is not clearly delimited in longitudinal sections, but in transverse sections the four groups of sporogenous tissue are more clearly defined. The structure of the anther at this stage shows nothing peculiar. As the stamen grows older the superficial cells have their walls thickened and are quite different in appearance from the cells beneath them (fig. 89). The sporogenous cells are now better marked and show the larger nuclei and denser contents usual in similar cells. Surrounding the masses of sporogenous cells are about three layers of cells forming the tapetum. These, as usual, are almost completely absorbed when the anther is mature. No especial study of the development of the pollen was made, as there seemed to be no peculiarities worthy of note, except the fact that not all the sporogenous cells give rise to spores; but a certain number are broken down and their free nuclei can be observed among the young spores (fig. 91, *b*). This recalls the similar behavior of the sporogenous cells of *Equisetum*. The pollen-spores are small globular cells, which contain two nuclei at maturity, a large vegetative nucleus, and a small generative one contained in a separate antheridial cell (fig. 91). Like the pollen-spores of *Naias*, no exospore is developed, and the ripe spore contains numerous starch granules.

A striking feature of the stamen is the development of its apex into a prominent appendage made up of large cells (fig. 90). The filament is traversed by a vascular bundle, which has a strand of tracheary tissue, showing in section usually two tracheids.

V. THE FEMALE FLOWER.

The pistillate flowers of *Zannichellia* form a cluster at the end of a short branch, the whole inflorescence being surrounded by a bell-shaped envelope of membranaceous texture, very like the similar sheaths below the nodes of the main axis. Botanists usually regard this whole carpellary complex as a single flower, and Magnus (1894, p. 223) compares it to the single flower of *Naias* and considers the envelope as the homologue of the carpellary envelope in the latter. Morong (1893, p. 56) in his description of the plant, however, evidently considers each carpel as a distinct flower, a view whose correctness is borne out by the study of the development. The number of carpels in a cluster varies from two to about eight. In the form studied by the writer there were usually five.

Each flower consists of a single flask-shaped carpel (fig. 104), having the ovary almost globular in form, and the style expanded above into a peltate stigma, which is much more strongly developed on the outer side, and whose edges are more or less evidently lobed. A very evident canal traverses the style. Schumann, following Irmisch, considers the inflorescence (or "flower") as the termination of the main axis, which is then replaced by a lateral shoot; but we have already seen that this view is incorrect, and the inflorescence is the result of the dichotomy of the main shoot, whose other member continues the growth of the axis.

Very soon after the stem-apex is divided, the young inflorescence becomes recognizable by its broadened form, the other member of the dichotomy remaining more pointed (fig. 85). It is soon evident that the broadening of the floral branch is due to a second dichotomy in it. The branch at this time closely resembles the young staminal one, but is somewhat larger. The arrangement of the tissues is very plain. The epidermis is separated from the axial plerome by a layer of periblem, which is more strongly developed on the lower side of the branch. At the time of the first dichotomy, the plerome consists of four rows of cells (seen in longitudinal section), but at the top it forks, one branch going to each of the branches of the inflorescence (fig. 92). In case there are but two carpels, there is no further division; but in all the specimens examined by me the dichotomy was repeated in each branch. The fifth carpel presumably is formed by a third dichotomy in one of the secondary branches, and where there are eight, it is natural to suppose that all of the branches have divided. It is plain from this that the so-called flower is really a branch system, arising by a true dichotomy of the primordium in precisely the same way that the latter arose from the dichotomy of the apex of the main shoot of the plant. Although the matter was carefully investigated there was no evidence that the flowers ever arose as lateral branches of a common axis.

The early stages of the development of the flower have been investigated by Schumann (1892) and Magnus (1894), but owing to the impossibility of tracing out the youngest of the stages except by the aid of microtome-sections, they failed to make out correctly the origin of the carpels, and especially the real nature of the ovule. Both describe the carpel as arising in the form of a ring-shaped wall, upon whose inner surface the ovule is formed as a secondary growth. A complete study of microtome-sections, through all the younger stages of the flower, has convinced me, however, that the ovule is really an axial structure, being the termination of a branch, and the carpellary leaf merely subtends it.

If an exact median section through the youngest stage in which the flower can be recognized is examined, it will be seen to consist of a very slightly elevated protuberance (fig. 93, *o*), which is the apex of the very short branch resulting from the last dichotomy of the floral axis. On the outer side of this is a crescent-shaped ridge, partially surrounding the apex, in section appearing as a pointed, almost horizontal protuberance (fig. 93, *c*). This is the carpellary leaf, but as its position shows, it is a structure entirely independent of the apex (*o*), or perhaps it may be better considered to be an appendage of it. The true relation of the two structures is still more evident in a later stage (fig. 94), where the tissues of the apex (*o*) show all the characters of the ordinary stem-apex. The base of the carpellary leaf extends around the base of the shoot and is confluent to some extent with it; but in no case do the two form a circular ridge of uniform height and thickness such as Schumann (1892, Pl. V, fig. 3) figures and describes as a circular carpel upon whose inner face the ovule arises later. If we compare with the stage just described a somewhat older one (fig. 95), it is seen that the growth on the side of the apex which is turned away from the leaf is stronger than it is on the inner side, so that the apex itself is beginning to be pushed over toward the inner face of the carpellary leaf. This continues until there is a ridge formed on the outer side of the shoot-apex, which is continuous with the margin of the growing carpel, and the two together constitute a tubular envelope extending above the shoot-apex and completely enclosing it (figs. 96, 99). The latter has been now forced over to a horizontal position by the strong growth on one side and forms a hemispherical projection, the young ovule, which has been erroneously supposed to be an outgrowth of the carpel itself. It is perfectly plain, however, from a study of its development, that the ovule is really the apex of the floral shoot, in which respect it may be compared directly to that of *Naias*. It is quite probable that a similar condition may be found in other low Monocotyledons. Thus in *Sparganium* the description and figures given by Dietz (1887, p. 45, Pl. III, fig. 15) would point to a similar origin for the ovule, although he states that the ovule arises from the wall of the circular carpellary leaf, which, however, is described as being very much higher on the side opposite the ovule.

The development of the ovule itself follows the normal type. The archesporial cell is very early evident as a large hypodermal cell (fig. 97), and can be detected before there is any appearance of the ovular integument, and while the ovule still has the form of a very broad but shallow prominence. From the primary archesporial cell there is cut off a single tapetal cell (fig. 98), and at about the same time the first integument becomes visible as a low ridge extending around the base of the ovule. The nucellus continues to grow, but remains relatively broad, and the apex is almost flat. The tapetal cell divides into two (figs. 100, 101), and the inner archesporial cell rapidly grows and divides so as to form, in all the specimens seen, a row of three cells, distinguished as usual from the neighboring cells by their size and contents. The lower cell is smaller than the others, and to judge from the appearance of sections studied (figs. 100 and 101), the upper and not the lower of the cells gives rise to the embryo-sac. The outer integument appears about the same time that the first divisions take place in the inner archesporial cell and grows with the developing ovule, but as in *Naias*, remains usually shorter than the inner integument, which forms the micropyle. The appearance of these in the mature ovule (fig. 105) shows nothing peculiar.

As the ovule develops, the growth continues stronger upon its upper side, so that it is forced over more and more, until it hangs almost vertically, having passed through an arc of nearly 180 degrees from the position it at first occupied.

The tube formed by the confluence of the outer margin of the shoot and the carpellary leaf grows rapidly and forms the cylindrical style, and its upper margins become widely expanded to form the large peltate stigma. There are no secretory papillæ formed within the ovary for the purpose of directing the pollen-tube, but the position of the ovule is such that the pollen-tube must grow along the integument as far as the opening of the micropyle. Whether some substance is then excreted by the ovule, which directs the tube into the micropyle, it would be difficult to prove; but it is quite probable.

The small size of the pollen-spores precludes the possibility of their depending upon the contained starch for the growth of the pollen-tube until it reaches the ovary. It is not surprising, therefore, to find several layers of cells surrounding the canal of the style, with abundant protoplasm and large nuclei, evidently secretory cells, presumably concerned with the nourishment of the pollen-tube in its passage through the style.

The embryo-sac, as usual, arises from one of the archesporial cells which destroys the others, and soon fills the space formerly occupied by them. Owing to repeated divisions in the tapetal cells, the young embryo-sac lies much deeper within the nucellus than was the case with *Naias* (fig. 102). The subsequent development in normal cases is of the usual angiospermous type and the details were not studied. After the nuclear divisions are completed, the egg apparatus and antipodal cells are formed in the usual manner, the latter as in *Naias*, having definite cellulose membranes. As in the latter, the two polar nuclei are much larger than any of the others (fig. 106), the nucleus of the egg cell being the next in size, and both the antipodals and synergidæ showing small nuclei. After these structures are formed there is a very decided enlargement of the embryo-sac before fertilization is effected, and during this growth it encroaches a good deal upon the surrounding tissues of the nucellus, but it does not occupy so large a space relatively as in *Naias*. Both the antipodal cells and those of the egg apparatus increase very much in size, and this is accompanied by a corresponding enlargement of their nuclei, especially that of the egg (fig. 108). The egg apparatus does not differ essentially from that of *Naias;* but the cells are all somewhat larger and not attached by so broad a base to the upper end of the embryo-sac.

The process of fertilization was not followed out in detail; but in one instance (fig. 108) the pollen-tube was seen entering the embryo-sac. So far as could be judged, the process was identical with that of *Naias*, but only one generative nucleus was observed in the tube. As in *Naias*, the pollen-tube pushes its way between the terminal cells of the nucellus and through the end of the embryo-sac, being much compressed above the point where it enters the sac.

Several cases were noticed where there was a departure from the normal type of development. The most common was an increase in the number of antipodal cells from three to four or five. This is obviously due to a secondary division of one or two of the primary antipodals.

A very much more marked departure from the type is that shown in fig. 110. Here the number of nuclei was much larger than usual, although it was difficult to determine just how many were present, as some of them were poorly defined. Two, which seemed to represent the polar nuclei, were distinct, and the three antipodal nuclei were pretty clear, but the others which were scattered through the granular protoplasm, which filled the whole cavity of the embryo-sac, showed no definite arrangement and did not stain strongly, so that the number could not be satisfactorily determined.

VI. THE EMBRYO.

The changes following fertilization in *Zannichellia* are the same as in *Naias*. One of the synergidæ persists for a short time, and the fertilized egg elongates before dividing. The latter has a rather broader base of attachment in *Zannichellia*, so that as soon as the first division in the embryo is completed, the suspensor cell already is decidedly larger than the embryo cell. As in *Naias*, the basal cell (suspensor) begins to enlarge at once, but undergoes no further division[1].

A curious variation was met with in one case shown in fig. 119. Here it looks as if one of the synergidæ had persisted and grown with the developing embryo, which was in contact with it on one side for nearly its whole length.

The following divisions in the embryo cell correspond closely to those in *Naias*, but here there seems little doubt that sometimes, at least, the two basal segments of the embryo are formed by division of the lower of the two cells into which the embryo cell first divides. It now consists of three cells (exclusive of the suspensor), and the next wall is in the terminal cell. This wall is nearly vertical (fig. 114), but not infrequently is more or less decidedly oblique. The exact succession of the subsequent divisions was not followed, but there are formed a series of transverse walls in all the primary segments, and also intersecting vertical walls in the upper ones, so that the embryo shows in its upper region a somewhat variable number of segments which are divided into quadrants, and these are separated from the suspensor by two or three undivided basal segments (fig. 116). The number of transverse divisions in the young embryo is greater than in *Naias*, and in consequence the mass of cells

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[1] Magnus (1870, p. 31) refers to this enlarged basal cell in *Zannichellia*, but gives no further particulars concerning the embryo.

constituting the embryo proper is more elongated in the early phases of development.

A more marked difference is seen, however, when we study the relation of the members of the embryo to the primary segments. In *Naias*, as in *Alisma*, the whole of the terminal segment develops into the cotyledon, while the stem-apex originates from the second segment. In *Zannichellia*, on the other hand, both stem-apex and cotyledon arise from the terminal segment, the separation of the two being determined by the first vertical wall in that segment; *Zannichellia*, therefore, forms another exception to the rule in Monocotyledons, that the stem-apex is of lateral origin. Solms-Laubach (1878) has shown a similar terminal origin for the stem in several members of the Commelynaceæ and Dioscoreaceæ; and Hegelmaier's (1874, fig. 33) figures of *Sparganium* and *Pistia* indicate that in these forms also the stem-apex is derived from the terminal segment of the embryo; but he makes no statement as to this. Solms' figures of *Heterachtia*, one of the Commelynaceæ, are strikingly similar to corresponding stages in *Zannichellia*, except for the almost complete absence of the suspensor.

The whole of the central region of the embryo of *Zannichellia* goes to form the root, the lower ones contributing to the root-cap, which is here well developed, and the secondary suspensor cells, of which there may be as many as four between the root-cap and the primary enlarged suspensor cell, which finally attains a very large size. As in *Naias*, the suspensor cell has densely granular contents and a very large nucleus.

The separation of the tissue-systems of the embryo is not determined so early in *Zannichellia* as in *Naias*, and the young embryo (fig. 117) shows a less symmetrical arrangement of the cells, the limits between the segments not being always perfectly definite. The formation of the dermatogen is not determined by the first periclinal walls in the segments, but is secondary; the first longitudinal walls cut off the plerome, and this is then followed by a separation of periblem and dermatogen in the peripheral cells.

VII. THE COTYLEDON.

The cotyledon is formed from one of the two cells into which the terminal segment is first divided. If the primary division is oblique it is the larger of the two cells which forms the cotyledon. In any case the latter grows more rapidly than the stem-apex, and is soon evident as a protuberance on one side of the apex (fig. 118), which continues to increase in size until it assumes a distinctly conical form. Its subsequent growth is very much like that of *Naias*, the main difference being the less completely developed sheath at the base and the characteristic elongated and outwardly curved apex (fig. 124). Owing to the slighter development of the stipular sheath, the cavity thus formed and surrounding the stem-apex, is not completely closed in front.

VIII. THE STEM.

The young stem-apex (fig. 118, *st*) is covered with a well defined epidermis, continuous with the rest of the embryo, and beneath this is a single layer of periblem cells, separating the epidermis from the plerome, which is connected directly with that of the cotyledon and root. As the embryo enlarges the stem-apex becomes more prominent and forms a projecting almost hemispherical prominence within a well marked cavity formed by the encircling base of the cotyledon (fig. 120). From it is formed later the second leaf (fig. 121, l^2). This arises as a protuberance upon the side of the stem-apex, opposite the cotyledon. Its tissues are continuous with those of the stem and show the same relative arrangement.

IX. THE ROOT.

As might be expected from the larger part of the young embryo which takes part in its formation, the primary root in *Zannichellia* is relatively larger than in *Naias*. The greater part of the root is formed from the second and third of the primary segments of the embryo, and in consequence is longer than that of the same stage in *Naias*. These segments probably always undergo regular quadrant divisions, and then each quadrant cell divides into an inner and an outer cell, the former contributing to the plerome. The separation of the dermatogen follows next, and this is soon followed by a second periclinal wall within the periblem, which thus becomes two-layered. All these tissues are more clearly defined in the root region of the embryo than in either the cotyledon or stem (fig. 118). The plerome extends only to the limits of the third primary segment, as in *Naias*, and from the fourth segment is developed the layer of periblem cells, and later the dermatogen. From the two segments below this layer are formed the cells of the root-cap, which is a conspicuous feature of the root. In most of the sections of the older embryos examined, there was a single layer of initial cells, common to dermatogen and periblem (figs. 122, 123), so that directly at the apex the plerome was separated from the inner cells of the root-cap only by a single layer of cells; but finally there is developed a dermatogen continuous over the apex and distinct from the periblem initials, such as we have seen occurs in the roots of the adult plant.

The end of the root is broad and truncated and the root-cap forms a lenticular body covering only the middle of the flattened root-apex (figs. 122, 123). At the time that the embryo is fully grown, the root-cap is about four cells thick in the middle where the growing part is situated.

The plerome is very sharply defined in the root of the fully grown embryo (fig. 123) and is more massive than in *Naias*. It does not show any evidence of a single initial cell at the apex, nor was any sign of the formation of tracheary tissue observed in any of the embryos examined. This probably is first formed after germination begins.

X. The Endosperm.

The endosperm formation corresponds very closely to that described for *Naias*. There is probably a fusion of the polar nuclei, but this could not be positively shown in all cases, and possibly may not always take place. As in

Naias, there is evident soon after fertilization a large nucleus just above the antipodal cells, which undergoes no division but increases very much in size. This is more variable in size than in *Naias;* not infrequently it could not be detected in the later stages, and in several instances it looked as if it were undergoing disintegration. The thick nuclear segments, which are usually so conspicuous in *Naias*, are much less so in *Zannichellia*, where the nucleus presents a more uniformly granular appearance. Whether this nucleus is in any cases the original lower polar nucleus must remain for the present unanswered; but it is by no means impossible. The secondary endosperm nuclei, which as in *Naias* arise entirely from the upper of the two primary endosperm nuclei, are rather more conspicuous, having a very definite contour and large nucleolus. They do not divide in the later stages of development of the embryo-sac, but increase a good deal in size. The formation of walls in the endosperm is either rudimentary or entirely wanting.

XI. THE FRUIT.

No particular study of the development of the fruit was made, but a few notes were taken which are here given. The outer tissues of the nucellus remain evident at the apex and base, but on the sides are almost completely destroyed by the growing embryo-sac. The thin testa of the seed is formed almost entirely from the outer integument. The walls of the ovary become much thickened and form the firm pericarp of the ripe fruit, and the style persists as a conspicuous beak at its upper end.

SUMMARY AND CONCLUSIONS.

A.—Naias.

1. A study of the development of *Naias flexilis* has confirmed the view as to the axial nature of the stamen and ovule.
2. The presence of tracheary tissue in stem, leaf, and

pedicels of the flowers was demonstrated, contrary to the conclusions of Magnus with reference to all species described by him.

3. The anther of *N. flexilis* is regularly unilocular, but not infrequently shows traces of a division into two loculi, which occasionally may be complete.

4. The large pollen-spores contain at maturity three nuclei, one vegetative and two generative. The early growth of the pollen-tube is entirely at the expense of the starch in the spore; only after it has penetrated into the ovary is it nourished by the cells of the pistil. In the ovary there are secretory papillæ at the opening of the canal of the style and also at the base of the funiculus.

5. Fertilization is of the usual type.

6. The first division of the embryo is transverse and divides it into two cells, suspensor and embryo cell. The former remains permanently undivided.

7. The embryo cell divides by transverse walls into a series of segments of which the terminal one forms the cotyledon; the second, the stem; the third and fourth, the root; the others, the secondary suspensor cells. No root-cap is present.

8. It is doubtful whether there is always a fusion of the polar nuclei. There is always present subsequently a single large nucleus at the base of the embryo-sac, which may perhaps represent the unchanged lower polar nucleus. Secondary endosperm nuclei are all derived from the upper of the two primary endosperm nuclei. The endosperm is rudimentary.

9. Deviations from the normal type of embryo-sac were noted in several cases.

B.—Zannichellia.

1. The anthers and ovules of *Zannichellia* like those of *Naias* are strictly axial structures.

2. The female infloresence is formed by the dichotomy of the main axis, but is not, as has been claimed, the

transformed axis itself; the carpels, or individual flowers, are formed by repeated dichotomy of the primary floral axis.

3. The envelope about the infloresence is the homologue of the tubular bract below each node of the main axis.

4. The male flower is also strictly terminal and arises by the dichotomy of a primordium in the axil of the lower of the two foliar leaves at each stem-node. The sister shoot developed from the primordium becomes a lateral branch.

5. The stamen corresponds closely in structure to the ordinary angiospermous type. The pollen-spores are small, with two nuclei at maturity; a conducting tissue is developed about the canal of the style, which nourishes the pollen-tube.

6. The ovule, like that of *Naias*, is the transformed apex of the floral axis.

7. The embryo-sac generally arises from the upper cell of the sporogenous complex; its development is normally of the ordinary type.

8. The first divisions in the embryo correspond to those in *Naias flexilis*.

9. Of the segments of the embryo cell, the terminal one gives rise to both cotyledon and stem-apex; the second, third, and fourth to the root, and the fifth to the root-cap; a secondary suspensor of three or four cells is developed from the lower segments.

10. The development of the endosperm is essentially as in *Naias*.

11. Abnormal embryo-sacs much like those in *Naias* were met with.

12. The primary root of the embryo, as well as those of the mature plant, have four distinct meristems; i. e., plerome, periblem, dermatogen, and calyptrogen.

Comparing *Naias* and *Zannichellia*, there are obviously many points of structure in which they agree. The general arrangement and development of the stem and leaves agree closely in the two, and the arrangement of the tissues is very similar. The origin of the flowers, too, as we have endeavored to show, is essentially the same in the two genera, although in *Zannichellia* the flowers are much better developed than in *Naias*. Whether the quadrilocular anther of the former is to be considered as derived from the unilocular form found in *N. flexilis*, through forms like *N. major* for example, can be better answered after the development of the anther in the latter has been more carefully studied.

Corresponding to the more highly developed flowers in *Zannichellia*, the tissues of the stem, especially the vascular bundles, are much better developed. Whether the same difference exists in the roots of the mature plants as is found in the embryos cannot now be stated. A further study of this point would be interesting.

The embryos of the two agree closely in their earliest divisions, and in both the suspensor remains permanently undivided. It is extremely probable that a further study of embryos of the same type will show that this is a common if not universal phenomenon. In regard to the origin of the different members of the embryo, however, there is one important difference; viz., the origin of the stem-apex from the terminal segment in *Zannichellia*. In this respect the latter approaches several Commelynaceæ and Dioscoreaceæ described by Solms-Laubach (1878), where there is a similar terminal origin for the stem-apex. This type of embryo is probably more common than has been supposed, as Hegelmaier's figures of *Sparganium* (l. c.) indicate a similar state of affairs there.

Corresponding to the greater part of the embryo devoted to its formation, the root in *Zannichellia* is better developed than in *Naias*, and the absence of a root-cap in the latter is also noteworthy, as this is a very uncommon phenomenon.

Comparing the embryos with those of other Monocotyledons, it is seen that in regard to the formation of the cotyledon and stem-apex, *Naias* approaches the type of *Alisma* and the Liliaceæ, while *Zanichellia* is more like the type of the Commelynaceæ or Dioscoreaceæ, where the stem-apex is terminal.

Attention has been called by the writer (Campbell, 1891, p. 253; 1895, p. 518) to the resemblance between the embryo of *Isoetes* and that of the typical Monocotyledons; and Kny (1875) has also suggested an independent origin for Monocotyledons from the Filicineæ. The lateral origin of the stem-apex in *Isoetes* is certainly suggestive of the similar origin in *Naias* or *Alisma*, and Hegelmaier's figures of *Pistia* are still more suggestive of the embryo of *Isoetes*, especially in the complete absence of a suspensor. The figures which Solms-Laubach gives of the embryo of *Heterachtia*, where the suspensor is also absent, are remarkably like the embryo of a typical Fern.

The ovules and anthers of *Naias* probably show the closest approach to the sporangia of the Pteridophytes of any angiospermous plant. The homologies of the ovules and pollen-sacs of the latter with the sporangia of the former have of course been recognized for a long time. The remarkable similarity to each other of ovule and anther in *Naias*, even to the investment of the anther with an integument like that of the ovule, is noteworthy as pointing to a very primitive condition in the differentiation of the macro- and microsporangia. It will be borne in mind that in all heterosporous Pteridophytes the two sorts of sporangia are much alike in their earlier stages of development, and it is extremely interesting to find an angiospermous Spermaphyte which so nearly resembles typical Pteridophytes in this respect. The writer, in a study of the sporangia in *Azolla* (Campbell, 1893, p. 162), has called attention to the remarkable resemblance between the macrosporangium there and the ovule of the Angiosperms, a resemblance that did not escape the earlier students of this plant. In this paper I defended the view that the indusium in *Azolla* is the homologue of an ovular integument, a view which I see no reason now to retract. The suggestion has also been made that possibly the velum in *Isoetes* may be of the same nature. It is true that these may be only analogies, but they are in any case of great importance, as showing how closely related, structurally at least, are the sporangia of the Pteridophytes and Spermaphytes. The different origin of the sporangia in *Naias* and *Isoetes*, however, as well as other structural differences, does not admit of any very close connection between such forms, and it would be useless to attempt a detailed comparison of the Monocotyledons and Pteridophytes until a great many more types of the former have been critically examined, especially those whose embryos are more like those of the Pteridophytes than is that of *Naias*.

The occurrence of deviations from the ordinary structure in the embryo-sac in both *Naias* and *Zannichellia* suggests the importance of further investigations on this point, as it is here that the surest clues to relationship with the Pteridophytes, if such exist, are most likely to be found. Recent investigations in this direction have shown that the type of structure is not so uniform as has generally been supposed, this being especially true with respect to the number of the antipodal cells. In both *Naias* and *Zannichellia* we have also seen that the number of nuclei, apart from the antipodal cells, may be considerably augmented. A few observations were made by the writer upon *Sparganium eurycarpum*, which showed that in this plant also the structure of the embryo-sac is not always constant. In fig. 129 is shown a case where there were about ten free nuclei in the upper part of the sac, and four very prominent antipodal cells. The latter may reach an extraordinary development in this species, as is shown in fig. 130. Other variations from the type were seen in the same species, although as yet these have not been critically studied. These instances are sufficient to show that there is much more variability than is usually supposed, and a further examination of these same parts in other low monocotyledonous types may be expected to yield further instances of the same kind.

The question of the position of the Monocotyledons in the system, and the relative positions of their different orders, is by no means settled. There is, however, a growing tendency to regard them as the most primitive of the Angiosperms, and not as Strasburger has suggested, a group derived originally from the Dicotyledons. So, again, as to the relative positions of Gymnosperms and Angiosperms, the writer has already expressed his belief that these two great divisions of the Spermaphytes are of entirely distinct origin. If we accept the view that there is a probable direct connection of the Monocotyledons with the Pteridophytes, it is among just such simply organized aquatics as *Naias* or *Zannichellia* that we should naturally look for the point of contact. It is true that these are generally looked upon as degenerate types derived from apocarpous forms, like *Alisma* or *Butomus* (Delpino, 1896; Bessey, 1893); but there seems no good reason for such an assumption. Inasmuch as nearly all the heterosporous Filicineæ, including *Isoetes*, are either aquatic or at least amphibious, it would naturally be expected that forms derived from them would inherit their aquatic habits, and the simple tissues which accompany such a habit. We should also expect in such forms an extremely simple type of flower, such as really exists in *Naias*. Taking into account, then, all of the similarities of the tissues of the mature plants, as well as the similarities in the embryo and sporangia, it may safely be said that at any rate the theory of a direct derivation of the Monocotyledons from forms related to the heterosporous Filicineæ, and especially the Isoetaceæ, is not weakened by what has been brought out in the course of these investigations.

As to the relationship of *Naias* and *Zannichellia* to each other, it does not seem sufficient to warrant uniting them in the same family, although they are with little question not very distantly related. For a clear understanding of their relationship to the other apocarpous Monocotyledons, further investigations of these forms will be necessary before we are in a position to decide with any degree of certainty.

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CALIFORNIA,
January, 1897.

SUPPLEMENTARY NOTE.

Since the foregoing paper was completed I have procured a copy of Hofmeister's paper (1861), in which he gives a somewhat extended account of the development of *Naias major* and a less complete description of the embryo of *Zannichellia*. In both cases he figures and describes correctly the earliest phases of the embryonic development, including the enlarged suspensor cell, but the details concerning the embryo-sac and the later stages of the embryo are very incomplete. No details are given as to the arrangement of the tissues in the older embryos, nor does he seem to have noted the absence of a root-cap in *Naias*.

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EXPLANATION OF FIGURES.

PLATE I.

Fig. 1. Stem-apex of *Naias graminea* Del., showing the arrangement of the appendicular organs—ff', ff'', ff''', fertile leaves; fst', sterile leaf; fl', fl'', floral rudiments; f', f'', lateral branches (after Schumann).

Fig. 2. This and all the succeeding figures are drawn from the author's own preparations of *N. flexilis* Willd. Fig. 2 is a cross-section of the terminal bud, × about 70. The older leaves are numbered; x, x', the apices of the main axis and oldest branch, *sq.*, squamulæ intravaginales; ♀, ♀′, ♀″, young female flowers.

Fig. 3. Longitudinal section of the stem-apex, × about 200; *v*, stem-apex; *k*, young primordium, subtended by the leaf, *l;* ♀, young female flower.

Fig. 4. Longitudinal section of an abnormal stem-apex, where the primordium had developed directly into a lateral sterile branch, v'; × about 400.

Fig. 5. Longitudinal section of a normal stem-apex, showing the youngest pair of leaves, l^1, l^2, and the primordium, *k*, subtended by the latter; × 400.

Fig. 6. Cross-section of a young internode of the stem, showing the arrangement of the tissues and the intercellular spaces, *i;* × about 300.

Fig. 7. Longitudinal section of a young internode, showing the central annular vessel of the vascular bundle; × 400.

Figs. 8-10. Early stages in the development of the male flower seen in longitudinal section, × about 400; *in*, inner envelope (integument), *p*, outer envelope.

Fig. 11. Section of a young primordium divided into the floral rudiment, *f*, and the lateral branch, *v*. The subtending leaf is seen below.

Fig. 12. Longitudinal section of male flower after the differentiation of the archesporium; × 200. The archesporial cells are the nucleated ones.

Fig. 13. Cross-section of an older anther.

Fig. 14. Longitudinal section of a male flower shortly before the separation of the sporogenous cells; × 70.

Fig. 15. Upper part of the same more highly magnified. The enlarged upper part of the integument, *in*, is conspicuous.

Fig. 16. Longitudinal section through the base of a slightly older flower, showing a rudimentary partition in the lower part of the theca; × 200.

Figs. 17-21. Successive stages in the first division of the spore-mother-cell. Leitz, immersion $\frac{1}{18}$, ocular 3; reduced by one-third.

Fig. 22. Two pollen-tetrads; × about 400.

Fig. 23. Young pollen-spore, with the primary antheridial cell; × about 800.

Fig. 24. A slightly older stage.

Fig. 25. A nearly mature spore, with the large vegetative nucleus, and the two small generative cells. The spore is nearly filled with starch granules; × about 400.

Fig. 26. A ripe pollen-spore; × 300.

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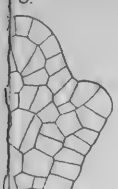

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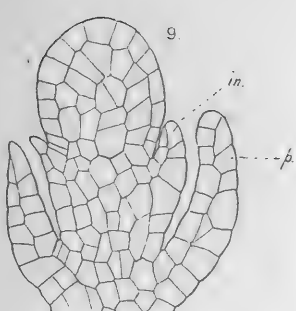

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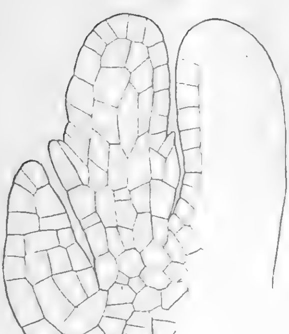

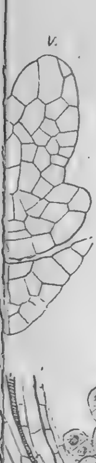

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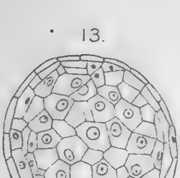

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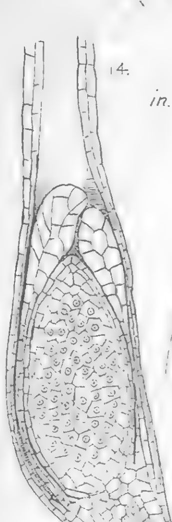

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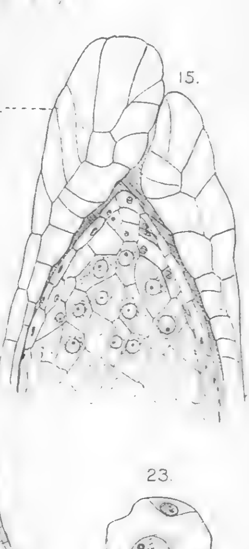

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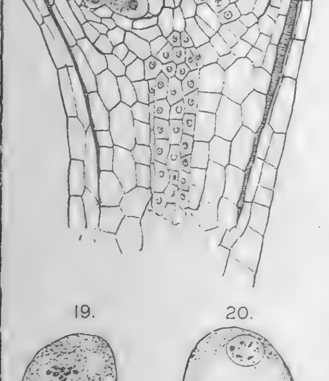

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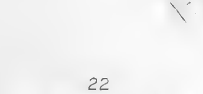

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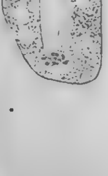

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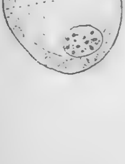

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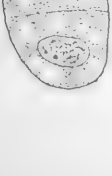

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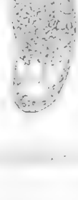


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PLATE II.

All figures refer to *Naias flexilis.*

Fig. 27. Mature male flower, showing the long pedicel; × 25.

Fig. 28. A male flower which has discharged the pollen, showing the lateral rupture of the floral envelope; × 25.

Fig. 29. Longitudinal section of a nearly mature flower, showing a complete division of the anther into two loculi; × 40.

Figs. 30, 31. Germinating pollen-spores; × 400.

Figs. 32, 33. Pollen-tubes, showing the granular protoplasm at the extremity. In fig. 33, the two generative nuclei, *k*, can be seen.

Figs. 34-39. Successive stages in the development of the ovule, seen in longitudinal section; × about 400, (except fig. 37, which is magnified about 200). The carpel is not shown except in figs. 34 and 37. The archesporial cells are shaded; *t*, the tapetum, in^1., in^2., inner and outer integuments.

Fig. 40. Young female flower, showing the young spiny lobes, *x*, and stigmatic lobes, *y;* one of the latter is still very small; × about 200.

Fig. 41. Section of young ovule, with the archesporium divided by longitudinal as well as transverse walls.

Figs. 42, 43. Young embryo-sacs, with two and four nuclei; × 450.

Fig. 44. A mature female flower; × 25.

Fig. 45. One of the stigmatic lobes; × 200

Fig. 46. A spiny lobe; × 200.

Fig 47. Longitudinal section of the ovary of a mature flower, showing the stylar canal and papillæ, *p;* × about 60.

Fig. 48. Young papillæ from the upper part of the ovary; × 400.

Fig. 49. Older papillæ from the same place.

Fig. 50. Upper part of mature embryo-sac, showing one of the synergidæ, *s;* the egg, *o;* and the two polar nuclei in close contact, *k;* × 400.

Fig. 51. The two synergidæ from a similar one.

Fig. 52. Egg apparatus from a slightly younger embryo-sac than that shown in fig. 50.

Fig. 53. (*a*) Upper part of the embryo-sac at the time of fertilization; *pt.* the pollen-tube, with two generative nuclei; *o*, the egg.

(*b*) The large endosperm nucleus, probably formed by the fusion of the two polar nuclei.


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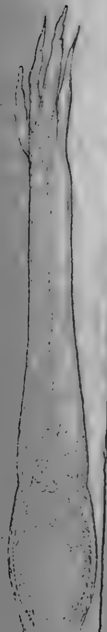

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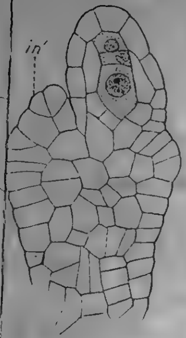

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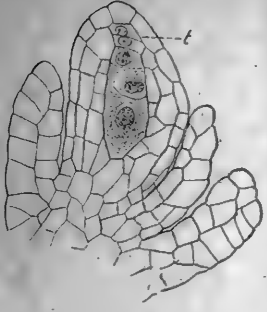

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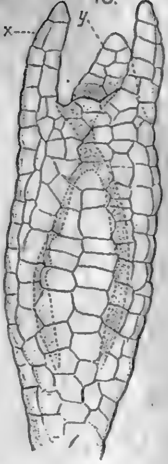

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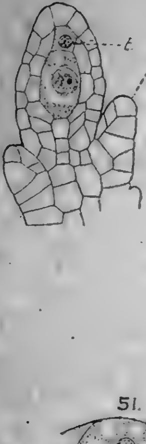

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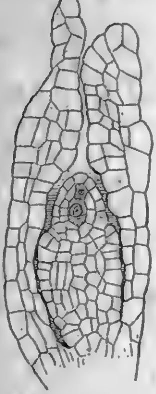

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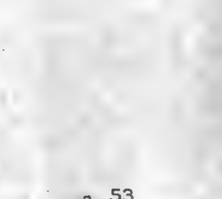

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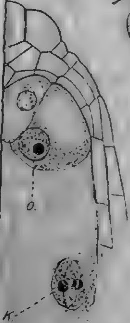

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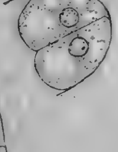

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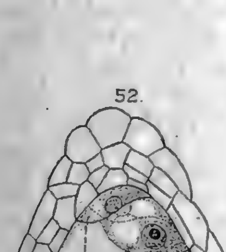

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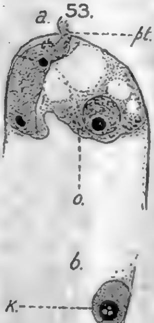

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PLATE III.

All figures refer to *Naias flexilis.*

Fig. 54. Two sections of an abnormal embryo-sac, in which apparently the upper archesporial cells were not absorbed as is usually the case, and no definite egg apparatus was formed.

Fig. 55. Lower part of the embryo-sac shown in fig. 54, with six antipodal cells (four only are shown in the section).

Fig. 56. Section of an ovule which apparently had not been fertilized; the embryo-sac is replaced by a mass of elongated cells; × 200.

Fig. 57. (*a* and *b*) Two sections through a normal embryo-sac, showing fertilization; *pt*, pollen-tube; *o*, egg; *s*, synergidæ; *k*, endosperm nucleus. (*c*) Lower part of the same embryo-sac, showing two of the antipodals; × 450 (about).

Fig. 58. An abnormal embryo-sac, in which only one cell of the egg apparatus could be certainly distinguished. The end of the pollen-tube was very much enlarged.

(*b*) Antipodal region of the same embryo-sac.

Fig. 59. Endosperm nuclei from an embryo-sac containing an advanced embryo. *(a)* The single large nucleus above the antipodal cells, which undergoes no division; *(b)* The smaller secondary nuclei from the upper part of the embryo-sac; × 400.

Fig. 60. Two sections of the upper part of an embryo-sac, showing the fertilized egg cell, *o*, and one of the synergidæ, *s*, which is still intact.

Fig. 61. (*a*) Upper part of embryo-sac, with two-celled embryo; × 250. (*b*) Endosperm nucleus of the same.

Figs. 62-66. Successive stages of the developing embryo, in longitudinal section; × 250. *sus*, primary suspensor cell; *k*, a secondary endosperm nucleus.

Fig. 67. Cross-section of an older embryo.

Fig. 68. Longitudinal section of an embryo, showing the primary segments 1, 2, 3.

Fig. 69. Longitudinal section of an embryo, showing the enlargement at the base of the cotyledon.

Fig. 70. Two nearly median, longitudinal sections of an older embryo; × 200; *st*, stem-apex; *cot*, cotyledon; in *a*, the boundary of the plerome is indicated by a heavy line.

Fig. 71. Median, longitudinal section of an older embryo.

Fig. 72. Similar section of a much older one; × 70.

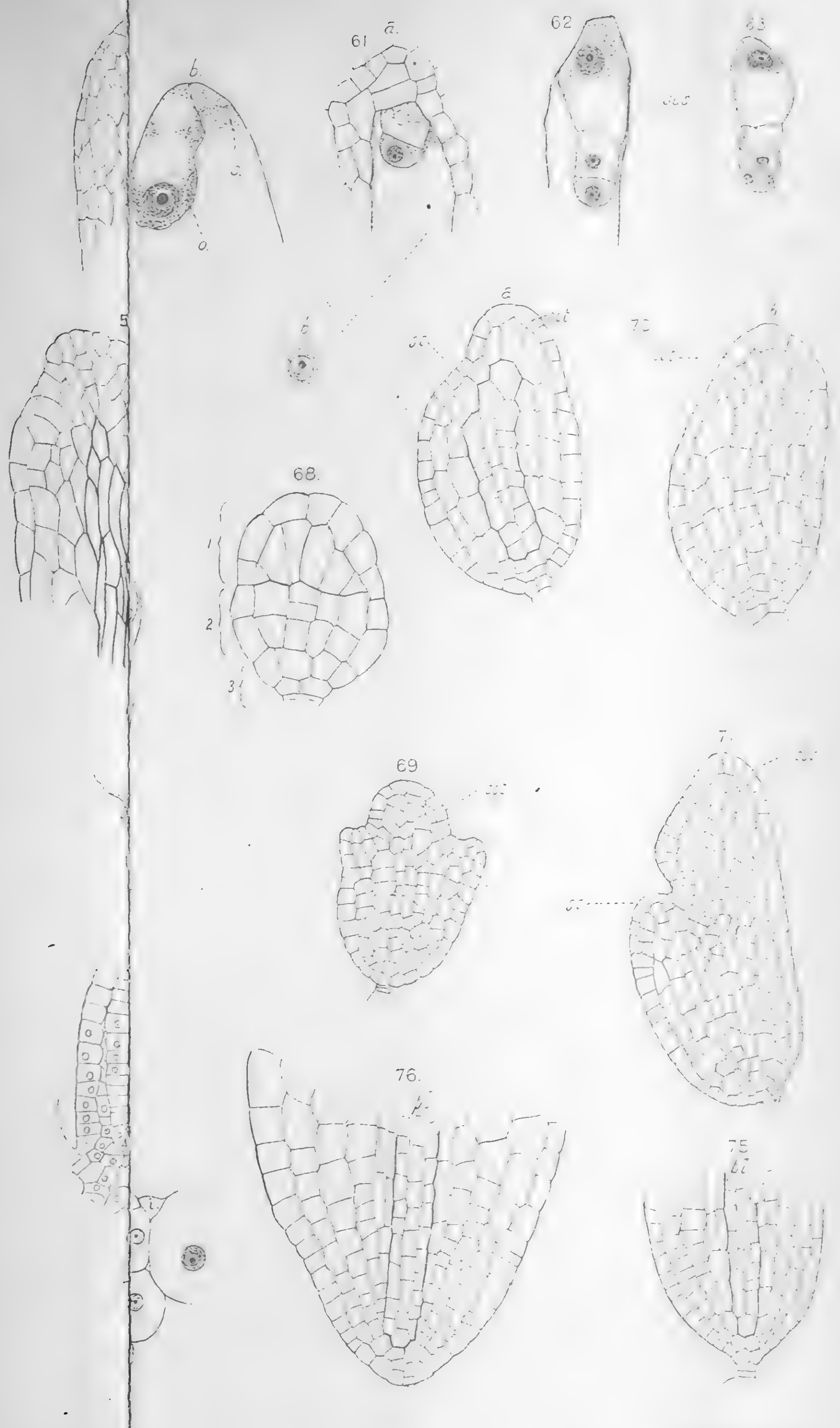
Fig. 73. Longitudinal section of an embryo from a nearly ripe seed; × 40.

Fig. 74. Two sections through the apical region of an embryo of the same age as the one shown in fig. 73.

Figs. 75, 76. Median, longitudinal sections through the root of advanced embryos; *pl*, plerome; × 200.

Fig. 77. Root of a full-grown embryo, showing the formation of intercellular spaces.

Figs. 78, 79. Two transverse sections of the root just back of the apex; *v*, vessel; *en*, endodermis; *i*, intercellular spaces; × 400


61
a.
b.
o.
62
63
68.
1
2
3
69
70
76.
75
5


54
57
55
58
59
73
pc
78
en
en

PLATE IV.

All the figures refer to *Zannichellia palustris* L.

Fig. 81. Nearly median longitudinal section through the stem-apex; × 70. The actual apex, *x*, was not included in the section, but its position is indicated by the dotted line; *sh*, the sheath below the node; l^1, l^2, the two "spathe leaves;" *i*, lacunæ in the leaves; ♀, female flowers; ♂, male flowers; *sq*, squamulæ intravaginales; *x′*, apex of a lateral branch.

Fig. 82. Transverse section of the terminal buds. The leaves are numbered; otherwise the lettering as in fig. 81.

Fig. 83. Longitudinal section of stem-apex; × 200. The apex, *x*, was divided into two parts, only one of which shows in the section.

Fig. 84. Transverse section of the staminal primordium; × 400.

Fig. 85. Longitudinal section of the stem-apex after its division into the carpellary branch, ♀, and the secondary stem-apex, *v;* × 200.

Figs. 86-88. Development of the stamen seen in longitudinal section; × 200.

Fig. 89. Transverse section of an older anther.

Fig. 90. Longitudinal section of an older stamen, showing the peculiar terminal appendage; × 60.

Fig. 91. Two nearly mature pollen-spores. In *b*, the primary nucleus is dividing. Two free nuclei, *k*, are shown, derived from disintegrated archesporial cells; × 400.

Fig. 92. Longitudinal section of young female inflorescence, showing the dichotomy of the plerome; × 400.

Fig. 93. A similar section through the margin of an older inflorescence, showing the ovular rudiment, *o*, and the subtending carpellary leaf, *c*.

Figs. 94-96. Early stages in the development of the female flower in longitudinal section; × 400. *o*, ovular rudiment; *car*, carpel.

Fig. 97. Section of the young ovule, showing the primary archesporial cell; × 400.

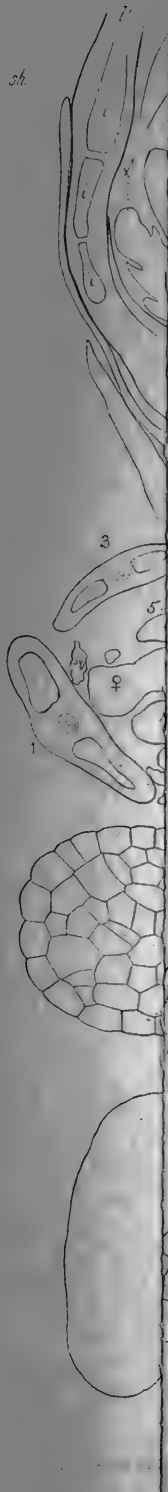
Fig. 98. Cross-section of a young flower; × 400. *car*, Carpellary leaf; *t*, the primary tapetal cell.

Fig. 99. Longitudinal section of an older flower; × 150.

Figs. 100, 101. Longitudinal section of ovules, showing the later divisions in the archesporium; *t*, tapetum.

Fig. 102. An older ovule, the nucleus of the embryo-sac already divided; × 400.

Fig. 103. Longitudinal section through the inflorescence, showing its connection with the main axis; *sh*, the involuere.



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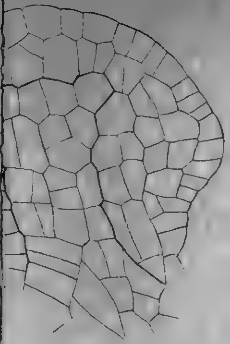

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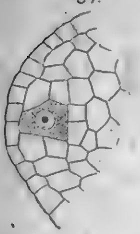

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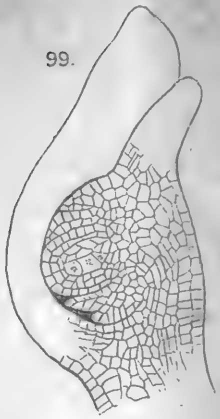

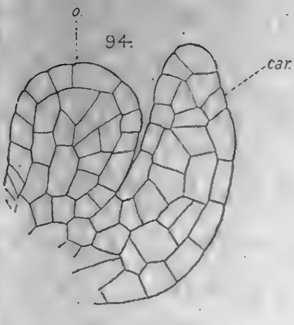

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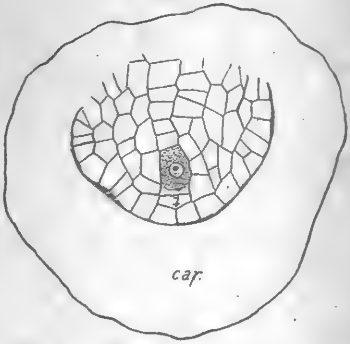

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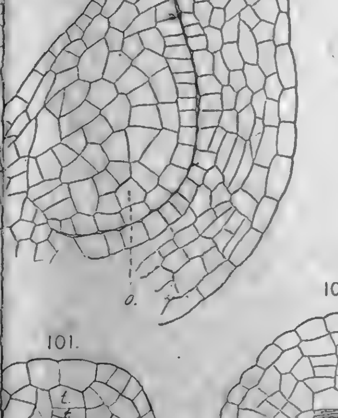

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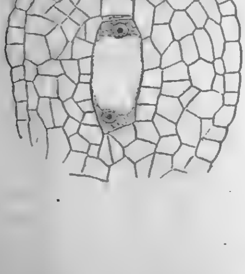
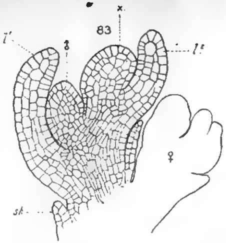


Lith Britton & Rey


81.
sh.
l¹
l²
l³
♂
♀
♂
sq


82.
3
2
5
2
♀
x
♂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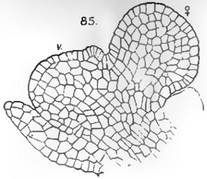
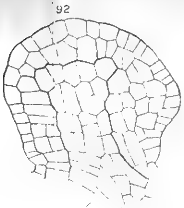
x
♂
l¹
l²
♀
sh.


85.
v.
♀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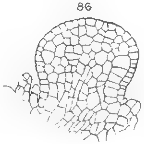
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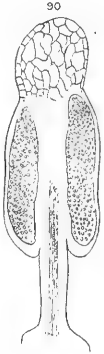
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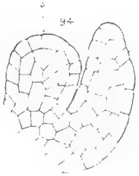
93
o
c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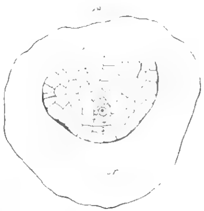

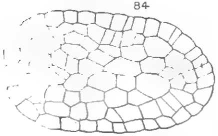
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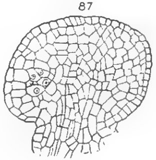
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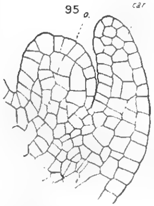
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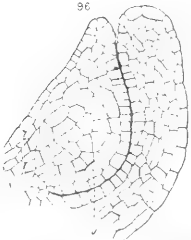
a.
car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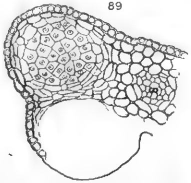
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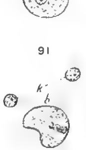
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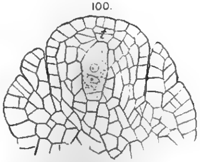
b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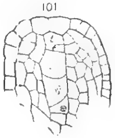
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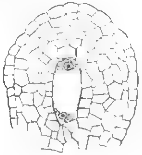
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PLATE V.

All figures except 128 and 129, refer to *Zannichellia*.

Fig. 104. Longitudinal section of a nearly mature female inflorescence; × 40.

Fig. 105. Longitudinal section of a nearly mature ovule; × 200.

Fig. 106. Two sections of an embryo-sac after the formation of the egg apparatus and antipodals; × 400.

Fig. 107. Lower part of a mature embryo-sac, with four antipodal cells; *k*, the lower polar (?) nucleus; × 350.

Fig. 108. Egg apparatus at the time of fertilization; *pt*, pollen-tube; *o*, egg; *s*, synergidæ; × 400.

Fig. 109. Antipodal region of mature embryo-sac.

Fig. 110. Two sections of an abnormal embryo-sac, with numerous free nuclei; × 400.

Fig. 111-116. Successive stages in the development of the young embryo; longitudinal sections × 400. The primary segments are numbered.

Figs. 117, 118. Older embryos; × 200; *st*, stem-apex; *cot*, cotyledon.

Fig. 119. Two sections of an abnormal embryo, in which, apparently, one synergid, *s*, was persistent, and adherent to the embryo; × 400.

Fig. 120. Section of an advanced embryo; × 70.

Fig. 121. Stem-apex of the same embryo; × 200. l^2, the second leaf.

Fig. 122. The root of an embryo of the same age. *rc.* root.cap; sus^2 secondary suspensor.

Fig. 123. Root of an almost full-grown embryo.

Fig. 124. Longitudinal sections of nearly mature embryos; × 40; *a* shows the stem-apex and root; *b*, the hooked cotyledon.

Fig. 125. Cross-section of an internode from the stem of a mature plant; × 70.

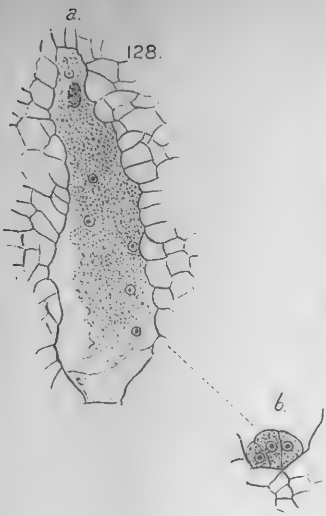
Fig. 126. Longitudinal section of the apex of a root from the mature plant, showing the four primary tissues; plerome, *pl;* periblem, *pb;* dermatogen, *d;* and calyptrogen, *cal;* × 200.

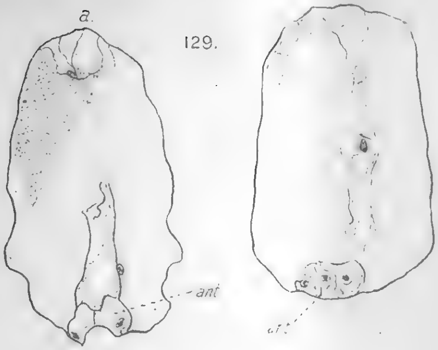
Fig. 127. Epidermal cells from near the root-apex, *a*, surface view; *b*, a vertical section; × 400. The cells with dense contents are apparently secretory cells.

Fig. 128. Embryo-sac of *Sparganium eurycarpum* Englm, with about ten free nuclui, and four antipodal cells.

Fig. 129. Two sections of an embryo-sac of *Sparganium eurycarpum* Englm, showing extraordinary development of the antipodal cells, *ant*.

[CAMPBELL.] PLATE V.





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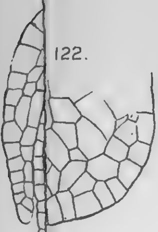

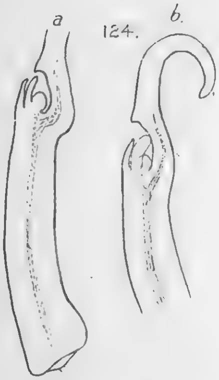

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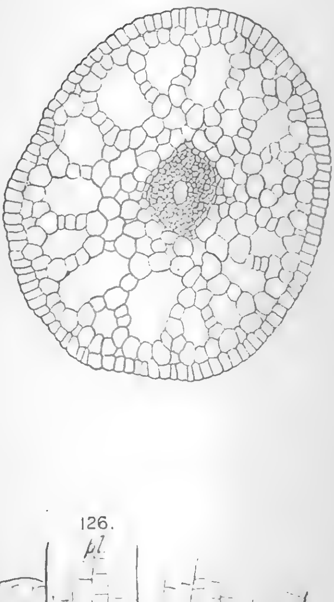

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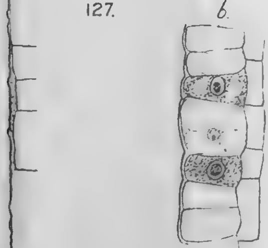

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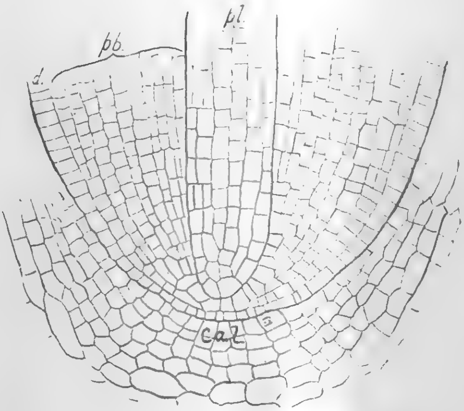

E. F. [illegible]

STUDIES IN THE HERBARIUM AND THE FIELD.—No. 1.

BY ALICE EASTWOOD,
Curator of the Herbarium.

CONTENTS.

PLATES VI–VII.

I.—REPORT ON A SMALL COLLECTION OF PLANTS FROM THE WHITE SANDS OF NEW MEXICO.[1]

SOME months ago, Professor T. D. A. Cockerell of the College of Agriculture and Mechanic Arts, New Mexico, sent me a small package of plants for determination. They were collected on the "White Sands" in August, 1896. They hint of a very interesting flora and indicate by a close alliance with well known species and by marked differences from the same, a peculiar environment and probably some

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[1] The traveler coming down Tularosa Creek, in the Sacramento Mts. of New Mexico, sees before him in the distance what appears to be the sea, with heavy breakers rolling towards the shore. As he descends to the valley, he gradually realizes that the apparent ocean is motionless, and is above, not below, the level of the plain. Coming at length within a few miles of it, he sees before him what are to all appearances great banks of snow; and were it not for the intense heat, the illusion might be complete. Actually arriving at the banks, he finds nothing but pure white sand, piled up perhaps to a height of fifty feet above the plain, from which it rises abruptly, and continuing in undulating hillocks as far as the view extends. It is this remarkable formation that is known as the White Sands. Prof. C. H. T. Townsend has described it in similar words in an unpublished paper on the Distribution of Life in the Southwest and Mexico; and I believe almost any one would receive the same impressions on visiting the locality for the first time.

November 23, 1897.

degree of isolation. The interesting description of the country, which Professor Cockerell has written, throws considerable light on the probable history of these plants.

Œnothera tubicula filifolia, var. nov.

PLATE VI, FIG. 1.

Stems slender, suffruticose; older parts with grayish brown, shreddy epidermis; younger parts and leaves slightly glandular, hoary-puberulent, with spreading short white hairs; leaves sessile, becoming almost terete with the involute margins, 5–15 mm. long, 1–1½ mm. or less wide, crowded at the ends of the branches and in small rosulate clusters in the axils; calyx-tube 3–3½ cm. long, funnel-form lobes spotted with dark purple, 1 cm. long, 4 mm. broad, with pointed tip 1 mm. long; corolla 3½ cm. in diameter, yellow, tinged with white when withered, petals rhomboidal, slightly acuminate, upper margin wavy; stamens with anthers 1 mm. broad, 7 mm. long, equalling the filaments;

The exact extent of the White Sands I do not know, but they are probably about forty miles long and a good many miles across. They lie to the east of the San Andreas range of mountains. They are composed of pure gypsum, undoubtedly deposited from a salt water lake, which must have been shut off from the sea and by degrees have dried up. Prof. A. Goss, of the N. M. Agricultural Experiment Station, has pointed out to me, that as the lake dried up, the gypsum would be precipitated early, being comparatively insoluble. Eventually the other salts would be deposited on the top of it. The more soluble salts have long ago been washed away, and we have remaining the beds of gypsum, which now rise considerably above the surrounding plain, the latter doubtless having been lowered by gradual denudation. While the plain itself contains a great quantity of gypsum, the banks are perfectly distinct and well defined—as well defined as a miner's dump. Somewhere in the sands, I am informed, there is a spring, and water is nowhere far from the surface.

It might be thought that no vegetation would grow on pure gypsum sand, but there is a scattered growth, consisting of various shrubby and herbaceous plants. I even found a small poplar, which looked to me like *Populus tremuloides*, though not typical; the poplar of the surrounding country, at least of the Rio Grande Valley, across the mountains, is *P. fremontii*, never *P. tremuloides*, at so low a level. One of the commonest shrubby plants on the sands is a *Rhus*, while a *Bigelovia* grows to a considerable size. When, last autumn, I visited this locality with Prof. C. H. T. Townsend, I was able to collect a few plants and insects; and my companion went somewhat further than I did, with the result of collecting two species of bees in quantity, and some other insects, which I had missed. Unfortunately, I was anything but well at the time, and we could not delay more than a short while, so that what was obtained was a mere fragmentary sample of the actual fauna and flora of the sands.

T. D. A. COCKERELL.

MESILLA, N. M., Feb. 28, 1897.

pistil extending 2 or 3 mm. beyond the stamens, stigma round and thick, more than 2 mm. in diameter; ovary 4-toothed at summit; capsule fusiform, contracted under the spreading, 4-toothed, reddish summit, 4-ribbed, splitting into four valves to within 1 mm. of the base and connivent at the top, persistent and becoming woody; seeds dark brown, irregular in outline, becoming mucilaginous when moistened; one row in each cell.

This differs from typical *Œ. tubicula* chiefly in the very narrow leaves and a more condensed habit of growth, the slender branches becoming almost fasciculate. The peculiarities are probably due to poverty in the environment, which by slow starvation would bring about a reduction in the size and form of its organs.

Œnothera albicaulis gypsophila, var. nov.

PLATE VI, FIG. 2.

Stems woody, corymbosely branched, canescent throughout, with dense, closely appressed pubescence; leaves narrowly oblong to lanceolate, acute, 8–20 mm. long, 2–5 mm. wide, cuneate at base, margin sinuate-dentate, with 3 or 4 short teeth on each side, midrib conspicuous, petioles 2 mm. or less in length; flowers axillary, 3 cm. in diameter; calyx with tube 3 cm. long, slender, divisions 15 mm. long, united in one or two sets, free at the tips and bases; petals white, rhomboidal, as broad as long, narrowed at base to a broad claw, slightly wavy on the upper margin; stamens shorter than the petals, about equalling the style; capsule 3 cm. long, almost perpendicular to the stem, variously curved or even inclined to coil, splitting almost to the base into four narrow valves; seeds 1–2 mm. long, ovate-lanceolate, acute, obtusely angled, usually mottled with purple, minutely tuberculate.

The description and figure were drawn from specimens without roots. The older parts of the stems present a ragged appearance due to the shreddy epidermis and the narrow spreading valves of the empty capsules.

The desert environment is suggested by stiff, dry stems, close branches and leaves, and rapid development of the fruit. The flowers show but little tendency to become pink as they fade.

Œnothera albicaulis is a variable species, easily recognized amid all its forms. Its most constant and distinctive characters are the white, shreddy epidermis, the capsules sessile by a hard, broad base, spreading from the axis so strongly as to make the stem somewhat zig-zig, valves separating almost to the base and widely spreading.

This variety is nearest to § *trichocalyx* Engelmann,[1] which has been named *Anogra pallida Engelmanni* Small.[2] The description of this variety is meager, but the erect and numerous branches of my specimen do not suggest "parce ramosa," nor are the seeds obtuse, as stated on page 334, Am. Journ. Sci. (II), Vol. XXXIV, under *Œ. albicaulis*. The leaves approach those of var. *v brevifolia* in size.

The plate was made by tracing after a photograph. It has, therefore, greater accuracy than would be possible with an ordinary drawing. The flower, however, was drawn from a dried specimen soaked and spread so as to show its shape.

Bigelovia graveolens appendiculata, var. nov.

PLATE VI, FIG. 3.

Stems light green, slightly tomentose except at the densely tomentose leaf axils; leaves involute, becoming terete, mucronate; heads in rather few-flowered, corymbiform cymes on pedicels, often divaricately spreading; bracts of the involucre carinate, ciliate, and scarious on the margins, obtuse or acute at the woolly apex; corolla with from one to four yellow, linear appendages of various lengths on the tube, and a few cobwebby hairs on the border.

This differs from all other forms of this variable species in the peculiar appendages of the corolla-tube. They are not transformed pappus bristles, being too far up on the tube, rather appearing like an outside corolla, as if the corolla were trying to become double. In other respects it approaches var. *hololeuca* Gray.

Thelesperma gracile *Gray.*

Bidens gracilis, TORREY, Ann. Lyc. N. Y., Vol. II, p. 215.

Habitat.—On the Canadian River.

The fragmentary specimen from the "White Sands" shows but little variation from the type; the heads are smaller than those of any of the species represented in the Herbarium of the California Academy of Sciences.

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[1] Am. Journ. Sci. (II), Vol. XXXIV, p. 335.

[2] Torr. Bull., Vol. XXIII, p. 176.

Muhlenbergia pungens *Thurber.*[1]

This is, according to C. J. Croft,[2] a valuable forage plant, and is known in Arizona as Black Grama and Grama China.

It was determined by Prof. Scribner, who reports it as "without unusual characters or special peculiarities."

There is also a branch of a shrubby Labiate, whose leaves in form and flavor suggest an *Audibertia;* but as it is without flowers or fruit, it cannot be identified.

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[1] Proc. Phil. Acad. Sci., 1863, p. 78.

[2] Proc. Cal. Acad. Sci. (I), Vol. III, p. 205.

II.—ON SPURLESS FORMS OF AQUILEGIA.

Aquilegia differs from allied genera chiefly in having five spurred petals and a column of staminodia surrounding the pistils. In some species a tendency to degenerate from the markedly specialized type exists, and the varieties are characterized by spurless petals. These cause the flowers to superficially resemble those of *Isopyrum*, *Clematis*, or *Anemone*, more than *Aquilegia*.

Double-flowered forms of *Aquilegia* are quite common in some species under cultivation, the stamens either becoming distinctly petaloid with spurs, or, together with the petals, becoming sepaloid, flat, and destitute of spurs.

Aquilegia vulgaris, which is widely spread through Europe and has, probably, been more extensively cultivated than any other species, has several varieties with ecalcarate petals. Two are given in De Candolle's Prodromus, Vol. I, p. 50: *A. stellata*, with double flowers, petals flat, spurless, and colored; *A. degener*, with double flowers, petals and sepals flat, spurless, and green. These are both figured in Clusius' "Historia Rarorium Plantarum," according to De Candolle. In the "Index Kewensis" another variety, *A. ecalcarata*, is given, which the name indicates to be spurless; but it is regarded by horticulturists as identical with *A. stellata*.

The attention of the writer has been called to these peculiarities by the occurrence of two species in Colorado, which have ecalcarate varieties. The first of these belongs to *A. cærulea*.

Aquilegia cærulea Daileyæ, var. nov.

PLATE VII, FIG. 1.

This is in all respects similar to the type except that the spurs of the petals are entirely wanting, sepals and petals flat, blue.

The plate indicates the peculiarities of the variety. The plant figured was drawn from specimens sent me by Miss

Anna L. Dailey. They were collected at Evergreen, Colorado, where Miss Dailey noted them during several years. It was her opinion that the plants had become more numerous since she first noticed them.

Mr. George E. Osterhout of New Windsor, Colorado, reports this form as frequent in Estes Park, Colorado.

Some years ago, the writer found several plants with the spurless petals growing among the typical form in Platte Cañon, Colorado.

In the "Gardener's Chronicle," Vol. XVI, 1881, p. 16, the following note occurs concerning *A. cærulea:*

"Mr. E. G. Loder sends us a spurless flower of *Aquilegia cærulea* quite similar to the European stellate Columbines. The long, white, spurred petals are, in this case, absent and replaced by an additional whorl of ovate, acute, blue sepals. A few years since, Mr. Loder tells us he 'collected seeds of *A. cærulea* at an elevation of 10,300 feet, not far from South Park, Colorado.' The seeds were sown in Northamptonshire in 1879. A few plants flowered last summer; but this year they have flowered most abundantly and the individual flowers are quite as fine as in their native habitat. Among the seedlings, one plant bears white flowers and others spurless flowers."

Aquilegia micrantha Mancosana, var. nov.

This is the plant that was first described in "Zoe," Vol. II, 1891, p. 226, as *A. ecalcarata.* Afterwards it was redescribed and figured from better specimens in Proc. Cal. Acad. Sci., Ser. 2, Vol. IV, p. 261. It is without doubt merely a degenerate variety of *A. micrantha,* which is extremely variable in both flowers and foliage, as I have indicated in Proc. Cal. Acad. Sci., Ser. 2, Vol. VI, p. 280.

It seems desirable to give this a more distinctive varietal name, so I take this opportunity and name it after the region where it occurs.

To Dr. B. L. Robinson, I am much indebted for the looking up of some references to which I had not access.

III.—THREE UNDESCRIBED CALIFORNIAN PLANTS.

Iris Purdyi, sp. nov.

PLATE VII, FIG. 2.

Rootstocks slender, scarcely thicker than the fleshy roots; leaves dark green or somewhat glaucous, glabrous, erect or laxly spreading, surpassing the scapes, 6–7 mm. wide, 2–4 dm. long, with long, acuminate apex and margins membranous and shortly ciliate, scapes 15–20 cm. long, slightly flattened; bracts generally overlapping, inflated, glaucous, striate, tinged with rose-color, acuminate; spathes usually 2-flowered, similar to the bracts, but more inflated and more rosy, especially on the margins; pedicels 1 cm. long, about equaling the tube of the perianth; perianth with throat slightly dilated above the junction of the style; outer segments oblong, 7 cm. long, 2 cm. wide, rich cream-color, beautifully marked with fine lines of yellow on the claw, and with dotted veins of purple on the spreading blades; inner segments cream-color, somewhat shorter than the outer, widely spreading, linear-oblong, with margins strongly sinuate; stamens with filaments 5 mm. long, 2 mm. broad, narrowing abruptly at the insertion of the anthers; anthers 15–18 mm. long, 3 mm. wide, the polliniferous margins less than 1 mm. wide, edged on each side with purple; style slender, 12–15 mm. long, stigmas about 4 cm. long, including the crests, which are 1½ cm. long, laciniate on the outer edge, tinted with pale rose-color to the ridge connecting the lobes of the stigma; stigma scale truncate, slightly undulate; capsules oblong, tapering equally at both extremities, valves about 12 mm. wide and 3 cm. long.

This elegant *Iris* is the species common in the Redwood region of Mendocino County, around Ukiah. It has heretofore been included under *I. Douglasiana*, which it resembles in its narrow, red-based, laxly spreading leaves, its cream-colored flowers, and its habitat. *I. Douglasiana* has always been considered an extremely variable species and includes a great number of forms, some of which may prove, as this had done, when carefully studied and compared, to be distinct species.

Iris Purdyi differs from other Californian species of *Iris* in the peculiar bract-clothed, flowering stems. From *I. Douglasiana* it differs in having larger flowers, leaves lighter green, less distinctly nerved, somewhat stiffer, and sometimes glaucous. The stigma scale is truncate instead of triangular-acuminate. The stamens are much broader, the capsule shorter, broader, and more uniform at each extremity. The flowers are fewer in the spathes, less exserted, and on shorter pedicels that elongate but little in age. It forms clumps similar to *I. Douglasiana*, but not so widely spreading.

It is most fitting to name this species in honor of Carl Purdy of Ukiah, since he first detected its identity as a species entirely distinct from *I. Douglasiana* and called attention to its peculiar characteristics.

Montia rosulata, sp. nov.

Plate VII, Fig. 3.

Annual, stems and leaves forming a compact, thick rosette, glaucescent, succulent; radical leaves terete or spatulate, 1–2 cm. long, 2–5 mm. wide; cauline leaves ovate-lanceolate, amplexicaul, 1–2 cm. long, 4–6 mm. wide; inflorescence almost concealed by the leaves, umbellate at first, becoming racemose, each cluster on a short, thick peduncle, subtended by a single lanceolate bract; flowers small, 3–4 mm. in diameter; petals white, unguiculate, oblong-obcordate; stamens with purple anthers on short filaments; capsule inclosed in the calyx, opening by three valves that become involute and acuminate; seeds three, black, glossy, almost 2 mm. long and 1½ mm. wide, minutely papillose, especially near the edge; strophiole white, conspicuous without the lens.

The seeds ripen rapidly and are shot to a distance of two or three feet by the elasticity of the valves. The empty valves form a 3-pointed star within the calyx. The flowers are ephemeral and the buds do not open in the house.

This species belongs to the group of which *M. perfoliata* Howell is the most common, and is intermediate between that species and *M. saxosa* Brandegee. It approaches the latter most closely, from which it differs in longer and narrower leaves, smaller flowers, fruits, and seeds, and less succulence and density of foliage.

The only locality at present known is on Mt. Tamalpais, where it was collected by the writer twice this year, on April 11th and 20th. On the trail to the Lone Tree, not far from Rock Spring, there is an outcrop of volcanic rock whitened by long exposure to the elements, and here only these little rosettes of flowers and leaves are to be found, scattered around but not abundant, and in a limited area of a few rods.

Newberrya subterranea, sp. nov.

PLATE VII, FIG. 4.

Stem brown, covered with broad, ovate or orbicular scales, which broaden as the stem becomes bulbous towards the inflorescence; scales surrounding the flowers becoming oblong-lanceolate, acuminate; flowers sessile on a disk-like receptacle 15 mm. in diameter; sepals of two brown, linear-lanceolate scales equalling the corolla, and two white membranous scales variable in length; corolla 1 cm. long, the four or five divisions as long as the tube, 2 mm. broad, oblong, obtuse, or emarginate, ribbed, densely hairy within, sparingly so externally, with ciliate margins; filaments varying in length, densely clothed with long hairs under the anther, sparsely hairy below, equalling or slightly surpassing the ovary. Anthers 2-celled, the half of each cell only polliniferous, ovate-elliptical; style thick, elongating with age, very hairy under the depressed, capitate stigma.

The snow-white flowers contrast beautifully with the dark brown scales and stem. In the plant from which the description is drawn, the middle flower is on the plan of five, while all the others are on the plan of four. This seems nearest to *Hemitomes pumilum* Greene, Erythea, Vol. II, p. 121.

It was communicated by Mr. R. A. Plaskett of Mansfield, Monterey County. He reports that he found it in bloom three inches below the surface of the ground,[1] growing in Willow Creek Cañon, under *Quercus densiflora*. This is the third plant that he has found under such unusual conditions, the other two having been lost before they could be sent. They all grew within a radius of forty feet and were from three to eight inches below the surface of the ground.

The genus *Newberrya* has heretofore been found only in Oregon and Northern California. The discovery of this interesting species extends its distribution from Mendocino County to the southern extremity of Monterey County. Willow Creek is not far from the southern limit of the redwoods and abounds in the vegetation peculiar to the Redwood Region; so that the conditions are quite similar to those under which the northern species flourish, and it is, therefore, really not surprising to find this northern genus here.

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[1] Leaf-mould 1 to 1½ inches; loam, or black soil, 3 inches; subsoil of coarse, loose, and mouldy nature, light-colored and very gravelly; on north hill-side, under heavy timber (Tanbark Oak and Redwood), where the sun never shines.—R. A. PLASKETT.

IV.—THE MANZANITAS OF MT. TAMALPAIS.

Across the Golden Gate from San Francisco lie the picturesque hills of Marin County. These reach their highest point on Mt. Tamalpais, which rises to an altitude of 2604 feet. The rocky slopes of this interesting mountain are densely clothed with a shrubby vegetation, except in some spots where a bluish gray volcanic rock becomes exposed. The chief shrubs are *Pickeringia montana*, *Eriodictyon glutinosum*, *Castanopsis chrysophylla*, *Adenostoma fasciculata*, several species of *Quercus* and *Ceanothus*, *Umbellularia Californica*, *Vaccinium ovatum*, and the different kinds of *Arctostaphylos* or Manzanita.

Of these manzanitas, there are at least four forms that appear quite different from each other; but the amount of variation is so great among some of them, and with one exception they are so different from all forms definitely described, that their identification is a puzzle that has been engaging the attention of the writer for more than a year on frequent trips to the mountain, at all seasons and over its many trails. If the manzanitas in other sections of California present as many variations as these on Mt. Tamalpais, it will be many years before the genus *Arctostaphylos* is understood, and then, probably, the results will be secured only through systematic cultivation of the various forms in Botanic Gardens. A beginning is already made in the Botanic Garden of the University of California, where several species are now growing.

The inadequacy of printed descriptions and the impossibility of deciding, without the types for comparison, to which species some of the Mt. Tamalpais forms are most closely allied, makes it seem necessary to describe and name each form, that seems undescribed, as a distinct species, leaving to the future monographer of the genus the task of assigning definite limits, if that be possible in so polymorphous a genus, which continually suggests hybridization or a very active and unlimited tendency to vary.

Arctostaphylos nummularia *Gray.*

This is distinct and can not be mistaken for any other species. It is in bloom at some place on the mountain throughout the year. It rarely grows amid dense brush, seeming to prefer somewhat exposed situations, and usually attains a height of about two feet, seldom more than four. It is quite common and always conspicuous, with young stems erect and slender, invested with a halo of white hairs, flowers small and very abundant, and leaves round and shining. The fruit, which is flattened longitudinally and without the mealy pulp of other manzanitas, differing also in the deciduous pericarp, which at maturity leaves the nutlets naked, sets this apart from all other species and renders the name of manzanita, or little apple, inappropriate when applied to this species.

Arctostaphylos glandulosa, sp. nov.

Shrubby, never arborescent, 2–8 feet high, young branches straight and erect, older ones divaricate; young shoots glandular-hirsute, with long and short spreading hairs; leaves erect on short petioles, oval to ovate-lanceolate, mucronate, thin, bright green, or sometimes thicker and inclined to be glaucous, sometimes spinulose-dentate even on flowering stems, an inch or two long, usually glandular-pubescent and glutinous; older stems smooth, dark brownish red, with thicker leaves, inclined to be orbicular, often glaucous, and without glandular hairs; racemes usually few in the panicles, loosely or densely flowered; bracts glandular, persistent, lanceolate-acuminate, green and foliaceous below, usually longer than the pedicels, shorter, often rose-colored and petaloideous above; sepals orbicular, glandular-ciliate, white, membranous, stellately spreading after anthesis, often revolute; corolla large, glabrous externally, hairy within, white or pinkish; stamens with filaments densely bearded but not glandular; style shorter than or equalling the corolla; ovary flattened horizontally, densely covered with white hairs more or less tipped with rose-colored or white glands; fruit spherical, horizontally flattened, transverse diameter about 1 cm., vertical diameter 5–7 mm. The immature but fully grown fruit is often tinged with red on one side; when ripe it becomes reddish brown, with the mealy pulp quite abundant. Sometimes it has a purplish bloom, and is generally slightly hairy and glandular. The pyrenæ are variously coalescent and frequently united into one.

This is the manzanita earliest in bloom on the mountain, the most beautiful, the most fragrant, most variable, and most widely spread. On the upper slopes and towards the ocean, the most glandular specimens are to be found; while on the Mill Valley Trail, the hills near Larkspur, and those above the reservoir of the San Rafael Water Company (localities somewhat protected from the ocean winds), it becomes almost glabrous except on the pedicels, the ovary, and the young growth, where some glandular hairs are always evident. When fresh shoots spring up where a fire has formerly swept over the mountain, they appear so different from the most common form as to suggest, at least, a good variety. The young leaves are often a bright red, appearing like a brilliant flower from a distance. Usually they are green, and often tinged with red, especially on the margins.

This species has been included under *A. tomentosa*, but its peculiar characteristics have been ignored in all descriptions of that species. In some of its features it resembles *A. Pringlei*, which was also formerly included under *A. tomentosa*. It resembles *A. tomentosa* in the shape and arrangement of the leaves and the erect tendency of the branches. The long, loose, woolly hairs so noticeable on young stems of *A. tomentosa* are in this species replaced by shorter and usually glandular hairs. The ovary and fruit are glandular and this, according to the various descriptions, is never the case with *A. tomentosa*. The glandulosity is so pronounced in typical specimens of this species that the leaves feel gummy when touched, and stick to each other if placed together. When drying, they are very fragrant.

While this species somewhat resembles *A. Pringlei* in the character of its pubescence, it differs from it in the shape and texture of the leaves, the persistent bracts, and the flattened instead of conical ovary.

Arctostaphylos montana, sp. nov.

Shrubby, widely spreading, young branchlets usually erect; lower stems glabrous, dark reddish brown; upper stems canescent, with a dense covering of short curly hairs; leaves venulose, minutely punctate, oval, 1–2 cm. long, with narrow cartilaginous margins and prominent mucro, canescent when young, becoming glabrous and glossy when old; petioles stout, 2 mm. long, pubescent, with minute blackish glands intermingled; panicles short, on rather stout peduncles; pedicels white, slender, glabrous, 5 mm. long; bracts short, 2-3 mm. long, canescent at base and minutely glandular, the apex brown, triangular-acuminate, deciduous; sepals green at base, thin and white above, involute, surrounding the ovary after anthesis; corolla small, 5 mm. long, with roundish, reflexed, ciliate lobes, externally glabrous, hairy within; filaments dilated at base, glabrous; ovary glabrous or slightly pubescent, conical; ripe berries glossy, reddish brown, variable in size and shape, 5-10 mm. in diameter, spherical or flattened either longitudinally or transversely, the pyrenæ either separable or coalescent into one, and extremely variable in shape; pulp thin.

This appears to be nearest to *A. Hookeri*, from which it is chiefly distinguished by thicker, less veiny leaves, shorter and stouter petioles, shorter bracts and longer pedicels, and much thinner pulp. This manzanita loves the exposed ridges, where the bluish gray volcanic rock crops out, and is usually found associated with *Quercus dumosa* var. *bullata*. The description was drawn from specimens collected near the cypress trees on the trail between the Eldridge Grade and Larsen's. It is abundant there, forming low, spreading bushes not more than three feet in height. It is also found around the reservoirs of the San Rafael Water Company and along the road from Fairfax to Larsen's. It is the last species in bloom, not coming into flower before April. The fruit is ripe in September or October and persistent for some time after ripening. The new growth is made after the flowering period, the canescent leaves and stems being very conspicuous contrasted with the dark green, glossy, older foliage.

Arctostaphylos canescens, sp. nov.

Shrubby, forming erect or low, spreading bushes, densely clothed throughout with short white curly hairs, with minute blackish glands intermingled on the stem, petioles, pedicels, bracts, and lower surfaces of the leaves; leaves oval, ovate, or obovate, shortly acuminate, mucronate, about 3 cm. long, 1½ cm. wide, on stout petioles 5 mm. long; racemes few or solitary, almost condensed into corymbs, with persistent foliaceous bracts 5-12 mm. long, surpassing the stout pedicels, red-nerved and margined or rosy throughout; sepals oval, white or rose-color, ciliate, densely hairy within, usually sparsely hairy externally, revolute, spreading after anthesis; corolla 7 mm.

long, with short, orbicular lobes, glabrous externally, hairy within, white or tinged with pink; stamens with filaments somewhat bearded; ovary densely covered with white hairs, but not glandular, slightly rounded at top; style a little longer than the stamens; fruit similar to that of *A. glandulosa.*

This manzanita, while very different in appearance from either *A. glandulosa* or *A. montana*, has some characteristics of both. The condensed raceme and the pubescence are similar to those of *A. montana*, the pubescence being that of the young growth of *A. montana;* while the size and shape of the flowers, the foliaceous bracts and stout pedicels resemble those of *A. glandulosa.* The fruit, also, is large and with abundant pulp.

It fruits sparingly. Its season of blooming is earlier than that of *A. montana*, but generally not so early as that of the first blooming bushes of *A. glandulosa.*

The bushes from which the description is drawn grow on the trail from the Eldridge Grade to Larsen's, and are to be found between the last bunch of cypresses and the Rock Spring. They are close to the trail and conspicuous in contrast with the bright green, very glandular specimens of *A. glandulosa* in the immediate vicinity. It is abundant on a trail recently cut from West Point to Rock Spring. Professor W. R. Dudley of Stanford University has sent me specimens of the same species from above Felton and from Loma Prieta in the Santa Cruz Mountains.

EXPLANATION OF PLATE VI.

Fig. 1. *Œnothera tubicula filifolia*, var. nov.

a. Longitudinal section of the calyx, showing pistil and stamens.

b. Node of the stem magnified to show leaves and pubescence.

c. Ripe capsule, actual size.

Fig. 2. *Œnothera albicaulis gypsophila*, var. nov.

Fig. 3. *Bigelovia graveolens appendiculata*, var. nov.

a. Flower magnified, showing corolla appendages, etc.

b. Capitula magnified, showing involucre, flowers, etc.

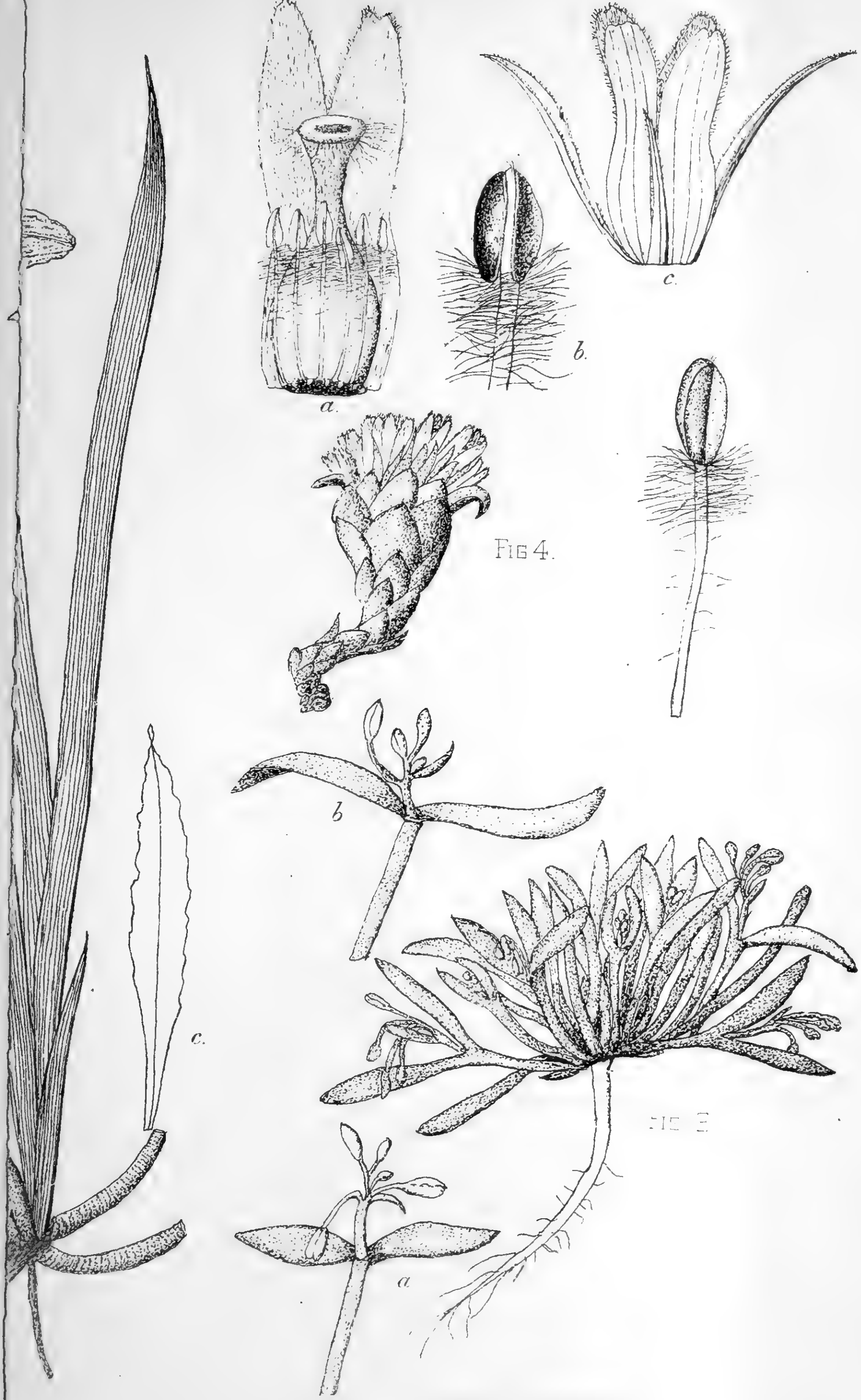
FIG. 2

[illegible]


Fig. 2

EXPLANATION OF PLATE VII.

Fig. 1. *Aquilegia cærulea Daileyæ*, var. nov.
  a. Node of the stem showing a leaf.
Fig. 2. *Iris Purdyi*, sp. nov.
  a. Inner side of one of the stigmas.
  b. Outer view of the above showing the stamen and stigma scale.
  c. One of the inner divisions of the perianth.
  d. One side of the three-sided capsule.
Fig. 3. *Montia rosulata*, sp. nov.
  a. and *b.* Flowering stems.
Fig. 4. *Newberrya subterranea*, sp. nov.
  a. Longitudinal section of flower magnified.
  b. Inner side of an anther magnified.
  c. Outer view of flower magnified.
  d. Side view of stamen showing the empty anther cell.



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STUDIES IN THE HERBARIUM AND THE FIELD.—No. 2.

BY ALICE EASTWOOD,

Curator of the Herbarium.

CONTENTS.

PLATES VIII–XI.

I.—NOTES ON THE PLANTS OF SAN NICOLAS ISLAND.

The plants upon which this report is based were collected in April, 1897, by Mrs. Blanche Trask. It is the first collection from this island of which any record has been made, and like all insular floras possesses peculiar interest.

Among the eighty or more species, nine are described as new species, three as new varieties. There are besides six insular types, though almost all the species are well represented on the other islands of the Archipelago as well as on the mainland. At least fifteen have been introduced, being plants of wide distribution and generally recognized as weeds. It is somewhat surprising to find *Rumex acetosella*, *Polygonum aviculare*, and *Erigeron Canadensis* absent from the list.

Under each species is given its distribution on the other islands, this information having been obtained from the

Sept. 5, 1898.

Herbarium of the Academy and from the list published in "Zoe," Vol. I, p. 129, in an article by T. S. Brandegee on "The Flora of the Californian Islands." The islands given are San Miguel, Santa Rosa, Santa Cruz, Santa Catalina and San Clemente. At the end is given a table similar to that in "Zoe," and a summary.

The following interesting account of San Nicolas has been copied from the report of Dr. Stephen Bowers, issued in the Ninth Annual Report of the State Mineralogist (1889, page 57):—

"San Nicolas Island belongs to Ventura County. It is nearly eighty miles south of the town of Ventura, the southeastern end being in latitude 33°, 14′ north and longitude 119°, 25′ west from Greenwich.

"The island is about nine miles long and four miles wide, containing 32.2 square miles, or twenty-thousand six hundred and eight acres. Its longer axis is northwest by west.

* * * * * *

"There is an abundance of water on the island but it is slightly brackish.

"San Nicolas is entirely destitute of timber, but evidently has not always been so. At the present time there is not even a bush growing on it except a stunted kind of thorn, scarcely two feet high, and a few species of the tree cactus.

* * * * * *

"Nearly all round the island, the shore-line is steep and about fifty feet high, from which the ground gradually rises in a sort of mesa or table-land, say one hundred to five hundred yards wide and terminates in a steep escarpment, which reaches an altitude of from five hundred to eight hundred feet. The high land is about seven by three miles in extent and sufficiently level to till. Much of it contains what appears to be good soil and ought to yield abundant crops if brought under cultivation. There are but few exposures of rock on the elevated portion of the island excepting near the upper termination of the escarpment mentioned, where they have been denuded by wind and rain. In a few places the sand-stone is capped with limestone bleached to chalky whiteness. Patches of small water-worn bowlders and pebbles of quartzite, porphyry, etc., are occasionally met with on the table-land. The escarpment is most abrupt on the south side of the island and in some cases is washed into picturesque cañons. The western end of the island is exposed to westerly winds which often blow for many days without intermission; as a result one meets with many sand dunes, with an occasional outcropping of shell heaps which have resisted the wind's force. In many places may be seen impressions or casts of roots of trees, ranging in size from coarse fibers to several inches in diameter. The loose soil and sand have been blown from around them leaving the casts of semi-petrifactions intact. They are so hard as to sound metallic when thrown on the ground or when struck with a hard substance. In other places thousands of columns of indurated sand, ranging in height from a few inches to several feet, may be seen. At a distance they look like stumps of small trees.

* * * * * *

"The only animals found on San Nicolas are a small fox, a kangaroo mouse, and a diminutive sand lizard. * * Seals, sea-lions, and other varieties of *Phocæ* are still found here but in limited numbers. In this connection, I may speak of the remains of two species of dogs found all over the island. One of them, which seems to have resembled the bull-terrier, is probably a distinct species, and, if I mistake not, was identified by Professor Baird. It was domesticated by the Indians, and found living here as late as 1853. * * * * * * * * * * *

"Several species of land birds are found. Amongst them may be mentioned the bald eagle, ground owl, raven, crow, and plover. Water fowl are abundant. * * *

"A noticeable feature of this island is the vast number of dead land shells strewn over the surface. * * *

"They are almost as numerous as the grains of sand driven before the wind, but not a living specimen is to be found. When they flourished there was vegetation on the island sufficient to support them, and their large size and vast numbers indicate anything but the arid waste that the surface now presents.

"Mr. Nidever speaks of a portion of the island covered forty years ago with trees, brush, and moss.

* * * * * *

"San Nicolas Island must have once supported a large population. In whatever direction one turns, he comes in contact with human skeletons, broken mortars, pestles, ollas, bone implements, ornaments, etc., and shell heaps."

The entire description is full of interesting facts, the account of the fossils being especially good. Dr. Bowers estimates that about two-thirds of the island is cultivable, the soil being apparently rich and fertile and the surface comparatively level.

Mrs. Trask to whom I sent Dr. Bowers' account finds conditions somewhat different now. This is what she writes: "I do not wholly agree with Dr. Bowers' account. There is no soil on the broad level top; but tons of pebbles, round as shot and of a like size. Even here the ice-plants flourish and an occasional gay patch of *Hordeum* or fox-tail is seen. Everywhere the rocks are visible and the soil thin.

"There are three routes which can be followed entirely around the island; one over the reefs, another on a flat or mesa, a third on the comparatively level top.

"The cañons are not what we usually call cañons; arroya is a fitter term. In them we hear no sound of bird, no whirr of wing; we see no bright flowers, only the ice-plants. There is no ripple of stream, only the briny tidal waters which glide but do not flow and gliding sink. Many a cañon, monster-capped and sculptured by sand and wind, is literally snowed-in by vast banks of sand. These are exquisitely marked by the action of the wind, as are the snow banks of colder climes.

"The shell heaps and rancherias are chiefly at the West End, thousands of them, while at the East End there may be a half dozen. One may tramp for miles at the West End upon nothing but shell sand, gathering bone implements, abalone ornaments, and other relics of the former inhabitants. The reason of the signs of habitation being concentrated at the West End is evident; there the fresh water drips from the rocks above the reefs, while no water is found at the East End, though Dr. Bowers says that there was an abundance of water on the island when he visited it. A tiny lake fringed with *Eleocharis* surprised me one day; near by were found *Lupinus micranthus*, several clovers, *Pectocarya* and *Orthocarpus*.

"In all the kitchen middens large heaps of charcoal yet remain. Great mortars, too heavy for a white man to lift, are found on the highest peaks, miles from fresh water; yet water they must have had near by.

"It is said that forty years ago the little harbor where we landed, known as Corral Harbor, was filled with sand—now, our schooner anchored in the surf outside, we took the waves at just the right moment, shooting in between the reefs where there was barely room, and entering the sand-bound bit of a key inside. I have seen seven breakers twenty feet high, without a lull, plunging in over the reefs into this same Corral Harbor. 'Harbor?' you say as you stand watching them.

"Another landing place is marked 'Anchorage' on the sea charts, situated near the sand spit on the south side; but there, a run has to be made through the breakers which are often so heavy that landing is impossible.

"Day after day, there is the cry of the gull and shag, the voice of otter and seal, the boom of the heavy surf, and the wind and fog and sand toiling on at their unending tasks."

GRAMINEÆ.

I am indebted to the great kindness of Dr. F. Lamson Scribner, Chief of the Division of Agrostology, U. S. Department of Agriculture, for the identification of these grasses.

1. **Bromus Trinii** *Desv.*

Trisetum barbatum STEUD.

Reported under the latter name from Santa Cruz Island. Found growing on San Nicolas in one locality, about *Opuntia Engelmanni.*

2. **Bromus Hookerianus** *Thurb.*—Reported from all the islands except San Miguel. On San Nicolas found growing about *Opuntia* and on a flat at about 100 ft. elevation.

3. **Bromus virens** *Nutt.*—This species has not before been reported from the islands. It also was found growing about *Opuntia.*

4. **Cynodon Dactylon** *Pers.*—This is the first record from the islands. It grew on a height above the brackish stream.

5. **Stipa setigera** *Presl.*—Reported from all the islands except San Miguel. On San Nicolas it was found in one locality, about *Opuntia.*

6. **Stipa robusta** *Vasey.*—The first record from the islands, growing in one locality, about *Opuntia.*

7. **Hordeum murinum** *L.*—Reported from Santa Rosa, Santa Cruz, and Santa Catalina. On San Nicolas it was found in fertile spots amid sand, at an elevation of 800 to 1000 ft.

8. **Avena barbata** *L.*—This is the first record from the islands. It also was found only about *Opuntia.*

9. **Phalaris Canariensis** *L.*—Reported from all the islands except Santa Rosa. This grew in one locality, a fertile flat 100 ft. above the sea.

10. **Distichlis spicata** (*L.*)—As *D. maritima*, this has been reported from all the islands except San Clemente. It grew only in the sand spit region.

11. **Polypogon Monspeliensis** *Desv.*—Reported from all the islands except San Clemente. Found growing in sand-swept arroyas.

CYPERACEÆ.

12. **Eleocharis** (probably *E. palustris* R. BR.)—This was collected on the borders of a small lake at 1000 ft. elevation.

LILIACEÆ.

13. **Brodiæa capitata** *Benth.*, Pl. Hartweg., p. 339, "In sylvis, prope Monterey."

Found on all the islands; infrequent on San Nicolas, in one locality, on a slope.

URTICACEÆ.

14. **Parietaria debilis** *Forster*, Weddell, DC. Prodr., Tome XVI, p. 235^{45}.

Reported from all the islands except San Miguel; found in one locality on San Nicolas in a clump of *Opuntia Engelmanni*.

CHENOPODIACEÆ.

15. **Chenopodium Californicum** *Wats.*, Bot. Cal., Vol. II, p. 48.—First mentioned by Moquin in DC. Prodr., Tome XIII^2, p. 74, as variety "? *hastatum*" of *C. anthelminticum*. "In California."

Reported from all the islands except Santa Rosa. On San Nicolas found only about *Opuntia* which occurs sparingly.

16. **Chenopodium murale** *L.*, Sp. Pl., p. 219, "In Europæ muris aggeribusque."

Reported from San Miguel, Santa Cruz, and Santa Catalina.

17. **Atriplex Californicum** *Moq.*, DC. Prodr., Tome XIII ^{2}, p. 98, "California, Coulter."

Reported from San Miguel, Santa Cruz, Santa Catalina, San Clemente. Mrs. Trask found this growing on the beach. Different plants varied greatly in size. The specimen from which the determination is made is larger in all its parts than any specimen in the Herbarium of the Academy. The leaves and other parts are less hoary.

18. **Atriplex decumbens** *Wats.*, Proc. Am. Acad., Vol. XII, p. 275, "near San Diego."

The plants from San Nicolas are too young for certainty. The species has been reported from Santa Catalina. On San Nicolas it grew on seashore sands.

19. **Suæda.**—Two species of this seem to have been collected, but the specimens are too young for determination. One resembles *S. Californica* Wats. *S. Torreyana* is the species reported from the other islands, but the plant from Santa Rosa Island, so labelled in the Herbarium of the Academy, is more like *S. Californica.* This is also true of one recently sent from Santa Catalina by Mrs. Trask.

20. **Aphanisma blitoides** *Nutt.*, Moq. in DC. Prodr., Tome XIII ^{2}, p. 54, "near San Diego."

This has rarely been collected. Besides the type locality it has been found on San Clemente and San Pedro (near Los Angeles). On San Nicolas it grew only at the foot of *Leptosyne gigantea.*

NYCTAGINACEÆ.

21. **Abronia maritima** *Nutt.*, in Herb. Bot. Cal., Vol. II, p. 4.—"On the sea coast, from Santa Barbara to San Diego."

Reported from San Miguel, Santa Cruz and Santa Catalina. Mrs. Trask records it on San Nicolas as "covering vast numbers of sand-mounds, the bright red flowers conspicuous."

22. **Abronia umbellata** *Lam.*—This is doubtful as the material is insufficient, the specimen being too young. Reported from all the islands except Santa Catalina. On San Nicolas it covered vast areas of drifted sands. Leaves shining, flowers red and fragrant.

23. **Abronia alba,** sp. nov.

Plate VIII, Figs. 4*a* and 4*b*.

Viscid-pubescent; stems brittle, prostrate or ascending; leaves orbicular to broadly ovate, obtuse, cuneate at base, sinuate, 1–3 cm. long, 10–16 mm. wide, with petioles equalling or longer than the blades; heads on slender peduncles 5–7 cm. long, about 12-flowered, with small involucre consisting of five thin, ovate, acute bracts 4 mm. long, 2 mm. wide; perianth white, very fragrant, with glandular, hirsute tube about 1 cm. long, and a border 6 mm. in diameter, of five divisions, each with two lobes, resembling rabbit's ears; fruit with ligneous body, at first rhomboidal in outline, becoming cuneate, more or less acuminate at apex, with four unequal wings, each 2 or 3 mm. wide above, narrowed to the base.

This belongs to § I. *Abronia* of the Bot. Cal.

It grew in sandy lowlands along the beach, but never on the sand-hills nor the true beach sands as do the other species. It was also less abundant.

CARYOPHYLLACEÆ.

24. **Silene Gallica** *L.*, Sp. Pl., Vol. I, p. 417. "Habitat in Gallia."

Reported from all the islands except San Clemente. On San Nicolas it was seen in one locality, a cliff overhanging a brackish stream.

25. **Spergularia macrotheca** *Heynh.*, Nom., Vol. II, p. 689; Robinson, Proc. Am. Acad., Vol. XXIX, p. 310.

Reported from all the islands as *Tissa macrotheca* Britt. The San Nicolas plant agrees with the form common on the Coast. It was collected on the beach.

PAPAVERACEÆ.

26. **Platystemon Californicus** *Benth.*, Trans. Hort. Soc., N. S., Vol. 1, p. 405. (Index Kewen.)

Reported from all the islands. On San Nicolas it covered sand-flats by the sea.

CRUCIFERÆ.

27. **Lepidium bipinnatifidum** *Desv.*, Journ. Bot., Vol. III, p. 165. (Index Kewen.)

This is the *L. Menziesii* reported from Santa Cruz Island. The San Nicolas plant is more loosely leaved and branched than the plant common around San Francisco, along roadsides. It was found in one locality, on a slope.

28. **Lepidium nitidum** *Nutt.*, Torr. & Gr., Fl., Vol. I, p. 116, "near Santa Barbara, Upper California."

Reported from Santa Catalina, San Clemente, Santa Cruz. The pods in these specimens are dull instead of shining as is usual with this species. Mrs. Trask found a few single individuals in two or three localities.

29. **Dithyrea Californica** *Harv.*, var. **maritima** Davidson. First described as *Biscutella Californica*, var. *maritima* Davidson, "Erythea," Vol. II, p. 179. "Sand dunes of Coast, Los Angeles County."

This is the first record of the above species or variety from the Coast Islands. Mrs. Trask collected it in "Kitchen Middens" in one locality. There were few individuals. The flowers are white tinged with pink, purple, or rose red.

RESEDACEÆ.

30. **Oligomeris glaucescens** *Cambess.* in Jacquem. Voy., Bot., Tome XXIV, T. 25. (Index Kewen.)

Oligomeris subulata WEBB, Fragm. Fl. Æthiop., p. 26 and Boiss. Fl. Orient, Vol. I, p. 435. (Index Kewen.)

As *O. subulata* it has been reported from all the islands except Santa Rosa. There are specimens from Guadalupe Island in the Herbarium of the Academy collected by Dr. F. Franceschi. On San Nicolas it was frequent, found on dry cliffs overhanging arroyas.

LEGUMINOSÆ.

31. **Lupinus micranthus** *Dougl.*, Bot. Reg., T. 1251.
This has been reported only from Santa Rosa and Santa Catalina. On San Nicolas, it grew on the borders of the small lake, 1000 ft. above the sea. The flowers are bluish white with black dots. This is similar to *L. micranthus* as defined by Watson, Greene, and others. Professor Greene has raised a doubt as to whether this common Californian plant is the true *L. micranthus.* Agardh's description, in Synopsis Gen. Lupini, page 14, drawn from Douglas' specimen in Herb. Lindl., differs first in respect to the leaves, which are said to be glabrous above, spreading pilose below, while this has leaves pilose on both surfaces; secondly in the seeds, which in Lindley's specimen were one colored, while these are mottled with brown. In Hook. Fl. Bor., Vol 1, p. 162, the following quotation from Douglas occurs: "It has much affinity with *L. bicolor*, differing in flowering from 4–6 weeks earlier, in being more slender, in the shortness of its alæ, its nearly sessile flowers, fleshy leaves, granulated roots, larger pods, and the color and size of the seeds." The leaves of the commonly accepted *L. micranthus* can scarcely be called fleshy.

32. **Lupinus albifrons** *Benth.*, Trans. Hort. Soc., N. S., Vol. I, p. 440.

The original description of this species is not available. That of Agardh,[1] drawn from Douglas' specimens in Lindley's Herbarium, agrees with this in almost all particulars. In Douglas' specimens, the bracts are said to be shorter than the flowers and the raceme is described as short. This has bracts surpassing the flowers in the bud, deciduous when the flowers are in full bloom, while the raceme is nearly a foot long. Mrs. Trask reports this as infrequent on San Nicolas, growing on bare stretches of sand; flowers bright blue. It is probably included under *L. Chamissonis* from San Miguel, Santa Rosa, Santa Cruz, and Santa Catalina.

33. **Trifolium microdon** *H. & A.*, var. **pilosum**, var. nov.

Entire plant, especially the young parts, pilose with soft, white, curly hairs; involucre wooly both interiorly and exteriorly, with the teeth of the divisions almost equal, entirely without the long middle tooth of the typical form; calyx viscid, but free from pubescence. The surfaces of the leaves are sparsely pilose. The plant is less robust and has smaller heads and flowers than the common form.

This was compared with the description and figure in Bot. Beech, p. 330, T. 79. *T. microdon* has been reported from Santa Cruz Island and collected on Santa Catalina by Mrs. Trask.

As represented in the Herbarium of the Academy, this species is variable. The specimen most nearly like this is one from near Tennessee Cove, Marin Co., Calif., collected by the writer. This variety was collected in two localities on moist slopes.

34. **Trifolium gracilentum** *T. & G.*, Fl., Vol., I, p. 316. "California, Douglas."

Not reported from the islands, but collected on Santa Catalina by Mrs. Trask. On San Nicolas two forms were

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[1] Syn. Gen. Lupini, p. 33.

found: one with purplish flowers and with each leaf marked with an inverted V-shaped white spot that disappears when the plant is dried; the other with whitish flowers and a more robust habit of growth.

35. **Trifolium stenophyllum** *Nutt.*, Journ. Phila. Acad., N. S., Vol. I, p. 151. "Island of Santa Catalina and San Pedro."

This is the true *T. stenophyllum* of Nuttall. It differs from *T. amplectens* T. & G.,[1] as Professor Greene has shown in Fl. Francis., Vol. I, p. 34. *T. amplectens* of the list in "Zoe" is probably this species.

36. **Trifolium Palmeri** *Wats.*, Proc. Am. Acad., Vol. XI, p. 132. "Guadalupe Island."

Also reported from Santa Catalina and San Clemente. On San Nicolas it was found in one locality, a moist slope.

37. **Trifolium dichotomum** *H. & A.*, Bot. Beech., p. 330. (Type locality not given.)

This has not before been reported from the islands, though *T. Catalinæ* is near it. The heads are smaller than the common form. It was collected in only one locality, a moist slope.

38. **Medicago sativa** *L.*, Spec. Pl., p. 778.

Stem, lower surface of leaves, and calyx pilose with long soft white appressed hairs; leaflets linear-oblong, apiculate from a truncate apex, about 2½ cm. long, 5–10 mm. wide, peduncles 8–9 cm. long, equalling the racemes; flowers 10–12 mm. long, with the filiform divisions of the calyx twice as long as the tube.

Reported only from San Miguel, but collected also on Santa Catalina by Mrs. Trask. On San Nicolas it was found in one locality, a flat above a brackish stream.

Since this island plant differs from the common form it seems best to give a general description.

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[1] Fl., Vol. I, p. 317.

39. **Medicago denticulata** *Willd.*, Sp., Vol. III, p. 1414. (Index Kewen.)

This has been reported from all the islands except Santa Rosa. On San Nicolas it was found on two slopes. The specimen at hand is unusually luxuriant. The leaflets are from 2–2½ cm. long and about 2 cm. wide; petioles 3–4 cm. long; peduncles 2–3 cm. long.

40. **Astragalus didymocarpus** *H. & A.*, Bot. Beech., p. 334, T. 81. "California."

This has been reported only from Santa Cruz. It has been collected on Santa Catalina recently by Mrs. Trask. On San Nicolas it was found only on the cliffs of a briny stream.

41. **Astragalus Traskiæ,** sp. nov.

PLATE VIII, FIGS. 6*a*–6*d*.

Stems densely white-tomentose, slightly viscid, several growing in a clump about 3 dm. high; leafy and branching: leaves shorter than the peduncles; leaflets canescent with appressed hairs, 20 or 25, alternate or opposite, oblong or obovate, obtuse, 10–15 mm. long, 3–5 mm. wide, one-nerved; stipules distinct, narrowly linear, 2 mm. long: peduncles 12–15 cm. long, erect, obscurely ribbed: raceme short when in bloom, elongating in fruit to about 9 cm.; bracts persistent, nigrescent, subulate; pedicels 2 mm. long, equalling or a little shorter than the bracts; calyx nigrescent, campanulate, 7–10 mm. long, with subulate divisions shorter than the tube; corolla yellowish white, glabrous; keel deeper yellow than the enfolding and surpassing wings, 5 mm. long without the claw; wings narrower, auriculate at base, 8 mm. long, with a claw 7 mm. long, equalling that of the keel; banner oval, attenuate to the claw, abruptly narrowing towards the emarginate apex, 15 mm. long, 6 mm. wide: legume coriaceous, transversely reticulate under the white wool, erect or spreading, exserted from the calyx on a stipe 5–8 mm. long; 2-celled from the intrusion of the dorsal suture, subfalcate, attenuate at apex to the long, persistent style; seeds immature.

This is closely allied to *A. Nevinii* Gray[1], which was collected on San Clemente Island by Nevin and Lyon. It differs from this species in its more robust habit, shape and size of the leaflets, and character of the pod. The specimen of *A. Nevinii* in the Herbarium of the Academy

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[1] Proc. Am. Acad., Vol. XXI, p. 412.

is one of the original collection. It has narrower, more falcate pods, perfectly glabrous and glossy. These two species are excellent types of insular variation; for undoubtedly they had a common origin. They seem most closely related to *A. arrectus* judging from the character of the pod.

It was collected in two places, in high, dry gulches, where it was abundant.

To name this in honor of the discoverer, the zealous collector, Mrs. Trask, is a small tribute to her courage and enthusiasm. It is one of the most showy plants on the island and perhaps the most interesting. The contrast between the white stems and leaves and the nearly black calyx would at once attract the attention of even careless observers.

42. **Hosackia venusta,** sp. nov.

PLATE VIII, FIGS. *2a–2d.*

Sericeous-tomentose, loosely branching from near the base, with stems 2–3 dm. long: leaves scattered at internodes of 2–3½ cm.; lower leaves unequally odd-pinnate, with two leaflets on the upper side of the rhachis, three below, and one terminal; upper leaves with five leaflets, two on each side and one terminal; rhachis 5–15 mm. long; leaflets oblong to obovate, obtuse or mucronate, 10–12 mm. long, 3–5 mm. wide: heads 2 cm. in diameter, on peduncles 2–3 cm. long, with one simple bract subtending the head; flowers yellow streaked with brown and turning brownish red in fading, on pedicels 1 mm. long; calyx densely villous, especially the narrow, linear divisions, which are longer than the campanulate tube; corolla surpassing the calyx by about 5 mm.; standard bright yellow, brown-veined near the base of the obovate-pandurate, emarginate blade; keel and wings brownish yellow, short clawed: immature pods densely pilose with ascending hairs, interiorly mottled with brown, exserted from the calyx and inclined to be falcate; immature seeds two, elliptical.

This species is one of several insular types closely related to *H. argophylla.* Two have been described by Professor Greene; one, as *Syrmatium niveum*[1], "Santa Cruz Island," and *Hosackia Ornithopus*[2], "Guadalupe Island." On San Clemente and Santa Catalina two others occur.

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[1] Bull. Cal. Acad. Sci., Vol. II, p. 148.

[2] Bull. Cal. Acad. Sci., Vol. I, p. 185.

A comparative study of these with drawings of similar parts would be a most interesting illustration of insular variation.

In the figures, the differences in the floral organs of this species and *H. argophylla* are given. It also differs in foliage and inflorescence.

Mrs. Trask reports this as rare and collected in the one moist flat above the brackish stream.

GERANIACEÆ.

43. **Erodium cicutarium** *L.'Her.*, ex Ait., Hort. Kew., ed. I, Vol. II, p. 414. (Index Kewen.)

Described first by Linnæus under *Geranium*, Sp. Pl., p. 680.

This has been reported from all the islands, uncommon on San Nicolas, collected on a moist slope. The specimen is a long, slender branch; the gynophore measures 4 cm. According to Mrs. Trask the flowers are bright red instead of the common magenta hue.

44. **Malva pusilla** *Smith*, Eng. Bot., T. 241. (Index Kewen.)

As *M. borealis* this was reported as common on all the islands. On San Nicolas it grew in one locality, a flat above the brackish stream.

ONAGRACEÆ.

45. **Œnothera viridescens** *Hook.*, Fl. Bor., Vol. I, p. 214. "Northwest Coast of America, Menzies."

There are specimens of this in the Herbarium of the Academy from San Miguel, Santa Rosa, and Santa Cruz Islands. It grew on San Nicolas on the sands of the shore and on the sand cliffs at 500 to 1000 feet elevation.

This is one of the forms included under *Œ. cheiranthifolia* in Bot. Calif., Vol. I, p. 225. It varies especially in the size of the flowers, amount of pubescence, and the margins and shapes of the leaves. These island specimens have smaller flowers than the mainland forms common along the southern coast of California; but they agree in the flowers fading green, in having similar capsules, and in the leaves forming small rosettes at the ends of the branchlets.

Since the original description of *Œ. cheiranthifolia* is not available and according to Professor Greene does not fit either this or *Œ. spiralis*, it seems best at present to leave these island plants under Hooker's name.

FICOIDEÆ.

46. **Mesembryanthemum nodiflorum** *L.*, Sp. Pl., p. 480. The specimens from San Nicolas are identical with those collected elsewhere in Southern California. They differ somewhat from a plant collected in Sardinia by Reverchon, (ex. Herb. Ball.) in the Herbarium of the Academy. In this genus it is very difficult to be certain of dried specimens where the species are closely related. On San Nicolas it was frequent on the beaches. The flowers are white.

46*a*. **Mesembryanthemum crystallinum** *L.*—This was abundant, growing on cliffs 1000 ft. high. No specimens were collected. Mrs. Trask writes that it grew knee high and that in walking through it her boots and leggins were soaked thoroughly with the sap. It rendered climbing dangerous as the rocks became very slippery and there were precipices everywhere on the cliffs. It is found on all the islands.

CACTACEÆ.

47. **Opuntia.**—This is probably *O. Engelmanni* Salm., var. *littoralis* Engelm.

Mrs. Trask reports it as identical with this species as she knows it on Santa Catalina. The specimen consists of a flower only and that without the ovary. It is reported from all the islands except San Clemente.

Wherever this cactus grew, it protected a small colony of grasses and tender herbs.

47*a*. **Opuntia prolifera** *Engelm.*—This also was seen but no specimens were collected. It has been reported also from Santa Catalina and San Clemente.

UMBELLIFERÆ.

48. **Daucus pusillus** *Michx.*, Fl., Vol. I, p. 164. "In campestris Carolinæ."

This has been reported from all the islands. It was collected on San Nicolas in sand gulches near the sea. Mrs. Trask reports the flowers as reddish purple.

This is the *Yerba del Vibora* of the early settlers of California and is widely accepted as an antidote for the poison of the rattlesnake.

49. **Apiastrum angustifolium** *Nutt.*, Torr. & Gr. Fl., Vol. I, p. 644. "San Diego, California."

Reported from San Miguel, Santa Cruz, and Santa Catalina. On San Nicolas it was found in one locality, a dry, riven sand flat.

50. **Sanicula Menziesii** *H. & A.*, Bot. Beech., p. 142. "California."

This is the first record of this species from the islands. It is a poor specimen but yet shows the characteristic pedicellate fruit and erect stem of this common species. It was frequent on dry rocky heights. Mrs. Trask has collected it also on Santa Catalina.

51. **Peucedanum insulare,** sp. nov.

PLATE VIII, FIGS. 1*a*–1*d*.

Acaulescent from a long, rather stout, woody root, sheathed at summit by persistent, dilated petioles which become fibrous with age; leaves from biternate to biquinate; leaflets cuneate, sharply dentate or incised, veiny;

petioles shorter than the blades: umbel with from 10–18 fruiting rays 3–8 cm. long; peduncles stout, solid, dilated at summit, 15 cm. tall, 5 mm. in diameter, slightly glandular-pilose when young, becoming glabrous and striate with age; involucre a single, elongated bract, palmately divided at the apex; involucels several, linear-attenuate, 5–10 mm. long, equalling the fruiting pedicels; sepals fleshy, triangular, inconspicuous; corolla yellow, petals ovate-acuminate, strongly nerved and incurved: fruit elliptical, cordate at each end; wings equalling or a little broader than the body; ribs filiform, inconspicuous; oil tubes variable in size and number, generally two in the intervals, six on the commisural surface, one occasionally in a wing. On the dorsal side the tubes vary from six to nine. Sometimes there will be one large tube between the ribs, sometimes two, either large or small, and occasionally one occurs, as in the figure, at the intersection of the wing. The oil is very abundant and has an odor almost identical with that of the oil of bergamot.

It was collected on sand cliffs overhanging briny arroyas and the plants were in flower but still retained the fruiting stems of the preceding season.

POLEMONIACEÆ.

52. **Gilia Nevinii** *Gray*, Syn. Fl., p. 411. "Guadalupe Island."

Reported from Santa Rosa, Santa Cruz, Santa Catalina, and San Clemente. On San Nicolas it was found on sandy heights above a brackish stream.

This specimen is too poor for certainty and seems to approach *G. multicaulis.* It differs from the plant common on Guadalupe and the other islands. The glandular, hairy pubescence is denser, the leaves less finely divided, with shorter divisions, the calyx and its divisions shorter, and the corolla smaller. The appearance is that of a depauperate specimen of *G. Nevinii.* The fruit is not ripe. The flowers were pale blue.

CONVOLVULACEÆ.

53. **Convolvulus macrostegius** *Greene*, Bull. Cal. Acad. Sci., Vol. I, p. 208. "Guadalupe Island, in the crevices of basaltic rocks."

This is found on all the islands. Mrs. Trask discovered but one plant on San Nicolas.

It is questionable whether this should be included under *C. occidentalis* or left as a distinct species. It looks quite unlike the common mainland form, but Mr. Brandegee in "Zoe," Vol. I, p. 85, describes plants that seem to inseparably connect the two. At present, it is most convenient to leave it under the above name.

Mrs. Trask writes as follows about this: "*C. macrostegius* is utterly different in every way from *C. occidentalis*, seen on Santa Catalina by hundreds. *C. occidentalis* is never two or more flowered within the bracts."

BORAGINACEÆ.

54. **Heliotropium Curassavicum** *L.*, Sp. Pl., p. 130.

Reported from San Miguel, Santa Cruz, and Santa Catalina. Collected on San Nicolas on the beach, seen in two localities.

These San Nicolas plants are singularly robust. The leaves are crowded towards the summit of the short stems, apparently very fleshy, oblong-spatulate, 2–5 cm. long including the broad petiole which equals or is twice as long as the blade, 10–15 mm. wide; flowers somewhat larger in all their parts than the common form.

55. **Pectocarya linearis** *DC.*, Prodr., Tome X, p. 120.

In Syn. Fl., Vol. II, p. 182, Gray mentions two forms. This resembles that under *P. Chilensis*. It has narrower and more pectinate teeth to a somewhat incurved wing and the nutlets arcuate, recurved in age. The type locality is in Chili, as the name indicates.

This is the first record from the islands. It was collected on the ridge 1000 ft. above the sea.

56. **Cryptanthe maritima** *Greene*, Pitt., Vol. I, p. 117.

Krynitzkia maritima GREENE, Bull. Cal. Acad. Sci., Vol. I, p. 204. "Guadalupe Island."

This from San Nicolas agrees almost exactly with a specimen collected by Prof. Greene on Guadalupe Island, the nutlets being identical on both plants. However, they are a line long instead of half a line, as in Greene's description. This difference is due probably to the varying age of the nutlets, which differ in size on the same plant and often seem ripe when they are dry but immature.

Mrs. Trask reports this plant as rare, growing in arroyas swept bare by sand and wind.

57. **Cryptanthe Torreyana** *Greene*, Pitt., Vol. I, p. 118.

Krynitzkia Torreyana GRAY, Proc. Am. Acad., Vol. XX, p. 271.

Type range: nearly throughout California and east to Nevada and southwestern parts of Idaho.

This is the first record from the islands; but it has recently been collected by Mrs. Trask on Santa Catalina. It was infrequent, found on bare, wind-swept heights. The nutlets are mottled with two shades of brown and slightly papillose towards the apex.

58. **Amsinckia St. Nicolai,** sp. nov.

PLATE VIII, FIGS. *7a–7e*.

Stems decumbent, branching at the base and at the inflorescence, somewhat viscid, very hispid with horizontally spreading, shining white bristles, pustulate at base, often yellowish at apex, from fine and short to stout and more than 1 mm. long: radical leaves broadly linear to oblanceolate; cauline ovate-lanceolate, 1–2 cm. long, 5–10 mm. wide at the sessile base, undulate, bristly ciliate, obtuse: spikes with bracts 5 mm. long; calyx with two oblong divisions free almost to the base, the other three united, 4 mm. long: corolla yellow, about twice as long as the calyx; limb short with uneven, rounded lobes; tube narrow, without folds, spots, or hairs in the throat; stamens versatile on very short filaments inserted in the throat of the corolla but not exserted; style extending to the stamens, surpassing the calyx; stigma capitate: nutlets ovate-triquetrous, carinate, incurved, granulate, irregularly muriculate especially on the keel and at the edges, indistinctly rugose, pale brown, mottled with darker brown.

This as well as the following species or variety was collected on seashore sands and dry cliffs at 1000 ft. elevation, growing in company with *Œnothera viridescens*.

59. **Amsinckia maritima,** sp. nov.

PLATE VIII, FIGS. 8*a*–8*c*.

Stouter than the last, more erect, with pubescence stiffer and foliage similar but larger: radical leaves wanting; cauline 3 cm. long, 2 cm. or more wide at base, scattered: spikes ebracteate except occasionally at the lowest flowers; calyx with three divisions united but cleft, the other two divided, 3 mm. long; corolla 5 mm. long with more spreading divisions than the preceding, throat without folds, hairs, or spots; stamens in the throat of the corolla similar to the preceding; style about equalling the calyx or slightly surpassing it: nutlets similar to the preceding but black and indistinctly transversely rugulose.

This appears similar to the common coast *Amsinckia* which has been called *A. lycopsoides* by both Dr. Gray and Professor Greene.

A. lycopsoides was named by Lehman without description or locality.[1] The earliest description is that of Fisher and Meyer,[2] for the following copy of which I am indebted to the Gray Herbarium: "*Amsinckia lycopsoides.*—A corolla fauce, barbata, limbo tubo triplo breviore; staminibus corollæ tubo paulo supra basin insertis.—*A. lycopsoides* Lehm., delect Sem. b. Hamburg, 1831.—Tubus corollæ 3½ lin. longus; limbus 2 lin. in diametro vix latior." De Candolle[3] gives the same description, adding "caule laxe ramosa" and "§ nuculæ rugosæ, inter rugos albo granulatæ, dorso convexæ, angulis parum distinctis."

The corolla with bearded throat and stamens inserted a little above the base of the corolla, as well as the rugulose nutlets, white granulate between the folds, excludes this island *Amsinckia*, as well as the plants described by Dr. Gray and Professor Greene under *A. lycopsoides.*

Recently, the writer collected specimens agreeing with the description of *A. lycopsoides.* They were found on a hillside on the range of hills separating Piedmont from Maragua Valley in Alameda County, Calif. The type locality is near Fort Ross, Sonoma Co., Calif. It would

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[1] Semina in Horto Bot. Hamb., p. 7, (1831.) (Index Kewen.)

[2] Ind. Sem. Hort. Petrop., Tome II, p. 26.

[3] Prodr. Tome X, p. 117.

not be unlikely to find the species in Alameda County, growing in the vicinity of *Vaccinium ovatum* and *Castanopsis chrysophylla.*

In a genus like *Amsinckia* where there are so many closely related forms, nothing definite can be discovered concerning the limitation of species until these various forms are represented growing in a botanic garden under similar conditions; nor is it possible to be sure of what characters are constant.

In view of all these doubts, it seems best to describe these two closely related island plants as distinct species. If the last proves upon further investigation to be similar to the common maritime species found all along the coast, the name will appropriately include them; while the other, perhaps Gray's *var. bracteosa* of his *A. lycopsoides*, is named in honor of the Island's saint.

SOLANACEÆ.

60. **Lycium verrucosum,** sp. nov.

PLATE VIII, FIGS. 3*a*–3*d*.

Glandular-puberulent, shrubby, 6–8 ft. high, divaricately branching, spinescent, bark light gray; branchlets verrucose at leaf axils from downy tufts at base of petioles: leaves spatulate, 5–15 cm. long, narrowing to the petiole, thick, obsoletely one-nerved: flowers small, solitary in the axils, on peduncles 2–7 mm. long; calyx campanulate, irregularly 4-cleft, divisions oblong, obtuse, thickish, reticulate, 1 mm. wide; corolla lavender, 8 mm. long, with tube slightly surpassing the calyx, hairy within below the throat, border of four rounded, spreading divisions, each 2 mm. wide; anthers thick, sessile in the throat of the corolla; ovary somewhat crested at summit; stigma capitate on a level with the anthers; immature fruit reddish.

This belongs to the same group as *L. Californicum* and *L. barbinodum* from which it can be readily distinguished by the floral organs.

It grew in several localities on arroya cliffs, with its branches hanging over the arroyas in many an inaccessible erosion.

61. **Lycium Californicum** *Nutt.*, in Herb. Bot. Cal., Vol. II, p. 542, "near San Diego."

This grew in sheltered, moist nooks with *Opuntia*. Reported from Santa Catalina and San Clemente.

SCROPHULARIACEÆ.

62. **Orthocarpus purpurascens** *Benth.*, in DC. Prodr., Tome X, p. 536. "Nova California, Douglas."

Reported from Santa Cruz and Santa Catalina. This from San Nicolas is a very poor specimen, not more than three inches tall, the spike about an inch long. It was collected in one locality, a moist flat on the ridge.

PLANTAGINACEÆ.

63. **Plantago insularis**, sp. nov.

Canescent with long, fine, silky hairs, very dense on the peduncles below the spikes: leaves broadly lanceolate-acuminate, narrowed to a broad petiole, a few callous teeth on the margin, 3-nerved, 5-9 cm. long, 5-12 mm. wide; peduncles 4-10 cm. long, rather stout: spikes oblong-linear, 1-2 cm. long, 8-10 mm. wide, densely flowered; bracts broadly ovate, about equalling the calyx; corolla 2½ mm. in diameter, with ovate-orbicular, abruptly acuminate lobes, brown at base; stamens and style exserted; seeds two, cymbiform as in *P. Patagonica* and its allies.

Found on sea-shore flats.

This might be included as a variety of the very polymorphous *P. Patagonica*, but owing to its different appearance, though the flowers are similar, it seems most convenient to consider it a distinct species.

COMPOSITÆ.

64. **Malacothrix indecora** *Greene*, Bull. Cal. Acad. Sci., Vol. II, p. 152. "Islets close to the northern shore of Santa Cruz Island."

This covered large areas on the ridge. It is almost identical with Professor Greene's type.

65. **Malacothrix implicata,** sp. nov.

Stems woody, purplish, glabrous or slightly viscid, branched above: leaves numerous and close together, irregularly bipinnatifid into numerous narrow, linear divisions which form a tangle so that individual leaves cannot be separated in the dried specimens; length of entire leaf about 6 cm., with divisions beginning at the base, varying in length from 4 mm. to 3 cm.: heads 2 cm. in diameter, closely cymose at the ends of the branches on short peduncles; ligules white, unevenly toothed and lobed; tube pilose with upwardly spreading hairs; akenes 2¼ mm. long, four or five angled, with one or two ribs between the angles, brown, minutely tuberculate, scar at base prominent, apex with white denticulate border. The receptacle, as in *M. saxatilis* becomes capitate, with the bracts of the involucre deflexed.

"Queens's Dairy," sand and wind carved cliffs.

It has been extremely puzzling to know what to do with this. It might just as well be made a variety of *M. saxatilis*.

From an inspection of allied *Malacothrix* from the other islands and the mainland it is found that all are more or less alike, differing in leaves, habit of growth, size of heads, and character of akenes. They are all evidently the offspring of a common parent and having been isolated, have developed peculiarities of their own. They are excellent examples of Darwinian species. This one from San Nicolas is most similar to one collected by W. G. W. Harford on San Miguel, but differs in having smaller heads and a more compact habit. There are no seeds on the San Miguel plant and we shall probably remain forever ignorant of its fruit, since, according to Dr. Gustav Eisen, who visited the island during the summer of 1897, the vegetation has been entirely destroyed by goats and the island has become a desolate waste of drifting sand.

I have provisionally included the San Miguel plant as well as specimens from Santa Rosa and Santa Cruz under this name. The last two have the divisions of the leaves broader and thicker, the inflorescence an open cymose panicle, and the heads smaller.

66. **Microseris linearifolia** *Gray*. Described first as *Calais linearifolia* DC., Prodr., Tome VII, p. 85. "California, Douglas."

Reported from Santa Rosa, Santa Cruz, Santa Catalina. On San Nicolas it was collected in one locality, a fertile flat. The few plants seen were in flower and fruit, with stems almost a foot in height and leaves varying from runcinate-pinnatifid to almost entire.

67. **Sonchus asper** *Hill*, Herb. Brit., Vol. I, p. 47. (Index Kewen.)

Reported from Santa Rosa, Santa Cruz, and Santa Catalina; collected on San Nicolas on a moist slope.

68. **Sonchus tenerrimus** *L.*, Sp. Pl., p. 794. "Montpellii., Florentiæ."

Reported from Santa Catalina. Two forms of this species were collected. In each the divisions of the leaves differ in width and both are much broader than in specimens from San Diego. One was found on cliffs of a water course, the other on moist slopes.

This species was first collected in North America by Nuttall in the vicinity of San Diego, and by him was named *S. tenuifolius*.[1]

69. **Sonchus oleraceus** *L.*, Sp. Pl., p. 794.

Reported from Santa Rosa and Santa Cruz. Collected on San Nicolas on a moist slope.

The leaves are much broader than in the form of this species common around San Francisco.

70. **Centaurea Melitensis** *L.*, ?—This has nothing but leaves. A spiny bud can be discerned among the uppermost leaves that suggests this species.

71. **? Artemisia** ———.—The odor and taste of the foliage of this plant suggest *A. Californica;* but the leaves

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[1] Trans. Am. Phil. Soc. N. S., Vol. VII, p. 438.

are quite different. There are no flower buds even. If an *Artemisia,* it is probably undescribed.

72. **Achillea Millefolium** *L.*, Sp. Pl., p. 899. "In Europæ pascius pratisque."

Reported from all the islands. On San Nicolas found on a cliff over a briny water way.

73. **Amblyopappus pusillus** *H. & A.*, Journ. Bot., Vol. III, p. 321. "Coquimbo," Chili.

This species has a peculiar distribution. It is represented in almost all the coast islands both of Southern and Baja California. On the mainland it extends as far north as Pt. Sal, where it grows in company with *Leptosyne gigantea;* while on the south it reaches the coast of South America, where it was first discovered. The following localities are known to the writer either from specimens in the Academy's Herbarium or from reports:

Coast of California, mainland—San Luis Rey, Coronado, Pt. Sal.

Coast Islands—Cedros, Santa Cruz, Santa Rosa, San Miguel, Santa Catalina.

Baja California—Lagoon Head, Carysito, Aqua Dulce, San Regius.

Chili—Macuma, Huasco.

There is some variation among all these specimens, those from San Nicolas being unusually large. The stem is about a foot high and becomes quite woody. It was frequent on uplands along the ridge.

74. **Baeria gracilis** *Gray*, Proc. Am. Acad., Vol. IX, p. 196. First described as *Burriela gracilis* DC., Prodr., Tome V., p. 664, "Nova-California, Douglas."

Cinereous with strigulose pubescence; leaves linear, 2–6 cm. long, 1–2 mm. wide; pappus of four upwardly barbellate awns almost equalling the corolla and gradually spreading to a paleaceous base; achenium strigose, especially on the angles; rays surpassing the involucre by about 4 mm.

It has been reported from Santa Rosa, Santa Cruz, and Santa Catalina. It covered the uplands on Santa Catalina.

A brief description of this island plant seems desirable owing to the great variability of this species.

75. **Hemizonia Streetsii** *Gray*, Proc. Am. Acad., Vol. XII, p. 162. "San Benito Island, Baja California."

Reported also from San Clemente, Santa Catalina, and Anacapa. On San Nicolas it was found on sea cliffs in only one place. These specimens have a more compact form than those from the other islands. This may be due to immaturity.

76. **Leptosyne gigantea** *Kellogg*, Proc. Cal. Acad. Sci., Vol. IV, p. 198. "Near Cuyler Harbor, San Miguel Island."

It is also found on the following islands: Santa Barbara, Santa Rosa, Santa Cruz, Santa Catalina, and Guadalupe. On the mainland, Mrs. Blochman discovered it at Pt. Sal and Mr. W. G. Wright obtained fine specimens from the coast of Ventura County.

When the stem is broken it exhales a strong odor of turpentine which, around Pt. Sal, has given it the name "Turpentine weed."

Mrs. Trask reports this as growing in four or five localities. About three plants were seen with eradiate heads, growing amid the ordinary plants with radiate heads. These eradiate heads are sterile and in the specimens examined appeared to be composed entirely of bracts, forming a globular head.

Mrs. Trask notes the leaflets of the San Nicolas plant to be fleshy and filiform, those on the Santa Catalina plant are not fleshy.

Franseria Chamissonis and *F. bipinnatifida* are two species inhabiting the sand hillocks along the coast and are almost always found associated together. They are most puzzling to the systematist who endeavors to make boundary lines, because they not only appear to run into each other but each is variable even in regard to what are supposed to be its own individual characteristics. Especially is this true as regards foliage, pubescence, and size of the heads.

F. bipinnatifida was first described in "Linnea" as variety *bipinnatisecta* of *F. Chamissonis*, and it may yet again be restored to its former position when all the forms are better known. Each of these is represented on San Nicolas, both differing from each other and the typical forms. One seems to fall under *F. Chamissonis* while the other is nearer *F. bipinnatifida*.

It is with hesitancy that I describe these forms as new varieties even; but after much deliberation it seems the best course.

77. **Franseria Chamissonis** *Less.*, var. **viscida,** var. nov.

Stems stout, striate, loosely villous with white hairs, viscid; leaves extremely variable; upper ones oblanceolate and entire to ovate-spatulate, cuneate at base, crenate-dentate; lowest leaves broadly ovate in outline, deeply parted with divisions crenate-dentate or incised and even becoming bipinnatifid; pubescence sericeous, dense, and appressed: sterile involucres 5 mm. in diameter, almost sessile; fruit with keeled, and channeled, spreading spines viscid even to the apex.

It is the viscid character of the spines to which the name is due.

78. **Franseria bipinnatifida,** var. **dubia,** var. nov.

Stem ribbed, less villous and viscid than the preceding; leaves broadly ovate in outline, bipinnatifid with divisions about 2 mm. broad, silvery silky with appressed hairs but less dense than the preceding; sterile heads 6 mm. in diameter on slender pedicels 4–8 mm. long; fruit with spines slightly villous and viscid.

Mrs. Trask notes these two as common on the sand-hills and as keeping their peculiarities even when growing together.

79. **Baccharis consanguinea** *DC.*, ? Prodr., Tome V., p. 408. "California, Douglas."

This is reported as the only tree and but one individual. It more properly ought to be considered as an arborescent shrub. It grew to a height of seven feet on a fertile flat. There were no signs of fruit or flower, so, though the foliage is exactly of the above species, there is some uncertainty about the identification.

As *B. pilularis* this has been reported from all the islands except San Miguel and San Clemente. Since this is the form described as *B. consanguinea* it seems advisable to list it under this name.

80. **Bigelovia veneta** *Gray*, or **Grindelia** ———.

This is fragmentary without flowers or even buds. It grew in a fertile flat near the sea in one locality. The only plant seen was about two feet in height.

TABLE OF SPECIES.

SPECIES.	San Miguel.	Santa Rosa.	Santa Cruz.	Santa Catalina.	San Clemente.	Mainland.
1. *Bromus Trinii* DESV. (*Trisetum barbatum* STEUD.)			*			*
2. *Bromus Hookerianus* THURB.		*	*	*	*	*
3. *Bromus virens* NUTT.						*
4. *Cynodon Dactylon* PERS.						*
5. *Stipa setigera* PRESL.		*	*	*	*	*
6. *Stipa robusta* VASEY						*
7. *Hordeum murinum* L.		*	*	*		*
8. *Avena barbata* L.						*
9. *Phalaris Canariensis* L.	*		*	*	*	*
10. *Distichlis spicata* L. (*D. maritima*)	*	*	*	*		*
11. *Polypogon Monspeliensis* DESV.	*	*	*	*		*
12. *Eleocharis* (*E. palustris* R. BR.)			*			*
13. *Brodiæa capitata* BENTH	*	*	*	*	*	*
14. *Parietaria debilis* FORSTER		*	*	*	*	*
15. *Chenopodium Californicum* WATS.	*		*	*	*	*
16. *Chenopodium murale* L.	*		*	*		*
17. *Atriplex Californicum* MOQ.	*		*	*	*	*
18. *Atriplex decumbens* WATS.				*		*
19. *Suæda* sp.? (*S. Torreyana* ?) *found on*	*	*	*	*		*
20. *Aphanisma blitoides* NUTT.					*	*
21. *Abronia maritima* NUTT.	*		*	*		*

SPECIES.	San Miguel.	Santa Rosa	Santa Cruz.	Santa Catalina.	San Clemente.	Mainland.
22. *Abronia umbellata* LAM. ?	*	*	*		*	*
23. *Abronia alba* sp. nov.						
24. *Silene Gallica* L.	*	*	*	*		*
25. *Spergularia macrotheca* HEYNH. (*Tissa.*)	*	*	*	*	*	*
26. *Platystemon Californicus* BENTH.	*	*	*	*	*	*
27. *Lepidium bipinnatifidum* DESV. (*L. Menziesii* of Bot. Cal.)			*			*
28. *Lepidium nitidum* NUTT.			*	*	*	*
29. *Dithyrea Californica* var. *maritima* DAVIDSON (*Biscutella*)						*
30.[1] *Oligomeris glaucescens* CAMBESS. (*O. subulata* WEBB.)	*		*	*	*	*
31. *Lupinus micranthus* DOUGL.		*		*		*
32. *Lupinus albifrons* BENTH. (*L. Chamissonis*)	*	*	*	*		*
33. *Trifolium microdon* H. & A. var. *pilosum* var. nov.						
* *Trifolium microdon*			*	*		*
34. *Trifolium gracilentum* T. & G.				*		*
35. *Trifolium stenophyllum* NUTT.				*		*
36.[1] *Trifolium Palmeri* WATS.				*	*	
37.[4] *Trifolium dichotomum* H. & A.						*
38. *Medicago sativa* L.				*		*
39. *Medicago denticulata* WILLD.	*		*	*	*	*
40. *Astragalus didymocarpus* H. & A.			*	*		*
41. *Astragalus Traskiæ* sp. nov.						
42. *Hosackia venusta* sp. nov.						
43. *Erodium cicutarium* L'HER.	*	*	*	*	*	*
44. *Malva pusilla* SMITH (*M. borealis*)	*	*	*	*	*	*
45. *Œnothera viridescens* HOOK.	*	*	*			*
46. *Mesembryanthemum nodiflorum* L.				*	*	*
46*a*.[5] *Mesembryanthemum crystallinum* L.	*	*	*	*	*	*
47. *Opuntia Engelmanni* SALM. var. *littoralis* ENGELM?	*	*	*	*		*
47*a*.[5] *Opuntia prolifera* ENGELM				*	*	*
48. *Daucus pusillus* MICHX.	*	*	*	*	*	*
49. *Apiastrum angustifolium* NUTT.	*		*	*		*
50. *Sanicula Menziesii* H. & A.				*		*
51. *Peucedanum insulare* sp. nov.						
52.[1] *Gilia Nevinii* GRAY ?		*	*	*	*	
53.[1] *Convolvulus macrostegius* GREENE	*	*	*	*	*	
54. *Heliotropium Curassavicum* L.	*		*	*		*
55. *Pectocarya linearis* DC.						*

SPECIES.	San Miguel.	Santa Rosa.	Santa Cruz.	Santa Catalina.	San Clemente.	Mainland.
56.[1] *Cryptanthe maritima* GREENE						
57. *Cryptanthe Torreyana* GREENE				*		*
58. *Amsinckia St. Nicolai* sp. nov.						
59. *Amsinckia maritima* sp. nov.						?
60. *Lycium verrucosum* sp. nov.						
61. *Lycium Californicum* NUTT.				*	*	*
62. *Orthocarpus purpurascens* BENTH.			*	*		*
63. *Plantago insularis* sp. nov.						
64. *Malacothrix indecora* GREENE			*			
65. *Malacothrix implicata* sp. nov.	*	*	*			
66. *Microseris linearifolia* GRAY		*	*	*		*
67. *Sonchus asper* HILL		*	*	*		*
68. *Sonchus tenerrimus* L.				*		*
69. *Sonchus oleraceus* L.		*	*			*
70. *Centaurea Melitensis* L. ?						*
71. *Artemisia* ?						
72. *Achillea Millefolium* L.	*	*	*	*	*	*
73.[2] *Amblyopappus pusillus* H. & A.	*	*	*	*		*
74. *Baeria gracilis* GRAY		*	*	*		*
75.[3] *Hemizonia Streetsii* GRAY				*	*	
76.[1] *Leptosyne gigantea* KELLOGG	*	*	*	*		*
77. *Franseria Chamissonis* LESS. var. *viscida* var. nov.						
* *Franseria Chamissonis* LESS.	*					*
78. *Franseria bipinnatifida* NUTT. var. *dubia* var. nov.						
* *F. bipinnatifida*	*		*	*		*
79. *Baccharis consanguinea* DC. ? (*B. pilularis*)		*	*	*		*
80. *Bigelovia veneta* or *Grindelia* ?						

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*Closely related species found on some of the other islands but different from the form on San Nicolas.

[1] Guadalupe Island, Baja California.

[2] Cedros Island, Baja California and S. America.

[3] San Benito Island and Anacapa Island, Calif.

[4] This might more correctly be considered a form of *T. Macræi* with the heads on long peduncles.

[5] Species reported but not collected.

SUMMARY.

82. Species recorded.
64. In common with the mainland, of which about 30 are Californian.
53. In common with Santa Catalina Island.
48. In common with Santa Cruz Island.
31. In common with Santa Rosa Island.
31. In common with San Miguel Island.
6. In common with Guadalupe Island; 1 with Cedros Island, 1 with San Benito Island and 1 with Anacapa Island; 7 species and 3 or 4 varieties peculiar to San Nicolas.

II.—NEW SPECIES OF CNICUS FROM SOUTHERN COLORADO AND UTAH.

1. **Cnicus bipinnatus,** sp. nov.

Cnicus Drummondii var. *bipinnatus* Eastwood, Zoe, Vol. IV, p. 8.

Glaucous and glabrous except for some slight arachnoid tomentum on the stems, petioles, and involucral bracts: stems stout, erect, leafy, 6 dm. or more high, branching from the base and also above; leaves with numerous linear-lanceolate divisions which are 2-6 cm. long, 5 mm. wide and irregularly parted near the base, generally on one side only, into similar lobes varying in length and sometimes as long as the main division, margin laciniate-dentate, spiny, lateral spines 2 mm. long, terminal 4-5 mm.; radical leaves petiolate, 1½-3 dm. long, 6-10 cm. wide; cauline, sessile, 10-15 cm. long, 5-6 cm. wide: heads corymbose at the ends of the leafy branches, almost sessile, narrow, cylindrical, 4½ cm. long, 1 cm. or more wide; involucre of appressed, imbricated bracts, successively shorter, in seven ranks, the lower ones pointed with a weak prickle 3-5 mm. long, the upper attenuate to a scarious tip, minutely puberulent; flowers purple; corolla with tube about half as long as the throat and divisions, throat about one-third as long as the linear, clavate-tipped divisions; stamens surpassing the corolla; style straight with the node 2½ mm. from the tip; akenes glabrous, shining, flattened, obovate-oblong, 6 mm. long, 3 mm. wide, surmounted with a yellow ring.

This is nearer to *Cnicus Rothrockii* than to *Cnicus Drummondii* but differs from the former in its foliage, narrower heads, short, weak spines, and general appearance. It formed a clump two feet or more in height and almost two feet in diameter.

Collected in Colorado in Johnston Cañon, near where it joins the Mancos River, in a locality but rarely visited by white men.

Closely related to this is the plant which the writer[1] described under the name *C. Rothrockii* var. *diffusus*. I take this opportunity of giving this, too, specific rank.

2. **Cnicus diffusus,** sp. nov.

Similar to the above in habit and surface: leaves narrower, less deeply divided, with more regular and triangular lobes; spines at the tips of the lobes 1 cm. long, stiff, yellow, those along the margins 1-3 mm. long: heads somewhat broader than the last, with outer involucral bracts tipped with stiff spines from 1-2 cm. long, deflexed-spreading in fruit, inner bracts attenuate

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[1] Proc. Cal. Acad. Sci., Ser. 2, Vol. VI, p. 303.

to a long spiny point; flowers purple; corolla with tube four-fifths of the throat and divisions; throat about one-third of the tube, divisions linear, abruptly acuminate, 18 mm. long; stamens surpassing the corolla; node of the stigma 2 mm. from the apex; coma 2½ cm. long.

Willow Creek, San Juan Co., Utah, Aug. 13, 1895.

3. **Cnicus Hesperius,** sp. nov.

Stem stout, simple, erect, leafy from the base, ribbed, almost glabrous, 3-4 dm. in height, 2 cm. in diameter: leaves 10-15 cm. long, 1½-2 cm. wide, upper surface glabrous, lower tomentose, ascending, linear-lanceolate, with numerous rounded lobes, spiny-margined with two to three large, yellow, subulate spines, 5 mm. long, and several shorter ones: heads sessile, crowded, in an oblong, terminal, erect, leafy, glomerule; involucre 2 cm. long, 2½ cm. wide, with bracts 3 mm. broad at the yellow, glabrous, ovate base, tapering to a long brown-purple spine 1 cm. long, arachnoid with silky wool except at the glabrous yellow apex: flowers light purple; corolla tube almost equalling the throat and divisions; throat fusiform, contracted under the divisions which are linear with thickened apex and about half as long as the throat; anthers surpassing the petals by 3 mm., sparingly arachnoid except at the pointed tips; style with inconspicuous node concealed by the anthers and stigma, exserted 2 mm.; coma 1 cm. long.

Mt. Hesperus on the Bear Creek Divide above timber line, La Plata Mountains, southwestern Colorado, Aug., 1892. Collected by the writer.

This *Cnicus* is nearest to *C. eriocephalus* Gray, under which it was placed by the writer in "Zoe," Vol. IV, p. 8. A recent inspection of the specimens of *Cnicus* in the Herbarium of the Academy has convinced me that this deserves to have specific rank and that it is not a hybrid with *Cnicus Parryi*, as I had formerly conjectured.

The involucral bracts are less densely tomentose than in *C. eriocephalus*, the glomerule erect, the flowers light purple or pink, the entire plant less arachnoid, and the stamens have not only the filaments wooly but also the anthers.

I have named it in honor of the mountain on which it is found, the highest in the La Plata Range. There were few individuals growing along the trail leading to the summit of the ridge.

III.—THE COLORADO ALPINE SPECIES OF SYNTHYRIS.

One alpine species of *Synthyris* is now recognized from the mountains of Colorado. This has been aptly named *S. alpina.*

1. **Synthyris alpina** *Gray.*

PLATE IX, FIGS. *1a–1d.*

This is found on most of the high peaks of Colorado, growing above timber line, in loose, rocky soil. Its low stature and short spike of dark purple flowers superficially distinguish it from the other species. There are always four calyx divisions, variable in shape and size even in flowers from the same spike, and conspicuously fringed with long white hairs. The corolla consists of two parts, united at the base; the upper broadly obovate, entire, and slightly concave; the lower two or three cleft, with laciniate or entire divisions varying in length and breadth. The stamens and style are moderately exserted and the flowers are erect.

In the little-explored mountains of southwestern Colorado two different species are found above the tree limit. One of these is so distinct that in a group so closely related as that to which *Synthyris* belongs, it might be taken as the type of a new genus; the other approaches *S. alpina.*

The placing of these two species in *Synthyris* necessitates a change in the generic characterization of the calyx. Instead of "calyx with four divisions" it must become "calyx with two, three, or four divisions." This difference in the number of calyx divisions arises probably from a union of parts not infrequent in other genera.

2. **Synthyris Ritteriana,** sp. nov.

PLATE IX, FIGS. *2a–2e.*

Sparingly pubescent with short, scattered hairs; scape stout, nearly 3 dm. high, closely covered from the middle of the stem to the spike with foliaceous bracts: leaves radical, 8-10 cm. long, 3½ cm. wide, oblong-elliptical, obtuse, cuneate and decurrent at base, crenate; petioles stout, 8-12 cm. long; bracts of the scape alternate, 1½-2½ cm. long, 10-18 mm. wide, ovate-acuminate, sessile by a subcordate base, crenate-dentate near the apex; floral bracts rhomboidal, acuminate, tapering at base to a short petiole which surpasses the pedicels: flowers white, erect on short pedicels in a spike 5 cm. long; calyx of three divisions varying in shape and size in flowers from the same spike, 4 mm. long, orbicular to obovate, entire, toothed or cleft, obtuse or acute, fringed with white hairs less dense and shorter than those on the preceding species; corolla of two divisions, surpassing the calyx by 2 mm.; upper part broadly obovate, acute, indistinctly spurred at base, ciliate; lower variously cleft with two to three laciniate, ciliate divisions; stamens with orbicular-ovate anthers 1 mm. broad and filaments inserted at the base of the corolla, surpassing it by 2 mm.; fruit unknown.

Collected by the writer in Cumberland Basin, La Plata Mountains, Aug., 1892. It grew in the alpine meadow where moisture was abundant. It is named in honor of Mr. and Mrs. B. W. Ritter of Durango, Colo., to whose kindness I owe the opportunity of visiting these mountains.

The plate shows the differences in the floral organs of the three species, all drawn to the same scale.

3. **Synthyris reflexa,** sp. nov.

PLATE IX, FIGS. 3*a*-3*d*.

Glaucous and somewhat viscid; scape erect, 1½-2 dm. high, clothed below the spike with broad, foliaceous bracts: leaves radical, 7 cm. long, elliptical-oblong, obtuse, truncate or cuneate at base, finely crenate, thin in texture; petiole 3-5 cm. long: bracts of the scape alternate, crowded, 2½ cm. long, 2 cm. wide, sessile by a broad subcordate or truncate base, broadly ovate, acute, entire or serrulate near the apex, diminishing upwards; floral bracts ovate to linear, fringed with long white hairs: flowers greenish white, reflexed on pedicels 1 mm. long; calyx of two divisions 5 mm. in diameter, orbicular, fringed like the bracts; corolla of two parts united at base, the upper broad, somewhat hood-shaped, 5 mm. broad, 8 mm. long, sparingly fringed; the lower two-cleft 5½ mm. long, 4 mm. wide, divisions laciniate, 2 mm. long; stamens two, anthers cordate, with cells not confluent, filaments inserted at the base of the corolla, surpassing it by 4 mm.; style shorter than the filaments, stigma capitate; fruit unknown.

Collected by the author in Kendall Basin, in the San Juan Mountains, near Silverton, Aug., 1890. It was quite rare.

This is the only *Synthyris* known to have reflexed flowers and two divisions to the calyx.

It is very doubtful if the genus *Synthyris* will stand in the future as it is now set forth in the Synoptical Flora; nor is it more certain that Professor Greene's transferrence of all the species to *Wulfenia* will be final.[1] In a group of genera so closely related and so polymorphous as those included under subtribe Veroniceæ in Bentham and Hooker's Genera Plantarum, botanists will always differ in regard to generic limits.

A difference in the arrangement of the leaves and habit of growth primarily separated *Wulfenia* from *Veronica;* the form of the corolla, the number of calyx divisions, the dehiscence of the anthers and the shape of the seeds separated *Synthyris* from *Wulfenia.* Professor Greene has shown the worthlessness of considering the number of calyx divisions as a generic character, and his position is reinforced by the two new species described in this paper and by two described under *Wulfenia* by Aven Nelson.[2] Professor Greene, however, does not give a diagnosis of *Wulfenia* nor tell why it, also, should not be included under *Veronica.*

If habit of growth is taken as a generic distinction, then *Synthyris* naturally falls into two genera, one containing *S. rotundifolia* and *S. reniformis;* the other, the remaining species and perhaps the original *Wulfenia.* If other characters are to be taken, many genera would result and the synonymy become much involved. It seems simplest to follow Bentham and Hooker and Gray and leave these uncertain problems to the future; so the new species of the Colorado mountains have been described as *Synthyris.*

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[1] Erythea, Vol. II, p. 80.

[2] Torr. Bull., Vol. XXV, pp. 281, 282.

IV.—FURTHER OBSERVATIONS ON THE MANZANITAS OF MT. TAMALPAIS.

Since the publication of the article on the "Manzanitas of Mt. Tamalpais,"[1] I have been able to explore parts of the mountain and the neighboring hills hitherto unknown to me. Scarcely a week has passed that I have not spent Sunday on the hills of Marin County. As a result of these frequent visits and the new territory explored, new facts concerning the distribution, time of blooming, and characteristics of the different species of *Arctostaphylos* have been observed.

1. **Arctostaphylos nummularia** *Gray.*— This I have found only on Mt. Tamalpais proper. It does not seem to grow on the hills around Fairfax, where the Big Carson and the Little Carson Creeks take their rise, nor on the ridge between Bear Valley and Bolinas. It is abundant on the Boot-jack and Throckmorton Trails, also on the trail leading directly from Mill Valley up the mountain and on the trail from the Potrero to the head of Cataract Gulch. While well formed fruit can be found at almost any time of the year, ripe fruit is seldom seen and never persists as does the fruit of all the other species.

2. **Arctostaphylos canescens** *Eastwood.*— This, too, seems to be confined to Mt. Tamalpais and apparently grows only on the southern slope. It loves bleak, gravelly hillsides, where it often holds exclusive possession. On the Throckmorton Trail a few bushes are to be seen, a few more on the Bill Williams Trail; but on the West Point Trail it is abundant, adorning the slopes during the winter with its blooming bushes.

On November 7th, the first flowers were seen. The plants on the Throckmorton Trail were beginning to bloom. The delicate pink blossoms have their beauty much enhanced by the gray-green foliage. From this date until

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[1] See this Vol., p. 81.

February 20th, it was seen in bloom every Sunday. Well formed fruit was observed on the bushes on the Throckmorton Trail before those on the higher West Point Trail had ceased blooming. Some plants only a few inches high, easily pulled up by the roots, and with but one or two branches, were laden with blossoms. The number of these small plants indicates a species full of vigor, seeking new territory for habitation. The roots of the larger plants are spreading rather than deep and are easily pulled up. During May the berries become ripe, and before the other species show ripe fruit this has usually lost all its berries.

3. **Arctostaphylos glandulosa** *Eastwood*.—On December 19th the first plant of this species was found in bloom. It may have been blooming also elsewhere on the mountain; but two weeks earlier flowers were not seen on the plants near the foot of the Boot-jack Trail, where I have always found them first in bloom. On May 1st, fully grown fruit was observed on bushes on the Boot-jack Trail. This species is the most abundant, found everywhere on the slopes and ridges of Mt. Tamalpais and the Fairfax hills. I am still uncertain whether two species ought to be recognized where I have described but one or whether, with all its forms, it ought not to be considered a variety of *A. tomentosa*.

4. **Arctostaphylos montana** *Eastwood*.—This has a wide range in Marin County. It is usually found only on the uplands and is especially partial to the bluish gray volcanic areas. Wherever *Cupressus Goveniana* and *Quercus dumosa* var. *bullata* are to be found this also will be seen. Besides Mt. Tamalpais, it is found on the Fairfax hills, where it covers large sections of country, being the most abundant manzanita there. It was first seen in flower February twenty-second, on the trail to the source of the Big Carson. Only one bush was in bloom, situated in a warm and sheltered spot. On May 1st it was still blooming

on Mt. Tamalpais, but evidently nearing the end of its season. Having had an opportunity of examining fresh specimens of *A. Hookeri* in bloom, sent me from Monterey by Miss Marion Rouse, I am confirmed in my belief in the identity of this species as distinct from *A. Hookeri.* The flowers of the latter are much smaller, the leaves not so thick, and the fruit, as noted before, has much thinner pulp.

V.—TWO SPECIES OF ERIODICTYON HERETOFORE INCLUDED UNDER ERIODICTYON TOMENTOSUM.

The genus *Eriodictyon* was founded on *E. crassifolium*, collected near San Diego, Calif., and described by Bentham in the Botany of the Sulphur, page 37. Previous to this, another species had been described and figured by Hooker and Arnott as *Wigandia Californica*.[1] In the Botany of the Sulphur, Bentham transferred this to *Eriodictyon*, giving it the appropriate name *E. glutinosum*. It again suffered a change of name when Torrey[2] restored its earliest specific name, calling it *E. Californicum*.

Bentham described still another species in the Botany of the Sulphur as *E. tomentosum*, differing from *E. crassifolium* in having pedunculate dense cymes, broader leaves, and very numerous, smaller flowers. This Dr. Torrey took as the type under which *E. crassifolium* should be included, and suppressed the former name, giving, as his reason, the numerous intermediates observed by Dr. Parry and himself around San Diego and elsewhere.

Gray accepted Torrey's view with the remark: "*E. crassifolium* Benth. was doubtless rightly united with this by Dr. Torrey, and this name should have been preferred, but the other is good and of the same date."[3]

Greene described a plant from Monterey County, Calif., collected by Mr. Brandegee in 1885, as true *E. tomentosum*, and restored the name *E. crassifolium* to the plant of Southern California.[4]

The attention of the writer was attracted to this puzzle by the rediscovery of Mr. Brandegee's plant near Jolon, in the San Antonio Valley, Monterey County, Calif. Truly it seemed that Professor Greene had solved the mystery; but to be certain, specimens of this from Monterey County and of the large flowered *E. crassifolium* from San Diego were sent to Kew for comparison with the types. The following

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[1] Bot. Beech., Pl. LXXXVIII, p. 364.

[2] Bot. Mex. Bound. Sur., p. 148.

[3] Proc. Am. Acad., Vol. X, p. 331.

[4] Bull. Cal. Acad. Sci., Vol. I, p. 201.

reply was received: "*Eriodictyon crassifolium* and *E. tomentosum* are conspecific and your plant named *tomentosum* is apparently an undescribed species which we also possess from J. G. Lemmon without locality, and from G. R. Vasey, Monterey, 438, coll. July, 1880."

Since Lemmon, Vasey, and Brandegee have all passed through Jolon when on their way to the Santa Lucia Mountains in search of *Abies bracteata*, doubtless the region of the writer's collection of this species coincides with theirs and will be considered as the type locality of the new species.

1. **Eriodictyon niveum,** sp. nov.

PLATE X, FIGS. 3*a*–3*d*.

Densely white-tomentose or flavescent; stems three or four feet high, growing in clumps, very leafy below the inflorescence: leaves thick, elliptical-ovate or obovate, 4–6 cm. long, 1–3 cm. wide, entire or crenate, except on the cuneate base, apex acute or obtuse, lower surface reticulate-rugose, upper with veins scarcely discernible; petiole broad, 5–10 mm. long: panicle terminating a long, naked peduncle, compactly or widely branched, the stout branches varying much in length on different plants; cymes densely flowered, with the lower bracts obovate or spatulate, tapering to broad petioles, the upper oblanceolate to linear; flowers small, almost sessile; calyx equalling the corolla tube, divisions linear-subulate, densely clothed with white silky hairs; corolla white or tinged with lavender, 4 mm. long, urceolate, glandular-hirsute externally, glabrous within, tube furrowed longitudinally, slightly contracted under the five small spreading lobes; stamens with the free portion short, inserted below the throat, anthers oval, 1 mm. long; styles shorter than the sepals; capsules orbicular, obtusely 5-angled, tomentose, especially on the angles; seeds four or sometimes five, brown, minutely favose, variable in shape, often keeled, more than 1 mm. long.

Collected by the writer near Jolon, Monterey County, Calif., in flower June 1, 1893, and in fruit Sept. 22, 1894.

The following specimens, besides, are in the Herbarium of the Academy:—

Lobb, San Antonio Valley (date not given); T. S. Brandegee, Monterey County, 1885; Dr. Palmer, "Perhaps from Monterey County," 1876.

There is also a specimen without flowers or fruit collected by T. S. Brandegee at Zapato, Fresno County, Calif. The foliage and pubescence are exactly of this species.

2. **Eriodictyon Traskiæ**, sp. nov.

PLATE X, FIGS. *2a–2c*.

Densely white-tomentose, except the dark-colored, glandular-hirsute calyx: leaves elliptical, 5 cm. long, 15 mm. wide, acute at apex, the base narrowed to a petiole 5mm. long, margins dentate except near the base, veins distinct on the lower surface, barely evident on the upper: panicle slightly surpassing the leaves, with branches spreading or curving upwards, rather slender, glandular and tomentose, bracts from elliptical with dentate margins to lanceolate or linear with margins entire; cymes densely flowered: flowers small, on pedicels 1 mm. or more in length; calyx divisions five, narrowly linear, not uniform in length, 4–5 mm. long; corolla purple, the tube equalling the calyx, 5 mm. long, contracted at base and throat, furrowed longitudinally, divisions of the limb irregularly orbicular, not uniform in size, glandular-hirsute externally as well as the upper part of the tube; stamens inserted half way down the tube, almost sessile; style branches glabrous, 1½ mm. long; ovary ovoid, glandular-hirsute; fruit unknown.

This was discovered May, 1897, on one volcanic upland on Santa Catalina Island, Calif., at an elevation of about 1500 feet, by Mrs. Blanche Trask, the indefatigable local botanist in whose honor it is named. Probably, this is the plant collected by Lyon on Santa Catalina, referred by Dr. Gray to *E. tomentosum*.[1] It approaches *E. niveum* but is undoubtedly a distinct species.

A plant slightly differing from the above was collected in the Santa Inez Mountains, Calif., by T. S. Brandegee, in 1888.

The peduncles are stout, with thicker and more spreading branches, leaves larger and coarser, pedicels much longer, 4 mm. long, while the filaments are short but distinctly evident, the corolla has the same shape, the lobes of the border being not quite so broad. As this, too, is in flower only and very young, comparisons of the fruit and seed cannot be made.

The plate shows the floral organs of *E. crassifolium* from San Diego, part of the collection sent to Kew, and also those of *E. niveum* and *E. Traskiæ*, all drawn to the same scale, five times the actual size.

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[1] Suppl. Synop. Fl., p. 420.

VI.—NEW SPECIES OF PACIFIC COAST PLANTS.

1. **Campanula angustiflora,** sp. nov.

PLATE XI, FIGS. *2a–2c*.

Annual, scabrous-hispid; stems slender, angled, 1–3 dm. high, branching diffusely from the base to the top with upwardly spreading branches: leaves sessile, ovate to orbicular, acuminate or acute, deeply dentate, 5–15 mm. long, 3–10 mm. wide: flowers axillary on stout, upwardly spreading peduncles, twice to four times the length of the flower; divisions of the calyx linear-subulate, almost equalling the corolla, connivent in fruit; corolla tubular, with five triangular lobes; stamens included, the anthers linear, longer than the thin, broadly triangular-subulate filaments; ovary obovoid, slightly constricted at the apex, ribbed; style short, thick, with three revolute stigma lobes; fruit strongly ribbed, irregularly humped with the three valves above the middle; seeds numerous, minute, shining, light brown, with a small darker spot at one end, 3-sided or keeled.

This has been included under *C. exigua* Rattan by Mrs. Brandegee, who first discovered it on Mt. Tamalpais, July 5, 1886, collecting it again in the same locality June, 1890, and July, 1893. She also found it on Mt. St. Helena, May to July, 1889.[1] It was rediscovered on Mt. Tamalpais by Mr. J. W. Congdon, and by the writer near the water tank at the head of the East Fork of Sequoia Cañon on the railroad track.

Besides the points of difference shown by the figures of the two species, there are differences in habit of growth and general appearance. *C. exigua* is lower, more slender, less branched, and with the branches divaricately spreading; the leaves are smaller and narrower, and almost hug the stem. The figures are drawn from a specimen collected by Volney Rattan on Mt. Diablo, Calif. It is probably part of the type. In the Herbarium of the Academy there are specimens from Mt. Hamilton, Calif., collected by W. W. Price, similar to those of the Mt. Diablo *Campanula.*

From Priest Valley in Monterey County, Calif., very young specimens of an annual *Campanula* were collected by the writer, May 12, 1893, resembling *C. angustiflora* in

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[1] Zoe, Vol. I, p. 83.

habit of growth, shape of corolla, and character of stamens and style. The leaves are much narrower, and the calyx divisions vary in length in the same flower and surpass the corolla. This I leave under *C. angustiflora*, as these small annual *Campanulæ* may be more common than is now supposed and the two species may vary a good deal among themselves. Their season is short, they grow in out-of-the-way places, and they are inconspicuous; so the chances of their discovery and collection are small.

2. **Romneya trichocalyx,** sp. nov.

Plate XI, Figs. 4*a*–4*c*.

Perennial, glaucous and glabrous except for the scattered, spreading setæ on the peduncles, rhachis, petioles, and lower margins of the leaves; stems many, suffruticose, laxly spreading from the base as they grow older, leafy, branched: leaves rather thin, with conspicuous venation, ovate-orbicular in outline, variable in size and divisions, pinnately 3–5 parted, the lower divisions entire, toothed or lobed, the terminal larger, cuneate, 3–5 cleft; leaves on the peduncle closely surrounding the bud, much smaller, the divisions linear, narrower, more numerous, and more setose-ciliate; petioles flat, 5 mm. to 2 cm. long: calyx of three imbricated sepals covered with upwardly appressed, scabrous setæ, except near the margins and on the underlapping parts; corolla white, texture crape-like, 8–15 cm. in diameter, variable in the shape, size, and number of the petals; stamens numerous, with linear-oblong anthers and slender filaments, the lower half brownish purple, the upper yellow; styles 10–11, viscid, incurved; ovary ovoid, densely setose; capsule oblong-ovate, the walls breaking irregularly from the stout, straight ribs of the framework; seeds not seen.

This has long been included under *Romneya Coulteri*, from which it is most markedly distinguished by the setose calyx. There is no doubt of the plant with smooth calyx being true *R. Coulteri*, since the description and figure of the type confirm it.[1]

Miss Kate E. Cole of Oakland first drew my attention to the fact that there were two kinds of *Romneya* in cultivation, describing the marked differences between them; but it was not until last fall when I myself saw the two kinds growing side by side in Golden Gate Park, San Francisco, that I began to look up the matter.

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[1] Lond. Journ. Bot., Vol. IV, p. 75, Tab. III.

So far as I have been able to discover, there are but two plants of *R. trichocalyx* in the Park. Both grow back of the statue of Halleck where two paths meet. *R. Coulteri* grows there too; but the best specimen is to be found near the Haight St. entrance. It is also very abundant in other parts of the Park, being more desirable as a cultivated plant owing to its greater size and compact habit.

Taking the plants in the Park for comparison, supplemented by the specimens in the Herbarium of the California Academy of Sciences, the following are the points of differences:—

Habit.—*R. Coulteri* forms large, erect, close clumps, with many strong branches from along the stems. *R. trichocalyx* does not form close clumps because the stems as they grow tall have a tendency to lean over as if too weak to stand; they are more leafy, less branched, and neither so tall nor so stout.

Leaves.—The leaves of *R. Coulteri* are thicker in texture, with fewer and larger divisions, becoming simple on the peduncle but never growing close under the flower, thus leaving the upper part of the peduncle naked. The differences in the leaves, however, are not always to be depended on as the leaves of *R. trichocalyx* are so variable, often closely approaching those of *R. Coulteri.* The upper leaves of *R. trichocalyx* however always become more dissected on the peduncle and grow close under the flower.

Inflorescence.—The peduncles of *R. Coulteri* are stouter and more spreading than are those of *R. trichocalyx.*

Calyx.—*R. Coulteri* has a smooth calyx; that of *R. trichocalyx* is setose.

Corolla.—In the specimens in the park, *R. Coulteri* has larger flowers, with the texture less crape-like than in *R. trichocalyx.* We have specimens of the latter in the Herbarium with corollas fully as large as any of *R. Coulteri.*

Fruit.—When the walls of the capsule break away leaving the skeleton of the pod, the ribs of the pod of *R. Coulteri* are more slender, becoming attenuated towards the apex and convolute; those of *R. trichocalyx* are stouter, uniform, and do not twist around.

The figures show the differences in the buds and the leaves of the peduncle. They were drawn from fresh specimens from Golden Gate Park, smaller than ordinarily because they were the last of the season. Both species bore fruit, but as it did not ripen, I was unable to compare the seeds. The pods from which the comparison was made came from herbarium specimens.

The following specimens of each species are in the Herbarium of the California Academy of Sciences:—

Romneya Coulteri, Anaheim, July, 1885, M. K. Curran, (with fruit and buds).
Baja California, W. G. Wright, (in flower).
Golden Gate Park, San Francisco, (cultivated).
Santiago Creek, near Orange, Orange Co., Calif., Miss Agnes Bowman, June, 1898, (with flowers and buds).
Romneya trichocalyx, Aliso, Baja Calif., T. S. Brandegee, May 30, 1893, (in flower and dry fruit).
Sausal, Baja Calif., T. S. Brandegee, June 4, 1893, (in flower).
Cañon de Gato, Baja Calif., T. S. Brandegee, June 5, 1893, (stem only).
Near Temecula, Riverside Co., Calif., No. 393, S. B. Parish, Oct., 1882, (in flower).
Matilija Cañon, Ventura Co., Calif., F. W. Hubby, May 18, 1895, (in flower).
Santa Maria R., Santa Barbara Co., Calif., Mrs. Ida E. Blochman, (a bud only).
Golden Gate Park, San Francisco, (cultivated).

3. **Sedum Congdoni,** sp. nov.

PLATE XI, FIGS. 5*a*–5*d*.

Stem 1–6 cm. high, simple or branched from near the base, with slender, erect, tortuous branches: leaves alternate, 2–4 mm. long, 1–2 mm. wide: very fleshy, ovate, obtuse, sessile, the place of insertion above the base; flowers yellow tinged with red, sessile in sparingly branched, few-flowered cymes terminating the branches; calyx with five short, broadly triangular divisions, acute and red-tipped; petals five, ovate-lanceolate, less than 2 mm. long, red at the apex; stamens ten, with thread-like filaments shorter than the petals; anthers kidney-shaped; ovaries five, tuberculate near the apex, 1-ovuled; styles curved outwards; fruit unknown.

This might be mistaken for *Sedum pumilum*, since both are small and have one-seeded follicles. The latter has much larger yellow flowers, linear-lanceolate petals, erect styles, and glabrous ovaries. The fringe of hairs at the suture of the follicle is much longer and finer in *S. pumilum* than in *S. Congdoni*. The former is farinose when young, becoming glabrous with age. The figures are designed to show the differences in regard to the petals and pistils of the two species.

This was discovered by Mr. J. W. Congdon, at Grant's Springs, Mariposa County, Calif., and collected April 9, 1898. It adds another to his namesakes in Mariposa County, appropriately associating his name with the flora which he has done so much to make known.

4. **Cercocarpus Traskiæ,** sp. nov.

PLATE XI, FIGS. *7a–7e.*

Tree, 10 to 25 feet high; trunk 2 to 10 inches in diameter, 6 to 8 feet to the lowest branches; bark rough, grayish brown externally, reddish on the inside; upper branches covered with a thin, downy tomentum: leaves orbicular to oval, 2–6 cm. long, 1–5 cm wide, with obtuse or acute apex, subcordate, truncate, or cuneate base; margin revolute from deeply dentate to entire; upper surface dark green, glossy, glabrous, except the downy young leaves; lower surface densely white-tomentose, veins large and conspicuous on both sides; petiole stout, about 5 mm. long. Inflorescence androgynous, the polygamous flowers numerous in axillary umbels; calyx white-tomentose, with tube 1 cm. long and border 5-toothed, open campanulate, 5–8 mm. in diameter, glabrous within; stamens numerous, anthers tomentose, with two linear-oblong cells united only at the insertion of the slender filament; perfect flowers with stigmas curved like shepherd's crooks, style exserted; akenes 1 cm. long, linear-oblong, covered with upwardly appressed silky hairs, tipped by the circinate, persistent style, about 5 cm. long, clothed with long, fine, silky hairs spreading horizontally.

This, the most beautiful of the Pacific Coast *Cercocarpi*, was discovered by Mrs. Blanche Trask at the southern part of the island in a volcanic region known as "Salte Verde." It is a wild place, too rough for men on horses, with no trails but those made by the goats. Even in winter the heat is great. She writes as follows concerning the place and the trees: "There are about forty or fifty trees in an arroya so small that there is but room to squeeze through, a southern exposure where Ruin and Earthquake have passed and in whose footprints but few plants have dared to rise." The sea dashes at the base of this arroya, the walls of which rise to a height of from 100 to 500 feet. The trees are all isolated, not at all forming thickets.

That any one should have found a new tree on an island that so many botanists have visited is surprising; but it is due to the great enthusiasm, the wonderful power of exploration, and the intense love for Santa Catalina Island and its flowers which Mrs. Trask possesses. It is with pleasure that I give her name to this tree.

Photographs of several of these trees taken recently by Mrs. Trask show them to have widely spreading branches and graceful habit, and to be well worthy of cultivation. The branches are abundantly adorned with rosettes of white tomentose flowers at all the leaf axils, the contrast of which against the dark, glossy green of the upper leaf surface is striking and beautiful. The same contrast occurs between the upper and lower surfaces of the leaves, the beauty of which is enhanced by the strong, even venation and revolute margins of the leaves.

This tree is unlike the other Pacific coast species and perhaps approaches *C. fothergilloides* H. B. K., the Mexican species, more nearly than any other. It seems to be a type of *Cercocarpus* isolated and distinct.

5. **Calochortus Purdyi,** sp. nov.

PLATE XI, FIGS. 8*a*–8*f*.

Glabrous and glaucous; stem 2–3 dm. high, rather stout, erect, branching, two to many-flowered, not bulbiferous at base: radical leaf solitary, sheathing the stem, linear-lanceolate, acuminate, 2 dm. long, 1 cm. wide, the upper surface bright green, the lower glaucous and ribbed with the filiform nerves; bracts foliaceous, lanceolate-acuminate, amplexicaul, upper ones opposite; pedicels equalling or slightly surpassing the bracts, erect in flower, recurved in fruit: flowers broadly open-campanulate; sepals from elliptical to narrowly ovate, abruptly acuminate, tinged with purple on the outer surface, purple-veined on the inner, two-thirds as long as the petals; petals broadly obovate-cuneate, acute or rounded at apex, creamy white or tinged with purple, bearded all over the inner surface with long hairs which are white on the upper half of the petals, purple on the lower, somewhat arched by the narrow, transverse, semicircular, conspicuous gland, the shallow pit of which is covered by a densely hairy narrow scale; anthers lanceolate, abruptly acuminate, cream color or purplish, shorter than the filaments, which broaden to the base; capsule 3 cm. long, 2 cm. wide, broadly elliptical, with the three thin wing-like valves transversely veined.

This belongs to the § *Eucalychortus* according to Watson's arrangement in the Botany of California. In habit it resembles *C. albus*, but in general is more like a giant *C.*

Maweanus. Its nearest relative is, however, *C. Tolmiei,* which belongs to the same region and from which it can readily be distinguished by the absence of the scale covering the gland of the latter. Most of the *C. Tolmiei* in herbaria is probably this species. It was compared with the original specimen of *C. Tolmiei* at Kew by J. G. Baker who says: "The Willamette plant differs a good deal from the original *C. Tolmiei. C. Tolmiei* has pale lilac petals bearded all over the face, no spot, no scale, no obtuse anthers." There is no true *C. Tolmiei* in the Herbarium of the Academy. We have specimens collected by Thos. Howell, from Grant's Pass, Oregon, from Prairies, Western Oregon, April 1881, and from Hillsboro, Oregon, May 1881, all marked *C. Tolmiei,* but each with a scale covering the gland and with flowers creamy rather than blue. It would seem as if the anthers were variable, since all of *C. Purdyi* that I have examined have acuminate anthers; but evidently the specimens sent to Kew had obtuse anthers.

C. Purdyi grows in the Willamette Valley, in the foothills on dry gravelly soil. It is never found in shaded woods.

It is named in honor of Carl Purdy who knows *Calochorti* more intimately than anyone, and whose work on the genus in the garden, the field, and the study has accomplished so much towards determining the true specific limits in this difficult and variable genus.[1]

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[1] Since the above description was written and the drawings made, a beautiful figure of this species has appeared in "The Gardeners' Chronicle," Vol. I, 1898, p. 305, fig. 147. The flower is much larger than that of any specimen seen by me. It is not unusual, however, that plants have larger flowers under the more favorable surroundings that cultivation produces. It is a well known fact that Pacific coast species vary considerably in the size and vigor of individuals according to the amount of moisture and fertility of the soil.

EXPLANATION OF PLATE VIII.

Fig. 1. *Peucedanum insulare*, sp. nov.
  a. and *b.* Parts of the same leaf, actual size.
  c. External view of carpels, magnified as shown in figure.
  d. Cross-section of a carpel, magnified as shown in figure.

Fig. 2. *Hosackia venusta*, sp. nov.
  a, Calyx. *b*, Standard. *c*, Keel. *d*, Wing. Figures magnified 5 times.

Fig. 3. *Hosackia argophylla* GRAY.
  a, Calyx. *b*, Standard. *c*, Keel. *d*, Wing. Figures magnified 5 times.

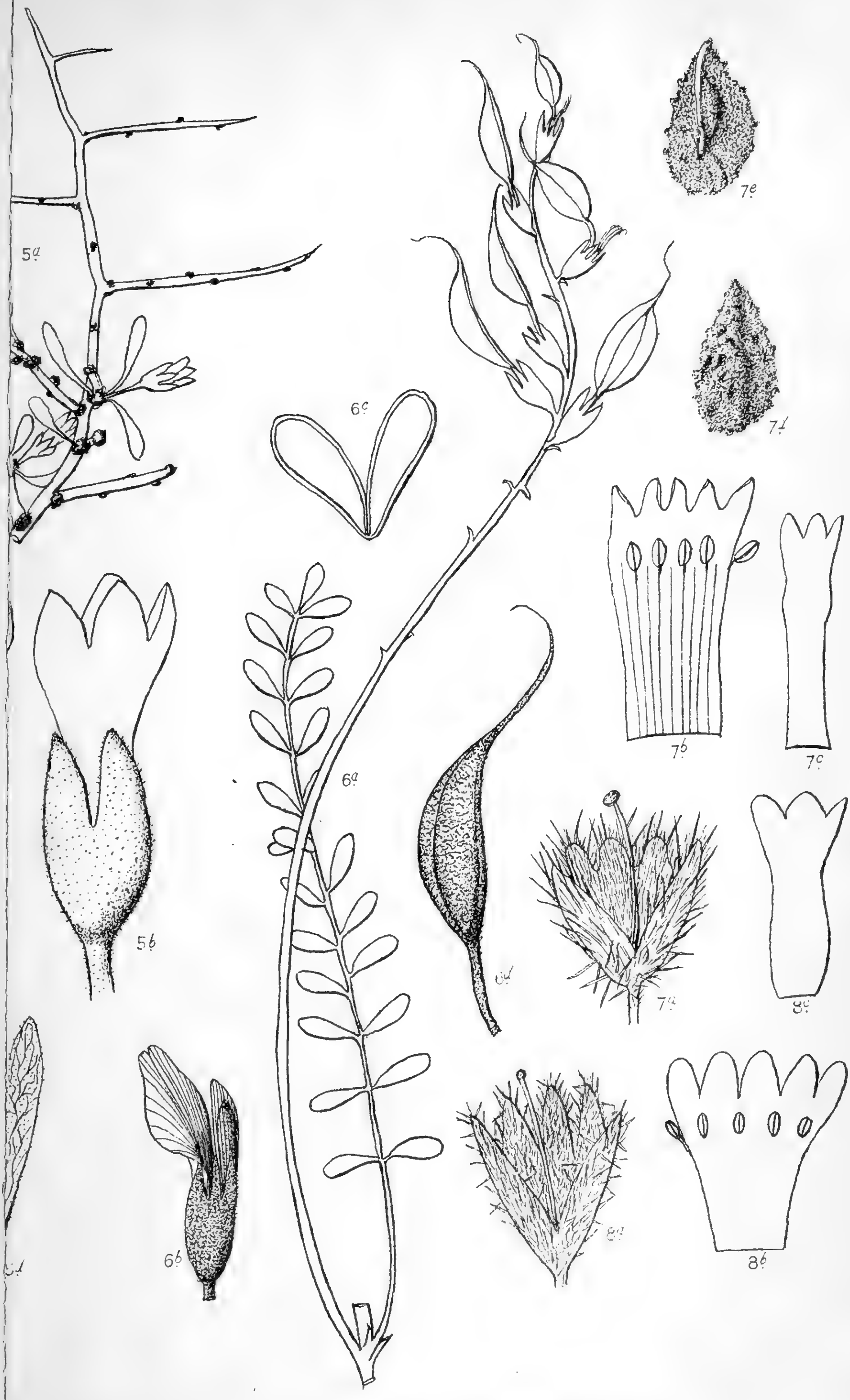
Fig. 4. *Abronia alba*, sp. nov.
  a, Flower. *b*, Immature fruit. Figures magnified 5 times.

Fig. 5. *Lycium verrucosnm*, sp. nov.
  a. Tip of branch, actual size.
  b. Flower magnified 5 times.
  c. Interior of corolla showing the position of the stamens.
  d. Interior of the calyx showing the pistil.

Fig. 6. *Astragalus Traskiæ*, sp. nov.
  a. Fruiting branch, actual size.
  b. Flower, twice the actual size.
  c. Cross-section of the pod.
  d. Mature pod.

Fig. 7. *Amsinckia St. Nicolai*, sp. nov.
  a, Calyx. *b*, Corolla spread open. *c*, Outline of corolla. *d* and *e*, two views of the akene. Figures about 5 times the actual size.

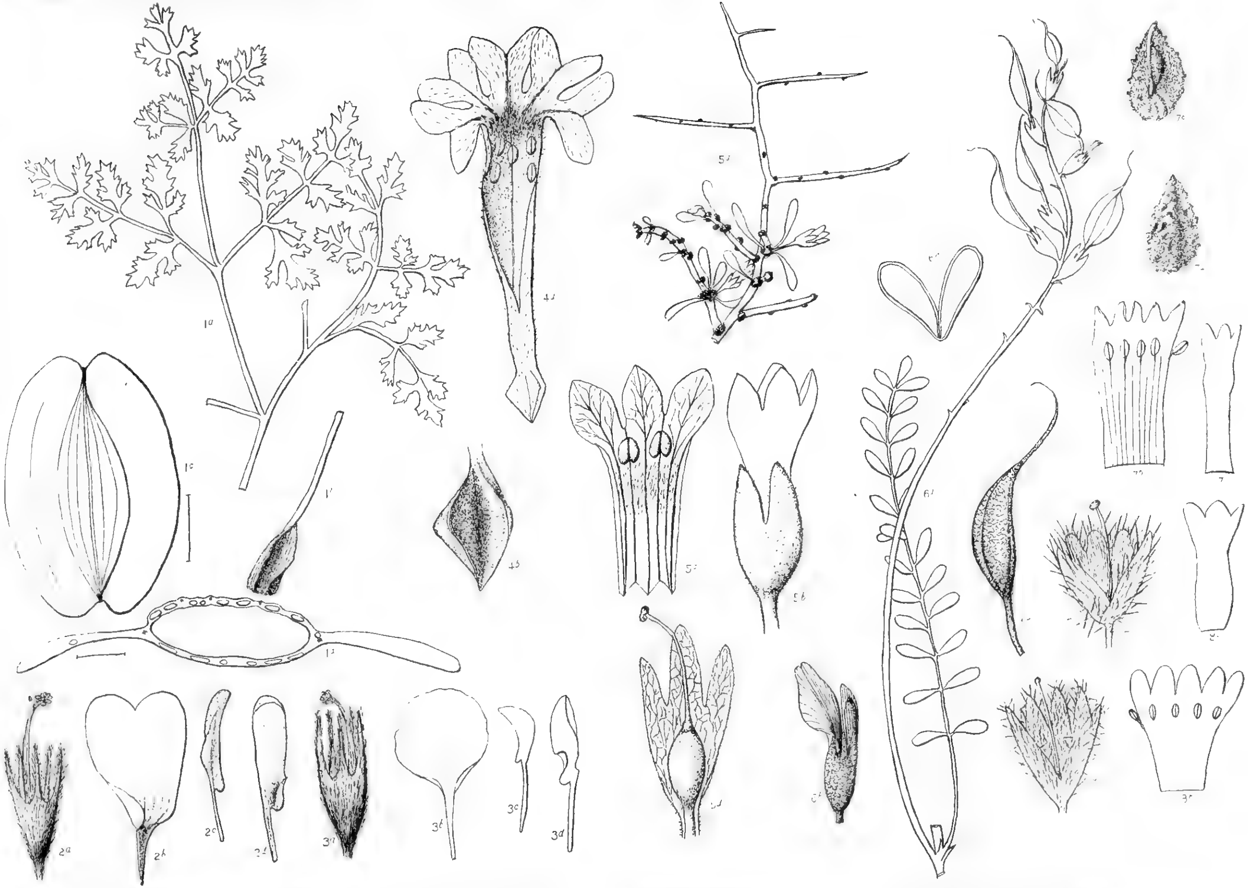
Fig. 8. *Amsinckia maritima*, sp. nov.
  a, Calyx. *b*, Corolla spread open. *c*, Outline of corolla. Enlarged as in fig. 7.



rrucosum. *Eastwood.*
s Traskiæ. *Eastwood.*

7. Amsinckia St. Nicholai. *Eastwood.*
8. Amsinckia maritima. *Eastwood.*

Lith. Britton & Rey, S. F.



1 [illegible]
[illegible]
3 Hosackia argophylla Gray.
Abronia alba. Eastwood.
[illegible]
6. Astragalus Traskiae. Eastwood
7 Amsinckia [illegible]
8 Amsinckia maritima. [illegible]

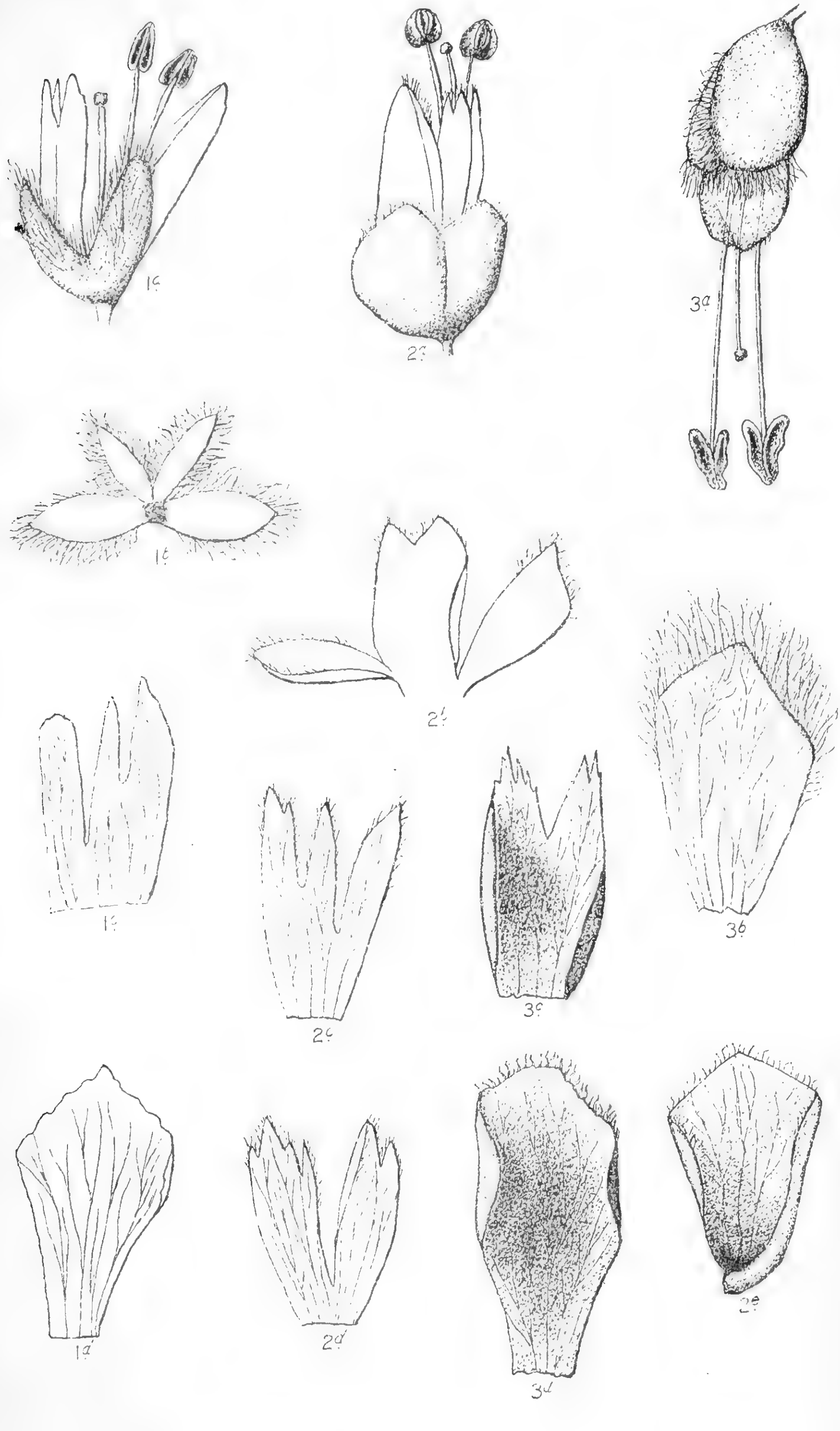
EXPLANATION OF PLATE IX.

All parts of the flowers are 5 times actual size.

Fig. 1. *Synthyris alpina* GRAY.
- *a.* Flower.
- *b.* Calyx.
- *c.* Lower part of corolla.
- *d.* Upper part of corolla.

Fig. 2. *Synthyris Ritteriana*, sp. nov.
- *a.* Flower.
- *b.* Calyx.
- *c* and *d.* Lower part of two different corollas.
- *e.* Upper part of corolla.

Fig. 3. *Synthyris reflexa*, sp. nov.
- *a.* Flower.
- *b.* One of the equal divisions of the calyx.
- *c.* Lower part of corolla.
- *d.* Upper part of corolla.



1. SYNTHYRIS ALPINA GRAY. 2 SYNTHYRIS RITTERIANA *EASTWOOD.*
3. SYNTHYRIS REFLEXA. *EASTWOOD.*

EASTWOOD, DEL.

LITH. BRITTON & REY, S.F.

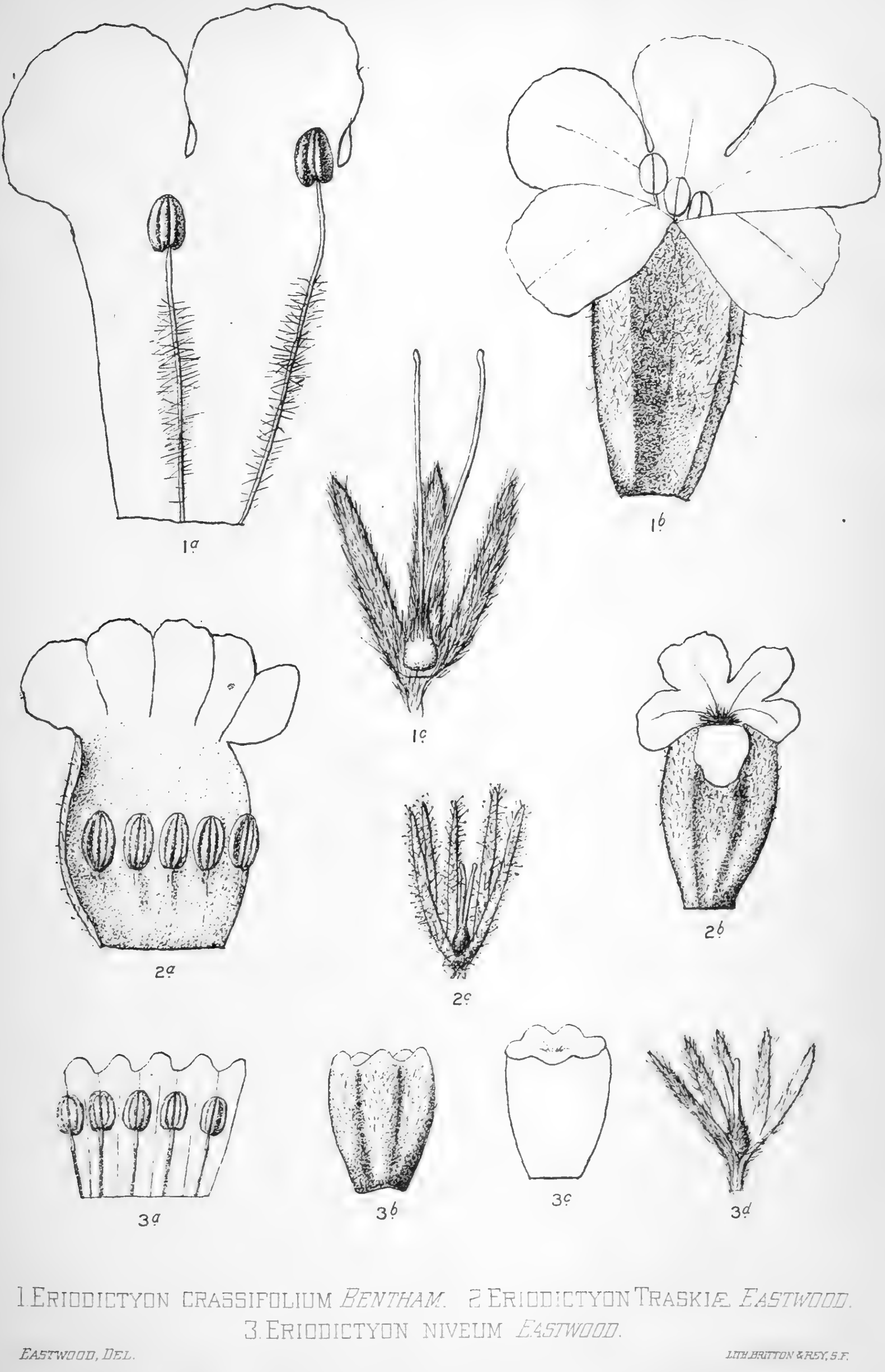
EXPLANATION OF PLATE X.

All figures are 5 times actual size.

Fig. 1. *Eriodictyon crassifolium* BENTHAM.
  - *a.* Part of corolla showing the stamens.
  - *b.* Corolla.
  - *c.* Part of calyx showing the pistil.

Fig. 2. *Eriodictyon Traskiæ*, sp. nov.
  - *a.* Interior of corolla showing the stamens.
  - *b.* Corolla.
  - *c.* Calyx spread open showing the pistil.

Fig. 3. *Eriodictyon niveum*, sp. nov.
  - *a.* Interior of corolla showing the stamens.
  - *b.* Corolla of a young flower.
  - *c.* Corolla with lobes fully expanded.
  - *d.* Calyx spread open showing the pistil.



1. ERIODICTYON CRASSIFOLIUM *BENTHAM*. 2. ERIODICTYON TRASKIÆ *EASTWOOD*.
3. ERIODICTYON NIVEUM *EASTWOOD*.

EASTWOOD, DEL. *LITH. BRITTON & REY, S.F.*

EXPLANATION OF PLATE XI.

Fig. 1. *Campanula exigua* RATTAN.
a, Flower fully expanded. *b*, Fruit. *c*, Pistil and stamen. Figures 5 times actual size.

Fig. 2. *Campanula angustiflora*, sp. nov.
a, Flower expanded. *b*, Corolla spread open. *c*, Fruit. *d*, Pistil and stamen. Figures 5 times actual size.

Fig. 3. *Romneya Coulteri* HARVEY.
a, Bud. *b*, Immature pod. Figures actual size.

Fig. 4. *Romneya trichocalyx*, sp. nov.
a, Bud. *b*, Immature pod. *c*, Leaf. Figures actual size.

Fig. 5. *Sedum Congdoni*, sp. nov.
a, Plant actual size. *b*, Flower. *c*, Follicle. *d*, Petal and stamen. The flower and its parts enlarged 10 times.

Fig. 6. *Sedum pumilum* BENTHAM.
a, Petal and stamen. *b*, Follicle. Enlarged 10 times.

Fig. 7. *Cercocarpus Traskiæ*, sp. nov.
- *a*. Tip of a twig, actual size.
- *b*. One of the larger leaves, showing the lower surface.
- *c*. Anther enlarged.
- *d*. Fruit.
- *e*. Flower.

Fig. 8. *Calochortus Purdyi*, sp. nov.
- *a*. Plant, actual size.
- *b*. Petal.
- *c*. Scale on petal enlarged.
- *d*. Sepal.
- *e*. Stamen enlarged.
- *f*. Ripe pod.

1 Campanula exigua *Rattan.*
Campanula angustiflora *Eastwood.*

3 Romneya Coulteri *Harvey*
4. Romneya trichocalyx *Eastwood*

Sedum Congdonii [illegible]
5 Sedum pumilum *Bentham*

7 Cercocarpus Traskiae [illegible]
8 Calochortus Purdyi *Eastwood.*

PHYCOLOGICAL MEMOIRS.

BY DE ALTON SAUNDERS.

CONTENTS.

PLATES XII–XXXII.

I.—SOME PACIFIC COAST ECTOCARPACEÆ.

Family ECTOCARPACEÆ *C. Ag.*

Ectocarpaceæ C. AG., Syst. Alg., XXX, 1824. Emend. Thur. Le Jol. List. Alg. Mar. Cherb., 1863.

Plant body arising from a mass of creeping filaments or a disk-like mass of cells mostly monosiphonous, more or less branched; reproductive bodies of two kinds—plurilocular sporangia formed of numerous small, densely aggregated, linear, lanceolate, or ovoid cells; unilocular sporangia cuboidal or globose.

SYNOPSIS OF GENERA.

The basal part of the plant consisting of branching filaments.
  The plurilocular sporangia intercalary with the cells of the vegetative filaments............ *Pylaiella.*
  The plurilocular sporangia not intercalary.
    Basal filaments mostly superficial .... *Ectocarpus.*
    Basal filaments ramifying through the tissue of the infested plant *Streblonema.*
The basal part of the plant consisting of a cellular, disk-like mass.
  No paraphyses............ *Phycocelis.*

I. **Phycocelis** *Strœmf.*

Phycocelis STRŒMF., Not., III, 1888, 383.

Plant small epiphytic, the basal part consisting of one or two layers, more or less circular in outline, increasing by peripheral growth. Erect filaments present; unilocular sporangia and paraphyses unknown; plurilocular sporangia sessile or stout; zoosporal cells mostly erect in a single row.

Oct. 29, 1898.

2. **Phycocelis reptans** (*Crouan*) *Kjellm.*

PLATE XII, FIGS. 8–12.

Phycocelis reptans (CROUAN) KJELLM. Handbk. I, 1890, 81.
Ectocarpus reptans CROUAN, Fl. Finist., 161, 1867.

Plant forming rounded patches 1–5 mm. in diameter, the disk-like base of one or two layers of cells 12–15μ broad. Erect filaments 2–4 mm. high, unbranched, ending in an abrupt, hyaline hair; cells 8–12μ broad, as long to twice as long as the diameter; chromatophores small, oval or band form; plurilocular sporangia lanceolate or linear-oblong, sometimes curved, 25–75μ (commonly 40–55μ) x 12–30μ, terminal on the erect filaments or rarely sessile on the basal ones.

On the leaves and air-bladders of *Nereocystis lutkeanus.* Pacific Grove, California.

3. **Phycocelis fœcunda** *Strœmf.*

PLATE XII, FIGS. 1–7.

Phycocelis fœcunda STRŒMF., Not., 1888, 383.

Spots orbicular, ½ mm. or so broad. Creeping filaments united to form a disk-like, unistratose, basal part; the erect filaments simple, of 2–6 cells which become transformed into sessile or stipitate, uniseriate, cylindrical, plurilocular sporangia, 27–40μ x 6–10μ; a cluster of long hairs in the center of each spot.

On *Macrocystis pyrifera*, *Desmarestia ligulata*, and *Pterygophora Californica.* Pacific Grove, California.

4. **Streblonema** *Derb. & Sol.*

Streblonema DERB. & SOL., Cast. Cat. Pl. Mars. Suppl., 1851, 100.

Plant body filamentous, consisting of two parts, the numerous branching filaments ramifying through the tissue of a host plant; erect filaments branched or sessile, usually ending in or bearing long hairs; unilocular sporangia large, subglobose; plurilocular sporangia simple or sometimes branched, one to many seriate.

5. **Streblonema fasciculatum** (*Thur.*) *Le Jol.*

PLATE XIII.

Streblonema fasciculatum THUR. in LE JOL. Alg. mar. Cherb., No. 100, Liste p. 73.

Vegetative filaments irregularly much branched, branches alternate, irregular, 6–9μ broad, cells 1–3 times as long as broad, slightly constricted at the joints; unilocular sporangia globose or ovoid, sessile or rarely stalked, 25–35μ x 21–30μ, borne on the main filament or the branches; plurilocular sporangia lanceolate or linear, obtuse at the apex, sessile or stalked, borne on the branches near the surface of the infested plant, 40–100μ x 8–12μ, often uniseriate.

In *Nemalion andersonii* Farl. San Pedro, California, Aug., 1896.

The plant is composed of an irregularly branching mass of filaments running through the soft central filaments of the *Nemalion.* Some of the branches extend out to the surface and are simple; others are once or twice dichotomously branched near the surface. The plurilocular sporangia are very irregular, born singly or sometimes aggregated on the outer sides of the branches, not at all branched. Long and colorless hairs are born on the branches with the plurilocular sporangia.

6. **Ectocarpus** *Lyngb.*

Ectocarpus LYNGB., Hydrophyt. Dan., 1819, 130.

Plant filiform, branching, attached to the substratum by branching, creeping filaments. Erect filaments monosiphonous, branched, occasionally corticated by outgrowths of superficial cells; unilocular and plurilocular sporangia terminal or lateral, never intercalary.

7. **Ectocarpus acuminatus,** sp. nov.

PLATE XIV, FIGS. 1–5.

Plant minute; creeping filaments forming a compact network; erect filaments simple, of the same size from base to apex, a mm. or so high; cells not at all constricted, 12–14μ broad, below as long as the diameter, above 2–3–5 times as long; chromatophores elliptical, much more abundant in the central part of the filament; plurilocular sporangia sessile on the base of the erect filaments or arising on a long or short stalk from the creeping filaments, lanceolate, very long-acuminate, sometimes tipped with a short hair, often more or less curved, 90–300μ (rarely 400μ) x 20–30μ.

Forms minute, light brown tufts in the conceptacles of *Cystoseira osmundacea.* Pacific Grove, California, July, 1896; San Pedro, California, Aug., 1896.

The creeping filaments ramify through between the paraphyses and attach themselves to the inner wall of the conceptacle; the erect filaments extend out of the mouth of the conceptacle a mm. or so; the plurilocular sporangia point toward the opening or extend just out of it.

8. **Ectocarpus ellipticus,** sp. nov.

PLATE XIV, FIGS. 6–9.

Plant minute, erect, tufted, attached to the inner wall of the cryptostomata or conceptacles by a colorless mass of creeping, branching filaments. Erect filaments unbranched or with a few unicellular branches, 9–12μ broad; cells at base once to twice as long as the diameter, above three times as long; chromatophores oval, numerous; plurilocular sporangia linear or linear-lanceolate, 75–100μ x 18–25μ, borne laterally at or near the base of the erect filaments or occasionally arising directly from the creeping filaments, sessile, or the lower on short stalks; zoosporal cells 5–8μ broad, one to few seriate; unilocular sporangia sessile, ovate or elliptical, 30–40μ x 12–18μ, borne on the same tufts with the plurilocular sporangia.

Forming minute, dark brown tufts 1 mm. high in the cryptostomata and conceptacles of *Fucus evanescens*. Pacific Grove, California.

9. **Ectocarpus chitonicolus,** sp. nov.

PLATE XV, FIGS. 1–4.

Plant 1–2 mm. high; creeping filaments numerous, branched, 15μ broad; cells once to twice as long as the diameter; erect filaments mostly unbranched, 14μ broad at base, somewhat narrowed above; cells below ½–2 times as long as the diameter, above 2–3 times as long, not at all constricted at the joints; chromatophores numerous, small and oval; plurilocular sporangia lanceolate or narrowly ovate, obtuse at the apex, 90–175μ x 20–35μ, borne laterally in the erect filaments or occasionally on the creeping ones; the lower sporangia on a long or short stalk, the upper sessile.

Forms minute tufts on the back of a chiton. Pacific Grove, California.

A variable species which approaches *E. cylindricus* in some of its forms but is separated from it by the more pointed, plurilocular sporangia and the uniformly smaller size of the vegetative parts.

10. **Ectocarpus cylindricus,** sp. nov.

PLATE XVI.

Creeping filaments irregularly branched, 12–20μ broad; cells 2–3 times as long as the diameter; erect filaments simple or giving off a few short branches below, of the same size throughout, 18–30μ broad; cells below and above 2–3 times as long as the diameter, in the central part as long as the diameter, not at all constricted; chromatophores numerous, disk shaped; plurilocular sporangia lateral, on a one- to several-celled stalk, erect, cylindrical or obovate, very obtuse above, 80–200μ x 35–45μ, opposite, most abundant below; unilocular sporangia on separate filaments, ovate or elliptical, 60–120μ x 30–40μ, usually on a one-celled stalk, or the upper occasionally sessile, often opposite.

The plant forms a compact, velvety mass 2–4 mm. high, of indefinite extent on the stems and rhizoids of *Egregia* *menziesii*, on the fruiting tips of *Cystoseira osmundaceæ*, on rocks, on *Codium adhærans* and *C. mucronatum Californicum*. Pacific Grove, California, 1895.

The form on *Cystoseira* averages slightly larger and many of the plurilocular sporangia arise directly from the creeping filaments; no unilocular sporangia were found on this form. In the forms that grow on a hard substratum, the creeping filaments are short and form a compact network on the surface; in those that grow on a soft substratum (*Codium*, etc.) the creeping filaments are much elongated and ramify between the loose threads of the host plant.

11. **Ectocarpus hemisphericus,** sp. nov.

Plate XVII.

Plant densely tufted, arising from a compact network of creeping filaments. Erect filaments unbranched at base, primary branches dichotomous, divergent, long, not at all narrowed upward, ending bluntly above, secondary branches numerous, short, clustered, many of them ending in a short, blunt hair; cells at base 15–20μ broad, 2–3 times as long as the diameter, above 22–30μ broad, 1–2 times as long as the diameter, slightly constricted at the joints; chromatophores small, numerous, linear or disk-shaped; plurilocular sporangia lanceolate or ovate, obtuse, short, 30–90μ x 14–20μ (rarely 30μ long), borne laterally on a short stalk in the upper part of the filament; unilocular sporangia short, cylindrical, 30–35μ x 20–25μ, on a one-celled stalk, on the same filament with the plurilocular sporangia.

The plant is very abundant, forming dense, hemispherical tufts 2–4 mm. high on *Pelvetia fastigiata* and *Taonia lennebackeræ*. San Pedro, California, Aug., 1896.

But one specimen was found of the form on *T. lennebackeræ*.

12. **Ectocarpus hemisphericus minor,** form. nov.

Plate XVIII, Figs. 1–3.

Vegetative filaments simple or but slightly branched, 16–21μ broad.

The plant forms small, dark brown tufts 1–2 mm. high on the fruiting tips and upper branches of *Fucus harveyanus*. The whole plant is smaller and does not form the dense rounded tufts as in the type. San Pedro, California, Aug., 1896.

13. **Ectocarpus paradoxus pacificus,** var. nov.

PLATE XVIII, FIGS. 4-7.

Erect filaments arising from a compact mass of creeping ones, 25-40μ broad, divergently branched, branches long, bearing above several short, pointed branchlets; cells about as long as broad, near the extremities one-half as long, slightly constricted; plurilocular sporangia cylindrical, ovate or lanceolate, obtuse or abruptly pointed at the apex, borne laterally on the main stem and branches on a long or short stalk, 70-150μ x 25-50μ; unilocular sporangia on short stalk or intercalary, globose, about 30μ in diameter.

Forming small tufts 2-5 mm. high on *Fucus evanescens*, most abundant on the fruiting tips; differs from the type in its smaller size, in the branching which is never opposite, and in the plurilocular sporangia which are longer and more pointed.

14. **Ectocarpus mucronatus,** sp. nov.

PLATE XIX.

Plant light olive-green, attached at base by a few long, colorless, creeping filaments. Erect filaments 1-5-6 cm. high, loosely intertwined, terminated above by a short, colorless hair, unbranched at base; main filament 30-40μ broad; cells one-third to as long as the diameter, below three times as long, not at all constricted, branches spreading, numerous, scattered, mostly short and pointed; chromatophores disk-form, numerous in each cell; plurilocular sporangia sessile, numerous, 50-155μ x 20-30μ, ovate or lanceolate, short-acuminate, borne on both the main filament and the branches.

Attached to *Zonaria tournefortii* which was washed ashore. San Pedro, California.

Also on *Petrospongium berkleyi* collected on rocks near San Pedro by A. J. McClatchie (1273).

15. **Ectocarpus corticulatus,** sp. nov.

PLATE XX.

Plant erect, 3 mm. to 3 cm. and more high, arising from a small, compact network of creeping filaments. Main filament 90-120μ broad, irregularly much branched below, above somewhat dichotomously branched; branches 50-70μ wide, spreading, irregular, some long and bearing many short branches, others short and few celled, all ending abruptly; the main stem and the branches densely corticated; cells one-half to as long as broad, but slightly constricted; chromatophores few, large, band-form, each containing several pyrenoids; plurilocular sporangia very variable in size and shape, lanceolate or narrowly ovate, short stalked or sessile, mostly 30-40μ x 12-18μ (occasionally 50–70μ x 20–30μ), most abundant on the upper side of the ultimate branches but found also along the main stem and primary branches, below apparently arising from the corticating filaments.

Forming small, loose masses, 2 mm. to 5 or 6 cm. high, on *Desmarestia ligulata*, Monterey; on *Zostera* leaves with *E. granulosus*. San Pedro, California.

16. **Ectocarpus mitchellæ** *Harv.*

PLATE XXI, FIGS. 1 AND 2.

Ectocarpus mitchellæ HARV., Ner. Bor.-Amer., I, 1851, 143.
Ectocarpus indicus SOND., Zoll. Verz. Ind. Arch. ges. pflanz., 3, 1854.

Plant arising from long, creeping filaments 10–15μ wide; cells 5–10 times as long as the diameter. Erect filaments unbranched below, bearing above many alternate branches which have numerous short, spreading branchlets; branches and branchlets pointed or ending in a short hair; main filament 25–40μ wide, 1–3 times as long as the diameter; chromatophores numerous, small, disk-form; plurilocular sporangia cylindrical, obtuse, 50–100μ x 18–35μ, sessile, mostly secund on the upper side of the branches.

Forming light olive-green tufts 1–2 cm. high on rocks at the low tide level. San Pedro, California.

A careful study of the plant showed it to be identical with the figures and description of *E. indicus* given by Askenasy in Ein. Austr. Meersalg., 8, 1894. The same plant was received from Prof. McClatchie named *E. mitchellæ*. From a careful comparison of the plates and descriptions of *E. indicus* and *E. mitchellæ*, the two species seem to be identical. Mr. F. S. Collins has received the same plant from San Diego, where it has been called *E. virescens* Thuret. He has "no doubt that Harvey's and Thuret's species are the same."

17. **Ectocarpus siliculosus parvus,** var. nov.

PLATE XXII.

Plants tufted, erect, 1–2 cm. high; primary branches numerous, alternate, gradually contracted above into long hyaline hairs, bearing many short, pointed branches. Cells with the main filament 21–30μ broad, 1–3 times as long, slightly constricted at the joints; plurilocular sporangia narrowly lanceolate or conical, 120–290μ x 20–27μ, pointed and often tipped with a long hair, borne on a long or short stalk, abundant on the main filament and the primary branches; unilocular sporangia ovate or elliptical, usually sessile, 35–55μ x 20–27μ, sometimes on the same filament with the plurilocular sporangia.

Forming a yellow fleece on sand-colored rocks. San Pedro, California, 1895. Collected by W. A. Setchell (1213).

The Pacific plant differs from the type and from the form *hiemalis* in the smaller size of the vegetative parts and the plurilocular sporangia; from the form *arctus* (Kuetz.) Kuck. in the much narrower vegetative filaments and larger plurilocular sporangia.

18. **Ectocarpus confervoides** (*Roth*) *Le Jol.*

Ectocarpus confervoides (ROTH) LE JOL., List. Alg. Mar. Cherb., 75, 1880.

Plants 2 cm. to 3 or 4 dcm. long, attached to the substratum by horizontal creeping filaments, often entangled at the base; branches alternate, gradually tapering, often corticated, cells of the larger branches 35–50μ broad, as long to one-half as long as the diameter; plurilocular sporangia narrowly lanceolate and subulate to ovate and acute, sessile to short or long stalked; unilocular sporangia ovate, globose, or elliptical.

Of this variable, cosmopolitan species two forms have been collected on the Pacific coast.

19. **Ectocarpus confervoides pygmæus** (*Aresch.*) *Kjellm.*

PLATE XV, FIGS. 5–9.

Ectocarpus confervoides pygmæus (ARESCH.) KJELLM., Handbk. I, 1890, 76.

Erect filaments arising from a compact substratum of short creeping filaments, unbranched or bearing above a few divergent, long branches, in figures 12–25μ in diameter, not at all narrowed above; cells at base 2–3 times as long as the diameter, above once to one-half as long; chromatophores large, irregular, band-form, few in each cell; plurilocular sporangia lateral and terminal, sessile or short stalked, lanceolate or conical, rather obtuse at the apex, 60–100μ x 20–30μ; unilocular sporangia lateral, abundant, ovate or globose, 25–40μ broad, often two to many seriate.

Forming an olive-brown, velvety covering on *Desmarestia ligulata* and *Dictyoneuron Californicum.* Pacific Grove, California.

20. **Ectocarpus confervoides variabilis,** form. nov.

PLATE XXIII.

Plant 2–8 mm. high, sparingly branched, branches alternate, distant, long drawn out at the tip, cells 10–30μ broad, 1–3 times as long as the diameter, not at all constricted; chromatophores large, band-form, few in each cell; plurilocular sporangia abundant, lanceolate, fusiform or narrowly ovate, usually on a one- to few-celled stalk, borne laterally on the main stem or branches, occasionally arising by a short stalk from the creeping filaments; 75–90μ x 16–35μ; unilocular sporangia globose or ovate, 15–35μ wide, single or 2–15 seriate, borne on a one- to three-celled stalk, mostly on the same filament with the plurilocular sporangia but much less common.

Forming light olive-brown tufts on *Laminaria andersonii*, *Iridæa laminarioides*, *Macrocystis pyrifera*, *Egregia menziesii*, *Nemalion multifidum*, *Alaria esculenta*, and *Lessonia littoralis*.

A very common species and one that varies considerably in the size of the vegetative filament and the plurilocular sporangia.

21. **Ectocarpus penicillatus** *C. Ag.*

PLATE XXI, FIGS. 3 AND 4.

Ectocarpus penicillatus C. AG., Syst. Alg., 1824, 162.

Plant densely tufted, dark olive-green, 1–4 cm. high; main stem and few of the primary branches corticated; cells of the primary branches 20–35μ broad, a little shorter than the diameter; secondary branches somewhat secund, short and very numerous; plurilocular sporangia linear or linear-lanceolate, sessile pedicillate, acute 85–165μ x 12–20μ, borne mostly on the secondary branches.

A dark, olive-green plant forming dense tufts on *Desmarestia ligulata*. Pacific Grove, California.

22. **Ectocarpus tomentosus** (*Huds.*) *Lyngb.*

PLATE XXIV, FIGS. 1 AND 2.

Ectocarpus tomentosus (HUDS.) LYNGB., Hydrophyt. Dan., 1819, 132.

Plants forming tufts 1–4 cm. long, of densely interwoven, irregularly, much branched filaments forming a rope-like spungy mass. Filaments 6–8μ wide; cells 2–4 times as long as the diameter; branches long, divergent, the ultimate ones standing at right angles, curved at the tip; chromatophores large, irregular, band-form, few; plurilocular sporangia linear-oblong, 40–110μ x 12–18μ, given out at right angles to the filament, sessile or occasionally short-pedicillate, often curved; "[1] sporangia almost elliptical, on short pedicels."

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[1] Hauck in Rab. Crypt. Fl. Vol., II, 330.

Common on *Fucus evanescens* and *Fucus harveyanus.* Monterey, California.

One of the commonest Pacific coast species; where it occurs in large quantities it appears to be very destructive to the "host" plant. The tufts average much smaller than those of the Atlantic coast specimens.

23. **Ectocarpus granulosus** (*Engl. Bot.*) *Ag.*

PLATE XXIV, FIGS. 3-5.

Ectocarpus granulosus (ENGL. BOT.), AG., Sp. Alg. II, 1828. 45.

Filaments 1-8 cm. high; main branches mostly opposite, many of them corticated, cells 40-75μ broad, one-half to as long as the diameter, secondary branches opposite, short, given off at wide angles, curved at the tips; ultimate branches secund, short and acute; plurilocular sporangia abundant, sessile on the secondary and ultimate branches, broadly ovate, obliquely truncate at the base, 60-100μ x 30 to 60μ; unilocular sporangia wanting.

On rocks, *Costaria mertensii*, and *Nereocystis lütkeanus*, Pacific Grove, California; and on *Zostera marina*, San Pedro, California.

The Californian plant agrees with Dr. Farlow's variety *tenuis* in the size and branching of the vegetative filaments, but has the plurilocular sporangia of the type.

24. **Pylaiella** *Bory.*

Pylaiella BORY, Dict. Class. IV, 1825, 393.

Plant filiform, monosiphonous, more or less branched, attached to the substratum by more or less branched creeping filaments. Unilocular sporangia globose, seriate, arising from the transformation of a part of the vegetative cells of any of the branches, opening laterally; plurilocular sporangia oblong or cylindrical, intercalary, opening laterally, or occasionally terminal and opening at the apex, single or many seriate.

25. **Pylaiella littoralis densa,** form. nov.

PLATE XXV, FIGS. 1 AND 2, 5 AND 6.

Vegetative filaments below densely intertwined into rope-like masses, penicillate above, branched. Branches numerous, long, opposite or alternate, bearing many short branchlets; main filament and branches 18-25μ, cells 1-3 times as long as the diameter, not at all constricted; unilocular sporangia globose, 2-15 in a series, most abundant in the branches and branchlets, 21-30μ in diameter; plurilocular sporangia scarce, mostly in the main filament, 20-50μ x 20-30μ, 2-10 or more in a chain.

The plant forms dense, ropey, dark olive-brown masses 3–8 cm. long on *Fucus* sp. Ilwaco, Washingion, near the mouth of the Columbia River.

On the southern Californian coast material was collected of what seems to be another well marked variety of *P. littoralis*. As the material was sterile I forbear making any further additions to the long list of varieties and forms of this species.

The description of the plant is given below:—

26. **Pylaiella littoralis,** var.

PLATE XXV, FIGS. 3 AND 4.

Plant composed of loosely intertwined, light olive-green filaments of indefinite length, bearing a few long attentuate branches 20–70μ broad, ½–2 times as long as the diameter, not at all narrowed upwards. Main filament and the branches bearing many one- to few-celled branchlets which stand at right angles to the filament.

Forming a light yellow flocculent mass of a few cm. long on *Amphiroa*. San Pedro, California, Aug., 1896.

II.—SPHACELARIACEÆ AND ENCŒLIACEÆ OF THE PACIFIC COAST.

Family SPHACELARIACEÆ (*Decne.*) *Kuetz.*

Sphacelariaceæ (DECNE.) KUETZ., Linn., XVII, 1843, 93.

Plant body arising from a larger or smaller mass of cellular tissue, polysiphonous, more or less branched, increasing by the division of a large terminal cell; reproductive organs (unilocular and a plurilocular sporangia) arising on a longer or shorter stalk directly from the basal tissue or borne laterally on the erect filaments.

The family includes at present about eleven genera, only one of which has been collected on the California coast.

27. **Sphacelaria** *Lyngb.*

Sphacelaria LYNGB., Hydrophyt. Dan., 103, 1819.

Plant olive-brown, tufted, filamentous, branching; basal plate fastened to rocks or in the tissue of other algæ as a substratum; both the axis and branches terminated by a large apical cell which by transverse, longitudinal, and oblique division produces a plant body, the external surface of which is composed of rectangular cells arranged in regular, transverse bands. Unilocular and plurilocular sporangia mostly extra-axillary on the branches, on a one- to few-celled stalk; propagula known in most species, on separate plants.

28. **Sphacelaria tribuloides** *Menegh.*

PLATE XXVI.

Sphacelaria tribuloides MENEGH., Lett. al Corinaldi 2, N. 1; Alg. Ital., 336, 1842.

Plant densely tufted, olive-brown; primary branches somewhat dichotomous, appressed, bearing above numerous alternate or opposite branches. Main filament composed of 4–8 siphons, 50–70μ wide, the external cells 1–½ as long as the diameter of the filament; propagula obcordate on the upper branches; plurilocular sporangia elliptical or obovate, 75–150μ x 50–70μ, on a one- to four-celled stalk.

The plant forms dense tufts 1–3 or 4 cm. high, on rocks at the low tide line. Collected by Prof. A. J. McClatchie.

Sphacelaria didichotoma, sp. nov.

PLATE XXVII.

Plant forming small, cushion-like masses 2–4 mm. high. Erect filaments arising from a small compact substratum, bearing many long, spreading, alternate branches; main filament 25–35μ broad; external cells ½ to as long as the diameter of the filament; axis of the filament of four or five siphons; propagula abundant, large, twice dichotomus, often standing at right angles to the main filament; stalk 2–300μ long, main branches 100–200μ. long.

Forming small, compact tufts on *Melobesia* and *Ahnfeldtia.* Carmelo Bay, California.

Family ENCŒLIACEÆ (*Kuetz.*) *Kjellm.*

Encœliaceæ (KUETZ.) KJELLM., Phyc. Gener., 336, 1843.

Reproductive organs developed from superficial cells or from one of the divisions of a superficial cell; plant tissue of parenchymatous structure; growth intercalary, growing point near the base.

Synopsis of Genera.

Plant body undifferentiated—of similar structure throughout.
  Plant thin, a flat, leaf-like membrane.................. *Homeostroma.*
Plant body differentiated—composed of at least two kinds of cells.
  Sporangia sunken beneath the surface, plant hollow, cylindrical, or club shaped....................................... *Coilodesme*
  Sporangia on the surface.
    Paraphyses none, plant a leaf-like membrane.
      Central layer of tissue composed of large, irregularly rounded cells............... .... *Phyllitis.*
      Central layer of tissue a loose web of slender branching filaments.................................. *Endarachne.*
      Central layer of tissue composed of a smaller, compact layer of cells reproducing by unilocular sporangia...... *Halorhipis.*
    Paraphyses unicellular.
      Plant body hollow, cylindrical................... *Scytosiphon.*
      Plant body hollow, irregulary rounded or oval..... *Colpomenia.*
    Paraphyses multicellular; plant body rounded or oval, plants mostly aggregated .... *Soranthera.*

30. Homeostroma *J. Ag.*

Homeostroma J. Ag., Anal. Alg. Cont., III, 1896, 3.
Punctaria Grev., Syn. in Alg. Brit., XLII, 1830, (in parte.)

Plant body membranaceous, of several (2-7) similar layers of cuboidal cells. Unilocular and plurilocular sporangia oblong or oval, formed from the outer layer of cells; paraphyses none, furnished with numerous clusters of hairs.

31. Homeostroma latifolium *J. Ag.*

Plate XXX, Figs. 4 and 5.

Homeostroma latifolium J. Ag., l. c.
Punctaria latifolia, Born. et Thur., Étud., phycol. p. 13.

Plant body arising from a minute disk, lanceolate-obovate, 1-5 dcm. long, tapering below to a short stalk 2-10 mm. long, olive-green, plaited on the edges; tissue consisting of 4 or 5 rows of cells; unilocular and plurilocular sporangia scattered, on the same plant.

Attached to leaves of *Zostera marina* washed ashore at Monterey, California.

32. Coilodesme *Strœmf.*

Coilodesme Strœmf., Eing. Meersalg. Isl., 173, 1886.

Plant body hollow, cylindrical or oval, on a short, solid stalk which arises from a minute disk-like base composed of two (or three) layers of tissue, an inner layer of large, mostly colorless, cylindrical cells and an outer layer of smaller colored cells. Unilocular sporangia solitary, scattered, developed from the outer layer of cells but surrounded by the continued growth of the outer layer of tissue; plurilocular sporangia, hairs, and paraphyses wanting.

33. **Coilodesme californica** (*Rupr.*) *Kjellm.*

PLATE XXIX, FIGS. 1-3.

Coilodesme californica (RUPR.) KJELLM. in Engl. and Prantl. Natürl. Pflanzenfam., Lief. 86, 202, 1893.

Adenocystis californica RUPR., Tange. Ochot, 29.

Plant olive-green, hollow, inflated, thin membranaceous or papery, cylindrical or ovoid, 2-6 dcm. long, ½-1 dcm. wide, abruptly contracted below into a short, solid stalk 1-3 mm. long. Sporangia abundant, scattered over the whole surface of the plant, ovate, 25-30μ x 12-15μ.

Abundant on the upper branches of *Cystoseira osmundacea*. Pacific Grove and San Pedro, California.

The plants appear in June as minute, smooth, air-tight sacks filled with a gelatinous liquid which is formed from the degeneration of the central tissue. They gradually increase in size, soon becoming wrinkled and folded and finally torn, especially at the ends. The walls are thin and delicate and are composed of two layers of poorly differentiated tissue. The single outer row of cells is rounded and though not well developed it is easily distinguished from the hypodermal layer. The hypodermal layer is composed of two or three layers of irregularly rounded or quadrangular cells; beneath this is the central layer composed of three or four layers of large cylindrical cells surrounded by many smaller ones. The hypodermal layer is supplied with one or two large oval chromatophores, and occasionally one is found in the central layer of tissue.

34. **Halorhipis**[1], gen. nov.

PLATE XXVIII.

Plant body solid, leaf-like, arising from a disk-like base, composed of two layers of tissue, the outer layer consisting of 2-3 rows of cuboidal cells, the inner layer of several rows of large, cylindrical cells; reproducing by unilocular sporangia collected in sori which are distributed over the whole surface of the plant; hairs numerous, forming the center of the sori; plurilocular sporangia and paraphyses wanting.

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[1] ἅλς=sea, ῥιπίς=fan.

35. **Halorhipis winstonii** (*Ands.*)

PLATE XXVIII.

Punctaria winstonii ANDS., Some New and Old Algæ, Zoe IV, 1896, 358.

Plant membranaceous, olive-brown, lanceolate, obovate, or spatulate, 8 cm.–2 dcm. long, 2–5 cm. broad, usually frayed and torn at the end, gradually narrowed below into a short stalk (2–8 mm. long). Unilocular sporangia elliptical, obovate, or pyriform, 30–45μ x 20–30μ, sori numerous, forming irregular, linear patches of various sizes.

On *Egregia menziesii* and on rocks at low tide level. Carmelo Bay, California.

In 1895 a study was made of material received from Dr. Anderson, and the distinctness of this plant from *Punctaria* was at once noticed. During the summer of 1896 several trips were made to Carmelo Bay, fresh material in all stages of growth was obtained from the same locality where the type specimens were collected by Mr. Winston and sent to Dr. Anderson.

36. **Phyllitis** *Kuetz.*

Phyllitis KUETZ., Phyc. Gener., 342, 1843.

Plant body solid, membranaceous, lanceolate or linear, tapering toward the base to a short round stem, of two layers of tissue, the cortical layer of small cuboidal cells, the inner layer of oblong colorless cells. Unilocular sporangia linear, covering the entire surface of the plant; plurilocular sporangia and paraphyses wanting.

37. **Phyllitis fascia** (*Muell.*) *Kuetz.*

PLATE XXX, FIGS. 1–3.

Phyllitis fascia (MUELL.) KUETZ., l. c.
Fucus fascia OEDER, Fl. Dan. Tav., 768, 1761.

Plant single or clustered, arising from a disk-like base, 2–30 cm. high, 1–5 cm. broad, linear, lanceolate, or elliptical, narrowed at base into a short stem, or sessile.

Two forms of this variable species have been collected on the Californian coast:

A.—Plants gregarious, linear or oblanceolate, 3–15 cm. long, 3 mm. to 1 cm. wide, gradually narrowed to a short stalk.

On rocks and *Phyllospadix* sp. Monterey and Pacific Grove, California.

B.—Plants single or somewhat clustered, broadly lanceolate, plaited on the margin, 5–9 cm. long, 1–2 cm. broad, basal stalk very short or none. San Pedro and Pacific Grove, California.

In external appearance this form is almost undistinguishable from *Endarachne.*

38. **Endarachne** *J. Ag.*

Endarachne J. AG., Anal. Alg. Cont., III, 1896, 26.

Plant plain, simple, without a rib, composed of three layers of tissue; the axillary tissue of slender, intertwined, articulate filaments, on each side of this a single row of slightly coherent hypodermal cells, outside of which there is a double layer of small cells, slightly elongated in a longitudinal direction; reproducing by plurilocular sporangia scattered over the whole surface of the plant.

39. **Endarachne binghamiæ** *J. Ag.*

PLATE XXX, FIGS. 6 AND 7.

Endarachne binghamiæ J. AG., l. c., 27.

Plant clustered, smooth, olive-brown, 5 cm. to a dcm. or so high, 1–2 cm. broad, obtuse above, tapering below to a very short stalk.

A single dried specimen of this plant, collected at San Pedro, California, was received from Prof. McClatchie about the time of the publication of Agardh's description; figure 7 was drawn before the publication was received. In external appearance the plant is almost undistinguishable from the broader form of *Phyllitis fascia;* it is, perhaps, a little thinner and more abruptly contracted at the base. Agardh places it between *Scytosiphon* and *Phyllitis.* It has been suggested that perhaps all that has been called *Phyllitis* on this coast is really *Endarachne.* A study of many specimens from Monterey and San Pedro seems to show that *Phyllitis* is quite abundant and *Endarachne* is found, so far at least, only on the Southern coast.

40. **Scytosiphon** *Ag.*

Scytosiphon AG., Sp. Alg., I, 1823, 160.

Plant body filiform when young, tubular when mature, composed of two layers of tissue, the outer of small quadrangular cells, the inner layer of thick-walled, vertically elongated, colorless cells. Plurilocular sporangia developed from the cortical layer of cells, covering the whole surface of the plant; paraphyses single celled, oblong-ovate, sometimes wanting.

41. **Scytosiphon lomentarius** (*Lyngb.*) *J. Ag.*

PLATE XXXI, FIGS. 8–10.

Scytosiphon lomentarius (LYNGB.), J. AG., l. c., 126.
Chorda lomentaria LYNGB., Hydrophyt. Dan., 74, 1819.

Plant body unbranched, tubular, arising from short (1 cm. long) filiform stalks, 1–4 dm. long, 1–10 mm. thick; constrictions regular and frequent, occurring at long intervals or entirely wanting.

On rocks, Pacific Grove, Monterey, Santa Cruz, San Pedro and San Diego, California (Averill's set).

One form found mostly below the low tide line is broad and short and the constrictions are regular and frequent; another form occurring on overhanging rocks at or above the high tide line approaches the variety *complanatus* of Rosenvinge. It is longer and more slender than the preceding form and the constrictions are seldom present. Between these two there is such an imperceptible gradation that it is difficult to draw a line of separation.

42. **Scytosiphon bullosus,** sp. nov.

PLATE XXXI, FIGS. 1–7.

Plant erect, membranaceous, hollow, dark olive-green, cylindrical to broadly ovate, 1–5 cm. high, 1–2 cm. broad, simple or lobed above, narrowed at base into a broad disk-like attachment; surface at first smooth, wrinkled, and often torn with age. Plurilocular sporangia, paraphyses, and hairs undistinguishable from those of *S. lomentarius.*

On rocks, exposed at low tide with *Leathesia* and *Ulva.* Pacific Grove, California, Aug., 1896.

A very variable species but apparently quite distinct from *S. lomentarius.*

43. **Colpomenia** *Derb. & Sol.*

Colpomenia DERB. & SOL., Phys. Alg., p. 11, 1856.

Plant body globose or oval, hollow, the walls entire or irregularly torn, composed of two layers of tissue; the inner layer consisting of a few large, rounded, colorless cells, the outer of small quadrangular colored cells. Plurilocular sporangia at first forming sori around the hairs, soon spreading over the whole surface of the plant, interspersed with unilocular, clavate, paraphyses.

44. **Colpomenia sinuosa** (*Roth*) *Derb. & Sol.*

PLATE XXXII, FIGS. 7 AND 8.

Colpomenia sinuosa (ROTH) DERB. & SOL., l. c.
Ulva sinuosa ROTH, Cat. Bot., III, 327, Tab. 12, 1806.
Asperococcus sinuosus BORY, of Anderson's list, etc.

Plant body sessile, thin, membranaceous, 4 cm. to a dcm. high, sunken and occasionally irregularly torn in the older forms, tissue .255 mm. in thickness, the outer row of cells consisting of one or two rows of cuboidal, colored cells, inner layer of two rows of large roundish cells; plurilocular sporangia 20 x 7μ, often containing the zoospores cells in two rows; paraphyses a little shorter and broader, 17 x 10μ.

The plant is usually found attached to other seaweeds and seems to prefer quiet coves. Carmelo Bay, Monterey Bay, and San Pedro, California.

45. **Colpomenia sinuosa expansa,** form. nov.

PLATE XXXII, FIGS. 4-6.

Plants aggregated, forming an indefinite expanded mass on rocks; plant tissue .425 mm. in thickness, the inner layer of tissue being composed of 5-7 rows of cells.

Santa Catalina Island near Avalon Bay, California.

46. **Colpomenia tuberculata,** sp. nov.

PLATE XXXII, FIGS. 1-3.

Plant coriaceous, olive-brown, sessile, hollow, hemispherical, 5 cm. to a dcm. or more in diameter; surface deeply convoluted, wrinkled, and folded, the whole surface covered in the mature plant with blunt tubercles 1 mm.-10 mm. high, 1-5 mm. broad. Plurilocular sporangia 22-25μ x 3-4μ, composed of 6-8 zoosporal cells in a single row; paraphyses 22 x 5μ, remaining after the zoospores have escaped.

Near San Pedro, California.

The plant forms large rounded brain-like masses attached to rocks by the whole under surface; the outer layer of tissue .65-.80 mm. in thickness, composed of 3-5 layers of cuboidal cells, the inner 5-8 rows of large irregular cells. The plant tissue is of firmer texture and much thicker than in *C. sinuosa*. The structure of the tissue is very similar to that of *Hydroclathrus cancellatus*.

47. Soranthera *Post. & Rupr.*

Soranthera Post. & Rupr., Illustr. Alg., 19, 1840.

Plant body hollow, inflated, composed of two layers of tissue, with a cortical layer of small, colorless cells, the inner of large, nearly colorless cells. Unilocular sporangia forming sori which are distributed over the entire surface of the plant; paraphyses unicellular, hairs abundant in the center of each sori; plurilocular sporangia unknown.

48. Soranthera ulvoidea *Post. & Rupr.*

Plate XXIX, Figs. 4 and 5.

Soranthera ulvoidea Post. & Rupr., l. c.

Plants gregarious, sessile, membranaceous, olive-green, globose or oval, 2–8 or 10 cm. high. Sori very abundant, evenly and closely distributed over the whole surface of the plant. Unilocular sporangia clavate, 70–100μ long, surrounded by numerous linear paraphyses which are nearly twice as long.

In sheltered coves, usually on *Rhodomela larix*, occasionally on rocks and other algæ. Monterey, California.

EXPLANATION OF PLATES.

PLATE XII.

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Figs. 1–7. *Phycocelis fœcunda* Strœmf. 148

Figs. 1–3 on *Macrocystis pyrifera*. 1 nat. size; 2 and 3 x 450.

Figs. 4–7 on *Desmarestia ligulata*. 6 nat. size; 4, 5 and 7 x 450.

Figs. 8–12. *Phycocelis reptans* (Crouan) Kjellm. 148

Figs. 8 and 9 nat. size; 10 x 80; 11 and 12 x 450.

PLATE XIII.

Streblonema fasciculatum (Thur.) Le Jol. 148

Figs. x 450.

PLATE XIV.

Figs. 1–5. *Ectocarpus acuminatus*, sp. nov. 149

Figs. 1 and 2 x 80; 3–5 x 450.

Figs. 6–9. *Ectocarpus ellipticus*, sp. nov.

Fig. 6 nat. size; 7 x 80; 8 and 9 x 450. 149

PLATE XV.

Figs. 1–4. *Ectocarpus chitonicolus*, sp. nov. 150

Fig. 1 x 60; 2–4 x 450.

Figs. 5–9. *Ectocarpus confervoides pygmæus* (Aresch.) Kjellm. 154

Fig. 5 nat. size; 6 x 60; 7–9 x 450.

PLATE XVI.

Ectocarpus cylindricus, sp. nov. 150

Figs. 1 and 6 x 80; the others by 450.

PLATE XVII.

Ectocarpus hemisphericus, sp. nov. 151

Fig. 1 nat. size; 2 x 65, 3–8 x 450.

PLATE XVIII.

Figs. 1–3. *Ectocarpus hemisphericus minor*, form. nov. 151

Fig. 1 x 65; 2 and 3 x 450.

Figs. 4–7. *Ectocarpus paradoxus pacificus*, var. nov. 152

Fig. 4 nat. size; 5 x 80; 6 and 7 x 450.

PLATE XIX.

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Ectocarpus mucronatus, sp. nov. 152
Fig. 1 x 80; 2–4 x 450.

PLATE XX.

Ectocarpus corticulatus, sp. nov. 152
Fig. 1 x 6; 2 x 80; 3–5 x 450.

PLATE XXI.

Figs. 1, 2. *Ectocarpus mitchellæ* Harv. 153
Fig. 1 x 65; 2 x 450.
Figs. 3, 4. *Ectocarpus penicillatus* C. Ag. 155
Fig. 3 x 90; 4 x 450.

PLATE XXII.

Ectocarpus siliculosus parvus, var. nov. 153
Fig. 1 x 65; 2–8 x 450.

PLATE XXIII.

Ectocarpus confervoides variabilis, form. nov. 155

Figs. 1 and 4 x 80; 2, 3 and 5 x 450; 6 one-half nat. size; 7 x 60; 8–10 x 450.

PLATE XXIV.

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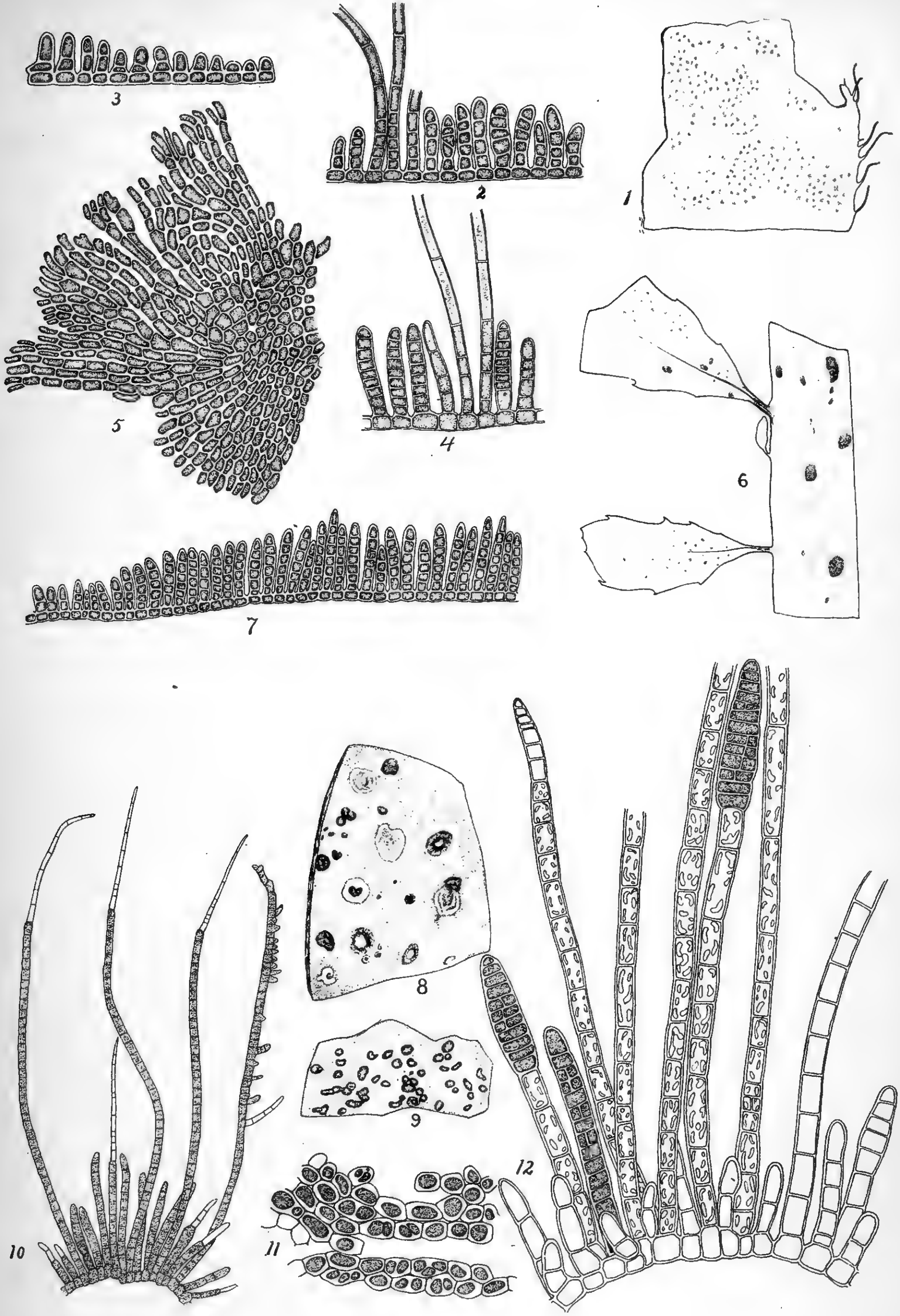

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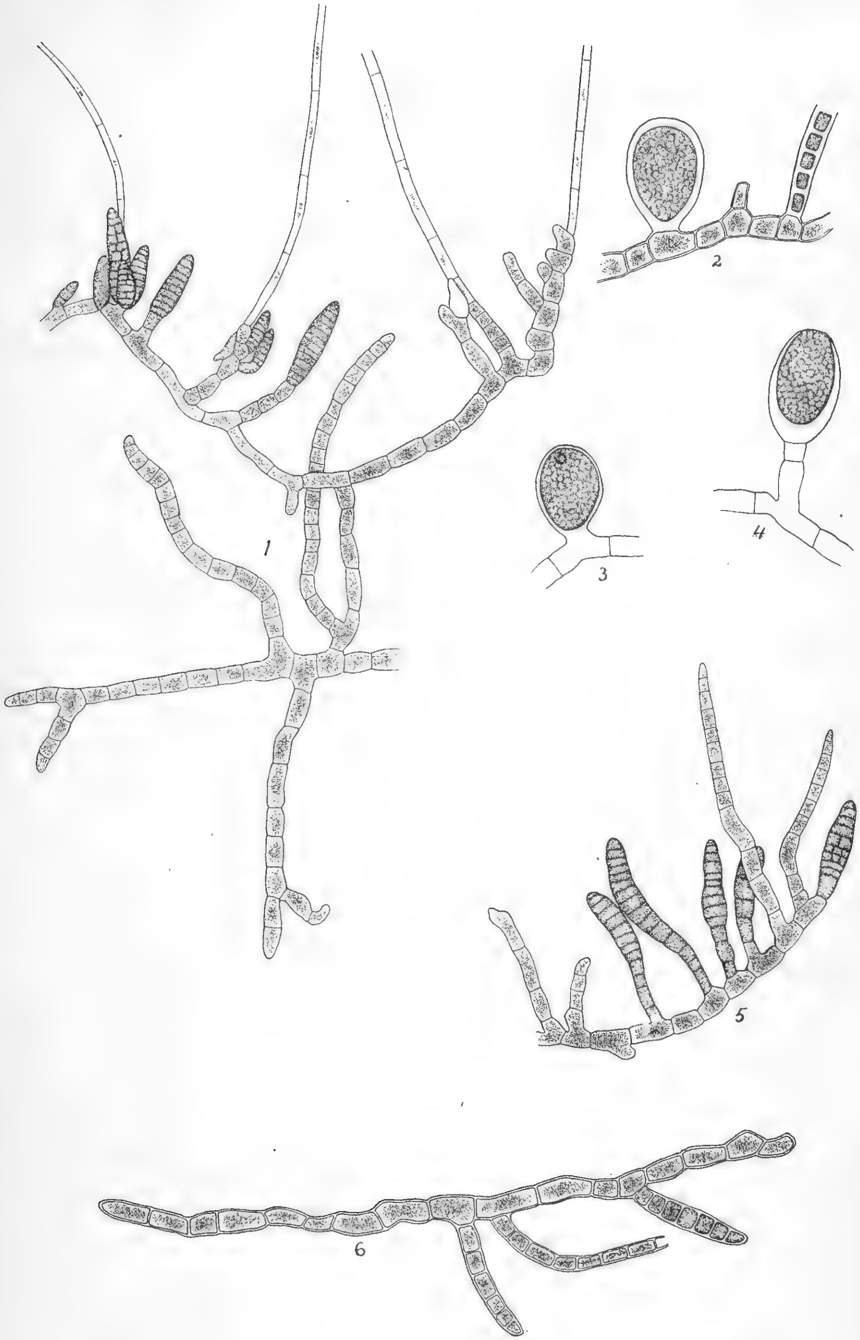
FIGS. 1 - 7. PHYCOCELIS FŒCUNDA *STRŒMF.*
FIGS. 8 - 12. PHYCOCELIS REPTANS *[CROUAN] KJELLM.*



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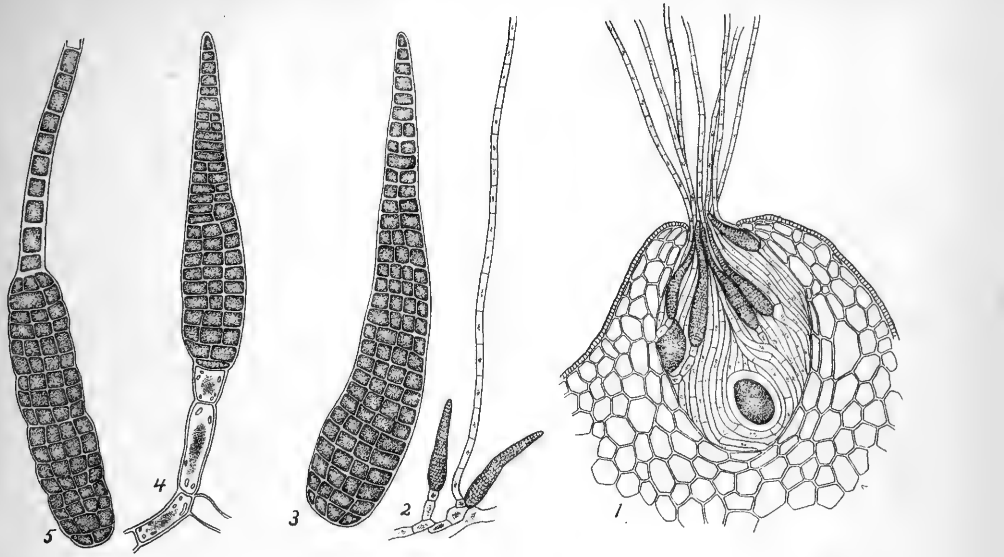
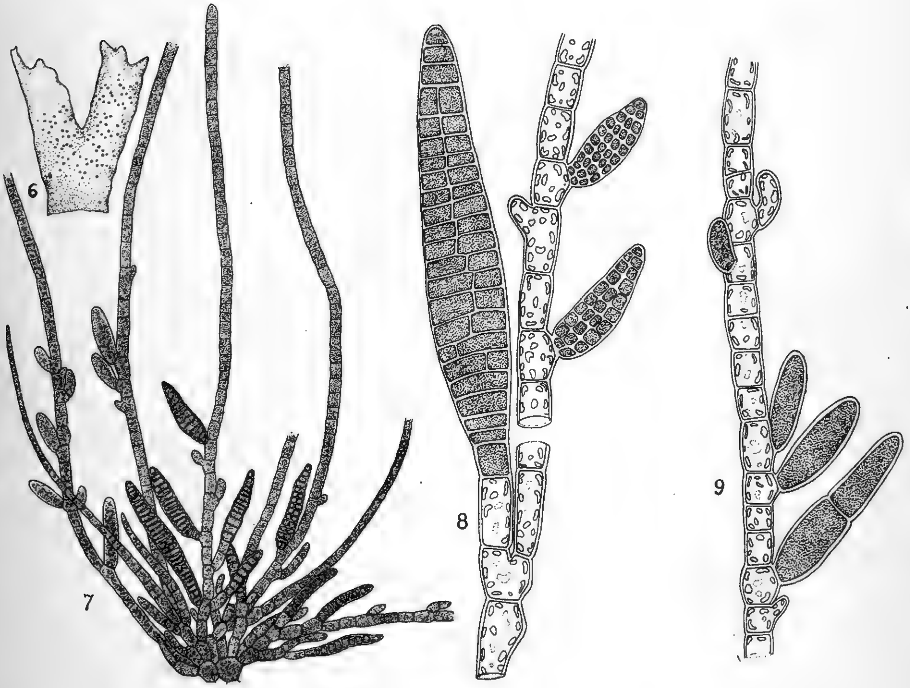
STREBLONEMA FASCICULATUM [THUR.] LE JOL.





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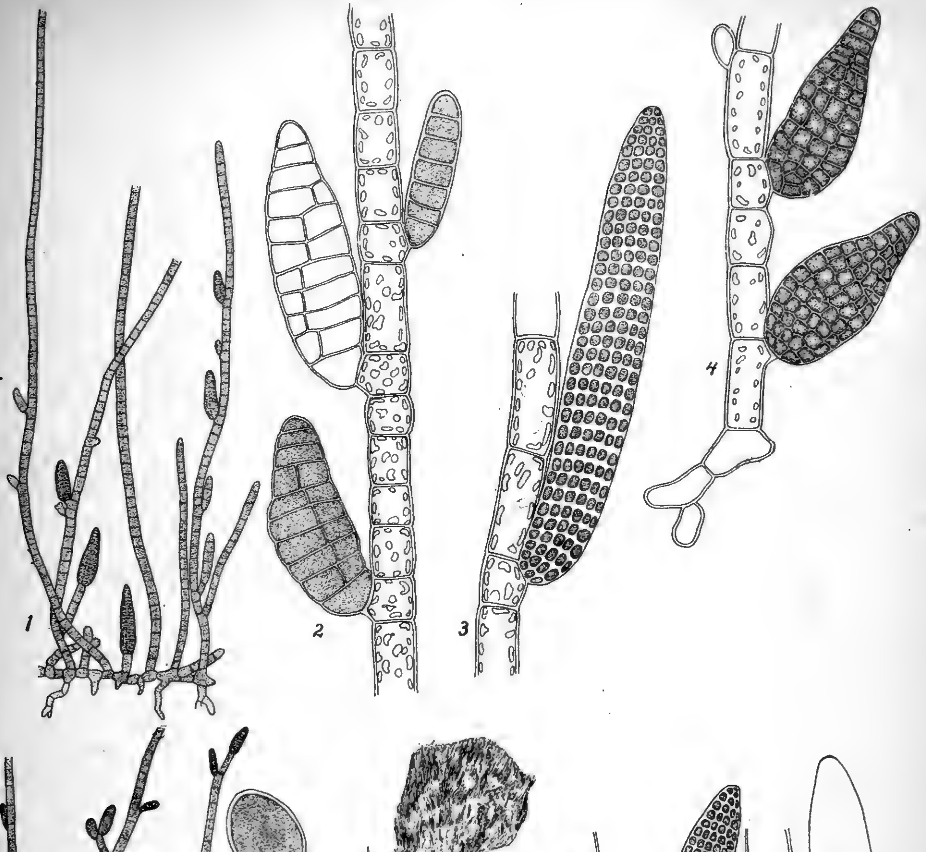
Figs. 1 - 5. Ectocarpus acuminatus, sp. nov.
Figs. 6 - 9. Ectocarpus ellipticus, sp. nov



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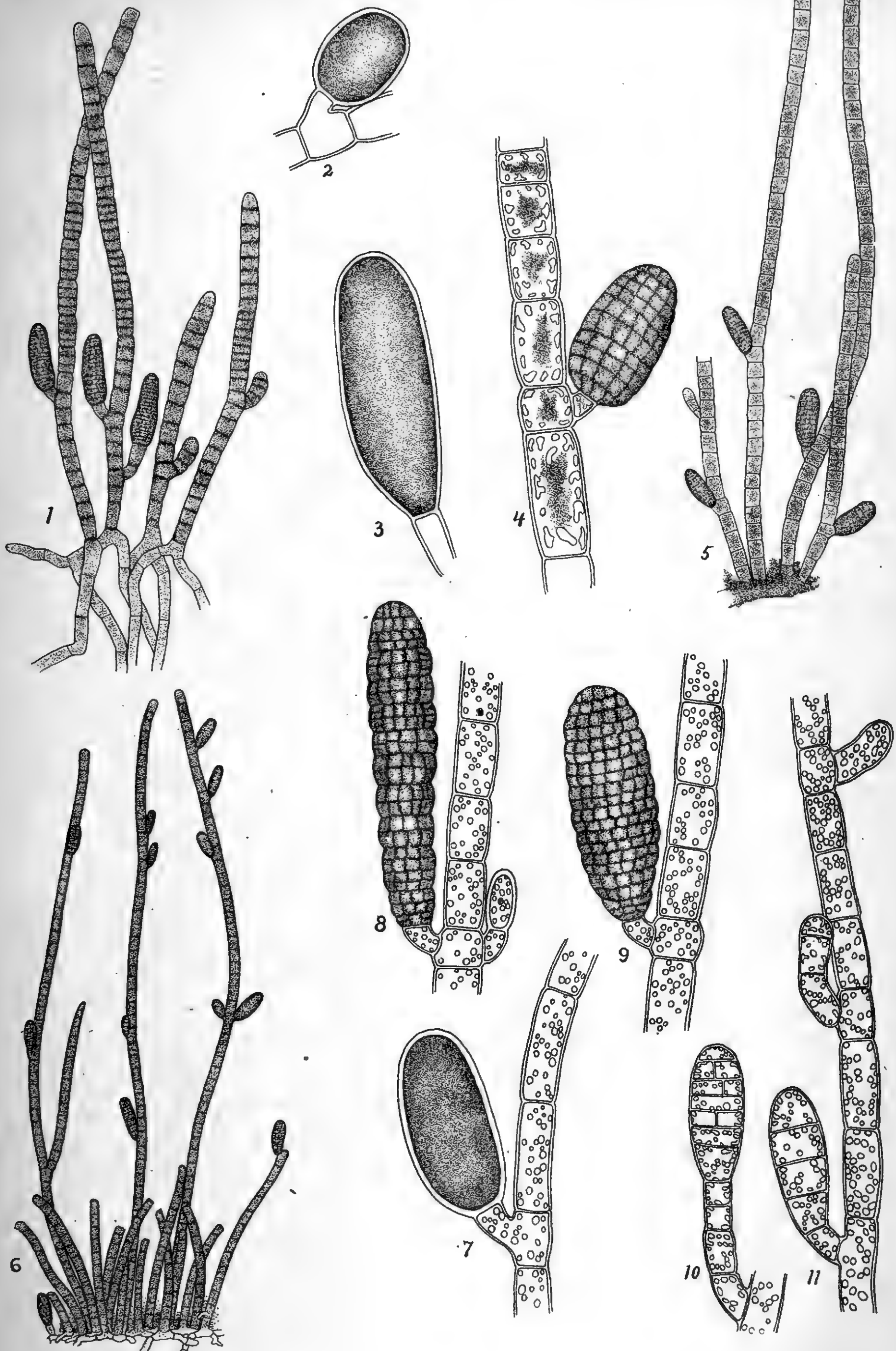
FIGS. 1 – 4. ECTOCARPUS CHITONICOLUS, SP. NOV.
FIGS. 5 – 9. ECTOCARPUS CONFERVOIDES PYGMÆUS, *[ARESCH.] KJELLM.*



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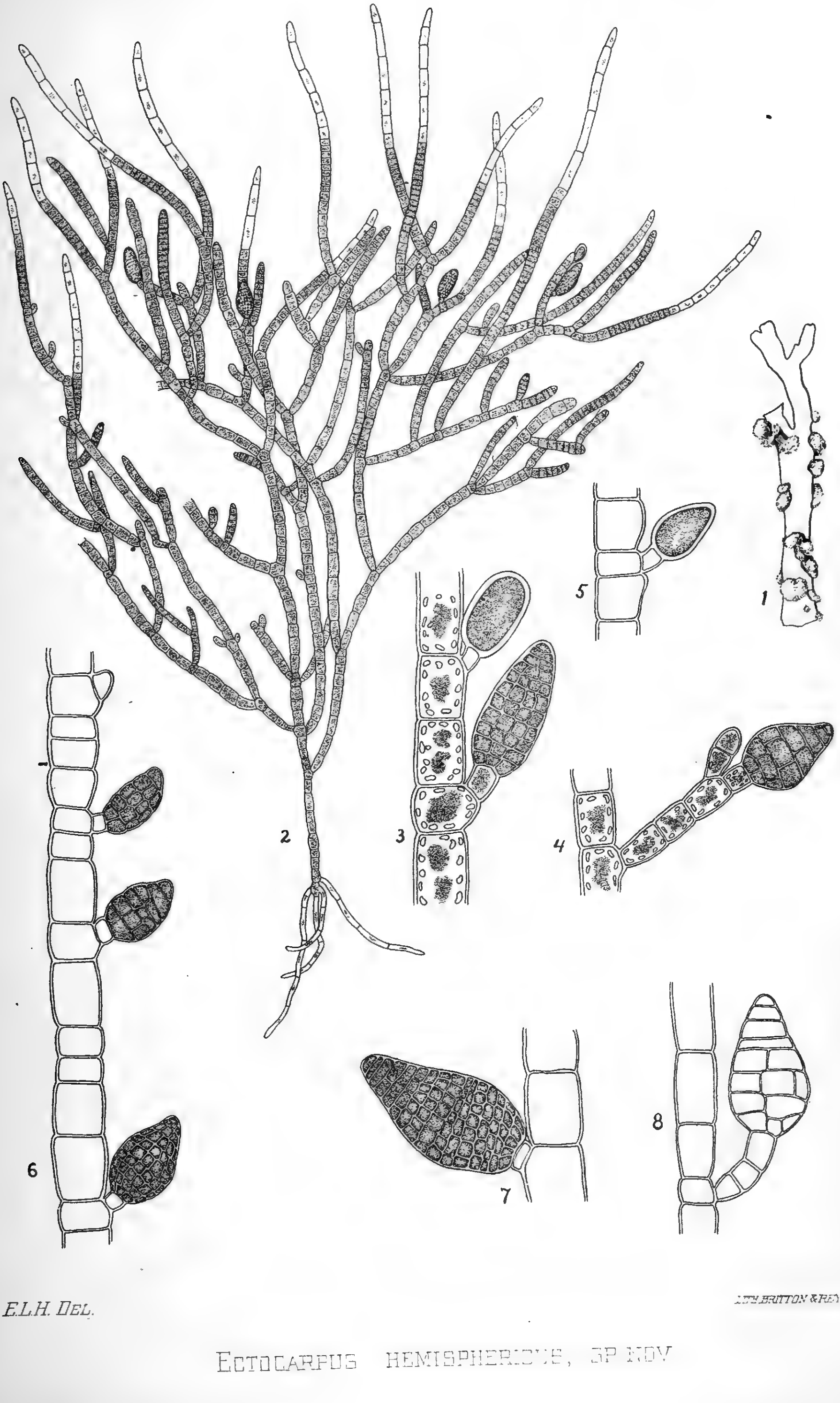
ECTOCARPUS CYLINDRICUS, SP. NOV.



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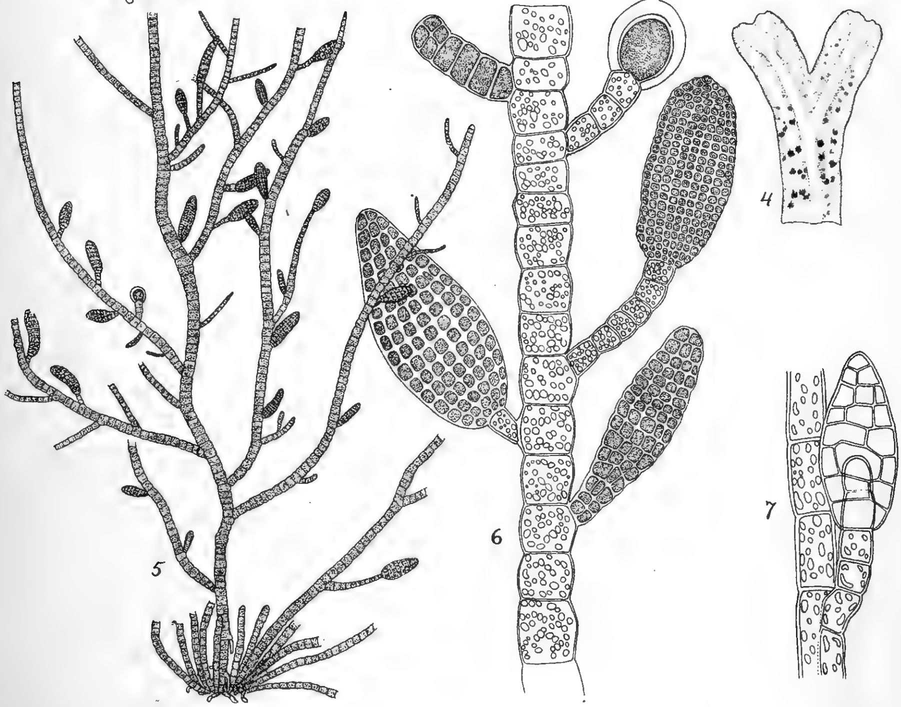
ECTOCARPUS HEMISPHERICUS, SP. NOV.



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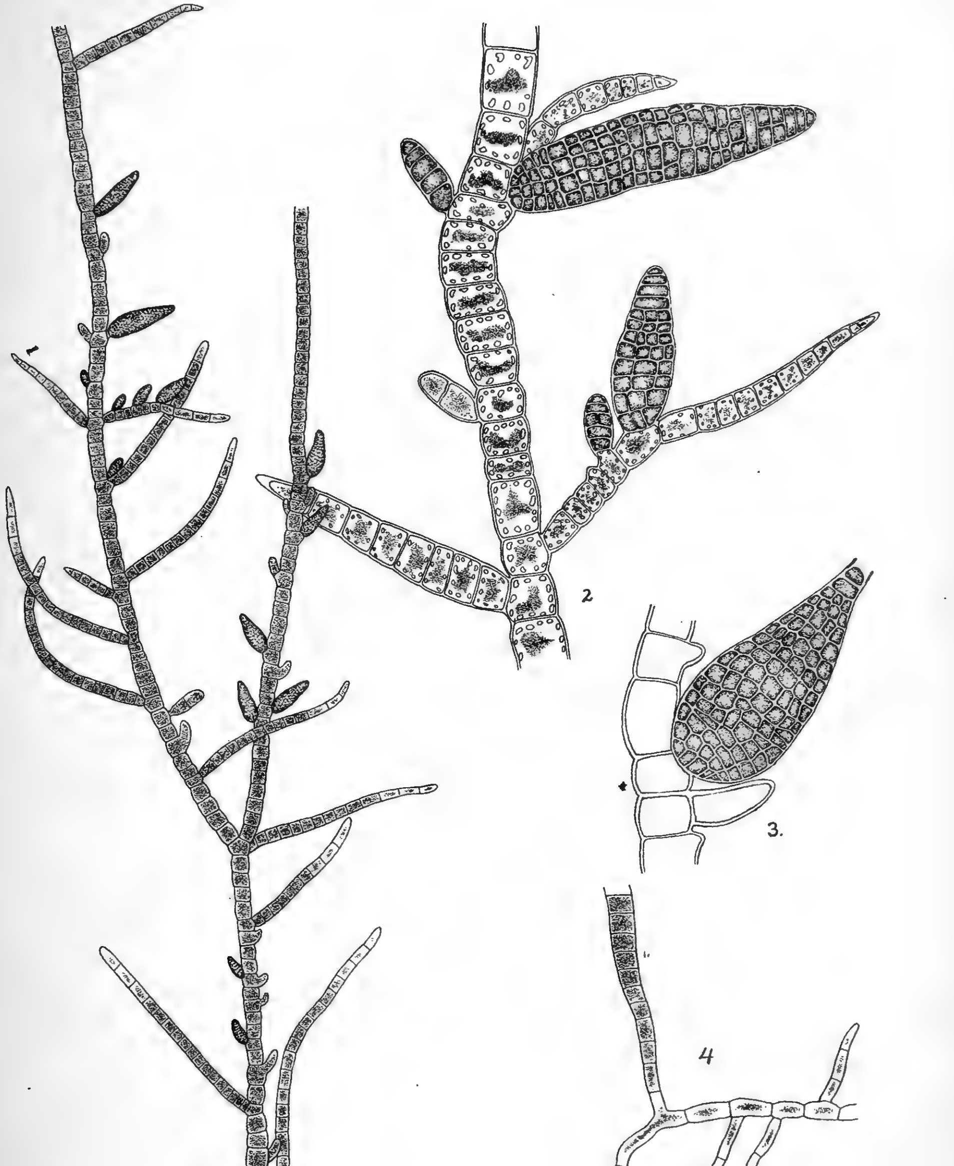
FIGS. 1 - 3. ECTOCARPUS HEMISPHERICUS MINOR, FORM. NOV.
FIGS. 4 - 7. ECTOCARPUS PARADOXUS PACIFICUS, VAR. NOV.



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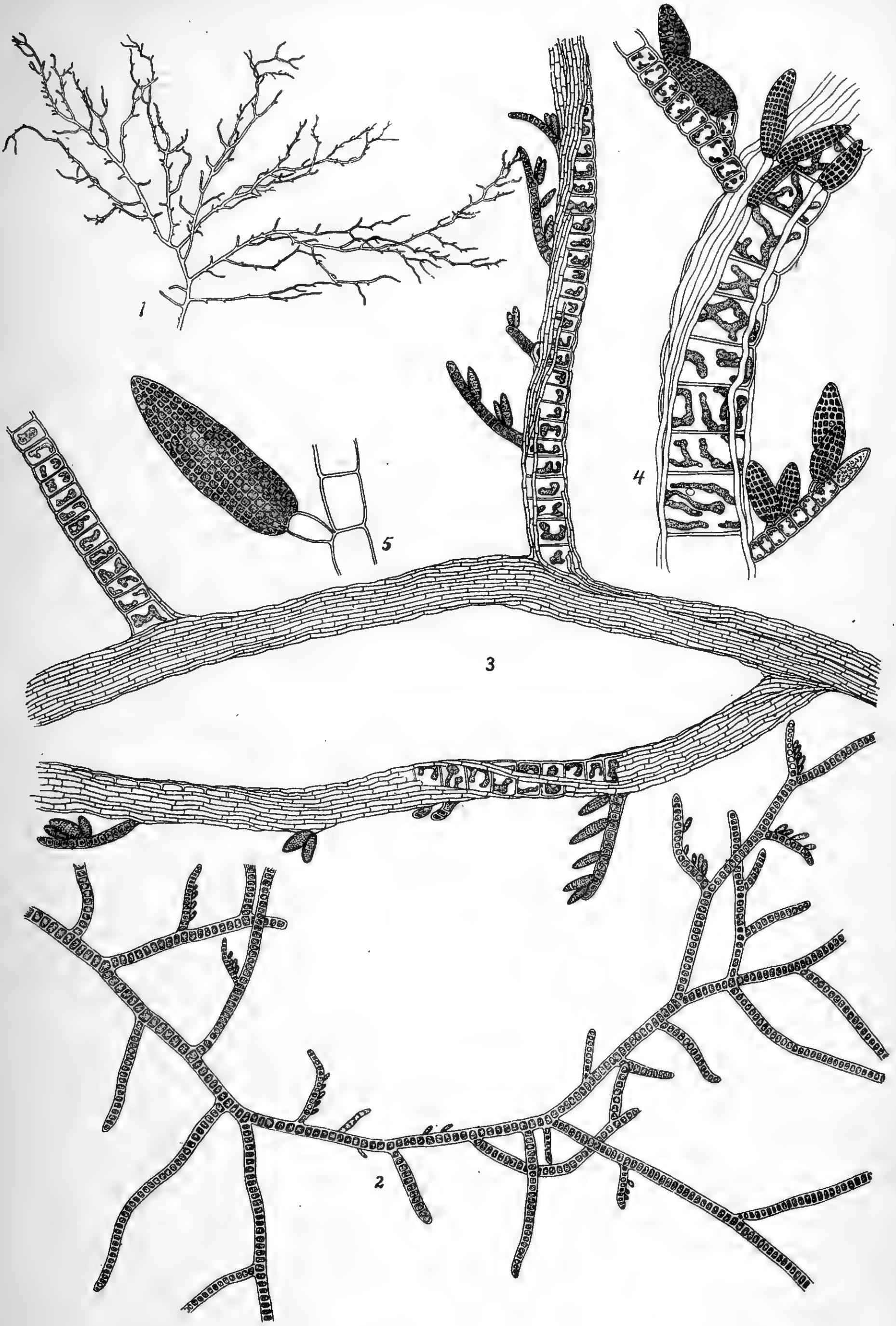
ECTOCARPUS MUCRONATUS, SP. NOV.



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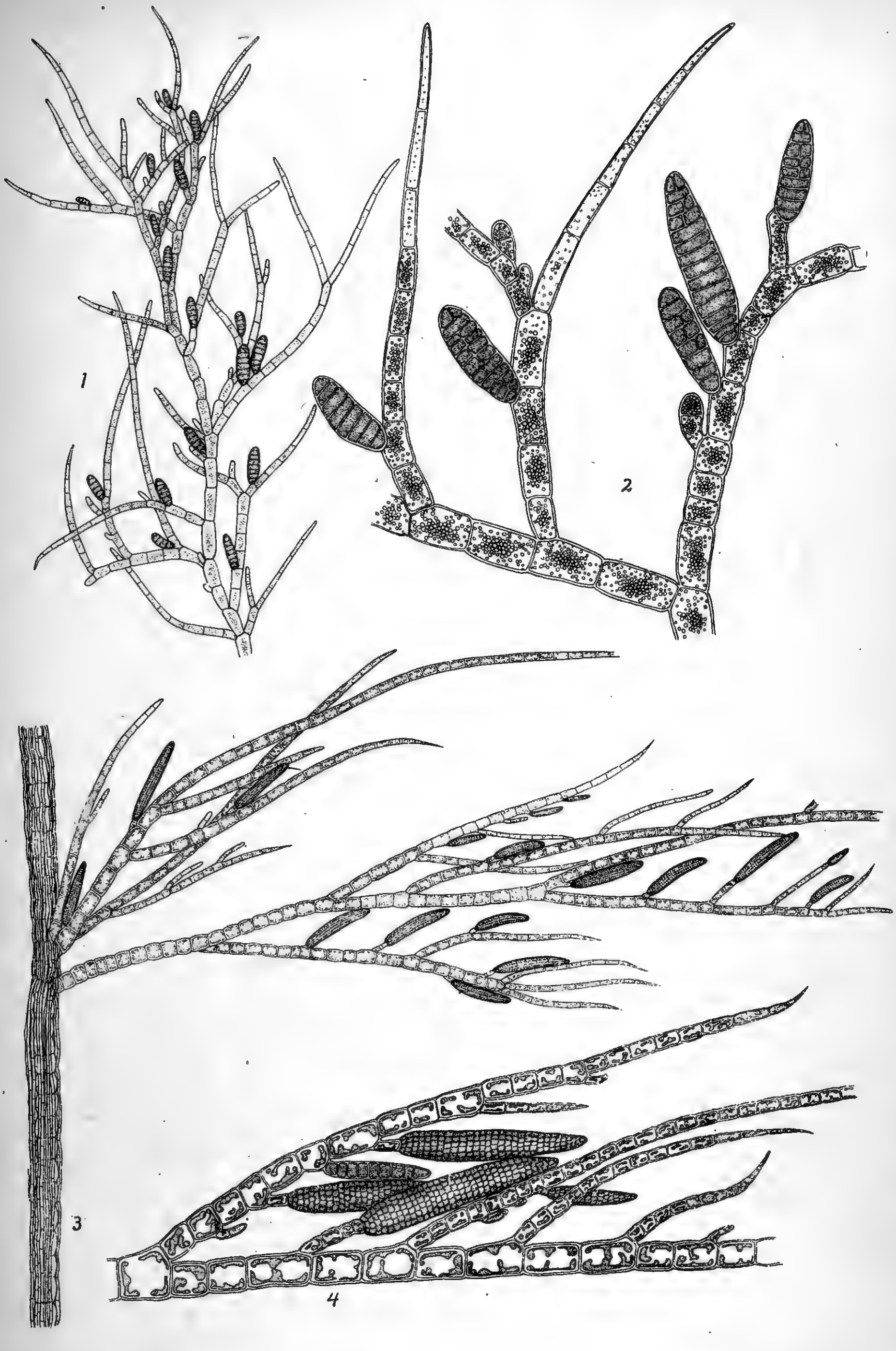
ECTOCARPUS CORTICULATUS, SP. NOV.



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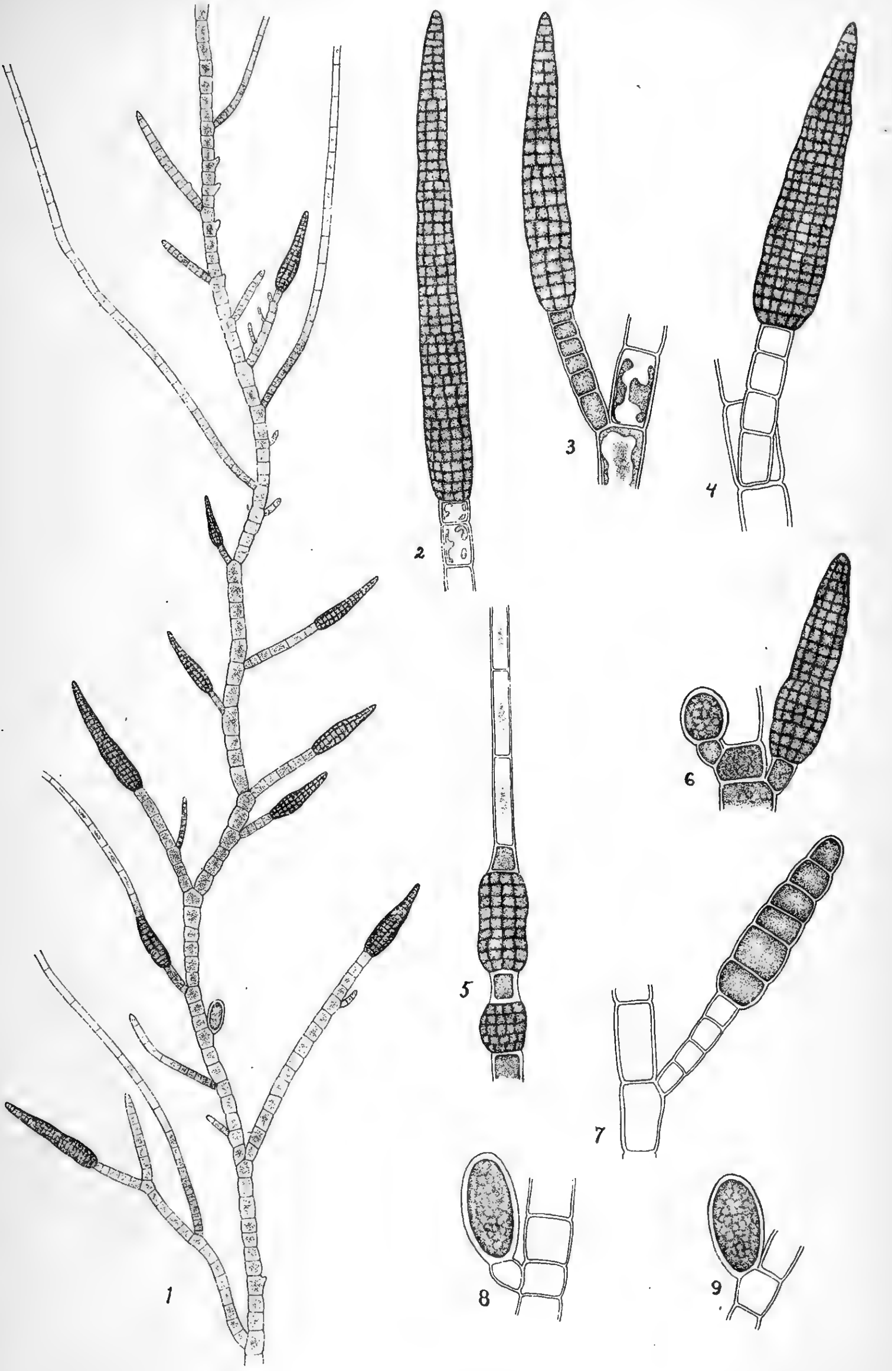
FIGS. 1 - 2. ECTOCARPUS MITCHELLÆ *HARV.*
FIGS. 3 - 4. ECTOCARPUS PENICILLATUS *C. AG.*



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ECTOCARPUS SILICULOSUS PARVUS, VAR. NOV.

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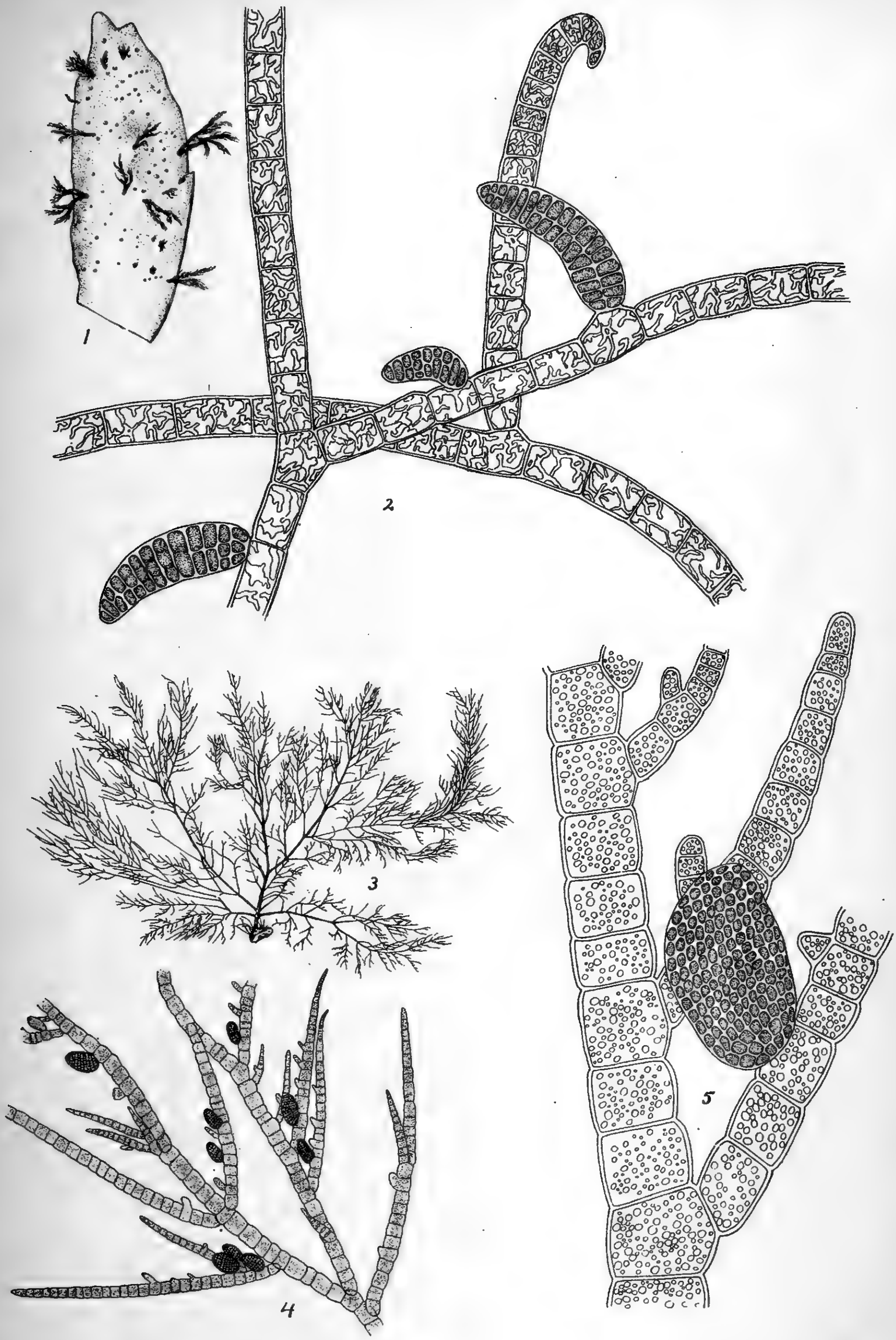
ECTOCARPUS CONFERVOIDES VARIABILIS FORM. NOV.



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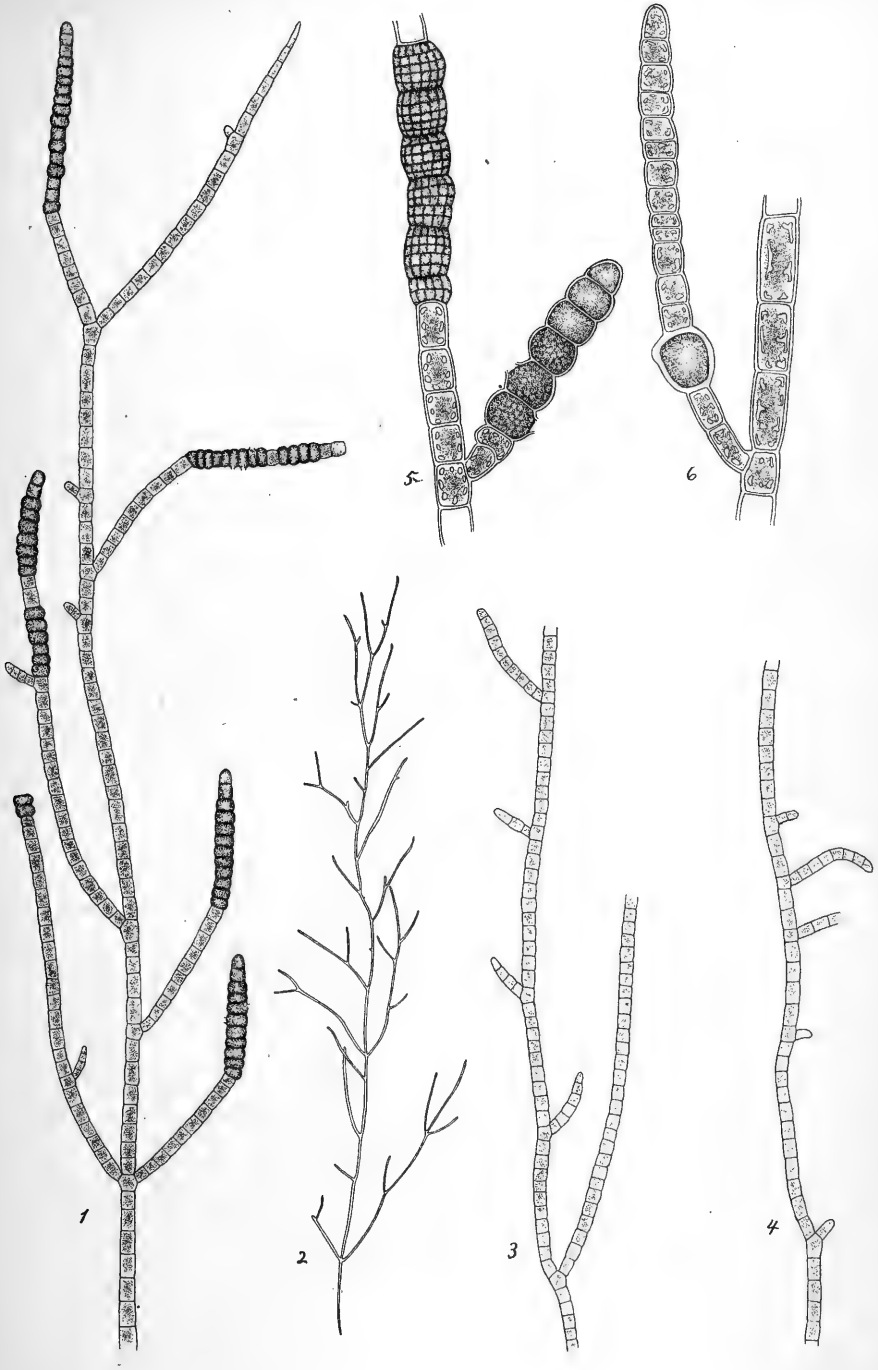
Figs. 1 - 2. Ectocarpus tomentosus *[Huds.] Lyngb.*
Figs. 3 - 5. Ectocarpus granulosus *[Eng. Bot.] Ag.*



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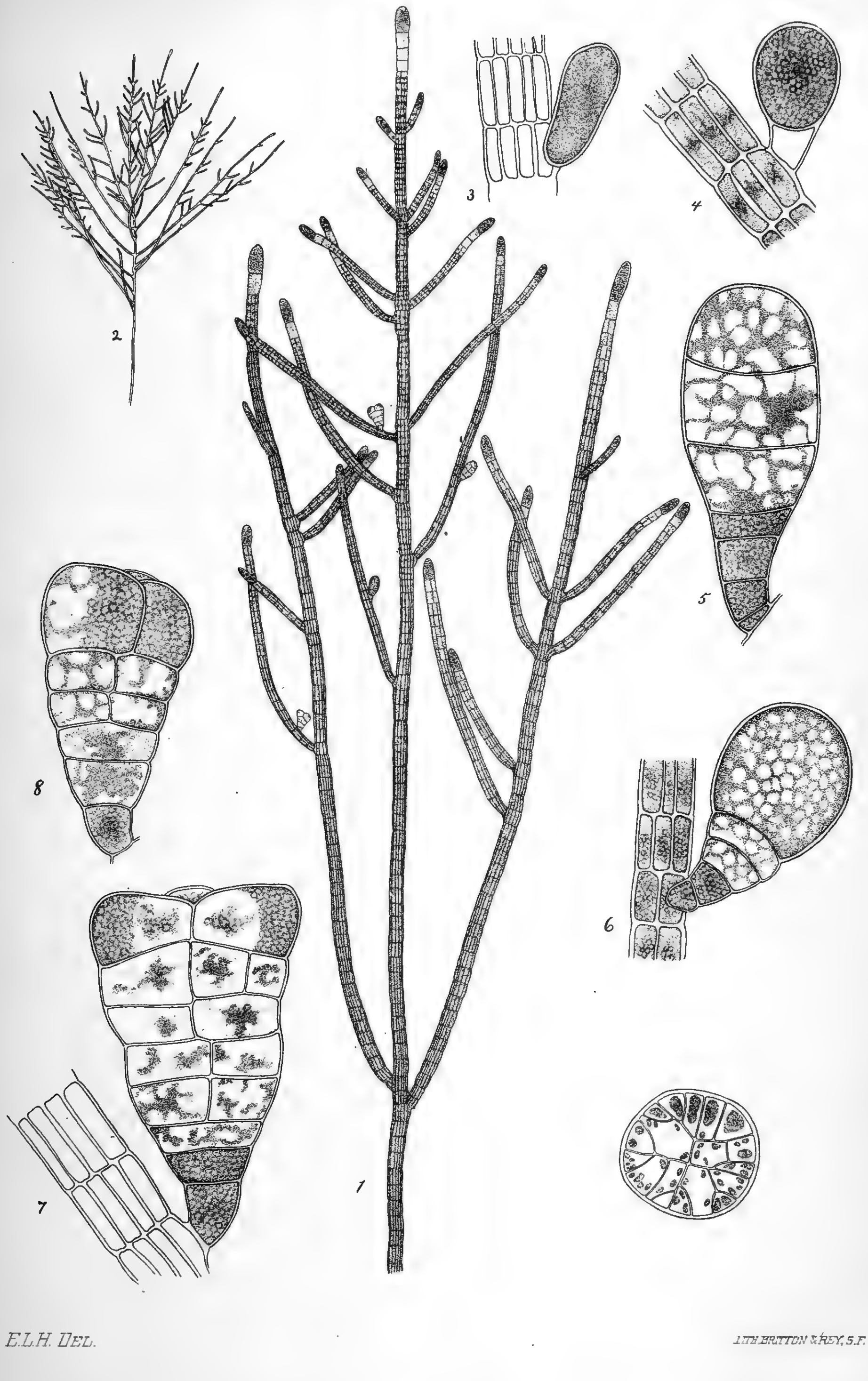
Figs. 1-2-5-6. Pylaiella littoralis densa, form. nov.
Figs. 3-4. Pylaiella littoralis, var.



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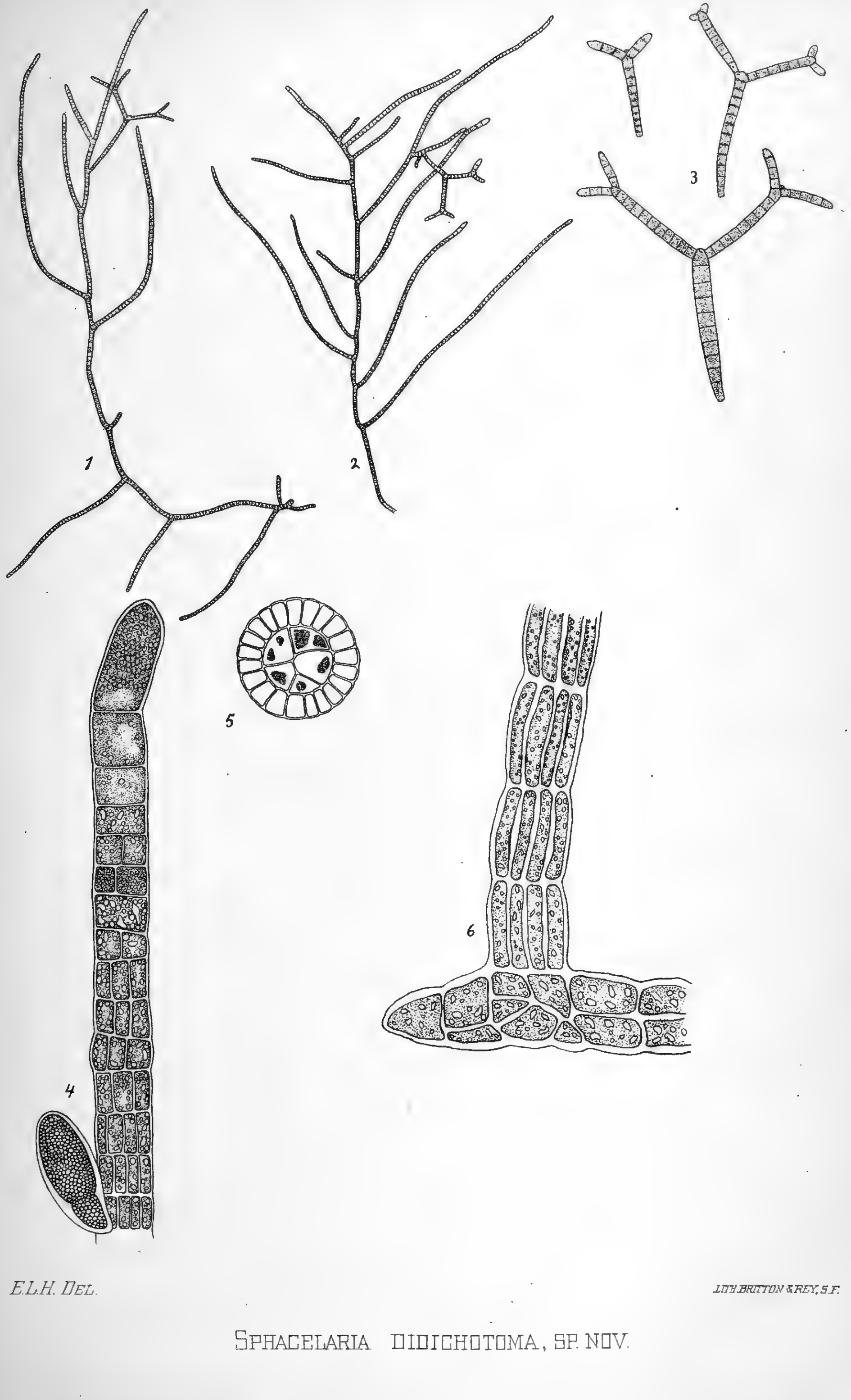
SPHACELARIA TRIBULOIDES *MENEGH.*



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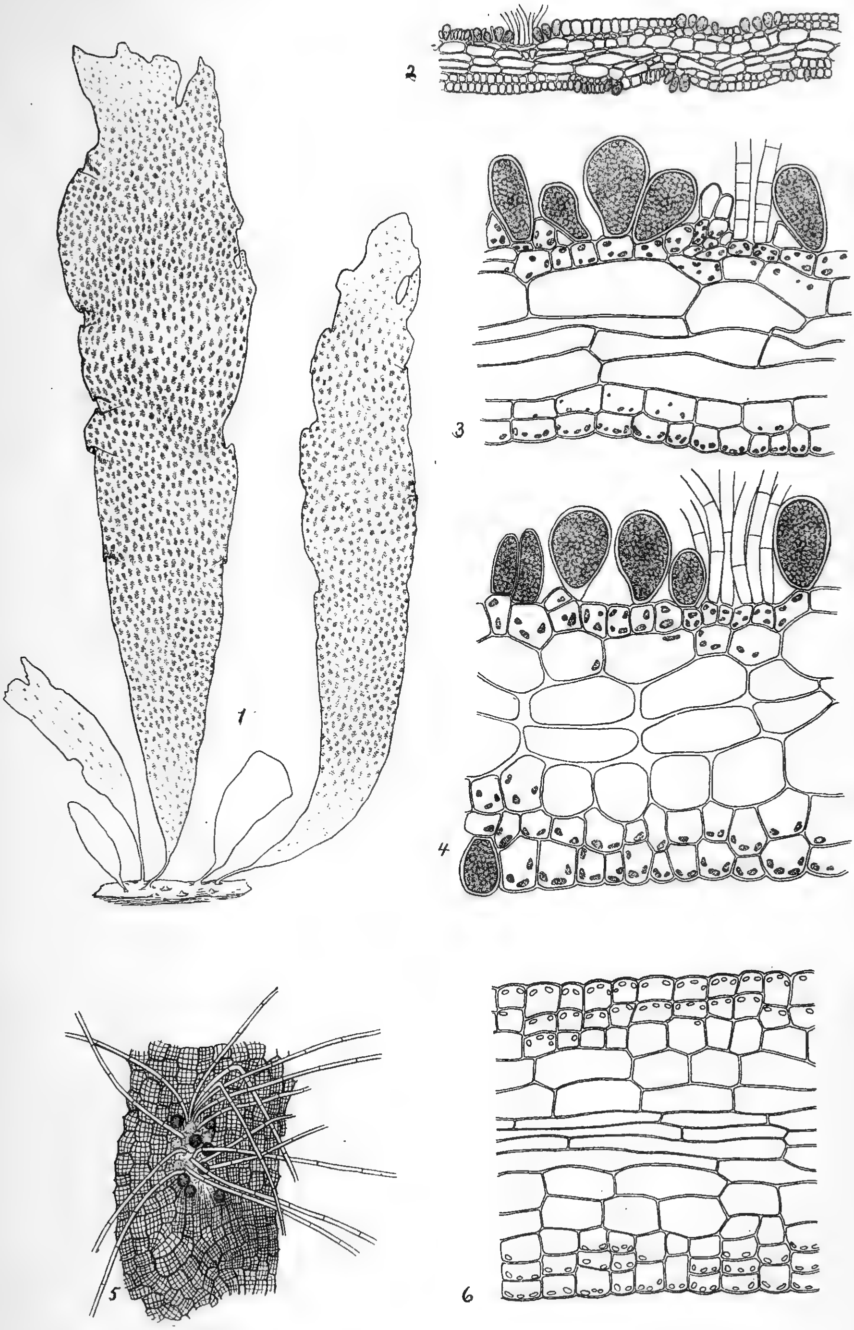
SPHACELARIA DIDICHOTOMA, SP. NOV.



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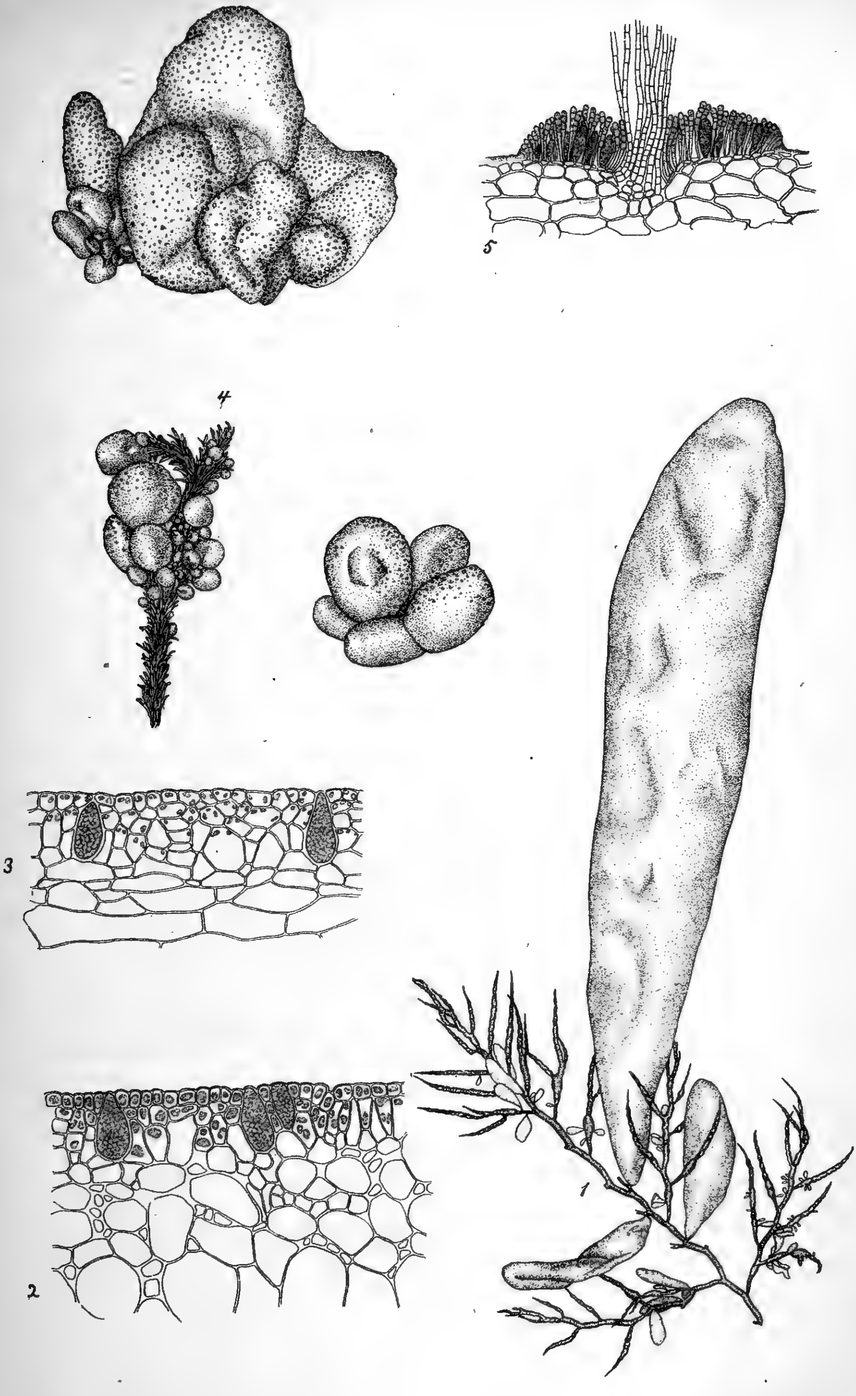
HALORIPHIS WINSTONII. [ANDS.] GEN. NOV.



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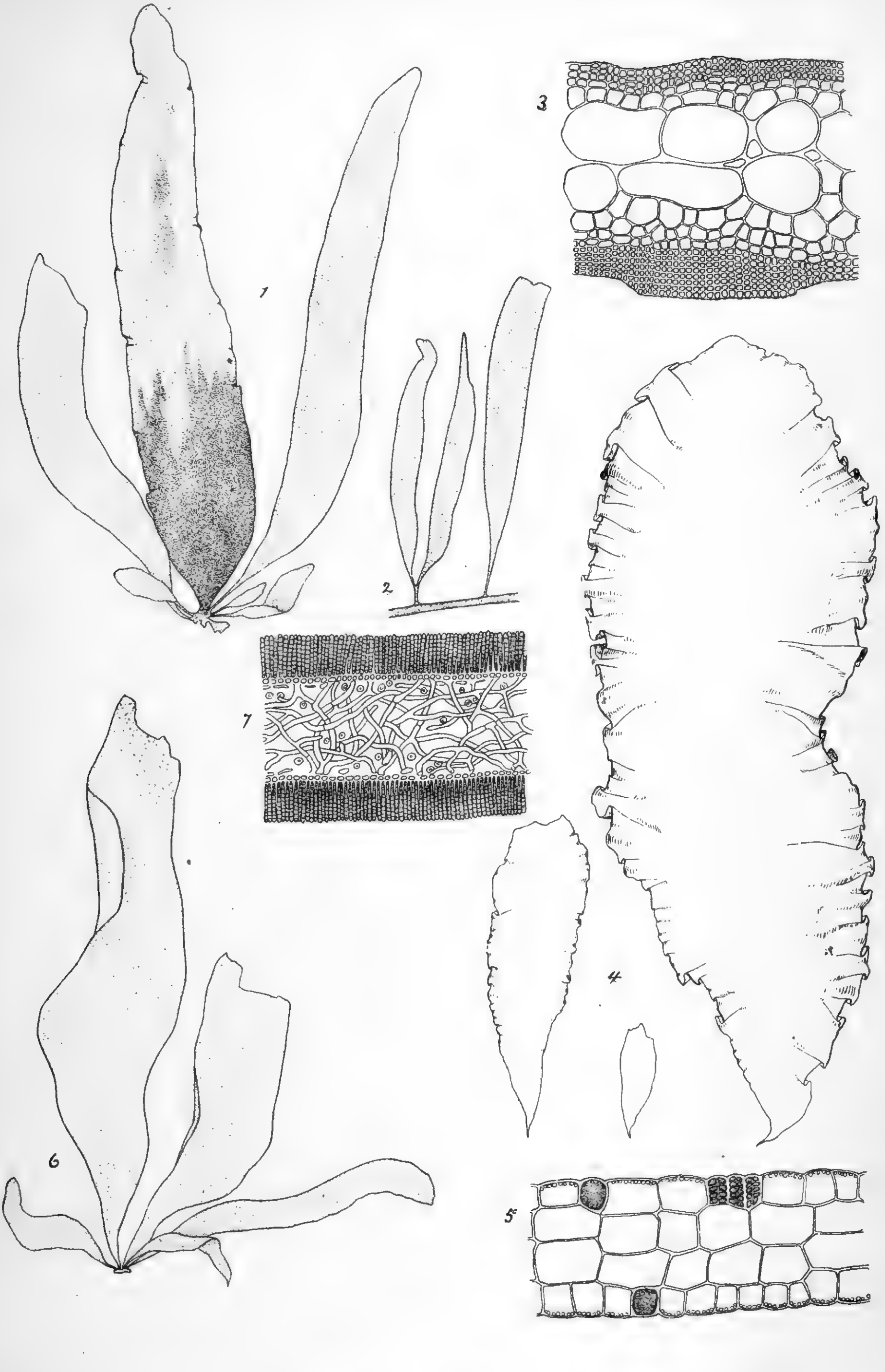
FIGS. 1 – 3. COILODESME CALIFORNICA. *[RUPR.] KJELLM.*
FIGS. 4 – 5. SORANTHERA ULVOIDEA *POST & RUPR.*



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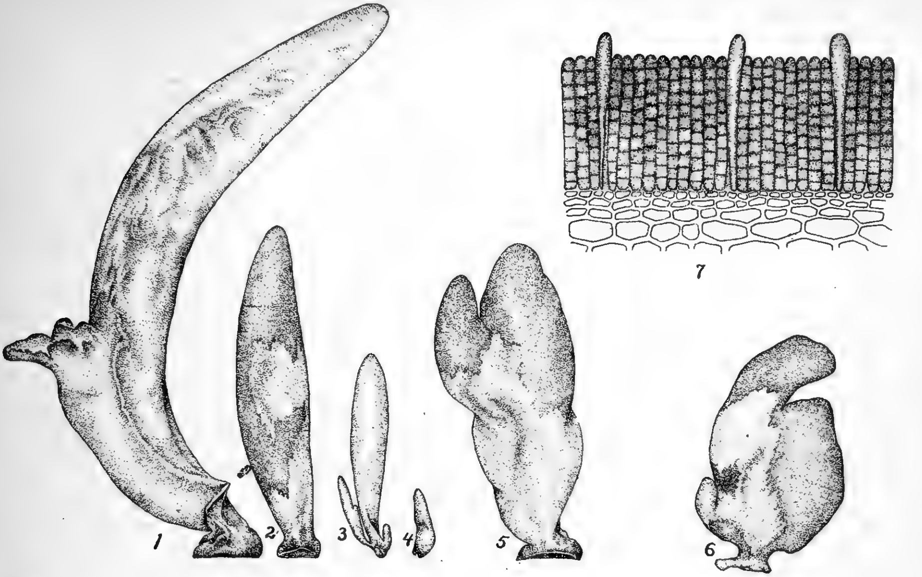
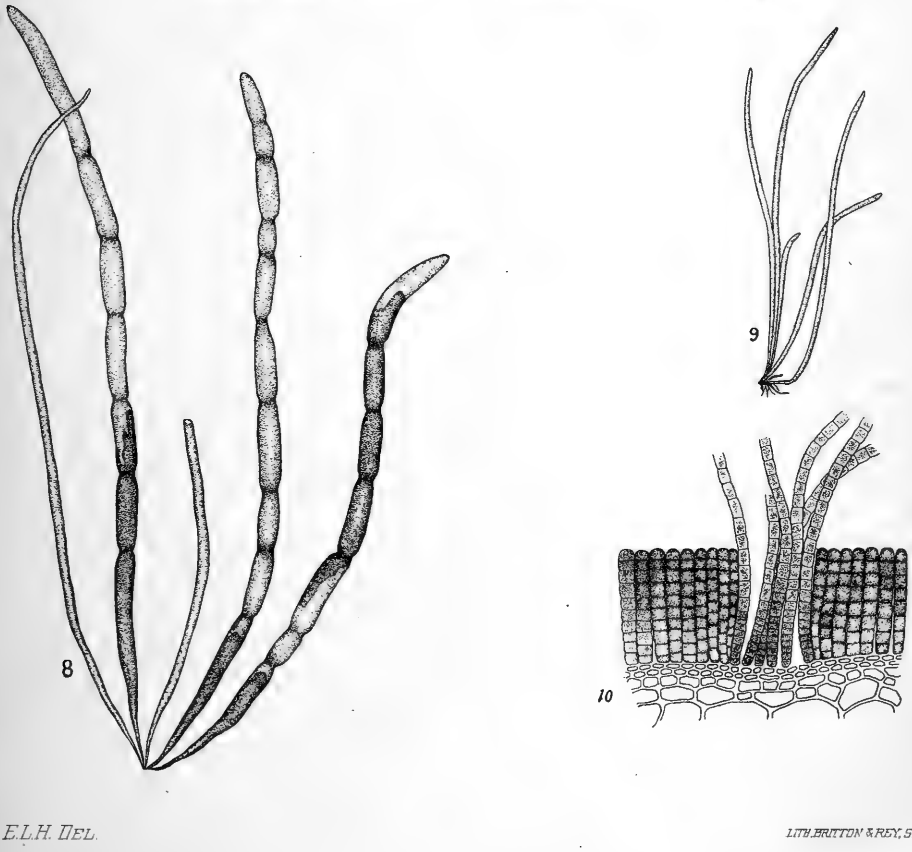
FIGS. 1 - 3. PHYLLITIS FASCIA *[MUELL.] KUETZ.*
FIGS. 4 - 5. HOMEOSTROMA LATIFOLIUM *J. AG.*
FIGS. 6 - 7. ENDARACHNE BINGHAMIÆ *J. AG.*





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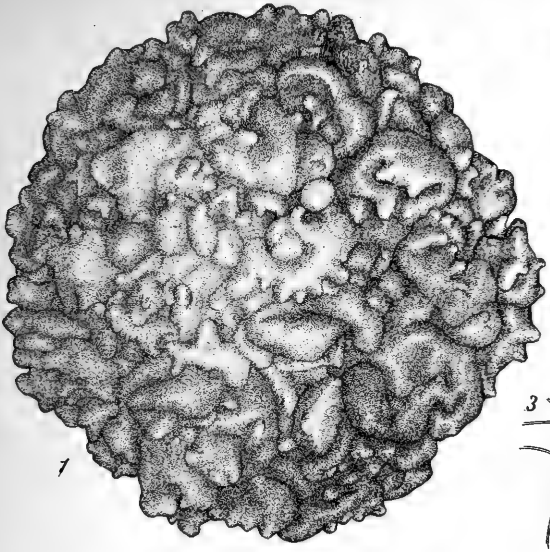
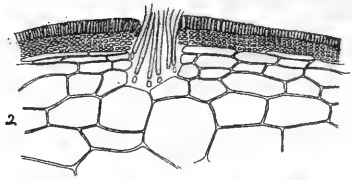
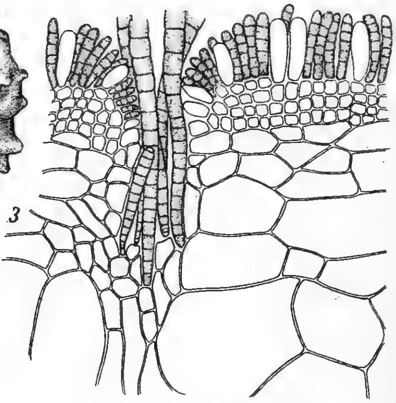
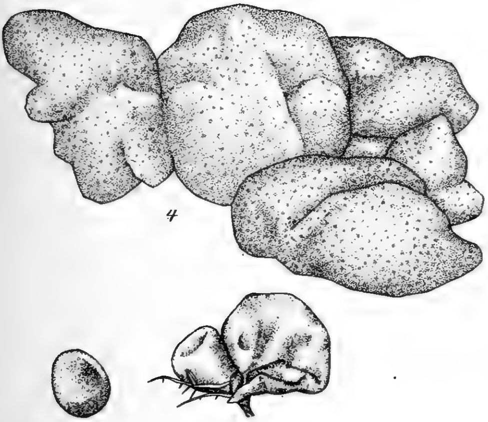
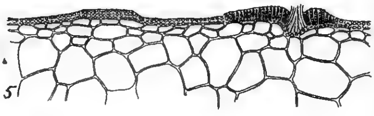
FIGS. 1 – 7. SCYTOSIPHON BULLOSUS, SP. NOV.
FIGS. 8 – 10. SCYTOSIPHON LOMENTARIUS *(LYNGB.) J.AG.*

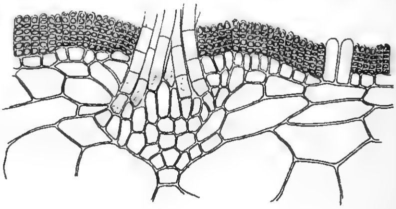


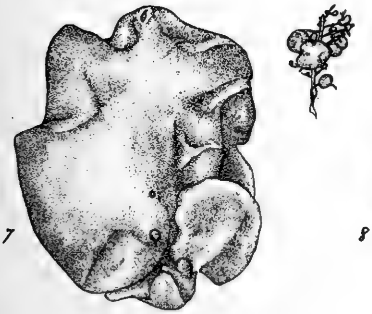


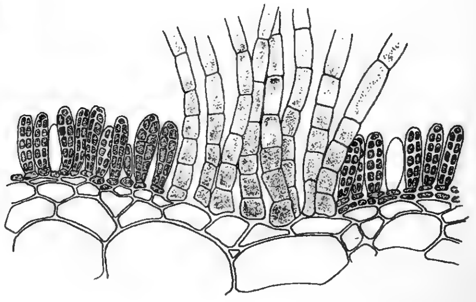












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Figs 1 - 3. Colpomenia tuberculata, sp. nov.

Figs. 4 - 6. Colpomenia sinuosa expansa, form. nov.

Figs. 7 - 8. Colpomenia sinuosa *[Roth.] Derb. & Sol.*

SOME OBSERVATIONS ON THE DEVELOPMENT OF THE KARYOKINETIC SPINDLE IN THE POLLEN-MOTHER-CELLS OF COBÆA SCANDENS CAV.[1]

BY ANSTRUTHER A. LAWSON.

PLATES XXXIII-XXXVI.

FROM the recent investigations of Strasburger (1897), Farmer (1895, *b*), Swingle (1897), Harper (1897), Mottier (1898), and others, we learn that centrosomes are present and take an active part in the formation of the karyokinetic spindle in certain of the lower plants. The most complete series of stages yet published showing the behavior of centrosomes in plants is found in the papers of Swingle (1897) and Harper (1897). Swingle investigated the apical cells of *Stypocaulon*, Harper the developing ascospores in the ascus of *Erysiphe*. In both of these cases, when the spindle is about to be developed, there is a body present which is surrounded by a system of kinoplasmic radiations. This body divides into two and the daughter-centrosomes thus formed migrate to opposite sides of the nucleus and form the spindle in much the same manner as in animals. Strasburger (1897, *a*) has described and figured well defined centrosomes in the oögonium of *Fucus*, and Mottier (1898) has also found them in the tetrasporangia of *Dictyota*.

In all of these cases it will be observed that the centrosome is described and figured as taking an active and very essential part in the development of the spindle. We have thus a very striking parallel between the formation of the spindle in animals and in the lower plants; but when we attempt to extend this parallel to the higher plants we meet

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[1] Contributions from the Botanical Laboratories of the University of California, No. 3. Presented for the degree of Master of Science. Prepared under the direction of Mr. W. J. V. Osterhout.

November 15, 1898.

with difficulties. In spite of the fact that Guignard (1891) and other writers have described centrosomes in the higher plants, recent investigations have rendered their existence very improbable. These investigations agree in showing that the spindle in its earlier stages possesses several poles, and later, by the fusion of these, becomes bipolar. In such a process of spindle-formation it is difficult to understand how a centrosome can have any part, nor has any observer, Guignard excepted, claimed to discover centrosomes in connection with it.

Guignard (1898), however, in a recent article, while admitting that the spindle goes through a multipolar stage in the course of its development, maintains that this does not prove the non-existence of the centrosome.

In the pollen-mother-cells of *Nymphæa* and *Nuphar* he describes centrosomes situated at the apices of the cones in the multipolar figures, and also at the poles of the mature spindle. But unfortunately he does not describe or figure a series of stages that would illustrate the behavior of these bodies. Moreover, Strasburger (1897, *b)* has already discussed this idea and concludes that it is highly improbable that a centrosome plays any part in this process.

Although multipolar spindles were previously described by Belajeff (1894), Farmer (1893), and Strasburger (1896), their significance was not fully understood until Osterhout's (1897) observations on *Equisetum* were made known. In this paper, which furnishes us with the most complete series of stages of spindle-formation yet worked out, the process is described as follows:—

The first thing to be observed in the formation of the spindle in *Equisetum* is a felted zone of kinoplasmic fibres surrounding the nucleus. These fibres grow out from the nuclear wall and take on a radial arrangement. By the coming together of their free ends these threads form a series of cones. The nuclear wall now breaks down and the fibres composing the cones grow in and become attached to the linin and chromosomes. The apices of the cones now approach each other and arrange themselves in two groups and then fuse to form a bipolar spindle. No bodies or granules that could be identified as centrosomes were observed in any stage of the process.

It seems very improbable that the occurrence of multipolar figures is an abnormal phenomenon. They have been found to occur in *Lilium* by Farmer (1893), in *Larix* by Belajeff (1894), and Strasburger (1896). They have been found in *Lilium*, *Fritillaria*, *Helleborus*, *Podophyllum*, and *Pinus* by Mottier (1897, *a* and *b*), in *Hemerocallis* by Juel (1897), in *Chara* by Debski (1897), and in *Zamia* by Webber (1897.) The writer has observed them in *Hesperlœ*, *Hedera*, *Disporum*, *Smilacina*, *Gladiolus*, *Iris*, *Cobœa*, and other genera. From this we can only conclude that multipolar spindles are of very general occurrence, and this throws considerable doubt upon the existence of centrosomes in the higher plants.

It must be observed, however, that in all cases where multipolar figures have been described, very little has been observed upon the very earliest stages in the development of the kinoplasmic fibres. It is with the hope of throwing some light on these stages that the following observations upon the pollen-mother-cells of *Cobœa scandens* have been made.

About two years ago Mr. Osterhout suggested that the writer undertake some investigations upon spindle-formation in anthers of different orders of flowering plants. In undertaking such a task it is very desirable to obtain material with large anthers and large pollen-mother-cells as well as large nuclei. The anthers of *Cobœa* are very good in all of these respects.

The anthers were gathered and immediately fixed in the field. The following fixing fluids were used:

Alcohol, 95 per cent.
Chromic acid, 1 per cent.
Flemming's mixture, chromic-osmic-acetic, strong solution.
Wilson's sublimate-acetic.
Boveri's picro-acetic.
Corrosive sublimate, saturated solution in 95 per cent. alcohol.

The best results were obtained by using Flemming's strong solution diluted with one volume of water. The material was washed in running water from six to eight hours. It was then carried through different grades of alcohol by means of an apparatus consisting of a tumbler with a cover and a glass funnel. The funnel was of such a size as to be supported in the mouth of the tumbler. A piece of parchment paper was folded and placed in the funnel in the same manner as for filtering. 10 per cent. solution of alcohol was placed in the tumbler and the anthers were placed in water in the funnel. The mouth of the tumbler was covered and the material was thus allowed to remain for an hour or two. The alcohol in the tumbler was changed at intervals to 25 per cent., 50 per cent. and 95 per cent. solutions. By this means the effect of the rapid change from a weak to a strong solution of alcohol was obviated. The anthers were then thoroughly dehydrated in absolute alcohol. They were then placed in a mixture of bergamot oil and alcohol and then in pure bergamot oil. From the bergamot oil they were transferred to a mixture of bergamot oil and paraffin, and from this to pure paraffin, where they remained at a temperature of 55°C. for twenty-four hours. Microtome sections of $3\frac{2}{3}\mu$ in thickness were used.

Many stains were tried; especially iron-hæmatoxylin and Bordeau red, ruthenium red and thionin, etc., but the best results were obtained from Flemming's triple stain, safranin, gentian violet, and orange G.

In the resting condition of the pollen-mother-cell the nucleus is quite large. It contains one or two large nucleoli which stain very readily with safranin and sometimes appear to be vacuolated. The chromatin, which is in the skein stage, stains blue with the gentian violet. As soon as the chromatin breaks up and forms the chromosomes it stains red with safranin. The chromosomes appear as small oval bodies which are invariably situated in contact with the nuclear wall. The largest number that was observed in polar view was twelve. On the chromosomes the writer has made very few observations. They will therefore not be discussed farther. The linin now appears in the form of a lumpy or granular thread; it stains blue and is invariably connected with the chromosomes.

The cytoplasm now appears in the form of a clear reticulum, as shown in fig. 1. The meshes of this network, which can be traced from the nuclear wall to the cell-wall, appear to be smaller and radially elongated in the immediate neighborhood of the nucleus; but as one follows them outwards they increase in size and are comparatively large towards the cell-wall.

Scattered irregularly through the cytoplasm are numerous small spherical bodies. These bodies have the appearance of oil-globules in the living cell, but after the cell has been killed in Flemming's fixing fluid they appear quite black. What the chemical nature or function of these bodies is, the writer is unable to state.

The cytoplasm does not maintain its clear, uniform appearance for a very long period, but soon undergoes a remarkable differentiation. This differentiation is shown in figs. 2-5. It is brought about by the gradual accumulation of a granular substance which forms a complete zone about the nucleus. The minute structure of this substance is difficult to make out, but it appears to consist of granules which vary in size. While some are very minute, others are comparatively large. They appear to be arranged in such a manner as to give the impression of a foam-structure.

This granular zone is so constant in *Cobæa* and in several other genera observed by the writer, that for convenience it will be called perikaryoplasm. While it is accumulating, the black bodies, which were previously scattered irregularly through the cytoplasm, take up a definite position. They arrange themselves along the outer margin of the perikaryoplasm, and in section present the appearance of a complete ring, as shown in fig. 5.

It is at this stage that the contrast between the outer cytoplasmic reticulum and the perikaryoplasm is greatest. The threads of the outer reticulum now appear to have no connection with the nucleus. They can no longer be traced through the perikaryoplasm. Where the outer reticulum abuts on the perikaryoplasm the meshes of the former are so compressed as to give the impression of a loose membrane.

These two constituents of the cytoplasm not only differ from one another as regards their structure but their staining properties stand in great contrast. While the outer reticulum stains a light or gray-blue with the gentian violet, the perikaryoplasm stains a decided orange with the orange G. The entire cytoplasm thus presents the appearance of two distinct and sharply differentiated zones, differing from one another as regards structure and staining properties. These zones are seen in fig. 5.

In case it should be thought that this is due to artifact, it might be well to state here that a large number of living cells were examined, and this striking differentiation of the cytoplasm and the ring of spherical bodies, together with the threads of the outer reticulum, could be readily seen. This, in the writer's opinion, is sufficient evidence to prove that the phenomenon is a normal one. There seems little doubt that it is the first step towards the formation of the spindle.

In fig. 6 we see the first indication of the breaking down of the nuclear wall. It evidently does not break down all at once. It commences to do so at one or more points where it becomes lost in a network which is now developed out of the linin and perikaryoplasm. Figs. 6-8 show stages in the breaking down of the nuclear membrane. It will be seen from these figures that the perikaryoplasm, where it is in the immediate vicinity of the breaks in the nuclear wall, is now undergoing a change. The linin has lost its lumpy appearance and now appears as fine, delicate threads (fig. 6) which are in direct communication with the perikaryoplasm. The latter is losing its granular nature in these places and is taking on the form of a network. In fig. 8 we see this network taking on a very definite form. It no longer stains orange, like the perikaryoplasm from which it develops, but stains deeper and deeper violet like the linin. At the points where the threads intersect granules are seen. In fig. 8 the nuclear wall is no longer continuous but is in the form of fragments. To what extent the linin enters into the formation of the network, the writer is at present unable to say, but it certainly appears to begin its formation. The amount of linin present when the nuclear wall breaks down is not sufficient to form the large central network that we see in fig. 9. This network increases in size and apparently grows at the expense of the perikaryoplasm. In fig. 9 the nuclear wall has entirely disappeared and the area once occupied by the nucleus is now filled by a perfect network which supports the chromosomes within its meshes. These latter bodies appear to be more frequently present in those places where the network is growing outward in the form of projections.

The contents of the cell is now beautifully differentiated into three parts: the outer cytoplasmic reticulum which stains light blue, the perikaryoplasm which stains orange, and the central network which stains violet. Between these latter two there is a transition place where the threads of the central network become granular and stain less deeply violet, until finally they become orange and pass over into the granular substance of the perikaryoplasm, where they can no longer be followed.

In fig. 9 we see that the central network has at three places formed definite projections. How many of these are generally formed it is difficult to make out from sections, but the number is nearly always more than two. In fig. 10 we see that the meshes of the network have become elongated in the directions in which the projections extended. In fig. 12 we see that the meshes have a drawn-out appearance, and we have the outline of a multipolar spindle. Figure 11 is probably a later stage than fig. 12, inasmuch as the meshes are drawn out to such an extent as to present the appearance of distinct fibres, and we now have the first spindle-fibres formed. In this figure it will also be observed that the nucleolus still persists, which shows that it has not been used to form the central network. This is the latest stage in which the nucleolus was seen, but what eventually becomes of it was not observed.

In the next figure we have a characteristic multipolar spindle. Here the fibres are straight and form cones which terminate in sharp points. We see extending from the apices of the cones fibres which have free ends. These fibres eventually become the mantle-fibres which are so characteristic of the mature spindle.

The multipolar figure becomes bipolar by the fusion of the cones in much the same manner as it does in *Equisetum*, as shown in figs. 14 and 15, but during the process the mantle-fibres have developed to a considerable length.

From the time of the breaking down of the nuclear wall the chromosomes have been in connection with the network from which are developed the spindle-fibres; so that this process differs materially from those cases where the spindle-fibres have been described as growing in and becoming attached to the chromosomes.

As shown in figs. 15 and 16, the mature spindle terminates in sharp points; there are three kinds of fibres present: The contractile fibres, which are in connection with the chromosomes, are compound in nature, being made up of a number of fine fibres. The continuous fibres extend from pole to pole uninterrupted. The mantle-fibres are remarkable for their great length and early development; they consist of very delicate straight threads; those from one pole cross those from the opposite pole in the manner shown in figs. 15 and 16. It should be observed that although the mantle-fibres are of great length they never extend beyond the perikaryoplasm.

After the mantle-fibres have reached their maximum development the contractile fibres commence to draw the chromosomes to the poles. This takes place in the usual way. It will be noticed, however, as shown in fig. 17, that during this process the mantle-fibres appear more divergent from their respective poles. When the chromosomes have reached the poles the mantle-fibres immediately lose their straight appearance and hang loosely alongside of the remaining continuous fibres, as shown in fig. 18. They soon after disappear. Although the continuous fibres now curve out towards the cell-wall as shown in fig. 19, there is no cell-plate formed until after the second division.

When the daughter-nuclei have surrounded themselves with a membrane the continuous fibres still persist, being attached to the daughter-nuclei as shown in fig. 19. In this figure we also see that the perikaryoplasm appears to be more plentiful at the ends of the cell where the nuclei lie. It surrounds the nuclei except where the continuous fibres are in connection with the nuclear membrane. The perikaryoplasm gradually surrounds the nuclei and apparently cuts off the continuous fibres. As shown in fig. 20, they can no longer be traced to the nuclear wall, and the perikaryoplasm has formed a complete zone about each nucleus.

The development of the spindle of the second division is identical with that of the first division, but on account of its small size, the stages in the process are much more difficult to work out.

In fig. 21 we see the last traces of the continuous fibres, and each of the nuclei is surrounded by a granular zone. It will also be noticed that the black bodies have formed rings at the outer margin of the zones of perikaryoplasm, just as they did in the case of the first division. These zones are as well defined and differentiated from the rest of the cytoplasm in structure and staining properties as in the first division.

In fig. 22 we see the two spindles of the second division lying at right angles to one another. In one the spindle is represented only by the cross-sections of its fibres. The other shows the entire spindle with the characteristic mantle-fibres, and the chromosomes on their way to the poles. This figure also illustrates the fact that the perikaryoplasm accommodates itself to the shape of the spindle. In one view it appears round and in the other oblong in outline, corresponding to the position and shape of the spindle.

In the next figure we see that the spindles are more nearly in the same plane. The mantle-fibres of the two spindles have reached over and have apparently united with one another. In fig. 24 we see three daughter-nuclei in the same plane. By means of the continuous fibres and mantle-fibres they are connected with one another. These fibres now occupy almost the entire cell-cavity. Cell-plates are now formed in the usual way. Swellings appear on the connecting fibres; these increase in size, and finally result in forming cell-walls which separate the daughter-cells from one another. During this stage there appears to be very little of the perikaryoplasm left and what is present is scattered irregularly through the cell.

Whether the method of spindle-formation observed in *Cobœa* is of general or exceptional occurrence must be left for future investigation to decide. From Belajeff's (1894) description of *Larix* it may be supposed that a similar process takes place here, but the origin of the network and the manner in which the spindle-fibres subsequently arise from it were not sufficiently investigated. The development of spindle-fibres out of a network, as shown in figs. 9-13, recalls Wilson's (1895) description of the formation of astral rays and spindle-fibres in *Toxopneustes*.

This method of spindle-formation differs decidedly in its earlier stages from that observed by Osterhout (1897) in *Equisetum*, although both agree in the formation of a number of poles which subsequently fuse to form the bipolar spindle. We have in *Cobœa* a zone of granular substance, the perikaryoplasm, whose function it is to take part in the formation of a network from which the spindle-fibres are developed; no such zone, however, is present in *Equisetum*. Similar zones have been figured by Belajeff (1894) (fig. 6) in *Larix* and Mottier (1897, *a*) in *Lilium*, but they have not been described as taking any part in the formation of kinoplasmic fibres.

In all other cases where multipolar spindles have been observed the earlier stages have not been sufficiently investigated to warrant any statement as to whether they follow the *Equisetum* type or that here described for *Cobœa*.

From the series of stages here figured the writer can only conclude that centrosomes or directive spheres can take no part in the formation of the spindle, and they confirm the idea that has already been expressed that in the vascular plants the method of spindle-formation is entirely different from that which prevails in the lower plants and animals.

In conclusion I wish to acknowledge my indebtedness to Mr. Osterhout for many valuable suggestions in the preparation of this paper.

SUMMARY.

The observations made upon the formation of the spindle in *Cobœa* may be briefly stated as follows:

A granular substance gradually accumulates and forms a complete zone around the nucleus. This zone is designated perikaryoplasm. Upon the breaking down of the nuclear wall the linin of the nucleus and the perikaryoplasm form a network which occupies the central portion of the cell.

This network grows out into several projections which become the cones in the multipolar figures.

The spindle-fibres are formed by the elongation of the meshes of the network in the direction of the projections.

The cones elongate and become sharply pointed. They fuse in two groups and form the bipolar spindle in the same manner as that observed by Osterhout in *Equisetum*.

The mature spindle is characterized by the great length and crossing of the mantle-fibres.

The spindle-formation of the second division is identical with that of the first division.

No bodies that could be identified as centrosomes were found in any stage of the process.

Botanical Laboratory,
University of California,
April, 1898.

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EXPLANATION OF PLATE XXXIII.

Figures drawn with Abbe's camera lucida. Zeiss, Apochromatic Immersion Obj. 12 mm. 1.30 Ap. Compensating Ocular No. 6.

Fig. 1. A young pollen-mother-cell. The cytoplasm is a clear network which stains a light or gray-blue. The meshes of the network appear to be smaller and radially elongated towards the nucleus. There are numerous spherical bodies scattered through the cytoplasm. They are stained black, probably by the fixing fluid. The nucleus is quite large and shows a large nucleolus and small oval chromosomes which lie immediately upon the nuclear wall. The linin, which stains deep blue, is of a lumpy or granular nature.

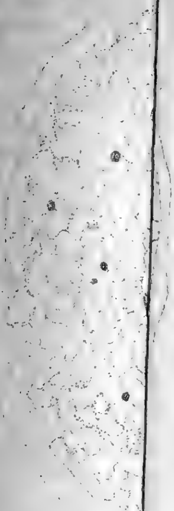
Fig. 2. This figure shows the commencement of a remarkable differentiation which takes place in the cytoplasm which immediately surrounds the nucleus. A zone of granular substance, the perikaryoplasm, forms around the nucleus, which differs decidedly both in structure and staining qualities from the surrounding network. While the outer cytoplasmic reticulum stains a light or gray-blue, the granular substance stains orange.

Fig. 3. This figure shows a later stage with an increase in the quantity of perikaryoplasm about the nucleus, otherwise it does not differ essentially from fig. 2.

Fig. 4. Shows a still greater increase in the quantity of perikaryoplasm about the nucleus. The black bodies are now beginning to form a ring at the outer margin of the granular zone.

Fig. 5. The perikaryoplasm has now reached its maximum and stands out in the greatest contrast from the outer cytoplasm. The meshes of the outer reticulum which abut on the perikaryoplasm are small and apparently compressed, giving the impression of a loose membrane which separates the two zones from one another. It is impossible to trace any of the outer meshes into the granular zone. They appear to have no connection with the nuclear wall. The black bodies have now taken up their position at the outer margin of the perikaryoplasm and form a complete ring about it.

Fig. 6. It will be noticed that in the preceding figures the linin is more or less of the nature of a granular thread. It now appears to have lost its granular structure and appears in the form of very fine threads. We now have the first indication of the breaking down of the nuclear wall, and at that part where the nuclear wall is broken, the perikaryoplasm is commencing to take on the form of a network and stains violet.



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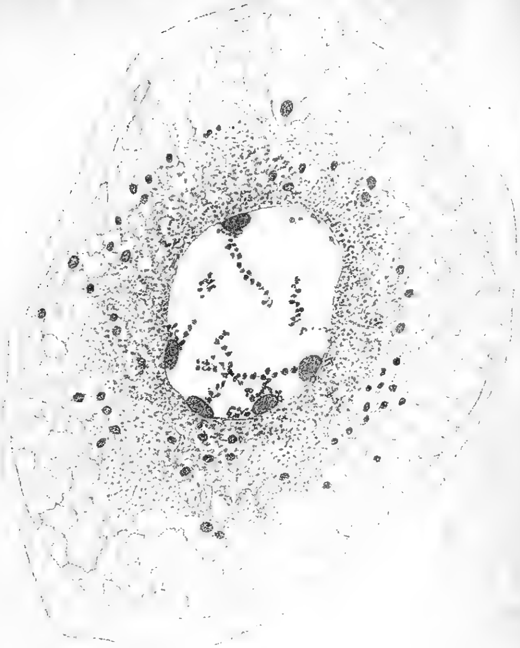

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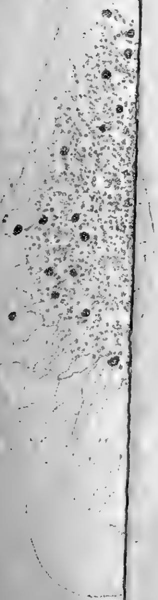

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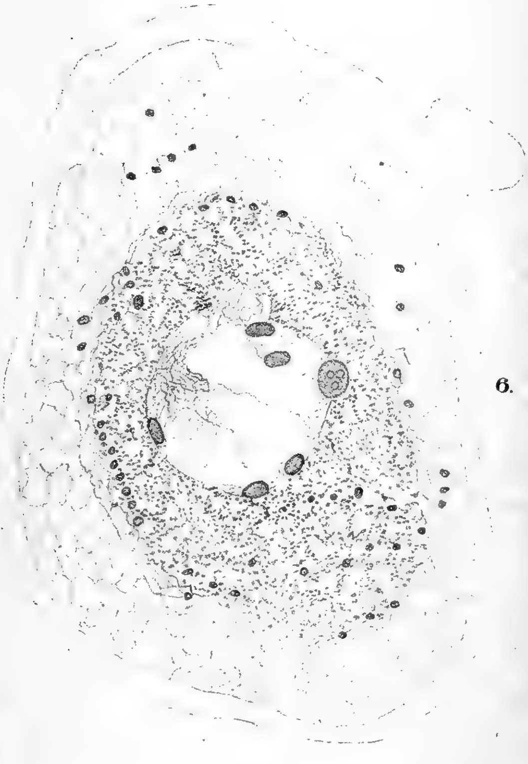

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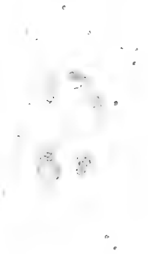
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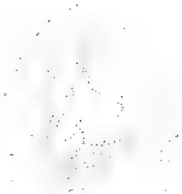
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EXPLANATION OF PLATE XXXIV.

Fig. 7. The nuclear wall has nearly all disappeared and the linin has now formed a network. The perikaryoplasm is being gradually transformed into a network of threads which stain deep violet, in contrast to the orange of the surrounding perikaryoplasm.

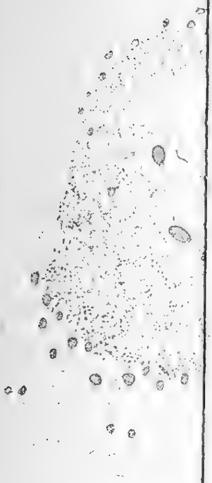
Fig. 8. This stage is about the same as fig. 7, only the network appears to be of a more definite nature.

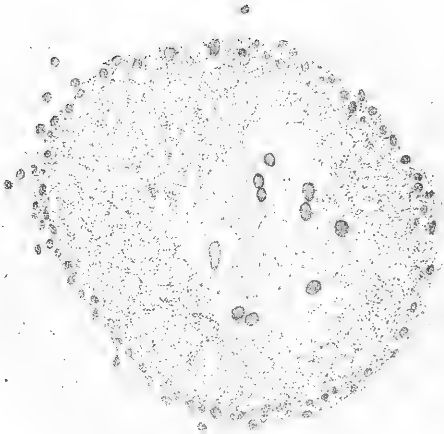
Fig. 9. The nuclear wall has entirely disappeared and the area once occupied by the nucleus is now filled with a clear network of threads; where the threads cross one another granules are present. The entire contents of the cell is now beautifully differentiated into three parts: the outer cytoplasmic reticulum which stains light blue; perikaryoplasm which stains orange, and the central network which stains deep violet. The figure also shows that the central network has in three places grown out into projections.

Fig. 10. This shows the projections to have grown considerably and the meshes of the central network are more elongated, as if pulled out.

Fig. 11. In this figure the projections have grown out to such an extent and the meshes have become so elongated that they form distinct fibres. The more definite the fibres, the more deeply violet they stain. The figure also shows the vacuolated nucleolus.

Fig. 12. This stage is probably earlier than fig. 11, as there are no fibres developed as yet. It shows the central network grown out in three distinct projections, and we have the outline of a multipolar spindle.





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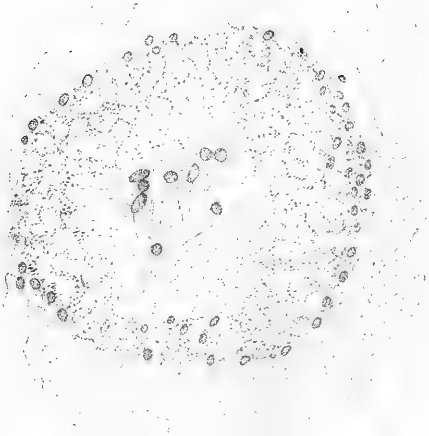

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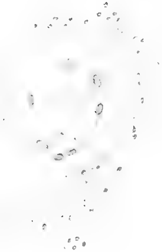
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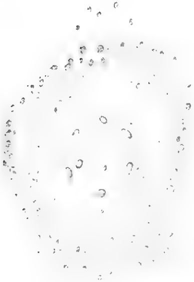
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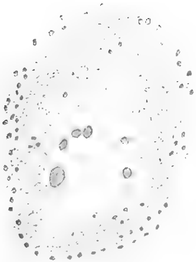
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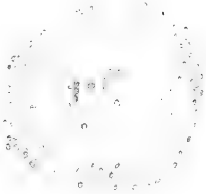
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EXPLANATION OF PLATE XXXV.

Fig. 13. Here we see a characteristic multipolar spindle, the fibres straight and definite, and the cones terminating in sharp points. We also see fibres with free ends projecting from the apices of the cones. These eventually become the mantle-fibres in the mature spindle. It will also be noticed that the chromosomes have taken up a more central position.

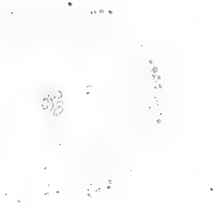
Fig. 14. This figure shows that certain of the poles have approached each other and we have the indication of a bipolar spindle. The mantle-fibres have also grown to a considerable length.

Fig. 15. This figure shows the mature bipolar spindle. The chromosomes lie in the equatorial plate. The mantle-fibres have developed to an extraordinary length; those from one pole cross those from the opposite pole. The mantle-fibres, although very long, do not extend beyond the perikaryoplasm. The contractile fibres, which are connected with the chromosomes, are plainly compound in nature. There are also continuous fibres to be seen which extend from pole to pole uninterrupted.

Fig. 16. This stage is a little later than that shown in fig. 15. The chromosomes have separated and have commenced to move towards the poles. The poles of the spindle terminate in sharp points. The mantle-fibres have reached their maximum development.

Fig. 17. By the contraction of the contractile fibres the chromosomes have been drawn toward the poles. The mantle-fibres now appear to be more divergent from their respective poles.

Fig. 18. The chromosomes have now reached the poles. The mantle-fibres have lost their straight appearance and hang loosely alongside of the remaining continuous fibres.



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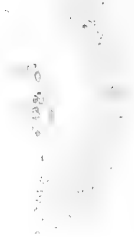

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EXPLANATION OF PLATE XXXVI.

Fig. 19. Here we see each of the daughter-nuclei surrounded by a membrane, with the chromatin stained blue, and in the form of a necklace. There is also seen a nucleolus in each daughter-nucleus. The continuous fibres still connect the nuclei with one another. The granular substance appears to surround the nuclei except where the continuous fibres are connected with the nuclear membrane.

Fig. 20. The perikaryoplasm now entirely surrounds each daughter-nucleus. The connecting fibres have curved out toward the cell-wall but can no longer be traced to the walls of the nuclei.

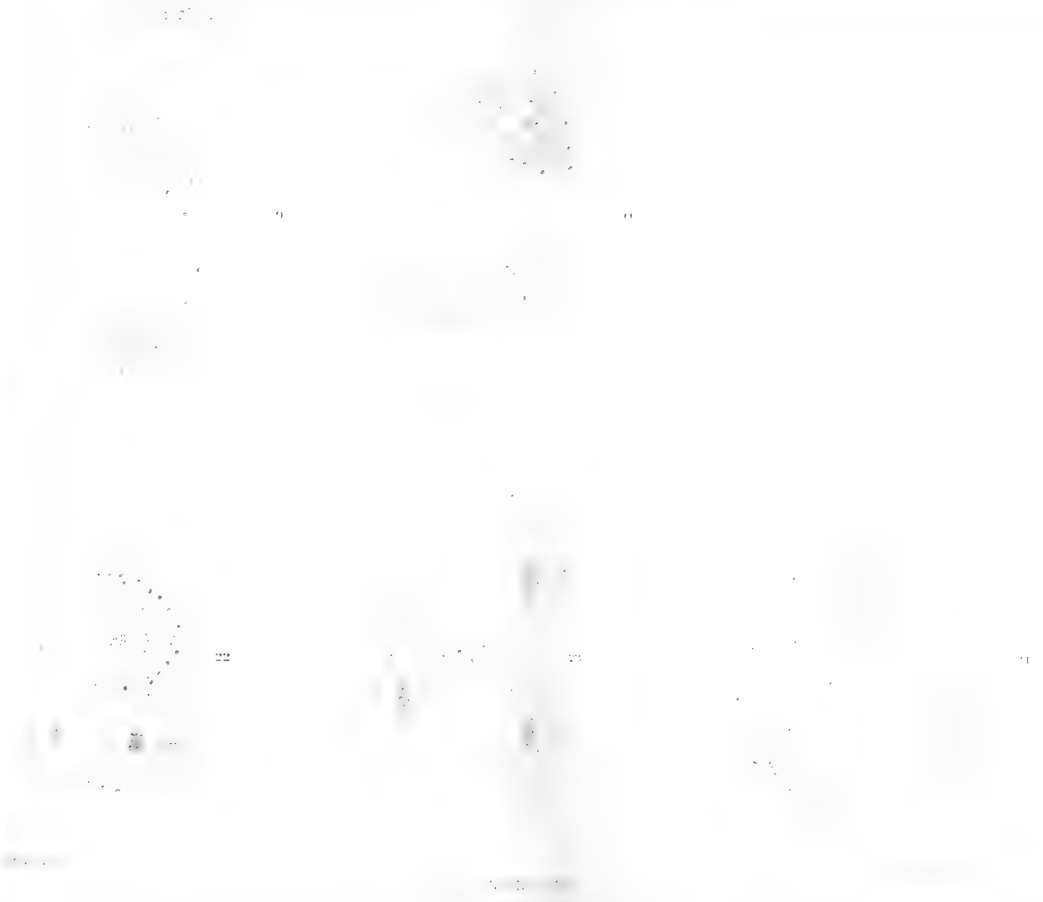
Fig. 21. The old spindle-fibres have disappeared and each of the daughter-nuclei is surrounded by a definite zone of perikaryoplasm. The black bodies form a ring at the outer margin of each zone.

Fig. 22. This figure shows the two spindles of the second division lying at right angles to one another. The one is only represented by the cross-sections of its fibres, the other shows the entire spindle with the chromosomes on their way to the poles and with the characteristic mantle-fibres. This figure also shows that the perikaryoplasm has accommodated itself to the shape of the spindles. In one view the zone is round and in the other oblong, corresponding to the size and shape of the spindle.

Fig. 23. Here the spindles of the second division are more nearly in the same plane than in the preceding figure. The chromosomes are at the poles. The mantle-fibres of the two spindles have reached over and united, thus connecting the nuclei with one another.

Fig. 24. Here we see three of the daughter-nuclei in the same plane, each surrounded by a nuclear wall. The chromatin is in the spireme stage. All the daughter-nuclei are connected by fibres which almost fill the entire cell-cavity. These fibres are curved out toward the cell-wall, and we see swellings on some of them. What little of the perikaryoplasm is left is scattered irregularly through the cell.

A.A.Lawso



THE ORIGIN OF THE KARYOKINETIC SPINDLE IN PASSIFLORA CŒRULEA LINN.[1]

BY CLARA L. WILLIAMS, M. S.

PLATES XXXVII–XL.

RECENT work on karyokinetic division has made it appear very probable that no centrosome is present in the higher plants. In view of this the origin of the spindle becomes a subject of especial interest. The study of karyokinesis in the pollen-mother-cells of *Passiflora cœrulea* was taken up in the hope of shedding some light on this question. The origin of the spindle is the sole question considered in this investigation other matters receiving only casual attention.

Among the fixing fluids experimented with in the preparation of material were Wilson's sublimate-acetic, Boveri's picro-acetic, Flemming's strong mixture, Flemming's strong mixture diluted with an equal part of water, and 2 per cent. iridium chloride. When anthers fixed in Wilson's, Boveri's, and dilute Flemming's solutions were crushed and examined in their respective fluids they showed such shrinkage that these fluids were not used in making preparations. Good results were obtained with iridium chloride, but no better than with Flemming's strong mixture (undiluted), which was used for fixing the greater part of the preparations studied.

The anthers were left in the fixing fluid for twenty-four hours, and afterwards washed in running water for six hours.

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[1] Contributions from the Botanical Laboratories of the University of California, No. 4. Presented for the degree of Master of Science. Prepared under the direction of Mr. W. J. V. Osterhout.

April 13, 1899.

They were then placed in the inner part of a dehydrator[1] and barely covered with water. The outer part of the dehydrator was filled with 95 per cent. alcohol. After remaining in the dehydrator for twenty-four hours, the material was removed to 95 per cent. alcohol and left for six hours. It was then run up successively through a mixture of equal parts of 95 per cent. of alcohol and absolute alcohol, absolute alcohol, a mixture of equal parts of absolute alcohol and bergamot oil, bergamot oil, a mixture of equal parts of bergamot oil and paraffin (43°), and a mixture of paraffin (43°) and paraffin (52°). The anthers remained six hours in each. When in bergamot oil they were placed on the paraffin oven. Paraffin (52°) was used for imbedding and the microtome sections were cut from 3 to 5 microns in thickness. The sections were fixed to the slide either with albumen (the sections being first spread out on a layer of water over the albumen, after which the slides were placed upon the paraffin oven to dry) or with 80 per cent. alcohol according to Eisen's method (Eisen 1897). The latter method is preferable as the sections may be stained almost immediately. After mounting, the sections were stained with the Flemming triple stain. They were first placed in safranin, where they remained twenty-four hours. On removal they were decolorized with 95 per cent. alcohol until the stain was removed from everything except the nucleolus. They were then washed with water and placed in gentian violet, where they were allowed to remain from five to fifteen minutes. There was then poured over the slide in rapid succession, a concentrated solution of orange G, 95 per cent. alcohol, and absolute alcohol. Clove oil was then poured upon the slide and the progress of decolorization watched under the microscope.

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[1] The dehydrator was made in accordance with the suggestion of Prof. W. A. Setchell, as follows: A funnel of appropriate size is deprived of its neck and supported in the mouth of a tumbler or beaker. A piece of parchment paper folded in the same manner as for filtering is placed in the funnel. A cover fits over the top of the tumbler to prevent evaporation. Alcohol is placed in the tumbler; the material is placed in the funnel and covered with water. The rapidity of dehydration depends upon the quantity of water, the strength of the alcohol, and the thickness of the parchment paper, and can be kept under perfect control.

When the sections were sufficiently decolorized the clove oil was removed by placing the slide in xylene for a few moments. The sections were finally mounted in Canada balsam.

In the young pollen-mother-cell, when the chromatin is still in the spireme stage (fig. 1), the cytoplasm is composed of two distinct elements. One is fibrous and forms a network throughout the cell from the nuclear wall to the cell-wall. The other is granular and is uniformly distributed within and upon the meshes of the network. The threads of the reticulum are knotted and sinuous and take the violet stain. The granular part of the cytoplasm usually stains yellow or yellowish brown. About the time when the chromatin thread breaks up a change takes place in the cytoplasm. The meshes of the reticulum immediately surrounding the nucleus are drawn out parallel to the nuclear wall and form a sort of weft about it (fig. 2). This condition of the cytoplasm is of short duration. Soon the meshes of the cytoplasmic reticulum assume a new arrangement. They become drawn out at right angles to the nuclear wall and appear as if radiating from the nucleus (fig. 3). A little later, irregular, deeply staining strands appear in the cytoplasm (fig. 4). For the most part, they are radially arranged and extend toward the cell-wall; some of them reach it. In one or two instances similar stages show groups of fibers outside the nuclear wall. These groups are conical with their bases directed toward the nucleus; they resemble the cones of *Equisetum* (Osterhout 1897, fig. 4). Their subsequent fate could not be determined; no trace of them was seen in later stages.

The radial arrangement of the cytoplasmic reticulum spoken of above disappears after a short time, and the fibers of the cytoplasm again form an irregular network as in figs. 1 and 2. The meshes show no tendency to be drawn out in any one direction, although a few deeply staining strands radiate from the nucleus (figs. 6, 7 and 9). Changes in the nuclear wall resulting in its transformation into a meshwork now begin. The first evidences of such change are the appearance of granules in the nuclear wall and an irregularity in its outline (fig. 6). Various stages in the transformation of the nuclear wall have been observed (figs. 7, 8, 9 and 10). As the figures show, this change continues until finally no definite nuclear membrane remains; in its stead, there is a zone of deeply staining meshes, the fibers of which contain many granules (fig. 11). This meshwork connects the linin reticulum with the cytoplasmic reticulum, forming one continuous network from cell-wall to cell-wall.

In the younger cells there are but few linin threads and these are delicate and stain but slightly. Later, however, they become coarse, exhibit thickenings and increase so that a linin reticulum entirely fills the nuclear space (figs. 8, 9, 10 and 11).

The granular constituent of the cytoplasm, which was at first uniformly distributed, soon becomes more or less massed in irregular patches midway between the nuclear wall and the cell-wall (fig. 4), leaving areas comparatively free from granular matter near the cell-wall and near the nuclear wall. This massing of the granular matter continues until a complete dense zone, the granular zone, is formed at the time when linin, nuclear wall, and cytoplasmic reticulum form an unbroken network from cell-wall to cell-wall (figs. 11 and 12). The granular zone is constant from this time on until the anaphase, and is occasionally seen even after the daughter-nuclei are formed. Such a zone has been figured by several observers. Juel (1897) shows it as a definite zone in multipolar and bipolar stages; Belajeff (1894) and Osterhout (1897) in the bipolar stage; and Mottier (1897, *a* and *b*) traces of it in prophase, in multipolar and bipolar stages. What the formation of the granular zone has to do with the origin of the spindle is uncertain. It appears to be simply an accumulation of the granular part of the cytoplasm in a definite area.

Soon after the formation of the continuous reticulum filling the cell, the fibers in the vicinity of the old nuclear wall cease to stain more deeply than the other parts of the reticulum. The entire network stains uniformly (fig. 12), although the fibers inside of the granular zone differ in appearance from those outside of it. They are delicate and clear cut, while those outside are much thicker, more granular and less fibrous in structure. This difference between the parts of the reticulum inside and outside of the granular zone is more marked in the later stages.

The first indication of the formation of the spindle poles is a decided change in the portion of the reticulum surrounded by the granular zone. At various points this part of the reticulum is drawn out into cones, which become the poles of the multipolar spindle (fig. 13). Each cone is composed of a reticulum whose meshes become stretched in the direction of the long axis of the cone and finally become fibers, many of which end free. A little later all traces of a reticulum inside of the granular zone disappear. The whole space limited by the zone is filled with free fibers which cross each other in all directions. Many of them converge at their extremities to form the poles of the multipolar spindle (fig. 14). At first the poles point in all directions, but soon they show a tendency to assemble in two groups (fig. 15), which are probably destined to form the poles of the bipolar spindle. The chromosomes assume a more central position than they have had heretofore and are more crowded together. The poles of these two groups gradually fuse (figs. 16 and 17) until finally a sharp-pointed, bipolar spindle results (fig. 18). In the equatorial plate stage, the spindle is usually long, very narrow, sharply pointed, and without mantle-fibers. Sometimes, however, there are long mantle-fibers which extend from the poles and pass obliquely to the cell-wall, the fibers from each pole crossing those from the opposite pole in their course. Often the poles extend to the cell-wall. In the metaphase, also, the poles may extend to the cell-wall; mantle-fibers are more often seen in this stage than in the equatorial plate stage. At this time, too, the spindle is usually broader than in earlier stages and its outline is more nearly elliptical. Often, in this stage, the groups of fibers which extend from pole to pole are not straight as if stretched, but are more or less wavy (fig. 19). This may be due to the drawing together of the poles. That the poles do approach each other appears probable from the fact that, although in the equatorial plate stage, the poles extend almost or quite to the cell-wall; yet the daughter-nuclei are always some distance from it.

The difference in the character of the threads of the inner and outer portions of the cytoplasmic reticulum, which has been mentioned above, increases as spindle formation progresses. The threads of the inner portion become less granular and more sharply defined, while those of the outer portion behave in exactly opposite fashion, becoming more and more granular, and finally coming to resemble accumulations of granules rather than threads. Sometimes in the bipolar stage only a few meshes remain and these lie close to the cell-wall (fig. 19). At other times in the same stage such a reticulum still extends throughout the cell (fig. 18).

Frequently, when the chromosomes have reached the poles, and also after the daughter-nuclei are formed, branching fibers extend in all directions from the poles almost to the cell-wall. At this time the granular zone may still be discernable, although it may be more or less obscured by the presence of granular matter both inside and outside of the zone (fig. 21). Before long the spindle fibers are separated from the daughter-nuclei by granular matter and each daughter-nucleus is surrounded by a dense granular mass of cytoplasm (fig. 22).

Many recent observations on spindle-formation in higher plants show that the developing spindle passes through a multipolar stage which becomes bipolar by the fusion of the poles, or by the withdrawal of some of them. Multipolar stages are figured and described by Farmer (1893 and 1895), Belajeff (1894), Strasburger (1895), Osterhout (1897), Mottier (1897 *a* and *b*), Juel (1897), Webber (1897) and Debski (1897). But the origin of the multipolar spindle has been worked out in only two or three cases. Osterhout (1897) describes it for the spore-mother-cell of *Equisetum* as follows: The process begins by the meshes of the reticulum immediately surrounding the nucleus becoming drawn out parallel to the nuclear wall and forming a sort of skein about it. This condition is transitory; soon the cytoplasm immediately surrounding the nucleus does not consist of a network, but of radially arranged fibers which gradually grow longer and push out into the surrounding cytoplasm. At first these cross each other in all directions but soon become parallel. Later, they bend toward each other and form numerous cones which begin to fuse, the nuclear membrane, meanwhile, disappearing in places. The threads of the cones penetrate into the nucleus and come into connection with the linin threads. The nuclear wall entirely disappears and the multipolar spindle is formed. Mottier (1897*a*) describes a similar origin of the multipolar spindle. The following is a summary of Belajeff's account of its origin in the pollen-mother-cell of *Larix:* The cytoplasm immediately surrounding the nucleus takes on an arrangement which, at first glance, produces the impression of a skein-like mass of threads wound around the nucleus, forming a distinct zone. It really consists of a network, the meshes of which are drawn out parallel to the nuclear wall. (In this, Strasburger's work on *Larix* agrees with Belajeff's). The nucleus soon becomes filled with a linin network. The nuclear wall disappears entirely and the inner linin network and the outer cytoplasmic one unite to form a continuous reticulum. Fibers pass from the "Centralkörper" (as Belajeff calls the central network) to the cell-wall, running radially or tangentially through the cell. The fibers, by their contraction, pull the "Centralkörper" out into a three- or four-angled body. Several fibers unite in a pole which is situated toward the periphery of the cell and is connected by fibers with the cell-wall, as well as with other poles. The chromosomes lie in the middle of the "Centralkörper," surrounded and held in place by a network whose fibers are gradually drawn out to form the spindle-fibers.

These are fastened to the chromosome in two groups, one at each end. All the fibers of the "Centralkörper" finally become directed toward one or another of the poles, whose number is finally reduced to two, probably by fusion.

It will be seen that the process in *Equisetum* has but little in common with that in *Passiflora*, and that the process in *Larix*, on the other hand, agrees with that in *Passiflora* in some very essential points. In both *Larix* and *Passiflora* the cytoplasm and linin take part in the formation of a central network which is pulled out to form cones, which later become composed of free fibers. The cones then fuse to form the bipolar spindle. Various details, however, are different in the two. The peculiar arrangement of the cytoplasm showing a zone around the nucleus (fig. 2) in which the meshes are drawn out parallel to the nuclear wall recalls Belajeff's description, but, as in *Equisetum*, is of short duration and it is difficult to say what part, if any, it plays in spindle-formation. The same arrangement has been described by Strasburger (1895) for *Larix*. He finds it to have about the same connection with the formation of the spindle as does Belajeff. Other observers have described a similar arrangement, but do not explain it.

The radial arrangement of the cytoplasmic network (fig. 3) corresponds very closely with Belajeff's description of the state of the cytoplasm of *Larix* before the meshes begin to be drawn out parallel to the nuclear wall. In *Passiflora*, however, the radial arrangement occurs *after* this stage. The radial arrangement described by Guignard (1891), Farmer (1893 and 1895), Osterhout (1897), and Mottier (1897*a*) seems to be due to the presence of free fibers, not to a network.

Belajeff speaks of fibers which extend out from the central network to the cell-wall; these run radially or tangentially. The appearance of fig. 4 certainly seems to indicate that there is a similar condition here. Some of the fibers can be traced to the cell-wall, but there is no evidence that they pull the central network out into cones as they do in *Larix*; indeed, their disappearance before the formation of the multipolar spindle would seem to prove that they have no such function.

The unbroken network stage in *Passiflora* (figs. 11 and 12) is much more striking than in *Larix*, and the cones are formed directly by the drawing out of this network without a preliminary converging of radial fibers such as Belajeff describes.

The conversion of a reticulum into spindle-fibers has also been described by Wilson (1895). In his work on the egg of the sea-urchin, he shows that the spindle-fibers are differentiated out of the linin reticulum.

To point out briefly the differences in the mode of formation of the multipolar spindle in *Equisetum*, *Larix*, and *Passiflora:* in *Equisetum*, the cones are formed solely by the converging of radial fibers and only come into contact with the linin network after they have reached their full size; in *Larix*, they are formed by the converging of radial fibers, and subsequently increase in size by the pulling out of the network at the places where they are attached to it; in *Passiflora*, they result from the simple drawing out of the network.

SUMMARY.

The cytoplasm of the cell in the spireme stage is composed of two separate elements. First, a reticulum stretching from nuclear wall to cell-wall, and, second, a granular substance uniformly distributed in and upon the meshes of the former. When spindle-formation begins the granular substance collects some distance from the cell-wall and forms a dense zone—the granular zone (figs. 11, 12, 13).

The spindle is formed as follows: The nuclear cavity gradually becomes filled with a linin network. The nuclear wall is transformed into a meshwork which connects the linin network with the cytoplasmic reticulum, making a single continuous network which fills the entire cell. That portion of the network which lies in the center of the cell,

surrounded by the granular zone (fig. 12), forms the spindle. It projects out at various points to form cones in which the meshes are gradually stretched and finally form free fibers (fig. 13). The whole reticulum inside of the granular zone finally becomes transformed into such cones. These at first point in all directions, but finally form two groups (fig. 15). In each of these groups the poles fuse to form a single one, thus producing the bipolar spindle.

The spindle is formed by the rearrangement of pre-existing structures, namely, of linin, nuclear wall, and cytoplasmic reticulum. No centrosome is present, nor could any special spindle-forming substance be recognized.

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BERKELEY, CALIFORNIA,
May 1, 1898.

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EXPLANATION OF PLATE XXXVII.

The Abbe camera was used in drawing.

Objective, Zeiss, oil immersion 1/12; ocular, compensating No. 6.

Fig. 1. Represents a cell with the chromatin in the spireme stage. The cytoplasm is composed of two distinct elements: One is fibrous and forms a reticulum throughout the cell from nuclear wall to cell-wall. The other is granular and is uniformly distributed within and upon the meshes of the reticulum. The meshes of the reticulum are irregular in form and are smaller immediately surrounding the nucleus than elsewhere. Its threads are sinuous and irregularly knotted. The nucleolus is large and contains a small vacuole.

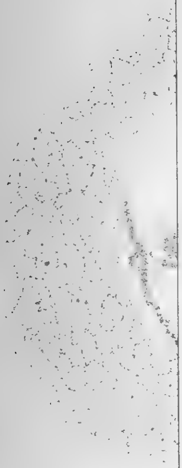
Fig. 2. The cytoplasm exhibits a peculiar structure. The fibers of the reticulum immediately about the nucleus are drawn out into long, narrow meshes parallel to the nuclear wall, forming a sort of weft about it. These appear, at first glance, as long, continuous fibers wound about the nucleus.

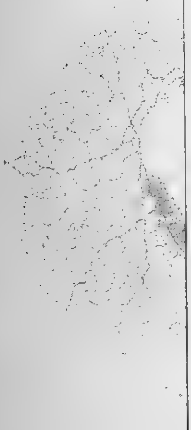
Fig. 3. The meshes of the cytoplasmic reticulum are drawn out at right angles to the nuclear wall and appear as if radiating from the nucleus. The chromosomes are very near the nuclear wall. The nucleolus is still about as large as that in fig. 1 and contains several vacuoles. Linin granules and threads partially fill the nuclear cavity.

Fig. 4. The granular element of the cytoplasm is beginning to accumulate in dense masses. Deeply staining, irregular strands are to be seen in the cytoplasm. They are radially arranged and some of them extend clear to the cell-wall. At first glance they appear as free fibers, but close examination shows them to be only thickened, more granular strands of the cytoplasmic reticulum. In other respects the figure resembles fig. 3.

Fig. 5. Three or four conical groups of fibers extend from the nuclear wall into the cytoplasm. Otherwise the figure is very much like fig. 4.

Fig. 6. The deeply staining, radially arranged, cytoplasmic strands seen in figs. 4 and 5 are less marked. There is a good development of linin. The chromosomes are very near the nuclear wall, which is irregular in outline and is beginning to be transformed into a meshwork.





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EXPLANATION OF PLATE XXXVIII.

Fig. 7. Differs but slightly from fig. 6. The transformation of the nuclear wall has progressed farther and the wall is interrupted at several points.

Fig. 8. Is similar to figures 6 and 7. The alteration in the nuclear wall, however, is still more marked; the linin is more abundant, its threads are coarser, contain more granules, and stain more deeply.

Fig. 9. The cell resembles that represented in fig. 8. The nuclear wall has apparently been transformed into a meshwork which forms one continuous network with the cytoplasmic reticulum on one side and with the linin reticulum on the other. The quantity of linin has increased.

Fig. 10. Is much like fig. 9, although the transformation of the nuclear wall has not progressed so far. The appearance of this and the two following figures might give rise to the suspicion that the sections of the nucleus are not median and that the appearance of the network filling the nuclear cavity is due to focussing on the inner surface of the nuclear wall. Careful focussing, however, shows conclusively that this is not the case.

Fig. 11. The nuclear wall, as such, is no longer to be distinguished. In some places it forms a fibrous belt two or three meshes in width. These fibers stain more deeply than any others; they are coarser and contain more granules; they help to form the continuous network which fills the cell. In one place every trace of the nuclear wall is lost; nothing remains to mark the transition from linin reticulum to cytoplasmic reticulum. The granular part of the cytoplasm now forms a complete zone between the fibrous belt representing the nuclear wall and the cell-wall.

Fig. 12. Every trace of the nuclear wall has disappeared. There is nothing to even indicate its position, and an uninterrupted network stretches from cell-wall to cell-wall. The granular zone referred to in fig. 11 is well marked.

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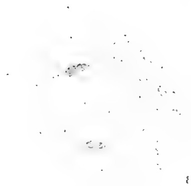

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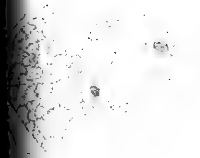

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PASSIFLORA CŒRULEA *LINN.*

EXPLANATION OF PLATE XXXIX.

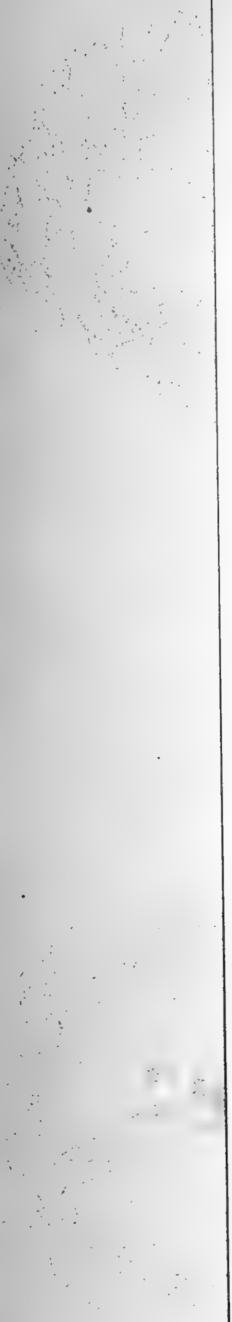
Fig. 13. Shows the part of the reticulum inside of the granular zone beginning to be drawn out into cones. In many places, the reticulum is still continuous from the chromosomes to the cell-wall.

Fig. 14. Represents an early multipolar stage. There is no longer a reticulum inside of the granular zone. It has been drawn out at various points to form cones in which the meshes have been gradually stretched until now they form free fibers. These cones and free fibers extend in all directions.

Fig. 15. The poles of the multipolar spindle lying within the granular zone show a tendency to gather into two groups which are probably destined to form the poles of the bipolar spindle.

Figs. 16 and 17. Represent very late multipolar stages with the poles fusing. The granular zone is clearly evident in each.

Fig. 18. The poles have fused completely, forming a sharply pointed spindle.



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PASSIFLORA CÆRULEA

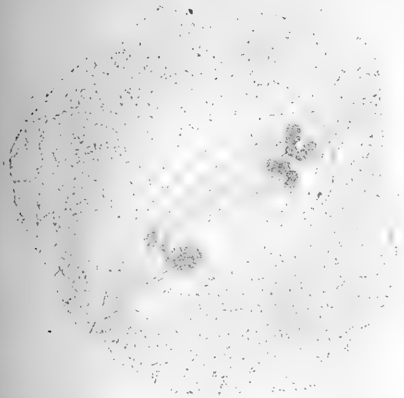
EXPLANATION OF PLATE XL.

Fig. 19. Shows a spindle in the anaphase. The granular zone is well marked. From the spindle irregular fibers, probably mantle-fibers, pass out and penetrate the granular zone.

Fig. 20. Represents a spindle in the anaphase. Branching fibers extend from the chromosome-groups toward the cell-wall. The granular zone is somewhat obscured by a more general distribution of granular matter between the spindle and the cell-wall.

Fig. 21. Shows the daughter-nuclei formed. The spindle-fibers still connect them. Branching fibers radiate in all directions from them.

Fig. 22. The spindle-fibers are separated from the daughter-nuclei, each of which is surrounded by a dense mass of granular cytoplasm.



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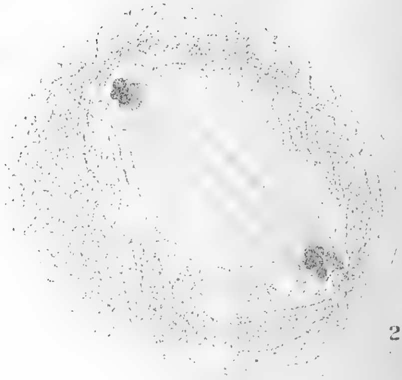

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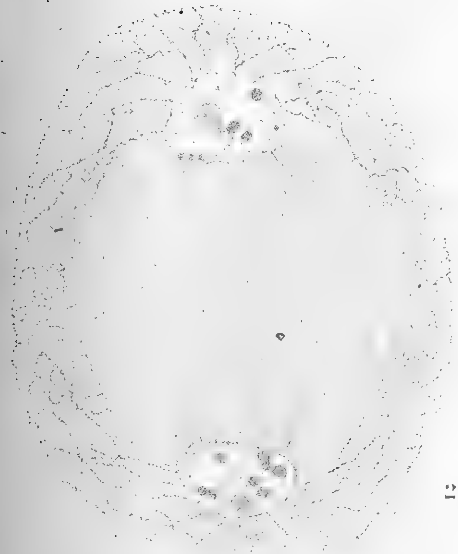

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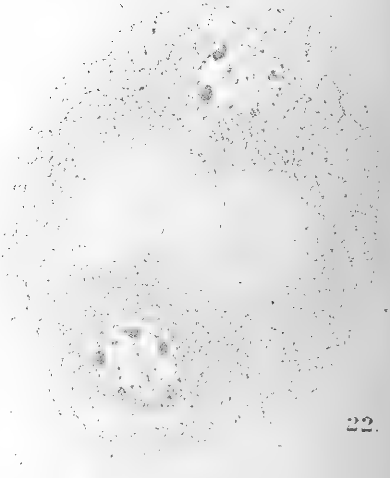

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PASSIFLORA CŒRULEA *LINN.*

THE NATURE OF THE ASSOCIATION OF ALGA AND FUNGUS IN LICHENS.

BY GEORGE JAMES PEIRCE,

Assistant Professor of Plant-Physiology, Leland Stanford Junior University.

CONTENTS.

PLATE XLI.

I. INTRODUCTION.

THE last few years have seen a revival of interest, gratifyingly widespread, in the study of lichens. Except during the few years immediately following the writings of DeBary, Schwendener and Reinke, which wrought a revolution in our conception of lichens, they have been studied mainly by systematists. These found in macroscopic characters all that was required to determine an old or to describe a new species. Every one must have felt, even before Reinke recently recalled the question so forcibly to the minds of botanists, that by no means the last word had been said about these interesting organisms, and that the study of other than superficial characters would repay the investigator. To the physiologist they especially appeal because they are not simple organisms, but an association of two simple organisms.

The nature of the association is variously regarded, from pure parasitism of one member upon the other, to association mutually beneficial, if not absolutely necessary, to the two. Schwendener has always regarded the association as pure parasitism of the fungus upon the alga, and his school advocates the same view. The opposite view is held by Reinke (1894) and his sympathizers, of whom Schneider (1896*a*) is at the moment perhaps the most conspicuous in this country. Reinke believes that the association is what he names Consortism, and that the "Consortium" is as "autonomous" as any plant.

A question to which there are such opposite answers by such eminent investigators cannot be regarded as answered at all. This paper is a contribution to the discussion, and I shall be glad if the account of my work and its results leads at all to the solution of the problem. I must remark at the outset that much of my work may not be new; how much I cannot say, for though I have tried, I have not been able to have access to all the literature on this subject. Furthermore, no one should venture, from the study of only a few forms, to draw conclusions regarding a great number, although the careful examination of a few forms will justify opinions regarding the others, if only these opinions are held tentatively, subject to modification by further researches.

Beginning with *Ramalina reticulata* Krplhbr., a lichen so large that it forms a conspicuous feature of the landscape in some parts of California, I have examined several species and genera of lichens occurring hereabouts, and not trusting merely to microtome sections of "fixed" material, I have had recourse to experiments and cultures on and of living material. The difficulty of minutely studying lichens alive is notoriously great, not least because of their extremely slow growth. Yet in their rates of growth there must be great diversity. I am inclined to believe that *Ramalina reticulata* grows more rapidly than most. My reasons are based on the universal occurrence of large specimens all about here, and also upon the behavior of this lichen in cultures. As emphasized by Benecke (1898) in a recent paper on the culture of Algæ, and earlier by Möller (1887), the difficulty of excluding bacteria from cultures made from vegetating, and even from spore, material, is very great. The presence of bacteria in a culture will at least delay and obscure, if it does not vitiate, the results; and yet to exclude the bacteria is impossible with our present crude culture-technique. The almost invariably gelatinous nature of the exterior of the lichen body renders the removal of the bacteria from the surface impossible. During the latter part of a long dry season, the surface of such a lichen as *Ramalina reticulata* must be so dry, at least by day, that it is not likely to hold the bacteria or the fungus-spores that fall upon it, though they may easily remain caught in some angle or slight irregularity. During and for some time after a rain, in a fog or on a dewy night, on the other hand, the gelatinous surface will be moist, at least sufficiently so in spots to cause whatever bacteria and fungus-spores fall upon it to stick. Möller (1887) recommends washing as thoroughly as possible in clean running water, the aim being to remove by the stream, as well as by floating, whatever may have fallen upon the surface. By this means he partially cleansed the apothecia from which he intended to collect spores for his cultures.

Defective as such cleansing is for the apothecia, which are not especially gelatinous on the surface, it is still more so for the much more gelatinous surface of the thallus. The running water does remove some of the foreign objects, but some of the most gelatinous of these (for example, bacteria in the vegetative condition) cling to the gelatinous surface of the thallus in spite of the most thorough attempts to dislodge them. For this reason, even if sterilized water be used for the washing, a discouragingly large proportion of the thallus fragments used for culture are accompanied by bacteria which multiply only too rapidly. In spite of thorough sterilization of the slides, cover-glasses, vessels and instruments used in connection with the cultures, and the utmost pains to prevent the introduction into the cultures of organisms from outside, I have failed in most cases to make pure cultures, because the lichen fragments themselves carried bacteria, and substances nutritious for them, into the culture-media. In many cases, however, the number of bacteria was constantly small.

For most of my cultures I used the "hanging-drop" method of the bacteriologist, employing for the purpose slides with two concavities, ground sufficiently deep to avoid contact of the drop with the bottom of the concavity. The cover-glasses were sealed upon the slide with vaseline. If the concavities are reasonably large and deep (e. g. 13 mm. diameter, 1 mm. depth) a hanging-drop surrounded by an adequate volume of air, and large enough to supply food-material for several weeks, may be used. It must be admitted, however, that hanging-drop cultures have only a limited usefulness, for the food-supply presently becomes exhausted, and there may accumulate in the drop undue amounts of the dissolved excreta of the organisms present.

Various methods have been employed by others in preparing material for culture. As culture-media for the spores and lichen fragments, I have experimented with boiled tap-water, with the moisture carried by the spores expelled upon the cover-glass, with a drop of the ordinary nutrient beef-gelatine of the bacteriologist, with similar nutrient agar-agar, and with the distilled water used for general purposes in the laboratory. The distilled water was poisonous. I did not consider it necessary to determine the reason for this, though one would suspect it of being acid and possibly of containing traces of copper or other injurious salts. The distilled water prepared in quantity in the chemical laboratory, and supplied by it to the other laboratories of this University, is sufficiently pure for ordinary purposes, but it is ill-suited to culture experiments on living organisms, as repeated experience shows. The effect of our distilled water on motile bacteria is marked and immediate. Bacteria actively motile in the media in which they are cultivated in the laboratory will continue to be motile at the same rate if placed in a drop of sterilized tap-water. Transferred either from the culture directly or from sterilized tap-water into which they have been inoculated, to a drop of distilled water, they promptly come to rest and will not recover their motility. The unsatisfactoriness of our distilled water for lichen cultures may, therefore, be attributed to some poison in it and not to the lack of oxygen, for boiled tap-water will be at least as free from oxygen as ordinary distilled water.

The nutrient agar-agar and gelatine above mentioned were made with tap-water (not distilled water) and had previously been proved to be well adapted to bacteria culture. In the lichen cultures also they were perfectly wholesome, as attested by the only too rapid growth of whatever bacteria were carried into the drops by the spores.

II. THE GERMINATION OF SPORES.

The generally practiced method of obtaining lichen-spores for cover-glass cultures is the following:—the thoroughly cleansed and sterilized cover-glasses, either dry or with a drop of some sterilized nutrient medium, are so placed that some of the spores discharged from an apothecium will strike upon them. The lichen material was prepared thus: fresh specimens of *R. reticulata*, brought into the laboratory from the trees on which they were growing, were brushed and shaken to remove loose dust, etc., from the surface, cut into small pieces, each piece having only one apothecium, and placed on moistened filter-paper in a Petri dish and covered. Near each apothecium, but not touching the lichen, was placed a cover-glass prepared as just described, and supported in such an inclined position that bacteria, etc., which might be floating in the air in the

Petri dish could not settle on the surface intended for the culture. The sterilized cover-glasses, although carefully kept "butter-side down," might readily become infected by air-currents set up by the necessary movement of the cover-glass and by lowering the cover of the Petri dish. Apart from such accidental infection, the possibility of which was carefully reduced to the minimum, the only bacteria which could get into the cultures were those carried in with the spores. The considerable force with which the spores are discharged is indicated, as others have repeatedly shown, by the distance to which they go. This force is developed by the swelling, when wet, of the gelatinous walls of the paraphyses and other cells forming the contents and the walls of the apothecia. In less than five hours, enough spores will usually be ejaculated upon the cover-glass to justify sealing it over a concave slide.

Spores collected thus upon cover-glasses spread thin with agar-agar or gelatine germinated in seven days. At the same time I collected spores upon cover-glasses introduced dry into the Petri dish. Owing to the cooling of the laboratory (from morning, when I set cover-glasses to collect spores, to afternoon, when I sealed the cover-glasses on the concave slides) there accumulated on the cover-glasses not only the moisture carried by the spores, but also that condensed from the damp air in the dish. Thus a supply of water at least adequate for germination was insured, whatever may be said of the nutrient value of such water. After the same lapse of time (seven days) spores had germinated on these cover-glasses.

In all the cultures the number of spores germinated was very small in proportion to the number sown. If I had sufficient confidence in the suitableness of agar-agar and gelatine for lichen cultures, and in the nutritive value of the condensed and spore-carried water, I might draw a definite and significant conclusion regarding the value of the spores of *R. reticulata* as reproductive bodies. I do not feel justified in doing this, though I will call attention to two things. First, there must be a very considerable number of spores discharged, both in nature and in the laboratory, before they are ripe and whenever the apothecia are wet. Second, that by bearing this in mind and by using trustworthy culture media for such cover-glass preparations, subjecting them to otherwise normal conditions of warmth, light and aëration, the percentage of ripe spores capable of germination could be determined. From these data the relative values of the spore-method and the purely vegetative method of dispersal could be ascertained. This is, however, hardly necessary, for, as I have shown in a previous paper (1898), the great majority of the specimens of *R. reticulata* to be found about here are evidently fragments, while only very few have grown where they are from the spore. This lichen may, earlier in its history, have produced even more spores in each apothecium and more apothecia than now, but this would seem hardly necessary, considering the ease with which fruiting specimens and an abundance of spores may be obtained at all seasons. It seems more probable that in this lichen, as is claimed also for others, superiority of the purely vegetative method of dissemination (by means of fragments torn away by the wind) is resulting in the decrease of the germinating power of the spores.

The superiority of the vegetative method of reproduction is two-fold: it insures the presence in the new place of both members of the lichen association—the hyphæ and the gonidia, as is the case in the soredia of other lichens—and it results in much wider dispersal than is possible with spores or soredia. The vegetative method of dissemination of this lichen, so evidently a very valuable one and perhaps the most perfect among lichens, may well react on the production of spores; if not already as to their number, then certainly as to their quality.

Although the spores germinated in the same length of time and in about the same numbers (proportionally) in the agar-agar, gelatine and water cultures, the subsequent development was unequal. In three days after the first germinations were observed, the germ-tubes had grown somewhat but had not branched in the agar-agar and very few if any more spores had germinated, whereas in the water culture the tubes were longer, some of them had branched, as fig. 3 shows, and the number of spores germinated had increased considerably. In eight days more, that is, in eighteen days after the spores were collected on the cover-glasses, growth had ceased in all the cultures. The differences between the water cultures on the one hand, and the agar and gelatine cultures on the other, were now still more evident. The germinated and ungerminated spores in the water cultures still looked healthy, and the number of bacteria in the cultures was comparatively small. In the other cultures, however, there were many spores evidently dead, the remainder looked unhealthy, the germinated ones least so, and the number of bacteria flourishing on and in the agar-agar and the gelatine was sufficiently large to justify the inference that they were an important if not the sole cause of the unsatisfactory condition of the spores.

The contents of the spores which appeared to be alive at all were far less highly refractive than at first; perhaps, but not wholly, because of the consumption of the oil which was stored in them in the form of drops of very considerable size (figs. 1 *a* and *b*, 2, 3 and 4). The death of the spores was marked by certain changes in the cell contents: the protoplasm lost its granular character and gradually became indistinguishable from the wall and the cell-sap, the oil drops spread, became confluent with one another, later appeared to fill the whole cavity of the cell, and finally disappeared altogether, leaving only the empty cell-wall. Minutely to follow the disorganization-phenomena ("Disorganizationserscheinungen") is very difficult, owing to the small size of these two-celled spores.

From what I have noticed, I can only suspect, not conclude, that the spores were killed and disorganized by the products of the discouragingly active bacteria. That the same appearances may be produced in another way is shown by a water culture made as above described, but with the hollow below the cover-glass filled with sterilized tap-water. In this preparation the spores all died within three days, the protoplasm disappeared, the oil drops became confluent and filled the cell-cavities. Excess of water, inadequate diffusion of oxygen and carbon-dioxide, checked respiration, the diffusion into the water of some poison contained in the vaseline used for sealing — all or any of these may have been the cause of death and of the breaking down of the cell-contents. Bacteria were practically absent.

If it were possible to clean an apothecium so thoroughly that no bacteria would be carried by the spores ejected upon the cover-glass, it seems probable that agar-agar would prove a good medium upon which to cultivate lichens from the spores. This is conceivable but not readily attainable. If practicable, agar-agar cover-glass cultures would be very useful, for they could be minutely watched with the high powers of the microscope.

In the cultures just described, made during the latter part of the rainy season, in February, only one cell in each spore put out a germ-tube. Water cultures begun about the middle of March, when it was warmer out of doors and the rains were practically over, were more successful in that both cells of some spores germinated, though in all of these the tubes from the two cells were unequal in length, and only one tube from a spore branched.

Having obtained germinated spores by means of these cultures, I attempted to reconstruct a *Ramalina* by putting these where they could easily reach gonidia from a *Ramalina* thallus. The method employed was this: Into a tap-water hanging-drop culture of *R. reticulata* fragments and isolated gonidia, obtained in the way described on page 218, I introduced by sterilized platinum loop a number of germinated spores, stirring gently so as to mix the spores with the gonidia. Germinated spores were thus brought close to isolated and apparently healthy gonidia. One would naturally expect the germ-tubes to be chemotropically attracted by the gonidia and to bend towards them. As illustrated by fig. 4, the hyphæ put forth by the spores did not bend at all. The hypha figured was about half as long when the germinated spores were sown in the gonidia culture. It continued to grow straight on, did not branch, and never united with the adjacent or with any other gonidium. The same is true of all the others, and although I kept the preparations until all the gonidia were evidently dead, though the hyphæ still looked healthy, no union of hyphæ and gonidia took place. Undoubtedly the bacteria, which overran these cultures within a week after they were made, are responsible for the failure of the gonidia to attract the hyphæ, of the hyphæ chemotropically to respond, and of the two to form a new lichen. That the failure of the attempts just described is not due to an unhealthy condition of the gonidia produced by the isolation is proved on page 220.

DeBary (1887) reports from Stahl's (1877) investigations on the formation of the lichen-thallus, that "smaller branchlets are formed at the points of contact" of the hyphæ with an algal cell, which closely embrace it and enclose it in fresh ramifications. Whether actual contact is necessary, whether the gonidia stimulate the germ-tubes to bend or to branch, whether the union of gonidium and hypha is always by branches of the germ-tube and not by the tube itself — these are questions which renewed investigations only can answer. When, by greater skill and better methods than I have possessed, one is able to put together isolated healthy gonidia and healthy germinated spores, in hanging-drop cultures free from bacteria, the formation and growth of the lichen can be followed, step by step, from the chemotropic behavior of the germ-tubes to the complete investment of the gonidia by the fungus.

III. THE RELATIONS OF GONIDIA AND HYPHÆ AS SHOWN BY CULTURES.

Although I have been unable to reconstruct a lichen, still I believe that by other means I have obtained some information regarding the questions which I hoped to answer in that way.

To isolate the gonidia of *R. reticulata* without injuring them is a matter of considerable difficulty owing to their position in the compact thallus. The methods described by others do not lend themselves to the species upon which I have worked. Baranetzky (1869) apparently made no attempt to isolate the gonidia from the hyphæ directly, contenting himself with making thin hand-sections of living lichens (*Collema*, etc.), and placing them in moist chambers. The result was that the gonidia multiplied and grew more rapidly than the hyphæ, coming out upon the upper surface of the sections and accumulating there practically free from hyphæ. Such a method as this, though satisfactory with filamentous gonidia in lichens of comparatively loose texture, is ill suited to lichens of close texture, containing spherical gonidial cells (*Cystococcus, etc.*) The gonidia do not become free under these conditions. The reason for this may lie in the absence of intracellular haustoria in Baranetzky's lichens and in the close investment and the penetration of the gonidial cells by the hyphæ of the lichens which I have studied. The gonidia of the latter seem to be too completely in the power of the hyphæ to be liberated in this way.

Teasing out thin sections in water by needles is a slow, tiresome and unprofitable task, for even in this way it is almost impossible to break up the small groups of gonidia closely invested and penetrated by hyphæ. These little masses placed in cultures behave like lichens, growing almost imperceptibly; the gonidia do not grow and multiply rapidly and so disrupt the little groups and escape to the surface.

When air-dry, *R. reticulata* is tough and leathery, difficult to section, readily bent, but not at all friable. Sections of the air-dry thallus cannot be pulled to pieces dry by needles, and, when placed in a drop of water on the slide, expand without at all loosening the hold of the hyphæ upon the gonidia. Teasing out sections cut dry and then placed in water is as unsatisfactory as though the sections were cut from a moist thallus.

The toughness of the thallus is due to the longitudinal direction and the compact arrangement of the rather thick-walled hyphæ near the surface. The surface is soft and gelatinous when moist, hard when air-dry. The gelatinous matter of the outer portions of the thallus both holds water very strongly and takes it up very quickly. Air-dry at the end of the long dry season, the lichen still contains 13.9 per cent. of water or nearly one-seventh of its weight, as shown by the following figures:

Weight air-dry	4.72	gr.
Weight constant at	4.06	gr. when dried several hours at 90° C.
Weight lost	0.66	gr.
Percentage of water	13.9	

The dried lichen must be weighed quickly, for it rapidly absorbs moisture from the air and returns to its original weight. When absolutely dry it is as brittle as it ordinarily is tough, and it may be ground in a mortar to a fine powder. Microscopic examination of this powder in water shows it to consist of minute fragments of hyphæ interspersed with isolated gonidia apparently uninjured by the grinding. It occurred to me to attempt drying the lichen at a temperature low enough to avoid injuring the gonidia. Warming in an oven for five hours at 36° C. (96° Fahr.), a temperature often attained, and sometimes maintained for several hours, on a summer day, proved to be perfectly harmless to the gonidia, but it did not dry the lichen to the point of brittleness. To attain brittleness without further heating, small pieces were kept for four days in a desiccator containing glacial phosphoric acid. Even after this treatment the fragments were not perfectly dry and brittle, though grinding rapidly in a mortar yielded powder of which the finest part contained isolated and apparently uninjured gonidia. Some of this was inoculated by needle into hanging drops of sterilized tap-water.

The individual behavior of the isolated gonidia, fairly scattered throughout the hanging drop, could be easily followed. Many of them were entirely free from any trace of hyphæ, while some had short pieces of hyphæ still attached to them. Of the latter, some gonidia, as shown by fig. 12, had haustoria in them, while others appeared to have the hyphæ only adhering or attached to the outside (fig. 7). A difference in size and in subsequent behavior between those gonidia absolutely free from the fungus, and those upon which and in which fungus fragments still remained, is to be noted. Those gonidia which, though enclosed within the lichen, have not been invested by fungus hyphæ, still less penetrated by haustoria, are larger, deeper green, and in every way healthier looking than the others. How is this to be accounted for?

The enclosed but not invested algal cells seem to me to be the only ones in the lichen thallus which are at all advantageously situated. They do have a more constant supply of aqueous solutions of food materials than their fellows outside, they are shaded from excessive light, screened from excessive heat, protected from excessive dryness, shielded perhaps from sudden changes of any kind, possibly manured by the excreta of the fungus. In these ways they may be better off than their unhoused fellows, and sometimes at least they are larger. They are not subject to the drain upon their vital energies which those gonidia invested and penetrated by hyphæ must withstand if they are to survive. The fungus can obtain from these gonidia with which it is not in permanent and intimate contact only such substances as diffuse from them into the water of the lichen-body; whereas it can withdraw through a haustorium within the cell, and even through the cell-wall with which a hypha is closely in contact, the foods elaborated by the gonidia for their own use. Gonidia not invested by hyphæ are to be found in every preparation. They are conspicuous from their larger size, deeper color and generally healthier appearance. It may have been these which suggested the notion that green cells are better off as gonidia than as independent algæ.

The next difference to be noted between the invested and uninvested gonidia is in their subsequent behavior in culture. Within a very few days (at the utmost six) the gonidia which contain haustoria, or which have hyphal fragments still attached to them, have either divided by internal cell-division at least once, or their cell-contents have contracted away from the wall. Figures 6, 7, 8, 9 show various stages in the division of invested gonidia, in fig. 6 into two, in fig. 7 into four, in fig. 8 another divided into four, in fig. 9 at *a* the same cell twenty-four hours after, when the wall of the mother-cell had become dissolved, setting free eight daughter-cells. In fig. 9 at the *, and in fig. 10, we have gonidial cells in which the haustoria, broken away from the hyphæ which formed and bore them, are plainly visible, the contents of the gonidial cells contracting away from, and in in this way escaping, the haustoria. Later the contracted mass surrounds itself by a new wall and behaves like the uninvested gonidia. These last do not divide in the culture for a very long time.

The only difference between the invested and uninvested gonidia in the culture being in their relation to an organism incapable of manufacturing its own food, it can be safely concluded that the cell-contents of the former divide, or contract away from the wall, in order to eliminate the foreign organism, and to produce individuals which will be free from it. The conditions prevailing in a hanging-drop culture cannot be entirely favorable to the green cells; if they were, all the gonidial cells would sooner or later divide. Haustoria within, or hyphal branches closely enwrapping them, must irritate the invested gonidia. The response to this irritation is an effort to get rid of it by contraction or by division. The uninvested gonidia, not subjected to this irritation, do not contract or divide.

The gonidia of *R. reticulata* are in rounded masses fairly compact and held together by hyphæ (figs. 5 and 11, and Peirce [1898], p. 412). Many of these masses are composed of small cells, and some of the cells are likely to be dividing internally (figs. 6 and 9). From such divisions there result new gonidia, but it is not necessary to infer, as some do, that the gonidia are thus only amiably doing their part toward the growth and the permanence of the lichen. On the contrary, as Hedlund (1895) describes for *Catillaria denigrata* (Fr.) and *C. prasina* (Fr.), and as I have just shown in the above, we have in both cases merely the attempt on the part of the gonidia to divide in such a way as to exclude the haustoria from as many of the daughter-cells as possible. That the gonidia cannot be benefited, but are evidently injured, by having haustoria within them, I shall show subsequently (page 226); and if the haustoria are injurious, is it not sensible to suppose that the gonidia will try to get rid of them? If they are harmless or beneficial why should there be frequent divisions which inevitably result in the formation of daughter-cells free from haustoria? In a culture, the conditions in which seem to be more favorable to the uninjured gonidia than to the much broken and greatly injured hyphæ, the gonidia succeed in eliminating the haustoria and in freeing themselves from enclosing hyphæ. Imbedded in the body of the lichen, surrounded on all sides by hyphæ, the advantage in the struggle is to the other side; but the struggle and the manner of it are the same. The gonidia in the lichen seek by division to escape the hyphæ. Some do—these flourish and grow large; most do not—these divide again as soon as possible and so remain small.

IV. THE RELATIONS OF GONIDIA AND HYPHÆ AS SHOWN BY MICROTOME SECTIONS.

So far as I know, very little use has been made of modern cytological methods in the study of lichens. This is to be regretted, for without recourse to these, the intimacy of the relations of gonidia and hyphæ must remain comparatively obscure. It has already been demonstrated that our culture-methods are still so defective, and the growth of the fungus-component of lichens is so distressingly slow, even under the most favorable conditions, that our knowledge of lichens, if it is based on hand sections and cultures only, must be incomplete. Hand sections are unsatisfactory at the best because they are so thick that important details are hidden by excess of material. Yet investigations of lichens which are based only on examinations of dead herbarium material, or even of freshly fixed, imbedded and sectioned specimens, are subject to the same danger of one-sidedness which sometimes threatens the work of those who know plants and animals only as embalmed tissues.

It is deplorable that we are still utterly unable to obtain, and to keep healthily alive, thin sections of living material. As Fischer (1895) and others have repeatedly emphasized, a technique which is based on the employment of poisonous acids and salts is one which can be implicitly trusted only when their effects on the living protoplasm are exactly known. The danger of being misled by the study of fixed material sectioned by microtome after imbedding is, however, minimized by examination of living material, both sectioned and in culture, as a control. When the question before the student can be answered in part at least by determining the relative position of cell-walls, nuclei, etc., the matter is still simpler. Such is in great measure the case with the questions which are under discussion in this paper. From microtome sections of lichens it is possible to obtain clearer views on the structural relations of hyphæ and gonidia than can be had otherwise, and from these data, supplemented by culture experiments, conclusions regarding their physiological relations may safely be drawn.

As reported elsewhere (Peirce, 1898*a*), the material was prepared as follows: freshly collected specimens of *R. reticulata*, *Sphærophorus globiferus* (L.) D.C., and an *Usnea*, after being thoroughly wet, were kept in a moist chamber near a window for twenty-four hours. This allowed the gonidia to resume their photosynthetic activities in the light, and the hyphæ to become reasonably plump, if they had become dried out of doors.

For fixing I used:

Chromic acid, 3 per cent., at room temperature.
Chromic acid, 1 per cent., just below boiling temperature.
Flemming's Chrom-osmic-acetic mixture, at room temperature.
Corrosive sublimate, saturated solution in 35 per cent. alcohol, at room temperature.
Corrosive sublimate, saturated solution in 35 per cent. alcohol, just below boiling.

The last proved the most successful. Penetration at room temperature is comparatively slow, owing to the large amount of air enclosed in even wet lichens, whereas the air is quickly driven out by the hot liquid. At room temperature, the fragments treated with the fixing agent float, and must be exhausted under the pump. Those treated with the hot fixing-solution sink in it almost immediately. There is, therefore, a saving of time, as well as greater certainty of rapid penetration, if the fixing agent is applied hot. Dehydration should not be carried on too rapidly, for the gelatinous walls, especially of the outer hyphæ, hold the water. After complete dehydration, the material was transferred from absolute alcohol to equal parts absolute alcohol and xylol, then to pure xylol, and to this were slowly added small fragments of paraffin melting at 55°. At the same time the temperature was slowly raised to about 40°. Paraffin was then added to the point of saturation and the xylol allowed to evaporate. When the xylol was driven off, the specimens were transferred to melted hard paraffin (melting-point about 59°), kept in this for two hours to remove the last trace of xylol and to insure perfect penetration, then blocked, and sectioned at leisure.

The gelatinous hyphæ, soft and easily cut when wet, are now hard and rather brittle. For very thin sections, and these yield the most trustworthy results, the knife must be even sharper than for most tissues. The best sections were 1 μ thick, made with a Zimmermann-Minot microtome, and fastened to the slide, after floating and straightening on warm water, by albumen fixative. Some were then stained with Czoker's Alum-Cochineal and Bismark Brown. Some material was stained *in toto* with the Cochineal, but this was less satisfactory than staining on the slide. Other sections were stained with Iodine-green-Fuchsin, washing out with Iodine in 80 per cent. alcohol, and still others with Anilin-safranin-Gentian-violet-Orange G., according to the directions given by Zimmermann (1893). Both of the double stains and the triple stain were very satisfactory in their different ways. The sections were examined with a Zeiss apochromatic 2 mm. oil-immersion objective and compensating eye-pieces 6 and 12. All of the drawings were made with Abbé camera.

Various gonidial cells of *R. reticulata* containing haustoria are shown in section in figs. 11, 13, 15. Figures 12 and 14 were drawn from isolated and not from sectioned gonidia, but, for the sake of comparison, they may be referred to here. Figures 11, 12 and 13 show gonidial cells into which the haustoria can have penetrated only comparatively recently, as the protoplasm and chromatophores are apparently perfectly normal and uninjured. Figures 14 and 15, on the contrary, are of gonidial cells completely emptied, in which the haustoria still remain, normally plump and with granular protoplasm. Figures 13 and 15 show the haustoria in profile, figs. 12 and 14 end on. In fig. 13, the haustorium, and the hyphal cell of which it is a branch, are shown to be continuous as to both wall and cavity. Figure 15 shows the haustorium within the cell, but the hyphal cell of which it is a branch was below the plane of the section. This gonidial cell was invested by a larger number of hyphæ than any other figured, and than the great majority of those examined. In the group of gonidial and hyphal cells shown in fig. 11, two gonidial cells show haustoria within them.

It is nothing new to find haustoria in the gonidia of lichens. They have been repeatedly seen and sometimes figured, perhaps most strikingly by Schneider (1896*a*). It is generally said, however, that the haustoria, though penetrating the walls of the gonidial cells, do not actually penetrate the protoplasm. Thus Hedlund (1895)—"Von der Seite einer Hyphe wächst ein kruzer Ast heraus, der die dünne Membran vollständig durchbohrt und innerhalb derselben mehr oder weniger kugelförmig anschwillt. Bei dem Eindringen der Hyphe zieht sich die Hautschicht des Protoplasmas zurück und bildet eine seichte Einbuchtung, in welcher das angeschwollene Haustorium seinen Platz hat—" and Schneider[1]—"The tip of the haustorium may pass through the algal cell-wall, forming a somewhat expanded filament between the wall and cell-plasm. In its highest development the haustorium, often entering the algal cell, develops a much branched network which encloses but does not penetrate the cell-plasm."

Neither in my sections, nor in the living gonidia, in which I found haustoria, could I detect the alleged "Einbuchtung" of the protoplasm, and certainly the haustoria do penetrate the protoplasm of the gonidial cells of *R. reticulata*, as the figures convincingly show. It may be that, at the time of penetration, the protoplasm may contract away from the intruding haustorium, but this condition is not permanent, the haustorium penetrates the cell, the essential and living part of the cell, as certainly as it penetrates the lifeless cell-wall.

Can one imagine that the presence of another body, whether living or lifeless, within the living protoplasm of a cell is not accompanied by profound disturbance of the living protoplasm, is not distinctly irritating to it, is not positively injurious to it? The contrast between the evidently healthy hyphæ and haustoria on the one hand, and on the other the haustoria-containing gonidial cells, many of which in sections and in free preparations had contents dead and shrunken or completely gone, at least suggests very strongly, though it does not prove, that the haustoria completely devour the contents of the gonidia.

It does not necessarily follow that the penetration of chlorophyll-containing host-cells by haustorial cells is fatal to the host-cells. This is the case, for example, in the host-

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[1] l. c., Pl. I and p. 445.

plants of *Cuscuta* (Peirce 1893), but no one would venture to intimate that this phanerogamic parasite, containing traces of chlorophyll and therefore less incapable of elaborating non-nitrogenous food than any fungus, does not distinctly injure every cell into which its haustorial cells penetrate. In the lichen, each green cell penetrated by a haustorium is obliged to manufacture non-nitrogenous food in quantity sufficient to supply both the haustorium and itself, and not only for the haustorium but also for the cell of which it is a branch and for the cells adjacent to it. How long can a green cell do this unusual amount of work? Certainly not for so long as it could do less work. The life of the individual cell is therefore shortened. Overwork, exhaustion, death, and finally the complete absorption of its contents, follow the penetration of a haustorium. Is the presence of the haustorium so beneficial or so pleasant as to compensate the gonidial cell for its increased work and and decreased span of life?

Turning once more to *Cuscuta* and its host for comparison, we find that both host and parasite are multicellular, that owing to the division of labor among the cells one cell can help another. For instance, if the photosynthetic or other food-elaborating activity of a green cell is reduced by the intrusion of a haustorial cell, the former will be supplied by its neighbors, in accordance with the laws of diffusion and osmosis, with those substances which it lacks. This is an inevitable physical as well as a regular physiological phenomenon, the result of the multicellular condition of the host. Thus the life of the penetrated cell, fed by its neighbors, may be prolonged; the struggle between host and parasite is more nearly equal, each haustorial cell draws upon more than one cell of the host to supply the more than one cell of the parasite. This last is also true of the fungus in the lichen, for there are many gonidial cells. But the gonidial cells are distinct from one another; the fungus is a multicellular plant, with the advantages of one; the gonidia—*actually* in *Ramalina* and in many other lichens, *virtually* in all—are unicellular plants with their corresponding disadvantages. The single gonidial cell must do everything itself or perish. The individual gonidial cells penetrated by haustoria are no better off as individuals than algal cells of the same species outside the lichen: they are obviously worse off.

Beside the gonidial cells penetrated by haustoria, there are a much larger number, to be seen both in sections and in free preparations, which are invested more or less closely either by the hyphæ themselves or by short branches therefrom. These last Schneider (1896*a*) calls "extra-cellular haustoria." The true haustoria, of which we have just been speaking, he terms "intra-cellular haustoria." Both are branches of hyphæ, are therefore morphologically the same; both are organs of nutrition, are therefore physiologically the same; but it seems hardly desirable to give to organs which do not penetrate, but only clasp, the same name which DeBary (1884) and so many after him have used with the original meaning only—"in's Innere der Zellen dringende Seitenzweige."

Whether we have to do with naked or enclosed masses of living protoplasm, their absorption of food is by the same means—by osmosis. The osmotic absorption of aqueous solutions of food substances into cells enclosed by thin cellulose walls is nearly if not quite as rapid as with naked cells. Through a thick cellulose membrane or through two cellulose membranes which, though closely applied to one another, are thicker than only one, osmosis is slower than through a thin cellulose membrane. Through a gelatinized membrane osmosis is also slower than through a cellulose membrane of the same thickness (Pfeffer 1897). From these considerations we see the means by which both the haustoria penetrating, and the hyphal branches investing, the gonidial cells obtain from them the nutrient solutions which the fungus must obtain from them or die. If the hyphæ become gelatinized as to their walls, their absorption of food will be diminished equally with their loss of water. The production of haustoria will, therefore, facilitate the absorption of adequate amounts of food. In many lichens, however, haustoria are never formed; the hyphal branches investing the gonidia osmotically absorb enough food to supply the whole body of the fungus. The principles underlying the absorption, and the results of the absorption, of food by the hyphæ from the gonidial cells are identical whether haustoria penetrate or hyphal branches only clasp the gonidial cells.

Microtome sections confirm the observations regarding the relative sizes, the number and kinds of division, the general appearance of the gonidial cells invested by and free from hyphæ, as reported in the foregoing chapter. Both the fixed and the living specimens show that fungus and alga are associated intimately enough, whether the fungus merely encloses or actively penetrates, for the organism absolutely unable to elaborate non-nitrogenous food to be able to absorb all that it needs from the one that can elaborate it. In both cases the absorption is by osmosis, and it must be almost, if not quite, equally effective in both cases, for the lichens which do not send hyphal branches as haustoria into the gonidia appear to thrive as well as those which do.

There must in both cases be irritation of the gonidial cells by the hyphæ. The irritation produced by haustoria must, however, be greater, and this conclusion is substantiated by the larger number of dead gonidial cells containing haustoria than of those with hyphæ merely attached. The observation of haustoria within gonidial cells, though not a step necessary to the conclusion that the fungus is parasitic upon the alga, is confirmatory evidence, for it proves that the fungus has the alga in its power—that it obtains all its food from it, that it irritates and exhausts it in proportion to the intimacy of its relation with the alga.

In the other two forms studied—*Sphærophorus globiferus* and an *Usnea*—microtome sections show that the relation between hyphæ and gonidia is intimate, the hyphæ closely investing the gonidia. Figure 19 is from a section through an old part of a *Usnea*, the species of which I did not determine, and shows a hypha, old and thick-walled, still closely applied to a gonidial cell which has begun to divide. Figure 20 is from a similar section of *Spærophorus* and demonstrates the intimacy of contact between the hyphæ and a gonidial cell also dividing. I did not succeed in finding haustoria in these two lichens, but from the closeness of the contact which, as these two figures show, exists between hyphæ and gonidia, and from the foregoing discussion of the physiology of this relation, one is certainly justified in concluding that the fungus and the alga stand to each other, in these two lichens as in *Ramalina*, in the relation of parasite and host. The algæ in these three lichens are the same, *Cystococcus humicola*, Näg.[1] It would be interesting to compare with these forms lichens which have other species of algæ as gonidia, but for various reasons I prefer to leave this to others or to later work of my own.

V. THE SIGNIFICANCE OF THE WATER-CONTENT OF *Ramalina reticulata*.

The amount of water held, and the force with which it is held, even in very dry air, is significant. The lichen cannot die from drought, and the alga is defended against extreme dryness by the gelatinous enveloping fungus, which holds water enough at least to keep the alga alive, and probably enough to enable it to elaborate some food each day. It is hard to conceive that the alga, supplied with any moisture at all, should be entirely inactive when daily illuminated by the sunlight; and owing to the affinity of the gelatinous outer hyphæ for water, the dews and the frequent fogs at night must furnish as frequent additions to the water-content of the lichen. It seems extremely probable, therefore, that the long dry season of California, checking the growth and many other activities of most plants hereabouts, is not sufficiently dry to stop the photosynthetic and other activities

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[1] Professor William A. Setchell, of the University of California, kindly informs me that this alga is now commonly called *Chlorococcum humicola* (Rab.) Näg.

of the gonidia of this lichen, much less to kill them; and hence the hyphæ, well supplied with food, may also, at least frequently, be active in growth and in other ways. For twelve months in the year these lichens can, and undoubtedly do grow, though the most rapid growth and the most growth must be during the warmer later part of the rainy season.

If this is the case with the lichen as a whole, what is the condition of those free algal cells entirely away from and uninvested by fungus hyphæ? Throughout a normal dry season on the west side of the Bay of San Francisco, the fogs at night and the dews are sufficiently frequent and heavy to wet fences, tree-trunks, branches, etc., etc. Though this moisture evaporates quickly after the sun appears, I doubt very much that *Cystococcus*-like algæ are so completely dried by day that they do not revive at night. Indeed, spherical unicellular algæ, *Cystococcus*, *Protococcus*, etc., although less abundant here on tree-trunks, fences, etc., than in many other parts of the world, can be found alive at all seasons. On almost every fence old enough, one may find the algæ alone, or with a few hyphæ among them, or with more but still not enough to cover and shield them from dryness, and so on up to mature and fruiting lichens of various species. In this region, at least, the survival of algæ like those in lichens is not dependent upon their being protected by fungus hyphæ against extreme dryness.

It is argued that because lichens are found flourishing where algæ alone could not possibly survive — for instance, on dry and sun-baked rocks — that this is evidence that the association of alga and fungus is mutually beneficial. Concerning this, *R. reticulata* offers a case in point. The algæ forming the gonidia of this pendant lichen could not possibly remain alive in the air even if they could float in it. Yet, is it any advantage to the gonidial cells of this lichen that they are living, growing, multiplying, where the force of gravitation and the insufficiency of food would forbid algæ free from fungus associates to survive? The answer to this question will be clearer if we use a homely analogy. A cow would never climb to the top of a twenty-story building, but once elevated to this position in opposition to her ordinary habits and to the force of gravitation, would she be any more advantageously placed than her more commonplace relatives in barn and pasture? Though algal cells cannot suspend themselves in mid-air, or live indefinitely exposed to excessive heat and dryness on sun-baked rocks, it does not necessarily follow that they are any better off when associated with fungus hyphæ and contributing to the formation of a lichen, than are their more commonplace relatives which are not in the air and have fallen on more advantageous places than exposed rocks.

VI. The Influence of Mechanical Strains on Growth.

As reported in a previous paper on *R. reticulata* (Peirce, 1898), the mere wetting of a thallus or thallus fragment, and the subsequent drying, bring about no material change in the length, breadth or thickness. During the rainy season, however, when the lichen remains wet for considerable lengths of time, growth will take place while the lichen is expanded and soft, thus permanently increasing the dimensions. The lichen will not contract, when it dries again after the rainy reason has passed, to the dimensions it possessed when the rains began; but how much of this increase in size is due to growth solely, and how much to stretching and the consequent change in position of the hyphæ, cannot now be stated. It is obvious that this pendant lichen, being more than twice as heavy (Peirce, 1898), as well as much softer, when wet than when dry, will be subjected in its different parts to a stretching force varying in the different parts with the weight of the parts nearer the tips. The parts nearest the branch from which it hangs will be subjected to the greatest stretching force or weight, the tip to the least. By stretching force I mean in this connection not the forcible expansions which follow the wetting and consequent swellings of a dry lichen, but the actual stretching strain which the distal parts exert by their own weight upon the basal upper parts, a strain which increases with the wetness and with the actual increase in substance. Once thoroughly wet, the lichen will not absorb still more water, but it may grow. We must distinguish, then, between growth which, in this connection at least, is a purely physiological process, and stretching, which is a purely mechanical one. The growth involves an increase in the size of the cells composing the lichen, is made possible by accumulated foods elaborated by the gonidia and hyphæ, and is very quickly followed if not accompanied by an actual increase in the weight as well as in the volume of substance either itself living or at least elaborated solely by the living substance.

The pull exerted upon itself by the wet and heavy lichen is parallel with the long axis of the thallus; it is stretched lengthwise, while growth takes place in breadth and thickness as well as in length. Hegler (1893) has shown for higher plants that a pull exercises two distinct influences; the mechanical one of stretching, the physiological one of irritating—a pull entirely insufficient for the former being in many cases quite sufficient for the latter. The irritation produced by pulling retards growth in the direction of the pull, stimulating it in other directions both as to the individual cells and also as to the tissues and organs as a whole. A pull so light that it does not stretch a stem or branch will lower the rate of elongation, raise the rate and degree of thickening of the walls, especially of those cells which contribute most to the mechanical strength of the plant, and in proportion to the actual increase in length there is more than the usual increase in diameter, by thickening the walls of already existing cells as well as by inducing the formation of new cells.

Without having made any measurements—a matter requiring infinite patience on account of the low rate of growth and because of the many sources of error to be eliminated — and merely from a study of the structure of this lichen (Peirce, 1898), I think we may justly infer in the light of the foregoing discussion, that the increase in length of *R. reticulata* is due in greater measure to that stretching of the thallus, by its own weight, which results in bringing the hyphæ from their diverse directions into a course nearly parallel with the long axis of the thallus (i. e., parallel with the pull) than to actual growth. The physiological process of growth in length, made less necessary if not retarded by the mechanical pull to which this lichen is constantly subject — a pull which is greater when the lichen is softest and weakest — is accompanied by growth in breadth and in thickness and by an increase, by thickening walls, in the mechanical strength of the hyphæ. These processes are at least not hindered and, judging from Hegler's work on higher plants, are likely to be stimulated by the longitudinal pull. As a result of the growth in thickness and breadth, the normal proportions of the thallus will be maintained and, furthermore, more hyphæ will be formed which, running at various angles to the long axis, may by the pull be drawn into courses parallel with it.

But Hegler has shown one other thing interesting in this connection, namely, that changes in the pull also affect the rate of growth, and that if the pull remains constant for a time the plant will recover its normal rate of growth in length, growing in diameter and increasing in mechanical strength in proportion to the force to which it is subjected. The decreasing weight of our lichen on drying, the gradual diminution of the pulling force, will stimulate it to some growth in length; but because the lichen stiffens as it dries, it cannot grow much at this time, and hence one can conceive of little more growth taking place than will suffice to fix the hyphæ in the direction into which they have been pulled. Since the pull does not remain constant in nature, winds and varying amounts of moisture forbidding this, the lichen cannot become accustomed to any one amount of force, cannot resume its normal rate of growth if, indeed, it may be said to have any one normal rate, though it must and does have normal rates.

VII. NUCLEUS OR PYRENOID AS THE CENTRAL BODY OF CYSTOCOCCUS CELLS.

There remains one more point to be discussed in this paper. In two papers which I have been unable to see but which are briefly reviewed in Just's Jahresbericht (Bd. XXII, 1, p. 148), Dangeard (1894) claims that the body generally regarded as the nucleus of gonidial cells is not nucleus at all but a pyrenoid, the real nucleus being at the side, small, inconspicuous, and formerly supposed to be a vacuole. Differential staining agents are alleged to prove Dangeard's assertion. As the species of gonidia investigated by Dangeard are not mentioned in the review, I cannot criticise his results and can only advance evidence to show that the central body in the cells which serve as the gonidia of the lichens reported upon in this paper, is certainly a nucleus, as the well known nuclear stains and the phenomena of division and cell-division plainly indicate. In a spherical cell, too, one would certainly expect to find the nucleus near if not at the center of the cell under ordinary conditions. In no case have I found a nucleus-like body far from the center of the gonidial cells of the lichens which I have studied. One would expect the nucleus to have the size in proportion to the diameter of the cell which this central body possesses, and not to be small, eccentric and inconspicuous. The form of the nucleus would be likely, for mechanical reasons, to approach that of the cell, though of course this is by no means always the case even in spherical cells. Pyrenoids occur always in chromatophores, as specially differentiated parts of them, not as independent organs.

In fig. 16 we have a typical gonidial cell in a thin microtome section of *R. reticulata*, stained on the slide with Iodine-green-Fuchsin. The central body, enclosed in cytoplasm in which the large rounded chromatophores are imbedded, is dense, granular and provided with a central homogeneous body of its own which, like nucleoli in general stained with this agent, has a deep red color. Figure 17 shows a gonidial cell in the same section in process of internal cell-division. For the sake of clearness, protoplasm, chromatophores and vacuoles are omitted from the drawing. Each daughter-cell, though not yet provided with its own cellulose wall, contains a dense, granular central mass, from which the nucleolus-like body is absent. This is what one would expect if the central mass is nucleus, for the nucleoli ordinarily disappear before division, reappearing in the daughter-nuclei only after the lapse of some time. Figure 18 is still another gonidial cell in the same section, which has divided still further, the eight daughter-cells, most of which are below the plane of the drawing, being already surrounded by their own cellulose walls and each containing its own central body.

From these figures, from the behavior of the nucleolus-like body both toward the stain and also in division, from the different staining of the central body, the cytoplasm and the chromatophores, and from its position, as far removed as possible from all the chromatophores, I cannot do otherwise than conclude that it is a nucleus.

Figures 19 and 20 show the nuclei of a gonidial cell of *Usnea* sp. (?), and of *Sphærophorus globiferus*, respectively, dividing and divided. These figures were made from thin microtome sections stained with Anilin-safranin-Gentian-violet-Orange G. The colors, though faint, differentiate nucleus and cytoplasm in the manner characteristic of this stain.

From the evidence it seems to be clear that the gonidia of these lichens have a central nucleus neither remarkable nor different from the nuclei of other similar algæ whether within or outside of a lichen thallus; that this nucleus is provided, in the "resting condition," with a typical nucleolus which disappears before the division of the nucleus and the cell; that nuclear division precedes cell-division. As to additional details of the processes of nuclear and cell-division, the small size of the objects makes study very difficult, and because this has no direct bearing on the main problem discussed here, I leave the matter as it now stands.

VIII. SUMMARY.

The results of this examination of a few forms, though admittedly of too few and too like forms to justify anything more definite than an opinion regarding lichens in general, may still be of value as a contribution to the discussion of the relation of fungus and alga in lichens and of the so-called autonomy of lichens. These results may be briefly stated as follows:—

I. Both cultures and thin microtome sections demonstrate
    1—that hyphæ and gonidia are in the most intimate contact;
    2—that the hyphæ develop branches which may merely clasp the gonidial cells or may, as definite haustoria, penetrate them;
    3—that such clasping or penetration stimulates the gonidia to internal cell-divisions in the effort to form individual cells free from hyphal investment;
    4—that the haustoria consume the protoplasmic contents of the gonidial cells which they have entered, leaving only the empty cell-wall.

II. 1—Since the fungus, being devoid of chlorophyll, must obtain already elaborated non-nitrogenous food;
    2—since the only constituent of the lichen capable of elaborating non-nitrogenous food is the gonidia;
    3—and since lichens ordinarily grow where they could obtain little or no non-nitrogenous food from the substratum even if they were dependent upon it for other than mechanical support and mineral salts, —it is obvious that the fungus is fed by the alga; the hyphæ, by the gonidia.

III. Though algæ may not always grow independently where they are found associated with fungi, forming lichens, it is neither logical nor sensible to conclude that their unusual position is beneficial to them.

IV. Though the percentage of water retained by the more or less gelatinous constituents of the lichen thallus is higher than that which the gonidia could retain as free organisms, the occurrence of healthy algæ on the spots subsequently occupied by lichens demonstrates that free algæ can thrive, at least for a time, wherever lichens can.

V. Though it may be claimed that the individual gonidial cells live longer in the lichen than the free individual cells of the same species of alga, there is no proof of this, and if there were, it is well known that in their resting forms free algæ withstand extremes of heat, dryness, etc., as successfully as do lichens and lichen gonidia.

VI. There is no proof that algal cells serving as lichen gonidia are any better off as to food, protection or situation than the average free algal cells of the same species; whereas it is evident that the fungus portion of every lichen is absolutely dependent upon the gonidia for all of its non-nitrogenous food.

VII. As to Reinke's claim that the lichens should be regarded as plants as truly autonomous as trees and shrubs because they have their own peculiar structure, growth, habit, color, etc., as well as because there can be no lichen without both components, an analogy may assist us to clearer views. Bacteria grown in bouillon cannot form the definite colonies of peculiar and characteristic structure, growth, habit, color, etc., which the same species will form on nutrient agar-agar or gelatine. To the formation of the colony, with its characteristic peculiarities, the living bacteria and the lifeless but nutritious solid substratum are both absolutely necessary. The bacteria may grow quite as well in a liquid medium as upon a solid one, but they will not aggregate into the same form. So the fungus component of a lichen, grown by Möller on liquid media and alone will not form a body like a lichen in structure, growth, habit, color, etc., although it will develop perfectly well. Both substratum and associate will affect the fungus, and *the lichen is the product, the resultant, of all these influences, not of one or two.*

VIII. The varying mechanical pull exerted by itself and by the wind upon *R. reticulata* influences its growth in the three dimensions of length, breadth and thickness.

IX. The central body of the gonidial cells of *Ramalina*, *Usnea*, and *Sphærophorus*, which are *Cystococcus humicola* Näg., is a nucleus, not a pyrenoid.

STANFORD UNIVERSITY,
CALIFORNIA,
December, 1898.

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EXPLANATION OF PLATE XLI.

The figures were drawn with Abbé camera over Leitz No. 7, or Zeiss 2 mm. apochromatic oil-immersion objectives, and Leitz eye-piece 3 or Zeiss compensating eye-pieces 6 and 12.

Ramalina reticulata.

Fig. 1, *a* and *b*. Ungerminated spores in water: *a*, smaller than the average and probably unripe; *b*, larger than the average. x 1300.

Fig. 2. Germinated spores, showing breaking up of the oil drops and their re-formation in the germ-tubes; both cells of each spore germinating. x 1300.

Fig. 3. Germinated spore; only one cell putting out germ-tube, but this branched. x 1300.

Fig. 4. Germinated spore; germ-tube growing close to and straight past a healthy gonidium. Is actual contact needed to produce stimuli? x 650.

Fig. 5. Group of invested gonidia and one uninvested gonidium separated by grinding; showing relative sizes of attached and unattached gonidia. x 650.

Fig. 6. Group of invested gonidia set free by grinding; showing gonidia dividing internally into two. x 560.

Fig. 7. An invested gonidial cell dividing into four. x 560.

Fig. 8. A similar one showing four enclosed daughter-cells. x 560.

Fig. 9*a*. The same cell as fig. 8, twenty-four hours later, showing eight daughter-cells liberated by solution of wall of mother-cell. x 560.

Fig. 9*. A gonidial cell containing a haustorium; the protoplast contracting and thereby escaping from the haustorium. x 560.

Fig. 10. Similar to fig. 9*. x 560.

Fig. 11. Group of invested gonidia, showing two haustoria within gonidial cells. x 650.

Fig. 12. Isolated gonidium containing haustorium; gonidium isolated and hypha broken off by grinding. x 1750.

Fig. 13. Gonidium, in a section, showing haustorium and the hyphal cell of which it is a branch. 12 and 13 comparatively recently penetrated by haustoria. x 900.

Fig. 14. Gonidium, isolated by grinding, entirely emptied by haustorium. x 1750.

Fig. 15. Gonidium, in a section, entirely emptied by haustorium and by investing hypha. x 900.

Fig. 16. Unusually large and healthy gonidial cell, free from investing hyphæ and showing chromatophores enclosed in peripheral cytoplasm; the central nucleus with its nucleolus and enclosing cytoplasm with radiating strands. x 1750.

Fig. 17. A gonidial cell dividing by internal cell-division into four daughter-cells, each with its own central nucleus; daughter-cells not yet surrounded by their own cell-walls. x 1750.

Fig. 18. Gonidial cell divided by internal cell-division into eight daughter-cells, each with its own central nucleus and its own cell-wall. x 1750.

Usnea.

Fig. 19. The central body, nucleus, of a gonidial cell dividing, preliminary to the division of this invested gonidial cell. x 1750.

Sphærophorus globiferus.

Fig. 20. Somewhat later stage in the division of the central body, nucleus, of an invested gonidial cell. x 1750.

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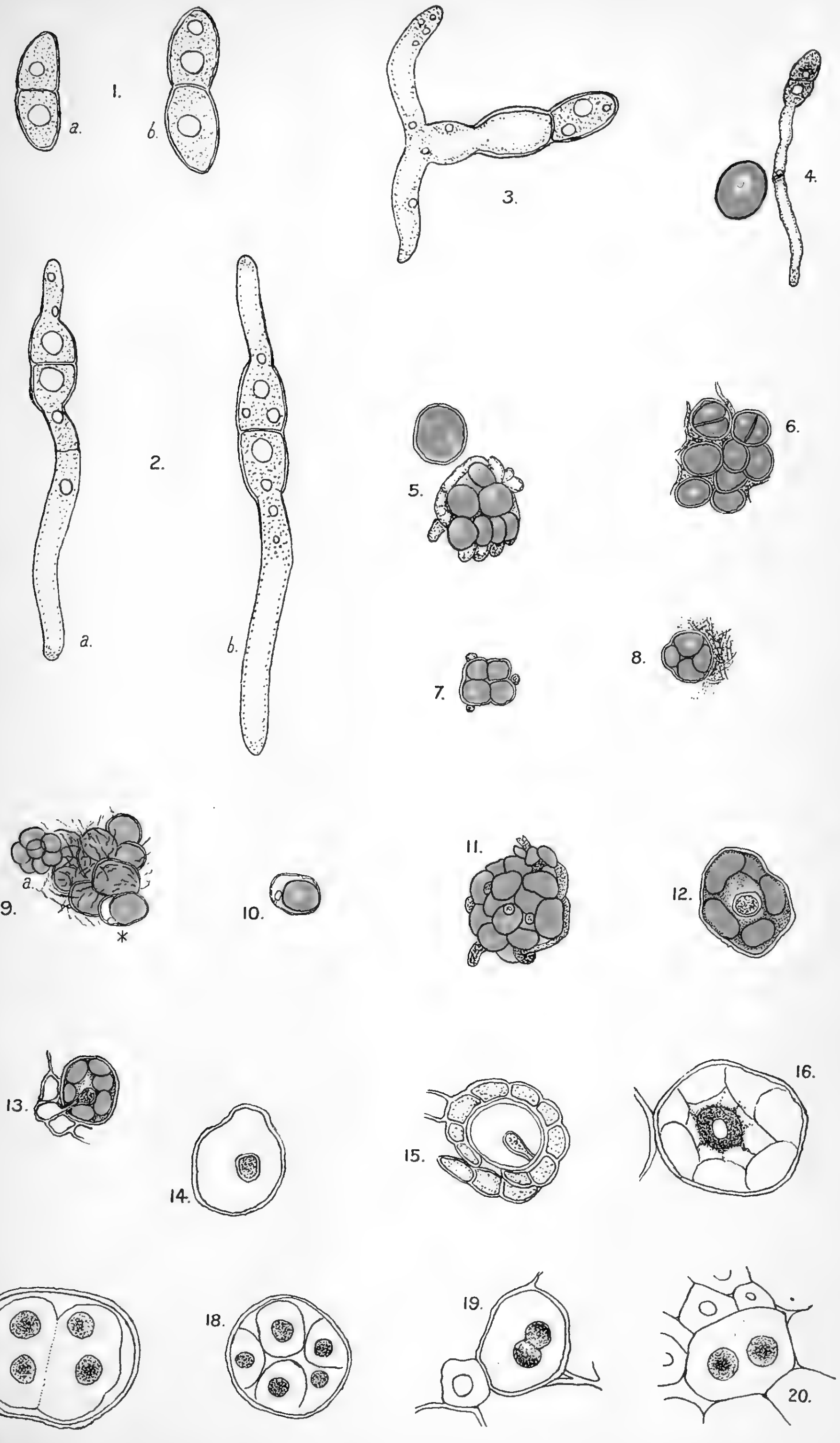
[PEIRCE] PLATE XLI



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LITH. BRITTON & REY, S.F.

CALIFORNIAN HYPOGÆOUS FUNGI.

BY H. W. HARKNESS.

Plates XLII–XLV.

Introduction.

For several years the author has contemplated the preparation of a monograph upon the Hypogæi of California, and whenever it was possible, search was made in order to secure specimens for the purpose. Ill health has, however, compelled the suspension of work for periods of many months duration, and has also prevented excursions for collecting material at seasons which are unsuited to the invalid.

I need not remind those who have given attention to this line of investigation that such a collection could only be brought together by long and persistent effort. Unless by accident, the material is obtainable only by removing the surface of the ground, the common garden hoe being the implement best suited for the purpose.

As there are but seldom any surface indications to mark the spot where the tubers grow, it will readily be seen that their collection depends largely upon chance. Experience, however, teaches the collector to seek such locations as are best suited to the growth and development of the desired material; but, with all his knowledge, it is only by persistent effort that he may succeed. It has been too frequently the case that the writer has expended hours of arduous labor without securing a single specimen.

The district within the limits of which excursions have been made is bounded upon the north by the California State line, on the south by the Tehachapi range, by the seacoast on the west, and the valley of the Donner lake upon the east—an area exceeding 400 miles from north to south,

June 26, 1899.

and some 300 miles from east to west, and within which are to be found the Coast Range mountains, with the dense forests of Sequoias, and the Sierra Nevada mountains rising to an elevation of 8,000 feet.

As will readily be seen, excursions for exploration to localities so remote must be, owing to unfavorable weather and other causes, too often barren of results. Many species may be found soon after the first autumnal rains, especially if the rain is followed by a period of sunshine and moderate heat. If these conditions continue during the entire rainy season much material may be collected during the winter. The most productive season, however, is that of early spring, as it seldom fails during these months that there are warm rains followed by sunny days. If, as it sometimes happens, there is an abundant precipitation of moisture, good material may be found even late into the spring. After the close of the rainy season but little is to be found, unless it be upon the banks of mountain rivulets, or in a few favored spots where there exists sufficient moisture combined with a suitable soil.

There being no visible indications to mark the spot where the fungi abide, to assure success in the search the characters of the trees and shrubs in the locality must be observed, as well as the nature of the soil. At times the fungi may be found beneath and amidst dense masses of decaying foliage of the Sequoias. When so found they will be in the immediate vicinity of the base of the tree. So far, however, as the writer's observations extend, the time during which the fungi are to be found among the Sequoias is of but short duration, as the mature plants are eagerly sought for by the rodents which are found in numbers in these forests. The most active of these foragers, and consequently the most destructive, are two species of wood-rats *(Neotoma)*. Where these are to be found one must be upon the alert if he would secure mature specimens of the fungus, as the active little fellows are tireless in their search for this dainty. Squirrels and other rodents are but little less active and add to the difficulties of the collector.

A few tubers are to be found in the high Sierras at an elevation of 7,000 feet or more; these are generally located at or near the base of *Pinus contorta*, and occasionally beneath other species of Coniferæ. So far as my observations extend, this section can be relied upon for specimens only in the late spring, as the snow generally falls too early in the autumn to allow of their development.

At a lower elevation—3,000 or 4,000 feet—we find the oaks, under which, at the proper season, good material may be obtained. At these elevations the banks of the streams may yield material as late as July. In the foot-hills, at an elevation of from 1,400 to 1,500 feet, we find the best localities for the greatest number of species, which are here most prolific.

Upon well drained hillsides, in sandy soil, a variety of *Ceanothus* is found growing in dense clusters and averaging about seven feet in height. When protected from fire, we find beneath these shrubs a large accumulation of decaying foliage which serves to fertilize and protect the fungi found here.

Upon the plains the Eucalyptus tree has been cultivated to a large extent, and here a few varieties of fungi may be found. It may be broadly asserted that but seldom are species to be found in localities where grass or weeds are seen, as the roots of these plants seems to be inimical to the development of the tubers. Neither are they to be found in places where water accumulates or remains for a length of time upon the surface.

The earliest date at which we may hope to find tubers (truffles so-called) is about the first of January. At this time the cell-structure of the gleba is in a perfect state but is still destitute of asci or spores, which makes the identification of species impossible. So far as I have seen, the spore does not arrive at maturity until April; much, however, depends upon the weather. In any event, the tuber is of slower growth than many others of this class of fungi. The genus *Tuber* is widely distributed throughout California but is exceedingly scanty in numbers.

As to the economic value of the Hypogæi of California: so far, we have found none of the edible varieties of the Continent of Europe, although *Tuber Californica* is nearly identical with an edible species found in Italy. All of the Californian species are, however, edible, and no doubt would be greatly esteemed as a luxury were it not for the fact that they are so rare as to practically prohibit their use as food. The writer has but recently discovered reliable traces of a variety which, if found in quantity, is certain to take its place as a table luxury, although as yet he has not been able to obtain a single specimen.

Some years ago the citizens of Marysville discovered large quantities of an earth fungus which was growing in the vicinity of the city and which was freely eaten by those who were so fortunate as to be aware of its value. In that city they were known as the potato mushroom. A trustworthy gentleman states that they never appeared upon the surface of the ground, but that the search for them was a comparatively easy matter. The first noticeable sign of their presence was a circular space a foot or more in diameter, which was free or nearly so from vegetation. A more careful examination showed minute cracks or fissures upon the surface of the ground, and a moment's work with trowel or hoe sufficed to unearth a number of white, globose fungi, varying in size from an English walnut to that of a small orange. My informant states that they were gathered with the greatest facility. Another gentleman states that they were found by himself and friends in the vicinity of Sacramento, where they were highly esteemed as a delicacy. His description of the method pursued in their collection and of the surface indications marking their presence was identical with that of the observer above mentioned. Neither of the gentlemen could say positively in what month the fungus was found, but both agreed that it was late in the winter or early spring.

This will undoubtedly prove to be a *Terfezia*, a variety of which is found in northern Africa and also in great abundance in Arabia, being sold in the markets of Bagdad as truffles. A *Terfezia* has recently been discovered in the valley of the Red river of Louisiana; this was recently distributed by Mr. Ellis in his "Centuries" (No. 1728) as *Terfezia leonis.* To what extent they are utilized as food in that locality we are not informed. Should the fungus again appear in the Sacramento valley in the same abundance as upon previous occasions, it will be sought for, as it is not only of value when fresh, but any excess of the product may be dried and would be an addition to any soup, and of value for many culinary purposes.

With these preliminary observations, which I trust may be of service in showing the methods pursued in the quest of material and its geographical distribution, I submit this monograph to the verdict of those who may be interested in this department of botany.

I should be lacking in courtesy did I fail to give due credit to my friend, Dr. Gustav Eisen, who has prepared the accompanying illustrations. The obligation is increased when I take into consideration the fact that his time was fully occupied in an entirely different line of biological investigation.

Hymenogaster *Vitt.*

Hymenogaster VITT., Monog. Tub., p. 20.

Peridium fleshy or thin, running down into an absorbing base. Cavities at first empty, radiating or irregular. Trama composed of elongated cells, but not of byssoid flocci, and therefore not easily separable. Spores various. (Berk. Outlines Brit. Fung., p. 295.)

1. Hymenogaster versicolor, sp. nov.

Subglobose, 2 cm. in diam.; color white turning to pink; common integument thick, corrugated, flakey externally, pinkish beneath, closely adherent; gleba firm; cavities sinuous, minute; spores ovate, attached by a slender but somewhat elongated pedicel, 5 x 8 μ.

Type, No. 174, Harkness Coll.

Under small oaks, Bishops, Mill Valley, Marin County, Calif., April.

2. **Hymenogaster Setchellii,** sp. nov.

Minute, 1.5 cm. in diam.; color white turning to brown, subglobose, smooth; gleba buff, elastic; cells large, sinuous; sterigmata elongated; spores citriform, guttulate, brown, 7 x 9 μ.

Type, No. 165, Harkness Coll.

Under *Vaccinium*, beneath vegetable humus, Mt. Tamalpais, Marin County, Calif., April.

Named in honor of Professor William A. Setchell, of the University of California.

3. **Hymenogaster utriculatus,** sp. nov.

PLATE XLII, FIGS. 6*a*–6*f*.

Large, roundly gibbous, 2 cm. in diam.; color chocolate-brown; smooth, with slightly concave depressions upon the surface; gleba brown; cells gyrose or subrotund; septa fleshy, elastic, fibrose; spores ovoid, upon a cylindrical pedicel 3 μ in length, inclosed within a winged utricle, color citron-brown, 6 x 10 μ.

Type, No. 244, Harkness Coll.

Among Sequoias and oaks, Mill Valley, Marin County, Calif., July.

The spores of the *Hymenogaster* are frequently inclosed in a semitransparent utricle; such investment is, however, so far as the writer has observed, uniformly saccate or subrotund in outline.

4. **Hymenogaster ruber,** sp. nov.

Oblong, 2 cm. in diam., rugose; peridium pale red, thick, fleshy; gleba brown, septa white; cells minute; spores briefly obovate, rough, 6 x 8 μ.

Type, No. 248, Harkness Coll.

In the forest, Mill Valley, Marin County, Calif., July.

5. **Hymenogaster globosus,** sp. nov.

Minute, globose, 1 cm. in diam.; color dirty white; gleba fuscous or nearly black; cells irregular; spores ellipsoidal, 6 x 12 μ.

Type, No. 246, Harkness Coll.

In damp ground, beside a rivulet, Mill Valley, Marin County, Calif., July.

6. **Hymenogaster candidus**, sp. nov.

Oblong-cylindrical, 3 cm. in diam.; color white; gleba ochraceous; cells large; spores elliptical, guttulate, color brown, 10 x 5 μ.

Type, No. 49, Harkness Coll.

Under *Pseudotsuga Douglassii*, Towle, Placer County, Calif., May.

Differing from *H. Klotzii* in the form of the fungus and in the shape of the spores.

7. **Hymenogaster luteus** *Vitt.*

Hymenogaster luteus VITT., Monog. Tub., p. 22, Tab. III, fig, 9.

Peridium very thin, soft and silky, white, then brownish, bright yellow within; spores even, ovate or elliptic, oblong, yellow. (Berk. Outlines Brit. Fung., p. 295.)

No. 12, Harkness Coll.

Under decaying wood, Oakland, Calif., December.

8. **Hymenogaster calosporus** *Tul.*

Hymenogaster calosporus TUL., Fungi Hypo., p. 70, Tab. X, fig. 4.

Globosus sat irregularis, sæpius depressus aut costato-sulcatus (subtus præsertim), ex albido brunneus et sordidus; peridio tenui vix solubili, humido; lacunis inæqualibus absque directione, vacuis; septis linea media obscuriore notatis nec scissilibus; pulvinulo subnullo; sporis lanceolato-acuminatis, saturate brunneo-rubiginosis, levibus.

No. 48, Harkness Coll.

In the forest, Towle, Placer County, Calif., May.

9. **Hymenogaster muticus** *B. & Br.*

Hymenogaster muticus B. & Br., Ann. & Mag. Nat. Hist., 2d Ser., Vol. II, p. 267.

Globose, quite white when young, then tinged with brown and cracked, pale yellow-brown within; spores obovate, oblong, very obtuse. (Berk. Outlines Brit. Fung., p. 295.)

No. 64, Harkness Coll.

Under Sequoias, Taylor's Mills and Mt. Tamalpais, Marin County, Calif., March.

10. **Hymenogaster lycoperdineus** *Vitt.*

Hymenogaster lycoperdineus VITT., Monog. Tub., p. 22, Tab. II, fig. 5.

Globoso-difformis; peridio albo-fuligineo, sericeo-levi; carne molli elastica dilute fuliginea; cellulis majusculis irregularibus, e basi ad centrum seriatim directis; sporis fusiformibus, pallide fuligineis. (Tul. Fungi Hypo., p. 64.)

No. 72, Harkness Coll.

Under oaks, Camp Taylor, Marin County, Calif, July.

11. **Hymenogaster arenarius** *Tul.*

Hymenogaster arenarius TUL., Fungi Hypo., p. 73, Tab. X, fig. 2.

Globosus amorphus obovatus, albidus immutabilis; peridio levi vel inæquali tenuissimo glabro, sicco; cellulis irregularibus, exiguis, parietibus, ferrugineis sporis obrutis; septis albidis subsericeo-nitentibus, tandem aquose obscuris; sporis minutis citriformibus, in superficie inæqualibus, luteo-brunneis, guttulam vix concentricam foventibus.

No. 79, Harkness Coll.

In the forest, Mt. Tamalpais, Marin County, Calif., March.

12. **Hymenogaster pallidus** *B. & Br.*

Hymenogaster pallidus B. &. Br., Ann & Mag. Nat. Hist., 1st ser., Vol. XVIII, p. 74.

Smaller, rounded, depressed, nearly smooth, white, then dirty tan-color, rather soft, within white, then yellow, then pale brown; sterile base obsolete; spores lanceolate, acute, shortly pedicellate, rather rough. (Berk. Outlines Brit. Fung., p. 296.)

No. 81, Harkness Coll.

Under oaks, Camp Taylor, Marin County, Calif., March.

13. **Hymenogaster caudatus**, sp. nov.

Large, globose, 5 cm. in diam., color fuscous, rough, caudate; appendages springing from the base; gleba brown; veins olivaceous; spores ellipsoidal, $6 \times 12\ \mu$.

The caudal appendage is fleshy, from 1–2 cm. in length by 0.2 cm. in diam., and has a bluntly pointed terminus. The appendage is formed by an aggregation of many rootlets which are enclosed in a delicate membranaceous investment.

Type, No. 240, Harkness Coll.

Beneath Sequoias and oaks, Mill Valley, Marin County, Calif., April.

14. Hymenogaster olivaceus *Vitt.*

Hymenogaster olivaceus Vitt., Monog. Tub., p. 24.

Globose, but angular; peridium whitish, then tinged with yellow, rufous when bruised; substance white, then of a dull buff, then rufous-olive, variegated with the white trama; spores pedicellate, mucronate, generally smooth. (Berk. Outlines Brit. Fung., p. 296.)

No. 167, Harkness Coll.

Collected during April, under *Sequoia sempervirens*, at Mill Valley, Marin Co., Calif., and under oaks, at Wire Bridge, Placer County, Calif.

15. Hymenogaster monticolus *Hk. Mss.*

Gautiera monticola Hk., Bull. Cal. Acad. Sci., Vol. I, No. 1, 1884, p. 30.

Dark brown, irregularly lobed, 10 cm. in breadth, uniformly about 3 cm. in thickness, nearly plane above and below; stipe short and slender; stroma ferruginous brown. basidia apparently two-spored; sterigmata filiform; spores pale brown, elliptic or obovate, apiculate, longitudinally or somewhat obliquely striate, 10–12 by 7–8 μ. With the odor of decaying onions.

Type. No. 113 (3543), Harkness Coll.

Under *Sequoia gigantea*, Mariposa Big Tree Grove, Calif., July.

16. Hymenogaster Bulliardi *Vitt.*

Hymenogaster Bulliardi Vitt., Monog. Tub., p. 23, Tab. III, fig. 5.

Globosus, ex albido aquilus; gleba firma densa, minutissime cellulosa, demum saturate ferruginea; loculis suboppletis; sporis levibus, late ovatis, breviter obtuseque acuminatis, basi rotundato-obtusis, guttulam crassam sæpius foventibus. (Tul. Fungi Hypo., p. 71.)

No. 233, Harkness Coll.

Mt. Tamalpais, Marin County, Calif., January.

17. Hymenogaster Behrii *De Toni.*

Hymenogaster Behrii De Toni., Syll. Fung., Vol. VII, p. 174.
Splanchnomyces Behrii Hk., Bull. Cal. Acad. Sci., Vol. I, No. 1, 1884, p. 30.

Cinnamon-brown, irregularly lobed, lacunose, 1–4 cm. in diam.; absorbing base inconspicuous; basidia 2-spored; sterigmata short, filiform; spores very unequal in size, yellowish brown, oval or elliptic, apiculate by the remains of the sterigmata, pitted all over with minute irregular depressions. 10–15 x 10 μ.

No. 104 (2911), Harkness Coll.

Growing in vegetable humus, Wildwood Glen, Sausalito, Marin County, Calif., December.

18. **Hymenogaster rufus** *Vitt.*

Hymenogaster rufus VITT., Monog. Tub., p. 23, Tab. III, fig. 17.

Subglobosus; peridio albo-rufescenti subsericeo; basi minuta; carne unicolore rubro-fusca; cellulis majusculis, irregularibus; sporis obovatis subsessilibus rufis. (Tul. Fungi Hypo., p. 64.)

No. 163, Harkness Coll.

Under shrubby oaks, Mill Valley, Marin County, Calif., April.

19. **Hymenogaster tener** *Berk.*

Hymenogaster tener BERK., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XIII, p. 349.

Small, globose, soft, white, silky; substance pale pink, then greyish-umber; sterile base conspicuous, white; spores broadly elliptic, with a papillary apex, minutely warty. (Berk. Outlines Brit. Fung., p. 296.)

No. 11, Harkness Coll.

Under oaks, Oakland, Alameda County, Calif. Date not given.

Hydnangium *Wallr.*

Hydnangium WALLR., in DIETR. Fl. des Kœnigr. Preuss., VII, 465.

Peridium fleshy or membranaceous. Sterile base none. Trama vesicular. Cells at first empty, then filled with spores. Spores echinate. (Berk. Outlines Brit. Fung., p. 293.)

20. **Hydnangium compactum,** sp. nov.

Globose, 5 cm. in diam.; color white, smooth; gleba dense, pale orange; cells minute, oblong or ellipsoidal; spores globose, rough, not echinate, white, briefly stipitate, guttulate, 6 μ in diam.

Type, No. 191, Harkness Coll.

Under *Ceanothus*, Auburn, Placer County, Calif., May.

21. **Hydnangium album,** sp. nov.

Globose, color dirty white; peridium attenuate, membranaceous; gleba ochraceous; cells minute; spores spherical, white, briefly echinate, 12 μ in diam.

Type, No. 178, Harkness Coll.

In the forest, Calistoga, Napa County, Calif., April and May.

Resembling *H. candidum* Tul., with the exception that the spores are spherical and unusually large.

22. **Hydnangium luteolum,** sp. nov.

Oblong or subrotund, color white turning brown, base not visible; gleba yellowish; cells minute; spores globose, white, briefly stipitate, crowded, echinulate, guttulate, 12 μ in diam.

Type, No. 100, Harkness Coll.

Found in somewhat sandy soil beneath *Libocedrus decurrens* in the mountain region about Alta, Placer County, Calif., July.

Closely resembling *H. Carotæcolor* Tul., except in its inconspicuous base and the form of the spore.

Octaviania *Vitt.*

Octaviania Vitt., Monog. Tub., p. 15.

Peridium continuous or cracked, cottony, running down into the sterile base. Trama byssoid, easily divisible. Fruit-bearing cavities or cells at first empty. Spores rough. (Berk. Outlines Brit. Fung., p. 292.)

23. **Octaviania brunneola,** sp. nov.

Globose, 5 cm. in diam., common integument smooth, absorbent base distinct, terminating in minute fibrillæ; cells various, subrotund or tortuous; basidia 4-spored; spores orbicular, brown, echinulate, 6–10 μ in diam.

Type, No. 82, Harkness Coll.

Mt. Tamalpais, Marin County, Calif., April.

24. **Octaviania rosea** *Hk.*

Octaviania rosea HK., Bull. Call. Acad. Sci., Vol. I, No. 1, 1884, p. 29.

Gregarious, peridium fibrillo-rugose, irregularly lobed, 1–3 cm. in diam., with distinct absorbing base, pale rose color, deepening within; basidia 1–2-spored; sterigmata filiform, capitate, as long as the diameter of the spore; spores globose, hyaline, pale; epispore covered with short, obtuse spines, 14–17 μ.

Type, No. 117, Harkness Coll.

Under shrubby oaks, at Golden Gate Park, San Francisco, Calif., January.

25. **Octaviania mutabilis** *Roum.*

Octaviania mutabilis ROUM., Revue Mycologique, Ann. VII, 1885, p. 23.

Subglobulosa, alba, tactu vinosa, dein nigrescens, basi fibrillis albis instructa; peridio separabili, tomento fugaci obtecto; gleba primum alba, dein, griseo-brunnea; cellulis irregulariter rotundatis, albidis, sæpe interruptis, centralibus majoribus; sporis globulosis, 12–15 μ in diam., echinulatis, brunneis.

No. 138, Harkness Coll.

Under *Arctostaphylos*, Auburn, Placer County, Calif., March; Calistoga, Napa County, Calif., March.

26. **Octaviania socialis,** sp. nov.

PLATE XLII, FIGS. 5*a*–5*d*.

Epigæous, large, 8 cm. in diam., surface deeply furrowed, furrows extending to its base; base distinct, with numerous branching threads; gleba rose-pink; cells irregular; spores globose, echinulate, having about ten pointed projections on the circumference, 12–14 μ in diam.

Type, No. 232, Harkness Coll.

In groups upon the surface of the ground beneath *Eucalyptus globulus*, Belmont, San Mateo County, Calif., January.

27. **Octaviania citrina,** sp. nov.

Globose, white; common integument flakey, imparting an earthy appearance; absorbent base spongy; fibrillæ wanting; gleba orange, cells irregular, basidia prominent, 4-spored; spores stipitate, brown, globose, echinulate, 10–12 μ in diam.

Type, No. 157, Harkness Coll.

Collected under *Arctostaphylos glaucus* at the following localities in California during April: Oat Hill Quicksilver Mine, Solano County; Camp Taylor, Marin County; and Calistoga, Napa County.

28. **Octaviania occidentalis,** sp. nov.

PLATE XLII, FIGS. 4*a*–4*d*.

Large, 2.5 cm. in diam.; color white turning brown, semiglobose; common integument flakey; absorbent base firm, terminating in branching fibrillæ; gleba white; cells oblong or subrotund, basidia 4-spored; spores briefly stipitate, white, globose, echinulate, having about twenty blunt projections on the circumference, 14 μ in diam.

Type, No. 137, Harkness Coll.

Wire Bridge, Placer County, Calif., March.

At irregular intervals, a flasked-shaped cystidium which springs from the parenchyma is to be found protruding from amid the true basidia for a distance of 18 μ and terminating in a conical point. These bodies are filled with what appears to be crystals and are destitute of sporophores.

29. **Octaviania compacta** *Tul.*

Octaviania compacta TUL., Fungi Hypo., p. 79.

Minor, polyrrhiza, nivea; peridio molliusculo insolubili tomentello-gossypino; cellulis rotundis oblongisve, minutissimis, mox obliteratis, oppletis; septis vix conspicuis; sporis innumeris minutissimis, sphæricis, scabriusculis, flavidis, tandem ochraceo-auratis.

No. 19, Harkness Coll.

Under oaks at Wire Bridge, Placer County, Calif., April. Collected by Chas. L. Phillips. Mill Valley, March.

Previously collected at Tamalpais, Marin County, Calif., and Blue Cañon, Placer County, Calif., under leaves, May-July.

30. **Octaviania Stephensii** *Tul.*

Octaviania Stephensii TUL., Fungi Hypo., p. 78.
Hydnangium Stephensii BERK., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XIII, p. 352, also Vol. XVIII, p. 76.

Irregular, oblong, externally rufous, plicato-rugose at the base, cribrose, white within, milky, at length, when exposed to the air, rufous; spores globose, at length echinulate. (Berk. Outlines Brit. Fung., p. 292.)

No. 148, Harkness Coll.

Collected at the following localities in California during March: under oaks at Laundry Farm, Alameda County; at Mill Valley and Kents, Marin County; amongst Sequoias at Mt. Tamalpais.

Previously collected at Tamalpais, Marin County, Calif., and Alta, Placer County, Calif., May–July.

31. **Octaviania monticola,** sp. nov.

PLATE XLII, FIGS. 3*a*–3*c*.

Large, 3 cm. in diam., irregular, globose, rough, flexible, buff; absorbent base prominent, fibres uniting, with earthy particles enclosed; gleba spongy, chestnut-brown; cells minute; basidia 4-spored, spores ovate, echinulate, 10 x 12 μ.

Type, No. 13, Harkness Coll.

Mountain regions in sandy soil, Auburn, Placer County, Calif., April.

Hysterangium *Vitt.*

Hysterangium VITT., Monog. Tub., p. 13.

Peridium entire, indehiscent, well marked, dissolving readily or splitting off naturally, either thin or somewhat thickish, firm, fibrous or membranaceous, provided with a mycelium; gleba perforated with cells which are at first hollow but are at length somewhat filled up, small, rounded or narrowly linear; partitions of the cells of very unequal thickness, tough, bearing basidia on both sides; basidia slender, generally 2-spored; spores ellipsoidal or lanceolate, with short sterigmata, very abundant, smooth and usually pale-colored and pellucid. Fungi of gregarious and hypogæous habits, of regular spherical shape; polyrrhizous, with the abundant white mycelium which is floccose in a peculiar fashion without being filamentous, either completely or partly covered, or at length attached to a nearly simple, rope-like mycelium and then naked, monorrhizous; with a distinct odor when mature. (Translated from the original.)

32. **Hysterangium cinereum,** sp. nov.

PLATE XLII, FIGS. 2*a*–2*b*.

Oblong-rotund, 5 cm. in diam., color brownish white, elastic. smooth; gleba ashy, cut surface showing abundant veins irregular in outline; spores elliptical, white, 6 x 14 μ.

Type, No. 31, Harkness Coll.

In vegetable humus under *Arctostaphylos*, Auburn, Placer County, Calif., February.

33. **Hysterangium Phillipsii,** sp. nov.

Plate XLII, Figs. *1a–1b.*

Large, 3–4 cm. in diam., color rose-pink, fibrillous; rootlets 12 cm. or more in length; gleba of a dark olive or greenish (verdatre) tint, profusely veined, coalescing at the base; cells minute, spores ellipsoidal, in groups of three or four, white, 2 x 5μ.

Type, No. 234, Harkness Coll.

Under oaks, Wire Bridge, Placer County, Calif., January. Collected by Chas. L. Phillips.

34. **Hysterangium occidentale** sp. nov.

Large, 4 cm. in diam., color dirty white; peridium soluble, subrotund, somewhat flattened or discoid; gleba chocolate-colored; cells gyrose, large; spores ellipsoidal, white, 12 x 7μ.

Type, No. 242, Harkness Coll.

Amongst Sequoias, Tamalpais, Marin County, Calif., May.

35. **Hysterangium nephriticum** *Berk.*

Hysterangium nephriticum Berk., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XIII, 1844, p. 350; Tul., Fungi Hypo., p. 82.

Depressed, springing from a white, flat, branched, membranous mycelium; peridium firm, elastic, distinct, tomentose; substance pale blue or grey, here and there greenish; cavities radiating from the base; spores minute, oblong, pale clay-color. (Berk. Outlines Brit. Fung., p. 294.)

No. 143, Harkness Coll.

Under oaks, Auburn, Placer County, Calif., March; Mill Valley, Marin County, Calif., April; Calistoga, Napa County, Calif., May.

36. **Hysterangium membranaceum** *Vitt.*

Hysterangium membranaceum Vitt., Monog. Tub., p. 14, Tab. IV, fig. 15.

Minus, rotundatum, radicatum; peridio tenui membranaceo albido subtomentoso; carne viridiuscula; cellulis difformibus et irregularissimis. (Tul. Fungi Hypo., p. 83.)

No. 176, Harkness Coll.

Mill Valley, Marin County, Calif., April; Auburn, Placer County, Calif., May.

37. **Hysterangium stoloniferum** *Tul.*

Hysterangium stoloniferum Tul., Fungi Hypo., p. 84, Tab. XI, fig. 8.

Sphæricum leve glabrum candidum, radice unica funiformi instructum; carne e cœruleo fusca, tenaci; septis crassis; sporis acervatim sordide fuscis.

No. 158, Harkness Coll.

Collected during April, under oaks, at the following localities in California: Calistoga, Napa County; Mt. Tamalpais and Camp Taylor, Marin County; Auburn, Placer County.

Previously collected at Tamalpais, March–May.

38. **Hysterangium Clathroides** *Vitt.*

Hysterangium Clathroides Vitt., Monog. Tub., p. 13, Tab. IV, fig. 2.

Globosum; peridio albido, mycelii gratia polyrrhizo, facile solubili; carne olivaceo-virente. (Tul. Fungi Hypo., p. 80.)

No. 156, Harkness Coll.

Collected in damp ground at the following localities in California during April: Calistoga, Napa County; Bishops and Tamalpais, Marin County; Wire Bridge, Placer County.

39. **Hysterangium australe** *Speg.*

Hysterangium australe Speg., Fungi Argent. Pug. IV, n. 237.

Primo subglobosum dein ob terræ pressionem irregulariter compressum, varie gibbose expansum, magnitudine ludens 5–20 diam., basi manifesta nulla, fibrillis radicalibus perfecte destitutum, album, levissimum, glaberrimum, peridio tenui a pulpa non v. difficile secedente, gleba autem pallide fulvo-olivascente, tremelloideo-subceracea, tubulis numerosis, minutissimis undique irregulariter percursa; tubulis gracilibus 150–250 μ diam., varie elongatis, vacuis, parietibus sporiferis cinnamomeis; sporis elliptico-elongatis, sursum plus minusve attenuato-rotundatis, deorsum acute attenuato-cuneatis basique truncatis, episporio ubique majuscule undulato-subverruculoso, saturate olivaceo-fuligineis, protoplasmate grosse granuloso farctis v. 1-guttulatis 15–20 = 8–10 μ; stipite longiusculo, gracili hyalino, monospermo fultis. (De Toni in Sacc. Sylloge Fung., Vol. VII, 1888, p. 157.)

No. 84, Harkness Coll.

Collected under oaks at the following localities in California during April: Tamalpais and Mill Valley, Marin County; Auburn, Placer County; Calistoga, Napa County.

40. **Hysterangium fuscum,** sp. nov.

Minute, dirty white, globose; mycelium flocculent at base; gleba elastic; veins white; hymenium brown; spores elliptical, 6 x 12 μ.

Type, No. 177, Harkness Coll.

Under *Arbutus Menziesii*, Mill Valley, Marin County, Calif., April.

Rhizopogon *Tul.*

Rhizopogon TUL., Fungi Hypo., p. 85, Tab. I, fig. 5, Tab. II, fig. 1, et Tab. XI, figs. 4–5.

Peridium continuous or cracked, adhering to creeping branched fibers which traverse its surface. Cavities distinct, at first empty. Spores smooth, oblong-elliptic. (Berk. Outlines Brit. Fung., p. 294.)

41. **Rhizopogon aurantius,** sp. nov.

Subglobose, 2 cm. in diam., color dirty white; peridium attenuate; gleba pale orange, the freshly cut surface showing a creamy exudation; cells large; cell-walls thin but firm; spores subglobose, with colorless oil globule, 8–10 μ in diam.

Type, No. 74, Harkness Coll.

Solitary in dense forests of Sequoias, deeply hidden by decaying vegetation, Mt. Tamalpais, Marin County, Calif., August.

Leucophleps, gen. nov.

Globose or roundly elongate, color white or citron, dense; gleba multilocular; cells crowded; veins pearly white; spores spherical or ovoid and borne upon elongated sterigmata.

42. **Leucophleps magnata,** gen. et sp. nov.

PLATE XLII, FIGS. *7a–7c.*

Large, 3 cm. in diam., subglobose or elongate, white, smooth, solid; peridium wanting, white; the freshly cut surface sometimes showing a blue tint which soon vanishes; multilocular cells irregularly decreasing in magnitude towards the surface and disappearing at the sterile base; veins pearly white; spores single, globose, smooth, enclosed in semi-opaque investments or utricles, with oil globules, supported upon somewhat tortuous sterigmata, 13 μ in diam.

Type, No. 154, Harkness Coll.

Under *Acer*, Calistoga, Napa County, Calif., April.

43. **Leucophleps foveolata,** sp. nov.

Subglobose, color white or faintly citron; peridium attenuate, minutely pitted; gleba white; veins white; cells rotund; spores white, smooth, guttulate, 7 x 12 μ.

Type, No. 209, Harkness Coll. A second specimen (No. 243) was collected in the same locality.

In moist earth beside a rivulet, Mill Valley, Marin County, Calif., July.

Differing from *L. magnata* in external characters and size of spore.

44. **Leucophleps candida,** sp. nov.

White, 2 cm. in diam., irregular, firm, surface completely studded with depressions of very variable circumference; peridium wanting; gleba of pearly whiteness; cells crowded and plentiful; spores globose, 8 μ in diam.

Type, No. 207, Harkness Coll.

Mill Valley, Marin County, Calif., June.

45. **Leucophleps odorata,** sp. nov.

PLATE XLIII, FIGS. 9*a*–9*b*.

Large, 3–4 cm. in diam., color orange, irregularly lobed or oblong, no fibrous attachment, slightly crepitating under pressure. Odor nauseating.

Type, No. 251, Harkness Coll.

Under oaks, Castle Crag, Shasta County, Calif., July.

The marked irregularity in form and color, together with the odor, serves to distinguish this from any other species, and although firm there is distinct crepitus to be observed upon pressure. The cells in the recently cut surface of the fresh plant present a glassy appearance.

46. **Leucophleps citrina,** sp. nov.

PLATE XLIII, FIGS. 8*a*–8*b*.

Subglobose, 2 cm. in diam., citron color, smooth; gleba firm, wavy; cells minute; spores roundly elliptical, guttulate, white, two to four spores form upon each basidium; basidia attenuate at the point of attachment, increasing in size towards the apex, oil globules interspersed for its entire length; spores $6 \times 8\ \mu$.

Type, No. 168, Harkness Coll.

Found amidst Manzanitas, Mt. Tamalpais, Marin County, Calif., April.

The fungus imparts a red tint to alcohol when immersed.

Melanogaster *Corda.*

Melanogaster CORDA in STURM'S Deutschl. Fl., Abth. III, Heft 11, 1831, p. 1.

Peridium adhering to creeping branched fibres which traverse its surface, without any proper or distinct base. Cells at first filled with pulp. Spores smooth, mostly dark. (Berk. Outlines Brit. Fung., p. 293.)

47. **Melanogaster Eisenii,** sp. nov.

Globose, smooth, 1.5 cm. in diam., color brown; gleba fuscous; veins brown; cells rhomboidal; spores globose, 6–8 μ in diam.

Type, No. 116, Harkness Coll.

Cabo St. Lucas, Baja California, January. Collected by Dr. Gustav Eisen.

48. **Melanogaster variegatus** *Tul.*

Melanogaster variegatus TUL., Fungi Hypo., p. 92, Tab. II, fig. 4, et Tab. XII, fig. 6.

At first ochraceous, then reddish-ferruginous, minutely downy; walls of the cells dirty-white, yellowish, or orange; pulp black; spores minute. (Berk. Outlines Brit. Fung., p. 293.)

No. 145, Harkness Coll.

Amongst oaks, Wire Bridge, Placer County, Calif., March.

Previously collected at Sausalito, Marin County, Calif., February.

49. **Melanogaster tuberiformis** *Corda.*

Melanogaster tuberiformis Corda., in Sturm's Deutschl. Fl., Abth. III, Heft 11, 1831, p. 1, Tab. I.

Hypogæus rotundatus, fusco-cupreus, intus ater, radiculis fibrillosis atris tectus; sporis atris obovatis, deorsum attenuatis. (Tul. Fungi Hypo., p. 95.)

No. 5, Harkness Coll.

Amongst small oaks, Mill Valley, Marin County, Calif., April.

50. **Melanogaster durissimus** *Cooke.*

Melanogaster durissimus Cooke., Grevillea, Vol. VIII, p. 94.

Subglobosus, compressus, difformis aut sulcatus, lævis, durissimus, atrofuscus, demum nigrescens. Peridio crasso, subnitido; carne mire lacunoso, ochraceo albo; lacunis majusculis, creberrimis, atris. Sporis oblongo-ellipticis, inæqualibus, brunneis .005–.008 x .003–.005 mm. Odore fortissimo.

No. 21*b*, Harkness Coll.

Collected amongst oaks at the following localities in California during April: Auburn and Wire Bridge, Placer County; Mt. Tamalpais and Sausalito, Marin County.

51. **Melanogaster aureus** *Tul.*

Melanogaster aureus Tul., Fungi Hypo., p. 97.
Octaviania aurea Vitt., Monog. Tub., p. 20, Tab. III, fig. 14.

Oblongus uniformis, basi radicatus; peridio levi subalbido; carne primo dura aurea, venis albidis (cellularum parietibus) variegata, demum molli et nigrescente; cellulis subcavis.

No. 68, Harkness Coll.

Amongst oaks, Wire Bridge and Auburn, Placer County, Calif., February.

52. **Melanogaster sarcomelas** *Tul.*

Melanogaster sarcomelas Tul., Fungi Hypo., p. 96.
Octaviania sarcomelas Vitt., Monog. Tub., p. 16, Tab. III, fig. 3.

Minor, difformis; peridio levi nigro; resticulis nullis; carne nigerrima unicolore; cellulis regularibus, substantia pultacea sporifera repletis; sporis ovalibus majusculis, levibus.

No. 128, Harkness Coll.

Collected at the following localities in California during April: amongst redwoods, Mill Valley, Marin County; under oaks, Wire Bridge, Placer County; in forest, Laundry Farm, Alameda County.

Elaphomyces *Nees.*

Elaphomyces Nees., in Fries Syst. Myc., Vol. III, p. 21.

Common integument thick, hard. Asci globose or obovate. Sporidia consisting of several concentric utricles. Internal mass of fungus at length dusty. (Berk. Outlines Brit. Fung., p. 378.)

53. **Elaphomyces variegatus** *Vitt.*

Elaphomyces variegatus Vitt., Monog. Tub., p. 68, Tab. IV, fig. 4.

Mycelium yellow (or yellowish grey), inconspicuous; cortex thick, hard, ochraceous-yellow or golden-yellow, rough, with thick pyramidal and obtuse, or narrow, pointed, and fragile warts, or only granulated; peridium reddish brown and variegated; asci 2–4-spored; sporidia opaque, blackish brown. (Cooke's Handbook, Vol. II, p. 749.)

No. 39, Harkness Coll.

Under *Pseudotsuga Douglassii*, Donner Lake, Nevada County, Calif., July.

54. **Elaphomyces Morettii** *Vitt.*

Elaphomyces Morettii Vitt., Monog. Tub., p. 71, Tab. IV, fig. 17.

Crusta fusco-purpurea; cortice duro, fragili, nigro-brunneo obtuseque verrucoso; peridio albido-fusco; sporis fusco-nigrentibus. (Tul. Fungi Hypo., p. 112.)

No. 38, Harkness Coll.

Under oaks, Santa Cruz, Santa Cruz County, Calif., May.

Hydnocystis *Tul.*

Hydnocystis Tul., Fungi Hypo., p. 116, Tab. IV, Fig. 7; Tab. XIII, Fig. 2; Tab. XIV, Fig. 1.

Receptaculum utriforme, globosum aut varie sinuoso-anfractuosum, penitus clausum, vel rima basilari inaperta, brevi s. longiuscula et gyrosa, pilisque adpressis confertis fungum intrantibus occlusa et velata quasi dehiscens, interius latissime uniloculare et vacuum. Integumentum, receptaculi extima corticula, indiscretum, minute papillosum, pilosum et coloratum. Hymenium quod fungi cavitatis paries est, albidum, ex fibris seu filamentis constans longissime linearibus, subdiscretis aut vix cohærentibus, parallele e receptaculo prodeuntibus, inæqualibus sterilibusque (paraphysibus), nec non et utriculis immistis paucioribus crassis longe cylindricis obtusis, in filum longum deorsum desinentibus, ascis scil. seu thecis octosporis. Sporæ uniseriatæ, sphæricæ aut ellipticæ, leves, pellucidæ, dilute coloratæ; nucleo oleoso, tandem homogeneo nec partito.

55. **Hydnocystis compacta,** sp. nov.

PLATE XLIII, FIGS. 11*a*–11*c*.

Minute, reddish brown, subrotund, cavernous without exterior opening, minutely and closely papillose; gleba compact, white; asci cylindrical, obtuse, 175 μ in length, 8-spored; spores globose, hyaline and unequally papillose, 25 μ in diam.

Type, No. 98, Harkness Coll.

Under *Libocedrus*, Alta, Placer County, Calif., May.

Genea *Vitt.*

Genea VITT., Monog. Tub., p. 27.

Common integument warty, with an aperture at the apex. Hymenium waved and sinuated, but not forming an intricate mass. Asci cylindrical. Sporidia globose [or subglobose.] (Berk. Outlines Brit. Fung., p. 378.)

56. **Genea compacta,** sp. nov.

PLATE XLIII, FIGS. 10*a*–10*c*.

Minute, 1 cm. in diam., irregularly stellate, color light brown, verrucose, distinct base with branching filaments; gleba white, irregularly cavernous; asci cylindrical, stipitate, 270 μ in length, 8-spored; spores ellipsoidal, verrucose, 25 x 18 μ. The fungus is exceedingly rare. The filaments composing the paraphyses are septate, extremely delicate, and of unusual length and wavy.

Type, No. 86, Harkness Coll.

Found in the forest, Mt. Tamalpais, Marin County, Calif., April.

The verrucosity consists in the surface of the spore being covered with small, round, knob-like projections, about sixteen being found in the circumference.

57. **Genea arenaria,** sp. nov.

Minute, color light brown, subglobose, lobed, verrucose, cavernous; gleba white, attenuate; asci linear, 8-spored; spores roundly ellipsoidal, 24 x 18 μ; paraphyses brief and not plentiful.

Type, No. 42, Harkness Coll.

In sandy ground. No locality or date.

58. **Genea hispidula** *Berk.*

Genea hispidula BERK., in Tul., Fungi Hypo., p. 121, Tab. XII, fig. 2, et Tab. XIII, fig. 3.

Small, brown, externally invested everywhere with rather rigid, adpressed, brown flocci; interior cavity very often simple, with the mouth almost hidden; radical fibres brown, adhering to the base; spores large, ellipsoid; warts thick and crowded. (Cooke's Handbook, Vol. II, p. 748.)

No. 115, Harkness Coll.

Beneath the surface of the ground under trees, San Rafael, Marin County, Calif., May. Under oaks, Wire Bridge, Placer County, Calif., April.

59. **Genea verrucosa** *Vitt.*

Genea verrucosa VITT., Monog. Tub., p. 28, Tab. II, Fig. 7.

Very irregular and polymorphous, gibbous, sulcate, or also somewhat many-lobed, black, verrucose ostiolate; ostiola sometimes very broad, radical filaments abbreviated; sporidia broadly elliptic, verrucose. (Cooke's Handbook, Vol. II, p. 748.)

No. 70, Harkness Coll.

Amongst decaying leaves under trees, Santa Cruz, Santa Cruz County, Calif., May.

60. **Genea sphærica** *Tul.*

Genea sphærica TUL., Fungi Hypo., p. 120, Tab. IV, Fig. 2; Tab. XII, Fig. 1, et Tab. XIII, Fig. 6.

Regularis et quasi perfecte sphærica, interdum depressa, atra glabra, verrucosa, comam ferrugineam siccam spissam longissimamque basi gerens, apice pervia, intus varie labyrintheo-cavernosa, rarius vacua et penitus utriformis.

No. 89, Harkness Coll.

Beneath the surface of the ground under oaks, Contra Costa County, Calif., May.

Balsamia *Vitt.*

Balsamia VITT., Monog. Tub., p. 30.

Common integument warty. Hymenium complicated with distinct lacunæ not leading to the surface. Sporidia cylindrical or oblongo-elliptic, even, pellucid. (Berk. Outlines Brit. Fung., p. 378.)

61. **Balsamia magnata,** sp. nov.

Subglobose, densely verrucose, 2.5 cm. in diam., color orange red; cavity gyrose; gleba white, firm; asci subovate, 8-spored, 50 x 38 μ; spores cylindrical, containing from one to three oil globules, 18 x 8 μ.

Type, No. 185, Harkness Coll.

In forests, Auburn, Placer County, Calif., May.

62. **Balsamia nigrens,** sp. nov.

Medium, semiglobose, irregular, black, verrucose, warts with polygonal base; openings stellar, sometimes extending through the mass; cavities large and somewhat regular; gleba white, firm, crossed by white wavy lines; asci semiglobose or ellipsoidal, briefly stipitate, 8-spored, 48 x 32 μ; spores oblong-elliptic, guttulate, 26 x 12 μ.

Type, No. 180, Harkness Coll.

Beneath *Ceanothus*, Auburn, Placer County, Calif., May.

63. **Balsamia alba,** sp. nov.

Large, color dirty white, subglobose, fissured, deeply verrucose; gleba firm; asci ellipsoidal, 8-spored; spores cylindrical, guttulate, 12 x 18 μ.

Type, No. 129, Harkness Coll.

Under oaks, Wire Bridge, Placer County, Calif., February.

This fungus is remarkable for the density of the gleba and the small number of its asci.

64. **Balsamia filamentosa**, sp. nov.

PLATE XLIII, FIGS. 13*a*–13*f*.

Large, oblong or irregularly globose, color ferruginous brown; densely verrucose; gleba filamentous; veins irregular; parenchyma pellucid; asci ellipsoidal, markedly stipitate, 42 x 24 μ; spores cylindrical, having two to three oil globules, 18 x 12 μ.

Type, No. 236, Harkness Coll.

Under *Heteromeles arbutifolia*, Auburn, Placer County, Calif., February.

The oil globules disappear from view when placed in a medium denser than that of water.

65. **Balsamia vulgaris** *Vitt.*

Balsamia vulgaris VITT., Monog. Tub., p. 30, Tab. I, Fig. 2.

Major, sæpissime sinuoso-exarata vel hinc et illinc excavata, minutissime papillosa, papillis interdum subnullis; lacunis latiusculis gyrosis; septis crassis in medio pellucidis; sporangiis paraphyses inter omnino nidulantibus brevioribusque vel breviter exsertis; sporis cylindricis angustis, guttulas oleosas tres subæquales includentibus. (Tul. Fungi Hypo., p. 123.)

No. 231, Harkness Coll.

Among decaying vegetation in shrubby thickets, Auburn, Placer County, Calif., December.

66. **Balsamia platyspora** *Berk.*

Balsamia platyspora BERK., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XIII, 1844, p. 358.

Small, globose, rufous, minutely warted, substance pallid yellow, minutely cellulose; sporidia at first broadly oblong-elliptic, with a large globose nucleus, at length slightly elongated trinucleate. (Cooke's Handbook, Vol. II, p. 747.)

No. 222, Harkness Coll.

Amongst shrubs under vegetable mould, Auburn, Placer County, Calif., December.

67. **Balsamia polysperma** *Vitt.*

Balsamia polysperma VITT., Monog. Tub., p. 31.

Minor, anguloso-tuberulosa, papillis minutis congestis ferrugineis vestita; carne subalbida cellulosa; substantia intercellulari (septis) alba opaca; sporis numerosissimis. (Tul., Fungi Hypo., p. 125.)

No. 220*b*, Harkness Coll.

Under shrubs in sandy soil, Auburn, Placer County, Calif., December.

Hydnobolites *Tul.*

Hydnobolites TUL., Fungi Hypo., p. 126.

Integument replaced by white, evanescent down. Hymenium complicated with sinuous lacunæ, ending at the surface. Asci elliptic. Sporidia globose. (Berk. Outlines Brit. Fung., p. 377.)

68. **Hydnobolites excavatum**, sp. nov.

1 cm. in diam., color brown; peridium smooth; gleba brown, cavernous; asci subrotund, 8-spored, 65 x 54 μ; spores globose, 25 μ in diam.

Type, No. 189, Harkness Coll.

Under vegetable humus in sandy ground, Auburn, Placer County, Calif., May.

Hydnotrya *B & Br.*

Hydnotrya B. & BR., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XVIII, 1846, p. 78.

Common integument minutely papillose, not distinct. Hymenium complicated with gyrose lacunæ, leading to the surface. Asci oblong. Sporidia globose, tuberculate. (Berk. Outlines Brit. Fung., p. 377.)

69. **Hydnotrya cerebriformis**, sp. nov.

PLATE XLIV, FIGS. 19*a*–19*f*.

Large, 3 cm. in diam., color salmon, subrotund, smooth, brain-like markings upon the surface; gleba white or faintly citron, canals gyrose; hymenium covered with clavate villi between and extending beyond the asci; asci cylindrical, briefly stipitate; spores globose, brown, foveolate, 25 μ in diam.

Type, No. 37, Harkness Coll.

Among fir trees, Donner Lake, Nevada County, Calif., July.

The slight pits upon the spore give it a rough appearance.

Pseudohydnotrya *Fischer.*

Pseudohydnotrya FISCHER, Tuberineæ in ENGLER & PRANTL'S Die Naturl. Pflanzenf., Teil I, Abth 1, p. 282.

Fungus irregularly rounded, perforated by hollow labyrinth-like passages and chambers which open out at several places on the surface of the fungus, and the walls of which are covered by hymenium. Surface of fungus covered with a pseudo-parenchymatic, hairy peridium, which often penetrates deeply into the interior chambers and then continues directly into the hymenium. Hymenium consists of paraphyses and of asci arranged like palisades. Paraphyses cylindrical, septate, at apex knob-like. Asci cylindrical or somewhat globular, 8-spored, spores ellipsoidal, smooth, without color, uniseriate or seldom biseriate. (Translated from the original.)

70. Pseudohydnotrya Harknessii *Fischer.*

Pseudohydnotrya Harknessii FISCHER, Tuberineæ in ENGLER & PRANTL'S Die Naturl. Pflanzenf., Teil I, Abth 1, p. 282.

Asci 140–160 μ long, 20–28 μ broad, generally 8-spored. Spores 25–28 μ long, 14–18 μ broad. Paraphyses 7–14 μ thick at the swollen end. (Translated from the original.)

No. 1, Harkness Coll.

Under shrubs among vegetable humus. Mill Valley, Marin County, Calif., April.

71. Pseudohydnotrya carnea, sp. nov.

PLATE XLIII, FIGS. 16*a*–16*b*.

Minute, 1.5 cm. in diam., common integument, color pale brown, subglobose, irregular, slightly tomentose, chambered; gleba white; parenchyma convolute; asci cylindrical, 125 μ in length, 8-spored; spores ellipsoidal, white, guttulate, 22 x 15 μ; paraphyses hidden.

Type, No. 181, Harkness Coll.

Among shrubs, Auburn, Placer County, Calif.; May; under oaks, Mill Valley, Marin County, Calif., April.

This species is much infested by a parasitic *Sphæria*.

72. Pseudohydnotrya nigra, sp. nov.

Large, 2 cm. in diam., color dark brown, inclosed, peridium loosely adherent, tomentose; gleba white; parenchyma convolute; asci 120 x 8 μ; spores guttulate.

Type, No. 216, Harkness Coll.

Under shrubs in firm ground to which it adheres by its hairy investment. Auburn, Placer County, Calif., November to April.

Stephensia *Tul.*

Stephensia TUL., Fungi Hypo., p. 129.

Common integument fleshy, cottony. Base distinct. Hymenium intricate. Asci cylindrical. Sporidia globose, even, at length verrucose. (Berk. Outlines Brit. Fung., p. 377.)

73. **Stephensia bombycina** *Tul.*

PLATE XLIV, FIGS 18*a*–18*c*.

Stephensia bombycina TUL., Fungi Hypo., p. 130, Tab. XII, Fig. 4.
Genea bombycina VITT., Monog. Tub., p. 29, Tab. III, Fig. 13, et Tab. IV, Fig. 8; BERK., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XIII, p. 357.

Subglobose, depressed; peridium rather soft, floccose, irregularly intruded into the cavity, destitute of rooting fibres; flesh gyrose-venose; sporidia pellucid, spherical. (Cooke's Handbook, Vol. II, p. 745.)

No. 173, Harkness Coll.

Found in forests, March. No locality.

This fungus varies slightly from the original description in the spores, which are generally biseriate and marked by irregularly foveolate depressions.

Pachyphlœus *Tul.*

Pachyphlœus TUL., Fungi Hypo., p. 130.

Common integument warty, opening by a terminal aperture. Base distinct. Asci clavate. Sporidia spherical. (Berk. Outlines Brit. Fung., p. 377.)

74. **Pachyphlœus carneus,** sp. nov.

PLATE XLV, FIGS. 33*a*–33*b*.

Subrotund, 1 cm. in diam., studded with slight warty elevations with stellate markings at their apex and an irregularly outlined base; gleba citron; veins obscure; asci elongate or ovoid and narrowed at terminus, briefly pedicellate, 8-spored; spores irregularly seriate, large, globose, verrucose, 14 μ in diam.

Type, No. 253, Harkness Coll.

Beneath Sequoias, Mill Valley, Marin County, Calif., July.

The spores are often seriate, at times, however, nearly biseriate. The fungus resembles *P. conglomeratus* B. & Br., but has a much larger spore.

75. **Pachyphlœus ligericus** *Tul.*

Pachyphlœus ligericus TUL., Fungi Hypo., p. 133, Tab. XIV, Fig. 5.

Exiguus verrucosus et nigricans; sporangiis ovato-globosis; sporarum verruculis crassis obtusisque.

No. 44, Harkness Coll.

Under pine trees in sandy soil, Towles, Placer County, Calif., May.

Myrmecocystis, gen. nov.

Fungus minute, irregular, lobed or gibbous, verrucose; gleba chambered by an irregularly stellate cavity not communicating with the exterior; asci subglobose or somewhat elongate, 8-spored; spores rough.

76. **Myrmecocystis cerebriformis**, gen. et sp. nov.

PLATE XLV, FIGS. 28*a*–28*e*.

Minute, 1 cm. in diam., color white or pale citron, lobed, verrucose, enclosed; gleba white, marked by an irregularly stellate-formed cavity without regular lines, the structure composed of large and uniform cells; asci subglobose or slightly elongated, 8-spored; spores globose, 24 μ in diam.

Type, No. 25, Harkness Coll.

In sandy places under oaks, Wire Bridge, Placer County, Calif., May.

77. **Myrmecocystis candida**, sp. nov.

PLATE XLV, FIGS. 29*a*–29*e*.

Minute, 0.5 cm. in diam., color white, irregular, lobed, verrucose; gleba irregularly chambered; asci subglobose, 8-spored; spores globose, rough.

Type, No. 18, Harkness Coll.

In rich sandy soil under oaks, Alameda County, Calif., June.

Differing from *M. cerebriformis* in magnitude and in the spore.

Geopora *Hk.*

Geopora Hk., Bull. Cal. Acad. Sci., Vol. I, No. 3, 1885, p. 168.

Subterranean. Integument woolly, continuous with the trama. Hymenium convolute. Asci cylindrical. Sporidia hyaline, oblong, smooth.

78. **Geopora Cooperi** *Hk.*

Geopora Cooperi Hk., Bull. Cal. Acad. Sci., Vol. I, No. 3, 1885, p. 168.

Irregularly globular, 2-4 cm. in diam., covered with dense brown wool which is continued inwards on the trama; absorbing base none; hymenium white, not closely packed; asci cylindrical, 8-spored, 220 x 26 μ; sporida hyaline, oblong, smooth, with a large shining, eccentric nucleus, 28 x 20 μ.

Type, No. 106 (3880), Harkness Coll.

Haywards, Alameda County, Calif., January. Coll. by Dr. J. G. Cooper.

79. **Geopora magnata,** sp. nov.

PLATE XLV, FIGS. 34*a*-34*d*.

Large, 6 cm. in diam., semiglobose, color brown, with brain-like convolutions marking its entire surface; septate hairs minute and in great abundance; gleba white and marked by labyrinthine cavities; asci cylindrical, 8-spored; spores white, destitute of oil globules, roundly ellipsoidal, 14 x 18 μ, much shorter than those of *G. Cooperi.*

Type, No. 255, Harkness Coll.

Amongst *Pinus insignis*, Golden Gate Park, San Francisco, Calif., January.

80. **Geopora brunneola,** sp. nov.

Irregularly globose, 3 cm. in diam., color brown, corrugated, tomentose, enclosed; gleba white; hymenium fleshy, densely crowded; asci cylindrical, 80 x 12 μ, 8-spored; spores obovate, hyaline, 12 x 18 μ. The asci are much shorter than in *G. Cooperi* and are densely crowded.

Type, No. 102, Harkness Coll.

In sandy ground, Golden Gate Park, San Francisco, Calif., April.

81. **Geopora mesenterica,** sp. nov.

PLATE XLIII, FIGS. 12*a*–12*c*.

Smooth, irregular, 5 cm. in diam., color dirty white; gleba ferruginous brown; parenchyma convolute; asci cylindrical, 102 x 12 μ; with elongated pedicel, 8-spored; spores white, ovoid, smooth, 10 x 12 μ.

Type, No. 37, Harkness Coll.

Under *Ceanothus* in decaying vegetable humus, Auburn and Wire Bridge, Placer County, Calif., May.

Tuber *Micheli.*

Tuber MICHELI, Nov. Pl. Gen., p. 221.

Asci short, saccate, disposed in sinuous veins. Sporidia elliptic, reticulate, often echinulate. Peridium warty or tubercled, rarely smooth, without any definite base. (Berk. Outlines Brit. Fung., p. 376.)

82. **Tuber (Eutuber) citrinum,** sp. nov.

PLATE XLV, FIGS. 30*a*–30*c*.

Subglobose, 2 cm. in diam., irregular, warty, fissured, color citron, turning to pale brown; gleba white; asci globose, enclosed in wavy filaments; spores two to three, seldom four; spores ellipsoidal, reticulate-alveolate, dark brown, 30 x 42 μ; about eighteen alveoli on the circumference of the spore.

Type, No. 123, Harkness Coll.

In forest, Tamalpais, Marin County, Calif., May.

Resembling *T. rapæodorum* Tul. excepting in form and the structure of the gleba.

83. **Tuber (Eutuber) monticolum,** sp. nov.

Minute, globose, 1.5 cm. in diam., smooth, color dirty white, fissured, with a slightly defined sterile base; gleba white, firm; asci globose, briefly stipitate, 2–4-spored; spores ellipsoidal, dark, reticulate-alveolate, 36 x 25 μ.

Type, No. 27, Harkness Coll.

Among firs in dense woods in Sierra Nevada mountains at Towle, Placer County, Calif., July.

84. Tuber (Eutuber) magnatum *Pico.*

Tuber (Eutuber) magnatum PICO, Melethemata, p. 79.

Ochraceo-pallens v. dilute virescens, subleve aut minutissime papillosum, difforme, globoso-angulosum et varie lobatum, basi obconica instructum; venis aeriferis tenuissimis, reticulatis; asci 1–3-sporis; sporis fuscis elliptico-rotundatis et alveolato-reticulatis, retis alveolis amplis. (Tul., Fungi Hypo., p. 150.)

No. 62, Harkness Coll.

In oak forest, San Rafael, Marin County, Calif., March; under oaks, Wire Bridge, Placer County, Calif., March.

85. Tuber (Eutuber) Borchii *Vitt.*

Tuber (Eutuber) Borchii VITT., Monog. Tub., p. 44, Tab. I, Fig. 3.

Globosum, vulgo regulare, puberulum, albidum, maculis candidis notatum posteaque rufescentibus conspurcatum, intus ex albido fuligineo-violaceum et etiam fusco-nigricans, venis albidis rariusque lineis obscurioribus marmoratum; sporangiis elliptico-rotundatis, sæpius 1–3-sporis; sporis crassis ovatis reticulato-alveolatis spisseque luteo-brunneis. (Tul., Fungi Hypo., p. 145.)

No. 54, Harkness Coll.

Amongst decaying leaves of oak, Mt. Tamalpais, Marin County, Calif., June.

86. Tuber (Eutuber) australe *Speg.*

Tuber (Eutuber) australe SPEG., Ann. de Sociedad Cientifica Argentina, Vol. XXIV, 1887, p. 122.

Globosum v. globoso-trigonum, superne integrum, inferne sæpius trilobatum, magnitudine valde ludens (4-30 mill. diam.), lævissimum, sordide album; cutis tenuis a carne inseparabilis; caro compactiuscula, alba, dein grisea, venis parcis crassiusculis, albidis, immutabilibus ramoso-anastomosantibus percursa; asci in pulpa dense dispersi, globosi v. globoso-elliptici, primo 2–3 spori, dein sæpius 1-spermi v. 2-spermi altero abortivo (70-90 μ x 60–80 μ): sporæ globoso-ellipticæ, pallide fulgineo-olivaceæ, areola hyalina, lata, reticulato-alveolata cinctæ (35–40 μ x 28–30 μ sine areola; 45–50 μ x 35–38 μ cum areola).

No. 203, Harkness Coll.

Amongst oaks in vegetable humus upon a well drained hillside, Auburn, Placer County, Calif., June.

87. **Tuber (Eutuber) gibbosum,** sp. nov.

Irregularly gibbose, 2 cm. in diam., color cinnamon-brown; gleba ochraceous; septa white, tortuous, obscure; asci subrotund, 3-4-spored; spores dark brown, ellipsoidal, echinate, markedly reticulate-alveolate, large, 24 x 36 μ.

Type, No. 162, Harkness Coll.

Under oaks, Mill Valley, Marin County, Calif., April.

88. **Tuber (Eutuber) excavatum** *Vitt.*

Tuber (Eutuber) excavatum VITT., Monog. Tub., p. 49, Tab. I, Fig. 7.

Subglobose, about an inch in diameter; peridium discrete, ochraceous, minutely verrucose, firm; flesh horny, cinerous-red, liver-colored, or tawny; veins pallid-ochraceous; the substance falls away in the center, so as to leave a cavity, which has an opening at the base of the tuber; asci numerous, ellipsoid, 2-4-spored; sporidia ellipsoid, yellowish, or pallid-tawny; epispore largely foveolo-plicate. (Cooke's Handbook, Vol. II, p. 740.)

No. 159, Harkness Coll.

Beneath oaks in clayey soil, Laundry Farm, Alameda County, Calif., April.

The spore is somewhat larger (42 μ in diam.) than in the dried specimen, and like it coarsely reticulate.

89. **Tuber (Sphærotuber) puberulum** *B. & Br.*

Tuber (Sphærotuber) puberulum B. & BR., Ann. & Mag. Nat. Hist., 1st Ser., Vol. XVIII, p. 81.

Gregarious, irregularly sublobate, clothed with short, erect down, which gives it to the naked eye a peculiar pearly appearance; the white spots are very visible, even in dried specimens; peridium very thin and delicate, so that the pinky-brown color of the flesh is apparent through it, often cracked; veins white from a radiating base, in some individuals very few; sporidia nearly spherical, reticulato-echinulate; odor of the radish. (Cooke's Handbook, Vol. II, p. 741.)

No. 36, Harkness Coll.

Growing amongst decaying pine bark in the forest, Donner, summit of the Sierra Nevada mountains, 7,000 feet, July; under *Libocedrus*, Towles, Placer County, Calif.

90. **Tuber (Sphærotuber) Californicum**, sp. nov.

PLATE XLV, FIGS. 31*a*–31*b*.

Subglobose, 1.5 cm. in diam., ochraceous, smooth; gleba firm, brown; veins conspicuous, not plentiful; asci subglobose, not stipitate, 3–4-spored; spores globose, large, brown when mature, reticulate-alveolate, 42 μ in diam., about ten alveoli on the circumference.

Type, No. 150, Harkness Coll.

Under oaks beneath vegetable humus upon a hillside, Laundry Farm, Alameda County, Calif., March.

This species is especially notable for the magnitude of its spore.

91. **Tuber (Oogaster) Caroli** *Bonnet.*

Tuber (Oogaster) Caroli BONNET, Rev. Mycol., Ann. VII, 1885, p. 8.

Globosum, brunneo-ferrugineum, verrucis plerumque 5-goniis asperatum, basi squamiformi, eximia instructum; gleba firma, sicca, pallide luteola, dein luteola, venis albis, numerosis, latissimis, e fungi basi exorientibus, gyrosis marmorata, lineis obscuris destituta; ascis globosis v. piriformibus, longe lateque stipitatis, 1–4-sporis; sporidiis ellipsoideis, dense et acute aculeatis, magnis, 20–22=14–15, luteo-brunneis. (Paoletti in Saccardo's Sylloge Fung., Vol. VIII, 1889, p. 894.)

No. 149, Harkness Coll.

In clayey soil beneath oaks, Laundry Farm, Alameda County, March; Howards, Marin County, Calif., May.

92. **Tuber (Sphærogaster) candidum,** sp. nov.

PLATE XLV, FIGS. 32*a*–32*b*.

Subrotund, 2 cm. in diam., smooth, color whity brown; gleba light brown; veins attenuate, white; asci subglobose; 3–4-spored; spores globose or ovoid, echinate, brown when mature, 24 μ in diam.

Type, No. 195, Harkness Coll.

Under dense clusters of *Ceanothus*, Auburn, Placer County, Calif., May.

Differing from *T. echinatum* Sacc. in the form of the spore.

93. **Tuber (Sphærogaster) Eisenii,** sp. nov.

Irregularly oblong, 3 cm. in diam., common integument smooth; gleba pale or whitish; veins large; asci ovate, stipitate, 1–2-spored, seldom more than one; spores globose, dark brown, echinate, 18 μ in diam.

Type, No. 196, Harkness Coll.

In sandy places beneath vegetable humus, Auburn, Placer County, Calif., May.

Named in honor of Dr. Gustav Eisen of the California Academy of Sciences.

94. **Tuber (Sphærogaster) olivaceum,** sp. nov.

Semiglobose, 2 cm. in diam., color ferruginous brown, smooth; gleba olivaceous; veins minute; asci ellipsoidal, markedly pedicellate, 2–4-spored; spores globose, echinate, dark brown, 24 μ in diam.

Type, No. 197, Harkness Coll.

Beneath vegetable humus, Auburn, Placer County, Calif., May.

Piersonia, gen. nov.

Integument scabrous or warty; gleba showing a multiplicity of brownish dots, orbicular or gyrose; asci nesting together; spores 3–4, alveolate.

Named in honor of William M. Pierson, a member of the California Academy of Sciences.

95. **Piersonia alveolata,** gen. et sp. nov.

PLATE XLIV, FIGS. 20*a*–20*e*.

Diameter 1 cm., integument scabrous, color white, turning to sulphur; gleba firm, citrine, cut surface showing a large number of orange-colored dots; asci clavate, 60 x 80 μ, pedicel elongated (70 μ), 3–4-spored; spores alveolate, citrine, 24 μ in diam.

Type, No. 183, Harkness Coll.

Beneath *Ceanothus*, Auburn, Placer County, Calif., May.

96. **Piersonia scabrosa,** sp. nov.

PLATE XLIV, FIGS. 21*a*–21*e*.

Semiglobose, irregular, 2 cm. in diam., color chestnut-brown, surface rough; gleba buff; asci obtusely saccate, pedicellate, 4-spored; spores globose, white, alveolate, 20 μ in diam.

Type, No. 201, Harkness Coll.

In the forest, Auburn, Placer County, Calif., June.

Differing from the preceding in color and in dimensions of the spore.

Delastria *Tul.*

Delastria TUL., Ann. Sci. Nat., Bot., 2d Ser., Tome XIX, p. 379.

Ascomata basi obtusa protuberante instructa, cortice tenuissimo, fibrilloso-byssoideo, passim rimoso aut evanido vestita. Gleba carnosa, humida, mollis, venis candidis anastomosantibus variegata et iisdem in glebulas rotundatas, quasi septis spuriis, divisa. Asci oblongo-reniformes, ampli, 2-4-spori. Sporidia sphærica, reticulato-alveolata, nucleo oleoso donata. (Sacc. Sylloge Fung., Vol. VIII, 1889, p. 904.)

97. **Delastria rosea** *Tul.*

PLATE XLV, FIGS. 27*a*–27*b*.

Delastria rosea TUL., Ann. Sci. Nat., Bot., 2d Ser., Tome XIX, p. 379.

Globosa v. obovata, depressa, vulgo gibberoso-mamillosa, interdumque sulcata et rimosa, fragilis, cortice adpresse byssaceo-tomentoso, subsericeo v. velutino, niveo dein fuscato involuta; gleba ex albido mox amœne rosea, dein rufa, venis candidis, immutabilibus, cum cortice continuis, areolata; ascis inordinatim sparsis, ovoideo-oblongis, sæpius incurvis seu reniformibus, nec in modum pedicelli deorsum angustatis, 2–3-rarius 4-sporis; sporidiis, sphæricis, reticulato-alveolatis, subaculeatis, maturis luteolis, 30–40 μ in diam. (Paoletti in Sacc. Sylloge Fung., Vol. VIII, 1889, p. 905.)

No. 182, Harkness Coll.

Under shrubs amongst vegetable humus, Auburn, Placer County, Calif., May.

This is the only species found of this genus. The characteristic rose-pink tint shown upon the cut surface of the gleba is still to be seen even after months of immersion in alcohol. About fourteen alveoli appear on the circumference.

Choiromyces *Vitt.*

Choiromyces VITT., Monog. Tub., p. 50.

Common integument, even. Base definite. Asci clavate. Sporidia spherical. (Berk. Outlines Brit. Fung., p. 377.)

98. **Choiromyces gangliformis** *Vitt.*

Choiromyces gangliformis Vitt., Monog. Tub., p. 51, Tab. II, Fig. 2.

Globosus, levis, fuscus; gleba albida, exiccatione vix mutata, grumoso-compacta, venis numerosissimis, interruptis, decolorantibus, mirabiliter anastomosantibus et areolas hinc illinc albas filisque minimis concoloribusque varie junctas, gangliformes, inter se relinquentibus; sporidiis sphæricis, verrucis conicis elongatis asperatis. (Paoletti in Sacc. Sylloge Fung., Vol. VIII, 1889, p. 901.)

No. 151, Harkness Coll.

Under *Arctostaphylos*, Calistoga, Napa County, Calif., April.

Terfezia *Tul.*

Terfezia Tul., Fungi Hypo., p. 172, Tab. VI, Fig. 4; Tab. VII, Fig. 5; Tab. XV, Figs. 3–5; et Tab. XXI, Fig. 15.

Integumentum crassum v. tenue, carnosum, clausum continuum v. hinc et illinc parce rimosum, leve, nonnunquam fibrillosum, in cuticulæ sorte qua tegitur primo albidum deinque plus minus et inæqualiter fucatum. Moles interior carnosa solida, scil. lacunis destituta, initio pallida et quasi similaris, matura uvida, molliuscula, in massulas s. glebulas rotundatas, rarius diversiformes, carnoso-humidas v. pulposas, fertiles et varie coloratas divisa, parenchymate sterili interposito laxiori ærifero pallido maculas que irregulares (areolas) s. venarum species in fungo secto fingente. Sporangia late elliptica v. globosa, utriculis genitivis imposita et in glebulis veluti inordinate creberrima nidulantia, octospora. Sporæ sphæricæ initio conglobatæ et leves, maturæ liberæ echinatæ (aliquando insuper reticulatæ) diluteque coloratæ; nucleo tandem oleoso.

99. **Terfezia spinosa,** sp. nov.

Plate XLV, Figs. 24*a*–24*b*.

Terfezia leonis Langlois in Ellis' Centuries, No. 1782.

Globose, white or citron, smooth; gleba variegated; asci subrotund or briefly elongate, 6–8-spored; spores globose, seldom ellipsoidal, 15–20 μ in diam.

Type, No. 108*a*, Harkness Coll.

Red River Valley, Louisiana.

The spores are furnished with large projections (only about twenty being found upon the periphera of each), which are slightly curved, somewhat blunt at the point, and confluent at the base.

As will be observed, there is a marked dissimilarity between this species and *T. leonis*, a specimen of which from the herbarium of Vittadini is in possession of the writer. A spore from this specimen is represented in fig. 25, and agrees in outline with that figured by Tul. in Fungi Hypo., Plate XV, fig, 3.

100. **Terfezia Zeynebiæ,** sp. nov.

PLATE XLV, FIG. 26.

Large, globose, 4 cm. in diam., color white, turning brown; gleba citrine when dried; asci subspherical, 8-spored, 36 x 40 μ (briefly pedicellate); spores with spine-like projections, 15 to 18 μ in diam.

Type, No. 212, Harkness Coll.

The valley of the Tigris, Arabia. This fungus was sent to me some years ago by the American Consul at Bagdad.

Named in honor of Zeyneb of the Arabian Nights.

T. Zeynebiæ is found in clusters in the alluvial soil of the valley and is readily discovered owing to the fact that slight fissures are to be seen in the overlying earth. The fungus is greatly esteemed as an article of food and is sold in large quantities in the markets of Bagdad.

The spine-like projections are short and blunt, generally some little distance apart, about 16 projections appearing on the circumference.

Chatin in La Truffe, page 78, describes two species from Mesopotamia, *T. Hafizi* and *T. Metaxasi*. The first, *T. Hafizi*, is figured by the author (Plate XV, fig. 1) as being rugose and destitute of spines. Paoletti in Saccardo's Sylloge Fungorum, Vol. XI, p. 445, refers to the same as possessing a reticulate spore, 18 x 20 μ.

T. Metaxasi, shown in plate XIII, fig. 2, Ibid., has a much larger spore with a very large increase in the number of its spines.

Terfeziopsis, gen. nov.

Ascomata smooth, globose or pyriform; gleba veinless, firm; asci globose or ellipsoidal, 2-4-spored; spores globose or ovoid, echinate; spines recurved or hooked.

This fungus is nearly allied to *Terfezia*, but is separated from *Terfezia* because of the form of its spore.

101. **Terfeziopsis lignaria,** gen. et sp. nov.

PLATE XLIV, FIGS. 23*a*–23*c*.

Subglobose, irregular, 1.5 cm. in diam., brown, smooth; gleba white; asci globose or ellipsoidal, 35 x 45 μ, briefly stipitate, 4-spored, spores globose or ovoid, echinate, 15 μ in diam.

Type, No. 206, Harkness Coll.

Among oaks in sandy pasture, Auburn, Placer County, Calif., June.

The spore is armed with delicate spines. In each instance the spine being hooked or recurved near the terminus, as is shown in fig. 23*c*. The same figure represents an ascus with spore *in situ*.

Endogone *Link.*

Endogone LINK, Diss. I, p. 33; FRIES, Syst. Myc., Vol. II, p. 295.

Hypogæous. Flocci collected into a globose, spongy mass. Vesicles globose, solitary, or collected in little fascicles at the ends of the branches. (Berk. Outlines Brit. Fung., p. 409.)

102. **Endogone macrocarpa** *Tul.*

Endogone macrocarpa TUL., Fungi Hypo., p. 182, Plate XX, Fig. 1.
Glomus macrocarpus TUL., Giorn. Bot. Ital., Ann. I, Vol. II, part 1, p. 63.
Endogone pisiformis BERK., Ann. & Mag. Nat. Hist., 1st Ser., Tome XVIII, 1846, p. 81.

Subamorpha, sordide grisea lutea auratave; peridio tenuissimo vel obsoleto; sporangiis crassissimis.

No. 99, Harkness Coll.

Under *Libocedrus decurrens*, Towles, Placer County, Sierra Nevada mountains, Calif., at an elevation of nearly 5,000 feet, July.

103. **Endogone microcarpa** *Tul.*

Endogone microcarpa TUL., Fungi. Hypo., p. 182, Plate XX, fig. 2.
Glomus microcarpus TUL., Giorn. Bot. Ital., Ann. I, Vol. II, part 1, p. 63.

Globosa, regularis, candida, intus vero luteola; sporangiis exiguis.

No. 237, Harkness Coll.

In forest, Mill Valley, Marin County, Calif., February.

104. **Endogone lanata,** sp. nov.

Subglobose, 0.7 cm. in diam., color white; gleba flocculent, white; concepticles numerous, wooly; asci brown, globose, 100 μ in diam.

Type, No. 45, Harkness Coll.

In forests in the Sierra Nevada mountains, Placer County, Calif., July.

The so-called ascus is crowded like others with more or less organized protoplasmic material.

105. **Endogone malleola,** sp. nov.

PLATE XLIV, FIGS. *22a–22b*.

Minute, 0.3 cm. in diam., convex surface inferiorly concave, fibers of mycelium extending from the concave surface; gleba white, flocculent; asci 48–70 μ in diam., spherical, attached to an elongated pedicel (6 x 180 μ); spore-like bodies numerous, globose, homogeneous, white, 7 μ in diam.

Type, No. 103, Harkness Coll.

Upon the surface of the ground in dense shade of *Sequoia sempervirens*, Mt. Tamalpais, Marin County, Calif., December.

The pedicel is much more minute than is that in *macrocarpa*.

106. **Sphæria (Hypocrea) Setchellii,** sp. nov.

PLATE XLIII, FIGS. *17a–17c*.

Parasitic, perithecia papillose discoid, minute, membranaceous; ostiolum hidden; spores heterogeneous, fifty or more in each of the perithecia, elliptical, black when mature, non-guttulate, 12 x 14 μ.

Type, No. 181*b*, Harkness Coll.

Parasitic within the parenchyma of *Pseudohydnotria carnea*.

There is a marked dissimilarity between this species and that of *S. Zobelii* Tul., not only in the general outline of the perithecia and its ostiolum but in the size of the spore.

Named in honor of Professor William A. Setchell of the University of California.

107. **Sphæria (Hypocrea) Zobelii** *Tul.*

Sphæria (Hypocrea) Zobelii Tul., Fungi Hypo., p. 186, Tab. XIII, fig. 1.
Microthecium Zobelii Corda, Icon. Fung., T. V., pp. 30 et 74, Tab. VIII, fig. 53.

Fungorum hypogæorum gregatim parasitica, sphærica, brevissime mucronata ore subintegro; perithecio membranaceo tenuissimo; sporangiis oblongis 3–8-sporis; sporis ellipticis et utrinque truncatis, levibus, atris. (Tul. Fungi Hypo.)

No. 255*b*, Harkness Coll.

Found with and upon the parenchyma of *Geopora magnata.*

In this specimen we find that the perithecia is globose or slightly oblong vertically, with a well developed ostiolum.

This parasite was discovered by Corda in *Choiromyces* and referred to a new genus, *Microthecium.* In his review of the work of Corda, Tulasne declines to accept his generic name and places it in the *Sphæriaceæ*, calling it *S. Zobelii.*

Sporophaga, gen. nov.

Parasitic and deeply seated within the ascus and spores of host-plant; a hypogæous fungus.

108. **Sporophaga cyanea,** gen. et sp. nov.

Plate XLIII, Figs. 15*a*–15*g*.

Ustilago cyanea Ces.

Hypogæous, produced within the spore of *Balsamia vulgaris* in groups of from three to six within each spore; the spores of the host-plant, together with the inclosing ascus, soon separate, when the spores of the parasite are seen to be grouped together; spores ovate, dark, 4 x 6 μ.

Type, No. 231, Harkness Coll.

The parasite does not appear until the spores of the host-plant are fully matured. After the disappearance of the spore and ascus the parasitic spores remain in groups of from twenty to forty, being kept in contact by the entanglement of the hyphæ; in due time, however, they separate and are dispersed.

Possibly the oil globules to be seen in the spores of a freshly cut *Balsamia* may for the moment be mistaken for the parasitic spores. It can readily be shown that there exists no connection between the two, as one has but to place the material in a fluid denser than water, and the oil globules will soon disappear from sight.

The affinities of *Sporophaga cyanea* are decidedly obscure and will probably remain so until the earlier stages of the development of its spore are noted. In the interval it may be placed either amongst the *Uredinæ* or the *Ustilagineæ*.

The freshly cut surface of the host-plant shows a decidedly blue tint, due to the presence of the parasite.

Host-plant found at Auburn, Placer County, Calif., April.

INDEX TO GENERA AND SPECIES

OF

CALIFORNIAN HYPOGÆOUS FUNGI.

New genera and species in **full face**, synonyms in *italics*.

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The colored illustrations have been mostly prepared after fresh material, a few after alcoholic preparations. The microscopic drawings have been made from glycerine preparations with the aid of a Zeiss Apochromat, Obj. 2 mm., Aperture 1.40, Compensating Oculars 8 and 12. Projection on working table.

EXPLANATION OF PLATE XLII.

Fig. 1. *Hysterangium Phillipsii*, sp. nov.
(a) Vertical section with fibrillose rootlets. (b) Section of gleba.

Fig. 2. *Hysterangium cinereum*, sp. nov.
(a) Fully developed fungus. (b) Transverse section.

Fig. 3. *Octaviania monticola*, sp. nov.
(a) External view. (b) Transverse section of same. (c) Section of gleba enlarged.

Fig. 4. *Octaviania occidentalis*, sp. nov.
(a) Section of gleba enlarged; Zeiss AA, Oc. 2. (b) Section showing hymenium and pseudobasidia; Zeiss AA, Oc. 6. (c) Pseudobasidia enlarged, showing spores round or ovoid. (d) Free spore.

Fig. 5. *Octaviania socialis*, sp. nov.
(a) Perfect plant. (b) Vertical section. (c) Enlarged spores *in situ*. (d) Basidia, sterigma, and spores.

Fig. 6. *Hymenogaster utriculatus*, sp. nov.
(a) Entire plant. (b) Section of gleba showing cells and hymenium. (c) Enlarged section of hymenium. (d, e) Two spores with utricle. (f) Isolated spore.

Fig. 7. *Leucophleps magnata*, gen. et sp. nov.
(a) Section of hymenium with basidia and spores. (b) Vertical section showing cell-structure. (c) Optical section of spore with spore investment.

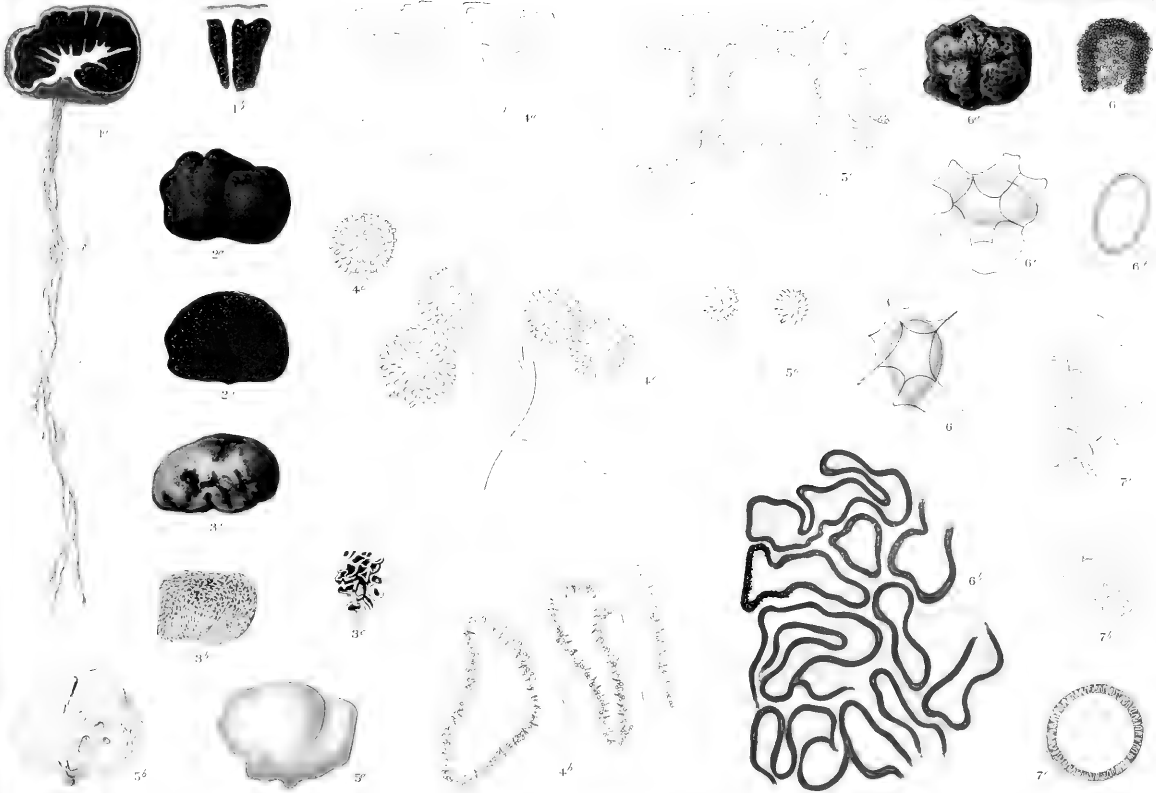

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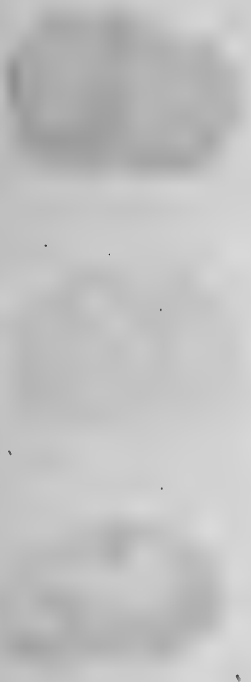
Fig 1 Hysterangium Phillipsii, sp nov Fig. 2. Hysterangium cinereum, sp nov Fig. 3 Octaviania monticola, sp nov Fig 4. Octaviania occidentalis, sp nov
Fig 5 Octaviania socialis, sp. nov. Fig 6 Hymenogaster utriculatus, sp. nov. Fig 7 Leucophleps magnata, gen et sp nov



EXPLANATION OF PLATE XLIII.

Fig. 8. *Leucophleps citrina*, sp. nov.
(a) Section of hymenium with basidia and spores. (b) Basidia isolated, 10 to 12 times the length of the spore (bb); (bbb) oil-globules shown within the basidia.

Fig. 9. *Leucophleps odorata*, sp. nov.
(a) Mature plant. (b) Vertical section showing cell-structure.

Fig. 10. *Genea compacta*, sp. nov.
(a) Section of gleba with asci and paraphyses. (b) Ascus with spores. (c) Isolated spore.

Fig. 11. *Hydnocystis compacta*, sp. nov.
(a) Ascus with spores. (b) Isolated spore. (c) Optical section of spore.

Fig. 12. *Geopora mesenterica*, sp. nov.
(a) Ascus with spores. (b, c) Isolated spores.

Fig. 13. *Balsamia filamentosa*, sp. nov.
(a) Fungus fully developed. (b) Longitudinal section. (c, d) Asci with spores. (e, f) Isolated spores with oil-globules.

Fig. 14. *Balsamia*, sp. ?
Immature fungus showing development of spores.

Fig. 15. *Sporophaga cyanea*, gen. et sp. nov.
(a) Optical section of spore of *Balsamia vulgaris* in the early stage of its development. (b) Section of the same showing the membranous investments of the spore. (c) *Balsamia* spore in a more advanced stage of development. (d) Ascus with spores of the host-plant; some of the spores already ruptured and the parasite set free within the ascus. (e) Group of parasites within a spore of the host. (f) Two parasites with hyphæ within a spore of the host. (g) Isolated parasite showing a double investment of the same, together with its septate hyphæ, the hyphæ having a branched terminus.

Fig. 16. *Pseudohydnotrya carnea*, sp. nov.
(a) Entire fungus, hairs faintly shown. (b) Transverse section.

Fig. 17. *Sphæria Setchellii*, sp. nov.
(a) Fragment of host-plant showing an ascus with spores and paraphyses; cell-wall of the perithecia enclosing parasitic spores. (b) Perithecia in different stages of development, one still destitute of spores; the asci of the host-plant faintly shown. (c) Isolated spore greatly magnified. Spores colored black for convenience, in life as in 17*c*.

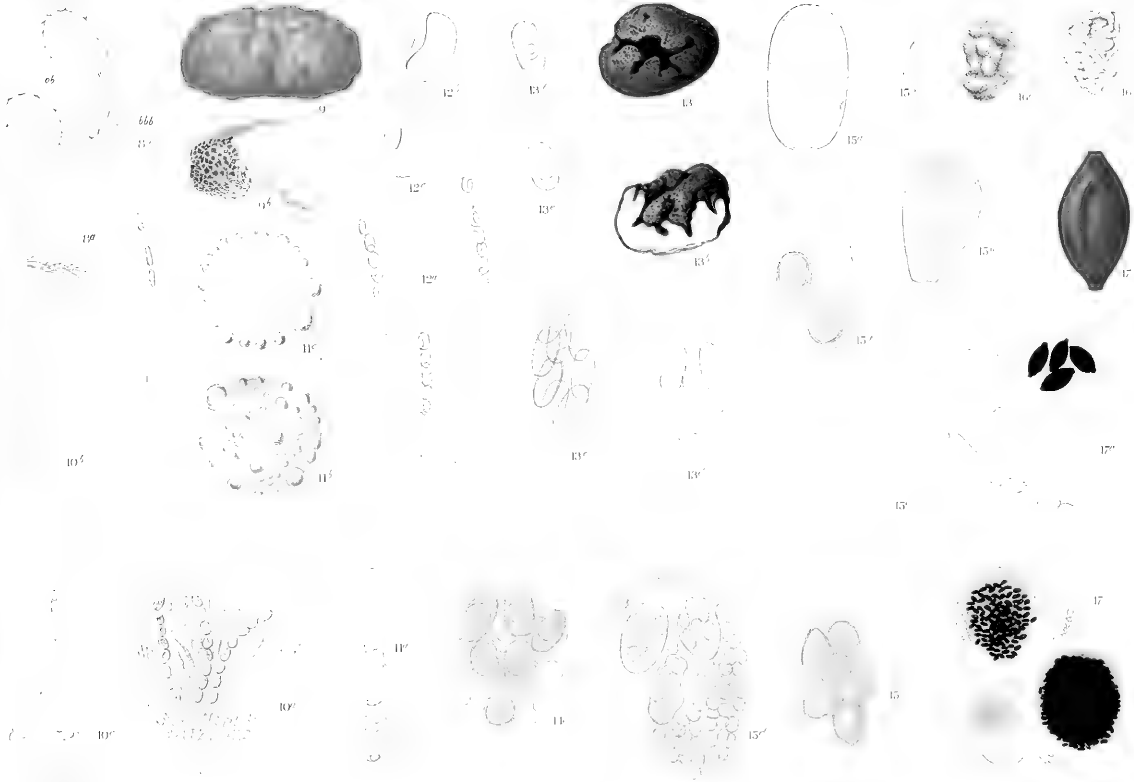


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Fig 8 Leucophleps citrina, sp. nov. Fig 9 Leucophleps odorata, sp. nov. Fig 10 Genea compacta, sp. nov. Fig 11 Hydnocystis compacta, sp. nov.
Fig 12 Geopora mesenterica, sp. nov. Fig 13 Balsamia filamentosa, sp. nov. Fig 14 Balsamia sp.? Fig 15 [illegible]
Fig 16 Pseudohydnotrya carnea, sp. nov. Fig 17 Sphaeria Setchellii, sp. nov.

EXPLANATION OF PLATE XLIV.

Fig. 18. *Stephensia bombycina* TUL.

(a) Fragment of gleba with asci. (b) Isolated spore showing its rugosities. (c) Optical section showing the periphery.

Fig. 19. *Hydnotrya cerebriformis*, sp. nov.

(a) Vertical section of fungus. (b) Enlarged vein-tracing. (c) Asci with paraphyses. (d) Isolated spore showing roughened surface. (e) Optical section of spore. (f) Section of the surface of spore magnified.

Fig. 20. *Piersonia alveolata*, gen. et sp. nov.

(a) Section of gleba showing veins, cell, and asci. (b) Asci (magnified) with spores. (c) Isolated spore. (d) Optical section of spore. (e) Section of spore showing alveolate surface.

Fig. 21. *Piersonia scabrosa*, sp. nov.

(a) Section of plant. (b) Enlarged section of cut surface. (c) Ascus with spores. (d) Optical section of spore. (e) Section of spore surface.

Fig. 22. *Endogone malleola*, sp. nov.

(a) Transverse section of fungus, full size of the mature plant. (b) Conceptacle with contents and fragment of pedicel.

Fig. 23. *Terfeziopsis lignaria*, gen. et sp. nov.

(a) Ascus with spores (spores round or slightly ovoid). (b) Optical section of spore (about 70 to 75 spines in its circumference). (c) Hooked spines on surface of spore.

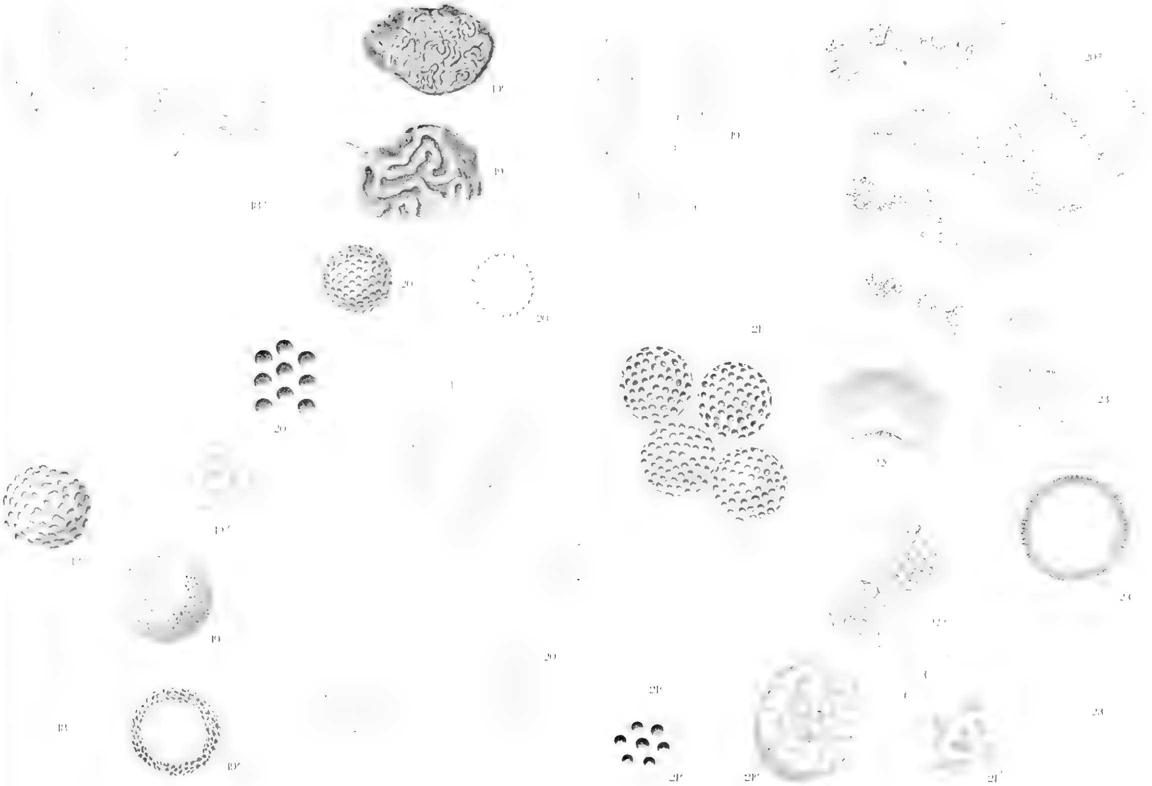

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FIG 18 STEPHENSIA BOMBYCINA TUL. FIG 19 HYDNOTRYA CEREBRIFORMIS, SP NOV FIG 20 PIERSONIA ALVEOLATA GEN ET SP NOV FIG 21 PIERSONIA SCABROSA, SP NOV
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EXPLANATION OF PLATE XLV.

Fig. 24. *Terfezia spinosa*, sp. nov.
(a) Isolated spore. (b) Spine on surface of spore.

Fig. 25. *Terfezia leonis* Tul.
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Fig. 26. *Terfezia Zeynebiæ*, sp. nov.
Isolated spore.

Fig. 27. *Delastria rosea* Tul.
(a) Section of gleba with ascus and spores. (b) Isolated spore.

Fig. 28. *Myrmecocystis cerebriformis*, gen. et sp. nov.
(a) Fully developed fungus. (b) Vertical section. (c) Detail of surface of fungus. (d) Ascus with spores. (e) Detail of surface of spore.

Fig. 29. *Myrmecocystis candida*, sp. nov.
(a) Section of gleba. (b) Asci with spores. (c) Isolated spore showing a rough surface. (d) Optical section of spore. (e) Detail of sculptured surface of spore. Asci in *c* and *d* improperly outlined, should appear as in *b*.

Fig. 30. *Tuber (Eutuber) citrinum*, sp. nov.
(a) Section of gleba with ascus and spores. (b, c) Isolated spores.

Fig. 31. *Tuber (Sphærotuber) Californicum*, sp. nov.
(a) Section of gleba with asci and spores. (b) Isolated spore.

Fig. 32. *Tuber (Sphærogaster) candidum*, sp. nov.
(a) Ascus with spores. (b) Isolated spore.

Fig. 33. *Pachyphlœus carneus*, sp. nov.
(a) Ascus with irregularly serrate spores. (b) Isolated spore.

Fig 34. *Geopora magnata*, sp. nov.
(a) Fully developed fungus. (b) Section of fungus. (c) Enlarged section of gleba. (d) Enlarged section of hymenium.

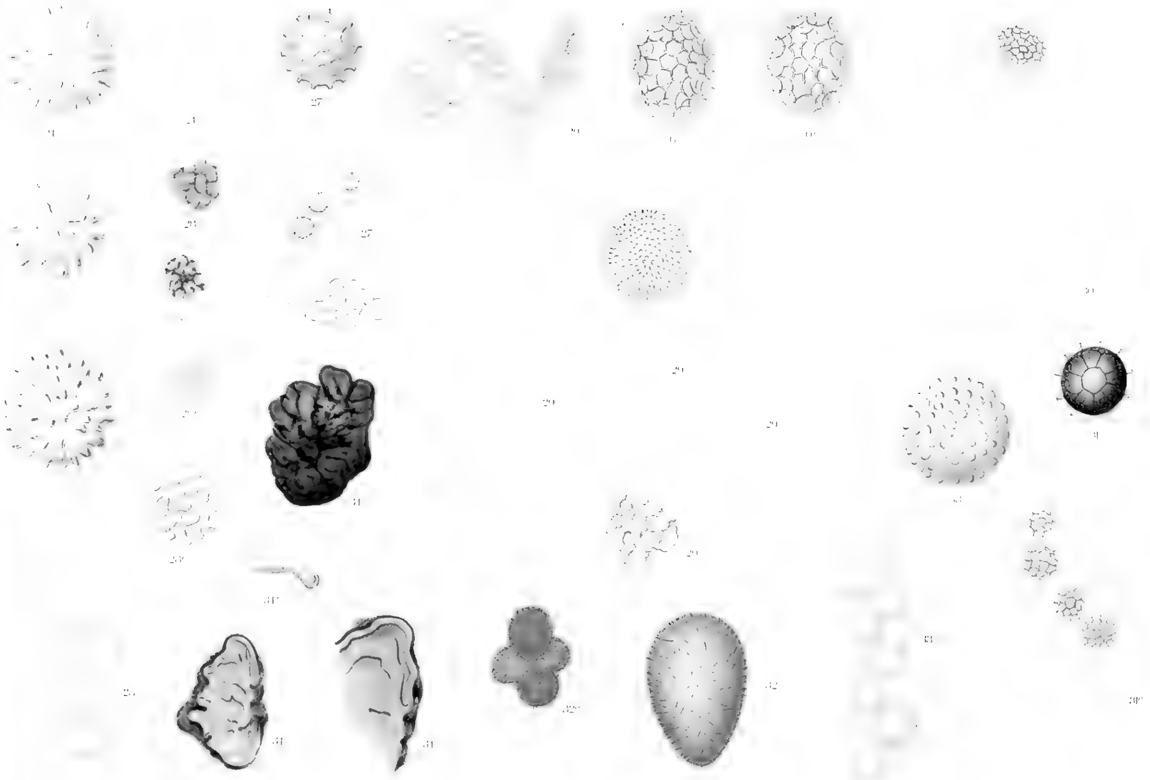

FIG 24 TERFEZIA SPINOSA, SP. NOV. FIG 25 TERFEZIA LEONIS TUL. FIG 26 TERFEZIA ZEYNEBIÆ, SP. NOV. FIG 27 DELASTRIA ROSEA TUL.
FIG 28 MYRMECOCYSTIS CEREBRIFORMIS, GEN. ET SP. NOV. FIG 29 MYRMECOCYSTIS CANDIDA, SP. NOV. FIG 30 TUBER CITRINUM, SP. NOV. FIG 31 TUBER CALIFORNICUM, SP. NOV.
FIG 32 TUBER CANDIDUM, SP. NOV. FIG 33 PACHYPHLŒUS CARNEUS, SP. NOV. FIG 34 GEOPORA MAGNATA, SP. NOV.

STUDIES ON THE FLOWER AND EMBRYO OF SPARGANIUM.

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CONTENTS.

PLATES XLVI–XLVIII.

THE genus *Sparganium* Tourn. includes about a dozen species distributed over the northern hemisphere, but also represented in New Zealand and Australia. The genus is a peculiar one, and there has been much diversity of opinion as to its affinities with other Monocotyledons. It has usually been associated with *Typha* in the family Typhaceæ, but the present view (Engler and Prantl, 1889) is that it should be considered the type of a separate family, Sparganiaceæ, with the Pandanaceæ or Screw-pines as its nearest allies.

The genus has not been extensively studied, but our knowledge of the development of the flower and embryo of the European *S. ramosum* is fairly complete (Hegelmaier, 1874; Dietz, 1887). The other species have, so far as I know, been treated from the standpoints of the descriptive botanist only, and no account of the embryo-sac has

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yet been published. Some years since I collected a small amount of material of the flowers of the common eastern species, *E. eurycarpum* Englm., and an examination of this material revealed several puzzling peculiarities of the embryo-sac, which were not clearly understood at the time. Figures of a few of these were published two years ago (Campbell, 1897), but lack of proper material, as well as other work, prevented any further study at the time. During the summer of 1896 a trip to Japan enabled me to procure a few specimens of the Japanese *S. longifolium* Turcz., and during the past season a good supply of *S. simplex* Huds. was collected in August at Tallac on Lake Tahoe. This species proved very satisfactory for study, and was made the principal subject of my investigations. In September, through the kindness of Miss Eastwood, a quantity of *S. Greenii* Morong. collected at Lake Merced, near San Francisco, was sent me, and served to supplement the work done on *S. simplex*. My material of the latter species was much more complete than that of any of the others, and moreover it proved easier to handle. The results obtained from a study of this species have been compared, so far as was possible, with those from the other species mentioned.

A preliminary statement in regard to *S. simplex* has already been published in a recent number of the "Botanical Gazette" (Campbell, 1899); but this refers simply to certain of the most striking points concerning the embryo-sac, and no account of the embryo is included.

Unfortunately all of the material collected was too old to show the earlier stages of development of the flower, so that the early history of the pollen and embryo-sac could not be traced. In the youngest flowers examined, the structures of the embryo-sac were already complete, and in most cases the embryo-sac was ready for fertilization. Hence in the present paper the study of the flower begins at the time when it is ready for pollination.

In the preparations of the material, various reagents were employed in fixing it: one-half to one per cent. chromic acid, saturated alcoholic solution of picric acid, saturated alcoholic corrosive sublimate, and weak Flemming's solution were employed, but of these the corrosive sublimate, on the whole, proved most satisfactory. The material was imbedded in paraffin and the sections were stained, usually with a double stain of Bismarck-brown and safranine, although in some cases they were stained *in toto* with alum-cochineal before they were imbedded.

I. THE FLOWER.

All of the species of *Sparganium* are monœcious, both staminate and pistillate flowers being aggregated in dense heads which are either sessile or borne on short pedicels. The lower heads are always pistillate and the upper ones staminate. The latter are usually much more numerous. In *S. simplex* and its allies the main axis is unbranched, while in the other species, e. g., *S. eurycarpum* and *S. Greenii*, the stem is branched.

Both sorts of flowers are exceedingly simple in structure. The individual flowers are borne in the axils of small bracts, and are themselves surrounded by a varying number of small membranous leaves which are usually considered to represent a very simple perianth. The male flower is composed of three or more stamens, while the female flower has either a single carpel, as in *S. simplex*, or a compound pistil composed of two completely united carpels, as in *S. ramosum* or *S. Greenii.*

The development of the flower has been studied to some extent in *S. ramosum* (Dietz, 1887), and is briefly as follows: Upon the primary axis are borne elevations which, in the lower part of the axis, where they are produced in axils of leaves, may develop into secondary axes, but in the upper portions of the axis, form at once the young inflorescences. In *S. simplex* and its allies, this axis does not branch, and all of the lateral axes develop into heads of flowers.

In *S. simplex* the lower three or four of these heads develop the pistillate flowers, while the number of staminate heads is usually larger.

The individual flowers, according to Dietz (l. c.), arise as small prominences upon the hemispherical fundament of the inflorescence, and upon these prominences arise secondary outgrowths which develop respectively into stamens or carpels. Dietz does not describe in detail the development of the stamen, and unfortunately my own material was too old to show this, so that it is not now possible to make a comparison with such Monocotyledons as have been investigated.

The scales of the perianth arise early, but Dietz does not describe their development.

To judge from his somewhat brief account and very diagrammatic figures, the development of the carpel and ovule is much like that of the low types like *Zannichellia* and *Lilæa*, which *Sparganium* resembles in these respects more than it does *Typha*, with which it has usually been associated. While further investigations are required before this can be decided, it looks as if in *Sparganium*, also, as in other low Monocotyledons, that the solitary ovule is of axial origin and not a product of the carpel.

The pistillate flower in *S. simplex* (fig. 1) consists of a single carpel surrounded by about six delicate membranaceous scales which form the perianth. Engler (Engler and Prantl, 1889) figures these in this species as having entire margins, but the form studied by me had the end of the narrowly spatulate scale sharply toothed (fig. 2), and the most recent figure (Britton and Brown, 1896) of this species shows the same thing, but with fewer teeth than my specimens. A delicate midrib traverses each scale. The ovary in this species merges gradually into the slender style which terminates in the narrowly sagittate stigma which is covered with minute papillæ.

In *S. longifolium*, which in many respects resembles *S. simplex*, the style and stigma are both shorter. In a second group represented by *S. Greenii* and *S. eurycarpum* the pistil is composed of two completely united carpels, and the resulting fruit is two-seeded. In both of these the style is very short or quite absent and the two stigmas are very long (fig. 4). The base of the ovary is also less tapering than in *S. simplex* and the perianth scales are heavier and nearly or quite entire at the apex.

S. simplex, which was the species principally studied by me, is a wide-spread form occurring throughout the northern hemisphere. In California it is confined to the higher mountains, the specimens collected by me being found near Lake Tahoe which has an elevation of over 6,000 feet above sea-level.

The Staminate Flower.

In *S. simplex* the staminate flowers form dense heads, each flower consisting of about six stamens. Just before the dehiscence of the anthers, the filaments elongate very much, so that the head becomes much looser, and the pollen is readily dislodged by the swaying of the slender filaments, much as in the grasses and sedges. The anther has four loculi as in most Angiosperms and offers no specially noteworthy peculiarities. The other species seem to agree closely in the structure of the stamen and were not critically examined.

The pollen-spores of *S. simplex* are small globular cells (fig. 6) and at maturity show the usual division of the nucleus into a larger vegetative one, and a smaller generative nucleus, but the latter was not seen to divide again while the pollen remained within the anther. Probably the final division of the generative nucleus takes place within the pollen-tube. Perhaps owing to its small size it was not possible to demonstrate the presence of a definite generative cell, the nucleus apparently lying free in the cytoplasm of the pollen-spore. As the cytoplasm of the ripe spore is very dense and stains strongly, it was not always easy, even in sections, to clearly distinguish the nuclei. The outer spore-membrane is marked with fine granulations but is not very thick. In this species there was almost always present in the ripe spore a structure which closely resembles the small vegetative prothallial cell in the germinating microspores of such heterosporous Pteridophytes as *Isoetes* and *Selaginella*. Chamberlain (1895) speaks of such a prothallial cell as an occasional occurrence in *Lilium Philadelphicum*, but except for this reference I am not aware of any reference to such a structure in the angiospermous pollen-spore. This prothallial cell, if such it is, in *Sparganium simplex* is lenticular in form (fig. 6), and separated from the body of the spore by a very well defined membrane which stains strongly with Bismarck-brown. While it was not possible to demonstrate positively the presence of a nucleus in this cell, there was usually to be seen a central body which stained more deeply than the rest of the cell with the usual nuclei stains and had much the aspect of a partially disorganized nucleus. While it seems very likely that this really represents a prothallial cell, homologous with the similar one in the microspores of *Isoetes*, for instance, its real nature cannot be positively assumed until its history has been followed.

The stamens of *S. Greenii* closely resemble those of *S. simplex*, but the pollen-grains did not show any trace of the prothallial cell, and the epispore is marked with fine reticulations. At one point (fig. 7) these were absent, and the clear area probably marks the point at which the pollen-tube emerges.

The Pistillate Flower.

The pistil may be composed of a single carpel, as in *S. simplex* and *S. longifolium*, or of two completely united ones, as in *S. Greenii* and *S. eurycarpum*. In *S. simplex* (fig. 3) a longitudinal section of the ovary shows the single anatropous ovule pendent from the upper part of the ovarian cavity. The narrow canal traversing the style opens into the ovary close to the base of the funiculus of the ovule.

The funiculus is rather slender and has a single axial vascular bundle. The nucellus is oval and there are two integuments usually found in the ovules of Monocotyledons.

The outer integument extends above the inner one and its upper margins are somewhat enlarged, so that the micropyle is quite closed.

II. THE EMBRYO-SAC.

The youngest embryo-sacs met with had the egg-apparatus and antipodal cells developed, and nothing can be stated as to their early history. As the ovule at the time of fertilization is of the ordinary type, it is not probable that there are any marked deviations from the type in its early development.

In *S. simplex* (figs. 3, 8) the mature embryo-sac is broadly oval in outline and is covered at the apex by about two layers of nucellar cells, the central ones somewhat elongated, so that the apex of the nucellus is slightly pointed. At the sides there are about four layers of cells in the nucellus, and these remain permanently and are not destroyed by the developing embryo-sac as so often happens. Within the embryo-sac the granular cytoplasm is principally confined to a thin parietal layer, except that surrounding the primary endosperm-nucleus there is a considerable amount of granular cytoplasm.

In *S. Greenii* (fig. 5) the two carpels are completely united. A section of the ovary shows a long central placenta formed by the coherent inner faces of the carpels, and from the upper part of the placenta depend the two ovules. These correspond in structure with those of *S. simplex* but are somewhat longer and more slender, although they are less constant in form than in that species. The embryo-sac is longer and narrower and more pointed at the ends. The part of the nucellus above the apex of the embryo-sac is thicker, there being usually about four layers of cells at this point.

Sparganium longifolium is much like *S. simplex* in the form of the pistil, except for the shorter style and small stigma. The ovule is of about the same size and shape, and the embryo-sac, so far as could be judged from the small amount of material available, closely resembles that of *S. simplex*, and as in that species there are but two, or at most three, layers of cells at the apex of the nucellus.

The common eastern *S. eurycarpum*, while resembling more nearly *S. Greenii*, differs from it in some details. The ovary is broader, due to an enlargement of the outer cells, and there are numerous enlarged cells present which contain bundles of rhaphides, or needle-shaped crystals, presumably of calcium oxalate. These spicular cells also occur in the placenta, and while not entirely absent from the ovary of *S. Greenii* are much less abundant. There are also found on the upper surface of the placenta papillate cells which are much less marked in *S. Greenii*. These are doubtless connected with the conduction of the pollen-tubes. The structure of the ovule itself, and the embryo-sac are much alike in the two species.

In all the species examined the cells of the nucellus persist, and the subsequent enlargement of the upper part of the integuments and the apex of the nucellus gives rise to the peculiar cap ("Samen-deckel" of Hegelmaier) which characterizes the ripe seed of all species of *Sparganium*.

The broadly oval embryo-sac of *S. simplex* is scarcely at all narrowed at either end. In all specimens examined the two polar nuclei had already completely fused, and it is evident that the fusion of them to form the primary endosperm-nucleus occurs some time before the fertilization of the egg-cell. The large endosperm-nucleus (fig. 10) is imbedded in a considerable mass of granular cytoplasm which is elsewhere confined to the thin parietal layer. The position of the endosperm-nucleus is not constant, and it was found in nearly all positions in the sac; sometimes it lay close to the egg-apparatus, sometimes it was near the antipodal cells.

The egg-apparatus is of the normal structure, and compared to the size of the embryo-sac is small. A good deal of variation in the size of the egg and synergidæ was noted, and these differences did not appear to be necessarily connected with the age of the egg-apparatus. The egg-cell was sometimes in the same plane as the synergidæ (fig. 8), and sometimes it was lower down and a good deal elongated (fig. 11). In either case it was nearly hyaline, with only a relatively small amount of granular contents surrounding the nucleus which is usually placed near the free end of the ovum, i. e., the end which projects into the embryo-sac (figs. 8, 11). The synergidæ are alike, somewhat smaller than the egg and filled with densely granular cytoplasm in which lies the small nucleus. All the nuclei of the egg-apparatus have a very distinct nucleolus which is especially conspicuous in material stained with anilin-safranine. The rest of the nucleus, however, does not stain strongly with this reagent, the nuclei preliminary to fertilization appear to have very little chromatin. The nucleus of the egg is somewhat larger than the synergidal nuclei but otherwise closely resembles them.

Above the synergidæ there was seen in many specimens what looked like the remains of the tapetal cells (fig. 8). This mass stained strongly with Bismarck-brown but showed little structure and probably represented the disorganized remnants of one or more tapetal cells. As the younger stages were lacking in my preparations the origin of this body can only be conjectured.

In none of the specimens of *S. simplex* were the separate polar nuclei observed. The large endosperm-nucleus resulting from their fusion is, however, conspicuous. It is much larger than the other nuclei of the embryo-sac, and has a very large nucleolus (figs. 10, 11).

The antipodal end of the sac in this species is almost flat, although there may be a slight depression where the antipodal cells are found. The early history of the latter could not be followed, as the material was all too old; but at the time the egg is mature, these cells are remarkable for their very small size, which is in striking contrast to their later development. Not infrequently where these cells had collapsed in the process of embedding, they could not certainly be distinguished, and may very easily be overlooked. There was nothing, however, to indicate that they are ever really absent. Where they are uninjured (fig. 12) they may usually be seen to be arranged in the same plane and are very shallow, projecting only very slightly into the cavity of the embryo-sac. The cytoplasm of these cells is finely granular but does not readily stain at this stage. The nuclei are very small and inconspicuous, and it is sometimes difficult to demonstrate them at all. In no case did they stain readily with the usual reagents.

In *S. Greenii* the appearance of the antipodal cells is somewhat different and this resembles more those of other Monocotyledons (fig. 21). The base of the embryo-sac is here prolonged into a narrow cavity within which lie the antipodal cells. These are not usually in the same plane, but one of them lies above the other two, to which it bears much the same relation that the egg-cell does to the synergidæ. The antipodal cells in this species are much larger than in *S. simplex*, and the cell contents denser, and the nuclei are larger and readily demonstrated, as they stain without difficulty.

So far as my observations go upon *S. longifolium* and *S. eurycarpum*, they are more like *S. Greenii* than *S. simplex* in the form of the antipodals, although *S. longifolium* is to some extent intermediate in character.

III. FERTILIZATION.

The small size of the pollen-spore and nuclei is not favorable to a study of the details of fertilization, and although in several instances the pollen-tube was detected within the embryo-sac, nothing was observed which indicated that the fertilization was in any way different from that of other Angiosperms. The pollen-tube after reaching the micropyle pushes down between the cells of the nucellus, which are not injured by its passage. On entering the embryo-sac, it apparently comes into close contact with one synergid, which is probably destroyed in most cases, although this is not necessarily the case, as in one instance, at least, the end of the pollen-tube was seen within the embryo-sac, although both synergidæ were still intact. The very small size of the generative nucleus makes it extremely difficult to detect, and only a few incomplete observations were made on its behavior after entering the sac. In one case (fig. 9) a small, deeply stained body was observed within one of the synergidæ, and this very probably was one of the generative nuclei on its way to the egg-cell. In another instance (fig. 13) there was visible within the egg a small body looking like a nucleus, but not staining as deeply as might have been expected of the male pronucleus. In the same preparation (fig. 14) there was a small granular mass attached to the end of the pollen-tube, and looking as if it might have been discharged from it into the cavity of the embryo-sac, but there was nothing to indicate the discharge of the second generative nucleus and its fusion with the endosperm-nucleus as described by Nawaschin; however, my observations were too incomplete to warrant any positive statement on this point. One of the synergidæ can usually be detected for a long time after fertilization has been effected, as has been observed in so many other cases.

After fertilization has been effected the egg-cell enlarges very little, and after the membrane is developed about it, it remains unchanged for a long time. At this time the unicellular embryo (fig. 24) is a more or less pear-shaped cell, sometimes in contact with the upper wall of the embryo-sac merely by a very small part of the pointed lower end, sometimes having a much broader base of attachment. In this condition it remains until the sac has increased a good deal in size and the development of the endosperm is well advanced. Owing to this slow development of the embryo the earlier stages between the unicellular condition and that shown in fig. 37 were missed.

IV. The Secondary Growth of the Antipodal Cells.

While the embryo-cell remains unchanged for a long time, the other structures of the embryo-sac undergo marked changes. Almost the first visible result of fertilization is a marked increase in the size of the antipodal cells. In

S. simplex where this was especially studied, and of which a preliminary account has already been published (Campbell, 1899), this is especially noteworthy. Before fertilization (fig. 12) the antipodal cells are extremely inconspicuous, but almost immediately after fertilization has been effected they rapidly increase in bulk, and at the same time show other marked evidences of active growth. The cytoplasm becomes more coarsely and densely granular, and the nuclei enlarge to several times their original size and at the same time take up stains much more readily than before (fig. 26). As the antipodals increase in size they project strongly into the cavity of the embryo-sac and form a conspicuous nearly hemispherical body. The three original cells now rapidly divide until finally a very large mass of cells (fig. 30) results, probably larger than in any other Monocotyledon. The number of antipodal cells may finally exceed 150, a number greater than that yet recorded for any other Angiosperm.

In position and general appearance the group of antipodal cells most nearly recalls that of many Gramineæ (Hofmeister, 1861; Fischer, 1880, etc.). An important difference is that in the latter the development of the antipodal complex is completed previous to the fertilization of the egg. The method of its development, however, is very similar in the two cases.

The embryo-sac in those grasses which have numerous antipodal cells has at first the ordinary number, three, and these subsequently divide to form the larger number ultimately developed. Hofmeister (1861) states that in the Triticeæ the number may be 6–12 and Körnicke (1896) found 36 or more, a large number, but very much less than the normal number finally developed in *Sparganium simplex*.

The first division of the nuclei of the antipodal cells occurs shortly after the first division of the primary endosperm-nucleus. Following the first division, the increase in size of the antipodal cells and the divisions proceed rapidly, while the endosperm at this stage remains slightly developed. There seems little question, that as Westermaier (1890) pointed out in the grasses, these enlarged antipodal cells replace physiologically for the time being the endosperm, and elaborate food materials for the growth of the developing embryo-sac and embryo.

The first divisions in both endosperm and antipodal cells take place before there has been any marked increase in the size of the embryo-sac; but later there is a rapid increase in the size of the ovule, which probably coincides with the first divisions in the embryo.

Körnicke (1896) in his studies on the antipodal cells of various Gramineæ was unable to detect any karyokinetic figures in these and was inclined to think that the divisions of the nuclei might be direct. This view appeared to be hardly likely, as the nuclei in the developing antipodal cell of *Sparganium* appeared entirely normal, and the cells were actively growing and dividing, not a condition in which one would look for direct nuclear division. Fortunately a preparation was finally secured in which some of the antipodal nuclei were actually in process of division (fig. 29), and it was seen that the division is the typical karyokinesis, which it is safe to say is the normal type of nuclear division, at least in the early stages. In the case under consideration the endosperm-nuclei were also dividing.

In most cases, possibly always, the first division of the nucleus in the antipodal cells in *S. simplex* is not accompanied by the formation of a division-wall, and the enlarged antipodal cells show plainly two conspicuous nuclei (fig. 29). Later, however, all the nuclei become separated by walls and each of the very numerous antipodal cells has evidently but a single nucleus (fig. 30). In some older ones, however, two nuclei were sometimes seen, so that it would seem that the last nuclear division, like the first one, may be independent of cell division. There is thus a certain analogy with the behavior of the normal endosperm-cells which would indicate that the antipodal cells are not markedly different in nature from the endosperm-cells, and may be really homologous with these.

The densely granular cytoplasm of the antipodal cells does not fill them uniformly, but there are usually present large vacuoles (fig. 28). The first division-walls in the antipodals of *S. simplex* are vertical, so that the mass has the form of a disc, but later transverse and oblique divisions may also occur, although the majority of the walls are vertical and the cells become a good deal elongated (fig. 30).

As the seed grows older the antipodal cells begin to show signs of disintegration, but in no cases where sections were made had they entirely disappeared, and traces of them probably persist even in the ripe seed.

The earlier stages of the antipodals were studied also in *S. Greenii* and *S. eurycarpum*, but material was not available for the later development which is probably not entirely like that in *S. simplex*. In *S. Greenii* the antipodals at the time the egg is fertilized are, as we have seen, much more conspicuous than in *S. simplex*. They are also differently arranged, not usually lying in the same plane, but one of them being above the other two (fig. 33). In one instance (fig. 16) there was present above the three antipodal cells a large cell which looked like a fourth antipodal, but as this was the only case seen, there was no clue as to its origin. Otherwise the embryo-sac appeared to be entirely normal. In this species *(S. Greenii)* the polar nuclei remained separate, although often in close contact (fig. 20) until after the fertilization of the egg, and in this respect it differs from *S. simplex* and probably from *S. eurycarpum*. There is also much greater variation in the size of the embryo-sac in *S. Greenii* than in *S. simplex*. As a rule the egg and synergidæ are larger also than in *S. simplex* and sometimes the former show a reticulate appearance in the cytoplasm, due to the presence of numerous vacuoles (fig. 18), an appearance which was not seen in the specimens of the latter species. The embryo-sac in *S. Greenii* is relatively narrower than in *S. simplex*, and there are three or four layers of cells at the apex of the nucellus, which is also larger than in that species. As we have already stated, the antipodal cells, before the fertilization of the egg, are noticeably larger than in *S. simplex*, and two are placed below the third one, and lie in the depression at the base of the embryo-sac. This is much narrowed, and may account for the fact that sometimes these two lower antipodal cells take no part in the formation of the group of antipodals formed after fertilization (fig. 36). In such cases they remain for a long time quite unchanged, and ultimately show signs of disorganization. The upper of the three original cells, however, enlarges greatly and assumes a vesicular form, projecting strongly into the cavity of the embryo-sac. The nucleus of this cell, as in the older antipodal cells of *S. simplex*, enlarges very much, soon undergoes division, and this is quickly repeated, so that four cells, arranged quadrant-wise, result. Where this was the case division-walls could be seen between the nuclei. Sometimes, however, the lower antipodal cells also enlarge (fig. 35) and the development proceeds much as in *S. simplex*, except for the relative positions of the cells. How far the antipodal cells may finally develop in *S. Greenii* could not be ascertained, as the next stages were absent from my material. So far as could be judged from the few stages examined, the cells show a tendency to become more inflated than in *S. simplex* and the granular contents are less abundant, but these peculiarities, which seem also to characterize *S. eurycarpum*, may not be constant, and a study of the later stages in these species will be necessary before the question can be definitely decided.

V. THE EMBRYO.

The development of the embryo does not, at first, keep pace with the development of the antipodal cells and endosperm, and for some time it remains without any apparent change in appearance. Although a large number of sections were made, it was impossible to find stages between the unicellular embryo and such advanced stages as that shown in fig. 37. It is therefore impossible at present to compare the first divisions in the embryo of *S. simplex* with the corresponding stages of that in *S. ramosum*, the only species hitherto examined. As the later stages agree quite closely in the two species, it is not likely that there are any very marked differences in the early stages. Nevertheless, it is much to be regretted that these early stages could not have been compared, and it is to be hoped that these may be examined soon in our American species.

According to Hegelmaier (1874) the embryo cell in *S. ramosum* divides into three superimposed cells, but it is not clear whether the second division is in the upper or lower of the two primary cells. Before any longitudinal divisions are formed there may be one or two more transverse divisions, making thus a single row of four or five primary segments in the embryo. A very similar account is given by Nörner (1881) for the young embryo of several grasses, except that he criticizes Hegelmaier's statement as to the time of the fourth and fifth transverse walls, claiming that these are probably not formed until after the first longitudinal divisions. He concludes that three is the regular number of the primary segments in most Monocotyledons. The more recent investigations in the embryo of the lower Monocotyledons (Schaffner, 1896; Chamberlain, 1895; Campbell, 1897, 1898, etc.) indicate that the basal cell, where this becomes enlarged, does not divide further, and that all the further transverse segmentation is in the terminal cells, but it is probable that in *Sparganium* the segments are the product of the division of the original basal cell.

So far as could be judged from an examination of the somewhat advanced embryo of *S. simplex* (figs. 37, 38, 39), it looked as if the first longitudinal divisions in the terminal segment occurred earlier than Hegelmaier gives for *S. ramosum*, and it is doubtful whether here there are more than three primary segments. A comparison of these stages with Hegelmaier's figures 5 and 13 indicated that possibly his segment 2 really belongs to the terminal segment.

The basal segment never becomes enlarged as it does in so many Monocotyledons, but remains usually very small and generally divides early by longitudinal walls into three or four cells, but sometimes a cross-section shows but two cells. The absence of the large vesicular suspensor cell found in *Naias*, *Alisma* and other Monocotyledons is largely a physiological phenomenon, doubtless connected with the nutrition of the developing embryo, and is intimately associated with the degree of development of the endosperm. Hegelmaier (1874) found that in *S. ramosum* the terminal segment gave origin to all the structures of the embryo except a portion of the root-apex. As he worked entirely with embryos which were simply rendered transparent, but not actually sectioned, he was unable to make out successfully all the details of the arrangement of the tissues in the older embryos. Nevertheless, his results, on the whole, were remarkable accurate, and show a close correspondence to my own preparations of *S. simplex* which were obtained from actual sections. He found that the cotyledon and stem-apex are both products of the terminal segment, and that the plerome of the root is also derived from this segment, and terminates at the wall separating segments I and II.

My own studies of the embryo were necessarily confined almost exclusively to *S. simplex*, as the material collected of the other species did not contain the proper stages of the young seed. The youngest embryos obtained are shown in figs. 37–40. While these agree in general with Hegelmaier's figures of similar stages in *S. ramosum*, there are certain differences which may be noted. The basal, or primary transverse wall (x) which corresponds probably to his wall (i), is regularly lower down than his figures, indicating that the terminal cell of the young embryo is from the first larger than in *S. ramosum*. It is possible that his segment II may be included in the portion above the basal wall, but this is not probable, as evidences of median vertical walls extending from the apex of the embryo to the basal wall can generally be made out, and from a study of the older stages it is evident that the plerome of the root extends quite to the basal wall, as Hegelmaier describes for *S. ramosum*. The hypobasal portion of the embryo narrows rapidly, and this portion shows ordinarily but two transverse segments, instead of the three or four found in *S. ramosum.* The small basal segment, which is in contact with the apex of the embryo-sac, varies a good deal in size, this being correlated with the form of the original embryo-cell. If this tapers much, so as to have a small point of attachment, the basal segment remains very small and pointed (fig. 42), but if the embryo-cell is flattened where it is in contact with the wall of the embryo-sac, the basal segment of the embryo is correspondingly broader and shows more divisions.

A median section of such an embryo shows the limits of the three primary segments still visible (fig. 38). This terminal segment is very much larger than the others, and, as already stated, relatively larger than in *S. ramosum.* The first divisions in all the segments are median vertical ones, and it is clear from studies of transverse sections that there are normally intersecting median walls which divide each segment into four equal quadrants. The divisions are less constant in the basal segment, especially when it is small, and transverse sections of this often show only two or three cells, one or both of the second median walls being suppressed. The next divisions are usually vertical also, but there is evidently no absolute rule as to their arrangement. In fig. 40 is shown a series of cross-sections of a young embryo, and it is clear that the divisions are not always entirely alike in the different quadrants of the same section (see fig. 44, *b*). Probably, in most cases, the first division-wall formed in the quadrant is curved, and extends from the quadrant-wall to the periphery. This is then followed by a series of periclinals which cut off the epidermis. Sometimes, however, it looks as if the first walls were periclinals, thus determining at once the separation of the epidermal layer. Hegelmaier shows much the same variation in *S. ramosum* (e. g. his figures 6 and 8).

The variations in the basal segment have already been referred to. It may divide into equal quadrants (fig. 44, *a*), but more commonly there is a suppression of one or both of the second quadrant walls. Where the basal segment is unusually large, transverse or oblique divisions may also occur (fig. 39). A transverse section of the second segment at this stage shows eight peripheral cells surrounding four central ones.

In the upper segment, the next divisions are transverse, and sometimes this gives the appearance of a complete transverse division across, and it is possible that the segment numbered II by Hegelmaier may in some of his figures really refer to a secondary transverse division in the terminal segment. The separation of the epidermis is brought about as in the second segment, and soon after another series of similar divisions separates the central group of plerome cells from the periblem. The plerome extends to the basal wall where it ends abruptly, not being found at all in the two lower segments. In cross-section (fig. 44, *c*) the young plerome shows four cells, one belonging to each quadrant, but there are soon found other longitudinal walls which increase the number of plerome cells.

The older embryo is not perfectly cylindrical in form, but is somewhat broader in the plane of the future cotyledon. Sections made in this direction have the upper segment nearly circular in outline, but the median wall is often somewhat oblique, so that the segment is not always perfectly symmetrical. In this view the small basal segment usually shows a vertical division into two nearly equal cells. In the cotyledon, which constitutes the major part of the terminal segment, the epidermis is already clearly differentiated, but this is not always so evident in the second segment, where the interlayer of cells usually undergoes another periclinal division, which is never the case, so far as I could determine, in the epidermis of the cotyledon. If the section is made at right angles to the face of the cotyledon (fig. 42) the embryo appears more pear-shaped in outline, and the basal segment may appear undivided. Cross-sections of similar embryos show that in such cases the basal segment is composed of but two or three cells. In a number of instances the second transverse wall was very oblique (fig. 42) and might even intersect the basal wall, and such embryos resemble very much the embryo of such grasses as *Triticum* and *Hordeum*, figured by Nörner (1881). Hegelmaier does not show these oblique walls in his figures of *S. ramosum*, and in this respect *S. simplex* is more like the grasses than is *S. ramosum*.

The primary tissues are now pretty well defined. The central plerome-strand extends to the basal wall and is separated from the epidermis by one layer of periblem cells (fig. 46). In the segment below, the superficial cells, as we have seen, divide again by periclinal walls, so that there are often two well defined layers of cells, evidently derived from a periclinal division of the primary epidermis. In the basal segment there are seldom more than four cells, and in case there is another segment between the basal one and the second segment (fig. 51) its divisions are quite irregular.

Hegelmaier's account of the origin of the different members of the embryo in *S. ramosum* corresponds closely to what was seen in *S. simplex*. Much the greater part of the embryo is taken up by the cotyledon which elongates rapidly, so that the embryo soon becomes several times longer than broad, this growth in length being mainly in the cotyledon, the stem and root remaining short. The stem-apex originates from the terminal segment, but on one side well toward the base. Its position and origin correspond closely to those in the grass-embryo, to judge from Nörner's account and figures (Nörner, 1881). In its origin from the terminal segment it differs from such Monocotyledons as *Alisma* and *Naias*, where the stem-apex belongs to the second segment. *Zannichellia*, however, has a terminal stem-apex, and Solms-Laubach (1878) describes several Monocotyledons with terminal stem-apices. In *Lilæa* (Campbell, 1898) the stem-apex is probably derived from the terminal segment as in *Sparganium*. *Sparganium* is, therefore, in regard to the origin of the stem-apex, intermediate between such extreme forms as *Zannichellia* and the majority of Monocotyledons investigated, in which the stem-apex arises from the second segment.

Cross-sections of the older embryo are usually more or less oval in outline, the longer axis coinciding with the face of the cotyledon. In sections made just above the basal wall (fig. 47), the first indication of the stem-apex (*st*) is evident in a more rapid division in the epidermis where the cells are decidedly narrower. At this time, the section of the plerome shows about nine cells, and the original quadrant divisions are very evident. The stem-apex appears to be the product of one only of the quadrants, and soon becomes sunk in a depression formed by the excessive growth of the basal cells of the cotyledon immediately adjacent to it (fig. 44). The stem-apex later becomes deeply sunk in the narrow cavity formed by the excessive growth of the base of the cotyledon, and this forms a sheath, such as is so frequently met with among the lower Monocotyledons (figs. 49 and 53).

The plerome-strand is continued upward into the cotyledon and downward into the root, but there is no trace of a cauline bundle. The other tissues of the root arise from the cells of the second segment of the embryo. This also divides at first by quadrant walls, and later a central growth of four cells (fig. 44, *b*) is separated from an outer row of cells. The latter again divides into two by periclinal walls. The initial group of cells, which contributes to the growth of the periblem, dermatogen and calyptrogen, is derived from the four central cells which may be said to constitute the initial for all the tissues of the root except the central plerome-cylinder.

Before the embryo is mature, the second leaf makes its appearance on the side of the stem opposite the cotyledon. The nearly flat stem-apex develops a protuberance on its outer side, and this quickly assumes the form of a short cylindrical body whose tissues are continuous with those of the stem, except that the plerome-cylinder connects with that of the root.

The embryo rapidly increases in size as the seed ripens, and finally occupies the whole axial part of the embryo-sac. The space between it and the wall of the sac has in the meantime become completely filled with the endosperm. The full-grown embryo (fig. 52) is a spindle-shaped body, of which the cotyledon constitutes much the greater portion. The outer edges of the sheath at the base of the cotyledon overlap so as to completely conceal the stem-apex and second leaf (fig. 54).

A longitudinal section through the base of the full-grown embryo (fig. 53) shows that the root is very broad and short. Occupying its axis is the conical plerome which in section shows about six rows of cells; this ends at the basal wall whose limits are still discernible. No single initial cell could be made out at the apex of the plerome, nor could any absolute regularity in the segmentation of the terminal cells be recognized. Connected with the main plerome-strand are smaller branches extending into the young leaves, but, as already stated, none is given off to the stem. Between the plerome of the root and the epidermis there are five or six layers of cells.

The origin of the other tissues of the root can be traced back to the central group of cells lying next the apex of the plerome and derived from the central cells of the second segment of the embryo. There are probably four of these initial cells, and two can usually be seen in longitudinal sections. Periclinal segments are cut off from those which add to the root-cap, and lateral segments are also formed which, dividing again, form the initials for the dermatogen and periblem. The primary root of the embryo of *Sparganium* therefore conforms closely to the type described by De Bary (1884), as found most commonly in Monocotyledons. The root-cap is well developed in the older embryo and has the form of a biconvex lens, as the central part of the root-apex is strongly concave.

A noticeable difference between the embryo of *Sparganium* and that of most other aquatic Monocotyledons hitherto examined, e. g. *Alisma*, *Naias*, *Lilæa*, etc., is the absence of the larger vesicular suspensor cell, so conspicuous in those forms. This cell is evidently of great importance in these plants, and directly concerned with the food supply of the young embryo. Its absence in *Sparganium*, the Gramineæ, and such Aroids as have been examined is no doubt to be sought in the better development of the endosperm in these forms, and possibly also in the presence of numerous antipodal cells, which assume temporarily the functions of the endosperm.

The first division of the primary endosperm-nucleus occurs almost immediately after fertilization. At this time the endosperm-nucleus is, usually at least, near the antipodal end of the sac. The divisions are repeated until there are formed in the usual manner many free nuclei arranged in a single layer in the parietal cytoplasm (fig. 30). These nuclei are more or less flattened and possess a single large nucleolus. At the apex of the sac they are more numerous, and the cytoplasm is more abundant and quite surrounds the young embryo. As usual, the first cell-division in the endosperm takes place at the apex and proceeds toward the antipodal region.

While the endosperm-nuclei have been dividing, and the peripheral layer of protoplasm is still very thin, the antipodals have increased enormously in bulk and divided rapidly to form the large mass of cells found at the antipodal end of the sac. We have already spoken of the karyokinetic division of the antipodal nuclei and it is very doubtful whether even in the binucleate cells sometimes found in the later stages this division is ever direct, as it has been found to be in the enlarged antipodal cells of a number of plants (e. g. in Ranunculaceæ, Mottier, 1895). As the embryo-sac enlarges it changes its form somewhat in *S. simplex*, becoming relatively much narrower at the upper end which early becomes completely filled with endosperm (fig. 37).

In the micropylar end of the sac the protoplasm early becomes much denser, the nuclei are larger than at the sides of the sac and not confined to a single layer. The nuclei increase a good deal in size before the cell-walls are formed between them (fig. 57).

As *Sparganium simplex* shows very clearly the endosperm formation, this was studied in some detail. Before the division-walls are evident, the nuclei are arranged at nearly equal distances. The delicate radiating lines connecting them are clearly evident (fig. 57), and in these the cell-plates are soon visible, and the nuclei are thus enclosed in polygonal areas which become cells by this transformation of the cell-plates into cellulose membranes (fig. 58). The cells at the apex of the sac are quite irregular in form and completely surround the embryo (fig. 37). At the sides of the sac these cells seen from the surface are often regularly hexagonal. The endosperm-cells at the apex have much denser contents than those at the sides, which are almost transparent. Figure 56 illustrates the way in which the development of the endosperm proceeds centripetally. This section is a nearly median one and shows how the nuclear divisions are mainly in a plane parallel to the periphery of the sac. The first-formed endosperm-cells are at first open on their inner face, and when the nucleus divides a division-wall is found closing up the outer cell, but leaving the inner one also open. This continues, one layer of new cells after another being added to the endosperm, until finally the whole upper part of the sac is filled up, but the lower portion remains open in the center up to a late enlarged period. Free nuclei can always be seen in this open part of the sac, lying in the layer of protoplasm covering the free walls of the inner endosperm-cells.

The endosperm-nuclei become a good deal enlarged before the division-walls are formed, and these enlarged nuclei generally show several nucleoli. The younger stages have only a single nucleolus and the outline of the nucleus is round and oval. As they increase in size, it was found that the nucleolus became elongated and constricted (fig. 58), finally resulting in a division into two, generally unequal, portions. This is probably repeated in the case of those which have more than two nucleoli. Each nucleolus is surrounded by a clear area, while the rest of the nucleus presents a granular appearance. As the nucleus itself becomes more or less distorted in outline with the division of the nucleolus, and often appears lobed, it was at first supposed that we had to do with a case of nuclear fusion, but in reality it is more nearly a case of fragmentation. Hegelmaier (1885) figures a number of similar cases, and they have been often observed, but so far as I know the origin of the secondary nucleoli has not been studied.

As the seed ripens, numerous very large crystalloids are formed, at least in *S. simplex*, in the endosperm-cells surrounding the embryo (figs. 63, 64). These are beautifully fixed by the action of alcoholic corrosive-sublimate, and stain readily with anilin-safranine. They vary in shape, the most perfect ones being rhombic in outline. Often they were aggregated in large masses, but usually it was evident that these masses were composed of separate crystals. *Sparganium simplex* may be recommended as an admirable subject for demonstrating these bodies. The material collected of the other species was either too young or had not been treated with the proper reagents, so that I cannot speak as to the occurrence of these crystalloids in the endosperm of the other species. They have, however, been noted in *S. ramosum* Sachs (1887).

No hard testa is formed about the seed of *Sparganium*, although this outer part of the nucellus and the integuments persist until a late stage, and probably permanently. Engler's statement (1889) that the endosperm is only separated from the pericarp by the integuments needs confirmation. In the oldest stages examined by me, there were several layers of nucellus cells still evident. The development of the hard inner pericarp is readily followed. The cells early have thickening layers deposited upon their walls, and these later become very thick and have deep pits developed in them. This sclerenchyma is rather better developed in *S. Greenii* than in *S. simplex*, and sometimes in the former the thickening is so great as to almost obliterate the lumen of the cell.

Hegelmaier (1874) has studied in *S. ramosum* the development of the curious structure to which he applies the name "Samen-deckel." The structure of this in *S. simplex* agrees closely with his account. It is formed from an enlargement of the micropylar part of the integuments, which become very much swollen, and form two caps, one above the other. The upper part of the nucellus is also included, but the cap is principally derived from the integuments (fig. 59). The margins of the inner integument are prolonged upward into a conical beak which fits closely into the opening in the outer integument. The whole structure is enclosed in the space at the top of the ovary which remains as a conical cavity in the pericarp.

The fruit of *Sparganium* is not very unlike the caryopsis of the grasses, but differs in the persistence of the integuments and probably also of a portion of the nucellus. By a further compression and disorganization of these a typical caryopsis would be formed.

VI. ABNORMAL EMBRYO-SACS.

In *Sparganium*, as in most other low Monocotyledons hitherto examined, there are occasional deviations from the normal development in the embryo-sac. Some of these have already been noted by the writer (Campbell, 1897) in the case of *S. eurycarpum;* indeed, it was these abnormalities which directed attention to *Sparganium.* In both *S. simplex* and *S. Greenii* similar deviations from the type were noted.

The most usual form is a multiplication of the nuclei within the embryo-sac without any noticeable increase in its size. As in such cases (fig. 68) the embryo cannot be detected, and the egg-apparatus has either not been formed, or has disappeared, the most probable explanation is that the sac had not been fertilized, but that the vegetative tissue of the gametophyte, i. e., the antipodal cells and the endosperm, are capable of a limited growth. This is quite comprehensible if *Sparganium* is, as it seems to be, a very low type of Angiosperm, and the case might be very well compared to the limited growth of the prothallium in the heterosporous Pteridophytes when fertilization is not effected.

Other abnormal embryo-sacs are shown in figs. 65 and 69. In the first case, taken from an ovule of *S. simplex*, the embryo-sac was very broad and divided longitudinally by a membrane—whether of cellulose or not was not determined. Three antipodal cells having the appearance of the normal ones in a recently fertilized sac could be distinguished. The structures at the micropylar end of the sac were not clearly distinguishable. The extremely broad form of the sac suggested the possibility of there having been two embryo-sacs formed in the ovule, but if this was the case, they had become entirely confluent.

Another puzzling form in *S. Greenii* is shown in fig. 69. Here the antipodal cells were apparently normal, but the polar nuclei, which were in close contact, were separated from the cavity of the embryo-sac by an evident membrane, and the upper portion of the sac was similarly shut off. Occupying the extreme upper part of this was a body looking like a very large nucleus, but the nucleolus (?) did not appear homogeneous, and it is possible that this apparent nucleus was really a cell, as the nucleolus-like body was quite similar in size and appearance to the nuclei of the surrounding nucellar cells. No other nuclei could be certainly made out in this region, except a deeply staining small body close to the wall of a vesicle which lay below the large apical nucleus. If the latter is really a nucleus it probably means that one nuclear division in the upper part of the young embryo-sac had been suppressed, and no egg-apparatus developed.

In another specimen of *S. Greenii* the embryo-sac was seen to be completely filled with granular cytoplasm, and a similar condition has also been seen in *S. eurycarpum*.

VII. RECAPITULATION.

1. The stamen in *Sparganium* is of the usual type: the ripe pollen-spore shows but one generative nucleus, but in *S. simplex* there is regularly a structure present which probably represents a vegetative or prothallial cell which was not observed, however, in *S. Greenii*.

2. The early development of the embryo-sac follows the normal course; the egg-apparatus is small in *S. simplex* and the polar nuclei fuse completely before the egg is

fertilized; in *S. Greenii* they remain separate until after fertilization.

3. The antipodal cells are three in number and in *S. simplex* are very inconspicuous; after fertilization there is a remarkable secondary growth in the antipodal cells, resulting finally in a large cell-mass, containing in *S. simplex* over 150 cells.

4. The process of fertilization, so far as it was studied, offered no anomalies.

5. The development of the embryo in *S. simplex* agrees closely with that of *S. ramosum*, studied by Hegelmaier. There are regularly three primary transverse segments, of which the terminal one gives rise to cotyledon, stem-apex, and part of the root. The suspensor remains undeveloped, and in this respect the embryo is like that of the Gramineæ. The slight development of the suspensor is associated with the complete investment of the young embryo by the endosperm.

6. The stem-apex is lateral in origin like that of most Monocotyledons, but is not developed from the middle of the three primary segments.

7. The primary tissues of the embryo are very early developed, especially in the terminal embryonal segment. The plerome of the root is derived entirely from the terminal segment; the initials for the other tissues of the root arise from the middle segment.

8. The development of the endosperm follows the usual course, but is rather late in forming the first division-walls. The enlarged antipodal cells doubtless function at first as endosperm.

9. The large endosperm-nuclei have often several nucleoli which are formed by a fragmentation of the original nucleolus.

10. Large crystalloids are abundantly developed in the older endosperm-cells of *S. simplex*.

11. The inner pericarp develops into sclerenchyma with thick, deeply pitted walls. The development of the "Samen-deckel" is the same as described by Hegelmaier for *S. ramosum*.

VIII. The Affinities of Sparganium.

The genus *Sparganium* has until recently been associated with *Typha* in the family Typhaceæ, but Engler (1889) has pointed out that the differences between *Typha* and *Sparganium* are so great as to make such a union unwarranted, and he proposes placing *Sparganium* in a separate family, following the Pandanaceæ. Until more is known about the development of the Pandanaceæ, however, it will be impossible to decide how closely the two families are related. A thorough study of some species of *Pandanus* would be of great value in solving this question.

Hegelmaier (1874) has referred to certain resemblances in the embryo of *Sparganium* to that of the Gramineæ, and my own study of *S. simplex* confirms this. The extraordinary character of the antipodal cells also is strongly suggestive of the grasses. The probably terminal origin of the single ovule is also like that of the grasses, and this it also shares with most other low Monocotyledons. Indeed the solitary uni-ovulate carpel is probably the most primitive type among the Monocotyledons, and is not the result of a reduction. In this particular *S. simplex* is probably more primitive than the forms like *S. Greenii* and *S. eurycarpum*, in which the ovary is compound.

The type of fruit in *Sparganium* is not unlike that of the Gramineæ. While the majority of the latter have a caryopsis, there are others in which the fruit is nut-like, corresponding to that of *Sparganium* (see Hackel, 1890). A comparison of some of these forms with *Sparganium* would be interesting.

The monœcious flowers of *Sparganium* also are shared by some grasses, e. g. *Zea*, so that the possibility of an actual relation between these two puzzling families may very well be considered. Of course the resemblances may be purely fortuitous, but it is more likely that they indicate a real, even if remote, affinity, and any further study of the flower and fruit of the Gramineæ should consider this. In short, so far as a comparative study has been made, *Sparganium* shows a closer affinity with the Gramineæ than with any other family, unless possibly the Pandanaceæ.

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EXPLANATION OF PLATE XLVI.

All figures except 1 and 4 were studied with Leitz lenses and drawn with a Zeiss camera. All figures slightly reduced.

Figs. 4, 5, 7, 15 and 23 refer to *Sparganium Greenii* Morong, the others to *S. simplex* Huds.

Fig. 1. Two female flowers of *S. simplex* enlarged about eight times; the one at the right with the perianth removed.

Fig. 2. A single scale of the perianth more enlarged.

Fig. 3. Longitudinal section of the ovary showing the single ovule; *ma*, embryo-sac. Oc. 1, obj. 3.

Fig. 4. Pistil of *S. Greenii;* × about 8.

Fig. 5. Section of the ovary of *S. Greenii.* Oc. 1, obj. 3.

Fig. 6. Sections of ripe pollen-spores of *S. simplex*, showing the large vegetative, and smaller generative, nucleus; *pr*, prothallial cell. Oc. 1, im. $\frac{1}{16}$.

Fig. 7. Sections of younger pollen-spores of *S. Greenii;* the nucleus is still undivided, and no prothallial cell is visible. The clear space on the surface probably marks the place of exit of the pollen-tube.

Fig. 8. Upper part of the embryo-sac of *S. simplex* just after the entrance of the pollen-tube; *o*, the egg-cell; *sy*, one of the synergidæ; *pt*, pollen-tube. Oc. 1, im. $\frac{1}{16}$.

Fig. 9. Another section of the same embryo-sac; the small dark body within the synergid is probably one of the generative nuclei from the pollen-tube.

Fig. 10. The antipodal end of the same embryo-sac, showing the single large endosperm-nucleus and two of the antipodal cells.

Fig. 11. The egg-apparatus and endosperm-nucleus from a mature embryo-sac. Oc. 1, im. $\frac{1}{16}$.

Fig. 12. (*a*) Two antipodal cells from a mature embryo-sac; (*b*) outline showing the position of the three small antipodals. Oc. 1, im. $\frac{1}{16}$.

Fig. 13. Section of the egg-apparatus showing the entrance of the pollen-tube, *pt*. A small body (the generative nucleus ?) is visible within the egg; both synergidæ are still intact. Oc. 1, im. $\frac{1}{16}$.

Fig. 14. Another section of the same; the pollen-tube has apparently discharged a small granular mass into the embryo-sac.

Fig. 15. Section of the nucellus and mature embryo-sac of *S. Greenii.* Oc. 1, obj. 7. A large cell (an extra antipodal ?), lies above the three antipodal cells.

Fig. 16. The antipodal region of fig. 16 more highly magnified.

Figs. 17 and 18. Two sections of the egg-apparatus of *S. Greenii.* Oc. 1, im. $\frac{1}{16}$.

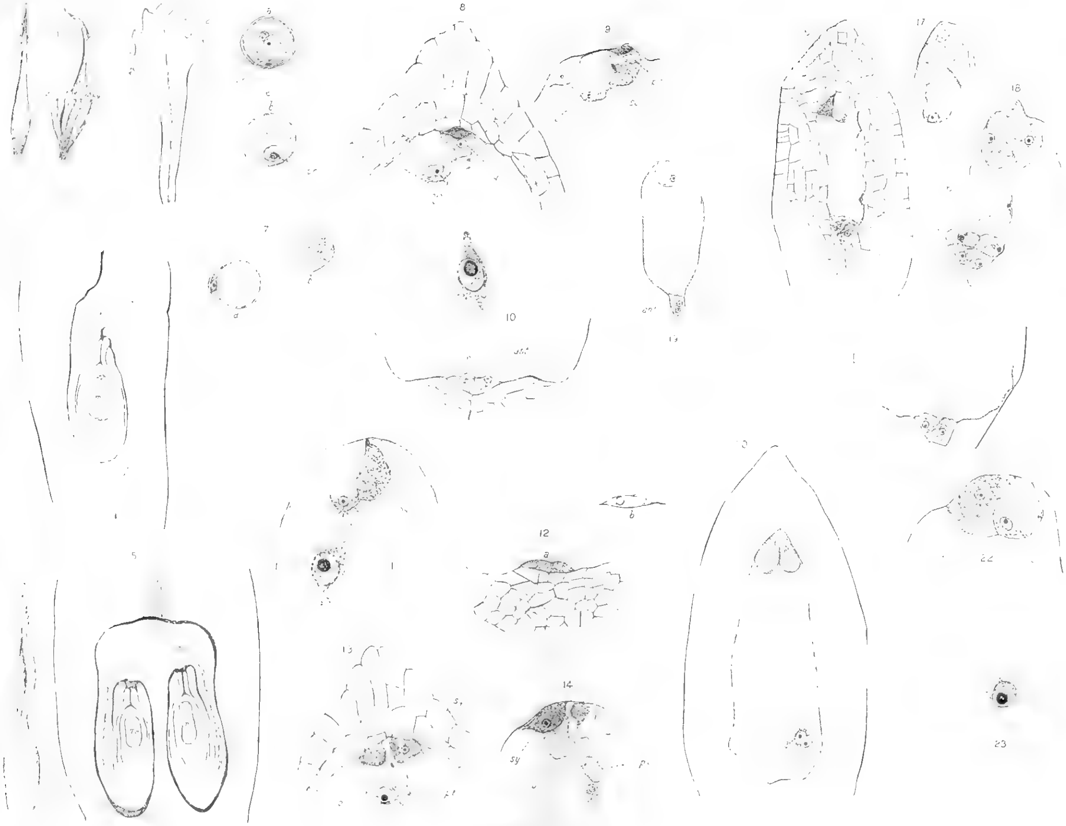
Fig. 19. Embryo-sac of *S. Greenii*, showing egg, *o*, and two antipodals, *ant.* Oc. 1, obj. 7.

Fig. 20. Unusually large sac of the same species; the section shows the two synergidæ and the still separate polar nuclei. Oc. 1, obj. 7.

Fig. 21. Two of the antipodal cells from the same sac more highly magnified.

Fig. 22. Section of egg-apparatus of *S. Greenii.* Oc. 1, im. $\frac{1}{16}$.

Fig. 23. Endosperm-nucleus from a similar sac.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EXPLANATION OF PLATE XLVII.

Figs. 33–36 refer to *S. Greenii*, the others to *S. simplex*.

Fig. 24. Apex of fertilized embryo-sac with one-celled embryo. Oc. 1, im. $\frac{1}{16}$.

Fig. 25. An embryo of the same age, but with a broader base of attachment. One synergid could be still made out.

Fig. 26. A recently fertilized embryo-sac; one of the enlarged antipodals, *ant.*, is shown. The endosperm-nucleus has divided once. Oc. 1, obj. 7.

Fig. 27. The antipodal region of the same more highly magnified; the three enlarged antipodal cells lie in the same plane; one of the two endosperm-nuclei is shown.

Fig. 28. Enlarged antipodal cells from an older sac; each of the cells shown has two nuclei; the whole number of nuclei was eight or nine. Oc. 1, im. $\frac{1}{16}$.

Fig. 29. Two sections of the antipodal group from a still older sac; some of the nuclei are dividing; twelve antipodal nuclei could be distinguished. Oc. 1, im. $\frac{1}{16}$.

Fig. 30. Nearly median section of the antipodal group from a much older sac. Oc. 1, obj. 7. Divisions have formed between all the nuclei; numerous free endosperm-nuclei, *en.*, are present.

Fig. 31. Part of the lining layer of protoplasm with a single endosperm-nucleus. Oc. 1, im. $\frac{1}{16}$.

Fig. 32. Surface view of a portion of the nucleated protoplasmic layer lining the wall of the embryo-sac.

Fig. 33. Antipodal cells from the unfertilized sac of *S. Greenii*. Oc. 1, im. $\frac{1}{16}$.

Fig. 34. Antipodal group shortly after fertilization; the upper cell has enlarged and divided; the two lower ones show indications of disintegration.

Fig. 35. Antipodal group of *S. Greenii* in which all the cells appear active.

Fig. 36. A somewhat older group of the same species; growth is mainly confined to the upper cell.

Fig. 37. Upper end of embryo-sac of *S. simplex* showing the young embryo surrounded by the endosperm-cells; the central nuclei, *en*, are still free. Oc. 1, obj. 7.

Fig. 38. The embryo from fig. 37 more enlarged.

Fig. 39. Median section of a similar embryo. Oc. 1, im. $\frac{1}{16}$; *xx*, the basal wall.

Fig. 40. Series of three cross-sections of an embryo of about the same age; *a*, the lowest segment.

Fig. 41. Two sections of an older embryo, cut in the plane of the cotyledon. Oc. 1, obj. 7.

Figs. 42, 43. Longitudinal sections cut at right angles to the plane of the cotyledon; the basal wall is decidedly oblique. Oc. 1, obj. 7.

Fig. 44. Three cross-sections of an embryo of about the same age as 42; the lowest segment is divided into four cells. Oc. 1, obj. 7.

Fig. 45. Upper part of embryo-sac showing the embryo surrounded by the densely granular endosperm-cells; the granular cell-contents of the embryo are not shown. Oc. 1, obj. 7.

Fig. 46. The same embryo shown in fig. 45, showing the differentiation of the primary tissues, the plerome ends at the basal wall, *xx*.

Fig. 47. A transverse section of an embryo of about the same age. Oc. 1, obj. 7.

Fig. 48. Section in the plane of the cotyledon of a similar embryo, with very regular arrangement of the tissues. Oc. 1, obj. 7.

Fig. 49. Median section of an older embryo, showing the stem-groove, *st.* Oc. 1, obj. 7.

Fig. 50. Embryo of about the same age, cut in the plane of the cotyledon.

Fig. 51. Median section of the base of the same embryo, more highly magnified; *pl.*, the plerome.


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EXPLANATION OF PLATE XLVIII.

All figures except 69, refer to *S. simplex*.

Fig. 52. Two sections of a nearly mature embryo. Oc. 1, obj. 3.

Fig. 53. Root-end of a somewhat younger embryo. The position of the original transverse, or basal wall (x) is still evident, l^2, the second leaf; *st.* the stem-apex. Oc. 1, obj. 7.

Fig. 54. Three cross-sections of a mature embryo. Oc. 3, obj. 3.

Fig. 55. Sections of the young seed before the endosperm has filled the embryo-sac; *e*, embryo; in^1, in^2, integuments.

Fig. 56. Section through the layer of developing endosperm lining the embryo-sac; many of the nuclei are dividing. Oc. 1, obj. 7.

Fig. 57. Larger endosperm-nuclei from the base of the sac at the time the walls are first beginning to form; some of the nuclei have more than one nucleolus; the fine fibres connecting them are plainly visible. Oc. 1, im. $\frac{1}{16}$.

Fig. 58. Transverse section of recently formed endosperm-cells showing the nucleolus fragmenting. Oc. 1, im. $\frac{1}{16}$.

Fig. 59. Upper part of the young seed showing the enlargement of the micropylar portion of the integuments. Oc. 3, obj. 3.

Fig. 60. Young sclerenchyma-cells from the pericarp. Oc. 1, obj. 7.

Fig. 61. Fully developed sclerenchyma-cell showing the deeply pitted walls. Oc. 1, obj. 7.

Fig. 62. Surface view of the pits more highly magnified.

Fig. 63. Endosperm-cells from nearly ripe seed, showing large crystalloids. Oc. 1, obj. 7.

Fig. 64. Separate crystalloids more highly magnified.

Fig. 65. Abnormal embryo-sac of *S. simplex;* the sac divided longtudinally with the endosperm-nucleus on one side. Three antipodals could be distinguished. Oc. 1, obj. 7.

Fig. 66. Micropylar end of the same sac.

Fig. 67. One of the antipodal cells of the same.

Fig. 68. Abnomal embryo-sac (perhaps unfertilized?) ; there has been little increase in size of the sac, but numerous endosperm-nuclei are present, and the antipodals have enlarged and divided. Oc. 1, obj. 7.

Fig. 69. Two sections of an abnormal embryo-sac of *S. Greenii;* three antipodals could be seen, and the polar-nuclei (*p.n.*), in close contact, were separated from the body of the sac. The upper part was also shut off by a membrane, and no definite egg-apparatus could be distinguished. Oc. 1, im. $\frac{1}{16}$.

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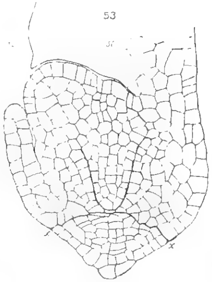

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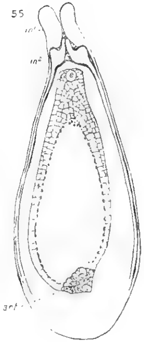

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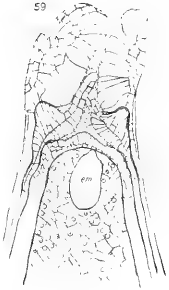

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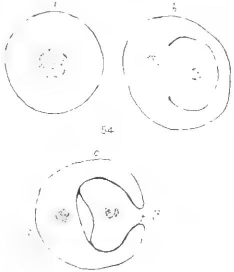

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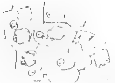

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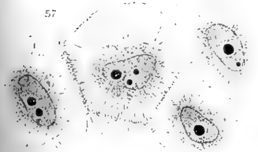

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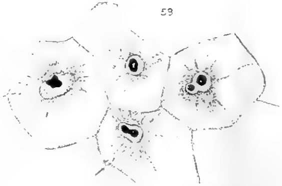

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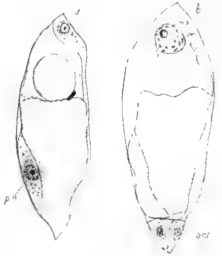

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A MORPHOLOGICAL STUDY OF THE FLOWER AND EMBRYO OF THE WILD OAT, AVENA FATUA L.

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CONTENTS.

PLATES XLIX–LIII.

I. INTRODUCTION.

THE grasses are said by Hackel to be a very isolated family, sharply defined from the other low Monocotyledons to which they are bound by only obscure relationships. For this reason they have been variously placed by systematists, but are now generally and probably best regarded as near the Aroids and the Palms. The life history of such grasses as have been studied justifies this conclusion, and it is the object of this investigation to add something to our knowledge of these forms in order that their mutual relationships may be better understood. Enough morphological work has already been done on types allied to the grasses to form a basis for comparisons. It remains therefore only for more extended and more thorough studies to be made on grasses before comparisons can be instituted. There have already been a few such studies published. The most important recent contributions to our knowledge of the life history of grasses have been by Lermer and Holzner (1888), and Koernicke (1896). The original of the former contribution was unfortunately not at hand and I was obliged

April 14, 1900.

to depend on citations and fragmentary reviews for my knowledge of it. It is an exhaustive work, describing the complete development of the floral and reproductive organs of the cultivated barley as well as its embryology. Koernicke, on the other hand, studied the development of the stamen and embryo-sac of the wheat with especial reference to cytological phenomena. Two studies which were made before the introduction of the modern methods of imbedding and sectioning, viz. by Fischer (1880), and Nörner (1881), were consulted in the preparation of this paper. Fischer's study deals with the development of the embryo-sac of various grasses, while that of Nörner treats of the embryology alone. All of the contributions mentioned above refer to grasses belonging to the branch of the family known as the Poaceæ, the members of which, besides being closely related, have very similar habits and habitat. It is to be greatly desired that future studies of the Gramineæ may include representative grasses of various habits and habitat of both branches of the family. In this way an adequate knowledge of the inter-relationships of the grasses, as well as their relationships to other Monocotyledons may be obtained, and also a better idea of the origin of plant structures. In addition to the papers already named there is a great mass of work on the comparative morphology of the different parts of the mature flower and of the mature embryo. Beginning with Malpighi (*Omnia opera*, 1687), and Gärtner one hundred years later, the series extends with little interruption to the present. For a review of these works the reader is referred to the studies by Bruns (1892), and to the recent one by Kennedy (1899).

Because the flower of the wild oat is the type grass flower, (it is described and figured in any good text-book of botany), it was selected for this morphological study. The wild oat is supposed to be the ancestor of the cultivated species, or at least the nearest relative of that ancestor, and is one of our commonest grasses. It was presumably introduced into California at an early date from Southern Europe, and has now a wide range throughout the state.

II. Origin of the Floral Organs.

The spikelet of *Avena* branches sympodially, the apex of the young spikelet developing into flowers and finally pistils. Each flower arises below the apex of the primordium of the spikelet and grows at right angles to it, so that the rachilla is sharply angular when young (fig. 1).

The primordium of the spikelet consists of three well defined series of tissues: (1) a dermatogen, (2) a single layer of large hypodermal cells—the periblem—which surrounds (3) an axial strand—the plerome cylinder. As the primordium increases in length the cells of the epidermis and of the periblem divide by anticlinal walls and form a continuous cap to the plerome. The plerome arises from a single cell, or perhaps a group of cells, that terminates the axial strand (fig. 3). All of these cells are well filled with protoplasm, are without conspicuous vacuoles, and have relatively large nuclei.

The floral organs all arise in much the same way upon the periphery of the primordium, beginning with the lower glume and ending with the carpel. Each begins as a ridge of tissue that extends part way around the primordium of the flower. The origin of each floral organ will be spoken of in the order of its appearance.

The lower glume and the young flower apex appear to arise simultaneously just below the tip of the primordium of the spikelet (fig. 4). At first these two rudiments are very similar, but the flower apex soon becomes broader, and the lower glume somewhat deeper by its growth and by the stretching out of that part of the rachilla that is immediately below it. At this time the glume is a semicircular organ, club-shaped in longitudinal section, composed of a well defined dermatogen enclosing about three layers of cells. As the lower glume increases in length it takes a direction which coincides with the direction of that part of the rachilla from which it springs, but it soon bends toward the tip of the spikelet (figs. 1 and 2). At that stage in the development of a flower when all of the floral organs are first to be distinguished, a narrow outgrowth appears near the base and on the inner surface of the lower glume. This outgrowth is at first on a level opposite the lodiculæ, but as the glume increases in length, it is carried upward somewhat (figs. 1 and 2). It becomes longer and broader and forms the lamina of the mature lower glume, while the original rudiment persists as the awn.

The upper palet and the lodiculæ arise apparently at the same time and from the same rudiment (fig. 5). A crescent-shaped ridge of tissue extends nearly around the primordium. This ridge does not form on the anterior aspect, but from the ends the lodiculæ develop, and from the anterior face the upper palet. The upper palet grows as the adjacent organs develop. When it can first be plainly recognized it is composed of three layers of cells, and later becomes thicker by periclinal divisions of the cells at its base (figs. 5 and 6). The upper palet is the last of the protective organs of the oat-flower to develop.

The lodiculæ appear as rounded shoulders jutting out from the lateral surfaces of the primordium and mark the ends of the rudiment that gives rise to the upper palet (fig. 5). The apex of the young flower grows up and leaves the lodiculæ in a lateral position below its tip. The lodiculæ are at first triangular with the broad base resting against the surface of the primordium. They gradually acquire the oblong shape characteristic of the mature organs.

The stamens of the wild oat arise as conical outgrowths at equal distances apart around the periphery of the apex of the flower. Figure 1 shows the relation of the anterior stamen to the lower glume; and figure 7, which is taken from a longitudinal section made a little to one side of the center of the flower, shows one of the lateral stamens and its relation to one of the lodiculæ. The stamens develop early, the filament appearing before the lamina of the lower glume is well differentiated and while the carpel is still small. It increases in length by cell-division in all parts and is always relatively slender. The pollen is generally shed before the stigmas of the flower have protruded from the spreading glumes.

The carpel is the last of the floral organs to arise. It appears as a single ridge of tissue on the anterior side of the floral axis (fig. 6), and gradually encircles the apex of the young flower (fig. *6a*). The young carpel is club-shaped in longitudinal section, and its structure is sufficiently indicated by the figures. Soon after the carpel has completely surrounded the tip of the flower axis, two protuberances appear on the sides and form the beginnings of the stigmas; later the rim of the carpel closes and shuts in the ovule.

A correct interpretation of the relations of the parts of the grass flower is of great importance, because upon it depends a right understanding of the relationships of this isolated family. These relationships are based mainly on the number and arrangement of the floral organs. The origin and development of the gynœceum and andrœceum of the grass flower, as well as the origin and development of the organs subtending these, are now fairly well understood, but the morphological significance of some of these organs is very much in doubt. It is not known, for instance, whether the lodiculæ represent a perianth or not, an important basal fact in determining the position of the grasses. There are concerning the lodiculæ two widely different views which have been held by botanists. In the first, the lodiculæ are considered to be the stipules of a leaf which has been suppressed, or the parts of a leaf of which the middle is wanting; and the posterior lodicula when present is held to be, according to this hypothesis, a leaf or palet which alternates with the lodicular palet and which therefore continues the distichous arrangement of the lower glume and upper palet. Or, in other words, according to this interpretation of the grass flower there are represented four alternating palets of which the two lowest persist, the others being rudiments. This explanation of the relation of the lodiculæ to the other organs of the grass flower is opposed to the law which is sometimes said to govern leaf arrangement among the grasses, by which the leaves of a branch are inserted on a plane at right angles to that of the leaves of the main axis. Further, this hypothesis excludes the idea of a perianth in the grasses, and with this a very important clue to the connections between the grasses and other low Monocotyledons is overlooked. The second interpretation recognizes a perianth which is represented by the lodiculæ. The two anterior members are present in most grasses, and the trimerous perianth is completed by a posterior member in the bamboos and certain other grasses. Neither of the hypotheses set up to explain the significance of the lodiculæ is entirely satisfactory—the first explanation for the reasons given, and the second, mainly because of the position of the lodiculæ in most grasses. The relation of the lodiculæ to the upper palet in *Avena* (and in some other grasses as well) in which there is a common origin for both, makes it difficult to look upon the lodiculæ as members of a perianth, for this, if present, ought to originate and therefore be placed on a higher plane than the upper palet. This intimate connection of the lodiculæ and upper palet is met also in *Oryza*, *Zea*, and *Solenache* (Eichler). The lodiculæ vary greatly in number in the different grasses and assume various positions, as in the Paniceæ they are mainly outside the upper palet, and in the *Ehrharta*-species similar bracts are associated with the lower glume. From this it seems reasonable to conclude that not all of the lodiculæ can represent rudimentary perianths. In addition to this variation in position of the lodiculæ there are present in the rye (Eichler) and certain other grasses four anterior lodiculæ placed on two planes; the two lower are connected with the upper palet ("stipular lodiculæ") and the two upper, originating evidently on a higher plane, are regarded as being two members of a perianth ("perianthal lodiculæ"). A comparison of the lodiculæ of *Avena* with those of the rye shows them to be homologous to the stipular lodiculæ of the rye, but in *Avena* the perianthal lodiculæ are wanting. In the bamboo a trimerous perianth of three lodiculæ is present, and in addition to this, two stipular lodiculæ also. The upper lodiculæ of the bamboo, by reason of their position and number, have been rightly considered to make up a perianth. They are homologous to the perianthal lodiculæ of the rye and cannot, therefore, hold similar relations to the lodiculæ of *Avena*. I conclude then from a comparison of the grass flowers that the lodiculæ in *Avena* do not represent a perianth, but that the perianth is entirely wanting; they are homologous to the stipular lodiculæ of other grasses.

From this it would appear therefore that not all those organs called lodiculæ are necessarily or even probably the same morphologically. In some grasses they are survivals or rudiments of a perianth, in others they are survivals or rudiments of extra-floral leaves, and in still others, where two rows occur, the inner row is morphologically perianth, the outer extra-floral bracts, and there is no evidence (Eichler) of a double perianth.

III. THE STAMEN.

The development of the stamen of *Avena*, as far as followed, corresponds rather closely with that of the stamen of wheat, (Koernicke, 1896). The stamens originate as crown-shaped projections at equal distances apart on the periphery of the floral axis. A cross-section shows the young stamen to be oblong in form (fig. 8). By more rapid growth in the portions where the loculi are to appear, the outline becomes irregular and characteristic of the stamens of Angiosperms (fig. 9). A constriction occurs very early at the base of the stamen, which indicates the beginning of the filament (fig. 7). The subsequent growth of the stamen until the time when the pollen grains are ripe is due almost entirely to the elongation of the anthers—the filament growing only immediately before the pollen is scattered. The primary tissues—plerome, periblem, and dermatogen—are clearly marked in the young stamen. As usual in Angiosperms, the pollen is derived from the periblem. In the increase in diameter of the anther, preceding the cutting off of the archesporium, the cells of the periblem in the parts where the loculi are to appear become larger than the intervening periblem cells and also than those of the plerome. They become separated from the epidermis by periclinal walls of more or less regular formation (fig. 10); but the hypodermal cells between the large periblem cells described divide by anticlinal walls only. This cell-formation results in the lobed condition characteristic of anthers.

A cross-section of an anther in which the loculi are visible shows one conspicuously large cell surrounded by two series of periblem cells and the epidermis. Of these three concentric cell series the middle one forms the endothecium, and with the epidermis persists until the anther is ripe. The inner series, according to Koernicke, divides by periclinal walls to form the tapetum and a middle layer, both of which are resorbed in the later stages of the development of the anther. This point, however, I did not see in the oat. The large cells which occupy the middle of each loculus and form, as longitudinal sections show, a single row, constitute the archesporium. Later these divide by radial walls and thus give rise to the pollen mother-cells. A median longitudinal section through a loculus in which the pollen mother-cells are formed (fig. 11) shows two rows of spore mother-cells, each of which reaches to the walls of the loculus.

The history of the division of the mother-cells into tetrads I did not follow. Koernicke gives a detailed account of this for the wheat, and we may suppose that the history of spore formation in the two nearly related genera is very similar.

The mature pollen spore is enclosed by two integuments, the inner of which is very delicate. The spore is densely filled with coarse granules of starch. Three bodies that stain strongly with the reagent used (Haidenhain's iron-alum-hæmatoxylin) are present in the spore.

The largest is oval and stains less strongly than the two spindle-shaped ones. These three are respectively the vegetative and the two generative nuclei. Some difficulty was encountered in distinguishing the nuclei from the cytoplasm in the generative cells, and it is probable that the nuclei form a larger portion of the cell contents than is indicated in the figure (fig. 12). Koernicke does not mention a division of the generative nuclei in the pollen grain of wheat, and this would be an apparent exception to the statement by Strasburger (1884), that the division of the generative nuclei is a constant character of the grasses.

The generative nuclei in the pollen grain of *Avena* occupy various positions with relation to the vegetative nucleus, but are always parallel to each other. The vegetative nucleus is oblong and as large as both the other two nuclei combined. The development of the pollen grain was not followed further.

IV. THE EMBRYO-SAC.

The initial cell of the embryo-sac in the oat is of subepidermal origin. It is the middle one of the epidermal cells of the primordium, as is generally the case (Fischer), and it is continuous with the axial plerome. At the time when both of the integuments of the ovary are clearly distinguishable, the archesporial cell is easily made out by reason of its relatively large size. At this stage it occupies in the oat, as in the wheat (Koernicke), over one-third of the nucellus, and is eight to ten times as large as the surrounding cells. There is no apparent difference at this time between the archesporial cell and those of the nucellus in density of cell contents.

When the archesporial cell is first recognizable the ovule is atropous. Parallel with the development of the sister cells and of the embryo-sac, the cells in the rachilla side of the nucellus divide and grow more rapidly than those in the opposite side, and push the micropylar end over so that finally the micropyle occupies a position almost opposite from that of the archesporial cell. During the revolution of the ovule (macrosporangium) the ovary increases greatly in size, and, from being somewhat flattened at first, it becomes spherical and at last oblong. The size and position of the ovule is intimately connected with the development of the archesporial cell and the embryo-sac.

When the axis of the ovule forms a right angle with that of the flower the archesporial cell has elongated, keeping pace with the elongating nucellus, and its nucleus has undergone one division (fig. 14). The cell is densely filled with granular protoplasm; no vacuoles are visible.

There are in *Avena* as in *Eichhornia* (W. R. Smith, 1898) apparently three ways in which the sister cells may be formed. In the first, the nucleus of the archesporial cell divides after the elongation of the cell, the two resulting nuclei divide, and the four sister nuclei lie free in the protoplasm of the cell, no walls separating them (fig. 15). Or (second) after the nuclei have divided, walls may appear between them (fig. 17). However, owing to faulty methods of staining, I could not in every instance be sure of the presence or absence of the separating walls, but the phenomena were observed at various times during the course of the study. In the third manner of formation of sister cells, dividing walls followed each nuclear division as in the section represented in figure 16. This variation in the formation of sister cells was not described by Koernicke for *Triticum*, or by Fischer for any of the grasses studied by him. Fischer did however describe a condition in the genus *Melica* which he says is constant, and is analogous to what has been described above for *Avena*. In *Melica* the division of the nucleus of the archesporium is followed in all cases by the formation of a dividing wall. The two nuclei thus formed divide each once, but without cell-walls being formed; so that in *Melica* there are two cells with two sister nuclei in each cell. It would be of importance to know whether this condition is as constant as Fischer states, or whether there really is in *Melica* that variation in the formation of the sister cells which is apparently the case in *Avena* and in *Eichhornia*.

In whatever way the sister cells are formed four superimposed nuclei always result, and of these the lowest becomes the spore mother-cell, the others becoming resorbed. The uppermost of the sister cells is the first to disappear (fig. 17), and after it the two next lower ones in succession, if cell-walls have been formed between them, or simultaneously if the nuclei are not separated by walls (figs. 18 and 19). The macrospore thus formed occupies the position recently occupied by the sister cells, and extends to the epidermis. No tapetum is formed. When they are present the walls separating the sister cells are not so strongly swollen as in *Triticum* (Koernicke) and in *Alopecurus* (Fischer, fig. 32). In this regard the oat agrees with the figures given by Fischer for *Sesleria*. The wall next to the epidermis in *Avena* is somewhat swollen as in *Sesleria* (l. c. fig. 10).

The macrospore nucleus divides into two nuclei which lie, one in the micropylar end and the other at a point distant about one-third the length of the embryo-sac from its chalaza end. The chalaza nucleus divides at right angles, and the upper nucleus divides parallel to the long axis of the embryo-sac (fig. 20). One large vacuole separates the two nuclear groups; and another separates the chalaza nucleus from the end of the embryo-sac. Each nucleus of each group divides again, the upper group at right angles to the plane of the first division. The embryo-sac now contains eight free nuclei (figs. 21 and 21*a*). During these divisions of the nuclei, the embryo-sac has increased greatly in length and diameter, and has absorbed the adjacent cells of the nucellus. Many large vacuoles have appeared in the protoplasm of the embryo-sac; prominent among them are the large ones surrounding the protoplasmic bridge that connects the two groups of nuclei, and the vacuole in the chalaza end.

In the micropylar end of the embryo-sac two (sister) nuclei form the synergidæ; and one that lies at one side of the synergids, the egg; while the sister nucleus of the egg becomes the upper polar nucleus (figs. 21 and 22). Three of the nuclei in the chalaza end of the sac give rise to the antipodal complex, and one forms the lower polar nucleus.

The egg is at first spherical, but as it increases in size it becomes oblong, and finally, when nearly ready for fertilization, balloon-shaped (figs. 24 and 25). It occupies a lateral position as regards the synergidæ, which is the position of the egg in *Sesleria* also (Fischer). The synergidæ are flask-shaped and do not appear to contain vacuoles. The egg-apparatus increases greatly in size but shows no other change up to the time of fertilization.

The upper polar nucleus moves to meet the lower polar nucleus in the region of the antipodal nuclei (figs. 21 and 22). The two nuclei then move towards the egg and remain in close proximity to it, in the protoplasmic bridge that connects the egg-apparatus and the antipodals. The polar nuclei do not fuse until about the time of the fertilization of the egg. The exact time was not determined. The nucleoli of the polar nuclei are the largest in the embryo-sac and with the ordinary staining reagents become deeply colored. The peculiar behavior of the polar nuclei of the oat does not agree with that in the grasses examined by Fischer; but Koernicke indicates that some such action of the polar nuclei occurs in *Triticum*, as he states that the two polar nuclei move towards each other. The sides of the polar nuclei that are in contact with one another are flattened, and each cell retains its delicate cell-wall up to the time of fertilization, when they fuse to form the endosperm nucleus. The time of the fusion of the polar nuclei of the oat appears to be the same as that in the wheat. There is no rule as to which side of the polar nuclei will come in contact, so that a line separating them may be parallel to the long axis of the embryo-sac, at right angles to it, or it may be at any angle between the two. The endosperm nucleus is imbedded in a dense strand of protoplasm which connects the antipodals and the egg, and strands radiate from this to the walls of the embryo-sac. This last is especially true of the younger sacs, the protoplasmic threads disappearing in the older stages. The protoplasmic bridge persists however until the antipodals disappear.

The embryo-sacs of all the grasses that have been studied, except *Melica* (Fischer), show a multiplication of the antipodal cells. This phenomenon has also recently been observed in the family which is probably the nearest ally of the grasses, viz. the Sparganiaceæ, and in the Araceæ.[1]

The antipodal nuclei of the oat begin to divide as soon as the lower polar nucleus is separated from them. They divide repeatedly and each nucleus becomes enclosed in a globular mass of protoplasm. The increase in number is accompanied by an increase in the size of the cells and also of their nuclei. A good idea of this growth of the antipodal complex may be had by comparing figures 22, 23 and 25. The multiplication of the antipodals and their increase in size takes place at the expense of the nucellus (*cf.* figs. 23 and 25). The greatest number of antipodals is found at the time of the fertilization of the egg. This number was not exactly determined, but it was at least 36, which corresponds with that given by Koernicke for the wheat. There is uniformly in *Avena* as in *Triticum* one nucleus in each cell. Fischer describes three antipodal cells only for *Alopecurus* and *Sesleria*, but says that there are four nuclei in each. *Melica*, on the other hand, does not show multiplication of the antipodals in any way. When they begin to divide, the antipodal cells of *Avena* occupy a position near, but not in, the chalaza end of the embryo-sac, and a line drawn through the long axis of the embryo-sac would bisect them. As the embryo-sac develops, the antipodals assume a lateral position and retain it until they disappear.

The antipodal complex shows, in section, a characteristic crescent form; the nuclei are large and stain deeply with the common staining agents. No vacuoles are visible in the young antipodal cells, but they appear as the cells grow, and are increasingly marked during their dissolution.

The disorganization of the antipodals begins simultaneously with the formation of the endosperm, and usually they can no longer be seen at the time when the micropylar end of the embryo-sac is being filled with endosperm. Figure 27 shows the condition of the antipodals when the endosperm is beginning to form. A few large vacuoles in each

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[1] Campbell, Bot. Gaz., March, 1899, and Proc. Cal. Acad. Sciences, 1899.

cell can be seen. Almost the last stages in the existence of the antipodals is shown in figure 28. The protoplasm of the antipodal cells is the first portion of the cells to disappear; traces of the antipodal nuclei are frequently met when they are quite disassociated from the protoplasm of the cells. The function of the great antipodal complex, in those forms in which it is present, undoubtedly varies with the time of its formation. In the oat, as in the wheat (Koernicke), the antipodals are formed prior to fertilization and disappear with the multiplication of the endosperm nuclei, being consumed by the endosperm in its development. In *Sparganium* (Campbell) the antipodals multiply enormously after fertilization, and evidently function as endosperm, and consequently serve to nourish the growing embryo.

V. FERTILIZATION AND THE BUILDING OF THE ENDOSPERM.

The pollen-tube enters the embryo-sac by pressing apart the cells of the micropyle. The two synergidæ do not usually disappear at this time, although one seems to do so. This point needs further study. One, or perhaps the two synergidæ, may sometimes be observed partly resorbed while the embryo is still in the proembryo stage, and it is likely here, as in the wheat (Koernicke), that both synergidæ are consumed as nourishment for the young embryo. The phenomena associated with the union of the sexual nuclei, as well as the further history of the pollen-tube, the vegetative nucleus, and second generative nucleus were not followed.

The endosperm nucleus begins to divide about the time when the egg is fertilized; but whether this precedes or follows the union of the nuclei was not determined. At the first division of the egg a few endosperm nuclei may be seen in the thin protoplasmic lining in different parts of the embryo-sac. These nuclei vary a great deal in size, and in shape also, from spindle form to a flattened sphere. Each endosperm nucleus generally contains several (three to eight) nucleoli. In the early stages in endosperm formation the nuclei divide in all parts of the embryo-sac wherever they are. With their increase in number they become larger in size, cease dividing, are usually spherical, and become enclosed in rather dense masses of protoplasm, which later become separated by cell walls. The lumen of the embryo-sac begins to fill first around the embryo, where the endosperm cells that closely invest it are long, somewhat crescent-shaped, and very dense.

The nucellus and embryo-sac increase greatly in length after the fertilization of the egg, the embryo-sac absorbing more and more of the nucellus cells, until little more than a single layer separates it from the inner integument. A change also takes place in the integuments. Before fertilization and more especially during the youngest stages of the embryo-sac, the two integuments are quite similar, each being composed of two layers of uniform cells. After fertilization the outer integument is compressed and finally destroyed, and the inner one takes on heavier cell-walls and becomes the outer seed-coat.

VI. THE EMBRYO.

The oöspore, which is relatively small and enclosed by a delicate membranous wall, increases considerably in size after fertilization and before any division occurs. The cytoplasm is granular and with few vacuoles. An interesting variation in the cytoplasmic structure of the cells of very young embryos was met in several instances. The cytoplasm appeared very coarsely granular and net-like. No conspicuous vacuoles were present in such embryos; growth and cell-division as far as it had occured were normal. No embryos beyond the proembryo stage presented this peculiar appearance of the cytoplasm.

The first division of the egg occurs near the distal end and is transverse, either at right angles to the long axis of the young embryo (proembryo), or at an angle more or less acute to it. I found one abnormal case in the first division of the egg, in which the cell-wall was a longitudinal one. Figure 29 shows an egg in course of the first division in which the wall is to be at right angles to the long axis of the proembryo. The section was cut not exactly in the median plane, and the figure shows what appears to be a large vacuole near the point of attachment of the embryo. Examinations of the neighboring section show that this is not a vacuole, the only visible vacuole present being in the neighborhood of the dividing nucleus. When the first wall is formed, however, vacuoles occur in both cells, and as the further history of the embryo is traced, the greatest number of these are to be found at and near its base.

The second division of the embryo occurs in the basal cell, so that the cell-walls of the pro-embryo are formed in basipetal succession. Nörner separates the grass embryos into three groups based on the direction taken by the first two walls. His "Type I" may be represented by figure 31, in which the first wall is at right angles to the long axis of the embryo, and the second parallel to it. Figure 32 represents "Type II" of Nörner in which the first wall is at right angles to the long axis of the embryo, but the second wall cuts this at an acute angle. Such embryos as that shown in figure 30 fall under "Type III". In this embryo the first wall is at an acute angle with the long axis of the embryo, and the second strikes the first at a sharp angle. As the figures indicate, the three types given by Nörner for all grasses studied by him are present in *Avena fatua*. Of these types the first is perhaps the most common; when the others are met in old embryos, the cell formation is so confusing that it practically defies solution.

The third cell-wall is formed in the distal cell of the proembryo, bisecting it parallel to the long axis of the proembryo, and is the first cell division belonging to the embryo proper (fig. 30). The fourth division is a transverse wall formed in the basal proembryo cell and cuts off the suspensor. No subsequent division was observed in the suspensor cell. At this stage in the development of the embryo there are four segments and five cells. There are two distal cells in the first segment, and between them and the suspensor two superimposed cells, of which the second belonged to the proembryo, and the third was derived from the basal proembryo cell, and is therefore not homologous to the cells above. For the sake of clearness in tracing its history in the developing embryo this last is designated as segment three.

The growth of the embryo is such as to obliterate these primary divisions, but a comparative study shows that probably the cotyledon and stem-apex are derived from the first segment, the hypocotyl and the initials which give rise to the root-cap, the cortex, and the dermatogen of the root from the second, and the coleorhiza from segment III. This is practically the conclusion of Nörner (l. c). As the boundary between the first and second segments particularly, in the advanced embryo, however, is not at all clearly defined, it was not possible for me to determine whether the stem-apex arose from the first segment, as in *Lilæa* (Campbell) and others, or from the second, as in *Alisma* (Schaffner, 1897).

In connection with the origin of the members of the embryo it is interesting to note that the position of the root and of the stem-apex in the embryo are the same with relation to the vertical as in the mature plant (which of course is the case in anatropous ovules in general). The reaction of the embryo to the influence of gravitation can here be traced to the one-celled stage. Experiments might be devised which would show not only the immediate influence of gravity on the embryo, but also which would give some grounds on which to base a plausible hypothesis to account for the anatropous condition of the ovule in this and in other plants where this condition occurs, and also its relation to the embryo.

Continuing the history of the development of the embryo, the next wall to be formed after the suspensor is cut off, the fifth wall in the embryo, is a vertical one in the second segment. Up to this time in the growth of the embryo the succession in cell formation is quite regular, but after this it varies considerably. The next wall to be formed is generally a vertical one in segment III, making a seven-celled embryo (fig. 33). This segment does not, however, always divide before quadrants are formed in the first segment. Quadrants are formed in segment I first, but there is no regularity in the quadrant divisions of the other primary segments. In some embryos quadrants are formed with regularity in all the primary divisions of the embryo, beginning with the distal primary segment; but in others, as in the embryo from which figure 35 was drawn, segment III has divided only once, although quadrants had been formed in the second segment, and in the first, octants. Segments I and II show greater regularity in cell formation than the third segment in the early as well as in the later stages in the growth of the embryo.

Octants are formed in the distal segment by anticlinal walls which strike the quadrants at an acute angle, generally below the middle, and not as stated by Nörner, at right angles to them. Of the octants thus formed the four uppermost form part of the dermatogen and divide subsequently by anticlinal walls only. The octants are usually formed as figure 35 indicates, while segment II is yet in the quadrant stage. This is, however, not at all uniform, and periclinal walls are sometimes met in the second segment before the octants are completely formed (fig. 36).

As just stated, the first periclinal divisions occur in the second segment. These are followed by similar division walls in the end segment. Segment III, in which the divisions are very irregular, does not take part in the periclinal divisions above mentioned. The plerome is cut off as in *Lilæa* (Campbell, 1898) in the two end segments at about the same time. This was found also in the grasses by Nörner (l. c.). In some cases in *Avena* it occurs, at least, in the end segment first (fig. 38).

An examination of the cells of the young embryo shows an increase in number and size of the vacuoles in the micropylar end. This peculiarity, together with the irregularity of cell divisions, serves in a way to mark the descendants of the third segment.

The suspensor, which is formed when segment III is cut off, remains small, does not divide, and plays an inconspicuous part in the history of the embryo. A large vacuole appears early in that part of the suspensor which touches the micropylar end of the embryo-sac. The protoplasm in the distal end of this cell (i. e. of the suspensor cell) rounds itself off, a membrane separates it from the large vacuole, and thus the embryo is attached to the micropyle by the proximal ends of the side walls of the old basal cell. The dotted lines in figures 33 and 34 indicate this attachment. The embryo remains connected with the micropyle in this manner until about the time when the primary tissues are differentiated, and then the attachment is broken and it lies free in the embryo-sac. The suspensor cell persists to form the end of the coleorhiza. It was not seen to divide, but it is not unlikely that in old embryos it may undergo a few irregular divisions.

The behavior of the suspensor resembles that of *Sparganium* (Campbell, 1899), but not of *Lilæa* (Campbell, 1898) and *Alisma* (Schaffner, 1896), in which the suspensor becomes a large and important absorbent organ. The degeneration of the suspensor of *Avena* is doubtless associated with the development of the endosperm cells, which closely invest the embryo, as well as with the prominent synergidæ which here, as in the wheat (Koernicke), serve to nourish the embryo in its youngest stages.

After the primary tissues are cut off, the embryo increases in size, mainly in length, by growth which is almost wholly confined to segments I and III. The embryo is club-shaped, pointed at the micropylar and blunt at the distal end. The periblem and plerome cells undergo few longitudinal divisions, dividing mostly by transverse walls. This makes the boundaries of the primitive segments difficult to trace. Cross-sections through the middle of the embryo show a plerome of about eight cells surrounded by a periblem two or three cells thick. The two are very similar, being composed of relatively large cells. The dermatogen is made up of regular and comparatively small cells. A cross-section near the micropylar end, through segment III, shows a greater irregularity in the structure of the dermatogen and internal tissues, which are not differentiated into plerome and periblem.

After the primary tissues are differentiated there are three very well-marked periods of growth, in which different sections of the embryo take part. The first is that succeeding the differentiation of the primary tissues and extends to the appearance of the stem-apex as a rounded elevation of the epidermis on the posterior surface of the embryo, and includes mainly the descendants of segments I and III. The second period is the elongation of that portion of the embryo which is above the stem-apex, the cotyledon, which takes place soon after the appearance of the plumule and plumule-sheath. The third occurs in the region of the radicle, in the descendants of the second segment of the proembryo, and takes place after the cotyledon has elongated. After these periods of growth and before the maturation of the embryo, plumule, cotyledon (scutellum), and root develop and grow simultaneously, retaining the same proportions. These periods of growth correspond very well with the further differentiation of the tissues of the embryo.

When the stem-apex is first discernible (fig. 41), the embryo is already relatively large, and all traces of its primitive segments are quite obliterated. The embryo at this period is oval with an obtuse cotyledonary and a sharp tapering radicle end. In cross-section, the embryo has changed from circular to oval. The stem-apex appears on the posterior side of the embryo about one-third the distance from the cotyledonary end, and becomes surrounded by a low ridge of tissue. From this, on the side of the stem-apex opposite, springs the epiblast, and on the cotyledonary side merely an augmentation of the boundary which separates cotyledon and plumule (fig. 41). An examination of the tissues at this stage of the development of the embryo shows several rows of elongated plerome cells in the cotyledon enclosed by a periblem of large and rather irregular cells. The epidermis of the cotyledon is beginning to assume the palisade-like structure it later develops as an absorbing organ. The elongation of the plerome cells is continued to the region of the stem-apex, but is not found in the root. This differentiation of the plerome is connected with the sudden shooting up of the cotyledon, and doubtless these elongated cells function as food carriers from the cotyledon to the developing plumule. The differentiation of corresponding tissues in the root occurs at a much later period, but the primary root tissues are already well defined. The group of cells at the end of the plerome cylinder, which give rise to the root-cap and to the dermatogen and cortex of the root, can be easily distinguished. The plerome initials are not developed until later; they do not, in fact, appear until one or two of the leaves of the plumule are cut off, and the embryo is approaching maturity. The plerome of the root is continuous with that of the cotyledon and that of the stem; the cortex and dermatogen of the root are continuous with the periblem of the embryo. A cross-section of the embryo through the region of the root shows a rather large central plerome-complex, as yet undifferentiated, surrounded by a periblem two or three cells in thickness, the outermost layer of which is beginning to take on the characters of epidermis. Surrounding all of these are one or two rows of cells which are the subepidermal cells of the embryo, enclosed in the dermatogen of the embryo.

A somewhat older embryo shows the third stage of growth, that is, the elongation of that part of the embryo within which is the root. This exhibits at the same time a further differentiation of the tissues of the root. A greater number of cells than before has now been cut off from the initials which give rise to the root-cap (by which this organ is very well marked) and to the extra-plerome root tissues. The plerome initials also have become well defined.

The tissues of the radicle correspond to those of the root-tip of the mature plant, and agree closely with those of *Hordeum* figured by Strasburger (1898). The region below the root-cap is made of large, irregular cells, with little protoplasmic contents. These form the coleorhiza of the mature embryo.

After the epiblast has been cut off, there appears on the cotyledonary side of the plumule, and just within the ridge of tissues spoken of above as surrounding the stem-apex

(p. 348), an outgrowth which partly and later entirely encircles it. This is the plumule-sheath. Subsequently a leaf, the first one, appears on the side of the stem-apex opposite the cotyledon, which agrees with the position of the first leaf in *Hordeum* (Lermer and Holzner, 1888). The plumule and first leaf thus appear precisely as the leaves in the mature plant, alternating on the stem.

The homologies of the scutellum, epiblast, and plumule-sheath have been abundantly discussed by many writers (see Introduction), and will only be touched upon in this paper. The scutellum is generally regarded as the cotyledon. Some authors (1) believe the epiblast to be part of the cotyledon, (2) others that it is simply a projection of the nature of a trichome from the hypocotyl, and (3) still others as a second rudimentary cotyledon. The plumule-sheath has been explained in various ways: (1) it is looked upon as an outgrowth of the hypocotyledonary internode, (2) it is regarded as a third leaf alternating with the epiblast, and (3) finally as a ligule-like growth proceeding from the scutellum. My observations on the embryo of *Avena* lead me to agree with Kennedy (l. c.) in his interpretation of the homologies of the epiblast and of the plumule-sheath. That is, the epiblast can probably be considered to be a second cotyledon, although it is not homologous to the true cotyledon, and the plumule-sheath may be regarded to be a ligule-like growth proceeding from the base of the cotyledon, forming an integral part of it, and to be homologous to the ligule of the grass blade.

While the plumule and plumule-sheath are forming and about the time of the growth in the region of the radicle (referred to as the third period of growth), the cotyledon begins to increase in length and in breadth to form the scutellum of the mature embryo. An examination of the epidermis on the side of the cotyledon next to the endosperm shows that the palisade-like cells, which are characteristic of the dermatogen of the scutellum in grasses, are already formed. These cells in *Hordeum* (Lermer and Holzner, 1888) exude an enzyme which dissolves the starch and proteids of the endosperm and renders them capable of being absorbed by the embryo in its germination. My attention has been called to the great similarity in appearance and in function between the epithelial cells of the scutellum of grasses and the cells at the tips of haustoria in certain phanerogamic parasites. The likeness between them and the epidermal cells in the haustorium of the Yellow Dodder is striking (Peirce, 1893). Both are epidermal cells modified to extract food from foreign tissues, and both exude solvents which can dissolve carbohydrates and proteids. A further and more careful comparison would be of importance, and might lead to some definite knowledge as to the reason of the peculiar parasitic habit assumed by the cotyledon of grasses.

As the region below the stem-apex increases in length, the epiblast, which was at first connected intimately with the plumule-sheath, becomes more and more removed from it toward the radicle end of the embryo. The epiblast increases somewhat in size although it is never as conspicuous an organ in *Avena* as in many other grass embryos. The epiblast is composed wholly of large parenchymatous cells and has no traces of conducting tissue.

VII. SUMMARY.

The principal points in this paper may be summarized as follows:—

I. (*a*). The spikelet branches sympodially, the flower and finally the ovary terminating the parent axis.

(*b*). The lodiculæ and the upper palet originate in the same rudiment.

(*c*). The awn of the lower glume appears before its lamina, the latter being an outgrowth from it. Thus the origin of the parts of the lower glume resemble that of the blade and ligule of the vegetative leaf.

(*d*). There is but a single carpel. This originates on the anterior side of the floral apex, which it encircles and finally encloses.

(*e*). According to the hypothesis put forward in this paper, attempting to explain the meaning and homologies of the lodiculæ in the flower of *Avena*, they are to be considered as homologous to the stipular lodiculæ of the rye. Perianthal lodiculæ are not present in the flower of the oat.

II. (*a*). The earlier growth of the stamen is mainly intercalary in the anther; immediately before the pollen is shed the filament elongates and causes the anther to protrude from the flower.

(*b*). The archesporium is composed of a single row of cells originating in the periblem.

(*c*). Each spore mother-cell reaches to the tapetum; none being bounded only by its fellows.

(*d*). In the young anther three concentric rows of cells intervene between the loculus and the epidermis. Of these the tapetum and the middle series are resorbed, and the endothecium persists to form with the dermatogen the anther wall.

(*e*). In the mature pollen-spore the generative nucleus has already divided.

III. (*a*). The archesporium of the embryo-sac is of hypodermal origin.

(*b*). The sister cells (potential macrospores) are variously formed. The nucleus of the archesporial cell divides to form four sister nuclei. These may be separated as soon as formed by cell-walls, or (2) they may somewhat later be separated by the subsequent formation of walls, or (3) they may never become separated, walls never forming.

(*c*). The lowest sister cell becomes the macrospore.

(*d*). There are no tapetal cells in *Avena*.

(*e*). The antipodals multiply before fertilization of the egg to the number of 36 or more, and disappear as the endosperm develops.

IV. (*a*). The synergidæ serve to nourish the young embryo.
(*b*). The lumen of the embryo-sac begins to fill first in the region of the embryo.
(*c*). All but one or two layers of cells of the nucellus are resorbed by the developing embryo-sac.
(*d*). The outer integument of the ovule is destroyed; the inner persists as the seed-coat.
V. (*a*). The first two cell-walls (which mark off the proembryo) in the development of the embryo appear in basipetal succession, and show the three "Types" of Nörner.
(*b*). The cotyledon and the stem-apex are derived from the distal segment of the proembryo; the root, the root-cap and the periblem initials of the root from the middle segment; and the coleorhiza from the basal segment.
(*c*). The suspensor is separated from the embryo by the fourth wall; it does not subsequently divide.
(*d*). The primary tissues are cut off in the first and second segments only; the divisions of the third segment are very irregular.
(*e*). The organs of the embryo originate in the distichous manner characteristic of the vegetative leaves of grasses.
(*f*). The scutellum appears to be analogous to the haustoria of certain phanerogamic parasites.

In conclusion I desire to express my gratitude to the officers of the botanical department, to Dr. D. H. Campbell in particular, for helpful advice and encouragement to me while pursuing the study of *Avena*. I ought to add also that the work was nearly but not quite finished prior to Dr. Campbell's departure for Europe in June.

STANFORD UNIVERSITY,
August 31, 1899.

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EXPLANATION OF PLATE XLIX.

(Reduced about one-third).

Fig. 1. Longitudinal section of a young spikelet: × 57; *lg*, lower glume; *c*, carpel; ♀, young ovary; ♂, young stamen.

Fig. 2. Section of older spikelet to show the beginning of the lamina of the lower glume: × 57; *l*, lamina; other lettering as in fig. 1.

Fig. 3. Median longitudinal section of the primordium of a spikelet: × 320; *d*, dermatogen; *pr*, periblem; *pl*, plerome.

Fig. 4. A similar section, not quite median, showing an older floral rudiment: × 320; *st*, floral apex; *lg*, lower glume.

Fig. 5. Longitudinal section of apex of flower in which the upper palet (*up*) and lodiculæ (*lo*) appear: × 320.

Fig. 6. Longitudinal section of floral apex: × 320; lettering as above.

Fig. 6*a*. Longitudinal section of young ovule with carpel (*c*): × 320.

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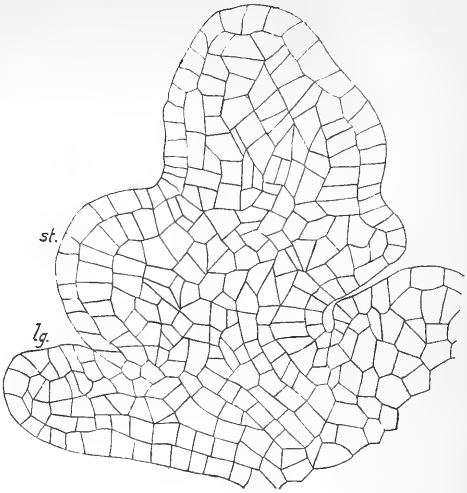

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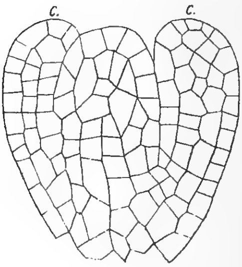

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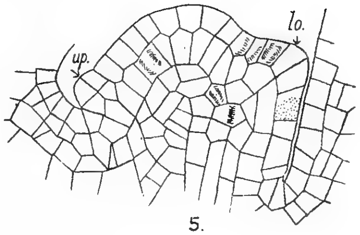

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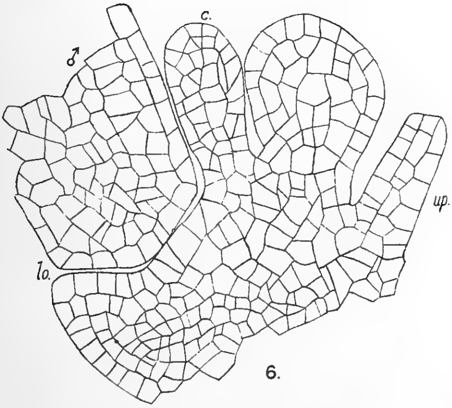

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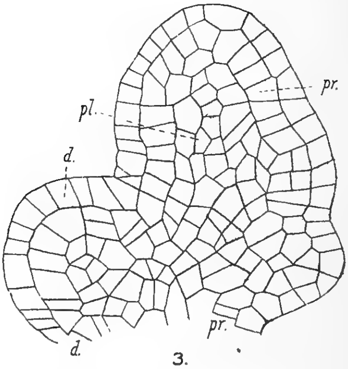

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AVENA FATUA L.

EXPLANATION OF PLATE L.

(Reduced about one-fourth).

Fig. 7. Longitudinal section, not median, of young flower showing a lodicula, and stamen: × 320; lettered as above.

Fig. 8. Cross-section of a young stamen: × 320.

Fig. 9. Cross-section of a somewhat older stamen than that represented in the preceding figure: × 320.

Fig. 10. Cross-section of stamen showing pollen mother-cells (*pm*): × 320.

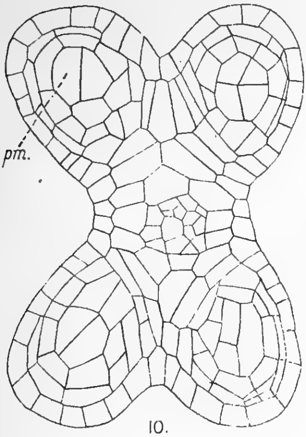
Fig. 11. Longitudinal section of stamen of the age shown in the preceding figure: × 320.

Fig. 12. Section of pollen grain showing one vegetative and two generative nuclei: × 320.

Fig. 13. Longitudinal section of ovule: × 320; *o*, outer integument; *in*, inner integument; *ar*, archesporial cell.

Fig. 14. An ovule with nucellus (*nu*); and archesporial nucleus that has divided once (forming two sister nuclei): × 320.

Fig. 15. Four sister nuclei: × 320.



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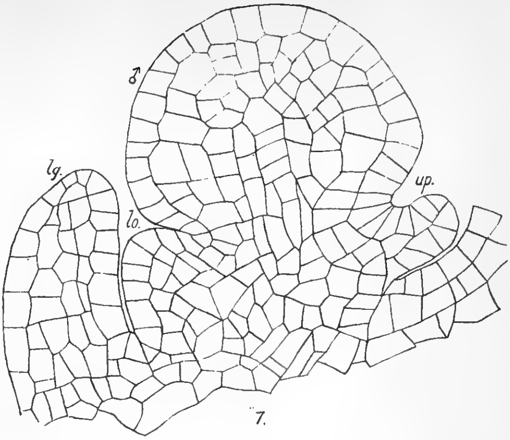

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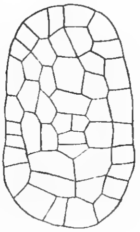

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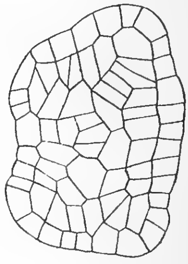

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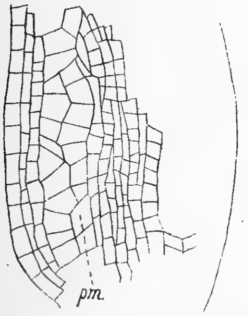

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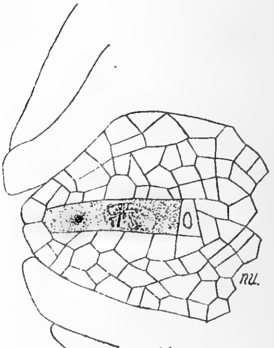

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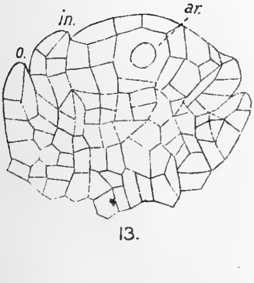

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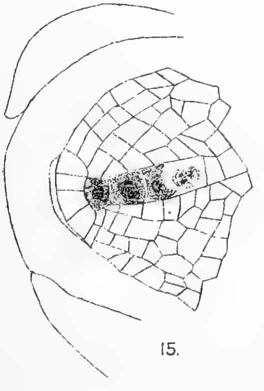

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AVENA FATUA L.

EXPLANATION OF PLATE LI.

(Reduced about one-fourth).

Fig. 16. Four sister cells in which cell-wall formation accompanied nuclear division: × 320.

Fig. 17. Sister cells of which the outermost, which shows in the adjacent figure (17*a*), has been absorbed: × 320.

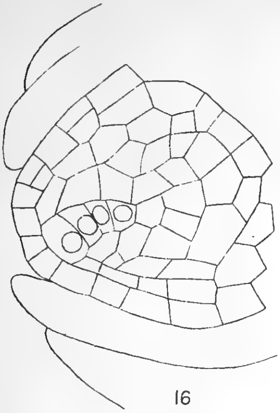
Fig. 18. Sister cells of which the outermost has been consumed: × 320.

Fig. 19. Longitudinal section of an ovule in which the macrospore has nearly absorbed the two middle sister cells: × 320.

Fig. 20. A four-celled embryo-sac: × 320.

Fig. 20*a*. Nucleus belonging to embryo-sac figured above.

Fig. 21, 21*a*. An eight-celled embryo-sac in which the polar nuclei are approaching each other: × 320; *ant*, antipodal cells; *e*, egg; *syn*, synergidæ; *p*, polar nuclei.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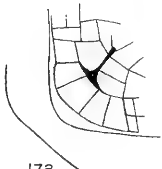
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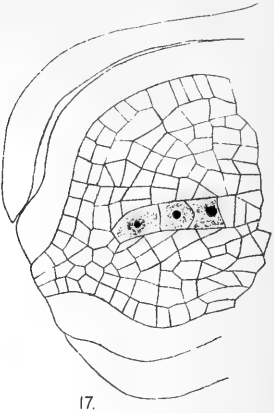
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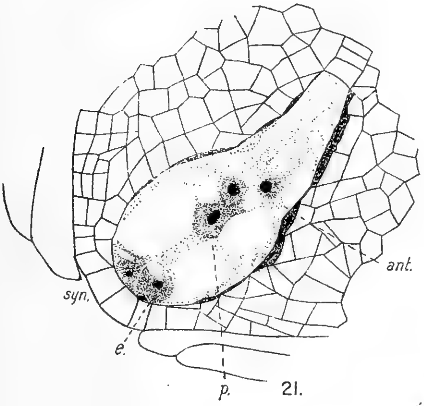

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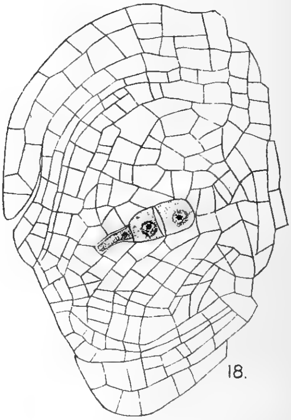
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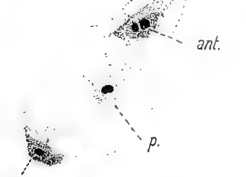

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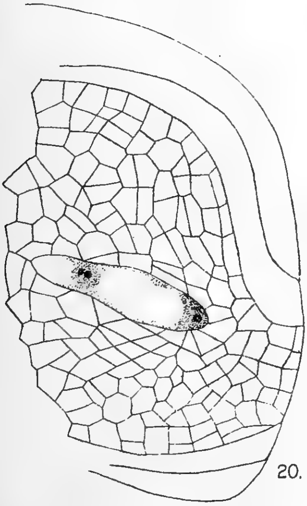
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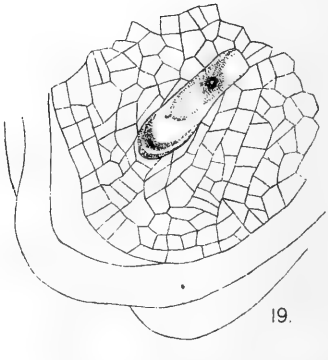
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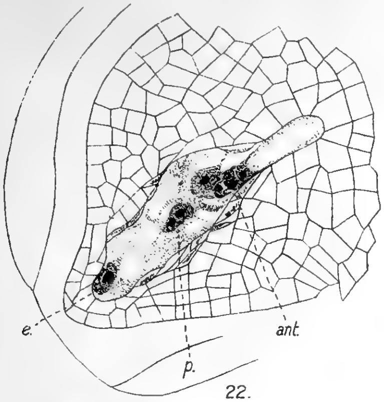
AVENA FATUA L.

EXPLANATION OF PLATE LII.

(Reduced about one-fourth).

Fig. 22.	Embryo-sac showing the beginning of the multiplication of the antipodals: × 320; synergidæ in the adjoining figure.
Fig. 22*a*.	Synergidæ of fig. 22.
Fig. 23.	An embryo-sac with young antipodal complex; shows the relation of the embryo-sac to the nucellus: × 110.
Fig. 24.	Detail of egg-apparatus: × 320; polar nuclei not yet fused.
Fig. 25.	A longitudinal section of ovule showing nucellus, embryo-sac, one-celled embryo, and the first division of the endosperm nucleus : × 110.
Fig. 26.	An ovule with nucellus, two-celled embryo, and dividing endosperm nuclei: × 57.
Fig. 27.	Antipodal complex of the embryo-sac shown in the preceding figure: × 80.
Fig. 28.	Antipodals that are undergoing disintegration: × 80.



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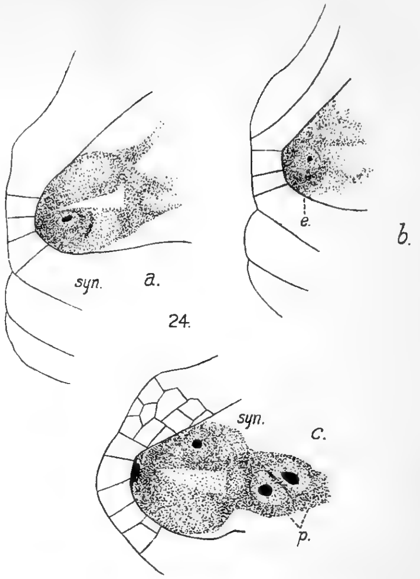

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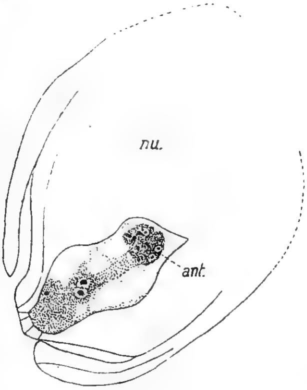

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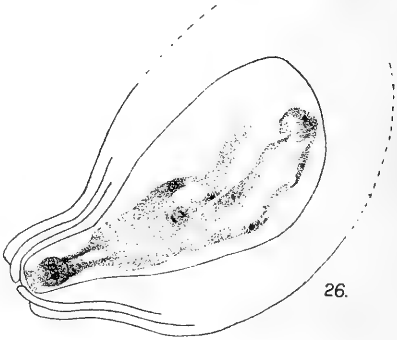

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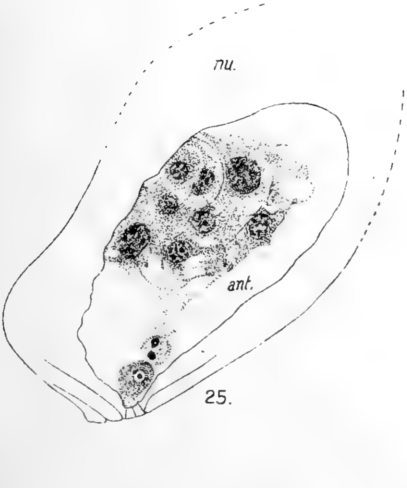

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28.

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Avena fatua L.

EXPLANATION OF PLATE LIII.

(Reduced about one-third).

Fig. 29. First division of the embryo: × 430.

Fig. 30*a*, *b*. Four-celled embryo; "Type III" of Nörner: × 430.

Fig. 31. Basal cell of embryo has divided to form the suspensor; "Type I" of Nörner: × 430.

Fig. 32. Same stage as fig. 31; "Type II" of Nörner: × 430.

Fig. 33. Seven-celled embryo; dotted lines indicate the connection of the embryo to the micropyle: × 430.

Fig. 34. Embryo in which quadrants have formed in the first segment: × 430.

Fig. 35. Embryo in which octants have formed in the first segment, quadrants in segment two, while the third segment has divided but once: × 430.

Fig. 36. Separation of plerome in the second segment: × 430.

Fig. 37. Differentiation of the plerome in the first two segments: × 320.

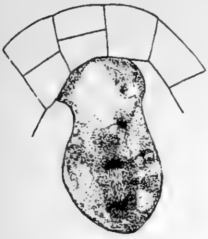
Fig. 38. Cutting off of the dermatogen: × 430.

Fig. 39. Section nearly median of young embryo, in which the primary tissues are cut off: × 400.

Fig. 40. Somewhat older embryo than that shown in the preceding figure: × 320.

Fig. 41. Nearly mature embryo; *st*, stem; *cot*, cotyledon; *r*, root: × 280.

Fig. 42. Cross-section of older embryo with the wings of the scutellum, the plumule sheath, and young leaves showing: × 140.



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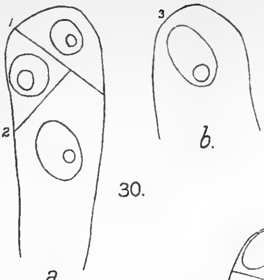

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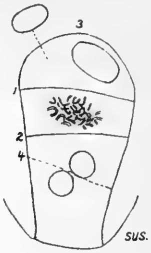

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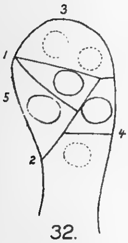

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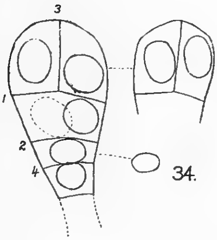

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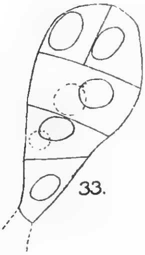

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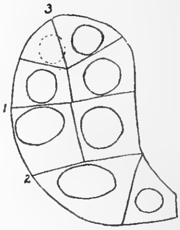

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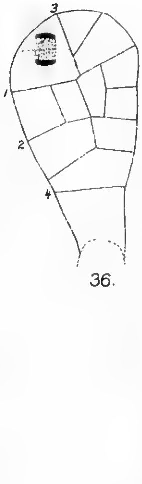

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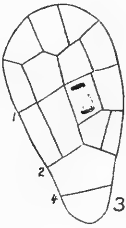

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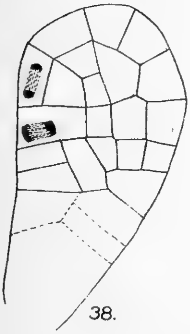

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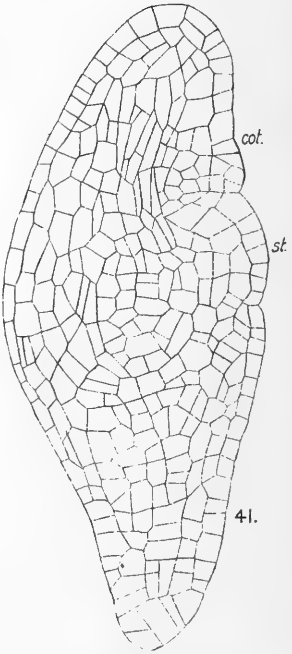

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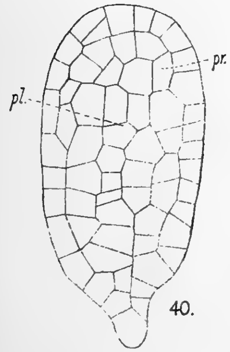

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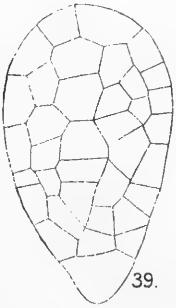

39.

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