ORGANOGRAPHY OF PLANTS

ESPECIALLY OF THE

ARCHEGONIATAE AND SPERMOPHYTA

BY

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AUTHORIZED ENGLISH EDITION

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PART II

SPECIAL ORGANOGRAPHY

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PREFACE TO THE GERMAN EDITION

THE aim of the Second Part of this book requires no exposition.

The large space devoted to the Bryophyta receives its justification in the fact that these plants offer an easily accessible and easily cultivated material for Experimental Organography, and that they, especially the Hepaticae, show particularly clearly how by different paths complex configuration has been reached from simple beginnings. Earlier accounts of these plants[1] have dealt with them almost exclusively from the purely formal standpoint, and in this offer a contrast with the work of the great bryologist of the eighteenth century, Hedwig, who was untrammelled by the limiting concept that has attached to the terms 'Morphology' and 'Physiology[2].' How incomplete is our knowledge of the phenomena of life of this group is everywhere apparent.

To give a comprehensive exposition is always a forbidding task; I hope that my readers will not consider the many new results of investigation[3] and the interpretations that are given in this book as a 'crambe biscocta,' and that what I have said may lead to new investigations.

To prevent misunderstanding I may say that teleological expressions are only used for shortness. My position with regard to the question of adaptations is fully set forth elsewhere[4].

The nomenclature of the Bryophyta is at present in great confusion. In respect of it I adopt a conservative attitude, and regard as a nuisance the practice of changing plant-names which have been long in use and appear in fundamental works like those of Hofmeister and Leitgeb purely on the ground of a shadowy priority. Fortunately the practice appears to have over-reached itself.

K. GOEBEL.

Ambach, 1898[5].

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[1] The most complete account of the Group is that of Douglas Campbell, The Structure and Development of the Mosses and Ferns, London and New York, 1895. This book is full of details of minute anatomy obtained by microtome-methods, and is specially valuable because of the records of the author's own researches.

[2] Compare, for example, the Preface of his 'Descriptio et adumbratio microscopica-analytica muscorum frondosorum,' where he gives free expression to his teleological instincts. Neglecting the physico-theological tone of the work we find that a separation of form and function was to the author unthinkable.

[3] I wish here to acknowledge my indebtedness for material for these investigations to Dr. E. Levier of Florence and F. Stephani of Leipzig.

[4] See an address by me, 'Über Studium und Auffassung der Anfassungserscheinungen bei Pflanzen,' München, 1898.

[5] The year of publication of the First Section of this Second Part. The last section appeared in 1901.

PREFATORY NOTE TO THE ENGLISH EDITION

THE reasons for this translation are given in the Preface to the First Part.

In preparing for English readers this Special Part of Professor Goebel's book, which abounds in facts and interesting interpretations, titles have been prefixed to the paragraphs, and to them a key will be found in the extended Table of Contents. By this, and by the Index, it is hoped that reference to the book will be facilitated.

Professor Goebel has read all the proof-sheets, and has modified the text in several places, and added additional notes. The paragraphs upon germination of microspores (p. 612) have been rewritten, and new figures have been introduced.

On the title-page of and throughout the First Part the word Spermaphyta was used in conformity with custom. In this Second Part the word appears in the more correct form of Spermophyta.

I should have preferred in the translation to restrict the term 'flower' to its established signification of that sporangiferous shoot which is found in flowering-plants. The extension of the term in the text to the Pteridophyta—adopted also by some English writers—is apt to lead to ambiguity, and encourages other loose expressions such as 'seed' of ferns. A change in the direction I have indicated would have involved, however, in default of another general term in use by which to designate the sporangiferous shoot of Pteridophyta and Spermophyta, so many modifications in the text as to have caused me to transgress the guiding principle of the translation—to produce the work as nearly as possible as minted by the author.

I. B. B.

Edinburgh, 1905.

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CORRECTIONS.

Part I.

Page 5, line 12 from bottom, *for* If *read* It.

10, line 13 from top, *for* Bilbergia *read* Billbergia.

39, Fig. 14, *for* Mortiziana *read* Moritziana.

46, Footnote 1, *for* lacustre *read* palustre.

113, line 2 from top, *for* Strobilanthus *read* Strobilanthes.

190, line 19 from top, *for* Weigelia *read* Weigela.

210, line 5 from top, *for* stipelles *read* stipels.

256, line 18 from top, *for* moschatellina *read* Moschatellina.

260, lines 12 and 13 from bottom, *for* Jussiaea *read* Jussieuea.

264, Footnote, line 1, *for* pyracantha *read* Pyracantha.

Part II.

68, line 2 from top, *for* moschatellina *read* Moschatellina.

97, line 10 from bottom, *for* remain *read* remains.

157, Fig. 123, *for* transverse *read* longitudinal.

210, Footnote, *for* aquatica *read* aquaticum.

222, line 3 from bottom, for *emergencies* read *emergences*.

315, line 9 from top, *for* Amphicosmia Walkerae *read* Hemitelia (Amphicosmia) Walkerae.

315, line 4 from bottom, *for* Amphicosmia Walkerae *read* Hemitelia (Amphicosmia) Walkerae.

350, line 4 from bottom, *for* O. Struthiopteris *read* Onoclea Struthiopteris.

445, line 9 from top, *for* Pumilo *read* Pumilio.

469, line 16 from top, for *Vivipara* read *vivipara*.

478, line 4 from top, for *Rupestris* read *rupestris*.

478, line 3 from bottom, for *Dimorphum* read *dimorphum*.

479, line 13 from top, for *Polycarpa* read *polycarpa*.

575, line 15 from top, *for* ARRANGEMENT *read* ARRANGEMENTS.

624, top line, *for* megaprothallium *read* megaprothallus.

SPECIAL ORGANOGRAPHY

INTRODUCTION

I HAVE endeavoured in the general part of this work to depict in some examples the general relationships of the formation of organs in plants; I have now in this special part to describe these relationships in the several groups with more detail. Various considerations, especially those of space, compel me to restrict my attention to the groups which fall within the limited scope of this book, namely, the Archegoniatae and Spermophyta.

In conformity with general usage, I include amongst the Archegoniatae the Bryophyta and the Pteridophyta. We might directly link on to these the Gymnospermae, whose relations to the heterosporous Pteridophyta have been proved in recent times to be very close by the discovery of spermatozoids in the Cycadaceae, with which group perhaps other forms will have to be reckoned; but the combination of groups between which actual connecting members are not known must always be a matter of convenience, and I have therefore preferred to keep together under the term Spermophyta the whole of the plants that produce seed. At the same time we must remember that the chief classes of Spermophyta embrace lines of development as different as are those of the groups Pteridophyta and Bryophyta which make up the Archegoniatae.

When we compare any one of the natural series of these groups in their different members, the first question that arises is, what is the relationship between formation of organs and adaptation? In other words, are the *specific* marks which separate from one another the several species, genera, and so forth, within one series, of a purely adaptive nature as the extreme disciples of the 'natural selection' school hold, or are the specific and the adaptive marks separable? In my opinion there can be no doubt that the latter is the case. The formation of organs must naturally always stand in conformity with the furtherance of life, but the special stamp it bears in each group, in spite of all differences in the individual adaptive configuration, shows that the 'inner constitution,' if we may use this expression which cloaks our ignorance, plays the chief part; were it not so the profuseness of the formation of organs could not be understood. What special advantage should it bring to the Anthoceroteae that their chloroplasts possess pyrenoids which are not seen in other Hepaticae? Or, that the mucilage which protects their apical region arises in mucilage-slits instead of in club-shaped papillae? Or, that their sporogonia are not stalked? Or, that their sporogenous layer is laid down in a way different from that in other Hepaticae? Or, that their archegonia are always embedded, and their antheridia are developed in pits? All these are specific characters which cannot be reckoned as adaptations. On the other hand, the production of water-sacs by species of Dendroceros, after the fashion of Metzgeria saccata and other forms, is an adaptation; the same may be said of the arrangements for collecting water which Anthoceros exhibits in common with many other Hepaticae; and also of the tubers which some species of Anthoceros produce, as do the prothalli of Anogramme amongst the Filices. Many other examples in this and in other series might be given.

Seeing that the phenomena of adaptation repeat themselves in different groups in like manner, they naturally must appear more conspicuously in the First Part of this book than they can in this Special Part. The appearance of characters of adaptation, everywhere or almost everywhere in a group, in all its members, for example the structure of the thallus in the Marchantieae, must be considered rather as an accidental concurrence with the specific marks—a conformity which we can understand if we assume that the adaptation is a very old one, that is to say, it took place before the separation of the group into isolated forms which developed in different directions.

The structure of the sexual organs and an abrupt alternation of generations are characteristic of the Archegoniatae. The name is based upon the structure of the female sexual organ, which throughout the whole group has an essentially similar construction in its mature state. The antheridium is a cellular body provided with an envelope if it is not sunk in other tissue, and this envelope almost always consists of one layer of cells. The archegonium is flask-shaped and encloses a single egg which is fertilized by the spermatozoids—male elements swimming freely in water, and of characteristic configuration and special origin. The elongated configuration of these is probably an adaptation which fits them to penetrate the mucilage investing the egg[1]. The peculiar transformation of the cells which leads to the formation of the spermatozoids finds its counterpart, so far as is yet known, only in the Characeae. I cannot, however, go further into that subject here.

Experience has shown us that the nature of the *sexual organs* is of quite special importance for the characterization of the groups we are dealing

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[1] We find them in Volvocineae. See Part I, p. 28, Fig. 4.

with, and we must therefore ask in the first place whether there is to be found in their structure any indication of a common line of genetic connexion. The more recent investigations into the history of development of these organs have in the main neglected the mature stage; yet the manner in which, for example, the antheridia open in the Bryophyta is of no less importance than is the succession of cell-divisions.

It would be instructive to give a comparative account here of the structure and of the development of the sexual organs of all the Archegoniatae, but for the reasons stated we must discuss these organs separately in the two archegoniate groups—Bryophyta and Pteridophyta.

In the following pages our subject is dealt with in the two sections:—

I. Bryophyta.
II. Pteridophyta and Spermophyta.

FIRST SECTION

BRYOPHYTA

BRYOPHYTA

It has been customary from of old to subdivide the Bryophyta or Muscineae into the two classes of the Hepaticae or liverworts and the Musci or mosses[1]. Each class embraces a number of series which are in part sharply separated from one another; at the same time they have so much in common that their combination even to-day appears still useful. Between Hepaticae and Musci there are no transition-forms, as there are none between Bryophyta and Pteridophyta; and as there never were such transitions[2] their absence is not caused by their having died out. If the development proceeded from very simple nearly related forms in definite and divergent directions we ought always to find a partial correspondence only in the simplest forms, and as a matter of fact we find these, as will be shown in the following pages. All of the speculations upon the relationship between the Hepaticae and Musci, Bryophyta and Pteridophyta, and other groups, which are based upon the highly developed Archegoniatae are therefore products of fancy; they spring from the tendency of our imagination to assume connexions even where they are not directly proved, but they have no sufficient support in the facts of experience, and their sole value lies in the new points of discussion they create.

The two groups of the Bryophyta behave quite differently in the formation of their *vegetative organs*. Everywhere in the Musci we find one and the same type of differentiation of the members of the vegetative body—that of the leafy stem. In the Hepaticae there is much greater variety:—starting from simple thallose forms which in their differentiation of members are far behind many of the Thallophyta, for example Sargassum, we have a rich variety in the construction of the vegetative body and its adaptation to external relationships. We gain the impression that the Hepaticae, apart from the Anthoceroteae, are a younger group,

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[1] It was Hedwig (Theoria generationis et fructificationis plantarum cryptogamicarum Linnaei, Lipsiae, 1798) who, I believe, framed this classification. He divided (p. 119) the Musci into 'Frondosi,' including those whose sporangium usually has a lid, and 'Hepatici,' including those whose sporangium has no lid, but opens by longitudinal valves. Micheli originally gave the name 'Hepatica' to Fegatella conica on account of a fancied resemblance to the lobes of the liver. Linnaeus had placed Jungermannia and Marchantia amongst the Algae.

[2] See Part I, p. 19.

still in a condition of flux, as compared with the older more fixed Musci. This is, however, a purely subjective representation, as the facts of Palaeontology leave us completely in the dark. The soft Hepaticae especially are but little favourable to preservation as fossils, and it is impossible to say whether many of the impressions which are described as 'Algae' are not to be ascribed to the thallose Hepaticae.

The structure of the *sexual organs* on the other hand supplies, as has been already indicated, a resemblance between the groups, and this, when we consider it from the standpoint of the theory of descent, appears to be an inherited portion from common ancestors. In other words, if we assume a descent in general it follows that the vegetative organs must have been greatly changed in different directions, whilst the sexual organs have altered but little. It is clear from this that the endeavours to refer back the sexual organs to parts of the vegetative body[1] must be futile. Further, the construction of the sexual organs is not the same in all Archegoniatae, but is rather characteristic in the individual groups, yet does not always exhibit quite constant differences. The development of the archegonia in the Bryophyta is everywhere different from that in the Pteridophyta, and the explanation of this is, as I tried to show long ago, that these two complex groups have from a *very early* time developed in diverging directions, and it is therefore impossible to prove a *direct* affinity.

An exposition of cytological relationships is not within the plan of this book. I may merely mention that Farmer[2] found in the dividing nuclei of the sexual generation of Blyttia (Pallavicinia) decipiens *four* chromosomes, whilst in the asexual generation derived from the fertilized egg there are *eight*. The sporocytes on the other hand show in division only four chromosomes—a reduction to one half. It is probable that this difference in the nuclei of the sexual and asexual generations exists also in other Bryophyta[3] and Archegoniatae. From many points of view this is an important difference, and it is to be wished that it will receive ere long full elucidation.

In what immediately follows, the grosser relationships of configuration and the structure of the sexual organs of the Bryophyta are shortly described.

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[1] With the morphological value of 'caulomes' or 'trichomes,' see Part I, p. 17.

[2] Farmer, Studies in Hepaticae: On Pallavicinia decipiens, Mitt., in Annals of Botany, viii (1894), p. 35.

[3] Farmer has already proved this in Pellia epiphylla. See Annals of Botany, ix (1895), p. 488.

SEXUAL ORGANS OF BRYOPHYTA

1. *THE ANTHERIDIUM.*

1. Structure and Position. The mature antheridium has the same essential structure in Hepaticae and Musci. The special body of the antheridium is seated upon a stalk (Fig. 2), the length of which varies in evident connexion with the relationships of life of the plant. It is short in the antheridia of the Hepaticae if they are sunk in pits, and then, as we shall see, the mouth of the pit supplies frequently a mechanism for the ejection of the spermatozoids; it is long in Musci, where the antheridia are not closely enveloped by leaves but stand more or less exposed and protected only by paraphyses. Relatively long stalks are found in antheridia, which stand in the axils of leaves as in the acrogynous Hepaticae, and there they secure that the contents of the antheridium do not remain in the axils of the leaves when they are discharged. We find similar relationships amongst the Musci in the antheridia of Buxbaumia (Fig. 105), where they are enclosed in an envelope like a mussel-shell and superficially resemble the antheridia of Hepaticae. The configuration of the body of the antheridium is connected also with the distribution of the spermatozoids. The deeply sunk antheridia of the series of the Marchantiaceae and those of Monoclea are club-shaped, whilst they have a more spherical form when they occupy a more exposed position, as is the case in most of the Musci.

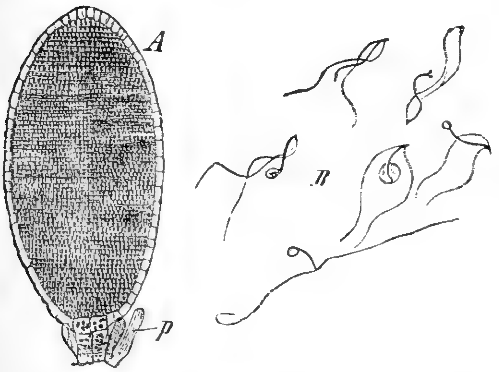

Fig. 1. Marchantia polymorpha. *A*, antheridium with mucilage-papillae, *p*, at its base. *B*, spermatozoids. *A*, magnified 90. *B*, magnified 600. After Strasburger.

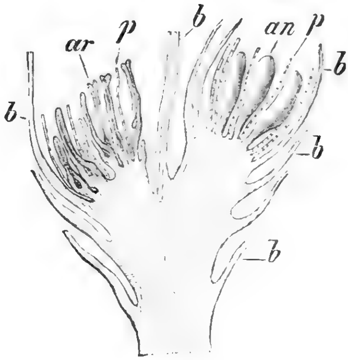

Fig. 2. Phascum cuspidatum. Stem in longitudinal section. *b*, leaves; *p*, paraphyses; *ar*, archegonium; *an*, antheridium. Magnified 45. After Hofmeister. Lehrb.

The body of the antheridium is composed of a wall investing a mass of spermatocytes. The spermatozoids[1] are always biciliate (Fig. 1). The

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[1] These were first described in Fossombronia pusilla by Schmidel, Icones plantarum, Norimbergae, 1747.

wall, which originally possesses chlorophyll, frequently shows in Hepaticae, such as Sphaerocarpus, Fossombronia, Anthoceros, and in many Musci abundant chromoplasts which give it a reddish or yellow-brown appearance, and we might with Stahl conjecture that this colouration promotes an increase of warmth to the antheridium. In support of the view that the colouration of the wall has a biological significance I may point out that in Sphaerocarpus the sac-like envelope in which the antheridia are enclosed has a reddish colour, and in Pellia the walls of the shallow pits in the thallus in which the antheridia are sunk is coloured frequently violet. The pits for the antheridia in Marchantia also are coloured violet. The wall of the antheridium is covered with a cuticle which is thicker in those which are exposed than in those which are in pits.

2. OPENING OF THE ANTHERIDIUM AND DISCHARGE OF THE SPERMATOZOIDS. The method in which the antheridia discharge their spermatozoids has not been much referred to in recent literature. If a ripe antheridium be touched with a drop of water it opens instantaneously and the spermatozoids are at once placed in favourable conditions. It has been commonly assumed that the wall of the antheridium is gradually ruptured at the apex through the pressure of its swelling contents[1] which then issue from it. I have satisfied myself, however, by the examination of a large number of antheridia of both Hepaticae and Musci that the wall plays an active part in the opening of the antheridium[2]. In most cases this is brought about by the same means as are employed in the annulus for the opening of the capsules of many Musci—a deposition of mucilage takes place in the cells, and this by its increase in volume through the absorption of water causes the dehiscence. So far as my investigations show there appear to be two types of opening in the antheridium of Bryophyta :—

(1) One cell or a sharply limited group of cells at the apex of the antheridium takes part in the opening; this cell or group of cells may be called the *opening cap*. This type occurs in the Musci with the exception of Sphagnum.

(2) No such limitation of the cells concerned in the opening is found, but a large number of cells of the wall take part in it. This type is found in the Hepaticae and in Sphagnum.

I shall now describe shortly a few examples of the opening of antheridia.

(*a*) **Hepaticae.** The opening of the antheridium of the Jungermanniaceae is brought about in the same way in all cases so far as we know. A deposition of mucilage takes place in the outside wall of the cells forming its wall, especially in the upper part of the antheridium. The

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[1] The wall of the spermatocytes becomes mucilage at a relatively early period.

[2] Goebel, Über den Öffnungsmechanismus der Moos-antheridien, in Annales du Jardin botanique de Buitenzorg, Supplement II (1898). The literature is cited here.

swelling of this mucilage stretches the cuticle, which finally splits. Frequently the cells of the wall separate from one another and curve in a direction the reverse of their original curvature (Fig. 5, 5). I have never observed that they act as 'ejaculatores seminis' as Gottsche suggested[1]. They may, however, remain in connexion with one another except at the point of splitting. In the series of Marchantiaceae I noticed a very great increase in the radial diameter of the cells of the wall of the ripe antheridium, which is here in a deep pit. In this case we have not to consider the tension induced by the cuticle of the antheridium, but that caused by the wall of the pit in which the antheridium is seated. The mouth of the pit is in many forms of this series raised above the surface as a projecting point, and this in my opinion has the same use as the nozzle of a syringe, and the wall of the antheridium acts like that of the india-rubber ball of a hand-spray. The emptying of the antheridium may also take place gradually, and drops containing spermatozoids are then found at the mouth of the pits, whence they can be either washed away or removed by small animals. The pit has then a definite function to perform in the ejection of the spermatozoids, and is not merely concerned with the protection of the antheridium[2]. We have as yet no certain knowledge of the method by which water gets from the outside into the narrow pits of the antheridiophore of Marchantia. Perhaps the mucilage which is formed in the pits by special mucilage-papillae (Fig. 1, *A*, *p*), and which accumulates at the mouth of the pits and so acts as a protection against dryness, may also act as an absorbent of water.

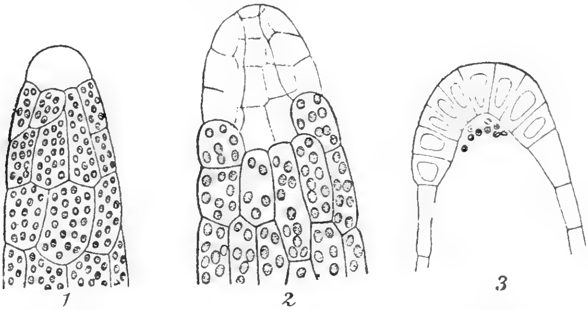

FIG. 3. Opening cap of the antheridium in Musci. 1, Funaria hygrometrica. Antheridium in profile; the opening cap consists of one cell. 2, Polytrichum. Emptied antheridium; the opening is in section. 3, Catharinea undulata. Apex of an antheridium in longitudinal section; the cells of the opening cap are marked by the deposition of mucilage in their walls.

(*b*) **Musci.** Funaria, Mnium, Catharinea, Polytrichum, were examined (Fig. 3). The process in all cases is the same excepting that the number

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[1] When an ejection of the contents of the antheridium occurs, as in Frullania, it is the sudden contraction of the previously stretched wall of the antheridium which causes this.

[2] In the Anthoceroteae the antheridia are laid down in intercellular spaces of which the covering is subsequently destroyed; the protection of the antheridia is in this case the only function of the pit.

of cells in the opening cap differs; in Funaria there may be one or two, in the others there may be more. The cap appears in water like a clear vesicle, as it was described and figured by Hedwig. The cuticle becomes greatly stretched and the cells of the opening cap suddenly burst and their contents pass either at first inwards to be subsequently discharged with the contents of the antheridium when the cuticle ruptures at the apex, or are discharged outwards at once if the cuticle at the apex ruptures earlier. In all cases a narrow opening only is formed which is bounded by the remains of the cells of the opening cap (Fig. 3, 2), and through this channel the slimy contents of the antheridium slowly pass out. There can be no doubt that the contraction of the previously stretched wall of the antheridium aids their passage, but at the same time their swelling into the form of a sausage is an important factor. The spermatozoids disperse afterwards when the mucilage in which they are embedded becomes more fluid.

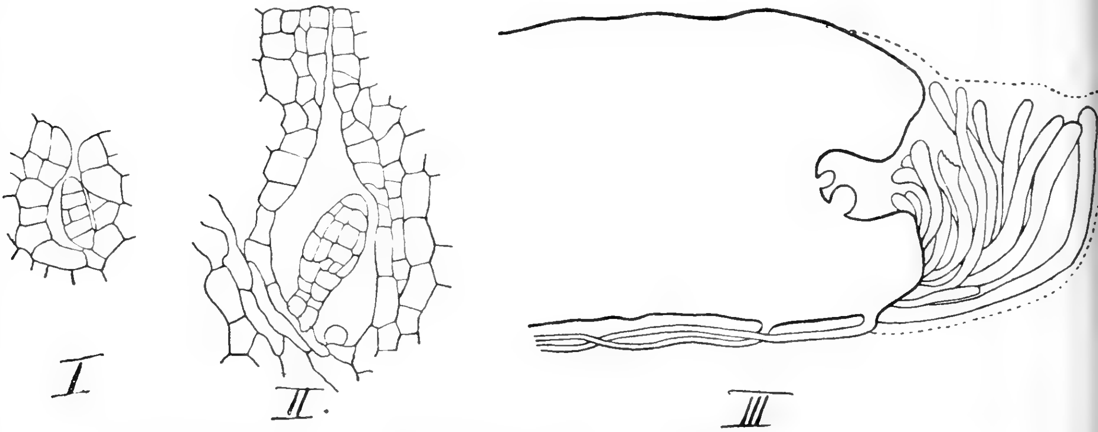

FIG. 4. Monoclea dilatata. *I*, *II*, young antheridium in a pit of the thallus. *III*, female plant in longitudinal section showing the inception of young archegonia in a pit behind the apex. Drawn by Ruge from material collected by me on the Cordilleras of the coast of Venezuela.

3. DEVELOPMENT OF THE ANTHERIDIUM. As we have such characteristic differences in the structure of the mature antheridium in the two classes of the Bryophyta it is not surprising that differences show themselves also in the manner in which they are built up out of cells. Are these differences then of systematic significance, and if so to what extent? We may say generally that they are of importance and the chief facts may be shortly stated here.

(*a*) **Hepaticae**[1]. Two types are exhibited, but they are connected by intermediate links:—

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[1] See Leitgeb, Untersuchungen über die Lebermoose, i-vi, Graz, 1874-1881; Satter, Beiträge zur Entwicklungsgeschichte des Lebermoosantheridiums, in Sitzungsberichte der Wiener Akademie, lxxxvi (1882); Douglas Campbell, The Structure and Development of the Mosses and Ferns, London, 1895. In this book the older literature is cited.

1. Construction by formation of transverse disks which is characteristic of the club-shaped antheridia in Riccieae and Marchantieae and of those of Monoclea.

This is the more primitive type, inasmuch as a separation of the wall from the inner cells of the antheridium takes place at a late period. Many tiers of cells arise, the lowermost of which goes to form the stalk (Fig. 4, *I*, *II*), and each tier becomes divided into quadrants and then the separation of the wall from the inner cells appears. We do not know what is the significance of the beak-like prolongation which is found in the antheridium of Corsinia.

2. Construction through growth in every direction as it is seen in the spherical antheridia of Jungermanniaceae and Anthoceroteae.

Sphaerocarpus may be first mentioned as it shows a transition from the first to the second type (Fig. 5, 1, 2). The mother-cell of the antheridium which has become club-like in form is divided by three cross-walls (1, 2, 3 in Fig. 5, 1, 2); the lowermost cell forms the stalk, the next lowest forms the under portion of the wall, the upper two cells divide into quadrants and make the body of the antheridium. In the other Jungermanniaceae the body of the antheridium usually is derived from *one* transverse disk. This commonly divides by a first longitudinal wall (1 in Fig. 5, 3) into halves; two longitudinal walls (2, 3 in Fig. 5, 3) then cut this obliquely; and the manner in which the inner space is formed is shown in Figure 5, 3. We do not know the reason for this remarkable deviation[1] from the customary formation of quadrants, but it is not quite constant, and Leitgeb[2] found the normal formation of quadrants in the antheridium of Scapanieae.

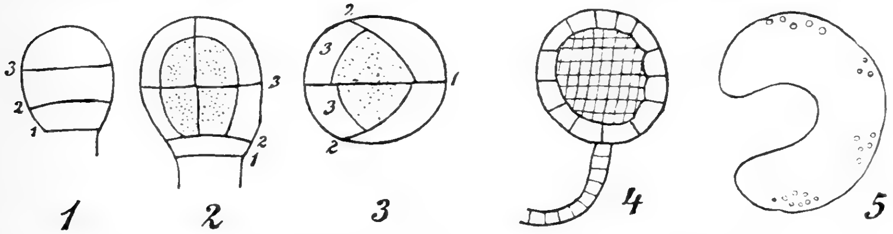

FIG. 5. 1 to 3, diagrams illustrative of the cell-division in the formation of the antheridium of Hepaticae. 1 and 2, Sphaerocarpus terrestris. 3, view from above of the apex of a young antheridium of one of the Jungermanniaceae. 4, diagrammatic representation of an antheridium of an acrogynous Jungermannia in longitudinal section. 5, Blyttia Lyelli. Cell from the wall of an opened antheridium. The side which is now concave was originally the convex outer side. Highly magnified.

(*b*) **Musci.** The cellular construction of the antheridia appears to be fairly uniform in this class so far as we as yet know[3], and the body of the antheridium is built up through the formation of a two-sided apical cell. The divisions through which the separation of the cells of the wall and the inner cells comes about correspond with those of the antheridium in Jungermanniaceae (Fig. 5, 3). In many forms the antheridium has a stalk which is a short cell-row in Nanomitrium

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[1] It is also found in the antheridium of Musci.

[2] Leitgeb, Untersuchungen über die Lebermoose, Graz, ii (1875), p. 43.

[3] For an account of the divergent type of Sphagnum see Leitgeb, Wachstum des Stämmchens und Entwicklung der Antheridien bei Sphagnum, in Sitzungsberichte der Wiener Akademie, lix. 1 (1869). In my view the case of Sphagnum requires further investigation. Its mature antheridium belongs to the type of the Hepaticae.

and other Phascaceae but a very long one in Buxbaumia (Fig. 105); in others the stalk is a short cell-mass.

2. *THE ARCHEGONIUM.*

1. Structure and Position. The form of the archegonium is everywhere uniform in so far as it consists of a neck which provides the path for the spermatozoids attracted by a substance exuded from its open mouth, and of a venter which contains the egg (Fig. 6). The Anthoceroteae (Fig. 83, 1) differ from all other Bryophyta in having their archegonia sunk in the thallus, and this of course involves a modification in the history of their development which in Anthoceros itself approaches in some measure the type of development which is exhibited by the Pteridophyta.

The 'free' archegonia of the other Bryophyta have either no stalk as in Riccia or a stalk (Fig. 2) which may be short or long and is longest in some Musci. The stalk, unlike that of the antheridium, has not merely the function of bringing the neck of the archegonium into a favourable position, but, where it is massive, is destined to be of use to the embryo, and after fertilization has taken place it may grow to a considerable extent (see Fig. 119). The embryo bores in the first instance into the stalk and may go no further, as in Nanomitrium (Fig. 120), or, as in other forms, it may penetrate into the tissue beyond the stalk. This subject will be discussed when the relationships of the embryo in Calypogeia are described[1].

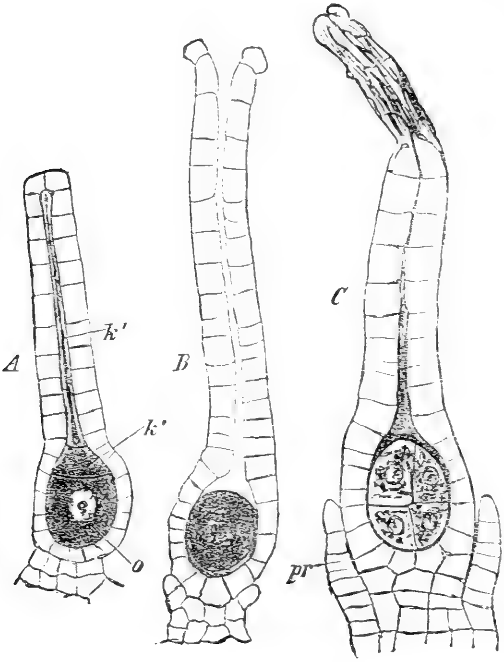

Fig. 6. Marchantia polymorpha. *A*, young archegonium. *B*, mature archegonium. *C*, archegonium of which the egg has been fertilized and a pluricellular pro-embryo is formed. k', neck-canal-cells already disorganized as a mucilage; k'', ventral canal-cell; *o*, egg; *pr*, perianth. Magnified 540. After Strasburger.

The mature archegonium possesses a neck traversed by a row of cells, the neck-canal-cells (Fig. 6, *A*, k') and a venter enclosing a central cell. This central cell divides by a transverse wall into an upper cell, the ventral canal-cell (Fig. 6, *A*, k''), and an under cell, the egg (Fig. 6, *A*, *o*); these two

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[1] See p. 90.

cells are often equal in size but commonly the egg is the larger. We do not know the significance of this division or whether the ventral canal-cell has any definite function such as that of the secretion of the attractive substance for the spermatozoids. Hypothetically we may regard the ventral canal-cell as the vestige of a second egg, but we know nothing definitely about it, yet its constant occurrence points to its possession of a physiological rôle. The neck-canal-cells furnish the mucilage which fills the canal of the neck after the opening of the archegonium. Their protoplasm, so far as it is not employed in the formation of mucilage, dies off, as does that of the ventral canal-cell. I have no doubt that the mucilage filling the canal of the neck at first protects the egg against contact with water. This is a function which very often attaches to mucilage even where it lies within a cell-membrane[1].

2. OPENING OF THE ARCHEGONIUM. The opening of the archegonium is brought about by the separation of the apical cells of the neck, and perhaps processes similar to those observed in the case of the antheridium occur here also.

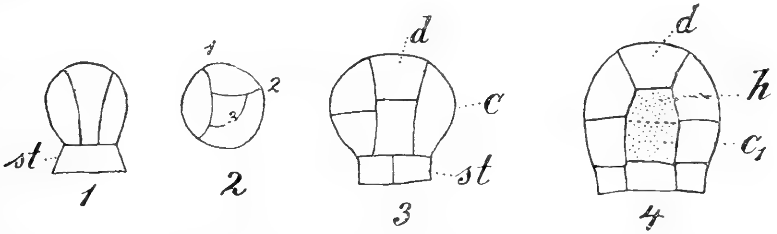

FIG. 7. Scheme of the development of the archegonium of the Hepaticae. 1, 3, and 4 in longitudinal section. 2, from the top. *d*, lid-cell; *st*, stalk-cell; *c*, primary central cell; the dotted line from *c* in 3 and c_1 in 4 should run to the central cell of the figure; *h*, mother-cell of the neck-canal-cells; c_1, secondary central cell which divides into ventral canal-cell and egg.

3. DEVELOPMENT OF THE ARCHEGONIUM. Passing now to the development of the archegonium, it may be asked if this conforms in any measure with that of the antheridium. I have elsewhere shown[2] that it is possible to establish amongst the lower plants homologies in the development of the male and the female sexual organs, but that the higher the differentiation the more do differences appear from the beginning in the construction of the two kinds of sexual organs. In the Bryophyta such differences exist, but they do not make impossible the occasional occurrence of malformations[3] which are half archegonia, half antheridia; even as amongst the Spermo-

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[1] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 233. See also Schilling, Anatomisch-biologische Untersuchungen über die Schleimbildung der Wasserpflanzen, in Flora, lxxviii (1894), p. 280.

[2] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 416.

[3] See Lindberg, Öfvergång af honorgan till hanorgan hos en bladmossa, in Öfversigt af Kongl. Vetenskaps-Akademiens Forhandlingar, Stockholm, 1879, No. 5.

phyta the appearance of pollen has been observed in ovules[1]. The presence of divisions like those in the antheridium within the mother-cell of the archegonium in the Bryineae is not to be considered as indicating a conformity of the formation of the archegonium with that of the antheridium, because they have nothing to do with the construction of the special body of the archegonium but only with that of its stalk[2].

How far the development of the archegonium[3] is alike in the two series of the Bryophyta and within each series is a matter in regard to which at present there is no agreement amongst observers.

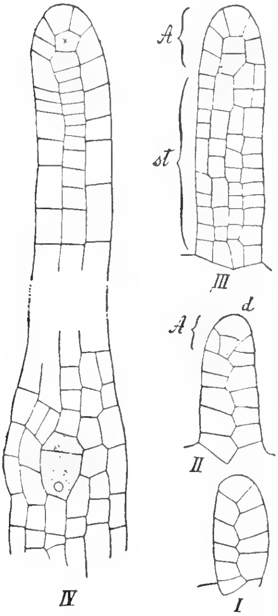

FIG. 8. Mnium undulatum. Development of the archegonium. *I, II, III, IV*, show successive stages. The archegonium, *A*, begins to be laid down in *II*. *d*, lid-cell; *st*, stalk, not shown in *IV*; × in *IV*, the lid-cell which acts as an apical cell.

(*a*) **Hepaticae.** The following is the scheme of development. The archegonium takes origin from a single cell here as everywhere else. This divides into a lower cell (Fig. 7, 1, *st*) which limits the archegonium below by forming the usually short stalk, and an upper cell. The upper cell divides by three longitudinal walls (Fig. 7, 2) into a central cell and three peripheral cells; the central cell then divides by a transverse wall into the lid-cell (Fig. 7, 3, *d*), and the primary central cell (Fig. 7, 3, *c*). The primary central cell next divides by a transverse wall into two cells (Fig. 7, 4, *h*, c_1). The cell *h* is the mother-cell of the neck-canal-cells and forms them by repeated transverse divisions. The cell c_1 is the secondary central cell and divides into the ventral canal-cell and the egg. The peripheral cells form the neck, the lid-cell *d* repeatedly dividing[4]. In the Anthoceroteae the general scheme is the same, but the mother-cell is sunk in the tissue and the mother-cell of the neck is cut off from the lid-cell *d*; this cell *d* has therefore no further share in the construction of the neck because this does not reach above the surface, but it divides by tranverse walls into four cells lying in one plane which separate from one another at a later period.

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[1] Compare the case of Begonia: Goebel, Beiträge zur Kenntniss gefüllter Blüten, in Pringsheim's Jahrbücher, xvii (1886), p. 246.

[2] Since this was written I have come to the conclusion that the homology between the construction of the sexual organs in Musci can be traced to their inception and that the archegonium corresponds to one half of the antheridium. See Goebel, Über Homologien in der Entwicklung männlicher und weiblicher Geschlechtsorgane, in Flora, xc (1902), p. 295.

[3] See Janczewski, Vergleichende Untersuchungen über die Entwicklungsgeschichte des Archegoniums, in Botanische Zeitung, xxx (1872), p. 377; Douglas Campbell, The Structure and Development of Mosses and Ferns, London, 1895; Gayet, Recherches sur le développement de l'archégone chez les Muscinées, in Annales des sciences naturelles, sér. 8, iii (1897), p. 161, where details regarding the number of canal-cells and so forth are given.

[4] Notwithstanding Janczewski's statement to the contrary. See Gayet, op. cit.

(*b*) **Musci.** According to the statements of Janczewski, Kühn, and Campbell, the development of the archegonium of Musci differs from that of the Hepaticae chiefly in this, that the neck-canal-cells do not arise by the division of *one* mother-cell but are produced in part by a peculiar growth of the lid-cell. This lid-cell acts as an apical cell (Fig. 8, *IV*, $^+$) and furnishes segments having walls parallel respectively with the axis and the base of the archegonium, the outer cells thus formed become cells of the wall of the neck, the inner ones become neck-canal-cells. Gayet contradicts this. According to him the course of the development is in essentials like that of the Hepaticae, that is to say, the lid-cell forms new cells of the wall of the neck but no internal segments. From my examination of Mnium undulatum (Fig. 8) I cannot confirm what Gayet says: I find in this plant confirmation throughout of the statements of Janczewski and others, and that the archegonium of the Musci is distinguished from that of the Hepaticae by its peculiar apical growth (Fig. 8, *IV*, $^+$). The stalk of the archegonium of Mnium undulatum which I select as an example is very strongly developed. It is furnished with plastic material which the young embryo uses up, and it contains also a definite nutritive tissue for the embryo, which after fertilization increases in amount; this feature which appears to have been hitherto overlooked corresponds to what we find in the development of the seeds in the Spermophyta. The primordium of the stalk precedes that of the body of the archegonium. In figure 8, *I*, the primordium of the stalk growing by means of a two-sided apical cell is alone visible. Out of its terminal cell the primordium of the body of the archegonium proceeds (Fig. 8, *II*, *A*), and this increases by apical growth in the way described.

From what I have said it will be seen that the relationships in the process of cell-construction, as well as those of the mature structure of the sexual organs, are characteristic of the large group of the Bryophyta. They have 'varied' less than has been the case in the vegetative organs.

HEPATICAE

I

VEGETATIVE ORGANS OF HEPATICAE

1. *RELATIONSHIPS OF SYMMETRY.*

THE statement made above[1] regarding the great variety of the formation of vegetative organs in the Bryophyta requires qualification in so far as the relationships of symmetry are concerned. Amongst Musci radial and dorsiventral forms of different construction are found[2], but amongst the Hepaticae the dorsiventral type, and in association therewith plagiotropous growth, predominates, and the vegetative body either clings to the substratum[3] or grows up obliquely from it. The group of Calobryaceae, which includes Calobryum and Haplomitrium, is however orthotropous; and so also are the sexual shoots of some forms and the shoots bearing gemmae. Some species of the remarkable genus Riella are also orthotropous, but they have only an apparently radial thallus; in reality the thallus is a modification of the dorsiventral[4]. The species of Riella possess a many-layered axis bearing a unilateral 'wing'. In some, for example Riella gallica, the axis lies upon the substratum, fastened to it by rhizoids on its under side. Such species diverge from the ordinary forms of Hepaticae merely in having the wing developed in a *profile* position, and this is also the case if the plant is fastened only at its base. In those species of Riella which grow erect the wing is arranged like a spiral stair round the axis. Its origin is always unilateral and the subsequent configuration may be attained to in one of two ways,—either the wing grows more in length than the thickened axis of the thallus, or a torsion of the whole vegetative body takes place. In the cases which I have investigated I have only met with the first of these, the thallus having a more or less strong *undulation*

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[1] See p. 15.

[2] See Part I, p. 100.

[3] The plagiotropous growth of most Hepaticae is connected, in my opinion, with their rooting. Their unicellular—usually very short—rhizoids cannot serve so well as anchoring organs and as absorption organs as the much longer usually pluricellular rhizoids of the Musci; therefore they make any great extension from the substratum disadvantageous. From this point of view the possession by the only radial Hepaticae, the Calobryaceae, of root-shoots instead of rhizoids is no accidental circumstance.

[4] See Part I, p. 87 and Fig. 41.

(Fig. 9), and Trabut[1] also who examined many living plants found the same in them. On the other hand Leitgeb[2], as the result of his study of dried specimens, describes a torsion extending over the wingless basal portion of the axis, the surface of which he compares with a strongly twisted cord. Probably both undulation and torsion occur. At any rate both states have the same significance in *biological* relationship—they place the wing not *vertically,* but *transversely* or *obliquely* to the light falling upon it from above. We may find an explanation of the whole process of the formation of the wing in the fact that submerged water-plants are sensitive to light of strong intensity, and in the case of small creeping forms, or even of those growing erect in shallow water, injury from the light would

FIG. 9. Riella Clausonis. Upon one side of the axis is seen the winding wing in which the antheridia are sunk. If these are not developed the wing is more prominent. Upon the under side large scales containing chlorophyll (leaves) are seen, which are larger in the figure than the wing. Magnified.

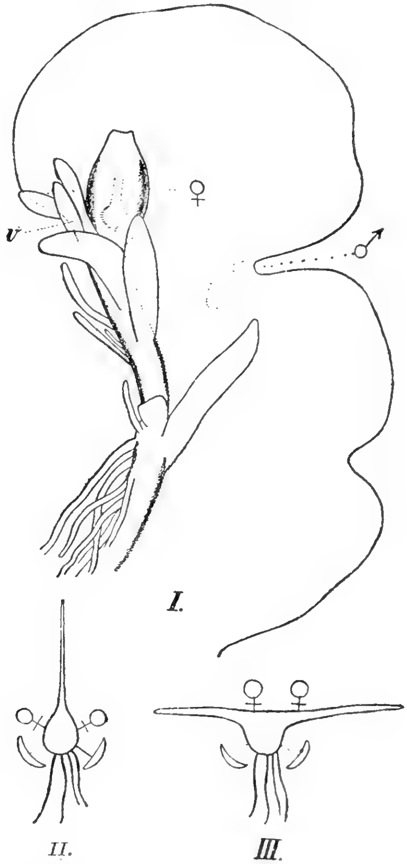

FIG. 10. I, Riella Battandieri. Upper part of plantlet in profile. At ♂ a pit in the wing in which a now emptied antheridium sat. At ♀ an archegonium surrounded by an envelope. *v*, vegetative point. II, scheme of Riella. III, scheme of one of the Marchantiaceae; the thallus seen in transverse section. Magnified.

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[1] Trabut, Révision des espèces du genre Riella, in Revue de botanique, iii (1891), p. 433.

[2] Leitgeb, Untersuchungen über die Lebermoose, Graz, iv (1879), p. 75.

be obviated by the development of the wing in the vertical plane. Larger forms of Riella are able to grow up in deeper water[1], and they live therefore in subdued light which they can use better by the oblique position of the wing, and this is attained by undulation or torsion. Leitgeb's conjecture that the germ-plants wind round a support after the manner of a twining plant appears to be extremely improbable, because the undulation of the wing or the torsion of the whole plant is connected in my opinion with the relationship to light and not with the fixation of the plant.

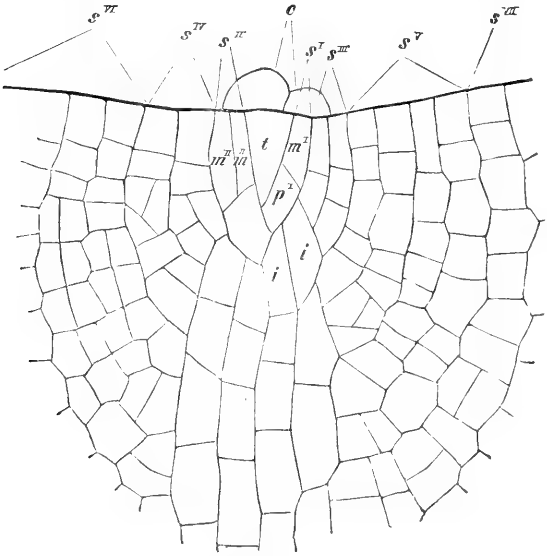

FIG. 11. Metzgeria furcata. Apical region of the thallus seen from above; *t*, the apical cell; s^{I} to s^{VII}, successive segments; *i*, *i*, portion of segment s^{III} devoted to the formation of the midrib; m^{I} to m^{III}, marginal cells of successive grades; *p*, surface-cell of first grade; *c*, mucilage-hairs upon the under side of the thallus. After Strasburger[2]. Magnified 540.

In other thallose Hepaticae the 'wing' of the thallus is spread out flat (see the scheme in Fig. 10, III). The central axis of the thallus is usually the thickest, and it serves as a place of storage of material as well as for its conduction; and it also acts mechanically as a 'rib,' which is particularly prominent in forms which possess a wing consisting of one layer of cells; Metzgeria and Blyttia for example. The thallus of Metzgeria and Aneura is a simple cell-surface in the juvenile condition; the rib only appears at a later period, and in Aneura it is not sharply marked off from the wing. The wing makes an indentation at the apex of the thallus in which the *vegetative point* lies.

2. *VEGETATIVE POINT AND ARRANGEMENT OF CELLS.*

The arrangement of the cells at the vegetative point has been the subject of numerous and thorough investigations; but few facts of importance from the point of view of the organography of the Hepaticae have resulted from these, and therefore they do not require to be spoken of here in any detail.

The vegetative point of most Hepaticae possesses a distinct apical cell which has been recognized by Leitgeb and others even in cases where the apex is occupied by

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[1] Montagne says that Riella helicophylla grows at a depth of seven decimeters.

[2] Strasburger, Das botanische Practicum, Jena, 1884, Fig. 112.

a number of cells like one another in form. In such cases, for example in Anthoceros, Blasia, Riccia, the apical cell cannot well be distinguished from its segments, and one might speak of an apical angle.

The configuration of the apical cell appears to be constant at corresponding stages of development within one genus usually and even within larger groups. Thus the Aneureae including Aneura, Metzgeria (Fig. 11), and Hymenophytum possess a two-sided wedge-shaped apical cell. But it may change even within *one genus*[1] and in the course of development in *one plant*. It is, for example, two-sided and wedge-shaped in the germ-plants of Preissia and Marchantia polymorpha, but it is four-sided and pyramidal in the mature plant. The interest of this lies in this,—it shows that the form of the apical cell stands in relation to the whole vegetative body. Forms of thallus which are thin cell-surfaces, as in Metzgeria where the midrib alone has many layers and in the germ-plants of Marchantia, have a two-sided apical cell which gives off segments only to the right and to the left. Those, on the other hand, which have a massive construction throughout have a four-sided or a three-sided pyramidal apical cell, which from the beginning gives off segments above and below also. Other factors, however, have also an influence. We find, for example, that Aneura pinguis with a thick thallus has a two-sided apical cell, and Cyathodium with its very thin thallus has an apical cell like Marchantia[2]. It is evident then that the factor of affinity operates also.

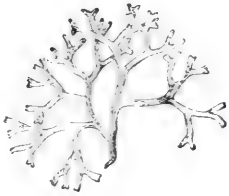

FIG. 12. Riccia fluitans. Forked branching thallus. No division of labour between the branches. Natural size. Lehrb.

3. *DIFFERENTIATION OF ORGANS.*

A. BRANCHING.

The branching of the thallus takes place partly in the plane of its flattening, partly upon its under side. The latter is predominant in Hymenophytum and many others; but it is rare elsewhere, for instance in the Marchantieae, and in Metzgeria it is limited to the sexual shoots, whilst in Pellia and many others it is wanting altogether[3].

Twigs which are not ventral always proceed from a new apical cell laid down in the vicinity of the old one. An actual bipartition of the apical cell so as to produce a forking such as the mature condition would suggest does not take place (see Fig. 15). It is characteristic of the branching that a 'middle lobe' shoots out between the two new apices and is the common basis for the wings of the two separating lateral shoots (Fig. 14).

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[1] Pellia epiphylla differs from P. calycina and Blyttia Lyallii from B. decipiens in this respect. See Leitgeb, Untersuchungen über die Lebermoose, iii (1875), pp. 54, 80; Farmer, Studies in Hepaticae: On Pallavicinia decipiens, Mitt., in Annals of Botany, viii (1894), p. 40.

[2] According to Leitgeb's figure.

[3] I have on the other hand met with ventral shoots in Aneura. Why these should be so conspicuous in some forms it is difficult to explain at present, but it is easy to see that dorsal shoots would be most disadvantageous.

The relationship between the configuration of the thallus and the kind and method of construction of the several branchings is of some interest. In the first place, it may be noted that in many thallose Hepaticae the formation of the wing on the thallus may be suppressed over a portion of its extent. This is seen at the base of lateral shoots, and also at the point of shoots of first order in Hymenophytum (Fig. 13), in Blyttia, and others. It also occurs in *etiolated* shoots of other Hepaticae through the absence

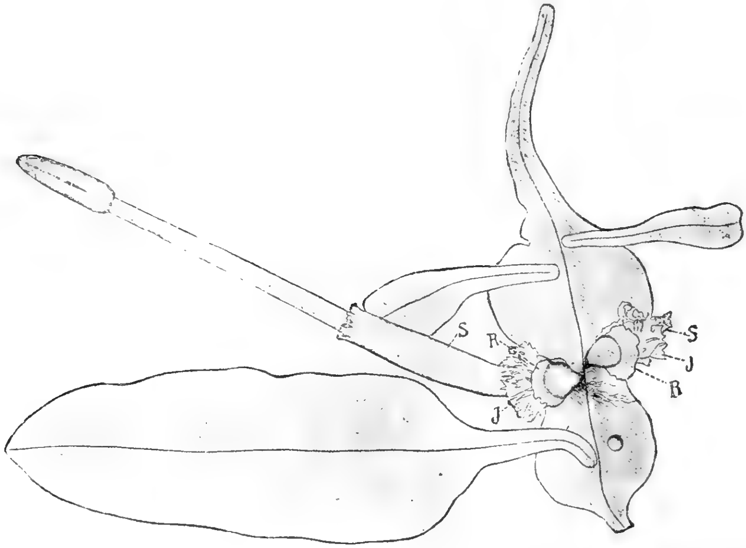

Fig. 13. Hymenophytum Phyllanthus. The plant seen from below. The thallus has a midrib and is grown out at the point into a stolon-like process. It bears five ventral shoots, and there is the primordium of a sixth at the right side of the lower part of the figure. Two of the shoots which remain very short are female sexual shoots, the one on the left has developed a sporogonium. *R*, margin of the sexual shoot; *J*, perichaetium; *S*, perianth. Magnified 5.

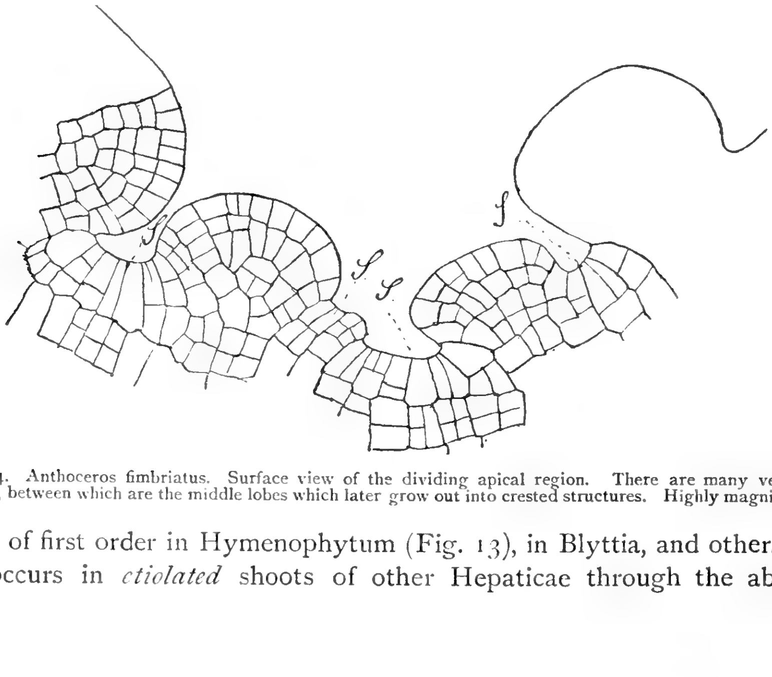

Fig. 14. Anthoceros fimbriatus. Surface view of the dividing apical region. There are many vegetative points, *S*, between which are the middle lobes which later grow out into crested structures. Highly magnified.

of light, but here it belongs to the normal course of development, inasmuch as the shoots which spring from the ventral side of the thallus are those which are at first wingless in correspondence with the fact that in their first developmental stages they obtain very little light. We observe then on these shoots a division of labour; the wingless portion serves to bring the assimilating portion into the light. A sharper division of labour occurs when the wingless portion serves also as an anchoring organ and as the absorber of nutriment from the soil, and thus in a measure corresponds with the root of higher plants. The assimilation-shoot has then no hair-roots; it raises itself above the substratum. If we imagine the wingless, apparently cylindric, but often somewhat flattened, portion to bore into the soil, and the winged portion to raise itself above that and to be endowed with limited growth, we obtain a form of thallus which occurs with a varying degree of limitation in the cycle of affinity of Blyttia, Symphyogyna, and others. Fig. 16 is an illustration of Symphyogyna sinuata in which the winged lobed thallus appears[2]. In it the winged shoots can again decrease at the apex and become stolons, but usually they conclude their growth after reaching a definite medium size, and then at their base they form a ventral lateral shoot which as a stolon continues the growth, subsequently rises above the substratum, broadens out, and then again forms a ventral shoot, and so on. In Fig. 16 there is a chain of five such generations, forming a sympodial

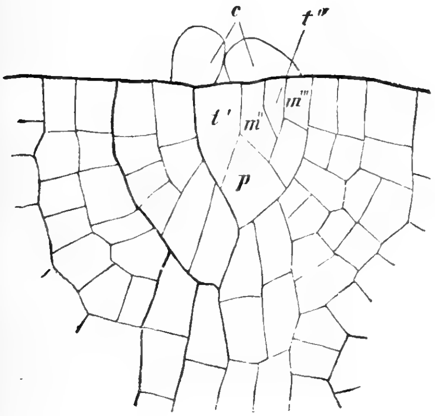

FIG. 15. Metzgeria furcata. Branching; *t'*, old apical cell; *t''*, new apical cell; *m''*, *m'''*, marginal cells of first and second grade; *p*, surface-cell of first grade; *c*, mucilage-hairs. After Strasburger[1]. Magnified 540.

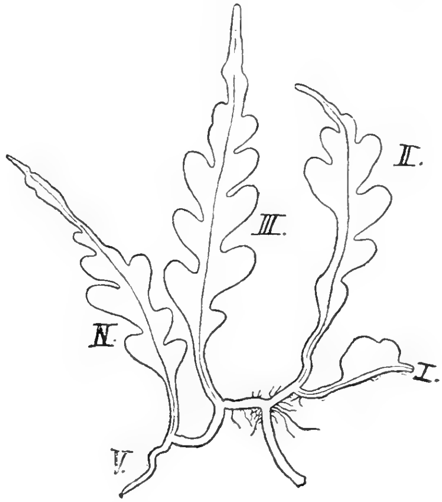

FIG. 16. Symphyogyna sinuata, or an allied form from Martinique. The thallus has leaf-like lobes which disappear in its upper part. The growth is sympodial. The successive shoot-generations are numbered I, II, III, IV, V; each begins with a stalk-like portion in the substratum, and gradually expands into the lobed portion above the substratum. Magnified 3.

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[1] Strasburger, Das botanische Practicum, Jena, 1884, Fig. 113.

[2] See what is said afterwards upon the transition to the formation of leaves, p. 37.

rhizome upon which assimilation-shoots stand as apparently lateral structures. In foliose forms we find exactly similar features, and the behaviour is biologically the same as that exhibited by the sympodial rhizome of species

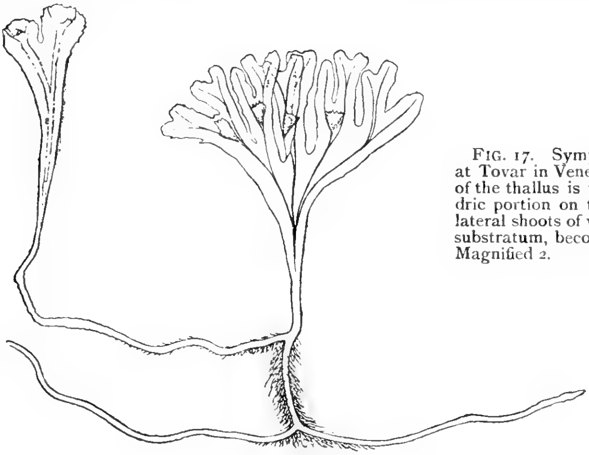

FIG. 17. Symphyogyna sp. I gathered this in 1890 at Tovar in Venezuela. The divided, fan-like surface of the thallus is the continuation of the nearly cylindric portion on the right. Upon it arise two ventral lateral shoots of which one, the upper, rises above the substratum, becomes flattened, and has begun to fork. Magnified 2.

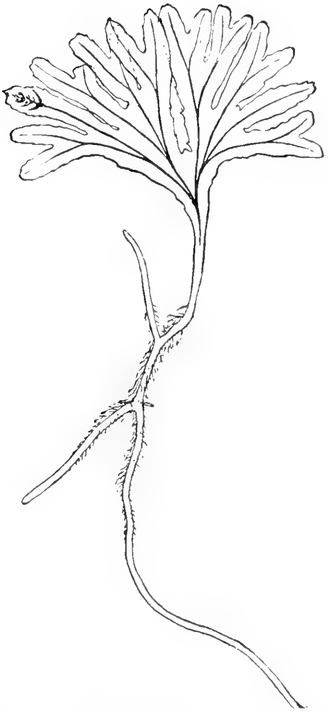

FIG. 18. Blyttia decipiens. I gathered this in 1885 at Nuwara Elyia in Ceylon. Illustration of the habit of a male plant with two cylindric ventral lateral shoots. Magnified 2.

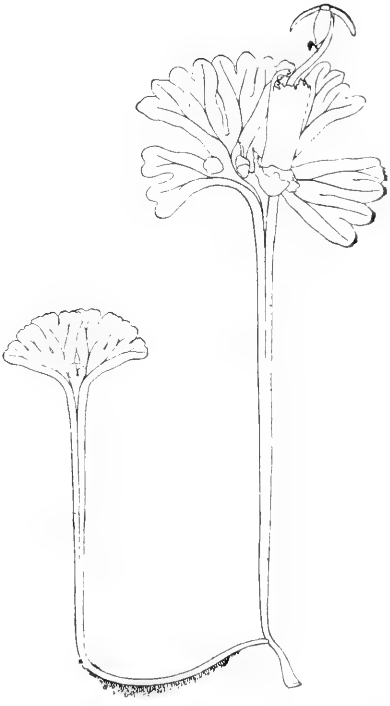

FIG. 19. Hymenophytum flabellatum. Seen from the under side. The plant on the right of the figure bears fructification, and a lateral shoot arising to the left has produced two small sexual shoots appearing as scales upon its under side. Magnified 2.

of Polygonatum. If the assimilation-shoots, which here have limited growth, possessed a leaf-like habit, and this would be more marked if they branched by repeated forkings, we should have structures like the leaves of many ferns[1]; and, indeed, from the point of view of their function, they would be exactly the leaves of a small Hymenophyllum. It is of special interest to note that in no fewer than three genera do we find this form of the vegetative body—namely, in Symphyogyna (Fig. 17), Blyttia (Fig. 18), and Hymenophytum (Fig. 19). They are, it is true, allied, but each of them begins as a creeping, simple thallose form, and independently of the others attains the configuration—shall we call it hymenophylloid?—depicted above. The figures will show how nearly these *parallel forms* correspond outwardly with one another, and we can only obtain evidence enabling us to say to which genus any individual plant belongs by an examination of the arrangement of the sexual organs.

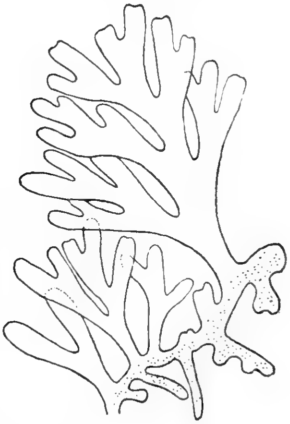

FIG. 20. Aneura bogotensis. From the rhizome indicated by dotted shading the forked thallus-branches have shot up. Magnified many times.

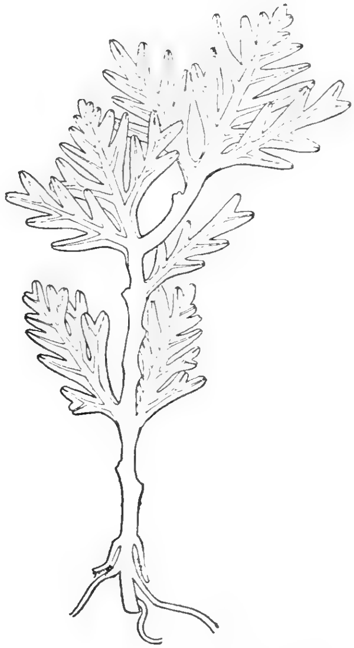

FIG. 21. Aneura eriocaulis. Habit of the plant. At the base 'roots.' The chief axis has been broken off above. Magnified 5.

In the genus Aneura there are many gradations up to the division of labour of the species with richly branched thallus. There are species like A. pinguis in which all the vegetative shoots behave alike[2], but it is different especially in epiphytic species, amongst which is Aneura bogotensis. A portion of a 'stolon' of this plant is represented in Fig. 20. Its vegetative body shows two parts—the one indicated in the figure by dotted shading lies on the substratum as a creeping rhizome which is not sympodial, the

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[1] See Farmer, Studies in Hepaticae: On Pallavicinia decipiens, Mitt., in Annals of Botany, viii (1894), p. 36.

[2] Those which bear the sexual organs we leave out of consideration here.

other consists of a number of dichotomously branched members which spring as lateral shoots from the creeping axis, and in a measure perform the function of leaves. In Aneura (Pseudoneura) eriocaulis (Fig. 21) we find a much higher division of labour. Its chief axis is differently constructed from the lateral axes, especially the terminal branchings of these, here of the third order. These terminal branches have limited growth, are organs of assimilation, although some of them also bear reproductive organs, and in correspondence with their function they are thin plates thickened only in their middle portion. The chief axis, on the other hand, whose function is partly a mechanical one, partly that of conveying nourishment[1], has almost a cylindric outline on cross-section, although there is a slight flattening visible upon the upper and the under sides[2]. Whereas in Aneura hymenophylloides (Fig. 47) and A. fucoides stronger mechanical claims are made upon the chief axis than upon the lateral axes, more of its cells exhibit thickened walls (Fig. 22), and the difference between the two axes is therefore greater. In other words, starting from a thallus with throughout similar branching (Fig. 12), a progressive differentiation into stem and leaf appears, and we are able clearly to follow its evolution. These species of Aneura possess also 'roots.' There are forms which no longer lie with the whole under-surface upon the substratum, but which fasten themselves to it by means of special anchoring-organs (Figs. 21, 23). These anchoring organs are distinguished from the

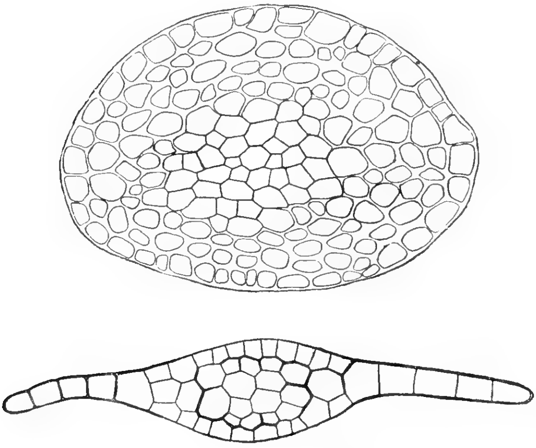

FIG. 22. Aneura fucoides. Upper figure; chief shoot in transverse section. Lower figure; lateral shoot in transverse section. Highly magnified.

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[1] See Part I, p. 34.

[2] The differences between the chief and lateral shoots in the species of Aneura are brought about through the suppression *from the first* of the formation of the wing on the chief axis, and through the assimilation-shoots in the middle region of the thallus undergoing only few divisions. There are of course transitions, that is to say, forms in which the difference between the chief axis and the lateral axis is simply one of the greater thickness of the former. Stephani's statement, in Hedwigia, xxii (1893), p. 12, that the thin membranous wing often thickens as it gets older until it becomes a stalk with a cylindric cross-section is, so far as I have observed, an error. The same author says (Colenso's New Zealand Hepaticae, in Journal of the Linnean Society, Botany, xxix (1892), p. 264) 'in Aneura fucoides, on the contrary, the thickness of the stem, similar to that of our forest trees, is continually increasing with advancing age.' Regarding this I may say that I believe a secondary growth in thickness in Aneura fucoides like that of tree-stems is entirely out of the question, because of the thickness of the peripheral cells.

assimilation-shoots by their direction and their configuration. They are smaller and lie clinging to the substratum. That they are no *new* formations, but merely transformations of the lower branches of the thallus, is proved by our finding not infrequently an assimilation-shoot grown out into a 'root' (Fig. 23), and there can be no doubt that assimilation-shoots could arise upon the 'roots,' although this does not usually happen. External influences probably determine these changes. Unfortunately there has been as yet no experimental examination of these forms, of which the organs are not so sharply limited from one another as they are in the higher plants, and the culture of such plants in Botanic Gardens would be of great interest.

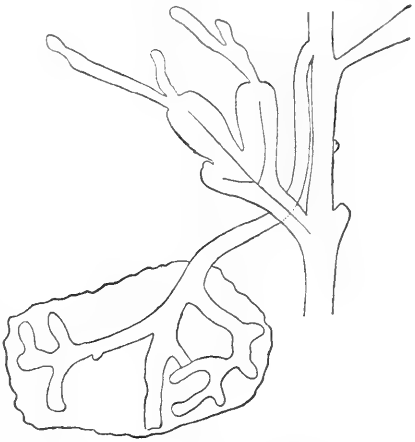

FIG. 23. Aneura fucoides. Basal part of a plant. A lateral shoot has become transformed into an anchoring-organ; it lies in close contact with the surface of the leaf of one of the Spermophyta; on the branches below it the apices have elongated into 'roots.' Magnified.

The higher differentiation of the vegetative body with which we have hitherto dealt has arisen through differences in the construction of the *branches* of the thallus; but this is not the only path along which the higher differentiation has been reached. A second way is that of the *appendages* of the thallus.

B. APPENDAGES.

1. Mucilage-hairs. Scales.

We find appendages in the lowest members of the Hepaticae taking the form only of hair-like bodies secreting mucilage which surround the vegetative point and often arise in definite order (see Figs. 11, 15). and ought to be considered as protective organs to the vegetative point. Such mucilage-hairs are wanting in the Anthoceroteae, where the vegetative point is nevertheless always covered with a thick pellicle of mucilage because *mucilage-slits*, another form of mucilage-organ, are present; secretion of mucilage is absent from the Riccieae, from many Marchantieae, and perhaps also from Riella, and its absence in the last-mentioned plant is the more striking because water-plants so commonly protect their young parts by copious secretion of mucilage[1]. The secretion of mucilage by most of the Hepaticae which live on moist spots serves not only as a means of protection against drought, but

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[1] At the apex of the 'leaves' of Riella which will be described later a papilla is frequently found which may perhaps secrete mucilage. Small papillae of unknown function are found in various places upon the thallus of Riella helicophylla.

also and specially against water. A similar protection, as will be explained presently, is given to the growing sporogonia by envelopes of different kinds. Mucilage-organs are also found in the foliose Hepaticae, in exceptional amount in Anomoclada mucosa[1], which is covered with a thick envelope of mucilage. Mucilage-organs may appear also in the thallose Hepaticae in the guise of simple papillae. These appendicular organs of the thallus deserve mention here, the more because their biological significance has hitherto received little notice, although the relationships between configuration and function are extremely evident. The series of the Marchantiaceae, of which we shall presently speak, supplies us with instructive illustrations. All thallose Jungermanniaceae and Marchantieae have at first appendicular organs for the protection of the vegetative point. Leitgeb's statement that they are wanting in Monoclea is an error (see Fig. 4, *III*), the result of the examination of unfavourable material. In Riccia crystallina[2] which, according to Leitgeb, possesses no scales, I found them as very delicate structures, but perhaps there are some forms of this species where the scales are wanting, because an observer like Leitgeb would scarcely have overlooked them were they present.

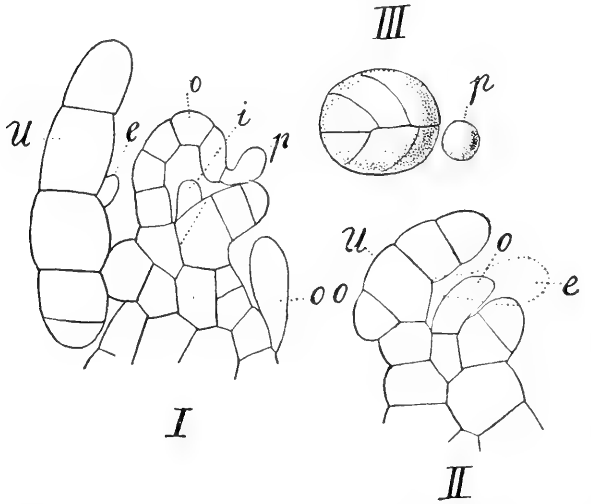

FIG. 24. Blasia pusilla. I, vegetative point in longitudinal section; *u*, amphigastrium with mucilage-papilla, *e*; *o*, leaf-auricle with outer papilla, *p*, as well as inner papilla, *i*; *oo*, papilla of the upper side of the thallus. II, similar section through a younger amphigastrium. Lettering the same. III, young leaf-auricle seen from above. After Leitgeb.

JUNGERMANNIACEAE. Mucilage-papillae are of common occurrence in this group. In Blyttia and Mörkia they are upon both sides of the thallus, in Metzgeria only upon the under side. They are simple and club-shaped in Metzgeria and Aneura, or the mucilage-secreting cell stands at the end of a cell-row as in Mörkia (Fig. 25, I), and this gives us a transition to the scales. These mucilage-organs arise in a definite order, for example, in Metzgeria.

Blasia. The relationships in Blasia are somewhat peculiar and complex. Besides the lateral leaves[3] which are inserted horizontally we find—

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[1] See Spruce, Hepaticae amazonicae et andinae, in Transactions of the Botanical Society of Edinburgh, xv (1884), p. 407.

[2] I am indebted to Dr. Levier of Florence for the specimens of this species as well as of many other interesting Hepaticae.

[3] See p. 37.

1. *Mucilage-hairs*: simple papillae springing out of the upper and the under side of the thallus (Fig. 24, I, *oo*).

2. *Amphigastria*: scales containing chlorophyll and standing upon the under side of the thallus with their under edge growing downwards beyond the point of insertion (Fig. 24, I, *u*); also half-shield-like scales which are arranged in two longitudinal rows in such a manner that usually an amphigastrium corresponds to one lateral scale. Each amphigastrium bears also originally at its apex a mucilage-papilla (Fig. 24, I, *e*), which is displaced subsequently to one side, as it is in many Marchantiaceae.

3. *Leaf-auricles*: spherical bodies (Fig. 24, III) formed by the incurving of a cell-surface rising above the surface of the thallus and then coming into contact again with it (Fig. 24, I, *o*). They are usually infested by a nostoc. They form mucilage, having in their interior a mucilage-papilla (Fig. 24, I, *i*), and another near the aperture leading into their cavity (Fig. 24, I, *p*).

One might describe the development of these different appendicular organs of Blasia by saying that they all proceed from mucilage-hairs. The scales would arise by the supporting cells of definite mucilage-papillae growing out and thus bringing these still nearer to the apex of the thallus, as happens also in Sphaerocarpus, Mörkia and others where the mucilage-papillae are borne upon cell-rows. Individual scales would then be transformed into leaf-auricles, perhaps primarily in consequence of external stimuli. We cannot at present say for what reason so richly membered an apparatus for the protection of the vegetative point has been produced in Blasia.

MARCHANTIACEAE. The formation of scales in Blasia may lead us on to the series of the Marchantiaceae in which we find the vegetative point almost exclusively protected by scales which appear in very different number and configuration.

Riccieae. The formation of mucilage is unknown in any Riccia, and it occurs but seldom in the Marchantieae. In Riccia the scales do not lie over the vegetative point but they only lean upon its outside. A longitudinal section therefore of the apex of Riccia exhibits an appearance different from that of the apex of Marchantia. The reason for this is that the vegetative point of the Riccieae lies in a cleft formed by the protuberant lateral portion of the thallus, and this needs to be closed by the scales only upon one side; the surfaces of the protuberant lateral portions of the thallus are often so closely apposed that their cells are interlocked.

Most of the Riccieae have only one row of scales[1] standing in the middle line of the thallus, and these, except in Riccia fluitans, subsequently

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[1] Contradictory statements are not infrequently found in the literature, but without the historical developmental basis which alone is of value.

become torn, and protection of the vegetative point against drought is effected by the air which is held between them, and the entrance of water is also thus prevented. In Riccia lamellosa the scales reach far beyond the lateral edges of the thallus; they are indented in the middle, which may perhaps be recognized as the first indication of the appearance of more than one row of scales; certainly it is an indication of fission. In Oxymitra pyramidata we find two rows of scales which, as is shown in Fig. 25, IV, form an extremely dense plug to the apical cleft by their interlocking one with the other. As this is a genus of drier habitats than the other

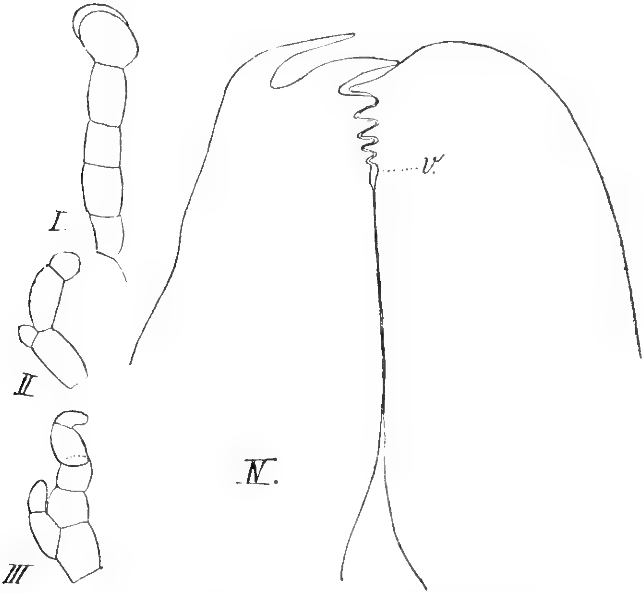

FIG. 25. I, Mörkia. Cell-row with a mucilage-papilla at its apex. II and III, Cyathodium cavernarum. Two cell-rows corresponding to scales. IV, Oxymitra pyramidata. Surface view. Narrow slit above the vegetative point *v* practically closed to the outside by the interlocking of scales.

Riccieae we can easily understand that the vegetative point requires more special protection. The features of Riccia natans will be described after the scales of the aquatic forms are described.

Marchantieae. The Marchantieae, including Corsinia, are distinguished by having their vegetative point in a flat depression over which the scales bend (Fig. 26); it is not in a narrow cleft as in the Riccieae. Cyathodium, a genus which inhabits very feebly illuminated spots, has cell-rows instead of scales (Fig. 25, II, III), evidently because an elaborate protection of the apex is superfluous; the germ-plants of Marchantia have a like arrangement. The scales in Marchantia and other genera stand immediately behind the vegetative apex. The tip of the young scale takes the form of a club-like hair, which in Targionia, Sauteria, and Dumortiera remains inserted upon the edge of the scale usually at the apex of a lobe-like projection. In others, again, there is formed upon the under side of the scale at its base *before* the construction of its apical papilla is completed an outgrowth which soon overtops the papilla and pushes it to the upper side, in the same way as the mucilage-papilla of the amphigastrium of Blasia[1] is displaced. This outgrowth, consisting at first of a single cell, becomes a cell-surface and may be called the *apical appendage*, and it shows beautifully how its form is conditioned by its function. In Fig. 27 we have an illustration of the under side of the thallus of Marchantia chenopoda. It bears two rows of scales, the majority of which still possess the apical appendage which is sharply marked off from the broad scale, is darker in colour than it, and has at its base a constriction at which its edges are bent downwards. *This constriction corresponds exactly to the width of the apical depression.* Over the apex these apical appendages alone are bent, and they lie upon it like the leaves of a book ; subsequently they are displaced to the under side of the thallus and then readily fall off. They have now become functionless, their work has been done ; but this is not the case with the scales. These have still an important duty. The scales lying upon the midrib form a canal within which the tufts of rhizoids run to penetrate the soil further back under the

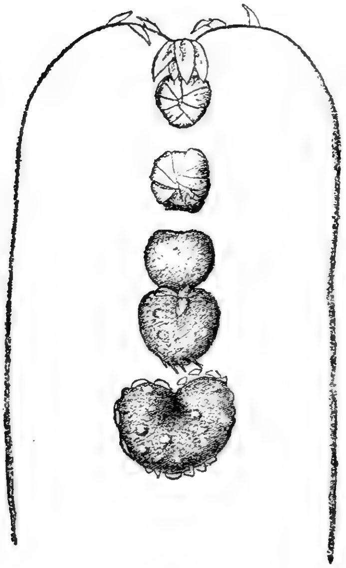

FIG. 26. Plagiochasma Aitonia. Male plant, with five antheridial groups, seen from above. The scales upon the under side bend over the vegetative point. The younger antheridial groups are protected also by overlapping scales which form their perichaetium. Magnified 8.

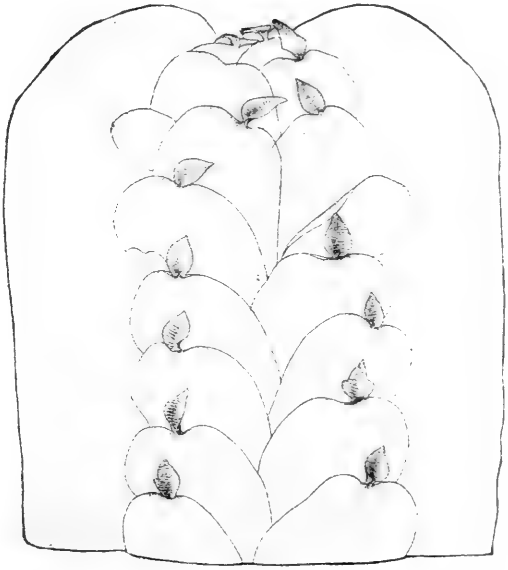

FIG. 27. Marchantia chenopoda. An Andine species. Apex of the thallus seen from below. There are two rows of scales. Towards the upper left side of the figure an additional one is visible. Each scale has an apical appendage which originally arched over the vegetative point and subsequently falls away. Magnified 15.

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[1] See p. 29.

thallus. The tufts of rhizoids are protected from loss of water by the scales, and are held together by them so that where they occur in great masses, as in xerophilous forms, they make wick-like strands and the water then does not pass merely into the lumen of the rhizoid but passes upwards between the rhizoids by capillarity. This relationship of the scales to the rhizoids is particularly striking in Marchantia polymorpha and other species in which there are not only scales in two rows approaching the midrib, but also over the surface of the thallus. It will not be superfluous to say a word here regarding these relationships.

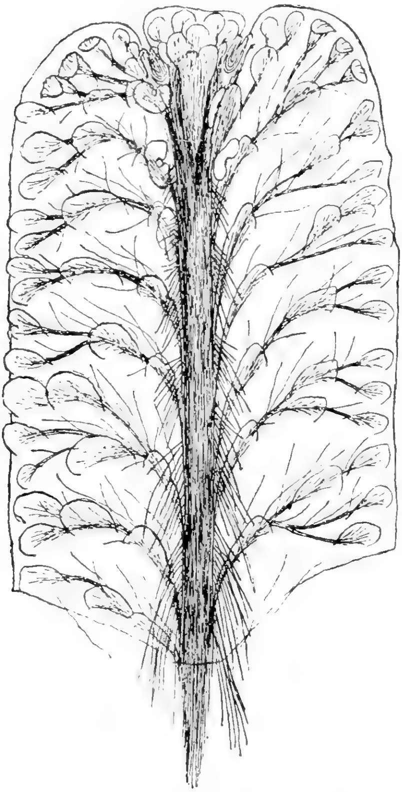

FIG. 28. Marchantia polymorpha. Thallus seen from the under side. A dense strand of rhizoids lies along the midrib and the strands of rhizoids which arise under the outer scales unite with this. Single free rhizoids spring out also from the thallus. Magnified about 5.

Marchantia polymorpha has been figured and described times without number, but the distribution of the rhizoids has not attracted much attention. We can recognize three series of scales in Marchantia polymorpha (Fig. 28). The *median scales*, which are provided with apical appendages like those represented in Fig. 27; *marginal scales*, which partially project over the edge of the thallus; and between these there stand scales which we may call *intermediate scales*. Underneath the median scales there runs a strand of rhizoids, the *chief strand*. Rhizoids also spring out both below and from the marginal and intermediate scales, wend their way united in thinner strands to the median scale, and there join on to the chief strand. It thus comes about that a series of strands is developed which we may compare with a system of irrigation. The lateral strands serve to conduct water to the marginal parts of the thallus. The scales at this point are chiefly organs of protection and direction to the rhizoid-strands, they are no longer protective organs for the vegetative point. Marchantia lamellosa, which inhabits the higher parts of the Northern Andes, has many more scales than M. polymorpha. This plant, notwithstanding that it lives upon a moist soil, has a xerophilous character, and the thick covering of scales upon the under side of the thallus between which the numerous strands of rhizoids run assures a sufficient supply of water even if the transpiration be profuse. It is further clear that the scales themselves standing close together will retain water by capillarity, as happens in Aneura endiviaefolia and other species [1].

Dumortiera. This genus has experienced a reduction in its anatomical structure, which is connected with its hygrophilous character [2]; it is found growing upon moist places, under the spray of waterfalls, or upon the banks of streams. In Dumortiera hirsuta, for example, the scales are represented by a few ridges upon the thallus, and can serve as no protection to the rhizoid. There is along the midrib of the thallus a strand of very thin rhizoids, but the remarkable arrangements of Marchantia polymorpha are not found here.

FIG. 29. Riccia natans. Apex of a thallus which has recently forked seen in transverse section. Large intercellular spaces are visible in the tissue. Scales upon the under side appear at each vegetative point in three rows. The scales of each lateral row overlap later those of the middle one.

We observe then that the configuration of the scales, and no less their number, stand in the closest relationship to the conditions of life, and of course also to the mass of the thallus. The narrow forms of Riccieae have *one* row of scales, the broad Riccia natans has *many* rows (Fig. 29). The

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[1] See p. 53.

[2] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 223.

narrower species of Marchantia have two rows of scales, the broad Marchantia polymorpha has many rows. Originally developed as protective organs to the vegetative point the scales when they are produced in numbers find their function in connexion with the supply of water ; they form cavities within which the strands of rhizoids run in the manner already described in the case of Marchantia polymorpha and others. We shall see afterwards that between the scales on the rays of the antheridiophore in Marchantia run strands of rhizoids to conduct water.

It is probable that these scales took origin out of *cell-rows*. The case of Cyathodium[1] indicates this as well as that of Corsinia in which the ventral scales possess a terminal process—the oldest part of the scale—consisting of a cell-row. In Hepaticae, such as Sphaerocarpus and Riella[2], which possess no elaters, we observe the same course of development. Sphaerocarpus possesses mucilage-papillae borne upon a cell-row. We find in place of these in Riella complete leaf-like scales, containing chlorophyll, which no longer serve merely as protective organs for the vegetative point, but are also assimilation-organs (Fig. 9). This no doubt is connected on the one hand with the direction of the thallus which exposes the scales to illumination, and on the other hand with the influence of the aquatic life. That the latter has an effect is shown by Riccia natans, the large *water-form* of which has strongly developed ventral scales which contain chlorophyll. These scales have here evidently the same biological significance as the water-leaves of Salvinia, they increase the surface by which water is absorbed ; they give the floating plant more stability ; they protect it by their secretions against the attacks of water-animals ; and further, on account of the chlorophyll which they possess, they co-operate in assimilation. They are much less developed in the *land-form*, and are present in it usually as protective organs to the vegetative point *only*. In the water-form they construct in front of the vegetative point a tuft which encloses air, and thus prevents the water from touching the apical region. Riccia fluitans (Fig. 12), on the other hand, which also lives in water, has scales which are not endowed with any new function, and are, as in the land-form of Riccia natans, only protective organs ; and this is so apparently because this species is more adapted to submerged life, as its anatomical structure indicates, and its delicate, richly-branched thallus can take up water through its *whole* surface ; whilst Riccia natans, which swims on the surface of the water, takes up water through the scales. There is an interesting parallel in the behaviour of the ventral scales in Riccia natans and in Riella, and these scales may be designated *leaves*[3].

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[1] See p. 30.

[2] These are in my opinion the lowest members in the series of Marchantiaceae, and approach Monoclea in some points.

[3] See p. 35.

2. Leaves.

Another series of appendicular organs includes those which in configuration and origin so much resemble the leaves of the foliose Hepaticae that we may designate them also leaves. We term these appendicular organs leaves if they are laid down in definite regular succession at the vegetative point and conform in configuration and function with the leaves of forms in which such organs have from the very oldest times been spoken of as leaves[1]. The formation of leaves in the Hepaticae has arisen in a large number of series *independently one of the other*, and this is characteristic. The so-called 'foliose' forms, in the narrower sense of the acrogynous ones, constitute only *one* of these series, and besides those amongst the Jungermanniaceae there are many others. If we leave out of consideration the ventral scales of Marchantieae and Riella described above—but as I have said we may always call them leaves in Riccia natans and Riella[2]—the series of Marchantiaceae alone, so far as we know, is wanting in the formation of leaves.

(*a*) LEAVES OF THALLOSE FORMS.

Anthoceros. There are a few cases of a like want of leaves amongst the Anthoceroteae, but these are not quite complete. In the genus Anthoceros itself we find leaf-like appendages in A. fimbriatus (Fig. 50), a species I found upon the Cordilleras of Merida. The one-layered crested appendages of the many-layered thallus are in this species really produced by the middle lobes which arise in the course of branching (see Fig. 14). There is a frequent division of the vegetative point with which is associated a corresponding formation of branches. Many of the vegetative points which are thus formed are arrested in development, and their apical cell loses its rich protoplasmic content and takes no further share in growth; but the middle lobes increase and become crested appendages, which will be mentioned again when I refer to the absorption of water[3].

Dendroceros. Some species of Dendroceros show, in addition to the leaves, other structures which are also connected with the supply of water. I have examined Dendroceros foliatus, a species described by Spruce[4].

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[1] See the remarks upon 'Formation of Organs and Division of Labour,' Part I, pp. 21–40. Many systematists who have studied the Hepaticae have raised objections to the use of the term 'leaves' for the organs under consideration here. Stephani (Treubia insignis, Göb., in Hedwigia, xxx (1891), p. 190), for example, made out the leaves of Treubia, Symphyogyna, and others to be no leaves but 'frond-lobes.' The altogether superfluous and almost fossil expression 'frond' instead of 'thallus' ought to be entirely discarded. But these 'frond-lobes' cannot be distinguished by any single essential character from the 'leaves' of the foliose forms. It would be different if they arose irregularly as outgrowths upon the margin of the thallus. But as Leitgeb has shown in Blasia and I have proved in the cases of Treubia and Symphyogyna this does not happen. To call the leaves of Calobryaceae 'frond-lobes' would be nonsense.

[2] See p. 34.

[3] See p. 56.

[4] Spruce, Hepaticae amazonicae et andinae, in Transactions of the Botanical Society of Edinburgh, xv (1884), p. 574. Professor Bayley Balfour was so good as to supply me from Edinburgh with Spruce's original specimens.

The plant (Fig. 51) possesses a number of relatively large hood-like formations, of which we can distinguish two kinds; one (Fig. 30, *M*) corresponding

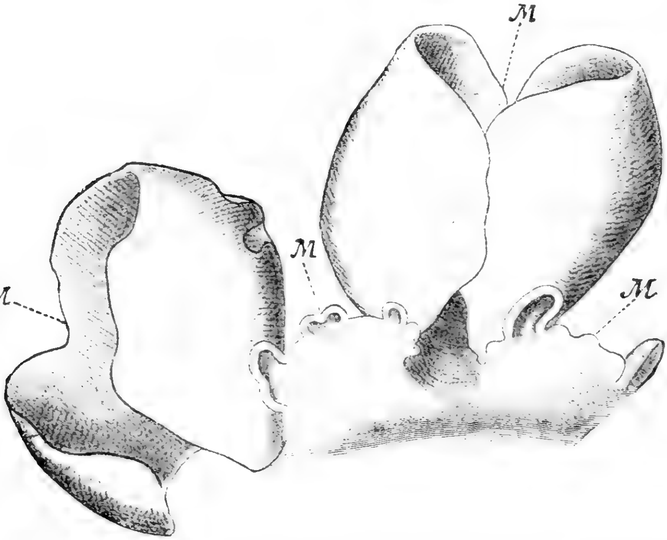

FIG. 30. Dendroceros foliatus. Apex of a thallus; *M*, middle lobes of different age, on the one to the left the formation of holes is seen on the upper right portion. Besides these the somewhat oblique hoods, 'the leaves,' appear as lateral shoots on the vegetative point. Magnified.

with the middle lobe developed by branching is recognizable by its deep emargination which indicates the beginning of a splitting; the other, in the form of a simple hood, arises as an independent outgrowth at the vegetative point and becomes hollowed at a subsequent period upon its under side. These 'leaves' are not attached to the midrib, but are bound to one another by the very slight wing-like part of the thallus. Dendroceros inflatus[1] and D. crispus show in their laminar folds an approach to the formation of leaves;

FIG. 31. Blyttia longispina. Apex of the thallus. On the edges the first indications of leaves are seen as cell-rows below the shallow indentations. Magnified 8.

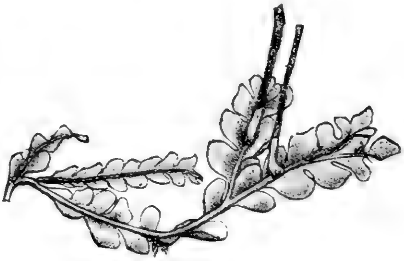

FIG. 32. Symphyogyna Brogniartii (Amphibiophytum dioicum, H. Karsten). A plant with two unripe sporogonia still enclosed in their calyptra.

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[1] G. Karsten, Morphologische und biologische Untersuchungen über einige Epiphytenformen der Molukken, in Annales du Jardin botanique de Buitenzorg, xii (1895), p. 125.

if these laminar folds were flat they would be like the leaves of Blasia. From a biological point of view their origin is easily understood. Leaves with a horizontal insertion, such as we meet with in different Jungermanniaceae, link on to them.

We have next to consider the features in the cycle of affinity of Blyttia and Symphyogyna.

Blyttia. Most of the species of Blyttia possess an unsegmented thallus (see Fig. 90). Blyttia longispina (Fig. 31) has appendicular organs in the form of cell-threads, which lie directed partly upwards, partly downwards, about the vegetative point, and so form a kind of protection. They sometimes also appear upon teeth which project from the edge of the thallus. These are more prominent in other species.

Symphyogyna. The plant represented in Fig. 16 has a thallus with evident segmentation into separate leaf-like lobes, and the segmentation may cease, and the thallus can, as the figure shows, grow on with an entire edge. The segmentation to form 'leaves' is more marked in Symphyogyna Brogniartii (Fig. 32). It reaches here almost to the midrib. The leaves approach the horizontal, are one-layered, and end in a short papilla, or a cell-row of two cells. They arise like the teeth already mentioned in regular progressive serial succession from the segments of the apical cell at the vegetative point[2]. Here also the formation of leaf may cease upon young shoots; and in all these cases it is evidently not yet fixed. The chief point is that the sproutings are laid down in *regular succession* at the vegetative point. Whether they are to be regarded as separate leaves or as small appendages depends upon their own growth and that of the axis of the thallus; according to the strength of the one or the other of these there appears at the vegetative point, in essentially similar primordia, a leafy stem or a thallus with appendages like that depicted above in Blyttia longispina.

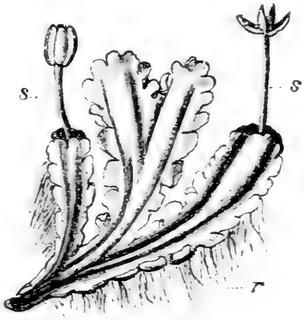

FIG. 33. Blasia pusilla. *s*, sporogonia open: *r*, rhizoids. Magnified 2. Lehrb.

Blasia. This and its nearly allied genus Cavicularia possess horizontally inserted lateral leaves, and these in Blasia (Fig. 33) are not sharply segmented from the flat portion which corresponds with the shoot-axis of other Hepaticae; usually the formation of leaves appears in slender plantlets.

One advantage the formation of leaves possesses over the unsegmented thallus is apparent even in forms provided with horizontal leaves: the development of leaves inserted obliquely or transversely to the long axis of a shoot provides for the protection of the vegetative point by the forma-

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[1] Goebel, Archegoniatenstudien: III. Rudimentäre Lebermoose, in Flora, lxxvii (1893), p. 98.

[2] Goebel, op. cit., p. 100, Figs. 16–20.

tion of an actual bud, which must of course be a very incomplete one when the leaves have an insertion parallel with the stem-axis; and, besides, the leaves are able also to retain water, and then the regular appearance of a number of sharply limited organs makes possible their adaptation to definite functions.

The foliose Hepaticae includes both anacrogynous and acrogynous forms.

(*b*) LEAVES AND SHOOTS OF ANACROGYNOUS FOLIOSE FORMS.

These forms belong to the cycle of affinity of the thallose group and call for attention first.

Fossombronia. The species of this genus (Fig. 34) possess two rows of obliquely placed lateral leaves which give the plant a crested aspect and favour greatly the retention of water. The shoot-axis has a two-sided apical cell and is much flattened upon the upper side. Upon its ventral side, which the edges of the leaves scarcely overlap, club-shaped mucilage-papillae occur which frequently in consequence of the growth and division of their supporting cells come to stand upon the summit of a leaf-like scale; this process is interesting because it furnishes a support to the suggestion given above in regard to the origin of the amphigastria of Blasia and other forms. Upon the dorsal side the edges of the leaves overlap almost to the middle, and here are found the sexual organs.

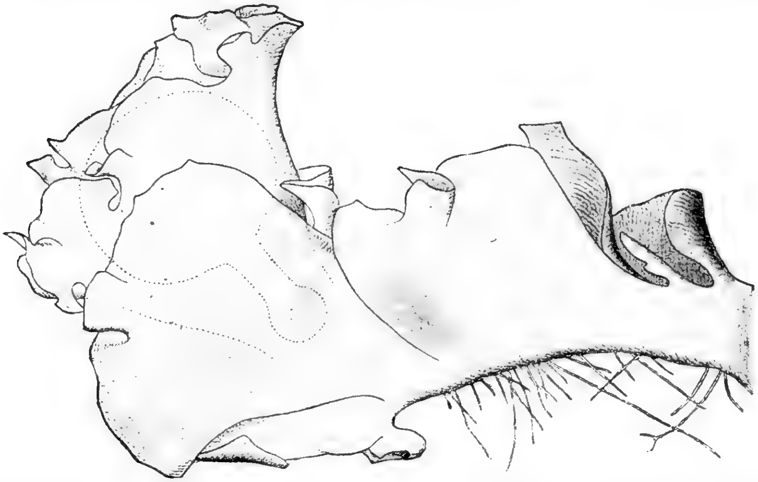

FIG. 34. Fossombronia tuberifera, Goebel. Lateral view of a distichously leaved plant in fructification. The sporogonium is surrounded by a bell-shaped envelope. The point of the plant begins to penetrate the ground where it would develop into a new tuber. Magnified 18.

Androcryphia and Petalophyllum. In Androcryphia and Petalophyllum the formation of the leaves is similar, the apical cell is, however, a three-sided pyramid, as in the acrogynous forms. The leaves overlap the dorsal side to a very slight extent. Mucilage-papillae occur upon the under side in Androcryphia.

Treubia. The largest of all the Hepaticae in this cycle of affinity is Treubia insignis, a species found by me in Java. In it there are two rows of large lateral leaves; the under side has no trace of appendages; the shoot-axis is not visible usually between the leaves, only on young and delicate examples are there internodes (Fig. 35, lower portion). The leaves which are over one centimeter long, are nearly horizontal, and are many-layered at the base, but one-layered higher up; the fore edge of the leaves is inserted deeper than the hinder edge, and when the position of the leaves is very close the hinder edge of each younger leaf covers the fore edge of the next older. The leaves are therefore succubous[1]. Upon the dorsal surface of the stem there are two rows of scales beside the leaves and surrounding the insertion of each, and their posterior part forms a zigzag comb (Fig. 36). They cover the sexual organs and the gemmae where these exist, and contribute also to the protection of the vegetative point which, however, is also enveloped in mucilage. The mucilage is derived from mucilage-papillae, which stand upon a wing-like growth on the under edge of the leaf, and thus replace or render superfluous the central mucilage-papillae which are found in other Hepaticae[2].

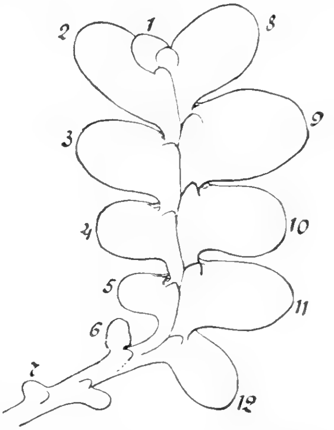

FIG. 35. Treubia insignis, Goebel. Young plant seen from above. The leaves are not numbered according to age. The hinder edge of leaf 2 evidently embraces the point of insertion of the fore edge of leaf 3. Beside and near the fore edge of each leaf stands a scale whose insertion is prolonged crestwise backwards. Under the scales stand the sexual organs if these are present. At the base of the shoot where the leaves are smaller the crest is less visible. The stem upon which the scales are inserted is quite evident. Magnified 1½.

Calobryaceae[3]. The Calobryaceae is the only group of Hepaticae in which orthotropous shoots occur; it has perhaps some affinity with Treubia. Fig. 37 shows the habit of Calobryum. Tristichous leafy shoots are borne upon a sympodial rhizome. The leaves, like those of Treubia, are many-

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[1] Stephani (Treubia insignis, Goebel, in Hedwigia, xxx (1891), p. 191) has made a number of statements which are not altogether in consonance with the developmental history of Treubia insignis. As our Fig. 35 shows, it is incorrect to say that 'the overlapping edges of two neighbouring leaves spring from *one* point.' The arrangement is, as I have satisfied myself by a renewed investigation, that the *anterior* edge of each leaf lies *deeper* than the posterior of the next younger. These are actual succubous leaves; they are not what Stephani calls them 'frond-lobes.' Stephani also misquotes when he says 'Goebel describes the midrib as cylindric in transverse section.' What I said was 'the stem does not usually show between the leaves, but on young and feeble examples, as well as at the base of the lateral twigs, one finds conspicuous internodes, and *here* the stem has an outline *approaching* the cylindric'; and what I have said is correct. Stephani is also incorrect in what he says about the dorsal scales. These are found here and there where there are no sexual organs as I made clear in my original description. Stephani takes as a basis of his definition of the notion of leaf exclusively the structure of that name in the foliose acrogynous forms. This is inadmissible. The formation of leaf has originated repeatedly in the *different* cycles of affinity in the Hepaticae.

[2] Leaf-born mucilage-papillae occur also in Fossombronia caespitiformis.

[3] See Goebel, Morphologische und biologische Studien: IV. Über javanische Lebermoose; 2. Calobryum Blumii, Nees, in Annales du Jardin botanique de Buitenzorg, ix (1892), p. 11. I have

layered, and like them also bear mucilage-papillae. Such papillae are, however, also found upon the cylindric shoot-axis. The Calobryaceae exhibit the highest stage of development of the anacrogynous Hepaticae, inasmuch as the shoots which bear the sexual organs possess terminal antheridia and archegonia, to which I shall refer when I speak of the position of sexual organs generally. Further, the cylindric shoot-axis is sharply demarcated from the transversely inserted leaves, and there is throughout a typical leafy shoot. It is interesting to note that occasionally anisophyllous shoots appear. The leaves of one lateral row have one side smaller than the other, and may indeed occasionally almost entirely abort, whilst the leaves in the other two rows have an oblique not transverse insertion. The importance of this case lies in its features being determined by external factors, and therefore showing that this construction of the leaves, which is the dominant one in the acrogynous foliose Hepaticae, may be reached experimentally[1].

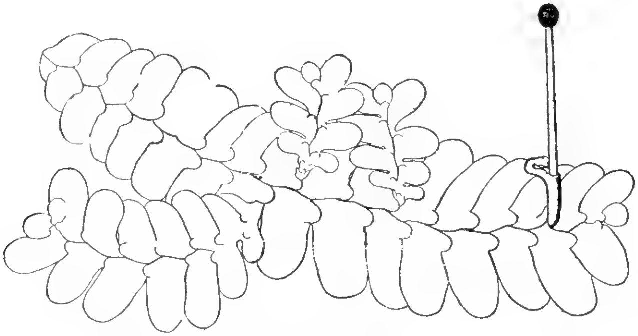

Fig. 36. Treubia insignis, Goebel. A plant seen from above. Natural size. It bears a sporogonium which is shown somewhat smaller than natural size.

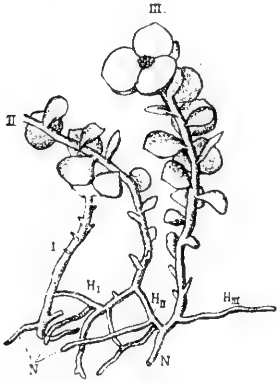

Fig. 37. Calobryum Blumii, Nees. Habit of a female plant. H_I, H_{II}, H_{III}, stolons united into a sympodial chain and serving as roots; I, II, III, their foliage-shoots; N, accessory stolons. Natural size.

(c) LEAVES AND SHOOTS OF ACROGYNOUS FOLIOSE FORMS.

In this group we have growth usually from a three-sided apical cell[2], which gives rise to a typical tristichous leafy stem, but the ventral row of

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here shown that Calobryum, which until now has been considered to be quite unique, should be united in one group with Haplomitrium, and I have called the group Calobryaceae. Schiffner's (Hepaticae, in Engler and Prantl, Die natürlichen Pflanzenfamilien, 1893, p. 60) alteration of the name to Haplomitrioideae is quite arbitrary.

[1] See Part I, p. 102. Also Goebel, Morphologische und biologische Studien: IV. Über javanische Lebermoose; 2, Calobryum Blumii, Nees, in Annales du Jardin botanique de Buitenzorg, ix (1891), p. 16.

[2] See Part I, p. 101.

leaves consists of the amphigastria, which are smaller than the leaves of the two lateral rows, and this is connected with the fact that only plagiotropous shoots occur in the vegetative region, with the exception of shoots which produce gemmae. The amphigastria are sometimes reduced to hair-like structures or are entirely wanting, as in Jungermannia bicuspidata, although there they occasionally if seldom appear. These features are entirely excluded in the case of Physiotium (Fig. 57, 1), in which the shoot-axis has a two-sided apical cell from which segments are cut off giving rise to lateral leaves[1]. On the orthotropous sexual shoots the amphigastria appear, although they may be wanting on the vegetative shoots, and the presence of a similar character upon the orthotropous shoots which bear gemmae in Calypogeia has been already pointed out[2].

In most members of this group the leaves are one-layered, but many-layered leaves are found in Gottschea pachyphylla, and a few others in which this character has probably the same significance as the succulence of the leaves of higher plants. There is commonly no midrib. Where a trace of this exists, as in Frullania Tamarisci, it is composed of cells with peculiar content different from that of the other cells of the leaf, and due perhaps to the accumulation of oil-bodies. This requires further investigation. An indication of a many-layered rib is found in Scapania, species of Plagiochila, and in Jungermannia albicans[3].

The early appearance in many forms of a division of the leaf into halves is very characteristic, but this often disappears as the plant grows; its occurrence precludes the apical growth which occurs in the leaves of the Musci. In consequence of it the mature lateral leaves of many Jungermannieae are two-lobed and possess an upper lobe and an under lobe which are frequently very different in form and size. This is never seen in the amphigastria. This bipartition distinguishes the leaves of the acrogynous species from those of the anacrogynous ones. The outgrowths which, in the form of lamellae, papillae, and so forth, are frequently found upon the leaves, will be spoken of when I discuss the arrangements for the taking up of water.

It has been already shown[4] that in many forms there is a displacement which may go so far that the leaves appear to have a horizontal insertion. This is by no means generally the case. Where no leaf-surface is formed. but the leaf consists merely of cell-rows, as in Jungermannia trichophylla, Lepidozia bicruris, Arachniopsis, there is no displacement. From this we may conclude that the displacement is connected with the obtaining of

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[1] Goebel, Archegoniatenstudien: V. Die Blattbildung bei den Lebermoosen und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 445.

[2] See Part I, p. 102.

[3] See Morin, Anatomie comparée de la feuille des Muscinées. Thèse, Rennes, 1893.

[4] See Part I, p. 101.

a favourable surface of assimilation, and it may be directly brought about by light, as it is in Jungermannia bicuspidata[1], or it may be inherited.

Concrescence of the leaves, either of the two upon the upper side, or of these with the corresponding amphigastrium, is met with in Plagiochila connexa and P. conjugata, species of Chiloscyphus and others, but we are unable at present to give any biological explanation of it.

Reversion to thallus-form. Some leafy Jungermannieae exhibit the remarkable feature of a reversion of their vegetative bodies in some degree to the form of a thallus. Cephalozia (Pteropsiella) frondiformis shows this. The vegetative body of this plant is, as its specific name implies, a flat band-like thallus from which *leafy* shoots bearing the sexual organs spring; but the apparent thallus is a leafy shoot, the horizontally-placed leaves of which have united with one another, or, which comes to the same thing, stand upon a wing-like outgrowth of the stem[2]. Transition-forms from the thallus to the leafy stem also occur. Zoopsis, which is a sub-genus of Cephalozia, shows similar features (see Fig. 97). Its leaves are small appendages of the stem, and the flattened large-celled dorsal surface of the stem does the work of assimilation; but at the vegetative point the same relationships are found as occur in other foliose forms, and the sexual shoots have well-developed leaves.

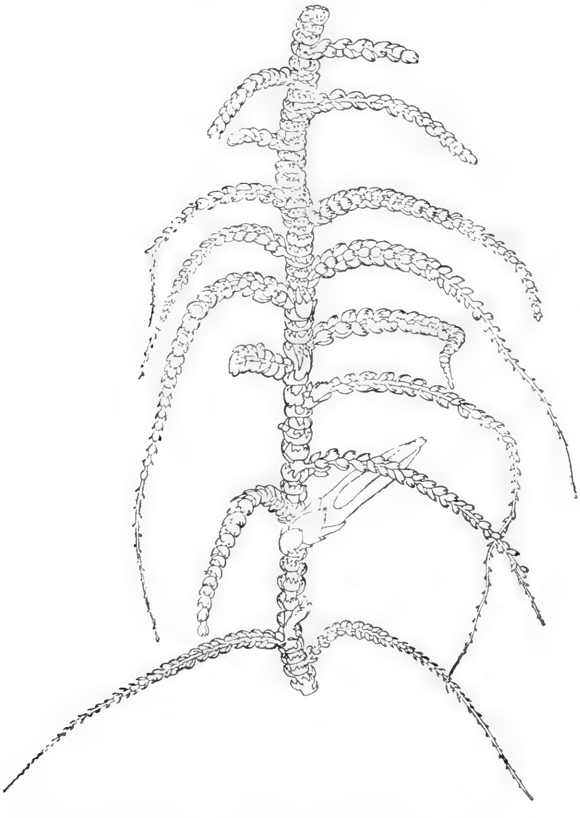

FIG. 38. Lepicolea cavifolia. A plant seen from below. The lateral branches have grown out into flagella which are clad with reduced leaves. Magnified 3.

Flagella. The reduction of the leaves on shoots which are constructed as *flagella*, and as stolons or rhizomes, comes about in another way. Flagella

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[1] Goebel, Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsberichte der bayerischen Akademie, xxvi (1896).

[2] Goebel, Archegoniatenstudien: III. Über rudimentäre Lebermoose, in Flora, lxxvii (1893), p. 83.

are shoots with thin long axes and reduced leaves. Lepicolea (Fig. 38) amongst others commonly has lateral shoots developing into flagella. These are usually richly provided with rhizoids, and apparently serve as a fixing-apparatus like the anchoring-organs in some species of Aneura[1]. In Mastigobryum these flagella arise ventrally. The shoots in this species do not cling to the substratum but rise obliquely from it, and the flagella have exactly the function of the rhizophores in Selaginella. They conduct water and the substances dissolved in it from the substratum to the plant, and like rhizophores they may be caused to develop as leafy shoots. Lembidium dendroideum (Fig. 39) has an oblique ascending shoot-system which develops no rhizoids. These are found upon shoots, bearing reduced leaves, which bore into the substratum, and penetrate it in all directions, being externally quite root-like. In many species of Plagiochila and Bryopteris (Fig. 40) the shoots in their lower part cling to the substratum, and raise themselves up as free structures in their upper part. What outer factors influence the development of these forms of shoots we do not yet know.

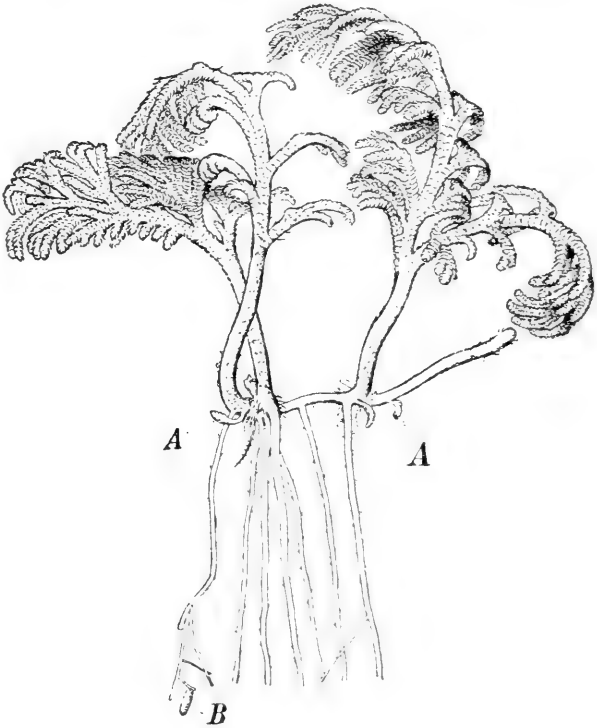

FIG. 39. Lembidium dendroideum. An isolated plant. The aerial shoot-system ascends obliquely with incurved ends. *A*. antheridial branches at the base of the shoot-system. Root-like subterranean shoots pass downwards on one of which is a tuber, *B*. The oldest aerial shoot is the broken stump on the right. Magnified 4.

Long shoots and short shoots. Of other kinds of division of labour among the branches of one shoot-system, apart from the supporters of the sexual organs, that of long shoots and short shoots, which as is known also occurs in the thallose forms, must be mentioned. It is very distinct in Bryopteris filicina (Fig. 40).

Tubers. The formation of tubers which takes place in some of the thallose Hepaticae, is unknown as yet in the foliose acrogynous forms (see, however, Fig. 39, *B*).

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[1] See p. 26.

Branching and the leaves. There remains to mention relationships of the branching to the leaves. In no case is branching axillary. The branches are either lateral or ventral, in correspondence with the dorsiventral character of the foliose Jungermannieae, just as in the thallose usually dorsiventral forms. In Anomoclada alone do the branches appear upon the dorsal side of the shoots, and the branching in this genus requires further investigation. In the lateral branching the formation of the branch takes place partly at the cost of one lateral leaf. A leaf, of say Frullania dilatata, from whose base a lateral shoot springs, wants its auricle, and in place of it there is the shoot. Whilst usually the whole lateral segment of the apical cell is claimed for the formation of the leaf, occasionally a few of the cells being devoted to the construction of a free stem-surface, here in the case of the branching the ventral portion of the segment is devoted to the making of a branch, and the upper part of it only is left for the leaf. Different in degree only is the laying down of the primordium of the branch in the basiscopic basilar portion of the segment, that is to say, the formation of the leaf out of the segment is complete, but one cell on the under basiscopic portion of the segment becomes the apical cell of the primordium of a branch, and when this develops we find, as in Radula complanata, the branch underneath a completely developed leaf.

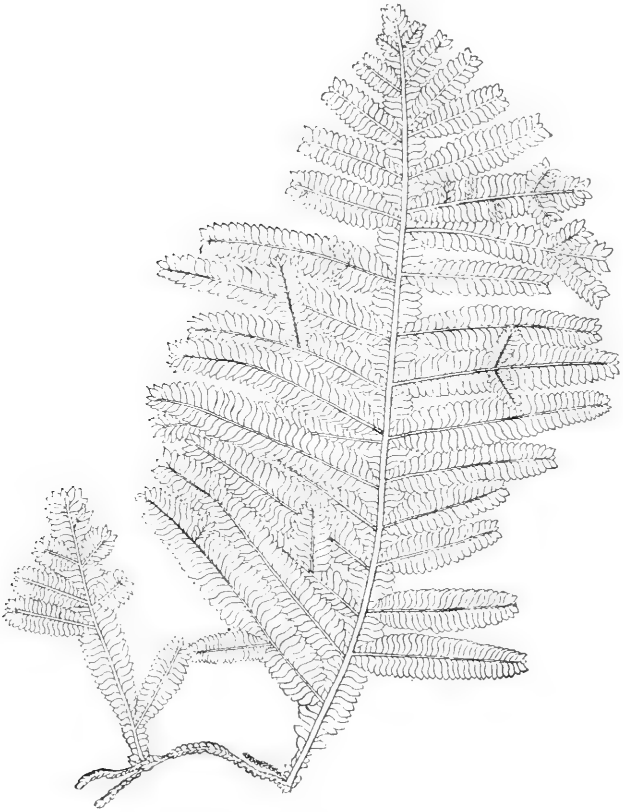

FIG. 40. Bryopteris filicina. Habit. The shoot branches in one plane. At the base are stolons with reduced leaves which can give rise to new shoot-systems and at the same time help in anchoring the plant. Magnified 4.

Resting buds. The lateral shoots of many species may become resting buds. In Lejeunia, for example, the first three leaves of the lateral shoot coalesce to form an envelope surrounding the primordium of the shoot which rests for an indefinite period. In the further development of the bud the envelope is broken through.

Endogenetic shoots. This leads us to what Leitgeb has described as the endogenetic origin of the ventral and lateral shoots of many species. He says that the flagella of Mastigobryum are formed from cells lying immediately under the outer cells, and the same is the case with the fructification-branches of this plant, as well as of Lepidozia, Calypogeia, and others. The disposition of these endogenetic branches in Lophocolea bidentata and in Jungermannia bicuspidata is peculiar. They are almost exclusively ventral, and the branches spread themselves out upon the substratum to both sides of the chief axis, so that the branch-system has the same facies as is produced by lateral branching.

3. Rhizoids.

Knowing now the relationships of configuration of the vegetative body, we have to cast a glance at the organs which anchor it to the substratum and draw therefrom, at least in many cases, water with the substances dissolved in it. These bodies are the *rhizoids*, hair-roots. All Hepaticae, whether thallose or foliose, possess unicellular rhizoids; the Musci, on the other hand, always have rhizoids composed of a single row of cells. These rhizoids differ in function. In some Hepaticae, for example epiphytic foliose forms, they are only anchoring-organs, in others they combine the work of fixing the plant and of absorbing water. They are absent in only few forms, and we can usually discover a reason for their absence. The Calobryaceae, for example, have no rhizoids [1], and they possess root-like shoots creeping in the substratum [2], and these render the rhizoids unnecessary. Physiotium cochleariforme also has no rhizoids, but it is provided with large water-sacs, and in this resembles Sphagnum [3].

The two species of Riccia, R. natans and R. fluitans, each of which possesses a land-form and a water-form, have no rhizoids in their water-form, and this because they are as unnecessary here as are the hairs upon the roots of many water-plants of higher groups, for example, Salvinia, Utricularia. In R. fluitans the water-form may produce rhizoids if it comes in contact with a solid body [4]. In many epiphytic forms, such as species of Lejeunia, a strong anchoring disk develops out of a bundle of rhizoids [5].

A division of labour occurs in the rhizoids of some thallose forms which attain a considerable stature, and particularly in those in which the upper

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[1] The germination of these Hepaticae is not yet known, and it is probable that as in Sphagnum the germ-plant has rhizoids.

[2] See p. 39, and Fig. 37.

[3] Trichocolea tomentella has well-developed rhizoids, although Nees thought it had few or none.

[4] See Part I, p. 269.

[5] For an account of this see Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 161, Fig. 66.

side of the thallus takes in no water, and the care of the water-supply devolves upon the rhizoids. Amongst such forms we know at present species of Monoclea[1] and the members of the series of the Marchantiaceae.

Monoclea. I had the opportunity of examining Monoclea dilatata in a living condition in Venezuela, and the interest of the species lies in this, that it foreshadows the peculiar features of the formation of rhizoids which belong to the Marchantiaceae[2]. It has two kinds of rhizoids; some wide and thin-walled, arising exclusively out of the under side of the thickened midrib of the thallus (Fig. 4, III), and at once piercing the substratum; others narrow and relatively thick-walled, which arise partly upon the edge of the thallus, partly upon its under side, and grow at first adpressed to the thallus, those that arise laterally converging to the midrib, beneath which runs a strand of rhizoids, keeping it moist by capillarity. These lateral rhizoids can irrigate the lateral parts of the thallus. The whole arrangement reminds one of that found in hygrophilous Marchantiaceae, especially in Dumortiera. Monoclea itself occurs like them in moist places. The arrangement, which is indicated in Monoclea, finds perfect development in the Marchantiaceae.

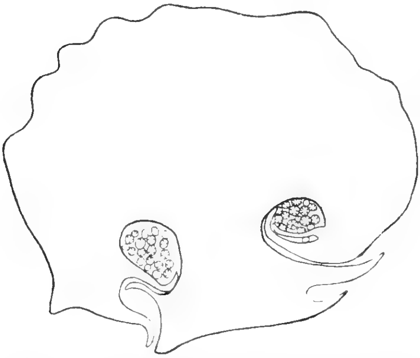

FIG. 41. Preissia commutata. Stalk of an archegoniophore in transverse section. The strands of rhizoids are sunk in two deep lateral channels.

Marchantiaceae. Here the rhizoids are frequently over two centimeters in length, and often form a thick felt on the under side of the vegetative body. The division of labour among them finds its expression in a difference between 'smooth' rhizoids, which have the usual construction, and 'trabecular' rhizoids, which have trabecular thickenings upon the inside of their wall. Germ-plants of Marchantia and plants which arise from gemmae possess at first only smooth rhizoids, and they it is which enter the soil directly from the under side of a mature thallus and anchor it. The trabecular rhizoids, on the other hand, lie upon the under side of the thallus in strands, the strongest of these running along the midrib, and only at some distance behind their point of origin do they enter the soil[3]. There is no doubt that these strands, which are also found under the rays of the disk of the sexual shoot and upon its stalk (Fig. 41), conduct water by capillarity, although at the same time the movement of water chiefly takes place through their lumen. The trabeculae within the

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[1] Which, however, can take up water directly from outside.

[2] See Ruge, Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893), p. 279.

[3] See p. 32.

rhizoids have also, as Kamerling[1] has recently shown, a connexion with the conduction of water. If the thallus draws water from the trabecular rhizoids, and a supply to replace it cannot be sufficiently quickly obtained from the soil, air-bubbles will be formed within the rhizoids which will interrupt the current of the water. The presence of the trabeculae compels the formation of these bubbles in the centre of the cavity of the rhizoids, and so the current of water can pass the bubble. The trabecular rhizoids then *make possible the maintenance of a more copious supply of water* than do the smooth ones. Concomitantly with this we find that the trabecular rhizoids are specially developed in forms with relatively great transpiration, whilst they are subordinated in forms in which this is feeble; for instance, in a Venezuelan hygrophilous species of Dumortiera they were present in extremely small numbers, and were entirely wanting in Cyathodium cavernarium.

Transformation of rhizoids. A portion of the rhizoids is transformed into thick-walled bristles in Dumortiera hirsuta, and the transition-forms to rhizoids show the true nature of the bristles, which may be considered protective organs for the thallus, although it is impossible to say precisely wherein the protection lies[2]. Change of function and transformation of rhizoids is otherwise unknown. Lindenberg speaks of segmented rhizoids in the land-form of Riccia natans, but this is either an error or a misdescription of the filiform adventitious shoots which sometimes occur upon old examples of species of Riccia[3]. So far as we know, the rhizoids in Hepaticae are incapable of a transformation or further development, and in this they contrast with their condition in the Musci.

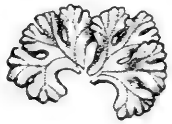
FIG. 42. Riccia natans. Land-form, seen from above. The branches of the thallus become isolated by the dying off of the parts behind. Natural size.

II

ASEXUAL PROPAGATION OF HEPATICAE[4]

Every asexual multiplication is fundamentally a process of division of the vegetative body in which the products of division may be very unequal in size. In creeping Hepaticae, as in many other plants, the branches may

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[1] Kamerling, Zur Biologie und Physiologie der Marchantiaceen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897).

[2] Compare with these the bristles arising upon the thallus of many species of Metzgeria which may be considered transformed rhizoids.

[3] A recent compiler has again mistaken these for rhizoids.

[4] Nees von Esenbeck, Naturgeschichte der europäischen Lebermoose, i–iv, Berlin and Breslau, 1833–8; Leitgeb, Untersuchungen über die Lebermoose, i–vi, Graz, 1874–81; Ruge, Beiträge zur

become independent plants through the dying off of the older parts behind (Fig. 42). Frequently, however, special propagative organs are developed which have been termed *gemmae* or *brood-buds*, and of these some examples must be given.

1. SEPARATION OF SPECIAL TWIGS FROM THE VEGETATIVE BODY[1].

This is the nearest to the ordinary processes of division. In its simplest form it is observed in Pellia calycina. Towards the close of the vegetative period of this plant there appear upon sterile plants, through repeated forking of the vegetative point, short-lived branchings filled with starch and other reserve-materials, but without rhizoids and frequently standing erect and overlapping one another. These readily break off, and clearly exhibit a primitive form of gemma (Fig. 43). If they do not break off they may grow in the succeeding spring as ordinary branches of the thallus. Fegatella supradecomposita shows a further stage of differentiation of these branches. In it they are borne upon thin stalks, and can therefore easily separate (Fig. 44). Superficially they resemble the similar structures in Marchantia and are nearly circular flat plates with a vegetative point on one side but they differ altogether in their origin. Whilst the gemmae of Marchantia are unicellular structures, which only before their separation, or it may be at germination, grow into cell-masses, those of Fegatella supradecomposita are merely modified branches of the thallus, and possess a series of scales covering the vegetative point in the manner usual amongst the Marchantieae.

FIG. 43. Pellia calycina. Branching of a sterile lobe of the thallus in autumn. Seen from below. Magnified.

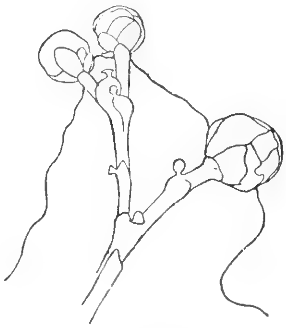

FIG. 44. Fegatella supradecomposita. Thallus with three gemmae seen from below. Magnified 12.

Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893); Schostakowitsch, Über die Reproduction und Regenerationserscheinungen bei den Lebermoosen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894).

[1] We leave out of account here the formation of tubers which will be referred to in a subsequent page. See p. 66.

2. GEMMAE (BROOD-BUDS) FORMED BY GEMMA-CELLS (BROOD-CELLS).

All other forms of gemmae can be traced back to a construction out of *gemma-cells* (*brood-cells*), but these frequently develop so far on the mother-plant that it is impossible sometimes to draw a sharp limit between them and adventitious shoots. This is particularly the case within the cycle of affinity of the Metzgeriae. Many species of Aneura have duplex gemma-cells which fall away from the thallus. They are discharged from their mother-cells with a slight jerk [1], probably by swelling of the inner layers of the membranes of these; the outer portion of the membrane remains behind. They often appear in large numbers. Allied to this is the copious formation of gemmae in Metzgeria conjugata. In this species some branches of the thallus become very narrow and develop as supporters of the gemmae. They ascend from the substratum, and, gradually losing their dorsiventrality, they become radial, whilst the gemmae, which appear close together at first and only upon the margin of the branch, are found later upon the upper and under sides of the thallus as well. The upright position evidently favours the distribution of the gemmae. The gemmae, at the moment when they are shed, are in the form of concave cell-plates, with a vegetative point having a two-sided apical cell, from which a new thallus is formed [2], and in the process of shedding a remnant of the wall of the mother-cell is left behind as is the case in Aneura. In Metzgeria furcata adventitious shoots are regularly developed instead of the gemmae, and each of them proceeds from a single cell of the margin or of the midrib. Gemmae of a more or less advanced stage of development before shedding are found in other thallose Hepaticae, for example in Marchantia and Lunularia, in which they have been so often described, and also in Treubia, Cavicularia, and Blasia. Blasia has two kinds of gemmae: the one is a nearly spherical cell-mass produced in a flask-like receptacle with a long neck, out of which it is squeezed through the swelling, when moistened, of mucilage formed by the mucilage-papillae at the base of the receptacle [3]; the other is a gemma-scale at the base of which there is to be seen at a very early period of development the cell from which the new thallus proceeds,—this gemma-scale arises upon the upper side of the thallus, especially upon shoots which bear neither sexual organs nor receptacles for gemmae [4]. Cavicularia has gemmae whose outer cells have thick walls, and each of them has an excrescence which has perhaps to do with the scattering of the gemmae by animals.

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[1] See Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882), p. 338; Ruge, Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893), p. 307.

[2] In Aneura the gemma is shed before these landmarks are developed.

[3] This also takes place in Marchantia, but in a less pronounced manner.

[4] These gemma-scales require investigation especially in their biological relationships. A similar dimorphism of gemmae appears probably in the genus Tetraphis amongst the Musci.

A description of the formation of the gemmae in the several forms of Hepaticae would have no general interest. Their appearance is sporadic within cycles of affinity, and even within genera. Anthoceros glandulosus, for example, is the only known species of the genus in which they are found, and in it they take the form of oval cell-masses. Amongst the Marchantieae, Marchantia and Lunularia alone possess them, and how profusely they are distributed in these genera is well known to gardeners. They overrun every pot in cultivation.

The occurrence of gemmae produced from shoots is not unknown in the foliose Jungermannieae, and they may be either unicellular or before their separation grow into cell-masses. The formation of gemmae occurs in many species, usually upon the edge or upon the tip of leaves, and the gemmae appear then often as long branched yeast-like chains. The several gemma-cells separate easily from one another in moisture. In Lophocolea bidentata aggregates of cells loosely joined together fall from the leaves. According as the formation of gemmae takes place at an early or late stage, the formation of the leaf is more or less influenced by it, and variations may be seen upon one and the same shoot. In Scapania nemorosa, for example, only the points of the upper lobes of the lower leaves of the shoot are furnished with gemmae; their formation therefore was relatively late. On the leaves higher up the under lobes of the leaves are first concerned in the formation

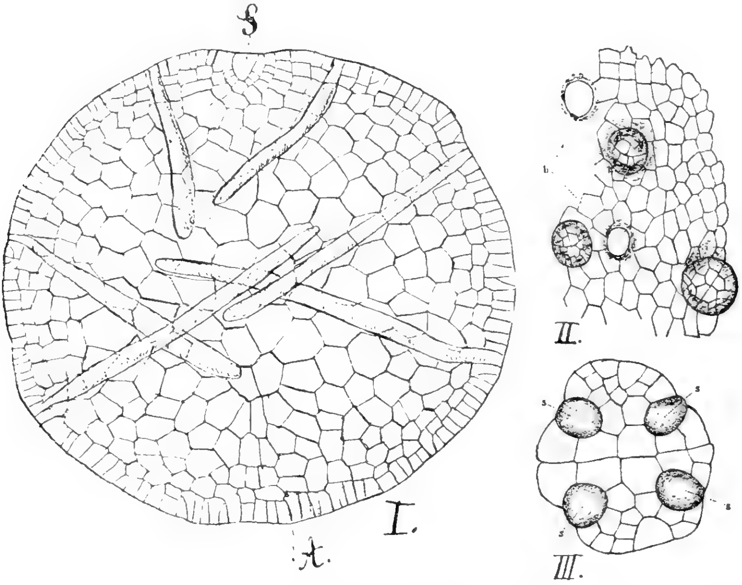

FIG. 45. Lejeunia. Formation of gemmae. I, Lejeunia (Odontolejeunia) mirabilis, Steph. Gemma; *S*, apical cell; *A*, point of attachment. Rhizoids in the form of long tubes have developed upon the under side from single marginal cells. II, III, Lejeunia (Cololejeunia) Goebelii. II, portion of a leaf with three gemmae still attached; *s*, *s*, indicate the points of attachment of two gemmae which have fallen off. III, gemma with four anchoring-organs, *s*, and two apical cells.

of gemmae, and the further up one goes the more is the development of the leaf-surface hindered, until finally, in the position of each leaf we find a group of gemmae issuing directly from the segment of the apical cell. The leaf-borne gemmae have thus become stem-borne, and we are furnished with an instructive example of a gradual transposition. The number of the gemmae in such cases is very large, as many as a thousand. The shoots which bear gemmae in many species, for example in Calypogeia Trichomanes, are orthotropous, as are those of Metzgeria conjugata [1]. In the genera Radula[2], Lejeunia[2], and Colura[2], gemmae in the form of cell-surfaces appear upon the leaves, and in these genera, which include mostly epiphytic species, they secure a rapid fixation to the substratum. The gemmae of Lejeunia (Fig. 45) have two vegetative points out of which shoots may subsequently develop, and they are furnished with anchoring-organs, which are merely arrested rhizoids (Fig. 45, I, III). The example figured in Fig. 45, I is of interest because there is only *one* apical cell, probably because the gemma is anchored not by its middle but excentrically. When the gemmae of Lejeunia have two apical cells (Fig. 45, III), a leafy plant may spring out of each of them, but the apical cell may also grow out into a thallus with a continued segmentation of a two-sided cell, like the product of a germinating spore. Such a formation of thallus takes place if the conditions are unfavourable for the formation of a stem, and it is particularly often seen in the germinating gemmae of Radula [3], where it furnishes the young plant with a firm fixation upon its substratum, which is the leaves of Spermophyta. These relationships of the development of the gemmae find their counterpart, both physiological and morphological, in the phenomena of the germination of the spore [4]. The germination of the gemma conforms generally with that of the spore. In Marchantia and Lunularia this is evidently not the case, but in these genera the profile disposition of the gemma, as in Riella, makes it impossible.

It is easy to establish that there is often a certain antagonism between the formation of gemmae and sexual reproduction. Gemmae appear either exclusively or preferably upon sterile individuals. Leitgeb, however, observed them upon the tips of the leaves about the antheridia in Scapania nemorosa, and Nees von Esenbeck recorded the occurrence of 'Jungermannia Sphagni,' bearing sporogonia and gemmae at the same time.

When the phenomena of regeneration were discussed, it was shown that

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[1] See p. 49.

[2] See Goebel, Morphologische und biologische Studien: I. Über epiphytische Farne und Muscineen, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 49.

[3] See Goebel, op. cit., Figs. 60–67.

[4] Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882), p. 339; Ruge, Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893); Schostakowitsch, Über die Reproduction und Regenerationserscheinungen bei den Lebermoosen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894).

the Hepaticae have a rich capacity of regeneration[1], especially by severed portions, and that there is a difference between them and Musci in this respect. In the Musci, regeneration always begins by the formation of the protonema characteristic of the germination of the spore, but in the Hepaticae cell-masses are produced in regeneration, even although the spore forms cell-surfaces or cell-threads in germination. I have been led by my investigations to the view that every cell in the Hepaticae has the latent capacity to develop further like the spore, but this is only called forth if there is an enfeeblement of the vegetative body. The proof of this was especially afforded by Metzgeria furcata[2], in which under definite conditions the cells did not grow out as usual directly into 'adventitious shoots,' but into cell-rows just as in the germination of the spore; and in support of this is an observation of Leitgeb that upon old, that is in my view enfeebled, plants of Jungermannia bicuspidata, cells of the surface of the stem could grow out into tubes like germ-tubes and form a shoot at their apex. In like manner on the *old leaves* of Lophocolea bidentata, and of a tropical species of Lejeunia which I observed, the same phenomenon may be noted. This subject cannot be discussed further here, but the facts are of the greatest importance for our comprehension of the development, although little attention is given to such phenomena in our times when the microtome is so popular an instrument.

III

PHENOMENA OF ADAPTATION OF THE VEGETATIVE ORGANS OF HEPATICAE

I. *RELATIONSHIPS TO WATER.*

The anatomical structure of the vegetative body of the Hepaticae is quite different according as it has or has not to take up water directly from the outside. A high anatomical differentiation is only reached in those Hepaticae which possess a vegetative body of which the surface cannot be wet. But such forms may revert again to a simpler relationship. It is easy to satisfy oneself that a Riccia, excepting Riccia fluitans, or a Marchantia, cannot be directly wet by water like a Pellia or one of the foliose Hepaticae, and this gives us the clue to their diverse structure which finds a parallel in the differentiation of tissues of the higher plants.

Most of the Hepaticae are *hygrophilous* and live in a moist medium, where they are seldom exposed to the danger of long drought, and therefore, as is

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[1] See Part I, p. 48.

[2] See Goebel, Archegoniatenstudien: VIII. Rückschlagsbildungen und Sprossung bei Metzgeria, in Flora, lxxxv (1898), p. 69.

the case with the lichens, the number of forms of the Hepaticae is greater as we approach moist mountainous regions. Epiphytic forms and those in unsheltered localities are subjected occasionally to a want of water, and they are endowed partly with the capacity of resisting drought of short duration, and partly with special contrivances to retain water. These contrivances also occur in terrestrial forms and in extraordinary abundance in many species.

I. ARRANGEMENTS FOR THE RETENTION OF WATER.

The arrangements for securing the retention of water imply a copious absorption of it. Their value to the plant is that even in drought the most delicately constructed forms are able to carry on the phenomena of their life, especially assimilation [1], and the longer the water is retained the longer and the more actively will their life-processes be maintained. Hepaticae in the tropics frequently live upon the leaves of the higher plants from which water readily flows off, and therefore we find in them arrangements for retaining water even in species which live in the wettest tropical hill-regions. Species of Physiotium furnish an example. In these species we have to deal with a relationship similar to that observed in Sphagnaceae, which, growing in localities which are always moist, have nevertheless a most remarkable contrivance for taking and retaining water. Why should this be so? I find nothing about it in the literature of Botany. The Sphagna chiefly live upon *rain-water*, and they take consequently ash-constituents from the substratum in only very small amounts [2]; they must therefore give off by evaporation a large quantity of water. Similarly the Hepaticae which live in the wet hill-regions take their necessary water from clouds and rain which contain but little nutritive matter, so that a large volume of water is necessary for them.

Although the arrangements for retaining water are essentially the same in thallose and foliose forms, it will be more instructive if we look at the two series separately.

A. In Thallose Forms.

a. JUNGERMANNIACEAE. The following are illustrations in this series:—

Aneura endiviaefolia is represented in Fig. 46. As its name indicates the thallus resembles a curled leaf of endive because the branches are curved inwards and downwards, and they thus provide in the thallus a sort of spongy construction which is favourable to the retention of water. The branches of the higher order differ from the chief axes in having a one-

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[1] Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 439. Air-dried, still living Frullania after eight hours' exposure to illumination had decomposed no carbon-dioxide. See also Jönsson, Recherches sur la respiration et l'assimilation des Muscinées, in Comptes Rendus, cxix (1894). He comes to the same conclusion:—'the more considerable the proportion of water, the more intense is the gaseous exchange.'

[2] This interpretation was first given to me by my deceased friend Sachs.

layered cell-surface except at the midrib. Similar arrangements occur in some Javanese species of Aneura (Pseudoneura). An investigation of living plants is required to determine whether the marginal cells of the thallus in species of Aneura absorb water.

Aneura hymenophylloides behaves in a similar manner (Figs. 47, 48). Its thallus in some measure resembles the feather-branched leaf of a species of Hymenophyllum, and it possesses an excellent arrangement for retaining water. The tips of the thallus are all strongly incurved downwards, and the branches, placed in two rows upon the chief axis, converge by their under sides, each branch having its edges concave downwards (Fig. 48, 2, 3). In addition, the thin-walled cells of the surface of the thallus are frequently convex outwards, and are excellently arranged for the retention of water. The branch-system does *not lie upon a substratum*, and a consideration of Fig. 48 will show the important difference there is between the cellular construction in the chief and lateral axes.

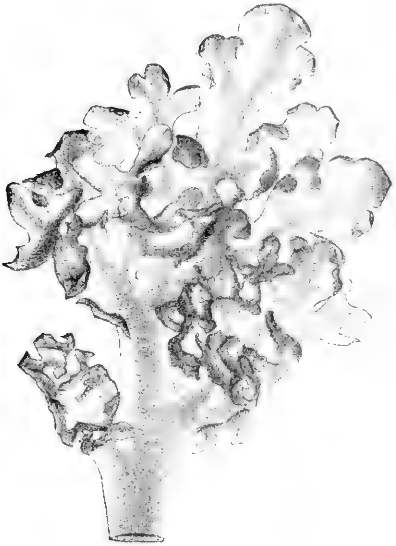

Fig. 46. Aneura endiviaefolia. Portion of thallus seen from below. The twigs are curled inwards and downwards. Magnified 9.

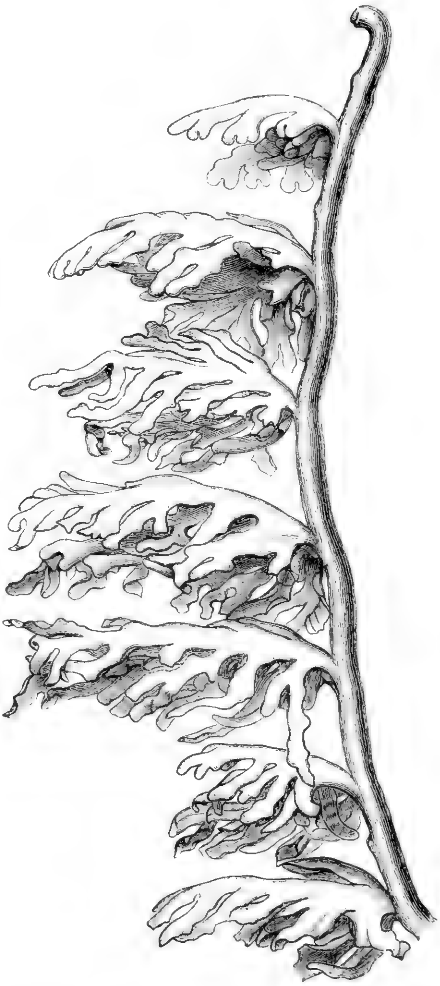

Fig. 47. Aneura hymenophylloides. Seen in profile. The vegetative point of the long shoot and all the branches are curved inwards and downwards. Magnified 8.

Aneura fuegiensis (Fig. 49) exhibits other arrangements. Upon the under side of the thallus we find lamellae, most numerous upon the chief axis, becoming always fewer upon the lateral axes of higher order. The margin of these lamellae is not smooth, but is provided with pluricellular 'hairs,' which increase the efficiency of the whole as a sponge. The cell-walls of the lamellae are thickened at their corners as they are in the cells of the leaves of many foliose forms. One may compare the lamellae with leaves inserted longitudinally, and they arise like the amphigastria of Fossombronia, each one behind a mucilage-papilla. They do not, however, run over the whole length of the thallus. In the lateral shoots of a higher order a lamella is not formed behind each mucilage-papilla.

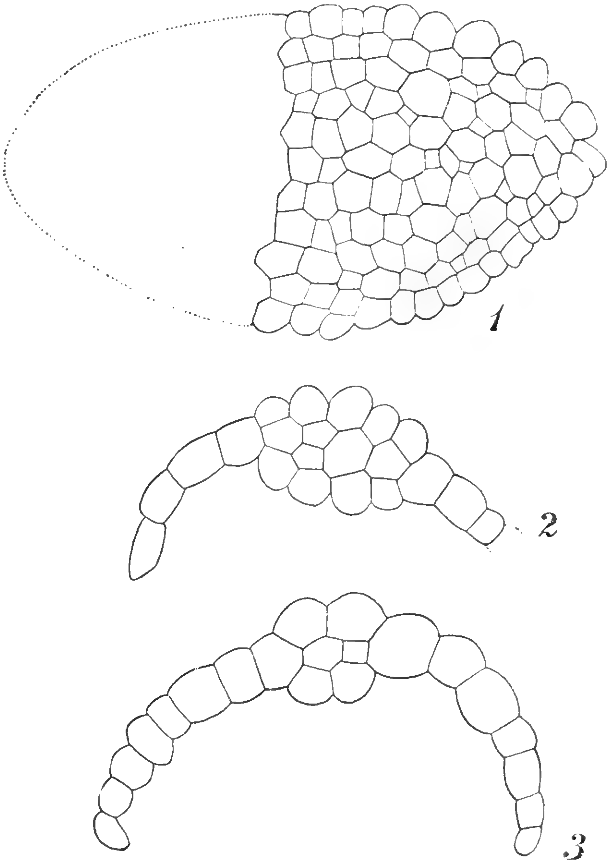

FIG. 48. Aneura hymenophylloides. 1, chief axis. 2, axis of the first order. 3, axis of the second order. All in transverse section. Highly magnified.

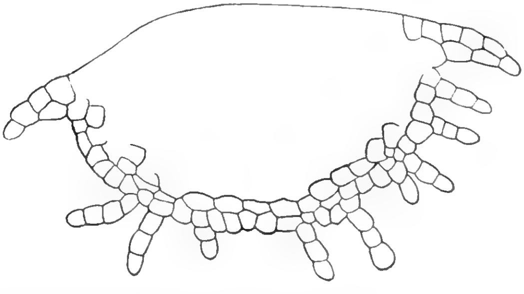

FIG. 49. Aneura fuegiensis. Thallus in transverse section, showing the lamellae upon the under side as cell-rows. Between these lamellae water is held. Highly magnified.

Metzgeria. Our indigenous species of Metzgeria have no special arrangements for retaining water if we except the papillae with which the thallus of Metzgeria pubescens is covered. On the other hand Metzgeria saccata[1], which lives between mosses on the bark of trees in

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[1] See Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 425, Fig. 1.

New Zealand, possesses *water-sacs* like those on the auricles of the leaves of Frullania, or like those which have yet to be described in Dendroceros foliatus (Fig. 51). On the edge of the thallus are found vesicular or hood-like appendages which are laid down near the apex by the concave infolding of isolated parts of the thallus. These become larger, fill with water, and so serve as water-sacs.

b. ANTHOCEROTEAE. Several species of Anthoceroteae repeat the arrangements which have been described above in thallose Jungermannieae.

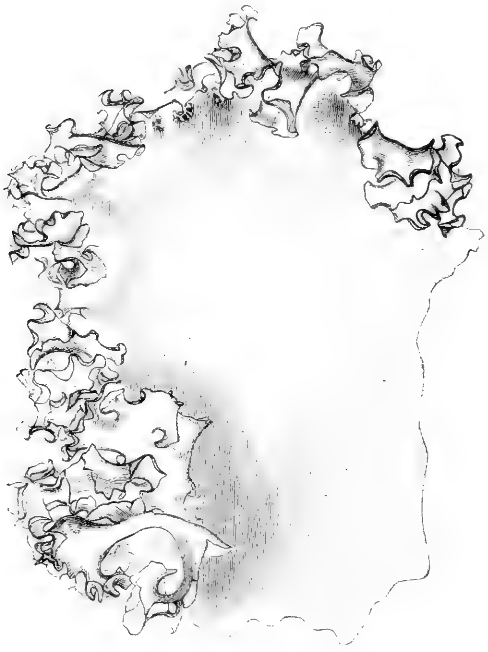

FIG. 50. Anthoceros fimbriatus. Portion of a thallus seen from below; the rhizoids are not shown. The one-layered crisped lobes at the edge hold water. Magnified.

Anthoceros. Our indigenous Anthoceros punctatus has upon the upper side of the thallus pit-like depressions which retain water. A. arachnoideus[1] has, instead of these, a net-work of low intersecting ridges, to which we must ascribe the same significance. On the other hand, A. fimbriatus (Fig. 50) is provided with a crisped one-layered cell-surface at the margin of its many-layered thallus, giving it a striking appearance as it grows upon the Cordilleras of Merida. The marginal fringe arises out of the 'middle lobe in the forking of the thallus[2], and it reminds us of the relationships which have been described in Aneura endiviaefolia[3].

Dendroceros. The remarkable relationships of Dendroceros foliatus (Fig. 51) were touched upon when speaking of the formation of leaves, and it was shown that on the edge of the thallus cap-like formations are found which are partly laid down as special shoots at the vegetative point and partly proceed from the middle lobes. These structures have evidently the same significance as the water-sacs of Metzgeria saccata. The same arrangement is found in Karsten's Dendroceros inflatus. The cells in the one-layered surface of the thallus of Dendroceros frequently separate from one another, and the schizogenetic intercellular spaces increase the spongy nature of the whole thallus.

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[1] See Stephani, Colenso's New Zealand Hepaticae, in Journal of the Linnean Society, Botany, xxix (1892), p. 265.

[2] See p. 21 and Fig. 14.

[3] See p. 53; adventitious shoots may arise from them.

These examples show that in *different* cycles of affinity the thallose Hepaticae exhibit *analogous* adaptations. When we deal with formation of tubers we shall find additional evidence of this.

B. In Foliose Forms.

As has been shown in the description of the formation of leaves, adaptations appear upon these which make possible the retention of water. They are indeed abundant, but are almost entirely wanting in plants which grow in moist localities.

A. PARAPHYLLIA.

The shoot-axis may share in such adaptations by the formation of outgrowths, which after the analogy of the Musci we may name *paraphyllia*. These are known in two genera which are not systematically nearly allied, Trichocolea and Stephaniella.

Trichocolea. They have been longest known in Trichocolea tomentella[1], but nothing has been said regarding their function. I find them only upon the upper side and upon the flanks of the stem, in the form of simple or branched cell-threads like those which are found upon the leaf-edges[2], and they make the whole plant a spongy mass. Trichocolea paraphyllina shows the same features. The paraphyllia without doubt act like the lamellae upon Aneura fuegiensis and upon the leaves of Polytrichum.

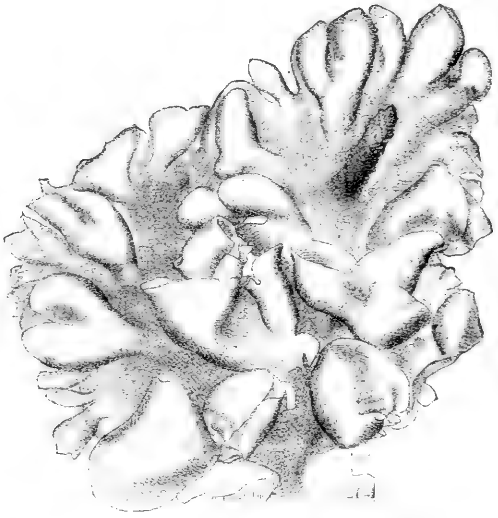

FIG. 51. Dendroceros foliatus. Seen from above. The 'middle lobes' are recognized by their emargination, and the other hood-like structures are the 'leaves.'

Stephaniella. Stephaniella paraphyllina[3] is a xerophilous form with remarkable formation of 'roots' which will be described later[4]. The leaves in this plant are hardly organs of assimilation; they lose very early their chlorophyll and become mere covers for the stem-bud and for the paraphyllia which clothe densely the surface of the shoot-axis and are at once an apparatus for holding water and organs of assimilation[5].

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[1] Nees von Esenbeck, Naturgeschichte der europäischen Lebermoose, iii, p. 109, mentions them in this species, but erroneously calls them 'leaf-appendages.'

[2] See p. 58.

[3] See Jack, Stephaniella paraphyllina, Jack., nov. gen. Hepaticarum, in Hedwigia, xxxiii (1894), p. 11.

[4] See p. 70.

[5] In Trichocolea the assimilatory activity of the paraphyllia is subordinate because the leaves retain chlorophyll.

B. LEAVES AND PARTS OF LEAVES AS WATER-RESERVOIRS.

A transformation of the leaves themselves more frequently provides the mechanism for retaining water than does the formation of paraphyllia.

1. Aggregation of Leaves. Of the simplest case, where capillary chambers are formed by the close aggregation of leaves, as is the case in Musci, we need not say much; only this, that in different genera there are species which hang in the form of strands from tree-branches, for example Frullania atrosanguinea, F. atrata, Lejeunia lumbricoides[1], in which the lateral leaves are not expanded flatly, as usual, but are incurved so as to form with the relatively large amphigastria a system of capillary chambers around the whole stem.

Of other arrangements the following may be noticed:—

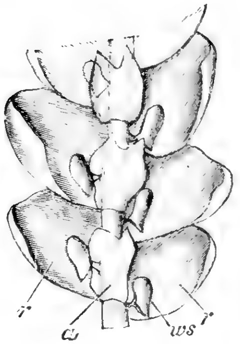

Fig. 52. Frullania Tamarisci. Portion of a shoot from below. *a*, amphigastrium; *ws*, water-sac, hood-like in form and formed out of the hollowed out larger portion of the under lobe of the leaf; *r*, upper lobe of the leaf. The 'stylus auriculae' is not shown. Magnified 36. Lehrb.

2. Outgrowths in the form of Cell-rows or Cell-surfaces upon the Margin or the Surface of the Leaf:

Trichocolea. In Trichocolea tomentosa we find a number of branched cell-rows springing from the margin of the leaf, and they also proceed from the under-surface of the leaf. They spread out in all directions and thus construct a spongy mass.

Lophocolea. In less degree the same thing is found in Lophocolea muricata[2].

Gottschea. In species of Gottschea[3] one or more lamellae spring from every leaf, and they form in Gottschea sciurea a remarkable water-apparatus.

3. By Transformation of Individual Portions of the Leaf Water-reservoirs are Developed:

A. *The under lobe of the leaf is so laid against the upper lobe that the two form a pocket-like or pitcher-like organ.* This occurs in Radula (Fig. 76), Phragmicoma, Lejeunia, and others. These organs have been called *auricles*[4].

Lejeunia. Heterophylly, a division of labour amongst the leaves, is a conspicuous feature in species of Lejeunia (Ceratolejeunia). Upon the

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[1] See Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 431, Plate viii and ix, Figs. 1, 2.

[2] See Goebel, op. cit., p. 430, Plate viii and ix, Fig. 3.

[3] See Goebel, op. cit., p. 430, Plate viii and ix, Fig. 18; id. Morphologische und biologische Studien: I. Über epiphytische Farne und Muscineen, in Annales du Jardin botanique de Buitenzorg, vii (1888), Plate v, Fig. 53.

[4] With regard to their configuration see Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 178, Figs. 78, 79. Although this was published in 1889 it has recently been asserted that these structures have not been recognized hitherto.

leaves at the base of the lateral shoots one or two relatively large water-sacs are formed, and there is almost no free leaf-surface, whilst on the upper leaves many small sacs occur, and there is a large leaf-surface formed by the upper lobe.

Radula. Radula pycnolejeunioides[1] is still more specialized. It has short shoots, the leaves of which become altogether narrow-mouthed water-sacs, with no free leaf-surface; whilst on the leaves of the long shoots the leaf-surface is quite conspicuous.

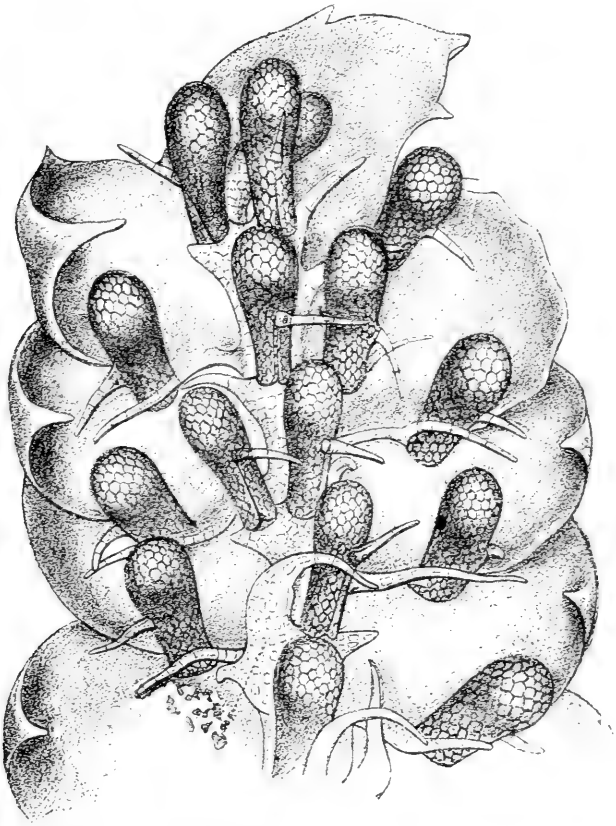

FIG. 53. Polyotus clavigea. Both on the amphigastria and on the lateral leaves there are water-sacs, one to two on each amphigastrium, one on each lateral leaf. Magnified.

B. *The under lobe of the leaf is laid against the upper lobe, but the under lobe alone constitutes the water-reservoir; it is concave upon the morphologically upper side, not, as in the previous case, upon the under side.* Frullania (Fig. 52) and Polyotus (Fig. 53) supply examples.

Frullania. In Frullania the under lobe of the leaf is much smaller than the upper lobe ; it is concave upwards and forms a hood-like structure,

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[1] See Goebel, Archegoniatenstudien : V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 433.

beside which stands a shorter body having a tip ending in a mucilage-papilla, the so-called 'stylus auriculae'[1]. Here as in other cases the water-receptacle is so formed that there is no wide opening to the outside so that the water can only slowly evaporate, and is taken up in great part by the cells of the leaf[2].

Polyotus. The genus Polyotus, as its name indicates, is richly provided with water-sacs. We find 'auriculae' not only on the lateral leaves but also on the amphigastria (Fig. 53), and the lateral leaves in many species are provided with marginal cell-rows which increase the sponge-like character.

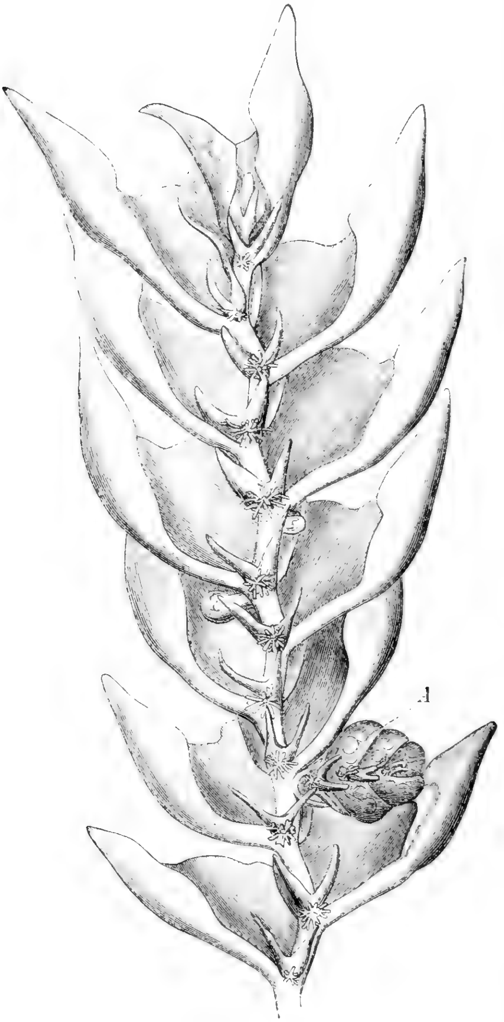

FIG. 54. Colura tortifolia. Beside each lateral leaf is an amphigastrium at the base of which rhizoids develop. The sac of the lateral leaves is turned with its point outwards, not well represented in the figure. At *A* a branch bearing antheridia. The figure does not show a characteristic development of Colura, namely that the leaves stand away from the substratum. Magnified 30.

All the species of Radula, Lejeunia, Frullania, and Polyotus have water-sacs more or less developed, but there are some genera, for instance Plagiochila, Chiloscyphus, and Jungermannia in which they occur only in isolated species: in Plagiochila cucullifolia[3], Chiloscyphus decipiens, C. cymbaliferus. Jungermannia curvifolia. I have proved that the formation of the water-sac is retarded in Frullania if it be cultivated for a long time in moisture. The formation of the water-sac is therefore an adaptation in direct relation to external factors. According as these influences affect the genus

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[1] The secretion of mucilage only takes place in youth, and serves for the protection of the stem-bud.

[2] With regard to 'Frullania' cornigera and others see Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 182, Fig. 82; id. Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 444.

[3] See Goebel, Morphologische und biologische Studien: IV. Über javanische Lebermoose; 4, Eine javanische Plagiochila mit Wassersäcken, in Annales du Jardin botanique de Buitenzorg, ix (1891), p. 34.

early or late in its history will the character of adaptation be of use or not as a systematic mark.

C. *Water-sacs which are closed by a hinged valve.* The genera Colura (Colurolejeunia) (Figs. 54, 55) and Physiotium (Figs. 56, 57, 58) exhibit the most highly developed adaptations for retaining water. They have water-sacs the opening of which is closed by a hinged valve. The valve crumples up in drought and opens the water-sac, in moisture it spreads out and closes it; and the arrangement is like that which occurs in the utricles of Utricularia.

Colura. Colura tortifolia (Fig. 54) is an epiphytic species which grows in South America [1]. The number of the amphigastria it is easy to see in the figure is double [2] that in the other foliose Hepaticae. The end of each lateral leaf takes on the form of a club-like sac into which a tube leads. There are two things to notice in the development of the leaves of Colura. First of all the under lobe of the leaf is rolled inwards against the upper lobe as in Lejeunia. It may become concrescent with the upper lobe and thus form the closed tube leading to the terminal club-shaped sac. The sac itself, which is not found in Lejeunia, is the result of an increased growth in surface of that part of the leaf which lies immediately above the tube just mentioned. The club-shaped sac arises then, not, as previous writers have assumed, by inrolling, but in exactly the same way as the water-sac of Frullania; and it is to be noted that the first sac-forming leaves which appear upon the germ-plant [3] of Colura, after a few flat leaves have been formed, conform in their configuration with these water-sacs in Frullania, and especially in the mouth of the sac which is directed downwards being not yet closed by a lobe. But the club-shaped sac here chiefly proceeds from the *upper* lobe, the inrolled under lobe of the leaf only forms the narrow tube leading up to the sac. The original apex of the leaf stands subsequently at the entrance to the club-shaped sac, and at this point the club-shaped papillae on the under lobe which secrete mucilage are found chiefly. It is extremely remarkable that the entrance to the sac is closed by a valve (Fig. 55). This lies upon a frame produced by a special outgrowth and partial overlapping growth of some cells of the wall of the sac. The valve is derived from a marginal cell of the under lobe of the leaf. It has at its base a joint [4] which provides that the valve can easily be bent inwards

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[1] For a description of the configuration of the leaf see Goebel, Morphologische und biologische Studien: I. Über epiphytische Farne und Muscineen, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 33: IV. Über javanische Lebermoose; 3, Colura ornata, Goeb., ibid. ix (1891), p. 28; id. Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Fora, lxxvii (1893), p. 437.

[2] This is brought about by the formation of a ventral segment after each lateral segment of the apical cell.

[3] For the germination of Colura ornata see Goebel, Morphologische und biologische Studien: IV. Über javanische Lebermoose; 3, Colura ornata, Goeb., in Annales du Jardin botanique de Buitenzorg, ix (1891), p. 28.

[4] The structure of the joint is not alike in all species; for details see Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893).

whilst the frame upon which it lies prevents its opening outwards. When the sac becomes emptied of water there can be little doubt that as in Physiotium it is opened by a crumpling up of the valve.

I observed Colura tortifolia in British Guiana living upon the leaves of trees. The leaves were not, as in other Hepaticae which live upon leaves, adpressed to the leaf but directed upwards [1]. The valve has here then not merely to hinder a free evaporation of water, but also the flowing back of water, and to this end the capillarity of the narrow sac is favourable. No animals were found in the sac, but these inhabitants will be referred to subsequently.

FIG. 55. Colura Karsteni. Diagrammatic longitudinal section through the saccate leaf at right angles to the closing valve. *K*, valve; *W*, the frame upon which the valve lies. The valve has a joint below and can only open inwards in the direction to which the arrow points.

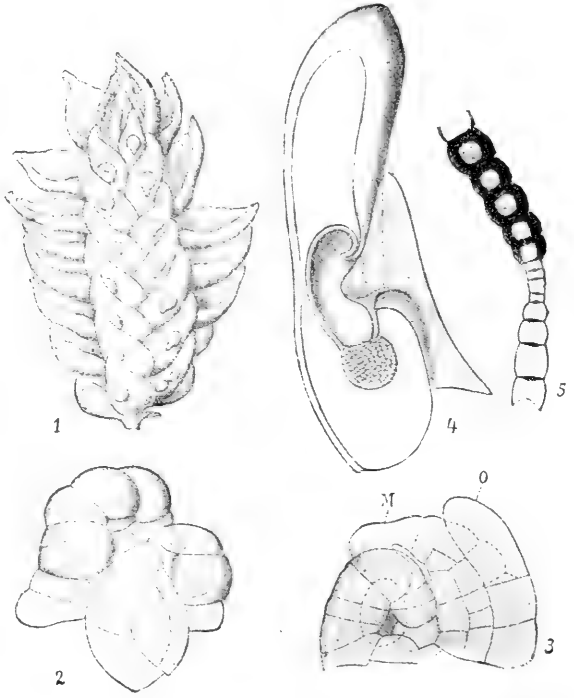

FIG. 56. 1 and 4, Physiotium giganteum. 2, 3, and 5, Physiotium cochleariforme. 1, stem seen from below. Through the water-sacs the depressions in which the apertures of entrance lie are visible. 2, stem-apex from above; two young water-sacs visible. 3, young water-sac seen from in front; *O*, upper lobe of the leaf; *M*, upper part of the under lobe. 4, water-sac in section through the middle. 5, longitudinal section through the point of origin of the valve. The hinge is indicated by smaller cells.

Physiotium. The remarkable configuration of the leaves of Physiotium next require notice. Physiotium is a genus inhabiting cool moist hill-regions in various parts of the tropics. In Europe only one species,

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[1] This is true probably of all species of Colura, at any rate of the beautiful large Colura Karsteni; see Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 427.

P. cochleariforme, remains as a relic of preglacial times in the same situations as the Hymenophyllaceae which share with it its history. Rhizoids are not present in the European species, of which I have examined living specimens in Norway. The water-sacs in the genus are very large, and are completely closed but for the special aperture of entrance. Their arrangement is shown in the transverse section represented in Fig. 57, and from it we learn that amphigastria are not present. This happens because there is a two-sided apical cell and not a three-sided one, as is the case in all the Hepaticae which have been mentioned until now ; consequently only two rows of segments forming leaves are produced [1]. The development of the water-sac cannot be described here, but it is noteworthy that the whole of the lower half of the segment is not used in its formation, and that an outgrowth on the upper side takes a part in its construction, as is the case in Frullania cornigera. In Physiotium microcarpum we find, as in some other species, a very simply constructed water-sac, the nature of which may be understood by a reference to Fig. 58,—water-sacs are usually more complex (see Fig. 56). They have a narrow mouth which lies in a depression. The special exit is bounded by two portions of the wall of the sac, lying upon one another like valves of a mussel, of which the one is stiff the other is movable at a joint. The valve consists of dead cells with delicate outer walls, and it shrivels when water is withdrawn from it, and thus gives a free entrance into the sac. At its base it possesses a joint like that in Colura. The water which is contained in the sac must, excepting a very small fraction of it, before evaporation pass

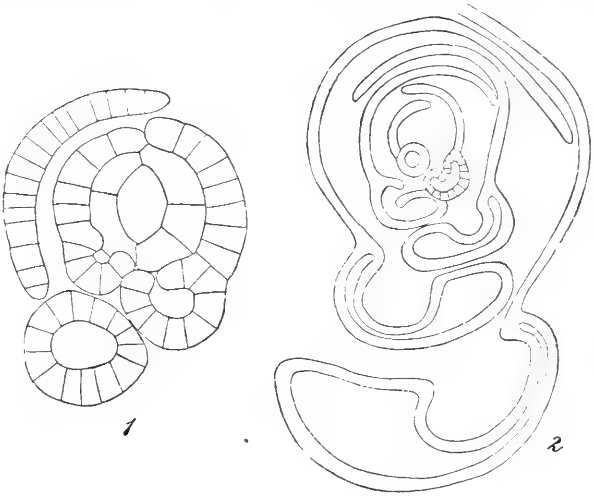

FIG. 57. Physiotium conchaefolium. Stem-bud in transverse section. 1, high up ; apical cell visible. 2, lower down. Magnified.

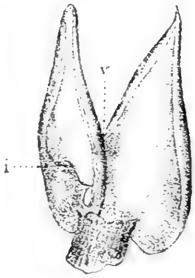

FIG. 58. Physiotium microcarpum. Dissected and spread-out leaf. To the left the simply-constructed water-sac. It is scaphoid and has a wide opening. Upon the upper side of the leaf a lamella springs out which embraces the point of insertion of the water-sac. Magnified.

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[1] The germination of Physiotium is still unknown. It would be interesting to know whether in course of the individual development there is a transition from the three-sided to the two-sided apical cell as is the case in some Musci, for example in Fissidens.

through the wall of the sac, and as this wall consists of living cells, these will not merely make use of the water, but also of all the substances dissolved in it. Evaporation through the dead cells of the valve is reduced to a minimum, because the aperture of entrance lies in a depression which itself contains water, and after the disappearance of this water it contains moist air. If the supply of water ceases, the water lying upon the surface of the plant evaporates first, the water-sacs by their position upon the under side are protected against *rapid* loss of water. They lose at first the water which is in the chamber in front of the entrance, and then the water in the sac itself. The air-bubble in its interior becomes greater, the water finally all disappears, and the valve and the whole sac shrivels, but it fills again with water in a short time on the addition of moisture, usually, however, one or two air-bubbles remain.

Capture of animals by water-sacs. Frequently, but not always, animals are found in the water-sacs of Physiotium, but by no means only in them. It has been long known that many Hepaticae have regularly a larger or smaller number of animals in their water-sacs. Rotifera are found in indigenous and tropical species of Lejeunia and Frullania, and also in the narrow water-sacs of Radula pycnolejeunioides. These aquatic animals, which are able to withstand drying up for a long time, find in the water-sacs favourable habitations, and similarly many lower forms of animal life inhabit moss-tufts. They are not necessary for the plant. That they may bring it some advantage is possible, as does the addition of animal manure to other plants. The conjecture, first put forward by Spruce and then afterwards by Zelinka, that the water-sacs have originated in consequence of a stimulus exercised upon them by the animals has no support. Even in the large wide water-sacs of Lejeunia (Ceratolejeunia and Lejeunia paradoxa)[1] *no* animals are usually met with. They seek out preferably the narrow water-sacs in which the water will naturally remain longer. The arrangement of valves in species of Colura and Physiotium recalls the utricles in Utricularia, and as these are traps for animals it was natural to suppose that the sacs of these Hepaticae were of like character. It is true that in Physiotium cochleariforme animals are often found in the sacs, but much seldomer than one would expect were the plants really carnivorous. Members of the most different affinities of water-animals were found, such as Tardigrada, Anguilluleae, Crustacea[2]. Once they have entered the sac, they cannot escape unless by breaking through its walls. If the water disappears and the valve shrivels a passage of exit is made, but being water-animals they cannot move in

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[1] Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 435.

[2] Goebel, op. cit., p. 451.

the absence of water. No animals were found in the sacs of Physiotium conchaefolium. It is probable that the rotting bodies of the dead animals in the sacs may supply soluble substances which can be absorbed by the plant. But this process must be quite a subordinate one to the chief work of the sacs as water-reservoirs.

2. ARRANGEMENTS FOR RESISTING DROUGHT FOR A PERIOD.

One must not reckon all Hepaticae as hygrophilous. That would be an error, for there are *xerophilous* adaptations. The configuration of Bazzania filum[1], one of the foliose Hepaticae, is xerophilous. This plant grows upon red clay soils which often become dry. The leaf-surface is but slightly developed, and the leaves are closely adpressed to the stem and have greatly thickened cell-walls. The whole plant has the stiff habit of many desert plants. The simplest of these xerophilous adaptations is seen in the capacity of many forms to withstand drying for a considerable period. The capacity exists in varying degree in different species, and is based upon the nature of their protoplasm. What interests us here is only the *peculiarities of the formation of organs* the advent of which are concurrent with resting stages under conditions of dryness. These special features will now be examined :—

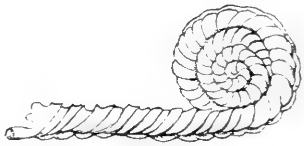

FIG. 59. Plagiochila circinalis. Apex of a shoot circinate in the dry state. Magnified. After Lindenberg.

(a) INVOLUTION OF PARTS. Riccia inflexa[2], protects its forked thallus in drought against *rapid loss of water* by the inbending of the edges of the delicate assimilation-tissue, and some Marchantieae do likewise[3]. Species of Plagiochasma, Reboulia, Grimaldia, Fimbriaria, Targionia, close up their thallus in such a way in drought that the assimilation-tissue is protected. The dark, or in some cases, almost black scales of the under side which were formerly invisible, now cover the thallus and give it a most peculiar appearance in its rolled up condition. The addition of moisture brings about again its expansion. The movements following upon loss of water, or absorption of water, take place in the membrane of the cells of the portion of the thallus containing no chlorophyll, and doubtless bring the assimilation-tissue into a position where it is protected. Grimaldia dichotoma may remain in the 'latent' condition in an absolutely dry atmosphere for seven years without losing its capacity for development, while

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[1] See Stephani, Hepaticarum Species Novarum, iii, in Hedwigia (1893), p. 206.

[2] Gottsche, Lindenberg et Nees von Esenbeck, Synopsis Hepaticarum, Hamburgi, 1844–7, p. 794.

[3] Mattirolo, Contribuzione alla biologica delle Epatiche, in Malpighia, ii (1888), p. 181 ; id., Nuove osservazioni sulla reviviscenza della Grimaldia dichotoma, Raddi, in Rendiconti della Accademia dei Lincei, 1894.

shoots of Grimaldia cultivated in a moist chamber soon die when placed in a drying apparatus.

The same kind of hygroscopic movement is found in the foliose forms. Fig. 59 shows the end of a shoot of Plagiochila circinalis, which is rolled up like a crozier in a dry condition, and the vegetative point is thus protected by an envelope of older tissue[1].

(b) FORMATION OF TUBERS. Further progress in the adaptation to periods of drought is observed in forms which produce in their resting stage *tubers* full of reserve-material.

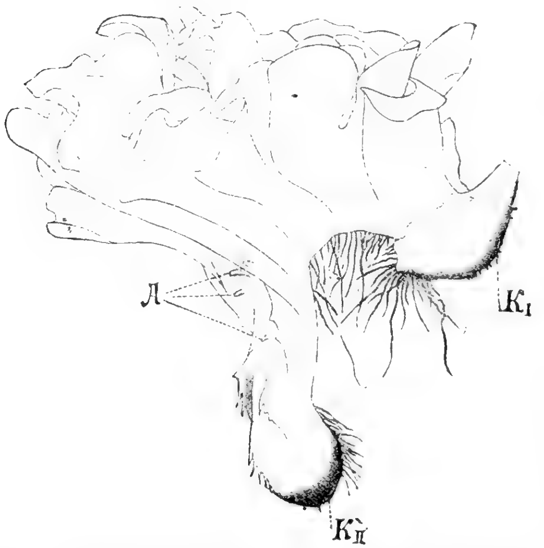

FIG. 60. Fossombronia tuberifera. Collected in Pelegua, Chili. K_{I}, old tuber which has given rise to a leafy shoot the end of which has bent downwards, produced then reduced leaves, and swollen up into a new tuber, K_{II}; A, archegonia on the upper side of the shoot. Magnified 17.

Historical. The formation of tubers in the Hepaticae is a process of so much biological interest that a short historical notice of the subject may be admitted here. Raddi appears to have been the first who observed this in Anthoceros dichotomus. Nees says[2]: 'Raddi found in the swelling at the end of the root-strand a white almost spherical little body which he considered a germ-bud.' Nees conjectured that this species of Anthoceros multiplied by shoots from the thickened end of its stout root-shoots, and Stephani[3] subsequently took this view. Meanwhile the formation of tubers was found in other species of Anthoceros. Taylor saw it in the Australian Anthoceros tuberosus[4]. Lindenberg[5] stated, regarding a species of Riccia from South Africa, that upon the under side 'here and there large shoots develop . . . which at their point are thickened into a spherical or elongated head, and this subsequently becomes a disk and probably ultimately grows into a new plant.' It is possible, however, that here ventral stolons only were observed, not formation of tubers. Regarding Riccia natans he says[6]: 'so soon as it approaches the shore or touches the mud there shoot out from the whole under-surface, and also out of the shreds belonging to this[7], thin, delicate, cylindric, hair-like, very

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[1] This, it must be stated, is concluded from the behaviour of dead plants only. No experiment relating to this point has been made with the living plant.

[2] See the account by Nees von Esenbeck, Naturgeschichte der europäischen Lebermoose, iv. p. 347.

[3] Stephani, Ueber einige Lebermoose Portugals, in Hedwigia, xxvi (1887), p. 6.

[4] Taylor, Novae Hepaticae, in Hooker's London Journal of Botany, v (1846), p. 412.

[5] Lindenberg, Monographie der Riccieen, in Nova Acta Academiae Caesareae leopoldino-carolinae naturae curiosorum, xviii. I (1836).

[6] Lindenberg, op. cit., p. 479.

[7] By this he meant the scales.

often segmented[1] root-threads, which are coloured at the junction of the segments like the under-surface of the thallus but are otherwise hyaline or granular. These fibres often thicken into a club-like or spherical form in which case the red or brown colouring-matter accumulates at these thickened ends which subsequently flatten and develop into new plants.' This statement by Lindenberg allows us to conjecture that here formation of tubers occurs, but it does not give us any insight into the matter. Formation of tubers has also been said to occur in Petalophyllum[2]. In a species of Fossombronia growing upon the Cordilleras of Venezuela I observed a formation of tubers[3]; and recently Douglas Campbell has made a careful investigation of the formation of tubers in a species of Jungermannia which he calls Geothallus tuberosus, and which is probably *very* near Petalophyllum[4].

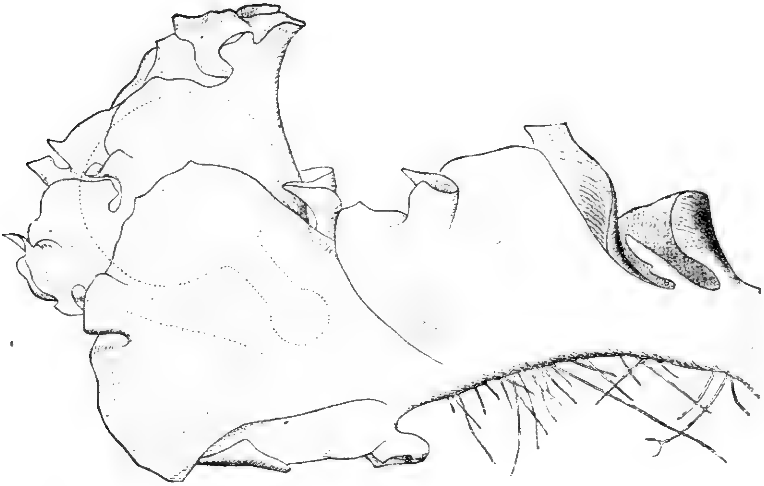

FIG. 61. Fossombronia tuberifera. Profile view of a distichously-leaved plant in fructification. The sporogonium is surrounded by a bell-shaped envelope. The point of the plant begins to penetrate the ground where it would develop into a new tuber. Magnified 18.

I shall describe here, upon the basis of my own investigations, the formation of tubers in one species of Fossombronia and two species of Anthoceros.

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[1] This is certainly wrong. The phenomenon is evidently one which can be observed in Riccia glauca, where on older plants single cells grow out as tubes which form at their end a disk like the germ-disk from the germinating spores. We have in this an example of what rarely occurs in the Hepaticae, namely, the development of the germ-phase in regeneration. When this is the case the plant is in unfavourable external conditions, and it is to be observed that the above-mentioned phenomena were specially seen upon *old* plants which had lasted through the winter. It has been stated recently that rhizoids might serve for regeneration, but this is certainly not the case. See Fellner, Keimung der Sporen von Riccia glauca, in Jahresbericht des akademischen naturwissenschaftlichen Vereins in Graz, i (1875).

[2] Gottsche, Lindenberg et Nees von Esenbeck, Synopsis Hepaticarum, Hamburgi, 1844–7, p. 792.

[3] See Ruge, Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893).

[4] Douglas Campbell, A new Californian liverwort, in Botanical Gazette, xxi (1896), p. 9; id., The development of Geothallus tuberosus, in Annals of Botany, x (1896), p. 489.

Fossombronia tuberifera, as I will name the species[1], lives in some ways like Adoxa moschatellina or Solanum tuberosum, that is to say, it forms alternately elongated shoots above the ground and tuberous shoots in the ground, and this alternation may be repeated many times on one and the same shoot-axis. In Fig. 60, for example, there may be seen at the hinder end of the plantlet the old tuber, K^1; out of it the leafy shoot developed which appeared above the ground, and which has upon its posterior side some archegonia, A. After the formation of leaves has reached the highest point—and this happens very soon, as the whole plant is very small—the shoot in its further growth curves very sharply downwards, the leaves become reduced and appear as but slightly projecting wings, and then root-hairs develop out of their edge, a development always absent from the epigeous shoot. The summit of the shoot then swells up into a tuber, K_{II}, the vegetative point remains covered by the youngest leaf-primordia, the epigeous parts die off with the advent of the dry period of the year, whilst the tuber persists. If it shoots out again it can branch, and so give origin to a small tuft of plants. If a sporogonium has been developed the plant nevertheless continues itself usually by a tuber-shoot (see Fig. 61).

FIG. 62. Anthoceros dichotomus. Portion of the thallus. From the thickened middle part two long-stalked tubers arise. On the left division of the right thallus-lobe the outline of a young tuber is visible. The dark spots on the left indicate colonies of Nostoc. Magnified 17.

The formation of tubers in Geothallus tuberosus is very like that in the Fossombronia just described, but the stalk which ensures the burying of the tuber in the ground, and which occurs in the species of Anthoceros as well as in Fossombronia tuberifera, is wanting. In Geothallus that portion of the tuber which contains the reserve-material is bounded by one or two layers of cells with thick, dark walls, and this is characteristic. The tubers arise both upon fertile and upon sterile shoots.

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[1] I found it along with Anthoceros argentinus, a form which also produces tubers, in a gathering from Pelegua in Chili. It is very nearly allied to a species I found at Tovar in Venezuela.

Anthoceros dichotomus and **A. argentinus.** The tubers of the two species of Anthoceros, A. dichotomus and A. argentinus, which have been examined, may be regarded as transformed branches of the thallus, whose ends have become swollen and filled with reserve-material. So far as material has sufficed for examination of the structure of these tubers, it corresponds with that of the tubers of Anthoceros tuberosus [1]. The tubers are surrounded by some layers of empty cork-like cells; their inner cells are filled with fat and small grains like aleurone. In Anthoceros dichotomus (Fig. 62) the tubers stand upon the under side of the thallus both upon sterile parts and upon fertile parts, but mostly upon the sterile. They arise from its thickened midrib-like portion, which is here not very sharply differentiated, and they have long stalks and are provided with rhizoids. They are laid down close behind the vegetative point, and are therefore not adventitious but ventral shoots. Instead of the stalk, which at a later period like the rest of the thallus dies off, there is sometimes found a thallus-lobe rich in chlorophyll. In Anthoceros argentinus [2] the tuberous shoots are partly lateral, partly ventral. Fig. 63 shows how lateral lobes of the thallus curve downwards, darken in colour, swell up, and become tubers.

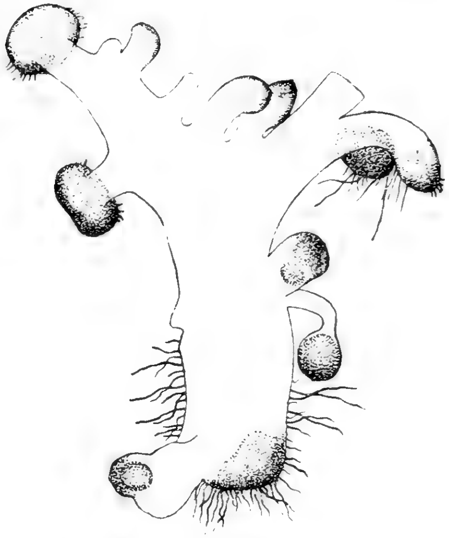

FIG. 63. Anthoceros argentinus. Thallus with tubers, apparently derived from the germination of a tuber which is still visible as a slight swelling at the base. Each tuber arises as a swelling of the end of a marginal lobe which bends downwards.

The method of germination of the tubers is unknown. Those taken from herbaria have lost their power of germination. If, as appears to be the case, the vegetative point of the tuber is not retained, we must assume that cells lying underneath the cork-envelope produce one or more new vegetative points, which rupturing the envelope grow out into lobes of the thallus.

I have recently observed formation of tubers in a cultivation of Anthoceros laevis sent to me by Dr. Levier of Florence. The tubers were whitish swellings upon the under side of the thallus near the vegetative point, and were filled with reserve-material and provided with rhizoids.

There can be no doubt that formation of tubers also takes place in the Riccieae.

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[1] See Ashworth, On the structure and contents of the tubers of Anthoceros tuberosus, Taylor, in Memoirs and Proceedings of the Manchester Literary and Philosophical Society, xli (1896), p. 1.

[2] See Jack and Stephani, Hepaticae Lorentzianeae, in Hedwigia, xxxiv (1895), p. 317.

In an Italian species of Riccia I found whole segments of the thallus developed as long tuber-like structures, the margins of the thallus being turned inwards, and the tissue lying under the chlorophyll-tissue being richly filled with reserve-material so that the body appeared white on the outside. Stephani[1] has lately described tubers in Riccia bulbifera, but the descriptions do not make clear what their morphological nature is.

The formation of brood-tubers as adventitious shoots upon the midrib of the thallus of Fegatella conica[2] may be mentioned in connexion with the tubers above described. The contents of these tubers may be drawn upon by others and they finally die off, but whilst they are undoubtedly a resting-stage they have no special relation to a period of drought, because Fegatella affects moist localities. Tubers dried for seven days were no longer able to form shoots. As in other cases the capacity to resist drying may sometimes be increased. It may be noted here that in the prothalli of ferns, for example species of Anogramme, analogous formation of tubers takes place[3].

(c) HYPOGEOUS ORGANS FOR THE ABSORPTION OF WATER. A further peculiarity of xerophilous Hepaticae is that they form organs which bore deeply into the ground to take up water. We leave out of account here the hair-roots of the Marchantieae, the length and bulk of which stand in relation to the fact that the surface of the thallus takes up no water.

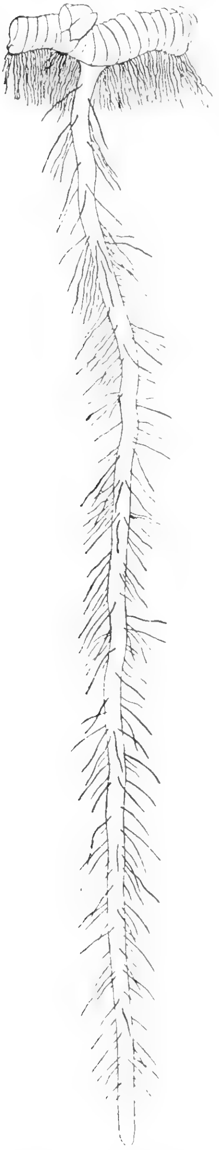

FIG. 64. Stephaniella paraphyllina. Profile view of a shoot. A lateral shoot springs from the side. Upon the under side a hypogeous rhizome clad with rhizoids which have been broken off short.

Stephaniella. Here we have specially to mention the behaviour of species of Stephaniella[4]. These are foliose Hepaticae which grow upon clayey soil liable to great dryness. They are small plants, two to four millimeters long, with a worm-like configuration recalling the condition under drought of the Marchantieae[5]. The position occupied by the scales in those Marchantieae is taken in Stephaniella by leaves closing together like the shells of a mussel, and these embrace the stem. Single plants form firm, compact, dry, hard covers, which provide a protection to the subterranean parts. These subterranean parts (Fig. 64) bore into the ground to a length of as much as thirty millimeters, quite eight times that of the leafy shoot, and this phe-

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[1] Stephani, Species Hepaticarum, in Bulletin de l'Herbier Boissier, vi (1898), p. 333. See also R. vesicata; Taylor, Novae Hepaticae, in Hooker's London Journal of Botany, v (1846), p. 416.

[2] G. Karsten, Beiträge zur Kenntniss von Fegatella conica, in Botanische Zeitung, liv (1887), p. 649.

[3] See p. 215.

[4] See Jack, Stephaniella paraphyllina, Jack, nov. gen. Hepaticarum, in Hedwigia, xxxiii (1894), p. 11.

[5] See p. 65.

nomenal length enables them to serve much more efficiently as organs for the taking up of water, than would short small hair-roots alone which are found upon them, and also upon the under side of the shoot. These hypogeous 'rhizomes' have greatly reduced leaves, and are the morphological equivalents of the flagella[1], which are found in so many Hepaticae, and they are able to grow out into leafy branches.

(d) ANATOMICAL STRUCTURE IN RELATION TO WATER. The influence which the kind and method of absorption of water has upon the anatomical construction of the thallus appears particularly clearly in the Marchantieae and Riccieae. The anatomical construction and the rooting of the Marchantieae stand in the most direct relationship to the absorption of water[2]. These Hepaticae are by no means all of them adapted to *dry* habitats. Many of them, like Dumortiera, have returned to the behaviour of the majority of the other Hepaticae, and some of them, like Riccia natans and Riccia fluitans, are floating water-forms. But the typical representatives of this group are distinguished by taking their water through their rhizoids, which are specially strongly developed, and not through the whole surface of the thallus[3]. In correspondence with this we find that in warm sunny areas like the south Tyrol, Jungermannieae have but a few representatives, but the Marchantieae and the Riccieae are abundant, and of them Grimaldia fragrans and Riccia ciliata occur in mass upon sunny localities. These forms have, in association with the strongly illuminated habitats they affect, a well-developed assimilation-tissue. In shaded localities the members of this cycle of affinity exhibit a very marked reduction in this respect.

Air-cavities. The existence of air-cavities in the assimilation-tissue is characteristic of the Marchantieae and Riccieae. They arise, as Leitgeb first showed, not schizogenetically like the intercellular spaces of higher plants, nor by a progressive rupture of the tissue from the outside inwards, but they are primarily depressions in the surface which result from the lagging behind in growth of the tissues at certain points, which are always those where four cells meet, and over these the adjacent parts then grow. These depressions then become deep pits, which are very narrow in the land-forms of Riccieae. It is easy to satisfy oneself that these pits retain air and do not allow the entrance of water. If a drop of water is placed upon the thallus, of say Riccia glauca, it does not disperse because the thallus cannot be wetted, and it does not enter into the pit. Even if the surface of the thallus be removed by a horizontal cut and laid in water the air-bubbles remain held between the cells. The uppermost cells of the dorsal tissue of the thallus have no chlorophyll in the Riccieae, and

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[1] See p. 42.

[2] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 222; Kamerling, Zur Biologie und Physiologie der Marchantiaceen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897).

[3] See p. 45.

in many they are somewhat broadened out, and so increase the difficulty of entrance of water into the air-canal. If, however, transpiration be arrested or made difficult, these cells without chlorophyll are able to give out water in liquid form, at least I have in some circumstances found Riccia lamellosa covered with small drops of water. They are evidently arranged for the purpose of the giving off of water-vapour, and they are rich in water and draw their supply to replace that which they lose from the cells containing chlorophyll. The Riccieae which live in dry localities have often many of the cells from the surface inwards wanting chlorophyll. This is the primitive form of an epidermis. In Riccia fluitans and Riccia natans the air-canal is replaced by a wide chamber, a structure the occurrence of which need not surprise us in plants living upon the surface of water or in moist localities. These chambers open by only a narrow aperture to the outside, and this in the water-form of Riccia fluitans is usually closed later. The chambers are overarched by the growth in surface of the epidermis. The chambers open to the outside in their whole width only in Riccia crystallina, a species which grows in moist localities, goes rapidly through its development up to the formation of the spores, and then dies. Such an easily attained to structure can only exist where no serious claim is made upon it.

The type of dorsal air-chambers opening to the outside by few or many pores, the 'breathing-pores,' is widely spread with a different construction in the series of the Marchantiaceae. Since Mirbel's beautiful exposition of the features of Marchantia polymorpha [1] this species has become, in textbooks, the representative of the Hepaticae. This is unfortunate, because it is really one of the most highly specialized forms. A detailed description of it is not necessary here, but an account of the relationships of its structure to the conditions of its life is required, as these are very instructive. The lid which roofs over the air-chamber is more or less sharply marked off as 'epidermis,' and consists in xerophilous species, like those of Oxymitra and Plagiochasma, of cells having no chlorophyll and possessing thickened cuticularized outer walls, but in forms like species of Cyathodium which live in moist localities, these cells of the epidermis, which are usually in two layers, contain chlorophyll. The other forms may be grouped, according to their conditions of life, between these two extremes. The 'breathing-pores' have a threefold aim, one only of which is expressed in the name: firstly, to give entrance and exit to carbon dioxide and oxygen; secondly, to hinder the entrance of water; thirdly, to regulate the evaporation of water. Whilst then they differ in their origin from the stomata upon the sporogonia of Anthoceros and of many Musci within the series of the Bryophyta, and from the stomata of Vascular Plants, they resemble them in their function.

In the construction of these breathing-pores many cells share and they

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[1] Mirbel, Recherches anatomiques et physiologiques sur le Marchantia polymorpha, in Mémoires de l'Académie des Sciences de l'Institut de France, 1835.

bound the opening. According as these cells divide by walls at right angles to the surface or parallel to it, *simple* or *canal-like* breathing-pores are formed. The latter are found upon the thallus in Marchantia (Fig. 65) and Preissia, and upon the sporogoniophore in other species which have simple ones upon the thallus. The simple breathing-pores are raised above the thallus upon a wart-like projection, so that water can readily flow away from them, and as the aperture is narrow water cannot enter. The canal-like openings also do not allow the entrance of water, and in the water-form of Riccia fluitans the openings are closed. This is the case also in a water-form of Marchantia polymorpha which Ruge has accurately described[1]. In it the submerged mode of life had hindered the formation of air-chambers in many parts of the thallus, but where these chambers did exist the breathing-pores were closed through papilla-like outgrowths of the cells of the lower tier of the pore. Finally in Dumortiera, which grows in the spray of waterfalls, on stones in streams, and other similar spots, there is a remarkable reduction evidently caused primarily by the conditions of its life[2]. The layer in which the air-chamber is formed is laid down at the vegetative point but is soon destroyed, and Dumortiera therefore behaves subsequently like a Pellia which usually lives upon land, but can also take up water directly from the outside. The reduction may go to varying lengths. In most species an areolation marking the outline of the destroyed air-chambers may be observed, and it is from these areolae that the assimilation-tissue subsequently shoots out free and exposed from the base of the air-chambers. In one species which I have examined this does not happen, and its older thallus

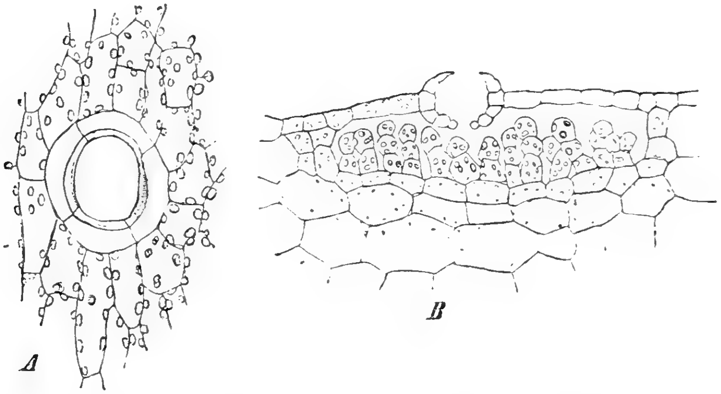

FIG. 65. Marchantia polymorpha. Breathing-pore. *A*, in surface view. *B*, in vertical section. Magnified. After Strasburger.

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[1] Ruge, Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893), p. 294.

[2] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 223.

therefore exhibits in section a structure like that of Pellia or Monoclea, that is to say, the chlorophyll is in its outer cell-layer[1].

With regard to the relationship of the breathing-pore to transpiration, it is clear that the narrower the opening the slower will be the evaporation of water. As a matter of fact we find the opening narrower in xerophilous forms than it is in hygrophilous. In many species a closure of the opening may take place, as I first showed in Preissia commutata. In Marchantia there is no power of closure. The lowermost tier of the breathing-pore is that which brings about its closure or the narrowing of it in Preissia (Fig. 66), and Kamerling has confirmed this in the case of the breathing-pores of the sporogoniophores in other species[2]. Closure takes place when water is withdrawn, when there is strong turgescence there is opening. In Preissia, which grows upon stones, walls, and similar places not always moist, the aperture of the pore is always narrower than in Marchantia; each of the cells of the lowermost tier—these are three to six in number, usually four—projects inwards so that the aperture is four-rayed. The surface of the cells which bound the canal of the breathing-pore is coated with wax granules, as in Marchantia; it cannot therefore be wetted by water; moreover, the breathing-pore is narrower at the outer aperture than it is in the middle. When then a drop of water falls upon a thin thallus of Preissia, it never can force out the air in the breathing-pore, and thus the tissue lying below is completely protected from wetting. A complete closure of the pore does not appear to take place in Preissia, but there can be no doubt that its narrowing is a provision for the regulation of transpiration. Simple breathing-pores have but limited capacity of closure. The presence of canal-like breathing-pores, which are usually capable of closure, upon the sporogoniophores in species where the vegetative parts have only simple breathing-pores, is no doubt due to the fact, as Ruge has pointed out, that an increased protection against transpiration is required in the former positions[3]. In the genus

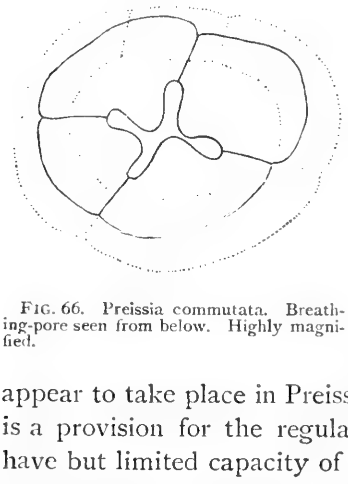

FIG. 66. Preissia commutata. Breathing-pore seen from below. Highly magnified.

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[1] It is an open question whether the species I investigated is the same as D. trichocephala in which Douglas Campbell (The Structure and Development of the Mosses and Ferns, London, 1895, p. 49) found analogous features.

[2] See Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882), p. 327, where I say:—'From what I have seen in Preissia, where the lowermost tier consists of four cells, I believe we may assume that they have the capacity to close the breathing-pore and thus to function as actual guard-cells.' Kamerling (Zur Biologie und Physiologie der Marchantiaceen, in Flora, lxxxiv, Ergänzungsband zum Jahrgang 1897, p. 37) is not justified then in his remark, that the opening and closing of the breathing-pores in Marchantiaceae has hitherto been unrecognized.

[3] This is very evident in the case of stalked antheridiophores, but not so in the sessile ones of Fegatella. The air-chambers are in this genus small, and chiefly serve for respiration. The diminu-

Exormotheca (Fig. 67) there is a peculiar disposition of the breathing-pores[1]. The air-chambers of the thallus are so high that seen from above the thallus appears white, and the breathing-pores are at the end of high chimney-like processes. The air-layer, which lies here in the thallus above the assimilation-tissue, acts as a kind of insulator against intense heat, in the same way as do the dead portions of the leaves which enclose air in many Musci, for example Bryum argenteum.

In Fegatella conica, which inhabits moist localities, there lie under the breathing-pores beak-like cells containing but little chlorophyll which, acting as evaporation-cells, increase the transpiration[2]. The construction of the assimilation-tissue in these Hepaticae stands otherwise also in evident relation to the transpiration as well as to the intensity of the light. In the simplest cases the side and ground walls of the air-chamber act as assimilation-tissue; in Cyathodium the roof does so as well. This is also the case in the germ-plants of Marchantia polymorpha, but subsequently confervoid septate cell-threads sprout from the bottom, sometimes also from the sides and roof, of the chamber; the same features are found in Boschia, Preissia, Lunularia, Fegatella, Targionia; on the other hand in Reboulia, Grimaldia, Fimbriaria, Duvalia, and some species of Plagiochasma, the whole of the tissue beneath the upper surface of the thallus exhibits an apparently irregular net-work of small and large air-chambers communicating with one another. This construction is brought about by the development of cell-plates from the walls and roofs of the air-chambers, and these project into the chambers and so divide them incompletely by septa. The narrower the communication between the several chambers and the breathing-pores the slower will be the transpiration. The several different conditions of life to which these forms are adapted have not, however, been thoroughly investigated.

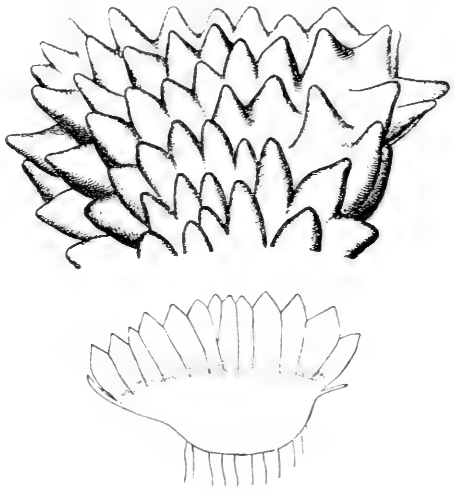

FIG. 67. Exormotheca Holstii. Upper figure: portion of a thallus seen from the upper side. Lower figure; thallus in vertical section. The assimilation-tissue is indicated by shading. Lower less highly magnified than the upper figure.

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tion of the transpiration may, however, be of use to the antheridia which require water for the discharge of the spermatozoids.

[1] See also Solms-Laubach, Über Exormotheca, Mitten, eine wenig bekannte Marchantiaceengattung, in Botanische Zeitung, lxiv (1897), p. 1.

[2] See Kamerling, Zur Biologie und Physiologie der Marchantiaceen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897).

Water-tissue. It is of less interest to us that in many Marchantieae and Riccieae, which possess a thick thallus, a storage-tissue lies under the assimilation-tissue, and in it water especially can be stored. The formation of mucilage may also be regarded as serving the purpose of storage of water, and it is found in many Hepaticae, both amongst Marchantieae and Anthoceroteae[1]. The mucilage-cells in the Marchantieae are partly isolated, partly in groups, as in Fegatella. In many species of Anthoceros, and evidently also in Dendroceros, mucilage-pits are formed in the thallus. They are present in great numbers in Anthoceros glandulosus, and have been described, even in recent times, as 'air-canals.' The formation of mucilage here is intercellular not intra-cellular as it is in Marchantieae[2]. We have no experimental proof of the importance of the formation of mucilage, but it is striking that it is so abundant in a hygrophilous form like Fegatella. Its relation, however, to water-storage is much more probable than the purely mechanical function ascribed to it by Leitgeb.

Sclerenchyma. It is not the plan of this book to deal with anatomical details, therefore I merely mention here that in many thallose Hepaticae, for example Preissia, Blyttia, and others, sclerenchyma-fibres are found. In many forms with strongly thickened cell-membranes the thickening has clearly not a mechanical function, but is chiefly connected with storage of water. The membranes are capable of swelling and can retain more water the thicker they are, and this is probably the reason for the occurrence of such membranes in the cells of the stem and leaves of Lepicolea ochroleuca. The differentiation of the tissue in the stems of the foliose forms is otherwise so simple that it requires no further mention here.

3. HYDROTROPISM.

The influence which their relationships to water have upon the disposition of the Hepaticae with reference to their substratum requires still more accurate investigation.

II. *RELATIONSHIPS TO GRAVITY.*

The relationship to gravity has only been studied in the Marchantieae. In the forms which live upon the bark and leaves of trees negative geotropism if it exists is only feebly expressed, as they grow clinging to the surface in all directions.

III. *RELATIONSHIPS TO LIGHT.*

Light has a powerful influence upon the configuration of both the thallose and the foliose Hepaticae. Etiolated shoots of species of Mar-

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[1] See Goebel, Zur vergleichenden Anatomie der Marchantieen, in Arbeiten des botanischen Instituts in Würzburg, ii (1878–82), p. 529; also Prescher, Die Schleimorgane der Marchantieen, in Sitzungsberichte der Wiener Akademie, lxxxvi, i (1882). For the Anthoceroteae see Ruge, Beiträge zur Kenntniss der Vegetationsorgane der Lebermoose, in Flora, lxxvii (1893).

[2] As in many alpine plants. See Lazniewski, Beiträge zur Biologie der Alpenpflanzen, in Flora, lxxxii (1896), p. 224.

chantieae and other thallose forms grow erect[1] and remain narrow and folded together; the development of the thallus as a surface, and with its characteristic anatomical construction, only takes place in light of sufficient intensity[2]. This influence of light upon the growth in surface may be limited only to one side of the thallus. I found a species of Blyttia upon the bark of a tree in Venezuela which usually had only one wing, that on the side away from the substratum; the other was only indicated or suppressed. Like appearances are presented by foliose Jungermannieae when they grow clinging to a pot and receive their light from above. One row of leaves then appears upon the side away from the substratum, that upon the other side is reduced to the smallest rudiments[3]. This conforms with what has been already said[4], that the leaves are arrested at an early stage of development in etiolated shoots of species of Jungermannieae. What is artificially and occasionally developed here occurs in nature regularly in some forms. In localities marked by feeble illumination, for example in hollows or in dark woods, Hepaticae grow with the peculiar habit which elsewhere is seen in germ-plants or in shoots which are half-etiolated; the leaves are feebly developed, chiefly in the form of cell-rows, and the function of assimilation is taken on mainly by the elongated shoot-axis. These are partly the forms which have been referred to as 'rudimentary.' In most of them we have to deal with an arrest at a stage of development which is passed by others, and this arrest stands probably in relationship to the conditions of the locality, especially those of feeble intensity of light. Experimental investigation of this subject is still wanting.

The peculiar colouration of the vegetative organs of many Hepaticae has in many cases a relationship to light. Green is the colour of most of them but not of all. Every one knows the dark copper colour of the tufts

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[1] This may take place also in illuminated shoots if they are cultivated in a very moist atmosphere. See Kamerling, Zur Biologie und Physiologie der Marchantieen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897).

[2] Plants of Marchantia developing from gemmae in feeble illumination grow very slowly, and are arrested at an early stage of the formation of their tissue; see Stahl, Über den Einfluss des sonnigen und schattigen Standorts, in Jenaische Zeitschrift für Naturwissenschaften, xvi. In etiolated shoots of Fegatella I find the assimilation-tissue only in the form of single cells instead of cell-rows, and not developed at all in the marginal portions.

[3] See Frank, Die natürliche wagerechte Richtung von Pflanzenteilen, Leipzig, 1870, p. 70. Frank does not express himself regarding the cause of the suppression, but seems to consider it as the result of want of room. In my opinion it is an effect of light. Let us suppose that the plant at first grows close upon the pot with the two rows of lateral leaves clinging to the substratum and equally developed. If the light now should fall directly upon them from above, the transversely heliotropic leaves as well as the shoot-axis would experience a torsion through 90°, and thus a row of leaves would come to lie between the stem and the pot, and would thus be entirely removed from light. I have observed the same phenomenon in the distichously-branched Musci, for example species of Hypnum. If these lie with one of the sides bearing twigs towards the tree-stem, the formation of twigs is suppressed on that side and appears only upon the other.

[4] See Part I, p. 241.

of Frullania upon the bark of our trees, and more striking still is the dark colour of Frullania atrata and F. atrosanguinea, which hang in long strands from the trees in the moist woods of the mountains of South America. The dark colouration is particularly striking in several Antarctic species of Jungermannieae collected by Will in South Georgia. The Gymnomitrieae which grow upon rocks have a similar dark colour which is only developed in them as in others on the portions exposed to light, and is brought about by the deposition in the cell-membranes of the colouring-matter by the protoplasm. Red colouring-matters are tolerably common, for example in Physiotium, Scapania undulata, and others; the scales of many of the Marchantiaceae, and also the under side of the thallus in part, have a purple colouration; the cell-wall of the rhizoids is violet in many species of Fossombronia. We may agree with Stahl in regarding the dark colouration of many Hepaticae as well as of many mosses as having a relationship to the absorption of heat[1]. But this point requires experimental investigation. The short statement by Jönnson[2] that dark-coloured individuals of Frullania Tamarisci respire and transpire more feebly than green ones is not sufficient basis for the settlement of the question.

We do not know whether the yellow colouring of many species of Lepicolea has any biological significance[3].

IV. *RELATIONSHIPS TO OTHER ORGANISMS.*

Reference has been already made to the animal lodgers of the Hepaticae, and now we have to consider the symbiosis of Nostoc with Blasia and Anthoceros, and the protection against animals which the Hepaticae exhibit.

The mucilage-pits of the Anthoceroteae are regularly inhabited by colonies of Nostoc. The hormogonia of Nostoc penetrate the mucilage-slits and grow into colonies. Their presence has a curious effect upon the mucilage-pit, it closes and the cells of the wall of the pit grow out into tubes which branch and enter into such intimate contact with one another and with the colony of Nostoc that the appearance is produced of a parenchyma-tissue within the intercellular space[4].

The leaf-auricles of Blasia are similarly inhabited by Nostoc, and other Cyanophyceae may also be met with in them. These cause an enlargement of the auricle and the formation of a much-branched tube which, spreading from a single cell, grows into the colony.

We have no experimental evidence giving us an explanation of this

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[1] Stahl, Über bunte Laubblätter, in Annales du Jardin botanique de Buitenzorg, xiii (1896), p. 168.

[2] Jönnson, Recherches sur la respiration et l'assimilation des Muscinées, in Comptes Rendus, cxix (1894).

[3] See Czapek, Zur Chemie der Zellmembran bei den Laub- und Lebermoosen, in Flora, lxxxvi (1899), p. 361.

[4] Leitgeb, Untersuchungen über die Lebermoose, Graz, v (1879), p. 16.

symbiosis. We can only say of it here, as elsewhere in Azolla and Gunnera, that the Cyanophyceae only enter depressions which form *mucilage*, and we gain the impression that the algae become shut up in them. They find in them protection and lodging. Whether they benefit the host or not we do not know; perhaps the colonies of Nostoc serve as reservoirs of moisture on account of their mucilage[1]. Other authors ascribe to them the capacity of assimilation of free nitrogen like the bacteria of the tubercles of Leguminosae. These are, however, all mere conjectures, and experimental proof can alone settle the point.

Many Hepaticae are not eaten by snails or other animals[2] because usually they possess a definite 'protective substance.' Mechanical protection by thickening of the cell-membrane is only seldom met with. It is easy to prove by chewing them that many Hepaticae have an unpleasant taste. Their peculiar smell is also a protection to many against animals, and this odour is naturally associated with the presence of oil-bodies[3]. Experimental proof of this is, however, wanting. The oil-bodies lie isolated in the cells of the Marchantieae or they may be in numbers in the cells, and they consist of a ground-substance or stroma in which the drops of fatty matter are embedded; and along with these tannin occurs in the Marchantieae and in other species, perhaps also small quantities of volatile oil. At any rate these substances so deposited must be regarded as excreta, and they are found in parts which are produced in the dark; but we are unable at present to say what is their significance in metabolism. Küster, who examined a large number of the Hepaticae, found them wanting only in Riccia lamellosa, Oxymitra pyramidata, two species of Clevia, Metzgeria furcata[4] and Metzgeria pubescens, Jungermannia bicuspidata and J. Michauxii, whilst other species of Riccia possess them. They appear to be altogether wanting in Anthoceroteae.

IV

FERTILE SHOOTS AND PROTECTION OF THE SEXUAL ORGANS OR THE SPOROGONIA OF HEPATICAE

The structure of the sexual organs and their products has been already described[5]. Here we have two points to notice, the disposition of the sexual organs, and the influence which the appearance of the sexual organs

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[1] Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882), p. 360.

[2] Stahl, Pflanzen und Schnecken, Jena, 1888.

[3] W. v. Küster, Die Ölkörper der Lebermoose und ihr Verhalten zu den Elmioplasten. Inaug. Dissertation. Basel, 1894. The literature is cited in this paper. Stahl has designated the oil-bodies 'protective bodies.'

[4] Whether the refringent bodies described by Stahl in Metzgeria as oil-bodies are really so or not requires further investigation.

[5] See p. 9.

has upon the vegetative organs, an influence which finds expression in changes of form of these, and in the development of envelopes for the sexual organs or the sporogonia.

1. DISPOSITION AND PROTECTION OF THE SEXUAL ORGANS OR SPOROGONIA.

No reference is required here to monoecious or dioecious conditions because they occur in one and the same genus, for example in Pellia. That dioecious forms, in the absence of male plants, are not fertile is a matter of course, but it may be seen in a very striking manner in Lunularia vulgaris, which for a long time has been known in North Europe in female examples only[1], this form having been introduced probably in orange-casks from South Europe. It has increased by gemmae, formed groups of archegonia but no sporogonia.

In the thallose forms the sexual organs always sit upon the dorsal or upper surface of the thallus. In Riella, where the existence of the wings gives an appearance of another arrangement, the disposition of the sexual organs is the same (see Figs. 9, 10); the antheridia are sunk in the many-layered wing; the archegonia are found on the two sides of it. Leitgeb has divided the Jungermannieae into the two groups of *acrogynous* and *anacrogynous* according to the point of origin of their archegonium. In the acrogynous group, to which the majority of the foliose forms belong, the apex of the stem is used up in the formation of archegonia; in the anacrogynous group this does not occur, yet Calobryum approaches the acrogynous forms inasmuch as there are here terminal groups of archegonia and antheridia (Fig. 37).

In the anacrogynous Jungermannieae and in the Marchantieae, two methods of disposition of the sexual organs may be observed; either they are disposed irregularly, as for example in Riccia, Fossombronia, the antheridia of Pellia, and others, or they are arranged in more or less sharply limited groups. In the former series of cases, and sometimes also in the latter, the shoots which bear the sexual organs continue their growth after the formation of these; but if they are constructed as short shoots (see Fig. 68), they are naturally more sharply marked off from the vegetative branches.

The primitive disposition is the diffuse as it is found in Riccia. Here the neck of the archegonium reaches beyond the surface of the thallus, whilst the lower portion is found in a pit. The antheridia are also sunk, and completely so. The mouth of the pit in which they sit projects more

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[1] The statement in books that male plants are rare in the South is incorrect. I found them everywhere when I looked for them in Florence, Rome, Naples, Sicily. That Lunularia seldom fruits in Italy is probably a consequence of its period of fertilization happening in spring when the requisite moisture for the process is often wanting. Cultivated examples fruit abundantly at Munich.

or less beyond the thallus and is pierced by a narrow canal ; in general the pit-mouth projects beyond the thallus as far as does the neck of the archegonium, but this requires further investigation. When the antheridia discharge their contents they press their mucilaginous content, including the spermatozoids, out of the narrow canal traversing the mouth of the antheridial pit, and owing to the narrowness of the canal there may be a gradual emptying of the antheridium. The spermatozoids may either swim freely to the archegonia which usually stand in a channel of the thallus, or they may be carried to the neck of the archegonium by small mites or other animals. As a matter of fact the Riccieae are usually found in very moist localities.

Monoclea forms groups of antheridia which resemble those of many of the Marchantiaceae. The shoot which bears the antheridial groups does not stop its growth upon their production, but that bearing the archegonia does so.

FIG. 68. Aneura (Pseudoneura) eriocaulis bearing antheridial branches. Magnified 5.

In Aneura (Fig. 68) the sexual shoots lag behind the sterile ones at a very early period in growth, and appear in consequence as lateral appendages upon the margins of the thallus. These shoots produce either antheridia or archegonia, and with their appearance the growth of the shoot ends. Male and female sexual shoots are found upon the same plant, for example in Aneura multifida, but they may be upon different plants. The antheridia arise in progressive serial succession and are sunk in the tissue of the shoot which bears them. As they stand close together in the greater number of cases the shoot has a wavy appearance.

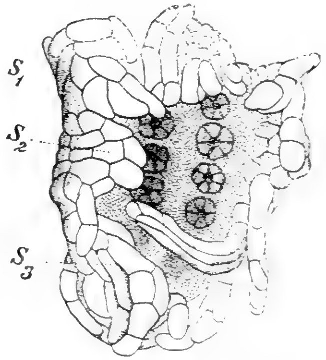

FIG. 69. Aneura sp. Archegonial shoot, seen from above. The margin is curved upwards and grown out into a number of scales, S_1, S_2, S_3. A scale-like outgrowth is also visible at the posterior end of the shoot; this is represented in the figure as directed upwards.

About the archegonia of Aneura there are arrangements which, whilst they protect the archegonia, are also specially fitted to retain drops of water which are so important for fertilization. This is a point which has been hitherto overlooked. Fig. 69 shows a group of archegonia from above. It is surrounded by an envelope, and this is formed from the two margins of the thallus first of all, and then by a scale-like growth from the posterior end of the sexual shoot. It is specially noteworthy that the margins of the thallus of the sexual shoot have grown out into a series of distinct scales, S_1, S_2, S_3, on the left side of the figure. These are to be considered as an indication of a formation of leaves and they appear *only upon the sexual shoots*, not upon the sterile ones. The long drawn-out lobes of this envelope form an apparatus which holds water-drops.

Whilst in Aneura modified *lateral twigs* of the thallus are formed for the purpose of bearing the sexual organs, in Hymenophytum and Metzgeria there are *ventral shoots* which perform this service. The species of Hymenophytum shown in Figs. 13 and 19, exhibit these short shoots which bear the sexual organs, in this case the archegonia, upon their upper side.

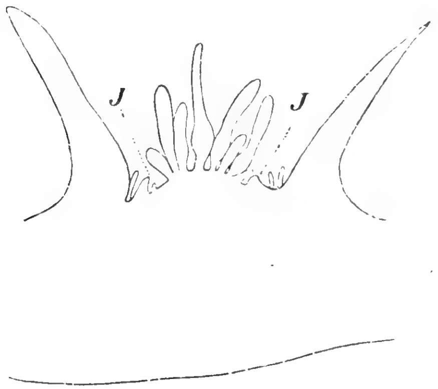

FIG. 70. Blyttia sp. Group of archegonia in vertical section. Surrounding the group is the cup-like perichaetium and within this the primordium of the 'perianth' J, J.

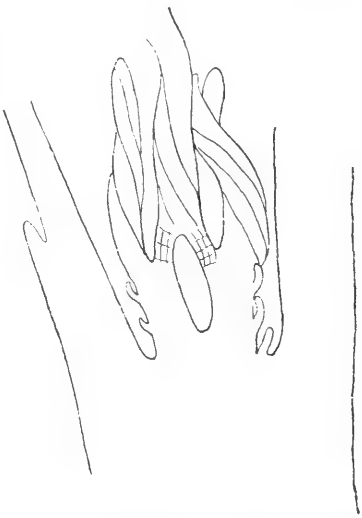

FIG. 71. Symphyogyna. Group of archegonia in vertical section. To the left the perichaetium which is composed of one simple scale only. To the right the thallus. The embryo has burrowed into the tissue of the stem beneath the archegonium, this tissue has originated by growth accompanied by cell-multiplication after fertilization.

The groups of archegonia are surrounded by a cup-like envelope, the perichaetium[1] (Fig. 13, *J*), which is split up into different scales, as in Blyttia (Fig. 70), and this slit perichaetium forms an apparatus for collecting water-drops, like the structure described in Aneura. Within the perichaetium there is developed after fructification a second envelope, the perianth (Fig. 13, *S*) for the protection of the sporogonium. This perianth is also seen in Blyttia (Fig. 70, *J*, *J*). In Metzgeria no special envelope

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[1] We shall, in order to avoid confused nomenclature and the coining of new words, name the envelope which invests the group of archegonia *before* fertilization, and which serves for fixing the drop of water, the *perichaetium*, and the envelope which grows out only *after* fertilization the *perianth*. Many Hepaticae have only a perichaetium, others, like Hymenophytum, have also a perianth.

exists[1], its place is taken by the concave curvature of the sexual shoot itself. In Symphyogyna (Fig. 71) the group of archegonia is protected by a single scale-like growth of the thallus which forms a perichaetial scale, whilst the antheridia stand singly, covered over by a small scale on the dorsal side of the thallus. This position I assume to be the original one for the archegonia. The behaviour of Mörkia points in this direction. In it there are, outside the perichaetium, some single scales; whilst in Blyttia these are united more or less to a scale-like envelope. Such a homology can only hold, however, within one genus or within a very near cycle of affinity, and in other Hepaticae the perichaetium arises certainly in another way than by the union of scales. In Pellia, at least in P. calycina, the perichaetium is like that of Blyttia, only that its mouth inclines towards the apex of the thallus, as there is formed, not only *behind* the archegonial group, reckoned from the vegetative point, but also *in front* of it, a growth which after fertilization grows out strongly and forms with the scales the envelope of the sporogonium.

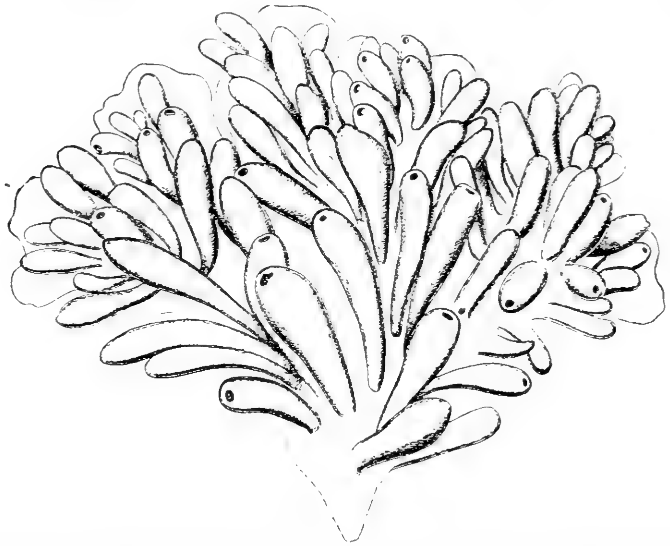

FIG. 72. Sphaerocarpus terrestris. Portion of a female plant seen from above. Many perichaetia, each surrounding one archegonium, cover almost the whole surface of the thallus. Magnified 12.

The combination of the archegonia in groups increases evidently the probability of fertilization. Usually only a single embryo develops into a sporogonium, and this bores into the tissue underneath the archegonium; in P. calycina I have occasionally found two sporogonia within one envelope, but they were unequally developed.

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[1] This is at least the case in Metzgeria furcata. According to Stephani, Hepaticae Australiae, in Hedwigia, xxviii (1889), p. 268, the perichaetium is present in Metzgeria australis, and therefore it is possible that it is a primitive structure in the genus which has been lost in most species in consequence of the strong incurving of the sexual shoot.

In Sphaerocarpus the sinking of the antheridia and archegonia in the thallus is impossible because this only consists of a few cell-layers. Here the cells lying around the incipient antheridium grow up around it, and this envelope forms the perichaetium which arches over the apex of the young antheridium and ends in a lobed projection with an opening at its point. A similar perichaetium surrounds the archegónium (Fig. 72). These perichaetia contain chlorophyll and evidently perform some work as organs of assimilation.

In Fossombronia (Fig. 61) and Haplomitrium, the antheridia stand free upon the surface of the stem; in youth they are protected by the leaves of the terminal bud. Occasionally they, as well as the archegonia, are protected also by scales which we may, with Leitgeb, consider as the remains of the protecting organ, no longer constantly formed, which the true thallose ancestors of Fossombronia possessed. With the appearance of leaves they became superfluous and degenerated. But the case of Treubia[1] shows that this hypothesis cannot be generally applied. In it the dorsal scales belong to organs of the plant which constantly occur, evidently because they share in the protection of the vegetative point. Calobryum forms a transition to, or rather a parallel formation with, the acrogynous Jungermannieae in so far as its archegonia and also its antheridia form terminal groups upon the leafy shoots, and conclude the growth of the latter.

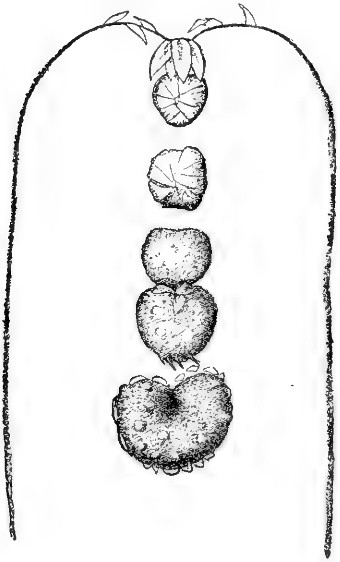

FIG. 73. Plagiochasma Aitonia. Male plant with five antheridial groups seen from above. The younger groups, like the vegetative point, are protected by overlapping scales. They form the perichaetium of the antheridial groups. Magnified 8.

MARCHANTIACEAE. The Marchantiaceae are distinguished by the fact that in them the transformation of the vegetative shoot-axis into sexual shoots reaches its extreme. The sexual shoots here form the peculiar antheridiophores and archegoniophores which we know in Marchantia, Preissia, and others. In the series all gradations from simplest up to the most complex development are found. We may distinguish three chief stages:—

1. *Diffuse disposition of the sexual organs*, as in **Riccia.**

2. *Combination of the sexual organs in groups without transformation of the branches which bear them.* This is the case in **Corsinia** where the archegonia stand in pits which are developed by the suppression of the

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[1] See p. 39.

assimilation-tissue; further, we find it in **Plagiochasma** (Fig. 73), where antheridial groups are repeatedly developed upon the back of the thallus and are protected by enveloping scales. The envelope-scales form the perichaetium and take origin in the same way as the ventral scales of the thallus already described[1]. The archegonial groups are ensheathed in similar perichaetial scales, which stand erect, and thus can readily hold water by their apices, and so favour fertilization. In Plagiochasma I found two groups of archegonia at the base of one papilla and enclosed by an outgrowth which formed a shell-like envelope. The papilla is constricted below and rounded above, and then, shortly before ripening of the archegonia, it grows out, so that the constricted part below the archegonia becomes elongated into a stalk. There is thus formed a structure very like the stalk of the archegoniophore in Marchantia and others, but which has quite another origin. There are in Plagiochasma then very simple means for the protection of the archegonia, for the furthering of fertilization, and for the favouring of the distribution of the spores. The head of the archegoniophore, if it develops chlorophyll-tissue, which is not always the case, has stomata of the usual canal-like form[2].

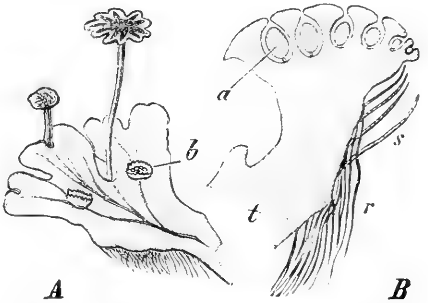

FIG. 74. Marchantia polymorpha. *A*, male plant with two antheridiophores of different age; *b*, cup for gemmae. *B*, vertical section of antheridiophore; *a*, antheridium sunk in the disk; *s*, the vertical scales; *r*, rhizoids; *t*, thallus. *A*, natural size. *B*, magnified. Lehrb.

3. *The sexual organs are borne upon special shoots* which are transformed into radiately branched axes of limited growth. **Marchantia** and **Preissia** furnish well-known illustrations of this, and the sexual branches in them owe their origin to a repeated forking of the vegetative point of the fertile shoot. The summit of the antheridiophore is disk-like (Fig. 74), and that of the archegoniophore is cap-like. These structures have been often described and yet their biological significance has not yet been explained. Why should male and female sexual branches have a radiating construction? Why should the male be differently formed from the female, and why should both be stalked, although this appears to be useful only for the female in connexion with the distribution of spores? What significance have the different envelopes of the sexual organs?

This disk is not actually radial but symmetrically divisible by only one plane. This appears much more conspicuously in species of Marchantia other than the endemic M. polymorpha. The fact that the disk of the antheridiophore consists of branches of the thallus each with progressive

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[1] See p. 30.

[2] See p. 74.

formation of antheridia at its vegetative point, may be connected with the fact that in this way spermatozoids capable of doing the work of fertilization become available for a long period.

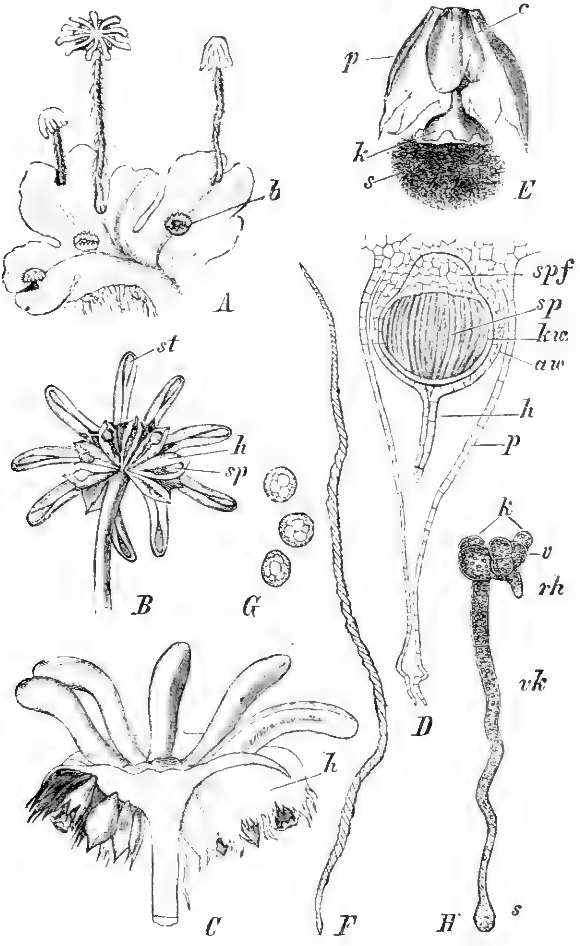

FIG. 75. Marchantia polymorpha. *A*, female plant with four archegoniophores of different ages; *b*, cup for gemmae. Natural size. *B*, cap of an archegoniophore seen from below; *st*, rays of the cap; *h*, perichaetium; *sp*, young sporogonium. Magnified 3. *C*, vertical section of the cap of an archegoniophore; *h*, perichaetium. Magnified 5. *D*, young sporogonium still within the archegonial venter in vertical section; *spf*, the seta; *sp*, sporogenous tissue; *kw*, wall of capsule; *aw*, wall of venter of archegonium; *h*, neck of archegonium; *p*, 'perianth.' Magnified 70. *E*, ruptured sporogonium from which the spores, *s*, and elaters are issuing; *k*, wall of capsule; *c*, venter of archegonium; *p*, 'perianth.' Magnified 10. *F*, an elater. *G*, spores. Magnified 315. *H*, germ-plant; *s*, spore; *vk*, germ-tube; *k*, germ-disk; *v*, vegetative point of the young plantlet; *rh*, its first rhizoid. Magnified 100. *C*, *E*, after Bischoff. *B*, *D*, *F–H*, after Kny. Lehrb.

As to the difference between the antheridiophore and the archegoniophore, it is evident that the antheridia remain permanently upon the upper side as in all other Hepaticae; the archegonia are laid down upon the upper side, but are displaced to the under side where they have a protected position.

The disk-form of the summit of the antheridiophore has relation to its function. The lie is directed somewhat upwards. If a drop of water, say a raindrop, fall upon the disk it spreads out quickly thereon it, as Strasburger has remarked[1]; and if the antheridia are ripe they empty their contents into the drop of water, and when a new drop of water falls upon the disk, it will wash off the greater part of the previous one containing the spermatozoids. The disk being stalked it is enabled to throw the water-drop with the spermatozoids further than it could were it unstalked[2]. If such a drop reaches the cap of the

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[1] Strasburger, Die Geschlechtsorgane und die Befruchtung bei Marchantia polymorpha, in Pringsheim's Jahrbücher, vii (1869–70), p. 49.

[2] Whilst the advantage of the stalk of the archegoniophore in facilitating spore-distribution is clear, that of the stalk of the antheridiophore is not so evident. Might it be a survival like the nipples in a male Mammal? The explanation I have given in the text seems to me the true one.

archegoniophore from below, the incurved rays of the cap hold it firmly. If the drop falls upon the upper surface of the cap, and it may do so easily so long as the cap is unstalked, it does not lie upon the convex surface of the incurved rays, but flows down in the grooves between them, carrying the spermatozoids to the groups of archegonia which in the unstalked cap have their necks directed upwards[1] and are therefore readily fertilized. The necks of the archegonia are subsequently, when the cap is raised up on its stalk, directed straight downwards, and fertilization can then only be brought about by water coming up from below; but such a movement of spermatozoids between the bundles of rhizoids upon the stalk appears to me to be highly improbable.

In addition to the incurving of the rays of the cap, which only later spread out if the sporogonium develops, the perichaetium also supplies a mechanism for holding drops of water (Fig. 75, *B*, *h*). This envelope corresponds to the mussel-shell envelope, which envelops the group of archegonia in Plagiochasma. In addition, there is around each archegonium a special envelope, the *perianth* (Fig. 75, *D*, *p*), which before fertilization appears as a low ring around the base of the archegonium, and subsequently grows over it. This envelope is, with reference to other Marchantiaceae, an entirely new formation, and it seems to be connected with the necessity of providing a strong protection against drought to the young sporogonia which are seated upon the stalked archegoniophore. It is absent in forms of Marchantiaceae, which grow in shaded localities, or in which the sporogonium is only borne on a long stalk at a late period of development.

We have thus endeavoured to bring the conformation of the antheridiophore and archegoniophore of Marchantia into relation with three factors:—

1. The distribution of the spermatozoids and the securing of fertilization.
2. The prolongation of the possibility of fertilization over a long period, and with this is connected the fact that several sporogonia may be found in each group of archegonia, and that there may be therefore more sporogonia than there are rays to the cap.
3. Protection of the sporogonium and the distribution of spores.

Let us compare now another nearly allied form which has an altogether different mode of life:—

The genus **Dumortiera**[2] develops the stalk of its archegoniophore only after fertilization has taken place, and from this we might conclude that the antheridiophore should be unstalked. This is the case. The stalk scarcely deserves the name, and at most it serves to facilitate the throwing off of water from the antheridial disk. As the genus is hygrophilous we should not expect a special envelope to the archegonium, and I have found no trace of

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[1] In response to what 'stimulus'?

[2] See p. 73. I examined two species which I collected in South America, and the Canary Island species D. irrigua.

it, and in this I differ from Leitgeb[1]. The cap of the archegoniophore is not provided at the time of fertilization with rays, but is only slightly nicked at the edge. The rays which appear later are a consequence of the strong development of the perichaetia surrounding the several archegonial groups. Each perichaetium has a narrow funnel-like mouth out of which the necks of the archegonia project to a considerable extent, and it is filled with mucilage[2]. The numerous scales which are found upon the cap are very striking; they are partly curved upwards, partly directed downwards, and they form a net-work for the firm retention of the water containing the spermatozoids. The entrance of the spermatozoids into the open neck of the archegonium is determined by chemotactic influences, and only one sporogonium is produced from each archegonial group. In Dumortiera the biological relationships, fertilization, distribution of spores, and so forth, are essentially the same as in Plagiochasma, whilst the morphological features are different, and we have here an instructive example of how the same end is reached by different means.

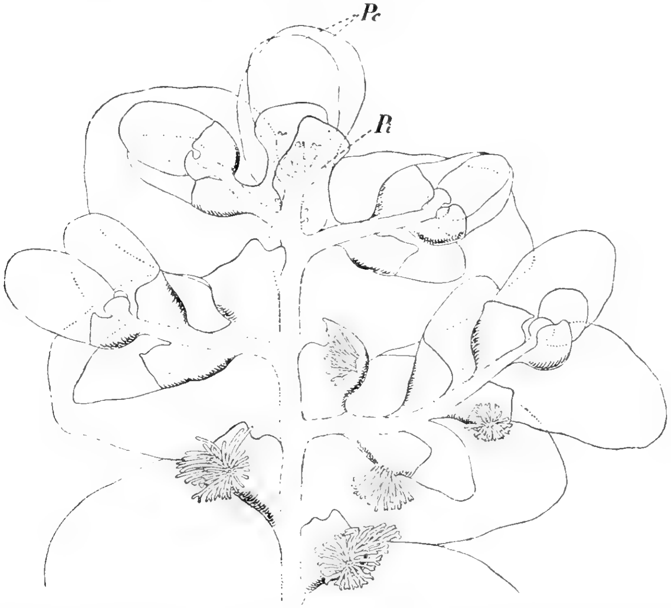

FIG. 76. Radula tjibodensis. An archegonial group at the end of the stem. *Pc*, leaves of the perichaetium; *Pi*, incipient perianth. Tufts of rhizoids are shown springing forth from the water-sacs.

ACROGYNOUS HEPATICAE. In the acrogynous Hepaticae the protection of the antheridium is effected by the leaves which are often characteristically formed for this purpose, and they have in their axil one or many antheridia. The archegonia also, which may be solitary as in Lejeunia and Phragmicoma, or in groups of two to three in Frullania, or of a larger

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[1] Leitgeb, Untersuchungen über die Lebermoose, Graz, vi (1881), p. 174.

[2] The envelope is, as in Plagiochasma, thicker than that in Marchantia.

number in Plagiochila, Jungermannia, of as many as a hundred in Lophocolea, are at first surrounded by leaves which form the perichaetium (Fig. 76, *Pc*). These leaves are distinguished from the vegetative ones mainly by their great size and by the absence of the adaptations of the latter, such as the formation of water-sacs. Where the sexual shoots are orthotropous amphigastria often appear in the perichaetium, even though they be absent from the vegetative shoots; but from sexual shoots which are not orthotropous, for example those of Radula, amphigastria are absent as completely as they are from the vegetative shoots. Further, most forms possess an organ which, at the time when the archegonia are ripe, appears as a low annular wall (Fig. 76, *Pi*); this grows out later as the perianth, and is commonly considered as being formed of three concrescent leaves, although I think the interpretation is doubtful. It appears to me to be much more likely that the perianth is the descendant by inheritance of an organ present in thallose ancestors. It is not present everywhere; it is wanting in Trichocolea, Gymnomitrium, and in the Jungermannieae of the group Geocalyceae.

Trichocolea. In Trichocolea pluma (Fig. 77), which I collected in Java, an archegonial group is found at the end of a thick branch clothed with leaves and numerous paraphyllia, and from this, as usual, only one sporogonium is formed. The archegonium in which fertilization is effected achieves only an insignificant growth, but the embryo penetrates at an early period into the tissue of the stem which furnishes it with the necessary protection, and acts as substitute for the wanting perianth. If we limit the notion of calyptra to an archegonial venter which increases in size after fertilization, Trichocolea has no calyptra. Such a limitation would be, however, alike useless and untenable. It is incorrect to say of this genus that the 'calyptra is woolly on account of the adherent involucral leaves[1].' There is no concrescence here, and the 'wool' is formed by the paraphyllia[2], which as in the vegetative shoot are organs for holding water.

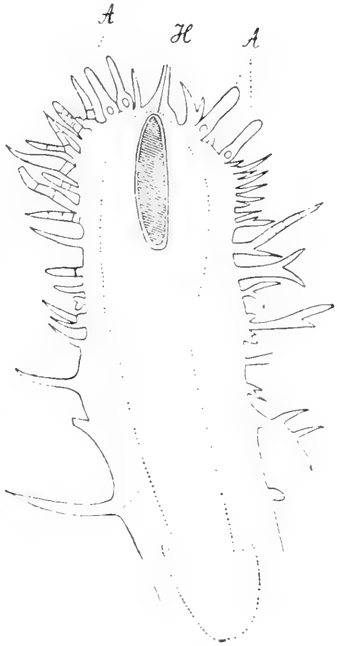

FIG. 77. Trichocolea pluma. Fertile branch in vertical section. Embryo is shaded. *H*, neck of the fertile archegonium; *A*, sterile archegonia. The dotted line gives the outline of an older embryo. The relationships are not quite correctly given in the figure because during development of the sporogonium the upper part of the fertile branch grows in length; it does not remain stationary.

The significance of the perianth (see also Fig. 85) for the ripening of

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[1] Schiffner, Hepaticae, in Engler und Prantl, Die natürlichen Pflanzenfamilien, p. 110.

[2] See p. 57.

the sporogonium is mainly this, it hinders the entrance of water and protects from drying up. Only in one form, Anthoceros, do we find water in the pit which surrounds the young sporogonium, and this water is secreted by separate cell-threads which project into the pit. Probably here, as in the case of some Musci in which the dilated calyptra exudes water, the water is required by the sporogonium; and this recalls the exudation of water in the flower-bud of many Spermophyta.

Calypogeia. A slimy fluid is also found in the narrow tube at the base of which sit the archegonia of Calypogeia ericetorum. Calypogeia belongs to a group of Jungermannieae which has been designated Geocalyceae, because the sporogonium is sunk in a hollow branch which in fructification is to a greater or less extent pushed into the soil. It has been long recognized[1] that this group is a *biological* one, not *systematic*, that is to say, its special feature is a character of adaptation which may occur in different groups, and we shall see that, notwithstanding opinions to the contrary, the adaptation appears in different forms and in different ways. No member of this group has a perianth[2]; other structures do its work and give the ripening sporogonium protection, especially against drying, a protection the more necessary because the water-supply available to these plants at the time of the development of their sporogonium is by no means a certain one. In Calypogeia ericetorum (Fig. 78) there arises upon the under side of the plant the hollow fertile branch which penetrates the soil like a root, reaching

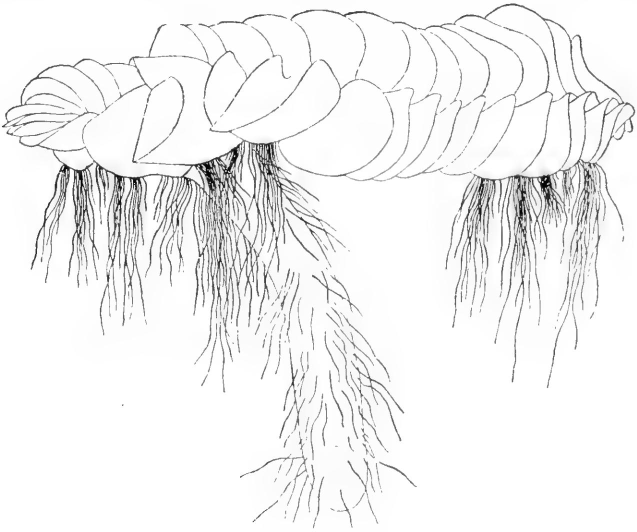

FIG. 78. Calypogeia ericetorum. Plant with fertile root-like shoot at the translucent end of which the fertile archegonium is visible.

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[1] See Spruce, On Cephalozia and some Allied Genera, Malton, 1882, p. 92. Spruce dwells upon the relationship of Acrobolbus (Gymnanthe, Taylor, pro parte) with Alicularia, and of Calypogeia with Southbya. The history of development he gives of the Geocalyceae is incorrect.

[2] There is a rudimentary perianth in some species.

a length of almost one centimeter. It is covered with hair-roots, and comes ultimately into a position which facilitates the intake of water, but makes difficult the drying up of the shoot. The inside of the hollow branch is lined with hair-like cells, and on these there are present special papillae (Fig. 79, *p*), which secrete mucilage and contribute to keeping the growing sporogonium moist; they are later pushed to one side by the developing sporogonium. The history of this sac, in which the sporogonium develops, has been examined by Gottsche and Hofmeister. The archegonia stand primarily upon the upwardly curved apex of a short ventral branch which is surrounded by some envelope-leaves. The summit of this branch later becomes concave, owing to the growth upwards of an annular portion of cell-tissue under the point of attachment of the archegonial group, in the same way as happens in the production of an inferior ovary, or of an inflorescence like the fig, and thus the fertile archegonium finally comes to lie at the bottom of a tube, on the outside of which are some leaves and numerous rhizoids. The zone from which the growth proceeds is recognizable also at a later period (Fig. 79). If it includes the points of insertion of leaves, then we find leaves on the surface of the tube as in Calypogeia Trichomanes; where the insertions are not included leaves are absent, as in Calypogeia ericetorum. The appearance of leaves on the outside of the tube has given rise to the incorrect assumption[1] that a vegetative point lies in an umbilicate pit at the base of the tube, and that this produces leaves. Whence could this vegetative point come? The vegetative point of the fertile shoot is used up in the formation of the archegonia: it must then belong to a lateral shoot, and this leads to impossible results. Lateral shoots occasionally appear on the fertile shoot of Calypogeia ericetorum, but in quite another position.

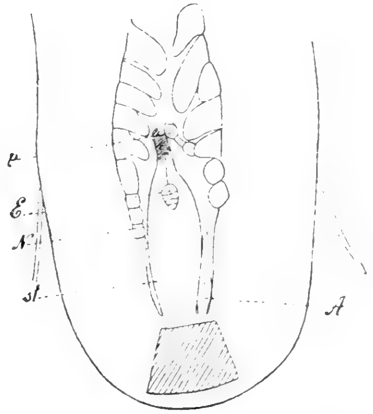

FIG. 79. Calypogeia ericetorum. Half-diagrammatic representation of a fertile sac in longitudinal section. *p*, mucilage papilla; *E*, embryo; *N*, nutritive tissue of the stalk, *st*, of the archegonium; *A*, sterile archegonium. The shading indicates the zone whence growth of the sac chiefly proceeds.

Gymnanthe. The method of formation of the tube or sac for the sporogonium in Gymnanthe saccata is somewhat different from that observed in Calypogeia, and has hitherto been incorrectly described. In Calypogeia the calyptra is almost completely concrescent with the tube of the fertile shoot, but this is not the case in Gymnanthe saccata. Springing from the under side and near the apex of its obliquely ascending stem (Fig. 80, 1), is

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[1] Schiffner, Hepaticae, in Engler und Prantl, Die natürlichen Pflanzenfamilien, p. 70.

a thick, fleshy, brownish body upon the outer side of which I found but few rhizoids. It appears to me, from an examination of dried specimens, doubtful if this sporogonial shoot is really pushed into the soil. It is possible that it bends down the plant by its weight ; this, however, can only be determined by the examination of living plants, In the juvenile stages *there is no sac only a solid fleshy body* upon the summit of which there are a number, about twenty, of archegonia. The archegonia are found, as a comparison of the longitudinal with the transverse section shows, in a shallow pit, covered in great measure by the neighbouring leaves. These stand about the apex of the shoot, and the tissue of the shoot has grown out somewhat about them and forms also underneath the archegonial group a tuber-like outgrowth. The embryo bores into the tissue which, in the case examined by me, contained no starch but inulin, and dissolves the central portion of it so that an actual sac arises, upon whose summit the sterile archegonia and the very slightly developed calyptras are found [1].

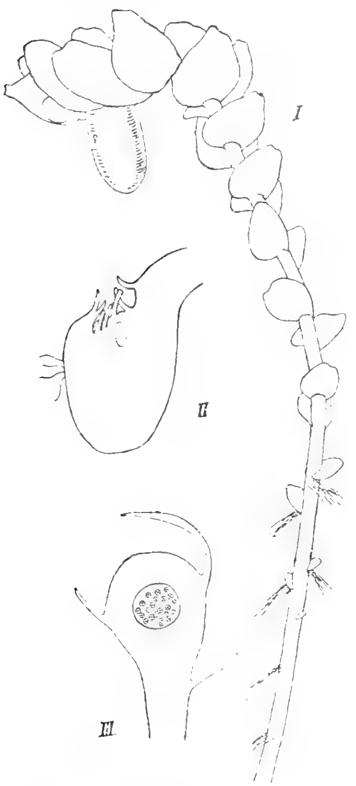

FIG. 80. Gymnanthe saccata. I, plant bearing a 'sac.' Magnified 2. II, 'sac' in longitudinal section ; the embryo indicated by dots. III, the shallow pit upon the upper side of the 'sac' in which the archegonia stand ; seen in transverse section.

But it is remarkable that the tissue which the embryo has to penetrate here is, at first, so massively developed, and the embryo follows it in its growth. Evidently the tuber is formed only after fertilization and doubtless furnishes the material at the cost of which the embryo grows. The fleshy character of the tuber is evidently connected more with the provision of an adequate food-supply than with that of water, because Gymnanthe saccata is adapted to a moist position. From the biological side then the sac-tissue does not correspond in essentials with the sac of Calypogeia, but with its archegonial foot, which is only developed after fertilization, and into which the sporogonium penetrates.

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[1] My investigations have led me to a different result from that reached by Stephani, Hepaticae Australiae, in Hedwigia, xxviii (1889), p. 276, who says 'the basal portion of the calyptra is soon concrescent with the wall of the sac, and as this elongates progressively the calyptra grows out into a long tube at whose base the sporogonium sits.' This description proceeds from the assumption that the development is originally like that in Calypogeia, and that there is formed an actual sac with which the calyptra is united. Such a concrescence does not take place, and the process is much more like that observed in the penetration of the embryo of Blyttia and others into the tissue lying below them. [I have, since the above was written, seen living specimens in New Zealand, and convinced myself that the 'sac' never touches the ground.]

A further obscure notion which is found in the literature of Hepaticae concerns these geocalycean Jungermannieae, that of the 'involucel.' This is said to be a special 'second envelope' which is developed 'within the calyptra'; but so far as I see it is only a collar-like outgrowth upon the suctorial swollen base of the sporogonium. To speak of an involucel seems to me superfluous. A similar collar is found, as Gottsche has shown, in Pellia epiphylla and elsewhere. We have here only a surface increase of the 'haustorium' in connexion with the peculiar configuration of the sac, not an 'envelope.'

2. SUMMARY.

If now we review the relationships which I have depicted, we see that the differences which the sexual shoots show as compared with the vegetative ones can be interpreted, at least mainly, from the *biological* standpoint. We have on the one side the securing of fertilization, and upon the other side the protection and nutrition of the growing sporogonium. A *phyletic* derivation of the different forms of construction is at the present time impossible, or only possible in a very limited sense. The several genera have indeed in many cases reached the present construction of their sexual shoot by very different ways, and as the result of 'inner' causes. In consequence of this many parallel formations occur. As such we may note the envelopes which are formed about the single archegonia in Sphaerocarpus and in the Marchantieae, the perianth of Blyttia, and of the foliose Jungermannieae and others. It is noteworthy that in the sexual shoots there is frequently an indication of leaf-formation, even in the thallose forms, as we see in Aneura and in the covering scales of the antheridia in Mörkia, and elsewhere, and this fact will be referred to again when the hypothesis of the phyletic origin of the acrogynous Jungermannieae is discussed[1].

V

THE SPOROGONIUM OF HEPATICAE

1. *STRUCTURE AND LIFE-RELATIONSHIPS OF THE MATURE SPOROGONIUM.*

The increased interest which has been shown in the developmental history of the Hepaticae during the past decades has brought it about that the structure and the life-relationships of the mature sporogonium has not received satisfactory consideration. I therefore put this subject prominently forward, as the mature condition is the ultimate aim of all development, and is therefore the most important[2].

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[1] See p. 115.

[2] See Goebel, Archegoniatenstudien: VI. Über Function und Anlegung der Lebermoos-Elateren, in Flora, lxxx (1895), p. 1.

The production of the spores is the common function of all sporogonia, as the name indicates, and the spores arise by division into four of mother-cells. The configuration of the sporogonium, in spite of its uniform function, is very different, and the function of distribution of the spores is frequently associated in it with that of the formation of spores, and both are accomplished in manifold ways. We have first of all to recognize two chief types, on the one side that of the series of the Anthoceroteae, and on the other that of the series of the Marchantiaceae and of the Jungermannieae. In both series there are parallel formations, for example, the appearance of elaters, although these have a different construction in the two groups.

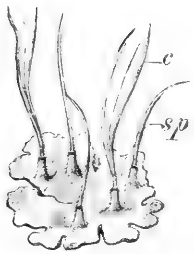

FIG. 81. Anthoceros laevis. Thallus with sporogonia. *sp*, unopened sporogonium. In the opened sporogonium the bristle-like columella, *c*, is visible. Natural size. Lehrb.

1. TYPE OF THE ANTHOCEROTEAE.

Anthoceros. We must start from the genus Anthoceros itself (Fig. 81). The long cylindric structure, which is not segmented into stalk and capsule, is here characteristic. The basal portion only is somewhat swollen and developed as a haustorium from which there pass out many suctorial tubes into the mother-plant. The sporogonium has, however, an abundance of chlorophyll, and is therefore able to assimilate. On this account the outer cell-layer is provided with stomata which have the same structure as those of the higher plants (Fig. 82). Stomata are known elsewhere amongst the Bryophyta only upon the sporogonia of some Musci, and they furnish thus a remarkable example of a parallel formation.

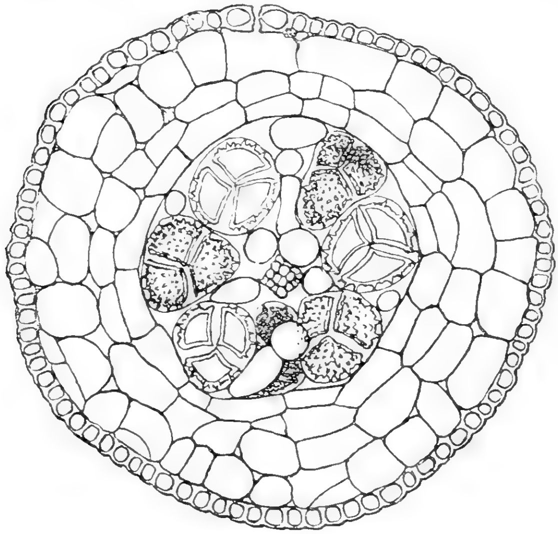

FIG. 82. Anthoceros punctatus. Immature sporiferous portion of sporogonium in transverse section. Small-celled columella in the centre, connected with the assimilating wall-layers by sterile cells which would become elaters. Between these sterile cells are the spore-tetrads. The epidermis shows one stoma.

In Fig. 82 we have a transverse section of a sporogonium of Anthoceros. The many-layered wall functions as an assimilation-tissue; in the middle runs a narrow-celled strand of tissue, which ultimately projects between the two lobes of the opening sporogonium as a bristle, this is the *columella*. At first it has a mechanical function in relation to the somewhat prolonged development of the sporogonium. It forms, in a certain measure, the frame-work upon which a net-work of sterile cells is fastened, between which the sporocytes lie. The columella has, besides, a nutritive function. It passes below into the basal portion of the sporogonium which is concerned with the taking up of water from the mother-plant. Transpiration from the surface of the sporogonium is considerable, especially as the sporogonium continues to elongate for a long time by intercalary growth; it opens indeed at the apex before the spores are formed in the lower part. The columella is then comparable with the 'central strand' of many of the Musci in serving as a channel for water. The columella can also supply to the sporocytes other substances, and this certainly takes place also through the sterile cells between the spores, as they are in connexion with the peripheral layer of assimilating tissue. These sterile cells take on another function at a later period. They separate in great part from the wall of the sporogonium and the columella, and as they dry exhibit movements of torsion which set the spore-masses in movement. The single spores, or it may be groups of them, are in this way thrown out along with these *elaters* from the open sporogonium, and this proceeds much more energetically in sunlight as will appear from what follows. Occasionally as in Anthoceros laevis, A. punctatus, and others these elaters exhibit a rudimentary spiral thickening of their cell-membrane[1], but in other species of Anthoceros, such as A. Vincentianus, A. giganteus, A. multifidus, A. denticulatus, and others, and in Dendroceros, the spiral thickenings are sharply marked. Elaters with prominent thickenings act as more energetic exploding organs than do those in which only rudimentary thickening is present. There seems to me to be no reason for considering the latter as reduced forms of the others: rather must we see in these elaters an illustration within the series of a progressive formation of one organ. The elaters in the Anthoceroteae are distinguished from the outwardly similar elaters of the Jungermannieae and Marchantiaceae, which may also show spiral thickening, by the fact that they are composed of cell-rows.

Notothylas. Douglas Campbell[2] has recently shown what the condition is in Notothylas (Fig. 83), the third genus of the Anthoceroteae, and has proved that Leitgeb's views, which were founded upon unfavourable material, are incorrect. The differentiation of archesporium and columella proceeds in exactly the same way as in Anthoceros, only the intercalary

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[1] Usually there are two thickening bands in the longitudinal direction, but they do not run with a straight course.

[2] See Douglas Campbell, The Structure and Development of Mosses and Ferns, London, 1895.

growth is less marked, and the division of the archesporium proceeds somewhat differently. The structure of the ripe capsule, however, shows remarkable differences. The sporogonium of Notothylas is *much smaller than that of Anthoceros* and has neither an assimilation-tissue in the capsule nor has it stomata. Whether the sterile cells share in the scattering of the spores is unknown[1]. Further investigation is required to determine whether some species of Notothylas want the columella, at least in the ripe sporogonium[2]. The Anthoceroteae, in all their characters, appear to be a group sharply differentiated from the other Hepaticae, and to be of a considerable age.

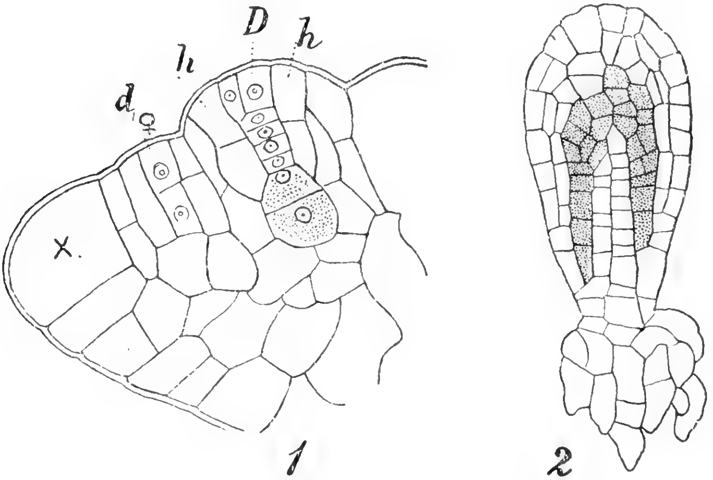

FIG. 83. Notothylas orbicularis. 1, thallus in longitudinal section; x, apical cell; to the right of this a young archegonium, ♀, and an older one; *D*, *d*, lid-cells; *h*, *h*, neck-cells. Magnified 600. 2, young sporogonium in longitudinal section. The shading indicates the archesporium. After Douglas Campbell.

2. TYPE OF THE MARCHANTIACEAE AND JUNGERMANNIEAE.

The sporogonia of the Anthoceroteae have reached a somewhat higher stage of differentiation than that of the lowest type of sporogonium in the Marchantiaceae, for in this there is no special arrangement for the scattering of the spores. Sporogonia without a distributing mechanism occur then amongst the Hepaticae as well as amongst Musci, but such sporogonia are either relatively small or if relatively large contain but few relatively large spores. Wherever we have numerous small spores there is always a special arrangement for their distribution and the sporogonium is differentiated into a capsule which contains, besides spores, some sterile cells which serve for the distribution of the ripe spores, and into a stalk whose basal portion is constructed as a suctorial organ. By the elongation of this stalk the

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[1] Probably they do so because their walls show spiral thickening.

[2] It may be suppressed early here as it is in the Ephemeraceae amongst the Musci.

venter of the archegonium is ruptured and the capsule protrudes. This elongation is a rapid one and is due to the great increase in size of the stalk-cells which use up the starch which lies within them. The wall of the capsule opens in a characteristic manner, the spores are scattered and the thin-walled cells of the stalk wither. In contrast with the course of events in the Anthoceroteae, the sporogonium has but a short existence here outside the venter of the archegonium. It lives chiefly as a parasite at the cost of the sexual generation which often forms a special nourishing tissue for it.

The simplest forms of sporogonia are cleistocarpic; the relatively large spores escape from them by rotting of the wall, and there is no special means for distribution. In the more complex sporogonia the wall, at maturity, ruptures by four valves in the Jungermannieae, and in different ways in the several genera of Marchantiaceae. According to investigations carried out in the Botanical Institute at Munich[1], a lid-portion always separates, except perhaps in Targionia in which the wall breaks up into several irregular pieces. This lid is either in one piece or it breaks up into single cells. The remainder of the capsule forms an urn in Reboulia, Grimaldia, and others, splits into four lobes which are afterwards divided in Lunularia, rolls itself together in Fegatella, and, in short, shows many variations. The illustration and description of the tufts of elaters hanging on the points of the lobes in Lunularia, which have been again put forth by Schiffner, are altogether wrong, although such an arrangement is found in Aneura. I cannot, however, discuss here these relationships, nor give the details of the deviations from the usual manner of opening that may be observed in the capsule of the Jungermannieae.

With regard to internal differentiation, we find in the Marchantiaceae and Jungermannieae the following types:—

1. THE SPOROGONIUM IS DIFFERENTIATED INTO A WALL-LAYER AND AN INNER SPACE FILLED ONLY BY SPORES; this in Riccia and Oxymitra. The wall-layer is absorbed early in Riccia and the spores are then set free by rotting of the thallus.

2. THE CELLS WITHIN THE INNER SPACE DO NOT ALL BECOME SPOROCYTES; A PORTION OF THEM REMAIN STERILE.

(A) *The sterile cells are only nutritive cells*, and the sporogonium has no stalk, but at the most a short appendage which acts as a sucker; this in Corsinia, Riella, and Sphaerocarpus.

Sphaerocarpus. The most primitive relationships are those of Sphaerocarpus, for here the difference between sterile and fertile cells sets in relatively late. It is remarkable that the wall of the sporogonium at an early period separates from the content (Fig. 84, *II*), which is surrounded by a slimy fluid comparable with that which is found in the 'water-chambers' of the calyptra of some Musci[2], and which there serves as

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[1] See Andreas, Über Bau der Wand und die Öffnungsweise der Lebermoossporogons, in Flora, lxxxvi (1899), p. 161.

[2] See p. 153.

a water-reservoir. The sterile cells are distinguished by their starch-content, whilst the fertile ones contain more proteid, a difference which appears also in Aneura. The fertile cells are the larger and the disposition of the two kinds of cells is such that at first groups of two to three sporocytes with a few sterile cells attached to them are formed. The fluid which fills the inside of the spore-capsule renders possible perhaps an exchange of material, for soluble materials may pass into it from the sterile cells and be again taken out of it into the fertile cells. At any rate the fertile cells are here chiefly nourished by the chlorophyllous sterile ones and by the chlorophyllous wall of the capsule; the short stalk of the sporogonium disappears so soon that the sporogonium has from an early period to depend upon itself for its nourishment. The division of the nuclei in the sterile cells[1] recalls rather the nuclear fragmentation of the tapetal cells in the anthers than the divisions within the sporocytes. The spores remain in tetrads (Fig. 84, *I*); the sterile cells are still visible when the spores are ripe.

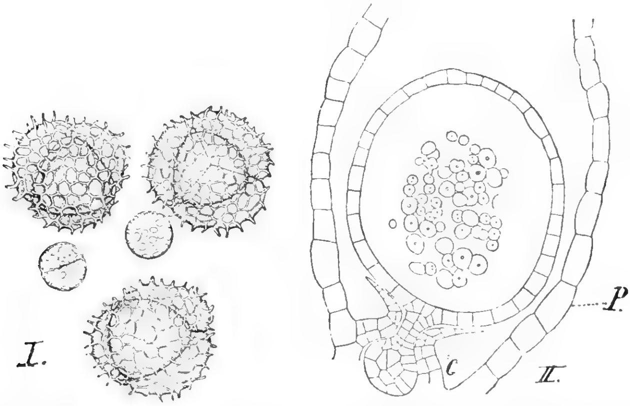

FIG. 84. Sphaerocarpus terrestris. *I*, three spore-tetrads and two sterile cells from a ripe sporogonium. *II*, longitudinal section through a sporogonium about half-developed, the sporocytes are not yet divided; *c*, calyptra; *P*, perianth.

The method by which the spores are set free, whether by rotting of the sporangial wall or otherwise, is unknown in Riella and Sphaerocarpus, as well as in Corsinia. Probably in them all the spores float away after the sporogonium has withered. In Corsinia the sterile cells, as in Sphaerocarpus, are still living at the time of the ripening of the spores, and are provided with small chloroplasts; they also serve as nutritive cells, but are externally much more like elaters than are those in Sphaerocarpus.

(B) *The sterile cells are provided with usually spiral thickenings;* they are spindle-formed and sometimes branched; they are dead at the time of ripening of the spores and they take a share in the distribution of the spores. This is effected in different ways; sometimes in the process

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[1] Frequently nuclear division is followed by a retarded formation of cell-wall (see Fig. 84, *I*, to the left).

of drying spring-like movements of the sterile cells are induced, and these are the more energetic the quicker the process of drying[1]; sometimes after the opening of the sporogonium hygroscopic movements bring about the formation of a loose framework which occupies a larger space than in the spore-capsule and from which the spores are gradually removed by air-currents.

The hygroscopic movements of different strength brought about by varying rapidity of drying must be kept in view in the following grouping of forms. The two groups, in one of which the elaters act as ejecting-organs whilst in the other they do not, are not sharply separated from one another, and in both groups there are different types to be distinguished.

I. THE ELATERS ACT AS ORGANS OF EJECTION.

A. There are no Elaterophores.

(*a*) **Type of Jungermannia.** The elaters are free; they are not fastened to the wall of the sporogonium and have no definite arrangement inside the capsule. The capsule opens by four valves, and the moist mass of spores and elaters is thus exposed to drying. So soon as the wall of the capsule ruptures the ejection of the spores begins; it lasts only a short time usually and is all over in a few minutes. The existence of the sporogonium finds in this its end. Different species of Jungermannia show this method, also Plagiochila, Chiloscyphus, and others. A modification of it, leading on to the next type, is observed in Jungermannia bicuspidata (Fig. 85), J. trichophylla, and others. In them the very long elaters are fastened by their base to the wall of the sporogonium; they converge inwards towards a zone free from elaters. In the open sporogonium the spores are seen invested by the elaters, which with their free end exhibit movements of torsion and then they jerk themselves off from their point of attachment and thus

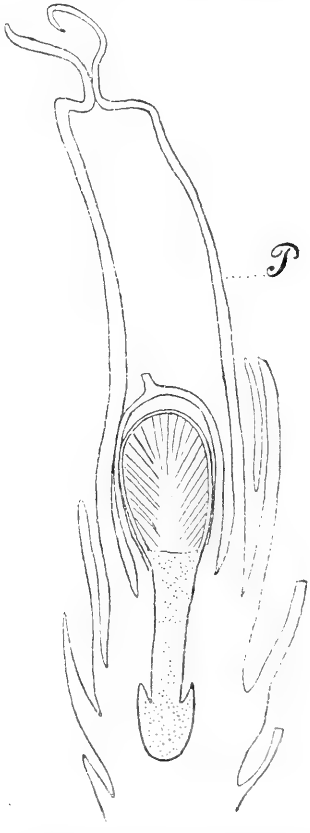

FIG. 85. Jungermannia bicuspidata. Stem in longitudinal section. *P*, perianth. The sporogonium has bored deeply into the stem.

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[1] In the Marchantieae, for example, there is usually no marked ejection of spores, but this may occur if conditions arise which, in the words of the renowned observer of last century, Kölreuter (Das entdeckte Geheimniss der Kryptogamen, Karlsruhe, 1777, p. 23), whose work contains many valuable observations, I may describe as follows:—'If one wishes that the threads of the capsule should show active movement one must, after the sporogonium has stood in the shade, place it in the sun, or where the sun's rays have access, and where there is little moisture. Then as the moisture

throw out the spores which are seated upon them. A few of them usually remain upon the wall of the capsule.

(*b*) **Type of Frullania.** Besides Frullania we have showing this type the allied genera Lejeunia, Colura, and Phragmicoma. The elaters lie nearly parallel with one another in the long axis of the sporogonium; their broadened ends are united to the inner surface of the capsule. When the sporogonium opens they rupture at their base and remain with their upper end seated upon the wall of the sporogonium. The opening of the capsule takes place very quickly in Frullania; a touch, and the spores are shed. The elaters are evidently stretched by the bending back of the valves; they break off from them, quickly spring loose, and throw off the spores. The hygroscopic movements which the elaters also exhibit have in this type only a subsidiary importance.

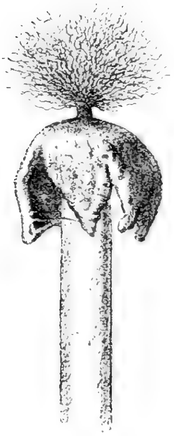

FIG. 86. Pellia calycina. Sporogonium opened and emptied showing the valves of the wall recurved, and an elaterophore of many threads.

B. Elaterophores are present.

(*a*) **Type of Pellia**[1]. The large capsules of the species of Pellia contain spores which exhibit the first stages of germination within the sporogonium, and therefore become cell-masses; consequently the spores are not usually thrown out to a distance. The dehisced sporogonium of Pellia calycina (Fig. 86) exhibits a tuft of many, often a hundred, long, thread-like, spirally-thickened cells seated upon the base of the capsule. In P. epiphylla the threads are fewer in number and are usually connected one with the other at their base. This tuft is the elaterophore; the special free elaters have been shed from it with the spores. A section through an unopened capsule shows in its centre in the lower part a cell-mass with radiating cells which will become the elaterophore. Sporocytes usually do not exist here. The work of the elaterophore is determined by the manner in which the capsule opens. In P. calycina I found the following, which I give in supple-

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evaporates from the sporogonium their movement becomes all at once stronger and more vigorous, and the spores thus loosened are thrown off in a cloud. This effect is most strongly seen if one focuses the light with a burning-glass upon the yellow woolly tuft. This experiment may be made with equal success upon the spikes of Equisetum.' This spring-effect of the elaters has been entirely overlooked by recent authors.

The mechanism of the movement of the elaters of Hepaticae has recently been the subject of a searching investigation at the hands of Kamerling (Der Bewegungsmechanismus der Lebermoos-elateren, in Flora, lxxxii (1898), p. 157). The mechanism is not the same in all elaters, that in Anthoceros for example differing from that in most of the Jungermanniaceae. Kamerling sees in this difference of mechanism a support to my view that the elaters are primarily nutritive cells which have taken on as a secondary duty the work of distribution of spores.

[1] See Goebel, Archegoniatenstudien: VI. Über Funktion und Anlegung der Lebermoos-Elateren, in Flora, lxxx (1895), p. 1. The literature is cited here. Also Jack, Beiträge zur Kenntniss der Pellia-Arten, in Flora, lxxxi (Ergänzungsband zum Jahrgang 1895), p. 1.

ment to my earlier statements. The capsule opens by four valves which spread out nearly horizontally. Elaters and spores exhibit lively movement, and some spores are occasionally shot out to a short distance. At first one sees nothing of the elaterophore, because it is spread like a web over the mass of spores or the four clumps of these. This mass of elaters and spores increases to a larger volume than it possessed within the capsule and rests first of all upon the valves, which then bend backwards more and more and the spores consequently fall off, if they have not been carried away before by the wind. But this does not happen all at once, because the elaterophore has still some hold on the mass, and forms a kind of support to it. Subsequently the elaterophore, which with the opening of the capsule became diffuse, again acquires a more erect form, and if spores are still sticking to it they can then be easily blown off. The elaterophore thus secures a *gradual sowing* of the spores[1], and when we know that Jack counted 4,500 spores in one capsule of Pellia epiphylla, it is clear that it is a matter of importance for the plant that these should not fall out of the capsule in great numbers together.

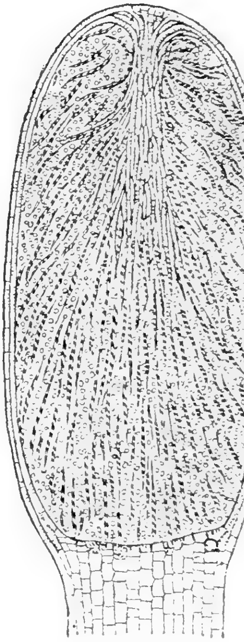

FIG. 87. Aneura pinguis. Ripe capsule in longitudinal section. From the summit the elaterophore hangs into the spore cavity in which are many spores and elaters. Magnified.

(*b*) **Type of Aneura**, including Aneura, Metzgeria, Hymenophytum. The elaterophore in this type is more specialized than in Pellia, where it may be considered as a peculiarly developed tuft of elaters. In Fig. 87 we have a representation of a longitudinal section through the ripe capsule of Aneura pinguis. The elaterophore appears as a tissue-mass projecting downwards from the upper wall of the capsule and the loose elaters are distributed in a radiating manner in the space between the spores. The elaterophore splits later into four parts, and the lines of separation are very early recognizable. The cells of the elaterophore have semi-annular thickenings, and the lowermost of the cells frequently grow into pointed cells like elaters. Between these projections of the elaterophore, as well as in other places, the ends of a number, not all, of the free elaters lie. The capsule opens by four valves which assume a nearly horizontal position, and the mass of spores and elaters divides similarly into four parts. Each one of the four masses thus formed and lying upon a valve undergoes a torsion of about 90° at its point of attachment to the elaterophore, and thus the spore-mass upon each valve stands erect. An energetic throwing off of the

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[1] Its nutritive function in the juvenile stage of the sporogonium will be referred to below. See p. 103.

spores now begins, and in about five minutes there is hardly a single elater left upon the elaterophore. It is evident that two things are achieved by this arrangement: firstly, the spore-masses being raised above the sporangial wall can be shot out further into the environment, and secondly, the elongated cylindric form of the sporangium results in a more thorough discharge of the spores; and in correspondence therewith we see that the elaterophore is more developed the longer the capsule[1].

II. Elaters are not, or not usually[2], Organs for the Ejection of Spores, but serve to hold the Mass of Spores.

Features of this kind seen in Pellia have been already mentioned. Fossombronia shows the same. The wall of its capsule separates into single pieces, leaving a lower scutellar portion which acts as a support to the mass of spores and elaters. By the movements of the elaters, which have little power as organs of ejection, the mass becomes more voluminous and can be readily gradually removed. The Marchantiaceae which have been examined behave in exactly the same way. In them there is formed before the opening of the capsule a voluminous framework, which reminds one of the capillitium in the sporangium of many of the Myxomycetes.

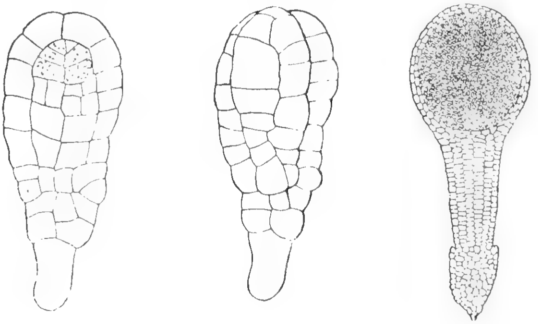

FIG. 88. Lophocolea heterophylla. Central figure. Young embryo seen from outside. Figure to the left. Young embryo in median longitudinal section. Figure to the right. Older embryo in median longitudinal section. Central and left figure magnified 300. Right figure magnified 53. After Kienitz-Gerloff.

The function of the elaters just described is only exercised in the mature condition. I do not doubt that they have also some significance during the development of the sporogonium. They may by their elongated form act as channels through which nutritive material may be transported to the sporocytes, especially in cases where the elaters or elaterophores are united with the sporangial wall, as in the types of Frullania, of Aneura, of Pellia, and in Jungermannia bicuspidata. Where the elaters lie scattered amongst the spores in the cavity of the sporangium they must always act

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[1] For an account of Metzgeria, see Goebel, Archegoniatenstudien: VI. Über Funktion und Anlegung der Lebermoos-Elateren, in Flora, lxxx (1895), p. 27.

[2] See p. 99.

as nutritive cells, giving up the greater part of their contents to the sporocytes. This service is facilitated by the wall of the sporocytes, like that of the incipient elaters, taking on a mucilaginous character at a middle stage of development. Under the elaterophore also in the young capsule in Pellia there is an accumulation of starch which we must regard as the surplus of the carbohydrate after the elaterophore has taken what it requires, and this starch is used subsequently and evidently not for the construction of the elaterophore alone.

2. *DEVELOPMENT OF THE SPOROGONIUM.*

We can recognize more than one type of arrangement of the cells in the earliest developmental stages of the embryo, but they are not strictly maintained:—

Type of the Jungermannieae (Fig. 88). This is the most common. The fertilized egg is first of all divided into an upper and an under cell by a wall at right angles to the long axis of the archegonium. The upper cell gives rise to the capsule and the stalk of the sporogonium, the under cell appears as an appendage at the foot of the stalk of the sporogonium and probably serves as a suctorial organ. A somewhat older embryo shows in its upper part a number of transverse disks, each of which consists of four cells disposed as the quadrants of a cylinder. The apex is occupied by four cells disposed as quadrants of a hemisphere. The division-walls of this mark the four lines of separation along which the capsule subsequently splits. In the simplest cases[1] the capsule proceeds from these four quadrants. Four outer cells, which are the primordium of the wall of the capsule, are separated by periclinal walls from four inner cells, which are the archesporium or primordium of the sporocytes. In most cases, however, the four cells of the transverse disk next these quadrants share in the formation of the capsule, as for example in Radula. We regard as the most primitive case in the group that in which all the cells of the embryo[2] form the archesporium and therefore the nearer to this the development of a sporogonium is, the later the differentiation of its archesporium will be completed. Within the sporogenous mass of cells which arises by the division of the archesporium, there are formed a number of sterile cells which become the nutritive cells and elaters already mentioned. This process of sterilization proceeds much further in the forms which are provided with elaterophores, for example in Aneura palmata[3] (Fig. 89). It is characteristic of this species that a separation at a *very early period* is observable in the sporogenous mass of cells by which two meristems arise, of which the one with less capacity forms the elaterophore which occupies the chief part of the capsule, whilst the other gives rise to the fertile cell-tissue which only subsequently differentiates into sporocytes and elaters. The cells within the capsule are primarily all alike, as in other Hepaticae. The peripheral series of the cells becomes subsequently marked out by a richer protoplasm-content, by chlorophyll, and by the absence of starch, and forms the secondary archesporium, whilst the inner cells form the

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[1] Which are precisely those furthest removed from the original configuration, for example in Pellia, Frullania, Lejeunia.

[2] With the exception of the wall-layer as in Riccia.

[3] Goebel, Archegoniatenstudien: VI. Über Funktion und Anlegung der Lebermoos-Elateren, in Flora, lxxx (1895), p. 24.

elaterophore. We may assume that the sterile cells serve as stores of food and as channels of food to the fertile ones, and that this is the reason of their early differentiation. Apart from the interest which this development possesses it is of importance because it offers an *ontogenous* procedure which upon comparative grounds we believe to be *phyletic* in Anthoceros.

Deviations in the cellular construction of the sporogonium within the series of the Jungermannieae are only known in Sphaerocarpus and Symphyogyna.

In SPHAEROCARPUS the embryo has an elongated form and is therefore divided at first into transverse disks lying one above the other, and these are later divided into quadrants.

The embryo of SYMPHYOGYNA has, according to Leitgeb, an apical growth like that in the case of Musci, and a later differentiation of the spore-cavity.

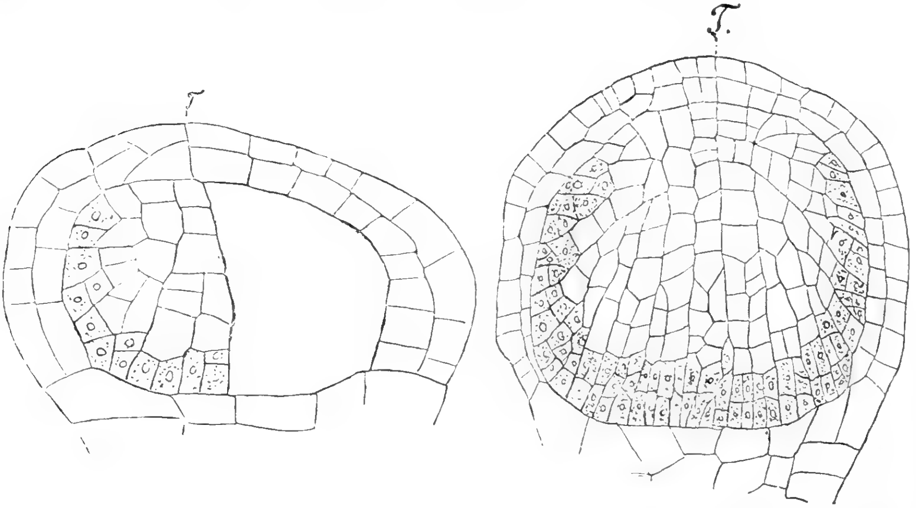

FIG. 89. Aneura palmata. Two sporogonia of different age showing their capsular portion in longitudinal section. The 'fertile' tissue is shaded. *T*, line of separation of elaterophore and wall of capsule.

When additional forms have been investigated we shall probably learn of more divergences oscillating around the type as in other cases.

The RICCIEAE and MARCHANTIEAE have a spherical or ovoid embryo, and the arrangement of the cells, a description of which here would offer no point of interest, corresponds. It may only be mentioned that Kienitz-Gerloff says of the Marchantieae that the first wall, which is at right angles to the long axis of the archegonium, separates the capsule and the stalk from one another. There are, however, variations, for in Targionia[1] transverse walls appear first of all in the elongated embryo, and there may be for a short time the formation of a two-sided apical cell, but later there appears in the upper part formation of quadrants. That the embryo of Riccia is the most primitive of which we have knowledge has already been stated[2].

TYPE OF ANTHOCEROS. As the mature sporogonium differs from that of other Hepaticae so also does its development, but the first stages of the development

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[1] Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882), p. 355.

[2] See pp. 97, 103.

resemble those of the type of Jungermannieae; the embryo consists of two to three tiers of cells arranged in quadrants. From the lower proceeds the 'foot,' from the upper one or two proceeds the capsule. The cells of these tiers are divided by periclinal walls into inner and outer cells (Fig. 83, 2). But whilst in the other Hepaticae the outer cells form the wall and the inner cells the archesporium, here the archesporium is separated off from the outer cells by further periclinal division, whilst the inner cells form the columella. The archesporium is a cell-layer in the form of a bell-glass with the mouth downwards, as it is in Sphagnum and Andreaea, amongst the Musci. Originally the inner cells were fertile, but sterilization has taken place, as in the case of Aneura, and this along with the fact that the layers of the wall of the capsule, which function as assimilation-tissue arise by further periclinal divisions, shows that we have here to do with a new and later formation. The archesporium gives rise to a net-work of sterile cells as well as to the sporocytes, which lie in its meshes as they do in Aneura. It has already been shown that the sporogonium of Anthoceros is an independent assimilating structure[1]. The embryos of other Hepaticae are usually, at least in the earlier stages of development, also chlorophyllous but, excepting in the cases of Sphaerocarpus, Riella, and Corsinia[2], this is of little importance for their nutrition, and they live mainly at the cost of the mother-plant. The basal portion of the embryo bores deep into it, and there is frequently a meristematic tissue which is developed after fertilization has taken place in Pellia, Aneura, and others. In Calypogeia there is a very greatly developed 'foot' to the embryo.

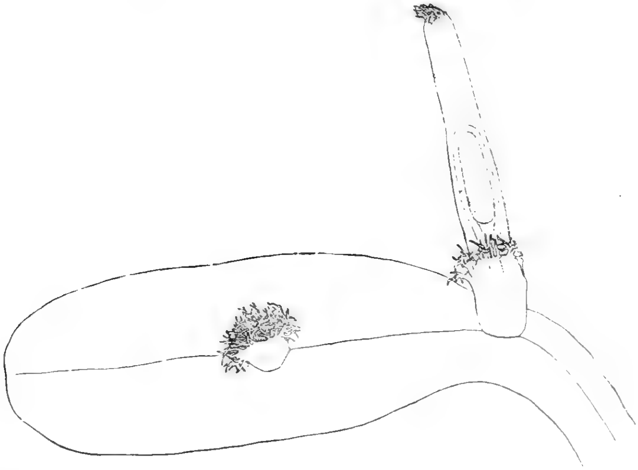

FIG. 90. Blyttia sp. from Ceylon. A young sporogonium arises from the upper surface of the thallus and is invested by the calyptra, the perianth and the perichaetium. Upon the group of archegonia to the left the perichaetium alone is visible and is provided with a tuft of hair-like outgrowths.

The effect of fertilization is not confined to the formation of the embryo alone, but is often seen in the production or the further development of envelopes to the ripening sporogonium as has been shown, but I may mention one further example.

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[1] See p. 94.

[2] See p. 98.

In Fig. 90 a young sporogonium of a species of Blyttia is seen to the right. It is surrounded by a two-fold or three-fold envelope, as well as by a calyptra. In its uppermost part only is this formed by the archegonial venter, it is in the main composed of the tissue lying below the archegonium into which the stalk of the sporogonium has burrowed. It appears indeed as if this 'calyptra' were the remains of the unfertilized archegonium. Outside the calyptra there is a much longer and wider envelope, the perianth, which when the archegonium is ripe exists only as a small annular wall, and receives by fertilization the stimulus to further growth. It is provided above with a tuft which prevents the entrance of water-drops into the interior. Outside and below this is the perichaetium, which is only slightly increased after fertilization.

VI

GERMINATION OF THE SPORES OF HEPATICAE

The spores of the Hepaticae are unicellular. Where pluricellular bodies occur in the sporangium, as in Pellia, Fegatella, and Dendroceros, we have cases in which germination has proceeded within the sporogonium, and they are not uncommon in the inhabitants of moist localities[1]. These pluricellular bodies, like the relatively large spores of Riccieae, are chiefly distributed by being washed away from the sporangium, whilst in the majority of the Hepaticae the spores are distributed by wind.

The size and investiture of the spores are very different even in nearly allied forms: Marchantia has small thin-walled spores, Preissia has large thick-walled spores. Formerly the cell-wall was said to be composed of a cuticularized exine, and a cellulosic intine, but Leitgeb[2] distinguishes three membranes: the *exosporium*, consisting of two different layers, of which the inner belongs to the spore itself and is the special exine, whilst the outer, the *perinium*, is laid down later upon the exosporium and is composed of parts of the sporocyte. In Fig. 91, is a representation of a perinium, which is an outer folded membrane. The function of the perinium is protective, especially against drought, and it is in general more strongly developed in xerophilous forms than in hygrophilous. Its relationships, however, are not clear. Leitgeb puts on one side the suggestion that the perinium is a protection against drought, and ascribes this to the exine because the perinium is well developed in Corsinia which inhabits moist places. But it may be asked if these places are really constantly moist. Certain is it, especially in the aquatic Riccieae, that the

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[1] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 133, where I arrange this phenomenon with the vivipary observable in higher plants.

[2] Leitgeb, Ueber Bau und Entwicklung der Sporenhäute, Graz, 1884.

perinium provides a protection against fungi. The perinium can certainly have nothing to do with a long resting period, because thick-walled spores like those of Corsinia, Preissia, Anthoceros, and Sphaerocarpus germinate a few days after they are sown. The vesicular swellings of the perinium, which are found so markedly in Grimaldia (Fig. 91) may, like the analogous structures on the pollen-grain of Pinus, be regarded as a parachute-apparatus, but at the time of the bursting of the capsule they contain no air. Leitgeb thinks their significance lies in this, that they increase the volume of the spore in germination, and at the same time are also a protective investiture. I confess that this explanation appears to me unsatisfactory[1] and that in order to obtain a clear idea of the relationships of the structure of the envelopes of the spores a thorough investigation of the conditions of life of the several species is necessary. We particularly want to know *when* in nature the germination of the spores takes place.

As in other groups we find amongst the Hepaticae forms whose spores are arranged for immediate development, and which cannot undergo a long period of drought, and those which can or must pass through a resting period. The germination is heteroblastic[2]. There is formed first of all a pro-embryo of simple configuration on which the plant then develops, but pro-embryo and plant are less sharply distinguished from one another than is the case in the Musci, because in most cases the plant arises from the terminal cell of the pro-embryo. The configuration of the pro-embryo varies greatly and is in part the result of external factors[3]. As some interesting questions crop up in connexion with the germination a few illustrative cases will be described.

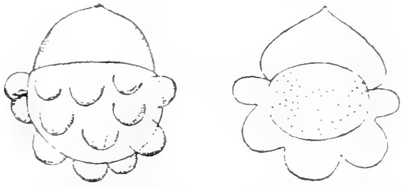

FIG. 91. Grimaldia dichotoma. Spore to the left seen in surface view. Spore to the right seen in section. Contents indicated by dots. The outer wall of the spore forms protuberances.

I. JUNGERMANNIACEAE.

THALLOSE FORMS. The phenomena of germination in Metzgeria and Aneura are very simple.

In **Metzgeria**[4] the spore divides, after increasing in volume, by a transverse wall into two cells which are usually of unequal size; in the one, the smaller, a two-sided apical cell is formed by a wall inclined obliquely to the long axis, and by its division a cell-surface which is one cell thick arises. Later a mucilage-papilla develops at its vegetative point, a midrib

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[1] In Corsinia the perinium consists of separate layers, which permit of the expansion of what is within.

[2] See Part I, p. 143.

[3] See Part I, p. 145.

[4] See Goebel, Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 15; id. Archegoniatenstudien: VIII. Rückschlagsbildungen und Sprossung bei Metzgeria, in Flora, lxxxv (1898).

forms, and thus the characteristic appearance of the thallus of Metzgeria is produced. The length of the first thread-like portion depends upon the intensity of the light ; the feebler this is the later is the cell-surface produced.

Aneura behaves in the same way, and in it branched germ-threads have been observed. The germination of its gemmae also corresponds with that of the spores.

The germination of Blyttia, Mörkia, Monoclea, Hymenophytum, and Symphyogyna is not known.

The spores of **Pellia** begin their germination within the sporogonium and form there a chlorophyllous cell-mass at one end of which—its position in the sporogonium is unknown—is a clear cell which grows out into the first rhizoid whilst the development of the plantlet commonly starts at the other end of the cell-mass. The cell-mass may, however, be so placed that rhizoids arise equally at both ends of it and the primordium of the plant appears in the middle of the pro-embryo. External factors apparently determine the position of the primordium, and the apparent polarity of the pro-embryo observable in the inception of the rhizoids is by no means fixed ; it only appears if the embryo stands erect and different species of Pellia behave differently in this respect.

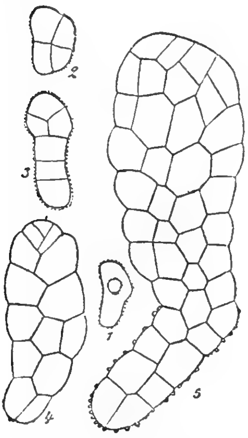

FIG. 92. Lejeunia. Germination of spore. 1–4, Lejeunia serpyllifolia. Exosporium, indicated by dotted line, is here as in many other forms not ruptured but greatly stretched. 5, Lejeunia sp. from South America. Pro-embryo.

ACROGYNOUS FORMS. The germination of **Frullania** and **Madotheca** after the sowing of the spores runs the same course as that of Pellia. An ovoid cell-mass arises out of the spore and becomes fastened to the substratum by rhizoids. An outer cell of this becomes an apical cell of the leafy stem. What the relationship of this method of germination to the conditions of life is we do not yet know.

On the other hand this relationship is quite evident in the case of Radula and in Lejeunia.

Radula. In Radula a cake-like cell-surface is produced out of the spore which has quite the same configuration as the gemma of this plant, only that the gemmae show at their base the point of attachment. From one cell on the margin of this cake-like pro-embryo the primordium of the leafy plant arises. It is clear that the configuration of the pro-embryo and of the gemmae fits them to anchor rapidly upon the rind of a tree or upon a leaf, and this would be a marked benefit to the epiphytic forms.

Lejeunia. The like is seen in the large genus Lejeunia. In Fig. 92, 1, we have an illustration of the elongated spore of Lejeunia serpyllifolia. It divides by a transverse wall, and this may be repeated (Fig. 92, 3) and thus a short germ-tube arises. Usually, however, shortly after the first division, the formation of a two-sided apical cell takes place in one of the two cells whilst the other divides by a longitudinal wall and then there is produced, according to the species and to the external conditions, a broader or smaller cell-surface (Fig. 92, 5), which can then multiply by adventitious shoots. The leafy plant finally proceeds from the apical cell of the pro-embryo. Comparing the construction of a gemma (Fig. 45, III), we find that the cell-surface of the gemma upon its short stalk has usually two wedge-shaped apical cells out of each of which a leafy shoot may proceed. *Such a gemma then corresponds with two pro-embryos united with one another at their base* or, what is the same thing, with a pro-embryo which is bipolar. The difference between the germination of the spore and of the gemma consists merely in this: in the spore there is a polarity which is not present in the gemma developing free upon the leaf[1]. If we consider these differences we shall find that there is no *essential* difference between the germination of spores and the germination of gemmae. We might also show for Marchantia that the apparently great difference between germination of the spore and the development of gemmae is conditioned purely by the lie of the gemmae as they are formed.

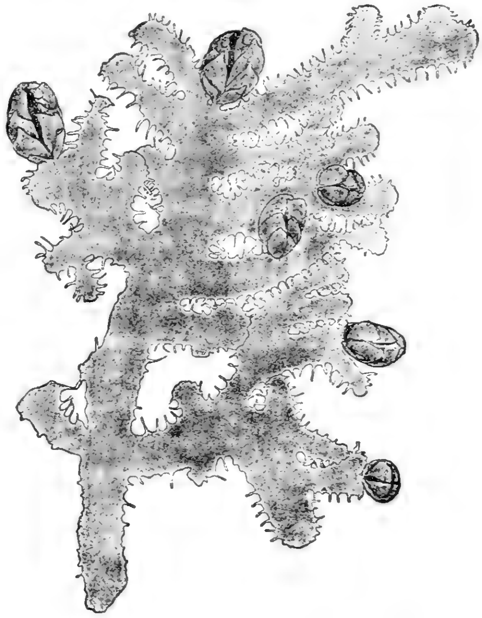

FIG. 93. Lejeunia Metzgeriopsis. Male plant. Description in the text. Magnified.

In Lejeunia also if the outer conditions are not favourable pro-embryo and gemma grow into a thallus before the leafy plant is produced, and this is normally the case in an epiphyllous species of Lejeunia which I found in Java and named L. Metzgeriopsis (Fig. 93). This remarkable plant has a thallus which is richly branched and bears appendages at the margin,—cell-rows which arise in regular serial succession at the vegetative point and may be considered as rudimentary leaves. This thallus, fastened firmly to the substratum by its rhizoids, propagates itself by gemmae. Leafy shoots appear as short appendages upon it, and these have the sole function of producing sexual organs, and their further vegetative development is not possible so far as we know. The thallus is then nothing else than a giant pro-embryo possessing a peculiar vegetative

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[1] It is attached somewhat differently from that in Radula.

body which elsewhere is only a rapidly passed over developmental stage. In Protocephalozia ephemeroides and amongst the Musci we shall find similar cases.

In other Hepaticae, such as **Lophocolea**, **Chiloscyphus**, **Calypogeia**, and **Cephalozia**, the spores, which have a finely granular exosporium, produce in germination a tube which becomes a cell-row by the formation of transverse division-walls. It forms then, as in Aneura and Metzgeria a cell-thread which may also branch, and it is of interest to note that in Calypogeia Trichomanes, for example, stages of germination similar to those of Lejeunia appear occasionally, that is to say, a cell-surface growing by means of a two-sided apical cell develops, and we have here a proof that this is only a modification or a further development of the filamentous stage. Out of the end-cell of the thread or cell-surface there arises a three-sided pyramidal apical cell, and thence the development of the leafy stem proceeds. Regarding the primary leaves of this plant I shall say something below. Here I will only point out that the amphigastria appear after the lateral leaves. In the position of amphigastria there frequently arise at first mucilage-papillae which are afterwards, by division of their supporting cells, carried up upon the point of scales. The germination of the gemmae conforms, so far as it has been examined, also here with the germination of the spore.

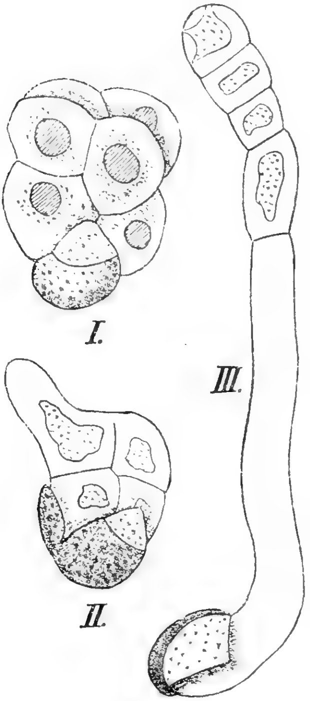

FIG. 94. Anthoceros. Germination. *I*, cell-mass produced in germination. *II*, cell-filament developing from the cell-mass. *III*, further stage of a cell-filament. After Leitgeb.

In **Cephalozia** (Protocephalozia) ephemeroides, found by Spruce in South America, the vegetative body is constituted by the pro-embryo which consists of branched threads upon which the short leafy shoots[1] bearing the sexual organs appear as appendages. The threads of the pro-embryo remind one much of those in the Musci especially in this that they consist of an epigeous part containing chlorophyll and a hypogeous part containing no chlorophyll.

A further group of the acrogynous Hepaticae is that in which, according to the external conditions, either a thread-like pro-embryo or a cell-mass arises in germination. We have examples in **Alicularia**, **Trichocolea**, **Jungermannia** trichophylla and J. hyalina, **Lepidozia** reptans. We do not know what are the external conditions which determine the point

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[1] Goebel, Archegoniatenstudien: III. Rudimentäre Lebermoose, in Flora, lxxvii (1893), p. 83. The literature is cited here.

whether a thread-like protonema or a cell-mass is to arise. It is probable that light plays a chief part, and that in feeble light-intensity the filamentous protonema is formed, whilst in stronger light-intensity we have a cell-mass. Moisture also may have a share. It has been already shown[1] that like variation occurs also in Anthoceros (Fig. 94) whilst in Dendroceros a cell-body arises at once. We shall find that the same problem, and in quite the same form, arises for consideration in the formation of the prothalli of ferns.

2. MARCHANTIEAE AND RICCIEAE.

Preissia. We may refer to the case of Preissia commutata (Fig. 95) which has been already mentioned[2]. The individual differences in the germination of the Marchantieae, when compared with the other thallose Hepaticae, depend upon the fact that the young plants are not developed in the same direction as is their pro-embryo. The pro-embryo is positively heliotropic. It forms at its end a flattened cell-mass, the *germ-disk*, at right angles to the direction of the light-rays, and out of one quadrant of this the new plant proceeds. This plant makes with the germ-tube primarily a right angle, but the sharpness with which this is marked varies in different forms[3]. By the withering of the germ-tube the plant reaches the soil and the whole arrangement is directed to bringing the plant into the light should the spores germinate lying between stones and in like stations; as the germ-tube is longer, within of course the limits imposed by conditions of nutrition, the more feeble the light-intensity, the attaining to the most favourable light-intensity is the more probable. In the Riccieae we observe similar germination[4]. The spores of Fegatella sometimes germinate within the

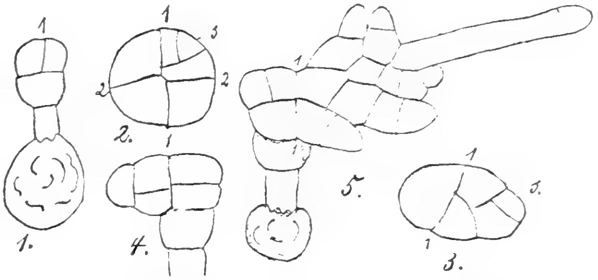

FIG. 95. Preissia commutata. Half-diagrammatic representation of the germination of spores. In figures 1 and 5 the spore is shown below. 1, the germ-tube is very short and bears at its end a cell-mass, the germ-disk, the end-cell of which is divided by quadrant-walls. 2, in one quadrant of the germ-disk seen from above the apical cell, *s*, of the young plant has been formed, 1, 1 the first segment-wall; 2, 2 the second segment-wall. 3, germ-disk seen from above showing apical cell, *s*, of the germ-plant formed from one of the halves resulting from division by the first segment-wall 1, 1. 4, the direction of growth of the young plant forms an angle of 90° with that of the pro-embryo; seen in optical longitudinal section. 5, the apical cell of the young plant has grown out into a germ-tube. See also Part I, Fig. 118.

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[1] See Part I, p. 240.

[2] See Part I, p. 239.

[3] For that of Marchantia, see p. 86, Fig. 75, *H*.

[4] According to Douglas Campbell (The Structure and Development of the Mosses and Ferns, London, 1895, p. 38) the axis of growth in the young plant of Riccia hirta is continuous with that of the germ-tube; but this is not borne out by his Fig. 9. The dorsal side of the thallus does not coincide with the long axis of the pro-embryo. In this method of germination as compared with that of other Hepaticae, we have primarily a more or less sharp adaptation; the original behaviour

sporogonium and form a cell-mass[1], as do those of Pellia. In other Marchantieae also the formation of the germ-tube may be occasionally suppressed, as it is in Anthoceros laevis, and this is the case in Targionia[2].

Let us now compare the behaviour of the gemmae of **Marchantia** and **Lunularia** with the germination of their spores. There are marked differences. The gemmae (Fig. 96) are lenticular cell-masses with an indentation on two opposite margins, and in these indentations lie the vegetative points out of which the new thallus develops. I regard *the whole gemma as a vertical germ-disk developing without a germ-tube*[3], *and it is not dorsiventral because it has a profile position*; dorsiventrality is only 'induced' in the germ-disk by light[4]. From the ordinary germ-disk the gemma is distinguished by its size and, apart from the structural peculiarities which are concurrent with this, by the possession of two vegetative points. We have this also in Lejeunia.

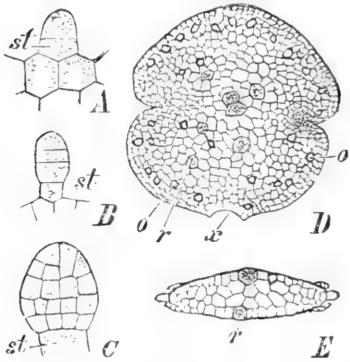

FIG. 96. Marchantia polymorpha. *A–C*, gemmae in different stages of development; *st*, stalk-cell. *D*, mature gemma in surface view, on each side is seen a vegetative point which can grow out into a new thallus; *x*, point at which stalk was attached; *o*, oil-cells; *r*, cells distinguished by their size and contents out of which the hair-roots develop. *E*, transverse section of *D* through the lateral vegetative points; *r*, as in *D*. After Kny. *A–C*, magnified 275; *D–E*, magnified 65. Lehrb.

We therefore arrive at the result, that *in all Hepaticae the method of germination of the spore conforms essentially with that of the development of the gemmae.*

Is there then in the germination of the spores a common type? I have hitherto endeavoured to answer this question by assuming that the formation of a germ-tube and its further development to a filiform branched protonema must be considered the original character. In support of this we find that in a number of forms the formation of germ-tubes regularly appears; in other forms it appears, at least under definite external conditions, and we can follow the filiform stage becoming gradually more limited in duration or we note the formation of a germ-tube being replaced by that of a cell-surface or a cell-mass. Further, this assumption, which is entirely a hypothesis, brings into conformity the formation of the pro-embryo of Hepaticae with that of Musci, and also, as we shall see, with that of the leptosporangiate ferns. The most primitive member of the Hepaticae appears to be one which develops a cell-

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is doubtless that which has been already described in Metzgeria. In Marchantia polymorpha the germ-disk is scarcely developed, but the difference in the direction of germ-tube and thallus is quite evident. If the germ-tube be laid upon the soil at an early period this difference in direction scarcely appears. See Kny, Botanische Wandtafeln, Abteilung viii, p. 338.

[1] See p. 108.

[2] According to Douglas Campbell, The Structure and Development of the Mosses and Ferns, London, 1895, p. 67.

[3] The germ-disk is also vertical in Riella; see Goebel, Archegoniatenstudien: IV. Zur Kenntniss der Entwicklung von Riella, in Flora, lxxvii (1893), p. 104.

[4] See Part I, p. 227.

mass on a simple or branched germ-tube, and this cell-mass bears the sexual organs. Sphaerocarpus approaches this inasmuch as the very young plant bears sexual organs, and the thallus is only a structure bearing these as do the leafy shoots in Lejeunia Metzgeriopsis and in Protocephalozia ephemeroides.

It has been already shown by an example drawn from the Myxomycetes[1] that a higher construction of the vegetative body ensues by the postponement of the formation of spores. If we apply this consideration to the development of the Hepaticae, their vegetative body has reached a stage in forms like those mentioned above in which it is able only gradually and after a long process of development to reach the construction which is competent to bring forth sexual organs. In the thallose Jungermanniaceae the changes which the germ-plant experiences are simple in correspondence with the simplicity of the structure of the mature plant[2], whilst in the Marchantiaceae the number of the developmental stages through which it passes is greater in correspondence with the higher differentiation at maturity. The young plants have at first a different construction of the vegetative point (as Fig. 95 shows), especially a wedge-shaped two-sided apical cell which later passes over into a prismatic four-sided one. The thallus is at first one-layered, and if it becomes many-layered it has at first no scales upon the under side and no air-chambers upon the upper side. Instead of the scales we find unicellular or pluricellular club-like papillae, at first like those of Metzgeria, and later like those of Mörkia or Cyathodium. With the germ-plants of the latter genera those of Preissia, Marchantia, and others also conform, in that their first air-chambers have not the characteristic assimilation-tissue spreading from their base. In other words, we see in the relatively highly differentiated Marchantiaceae the embryo-plant pass through developmental stages which in the other Hepaticae are present in a permanent condition, and this is a fact of extreme interest. Moreover in Marchantia the air-chambers appear relatively late, and it is also characteristic of the genus that the young plants at first have only the 'median scales,' and in this show a construction which in other Hepaticae is the permanent one, whilst in Marchantia itself the further copious development of the scales, which has been already described, subsequently takes place[3]. If we can imagine a germ-plant of Preissia or of Marchantia bringing forth sexual organs before the appearance of the air-chambers, then we should have a condition like that in Sphaerocarpus.

The thallus of **Plagiochasma** Aitonia[4] shows at first upon its upper

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[1] See Part I, p. 25.

[2] See what is said about Metzgeria on p. 107.

[3] See p. 32.

[4] Schostakowitsch, Über Reproduktion und Regenerationserscheinungen der Lebermoose, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 360.

side pits with broad mouths, and only subsequently do the air-chambers appear which have only a narrow breathing aperture towards the outside. The first construction is, like other peculiarities of the germ-plant, only possible in a small plant growing in shaded and moist places.

In the anacrogynous foliose forms the germ-plant is remarkable for two things; first of all, the configuration of the primary leaves, and secondly, the appearance of the amphigastria. The lateral leaves appear first and as short cell-rows. One may cause, as I have shown in Jungermannia bicuspidata, the shoots again to form primary leaves if the conditions are unfavourable; these primary leaves are purely arrested formations. Whilst now most forms produce completely developed leaves more or less quickly, and always long before the appearance of the sexual organs, this is not the case in those which I have termed 'rudimentary[1].' In them the formation of leaf upon the *vegetative* shoot usually remains stationary at a stage which in other plants is only found in the germ-plant, and only upon the sexual shoots are further developed leaves found. This procedure recalls in a certain measure the fact that the formation of the pro-embryo is prolonged, only this temporary prolongation reaches here to the stage following the formation of the pro-embryo.

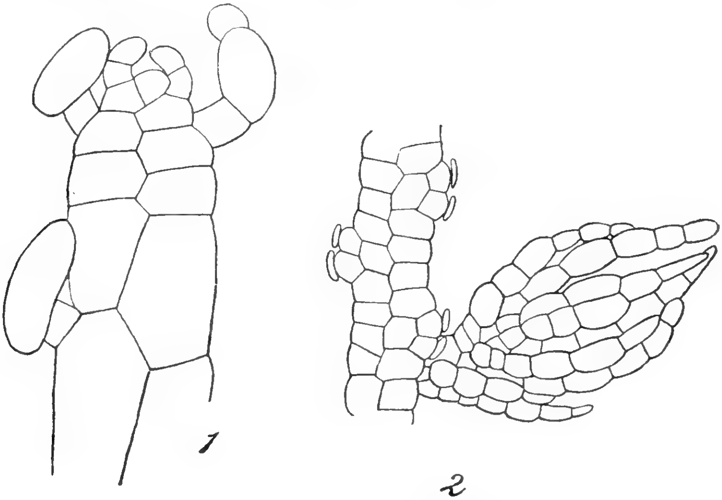

FIG. 97. Zoopsis argentea. 1, young plant with stem composed of but three cell-rows. The 'leaves' are cell-rows which serve only for the protection of the vegetative point. 2, portion of an older plant. A ventral lateral shoot with well-developed leaves bears the archegonia. Highly magnified.

The Hepaticae which come into consideration here are distinguished, like Lejeunia Metzgeriopsis and Protocephalozia ephemeroides, from the great majority of the others in that they are very small. They have thin stems which give them, living as they do in shaded and moist localities, the

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[1] See page 77.

appearance of an Alga[1]. Amongst them are the descendants in the most different cycles of affinity of the foliose Hepaticae. Some examples may be given. The genus Zoopsis, a sub-genus of Cephalozia, is widely distributed, and its lateral leaves are unequally developed in the several species upon the sterile shoots. In Zoopsis argentea (Fig. 97) and Z. setulosa they consist of only two cells, each with an appendage, and they are laid down as in all other Hepaticae, but are displaced completely into the horizontal position. The amphigastria do not reach beyond the condition of primordial papillae, two club-like papillae standing near one another. The sexual shoots are quite different. They have well-developed leaves formed as cell-surfaces. The leaves are more developed in Lepidozia bicruris and Arachniopsis. Here they are composed of two cell-rows, and on the fertile shoots they form cell-surfaces. The same is the case in Lepidozia goniotricha and some others. Of the relationship of the formation of organs of these Hepaticae to their habitats mention has already been made[2].

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[1] One form has indeed been described as an Alga under the name Kurzia crenacanthoidea; see Goebel, Morphologische und biologische Studien: IV. Über Javanische Lebermoose; 5, 'Kurzia crenacanthoidea,' in Annales du Jardin botanique de Buitenzorg, ix (1897), p. 37.

[2] See p. 77.

MUSCI

I

GERMINATION OF THE SPORE IN MUSCI

In dealing with the Musci I shall, for reasons which will appear presently, start from the germination of the spore.

From the time when Hedwig first of all described the germination of the spores of the Musci the subject has evoked many investigations and many interpretations, notwithstanding which our knowledge is not yet without gaps. It is true that we no longer regard the pro-embryo as an Alga, nor do we consider it with Hedwig as a cotyledon, nor suppose like Nees von Esenbeck that the buds are formed by the weaving together of protonema-threads; nevertheless there is much that is still controversial and obscure. When we use the word 'pro-embryo' we naturally do not say anything about the morphological or biological significance of this structure which precedes the leafy shoots.

1. *THE CONFIGURATION OF THE PRO-EMBRYO.*

The pro-embryo in most cases consists of branched cell-threads, and is distinguished from the filiform pro-embryo of the Hepaticae by the absence of *unicellular rhizoids*; but it produces *segmented cell-threads*[1], designated also rhizoids, which are not the morphological equivalents of the rhizoids in the Hepaticae. They are subterranean axes of the pro-embryo, not appendages of the pro-embryo. The degree of development reached by the pro-embryo differs in different forms, as is also the case in the Hepaticae.

Physcomitrium pyriforme[2] furnishes a very simple case. The germinating spore grows out into a cell-thread segmented by cross-walls and containing chlorophyll, and this thread branches. Rhizoids also arise which are thinner than are the protonema-threads exposed to the light, and like these they are provided with cross-walls which are *quite transverse*. Cell-division takes place as a rule only in the end-cells not in the segment-cells in all the axes of the pro-embryo. The different construction of these axes

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[1] Protocephalozia ephemeroides alone amongst the Hepaticae approaches the Musci in this feature; see p. 110.

[2] See Goebel, Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 1.

of the pro-embryo is evidently conditioned by their different physiological work.

In pro-embryos of greater bulk we find also at first a similar slightly marked difference between hypogeous and epigeous axes. The hypogeous axes, at least the stronger ones, are provided in such cases mostly with brown outer walls and cross-walls *oblique* to the long axis. Such rhizoids are also found upon the leafy moss-plants, but there they are more richly branched and the several branches exhibit a division of labour:—the last thin branchings may be compared in their function with the root-hairs of the higher plants, and they grow round the particles of soil; the thicker branches become anchoring-organs, and they may also serve for the conduction of food-material (Fig. 98).

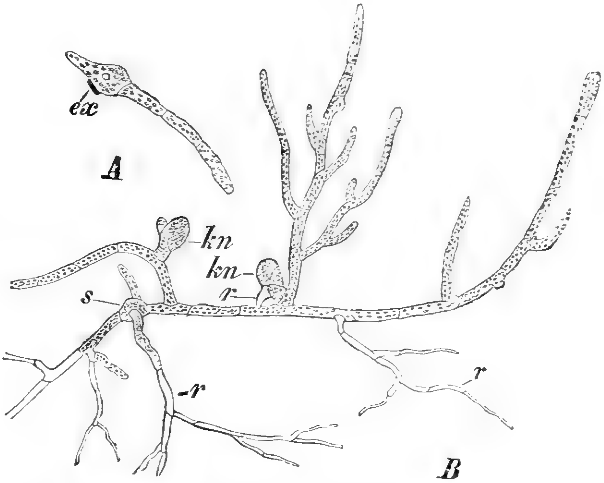

Fig. 98. Funaria hygrometrica. *A*, germinating spore; *ex*, exine. *B*, protonema; *kn*, buds; *r*, rhizoids; *s*, spore. Magnified. Lehrb.

Oblique walls in rhizoids. The oblique direction of the walls in the rhizoids is a remarkable fact which invites an explanation both from the *biological* and from the *morphological* side.

First of all it may be noted that we have illustrations of a like feature in plants outside the group of Musci. In the rhizoids of Chara the walls are not simple transverse walls but are somewhat oblique, yet they always join on to the walls they intersect at a right angle. This, as Errera[1] was the first to point out, and as de Wildeman[2] has also shown, is also the case in Musci. The walls originally are set on to the outer wall of the thread at a right angle, but they have a double curvature; they are not laid down as flat plates and then displaced, but from the beginning have this double curvature. When they, at a later period, appear as placed in an oblique position, that is due to subsequent growth[3]. It is in this way, as various

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[1] Errera, Über Zellenformen und Seifenblasen, in Biologisches Centralblatt, vii (1888), p. 729.

[2] De Wildeman, Études sur l'attache des cloisons cellulaires, in Mémoires couronnés, publiés par l'Académie Royale des Sciences de Belgique, 1893.

[3] I have not been able to convince myself in my study of the process of division that the walls are always set on at right angles to the outer wall. Certain is it that the wall is from the beginning oblique to the long axis, and on one side I often saw plainly that it was set on at a right angle, but, that the walls are set on throughout at right angles, I am not satisfied. Moreover, as the example

authors have shown[1], that the surface by which two superposed cells touch is increased, and that a more rapid interchange of material between them is provided for. The thin lateral branches of the last order of the rhizoids are abundantly provided with straight cross-walls which, however, may also occur in the chief axes, especially when intercalary division takes place. In the *epigeous* parts oblique walls occasionally occur, but the most of the walls are transverse.

The *teleological* 'explanation' of the oblique position gives no clue as to the conditions under which it arises. One may cause *hypogeous* rhizoids to pass over into protonema-threads provided with chlorophyll and having straight walls; but this is not a simple effect of light, as might at first be supposed. My researches with Funaria furnished the proof of this. This plant, cultivated in the dark upon a sugar-solution, grew out to a relatively large size; the cross-walls remained transverse and were not oblique[2], and the rhizoids which developed in the light upon the moss-plants possessed oblique walls, although green threads with straight walls might arise upon them. It is in the highest degree probable that light is a condition for the development of a rhizoid into a green protonema-filament, but in addition other factors are operative, and especially the relationships of correlation.

The oblique position of the wall in the rhizoid has also received a *morphological* explanation. Sachs[3] first of all expressed the view that the protonema and its equivalent rhizoids in the Bryineae are only a very feeble form of the moss-stem. Müller-Thurgau[4] has endeavoured to support this view by showing that the segmentation in the apical cell of a rhizoid is the same as in that of the stem of a moss, only that the chief walls of the segments which follow one another are so far apart that they no longer intersect. This view is altogether untenable, as I showed some years ago[5], and have subsequently again proved. As, however, in a recent compilation[6], showing altogether a want of knowledge both of facts and of literature the Sachs-Müller idea has again been brought forward, it is necessary once more to state the grounds which show its futility:—

1. The regularity in the orientation of the oblique walls which Müller-Thurgau assumed does not always exist. The walls are not always inclined successively

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of Ephemeropsis shows (Fig. 99, 6, where the segment-walls show a double curvature whilst retaining their attachment at a right angle), the surface-development of the wall is more important for the plant than to have it in any definite position. That its position is mostly oblique is only of secondary importance.

[1] Haberlandt, Physiologische Pflanzenanatomie, Ed. 2, Leipzig, 1896, p. 196.

[2] See Part I, p. 233, Fig. 114.

[3] See Sachs, Textbook of Botany, 2nd English edition, Oxford, 1882, p. 363.

[4] H. Müller-Thurgau, Die Sporenvorkeime und Zweigvorkeime der Laubmoose, in Arbeiten aus dem Botanischen Institut in Würzburg, i (1874), p. 475.

[5] Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882), p. 385.

[6] Carl Müller, Musci, in Engler und Prantl, Die natürlichen Pflanzenfamilien, 1898.

in three directions in space as are those of the apical cell of the stem. Thus in Fig. 99 the third wall is parallel with the first, the fifth with the fourth. In the absence of a regular arrangement of the walls in three directions in space the whole analogy with the apical cell fails.

2. Even if the regularity claimed by Müller-Thurgau existed, the walls, which are curved, have quite another character from those of the apical cell of the stem.

3. The oblique position is found only in the *rhizoids*, but not everywhere. But the rhizoids are only a *part* of the protonema, and with that portion of it which has straight walls the hypothesis does not fit. In Sphagnum its impossibility is quite clear.

4. The hypothesis does not fit the pro-embryo of the Hepaticae. The protonema is certainly a simpler form of the vegetative body, but the simplification expresses itself in this, that the cell-divisions proceed in it otherwise than they do later. The oblique position of the wall in the hypogeous protonema is simply a modification of the transverse position, is called forth by the change in the requirements in relation to environment, and has no more morphological significance than it has in Chara.

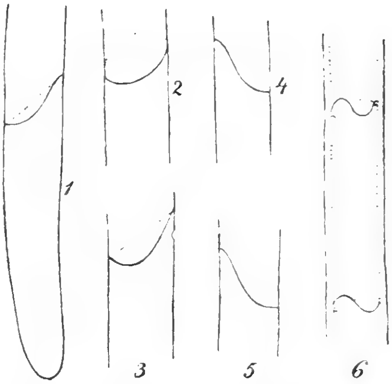

FIG. 99. Arrangement of the segment-walls in protonema-threads. 1 to 5, serially successive segment-walls in the rhizoid of an undetermined species of moss. 6, segment-walls in a protonema-thread of Ephemeropsis tjibodensis; the walls show a double curvature whilst retaining their insertion at a right angle. Highly magnified.

Short shoots and long shoots of protonema. The epigeous parts of the protonema frequently exhibit a differentiation into short shoots and long shoots. This may be illustrated by a moss which I found in Java and have named Ephemeropsis tjibodensis, a very instructive form which is epiphyllous, especially upon Monocotyledones[1]. It shows clearly how the protonema is adapted to external conditions, and particularly in its relationships of symmetry (Fig. 100). The protonema is strongly dorsiventral. Its chief axis creeps upon the leaf-surface. Distichously-branched branches of limited growth arise upon the dorsal side and end in long bristles. Upon the flanks are formed branched anchoring-organs (Fig. 100, *H*), which glue themselves closely to the surface of the leaf and occasionally grow out into lateral twigs. There is no richly developed system of rhizoids; their place is taken by the short anchoring-organs, and the dorsal assimilating shoots are specially fitted by their length and stiffness to retain water-drops, and thus to make possible the nourishment of this peculiar protonema. The gemmae also, which appear upon the protonema, are, as will be pointed out below[2], adapted in a special manner to the epiphyllous life.

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[1] The plant is unfortunately only imperfectly known, and its systematic position can only be decided when female specimens bearing sporogonia are discovered. They have been found lately, since the above was written, by M. Fleischer, Diagnose von Ephemeropsis tjibodensis, in Annales du Jardin botanique de Buitenzorg, sér. 2, II (1901).

[2] See p. 126.

Rhizoid-strands. Other adaptations are observed in some geophilous species, for example amongst the Polytrichaceae, where, especially upon the plant itself, rhizoid-strands are found, which Koch[1] compared with a badly twisted string. The lateral branches of the rhizoids lay themselves along the chief axis and partially invest it; they are not coloured brown. There can be little doubt that we have here structures analogous with the rhizoid-strands of the Marchantieae, and that here also a 'wick-mechanism' comes into play, and thus the most of the Polytrichaceae, amongst which Atrichum, however, is an exception, are able to live in relatively dry stations. To many of the Polytrichaceae which reach a considerable size the rhizoids are also of mechanical benefit, but this is only a secondary service.

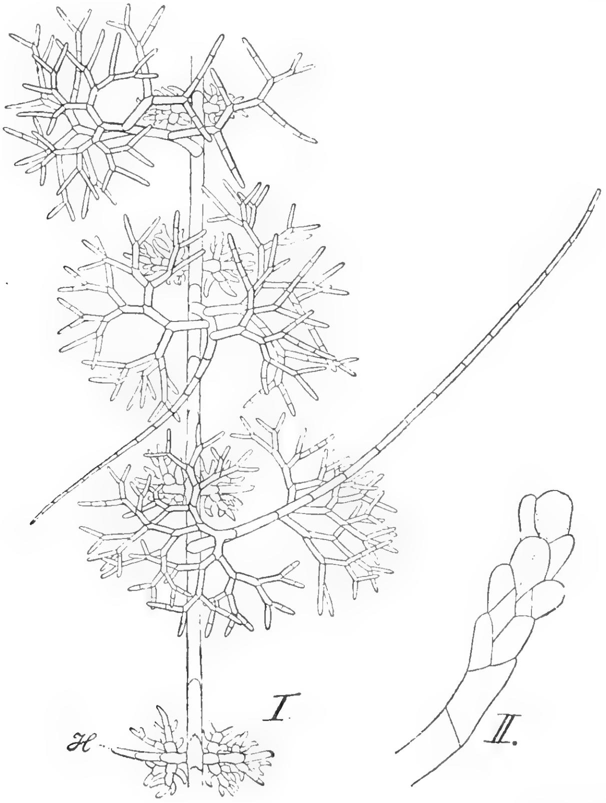

FIG. 100. Ephemeropsis tjibodensis, Goebel, from Java. *I*, habit of the protonema, seen from above. Anchoring-organs, *H*, shoot out from the flanks of the chief axis. Assimilating distichously-branched short shoots arise from its dorsal surface. *II*, male plant which shows an abnormal arrest of the leaves.

Luminous protonema of Schistostega. Schistostega osmundacea[2] has

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[1] H. Koch, Bryologische Beiträge, in Linnaea, xvi, 1 (1842), p. 69.

[2] See particularly Noll, Über das Leuchten von Schistostega osmundacea, in Arbeiten aus dem Botanischen Institut in Würzburg, iii (1887), p. 477.

partly ordinary protonema-threads, partly branches which consist of strongly convex lens-like cells instead of ordinary cylindric cells. The branches which consist of these lens-like cells, spread out in one plane at right angles to the direction of the light (Fig. 101). The peculiar conformation of the cells of the protonema has a relation to the habitat, for the plant grows usually in clefts of rocks, which are illuminated only feebly and from one side. Owing to the lens-form of the cells the light-rays falling upon them are concentrated upon the chloroplasts which lie at one end of the cells, and these are consequently subjected to a greater light-intensity. A portion of the light-rays are reflected after they have reached the chloroplasts, and thus cause the 'luminous' appearance of the protonema of Schistostega. The lens-like cells may pass over into ordinary cylindric cells, as I have observed, but we do not know what are the external conditions which bring this about.

Concrescence of protonema-threads. In the Buxbaumiaceae, which includes Diphyscium and Buxbaumia, the branches of the protonema, both those containing chlorophyll and those having none, become concrescent at their points of contact. The possibility therefore is created of a copious passage of food-material to the places where it is required, and especially to the points of origin of the moss-buds.

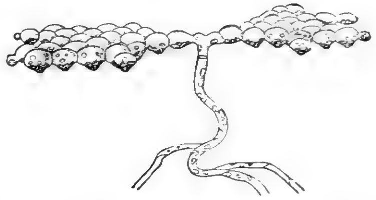

FIG. 101. Schistostega osmundacea. Protonema. Magnified 90. After Noll. Lehrb.

Special organs of assimilation of protonema. Diphyscium[1] has a peculiar organ of assimilation on its protonema, usually in the form of an upwardly concave plate, which sits upon a stalk composed of a cell-mass; even the end of the germ-thread itself is commonly constructed in the form of such an organ of assimilation. From the base of this organ of assimilation rhizoids proceed. I have usually found the primordia of the moss-buds springing from the protonema-thread, and not, as one would expect, from the base of the organ of assimilation, a phenomenon which is less striking in view of the concrescence of the threads. In Diphyscium the surface of the organ of assimilation is occasionally not at right angles to the stalk but it passes directly into this. Such flat leaf-like organs of assimilation are also found in Tetraphis[2], Oedipodium, and Tetrodontium. All these genera grow in relatively very shady places, and the organs of assimilation are therefore well developed in them. They have been described so frequently in recent years that it is unnecessary for me to say more about them.

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[1] See Berggren, Proembryot hos Diphyscium och Oedipodium, in Botaniska Notiser, 1873, p. 109; Goebel, Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 9.

[2] See Part I, p. 249, where is quoted the observation of Correns regarding the development of protonema-tufts under feeble illumination.

The pro-embryo in Andreaea. The remarkable behaviour of Andreaea[1] stands in intimate relationship to its locality, as I have before now pointed out. In the germination of this plant a cell-thread does not arise, but a cell-body like that of many Hepaticae, and this is probably a protection against drought. One to three peripherally-placed cells of this cell-mass grow out into threads in which both transverse and oblique walls appear, and also longitudinal walls. Where the protonema lies upon a stone it broadens out into a much lobed and branched plate of tissue, which evidently forms a very satisfactory anchoring-organ for this exclusively lithophilous moss. Another form which is met with in the pro-embryo of Andreaea is that of the tree-pro-embryo. It is a roundish, radially branched, orthotropous structure which grows isolated occasionally, but mostly associated with others. Its outer surface is covered with a thick cuticle, evidently a protection against drought in its station. Leaf-like structures, like the organs of assimilation of the pro-embryo of Tetraphis, are found also in Andreaea, which belongs to the most highly developed of the Musci. The dependence of its configuration upon external factors requires investigation.

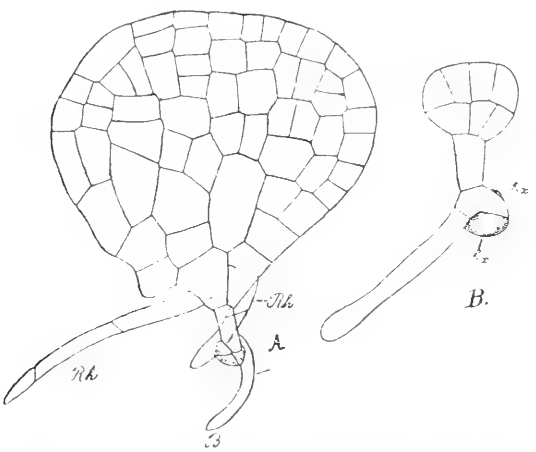

FIG. 102. *A*, Sphagnum acutifolium. Protonema five weeks old; *Rh*, rhizoid. *B*, Sphagnum cuspidatum. Younger protonema; *Ex*, exosporium.

The pro-embryo in Sphagnum. The formation of the pro-embryo in Sphagnum is well known, but was commonly described incorrectly until recent times. Hofmeister[2] was the first who found that there is developed here a frilled surface somewhat like that found in Anthoceros instead of a branched filamentous pro-embryo. Schimper[3] believed that he had found that when the spores germinated in water the pro-embryo was thread-like. In 1882 I threw out the suggestion, and in 1889 I proved[4], although later authors have entirely overlooked this, that Schimper's statement rested upon an error.

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[1] Berggren, Studier öfver mossornas byggnad: I. Andreaeaceae, Lund, 1868; Kühn, Studien zur Entwicklungsgeschichte der Andreaeaceen, in Schenk und Lürssen, Mittheilungen aus dem Gesammtgebiete der Botanik, i (1874).

[2] Hofmeister, Zur Morphologie der Moose, in Berichte der sächsischen Gesellschaft der Wissenschaften, August 1854.

[3] Schimper, Histoire naturelle des Sphaignes, in Mémoires présentés par divers savants à l'Académie des Sciences, xv (1858).

[4] Goebel, Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 11.

It is of course possible, by feeble illumination and other external factors, to hinder the formation of the flat surface, but in the normal relationships this arises in germination in water just as it does upon the land. It has further been shown that the flat pro-embryo is nothing but the broadened cell-thread; in germination a chief axis is first of all developed, and this soon passes over into a cell-surface in which the arrangement of the cells is varied. In weak pro-embryos one finds not infrequently a two-sided apical cell; in pro-embryos which are more strongly nourished most of the marginal cells show differences in growth which here are evidently quite subsidiary. In the case represented in Fig. 102, *A*, the formation of the surface takes place in the second cell, in Fig. 102, *B*, it appears in the third cell of the germ-thread; rhizoids in the form of filiform branchings segmented by oblique walls arise from both the short germ-thread and the cell-surface. The fact that the flat pro-embryo is derived from a filiform one is also shown by this, that the *rhizoids are able to pass into cell-surfaces at their end.* What are the external factors which cause this are unknown. Light is probably favourable to it, as perhaps also is an arrest in the growth of the chief cell-surface[1]. It must suffice for us that these facts show that the pro-embryos of all the Musci can be referred back to the filamentous form. Sphagnum has this further interest, that occasionally pro-embryos are met with which resemble the assimilation-organs of the pro-embryo of Diphyscium.

I have observed remarkable relationships in Eucamptodon Hampeanum and Dicnemon semicryptum[2], two allied genera of which the development of the spores differs so much from that of the other Musci that Montagne[3] believed that there were no spores in the sporogonium of Eucamptodon but only gemmae like those of Marchantia.

Eucamptodon Hampeanum. If one examines an as yet unopened sporogonium of Eucamptodon one finds that the 'spores' are not simple cells, but pluricellular bodies of a flat form and somewhat elongated irregular outline. A better idea of them can be obtained from Fig. 103 than from a description. Many are cell-surfaces, in others divisions have taken place parallel with or obliquely to the surface; I have seldom found more than two cell-layers in any one body.

Dicnemon semicryptum has much larger cell-masses with a roundish outline within the sporogonium. The 'spores' from an as yet unopened sporogonium are easily visible to the naked eye, and therefore are giant as

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[1] I cannot here discuss the phenomena of regeneration in the pro-embryo of Sphagnum, or other subsidiary points.

[2] I have to thank Dr. Carl Müller-Halle for specimens of these two mosses.

[3] Montagne, Plantes exotiques nouvelles, in Annales des sciences naturelles, iv (1845), p. 120. Montagne examined Eucamptodon perichaetialis, Montag., and when he says 'one cannot regard these organs as true spores' he refers to the spores which germinated in the sporogonium. Montagne's species grows in Chili, probably in a moist climate.

compared with the spores of other Musci. They are green pluricellular bodies flattened upon one side whilst the other is somewhat flatly trigonous (Fig. 103, *I*). Here then, as in Pellia and Fegatella amongst the Hepaticae, the germination of the spore has taken place within the sporogonium, but the pro-embryo found in Dicnemon semicryptum is composed of many more cells than is the pro-embryo in the Hepaticae mentioned, and has not the entirely flattened form it possesses in them. The small brown spheres which are visible at different positions of the cell-mass, are probably the remains of the strongly stretched exosporium; they can also be seen on the outside of the spores of Eucamptodon. A number of cell-walls, which by their colouring appear specially prominent, are the first to arise. How further development proceeds I do not know, as I had only dead material to examine. It is most probable that out of the germinated spores a filamentous protonema is formed, just as it is out of the gemmae of Tetraphis. The habitat of this moss on the south side of the South Island of New Zealand confirms me in the view I put forward long ago, that its peculiar vivipary is the result of its living in a moist locality. The appearance of this peculiar method of germination amongst the Musci, whose spores otherwise only form a filamentous protonema, speaks again strongly in favour of the view that other variations also in the form of the pro-embryo, are only later changes of the primitive filamentous protonema.

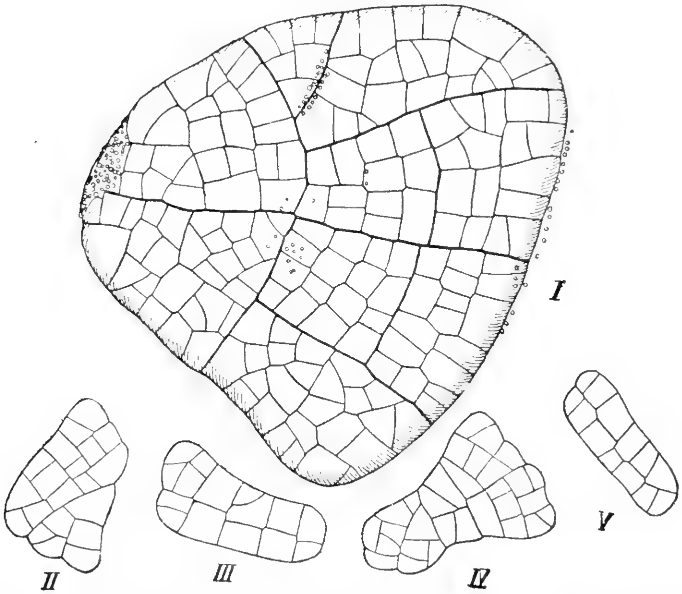

FIG. 103. Germinated spores taken from sporogonia which had not opened. *I*, from Dicnemon semicryptum, Carl Müller-Halle. *II–V*, from Eucamptodon Hampeanum. Magnified.

2. *GEMMAE (BROOD-BUDS) ON THE PRO-EMBRYO.*

The pro-embryos of many Musci possess propagative organs which are known as *gemmae* (*brood-buds*). Here we can only show some of the manifold ways in which these may arise.

The simplest case is that of the breaking up of the pro-embryo into simple cells under the stress of unfavourable conditions.

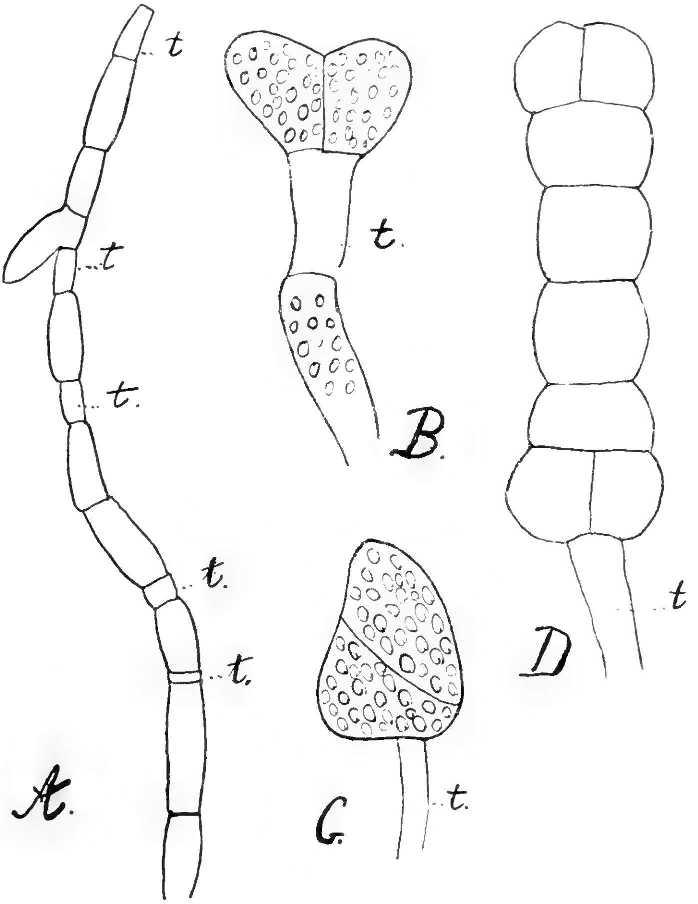

FIG. 104. Funaria hygrometrica. *A*, *B*, *C*, *D*, protonema-threads showing colourless separation-cells, *t*, between gemmae which contain chlorophyll, and which subsequently may become cell-masses. Magnified.

Funaria hygrometrica. We find this[1] in Funaria hygrometrica (Fig. 104) and in Bryum pseudo-triquetrum (?). Separation-cells which have colourless contents and whose walls swell up are formed by intercalary divisions. The remaining portions of the pro-embryo which contain chloro-

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[1] Goebel, Über die Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsberichte der bayerischen Akademie, 1896.

phyll may then grow out into new protonema. This division of the protonema into single cells, or it may be into cell-masses, is the most primitive method of the formation of gemmae, and it happens especially when the external conditions for vegetative growth are unfavourable.

Schistostega. In Schistostega[1] the end of the filament, composed of a row of cells, separates off in quite the same way by a separation-cell, but there is evidently here a little more specialization of the gemma as such.

Ephemeropsis. The formation of an anchor at the base of the gemma of Ephemeropsis is remarkable[2]; the gemma after its separation can fix itself firmly, by means of the projecting arm of its anchor, to the surface of the leaf if this should offer a slightly rough surface.

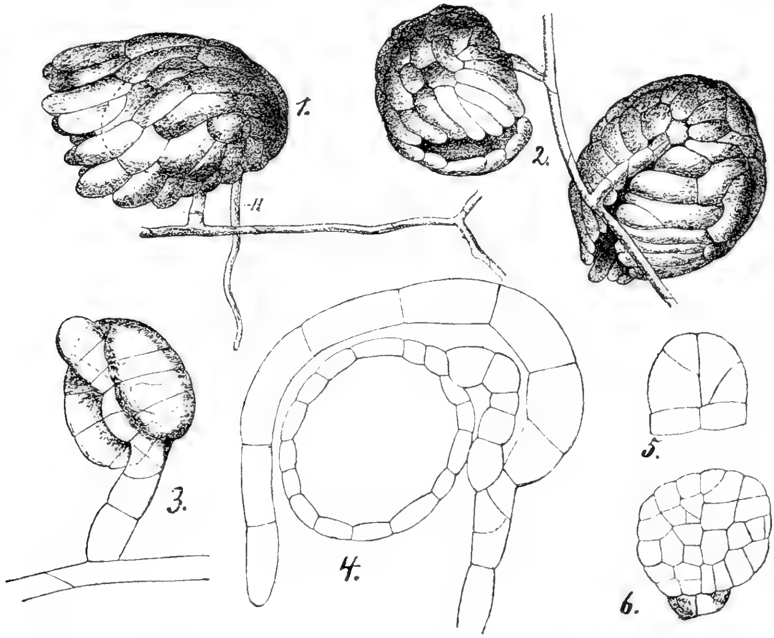

FIG. 105. Buxbaumia indusiata. 1, protonema-thread bearing a male plant; *H*, rhizoid. 2, protonema-thread with two male plants, one seen from in front, the other from behind. 3, young male plant on a protonema-thread. 4, half-diagrammatic longitudinal section of a male plant. 5, 6, cell-grouping in young leaves. 1 and 2, magnified 200. 3, more highly magnified.

The gemmae of the protonema of many other Musci are cell-bodies which are adapted to a period of rest and possess thickened, often brown, outer walls. To describe these structures here would carry me too far. In many cases, although not in all, they are arrested stages of buds of moss-plants. Investigation is required to show whether they do not play fre-

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[1] Noll, Über das Leuchten der Schizostega osmundacea, in Arbeiten aus dem botanischen Institut in Würzburg, iii (1887), p. 477.

[2] See Goebel, Morphologische und biologische Studien: I. Über epiphytische Farne und Muscineen, in Annales du Jardin botanique de Buitenzorg, vii (1888).

quently the part of reservoirs of reserve-food for the protonema, in which case all these gemmae would not exhibit further development [1].

3. *SIGNIFICANCE OF THE PROTONEMA.*

In the life of the moss-plant the formation of the protonema has a double significance: on the one hand it secures that a large number of moss-plants may proceed from one spore, and on the other it secures a vegetation under conditions which would not allow of the development of the leafy moss-plant [2]. The relationship of the protonema to the moss-plant is, as in the Hepaticae, of a varying character. In most cases it is a juvenile stage rapidly passed through, whilst in others it is the special vegetative body, and the 'leafy' plant is nothing more than the bearer of sexual organs.

Buxbaumia. Buxbaumia, one of the most remarkable of the Musci in other respects [3], shows an extreme in this direction. The male plants are extremely simple, about the simplest moss-plants we know (Fig. 105). At the end of a branch of the protonema there is found a long-stalked antheridium, which is surrounded by a chlorophyllous envelope shaped like a mussel-shell. This envelope is the only 'leaf' of the plant. These extremely small male plants, which cannot be seen by the naked eye, have usually no rhizoids, although these may appear occasionally upon the envelope (Fig. 105, 1, *H*), and *the plants obtain their food therefore from the green protonema.* There is no formation of a proper stem here, that is replaced by a very slightly changed branch of the protonema. The female plant has a slightly higher organization than the male, consisting as it does of a cell-body which forms a little stem at the apex of which lies an archegonium. A number of leaves, which contain no chlorophyll, invest the archegonium as an envelope. We can understand that the female plant is more differentiated because it has to provide for the sporogonium which appears later, and like differences between the supporters of the male and the female sexual organs will be noticed afterwards in the case of the fern-prothalli also. The question then arises, Is this simple construction of the plant in Buxbaumia a primitive one, or is it a reduced one? In considering this question inquiry must first of all be directed to the point, Are there yet other characters in Buxbaumia which can be called primitive? There are. In the first place, the leaves of the plants of Buxbaumia have a different arrangement of cells from that of all known Musci, with the exception of species of Andreaea. The leaves of other Musci develop by means of a two-sided apical cell (Fig. 106), whereas Buxbaumia has no apical cell to the leaves but only a cell-grouping more or less resembling that of the leaves of the Hepaticae (Fig. 105, 5, 6) [4].

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[1] See what is said on p. 216 about the tubers in the Filicineae.

[2] See Part I, p. 207.

[3] Goebel, Archegoniatenstudien: I. Die einfachste Form der Moose, in Flora, lxxvi (Ergänzungsband zum Jahrgang 1892), p. 92.

[4] That acute observer Robert Brown so long ago as 1819, said: 'I have lately ascertained, however,

Another primitive character of the leaves is their production of many rhizoids, which occurs but rarely elsewhere in moss-leaves. Further, the build of the sporogonium, especially the device for the throwing off of the lid, shows a primitive structure. In support of the view that we have in Buxbaumia a reduced form it might be advanced that the plant is a saprophyte, and in saprophytes and parasites elsewhere reductions commonly occur. That Buxbaumia leads a saprophytic life is concluded from the localities—rotting wood, soil of woods rich in humus—in which it occurs, as well as from the absence of chlorophyll in its leaves. It is possible that saprophytism does occur here, yet in other Musci which live on the dead bodies of animals, their saprophytism has not brought about reduction. But saprophytic life has not been *proved* for Buxbaumia, and its protonema in the parts exposed to light, as well as its sporogonium, contain chlorophyll[1]. If Buxbaumia is a saprophyte this habit would account at any rate for the

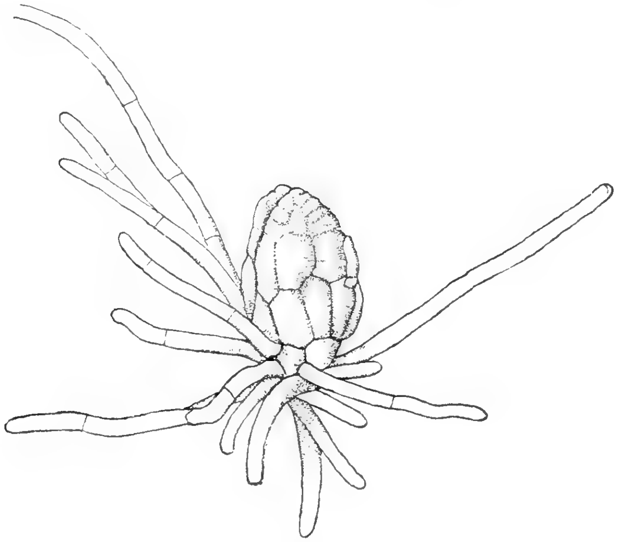

FIG. 106. Funaria hygrometrica. Young plant. At the base of the shoot protonema-threads spread out. The two-sided apical cell is visible upon each of the upwardly-directed leaves.

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that Buxbaumia aphylla is always furnished with perfect leaves, which more nearly resemble, both in texture and division, those of a Jungermannia than of any species of moss properly so-called . . .'; see Miscellaneous Botanical Works of Robert Brown, London, 1867, II, p. 351.

[1] This extends to Splachnum also. I sowed spores of several species of Splachnum (S. sphaericum, S. rubrum, S. luteum) upon fresh cow-dung and obtained quite normal green protonemata, upon which arose subsequently partially formed sporogonia. That the species of Splachnum which grow upon dung take organic substances from their substratum is probable, as it is in the case of the species of Tetraplodon.—T. Wormskjoldi upon the dead bodies of lemmings, see Bryhn, Beobachtungen über das Ausstreuen der Sporen bei den Splachnaceen, in Biologisches Centralblatt, 1897, p. 48; T. augustatus upon dead mice and excrement. Saprophytism can never be proved, however, on purely *morphological* grounds (the behaviour of the rhizoids), and up till now we know of no moss (if we except Buxbaumia) which has experienced reduction in consequence of saprophytic life-relationships.

absence of chlorophyll from the leaves and their small number, but would not explain its other relationships. I have therefore arrived at the conclusion that—if one rests mainly upon phyletic hypotheses—Buxbaumia is a form which has *stood still* in a stage which other Musci have passed, and that it has a primitive character. We might imagine such a form to arise from a filamentous Alga in which the branches bearing sexual organs have developed somewhat differently from the vegetative branches, especially in the direction of providing envelopes for the sexual organs. If the formation of the sexual organs is postponed to a later stage and the envelopes became purely vegetative, a leafy moss-stem would then arise.

Phascaceae. Only a little more developed than in Buxbaumia are the plants of some small Phascaceae. In them the protonema perennates and the moss-plants are mere supporters of the sexual organs. They always exist, however, from the first as cell-bodies constructed out of the three-sided pyramidal apical cell which is almost universal in Musci, and the segments of which are devoted to the formation of leaves. In the simplest Musci the leaves consist of but *one* cell-layer, and they can act as organs of assimilation because they contain chlorophyll, but as a fact they are at first used only as envelopes to the sexual organs. In this relation it is interesting to observe that the first 'leaf' of Ephemerum serratum (Fig. 107) is sometimes a simple protonema-thread, so that the primordium of a moss-bud up to a certain stage of development can be caused to grow out into protonema[1].

FIG. 107. Ephemerum serratum. Portion of a protonema-thread with two young plants. Three antheridia are visible in the plant to the left, and one archegonium in the plant to the right. The first leaf of the female plant is seen turned to the front and consists of a simple cell-row. Magnified.

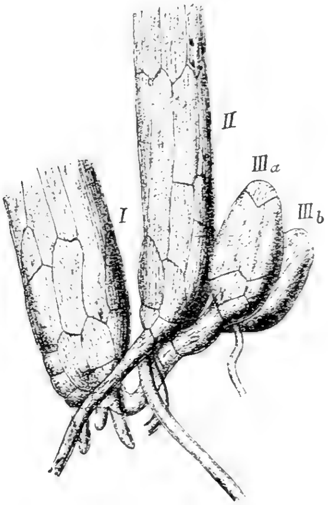

FIG. 108. Schistostega osmundacea. Social growth. *I*, the oldest shoot. *IIIa* and *IIIb* issue from *II*.

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[1] Goebel, Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsberichte der bayerischen Akademie, 1896.

Schistostega. The next stage is one where the stem passes on to the formation of the sexual organs at a later time than in the case of Ephemerum. It still, however, has a simple conformation as it remains unbranched. We see this in Schistostega. The several foliage-shoots of this plant have limited growth, and, according to the hypothesis above stated, were originally all supporters of the sexual organs, whilst now only a relatively small number of them are of this nature; the others remain vegetative. All are alike incapable of branching[1]. New shoots arise out of protonema-threads which are formed at the base of the old shoots. These protonemata remain very short, and each at its apex passes at once into the formation of a moss-bud (Fig. 108), evidently because assimilated material flows into them from the old shoot. They issue from the leafless under-region of these old shoots, and in this way arises the social growth of the stems. If we suppose the protonema-threads which will grow out into shoots to be still more shortened, the resemblance to an actual branching would be even more conspicuous.

Fissidens bryoides. An interesting transition in this respect is found in the male branches of Fissidens bryoides[2]. This moss retains in its branching a primitive character—the chief shoot ends with the formation of archegonia. In the axils of the leaves numerous bud-like groups of antheridia are found, and in the position occupied by these in the lower region a protonema-thread appears. The cell which becomes a male branch projects outwards beyond the surface of the shoot, as if it were about to grow into a protonema-thread, but then, *without forming a protonema-thread*, it passes at once into the formation of an apical cell of a shoot.

The case of Fissidens bryoides brings us evidently very near to that of Schistostega, and only one step further is necessary for the complete suppression of the protonema in the origination of the shoot. At all events we could establish a series from Buxbaumia up to the ordinary type of the Musci, and we have seen analogies in the Hepaticae. Whether it is really an ascending series, or perhaps a descending series, and whether what we have regarded as primitive forms are not really reductions, is not at first to be determined, and it is therefore superfluous to dispute about it. The chief point is *to establish such series* as will bring different forms into relationship one with another.

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[1] Contrary statements which appear in the Bryologia europaea are based upon incorrect observation. I have not found a single branched individual amongst hundreds of plants of Schistostega which I have cultivated and examined. Leitgeb also never found a branched plant; see Leitgeb, Das Wachstum von Schistostega, in Mittheilungen des naturwissenschaftlichen Vereines für Steiermark, 1874, p. 1.

[2] See Leitgeb, Zur Kenntniss des Wachstums von Fissidens, in Sitzungsberichte der Wiener Akademie, lxix, 1 (1874).

II

CONFIGURATION OF THE MOSS-PLANT

The disposition of the cells, the formation of the leaves, and the branching of the 'typical' moss-stem, are described in the textbooks, and nothing new has been brought forward within the last twenty years. It will suffice therefore for me to mention here the chief points. These are :—

1. In all moss-stems which have been examined an apical-cell has been found, and a leaf arises from each segment of this. The apical cell is usually a three-sided pyramid (Fig. 109). In Fissidens, Phyllogonium, and perhaps also in other Musci with distichous leaves it is two-sided. This is a derived condition, as Fissidens clearly shows.

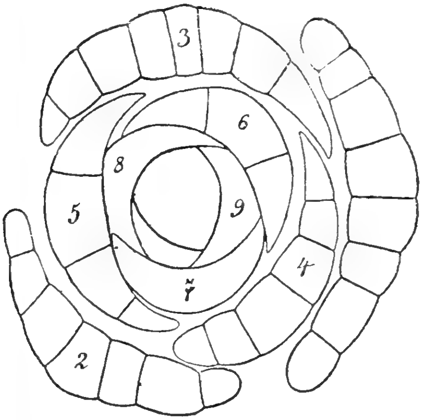

FIG. 109. Thuidium abietinum. Shoot-apex of a bud seen in transverse section. After Kienitz-Gerloff.

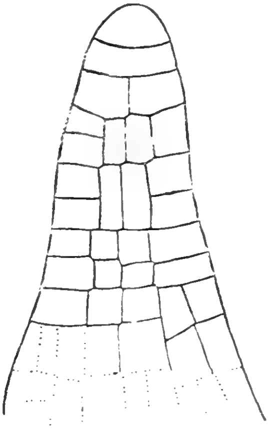

FIG. 110. Andreaea rupestris. Young leaf. There is no two-sided apical cell. Highly magnified.

2. The phyllotaxy is determined by the segmentation of the apical cell. Schwendener's mechanical hypothesis of position of leaves finds therefore no support in the Musci. Where the phyllotaxy deviates from one-third there is an 'encroachment of the segment-wall in the anodic direction' (Fig. 109), as Hofmeister proved, and there is therefore an appearance of a torsion of the stem.

3. Branching is not axillary. Each lateral twig shoots out *below* the leaf with which it shares origin from a common segment-cell.

4. The arrangement of the cells in the leaves is characteristic. The leaf grows chiefly by a two-sided apical cell (see Part I, Fig. 26, to the right) in the great majority of the cases that have been investigated. We have seen an exception in the case of Buxbaumia. In other genera which have primitive characters like Andreaea there are also deviations from the ordinary arrangement[1]. There are leaves which

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[1] Berggren, Studier öfver mossornas byggnad: I. Andreaeaceae, Lund, 1868; Kühn, Studien zur Entwicklungsgeschichte der Andreaeaceen, in Schenk und Lürssen, Mittheilungen aus dem Gesammtgebiete der Botanik, i (1874).

have the ordinary arrangement, and there are leaves which show at first a two-sided apical cell, and then pass over into a condition of simple anticlinal and periclinal segmentation, as in A. petrophila; finally, in A. rupestris this latter arrangement is present from the first. Fig. 110 illustrates the arrangement of the cells in a young leaf of Andreaea rupestris. The earliest stages in the development I have not examined, and I find no account of them in the authors quoted, and it is possible that at first an obliquely inclined wall, which would be the first indication of the formation of a two-sided apical cell, appears, and then the cross-walls. I have noticed this arrangement in the primary leaves of Schistostega, which not infrequently consist of a cell-row like that which has been described above in the case of Ephemerum. At all events in the leaves of Andreaea rupestris we have a construction which resembles that of the leaf-like structures which appear also upon the protonema of Andreaea, and this construction appears to me to be more primitive, as it is in Buxbaumia, than that which occurs in other Musci. Diphyscium, which is nearly allied to Buxbaumia, shows in the formation of its leaves the same transition to the ordinary arrangement of the cells of Musci as is observed in the leaves, especially the broader ones, of Andreaea[1].

1. *THE CONFIGURATION OF THE SHOOT.*

a. RADIAL SHOOTS.

When we consider the configuration of the shoot of the moss-plant we designate as simplest Musci those which possess radial orthotropous shoots with only foliage-leaves. Different forms exhibit that *division of labour* to which reference in general terms has already been made[2], and especially in the appearance of shoots with limited growth. The limitation of growth in the lateral shoot is mainly the result of correlation, but it also occurs in chief shoots, and here I believe that as in the Hepaticae the conditioning cause is mainly the water-supply. So far as I know the cushion-like Musci which grow out radially have shoots of unlimited growth, and these die off below as they grow above. This is not the case in segregate forms. Climacium dendroides, for example, has, as its specific name indicates, a tree-like stem through which its characteristic habit is acquired, and it only forms twigs of limited growth at a certain height. But these shoots are capable of further development if they come to lie upon the moist soil. The plagiotropous lateral shoots of the radial shoot of Mnium undulatum show similar features; if they reach the soil they root and grow as creeping shoots, and only subsequently when they acquire sufficient strength do they rise as orthotropous shoots and produce sexual organs[3]. In support of the

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[1] An oscillation between the two types of cell-arrangement, that is to say with or without a two-sided apical cell, occurs also in the 'paraphyses' ending in cell-surfaces that are found in the antheridial groups of different species of Polytrichum. Paraphyllia also exhibit like differences, as will be shown on a subsequent page (see p. 146).

[2] See Part I, p. 21.

[3] See the description in Bryologia europaea.

view expressed above may be cited the fact that the creeping chief axes of Thuidium and of many other Hypneae and other Musci have unlimited growth.

In radial Musci which attain large dimensions we find frequently in the leaves of the epigeous shoots the same division of labour that is observed in many Spermophyta, namely, the shoot is beset in its lower part with scale-leaves, which are protective organs merely and are not organs of assimilation or function as such only in a slight degree. The shoot of a bamboo, for example Dendrocalamus giganteus, which reaches giant-dimensions, produces at first scale-leaves alone, and these protect the bud of the stem; only when the shoot comes above the ground are assimilating lateral shoots produced. If we compare with such a shoot the representation in Fig. 111 of Bryum giganteum we shall see the same features. The shoot of Pterobryella longifrons is clothed at first with scale-leaves which contain no chlorophyll and glisten like silver. They are composed, with the exception of the basal portion, of elongated sclerenchyma-like fibre-cells with membranes so thickened that the lumen almost disappears (Fig. 112, 3), a remarkable deviation from the soft structure which is characteristic of most leaves of Musci. These scale-leaves fall off at a later period and the shoot produces in its upper part branches with foliage-leaves which are plagiotropous and distichously branched, and the whole resembles closely the leaf of a fern with a thick stalk. The production of scale-leaves in this plant is connected with the struggle in which it engages with its fellows to raise itself

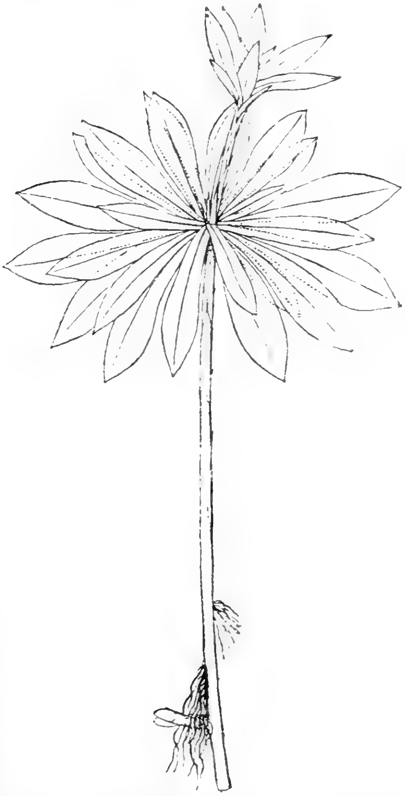

FIG. 111. Bryum giganteum. Showing the habit of the plant. Natural size.

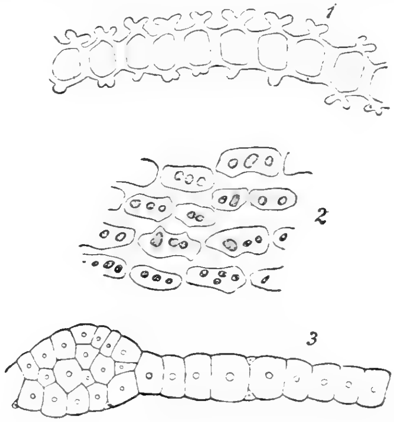

FIG. 112. 1 and 2, Hedwigia ciliata. 1, portion of a leaf in transverse section. 2, portion of a leaf-surface, the protuberances shaded. 3, Pterobryella longifrons. Bud-scale in transverse section. Magnified.

above the substratum. In other cases scale-leaves are produced upon shoots creeping in the substratum, and then it is the want of light which conditions their appearance, and they are arrested states of the primordia of foliage-leaves, as I have previously pointed out is the case in Mnium undulatum[1]. These scale-leaves here remain stationary at a somewhat late period of development after the inception of the midrib, and their cells remain small and like one another, whilst a division of labour subsequently appears in the foliage-leaf between the marginal cells and those further in; but in Pterobryella, as we have seen, there is a more far-reaching transformation which is dependent upon the fact that the scale-leaves appear in it upon *epigeous* shoots. True leafless shoots of Musci are unknown to me, although they have been described in systematic works as occurring, for example in the stolons of Climacium dendroides, but these have scale-leaves which act as a protection to the bud of the stem. There would be no object in discussing the transitions between scale-leaves and foliage-leaves. The genetic relationship between the two naturally leads to the occurrence of transition-forms.

All the moss-shoots which bear scale-leaves produce foliage-leaves if they reach the light. We know of no forms which persist, as in many Hepaticae, as rhizome-shoots. Fontinalis, the water-moss, preferring to live in rapidly flowing water, shows some interesting features. The base of the shoot is fastened by numerous rhizoids to the substratum. Its upper part floats. The leaves on the lower part are rudimentary. If, however, Fontinalis be cultivated in still water in the laboratory there are formed, especially in spring, many curved young shoots which are clad with small tufts of rhizoids and rudimentary leaves—an indication that adaptation to habitat has here become hereditary.

Leaves on radial shoots. The configuration of the leaves of the radial stems of Musci is wonderfully uniform, and their adaptation to external conditions is expressed more in the anatomical structure than in the external form. Upon this more will be said hereafter[2]. Here it may be pointed out that all the leaves of Musci are simple and unbranched, and are originally simple cell-plates. In the smallest Musci they remain in this condition, for example, in Ephemerum, Nanomitrium, and elsewhere. But in others the primary leaves only are so simple, the later ones have a midrib which is a *subsequently* formed thickening of the middle portion of the leaf produced by cell-divisions parallel to the surface of the original one-layered primordium. The leaves of some Musci have more than one nerve. The highest degree of differentiation is that possessed, for example, by the leaves of Polytrichum, in which one can recognize a lamina and a vagina.

Notwithstanding their simple relationships of configuration the leaves of

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[1] Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880), p. 787.

[2] See p. 143.

different forms frequently show differences, but we do not know in most cases whether these are connected with the conditions of life or not. One is inclined, for example, to consider that the form of the keel-shaped leaves of Fontinalis antipyretica, which grows in rapidly flowing water, has some connexion with facilitating the gliding off of the water. But it is unknown whether, and in what manner, the direction to *one* side of the apices of the curved sickle-like leaves of many species is connected with the life-conditions. Wichura[1] has pointed out that in Hypnum uncinatum, H. aduncum, H. revolvens, H. cupressiforme, and others, the leaf-apices are turned towards the shaded side, whilst in the Dicranaceae, for example D. scoparium and D. undulatum, they are turned towards the light, and therefore a kind of secondary dorsiventrality comes to pass here as lighted and shaded sides are differently constructed. One might believe that the retention of water-drops was favoured by this, but then we find the same appearances in aquatic Musci like Dichelyma falcatum and others. We must therefore regard the question of the utilitarian side of these configurations as one that is open, and it has not yet received sufficient attention[2]. There are some phenomena of adaptation in the configuration of the leaves which stand in relation to the uptake of water, and these will be noticed presently; here I wish to note the occurrence of '*hypsophylls*'[3].

Hypsophylls. These are present as the envelopes of sexual organs, and they diverge as do the perichaetial leaves of the Hepaticae, from the ordinary form of foliage-leaves, especially where the foliage-leaves exhibit definite adaptations to outer factors, because then these adaptations are absent or are reduced in the hypsophylls. Thus the leaves of the envelope about the antheridia of Fissidens bryoides want the characteristic wing of the foliage-leaf; in other species the wing is present in a reduced condition.

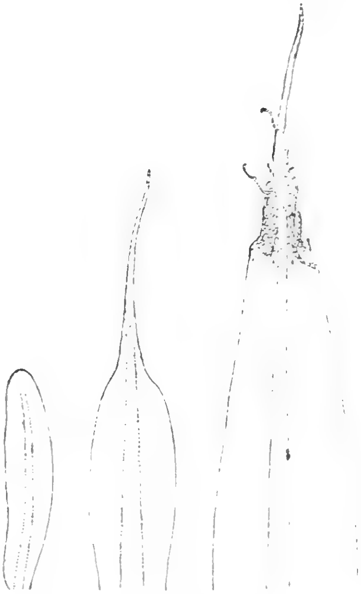

FIG. 113. Diphyscium foliosum. Leaf on the left a foliage-leaf. Two leaves to its right are from a female shoot; the middle one from lower down the shoot than the envelope-leaf on the right, and it forms a transition from the foliage-leaf to the envelope-leaf. Magnified 20.

In Polytrichum the leaves which envelop the groups of antheridia arrive at their condition in quite the same manner as the hypsophylls in

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[1] Wichura, Beiträge zur Physiologie der Laubmoose, in Pringsheim's Jahrbücher, ii (1860), p. 194.

[2] We may say the same of the analogous cases, for instance that of Mastigobryum, amongst the Hepaticae. Why should the leaves by their curvature (which in Mastigobryum is always towards the under side of the shoot) assume a kind of profile-position?

[3] See p. 389.

many Spermophyta. The sheath of the leaf enlarges, whilst the lamina is only slightly developed, and thus it forms a large membranous expansion. The perichaetial leaves of Diphyscium are also markedly different from the vegetative ones. The vegetative ones (Fig. 113 to the left) are simple tongue-like: the leaves of the envelope around the archegonia are much larger and broader, and they end in a long bristle, such as we find in the vegetative leaves of many xerophilous Musci, and they have 'cilia' on the margin in the upper part (Fig. 113 to the right). These cilia are arrangements for the retention of water, which has the same function in fertilization here as in the Hepaticae. The bristles, as we shall see, are essentially protections against drought.

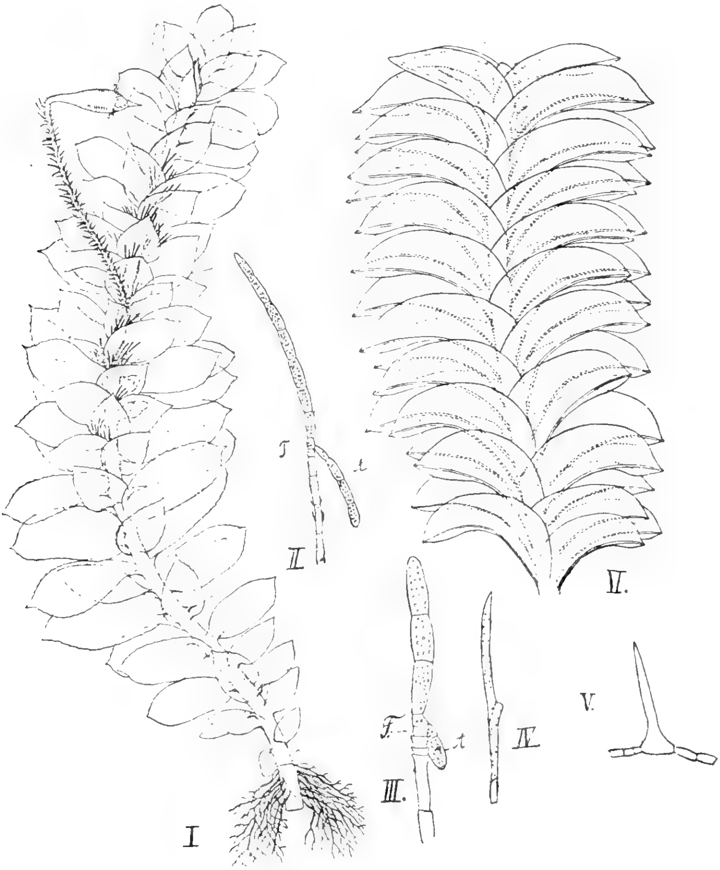

FIG. 114. *I–V*, Eriopus remotifolius. *I*, plant with fructification, showing habit. *II* and *III*, gemmae; *A*, outgrowth of the gemma; *T*, separation-cell. *IV*, 'hair' from the calyptra. *V*, 'hair' from the seta. *VI*, Drepanophyllum fulvum. Portion of shoot to show habit. *I* magnified about 4. *II* and *III* highly magnified. *VI*, magnified 12.

Musci possess also bilateral and dorsiventral shoots besides radial ones, and, as I have already shown[1]:—

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[1] See Part I, pp. 66 and 100.

1. The bilateral or dorsiventral shoots proceed from radial ones.
2. The bilateral or dorsiventral shoots are an adaptation, in varying degree, to external relationships, especially to feeble illumination.

It will suffice if I here point out a few peculiarities.

b. Bilateral Shoots.

These are flattened upon two opposite sides, and frequently the position of the leaves has passed over from a tetrastichous into an apparently or really distichous arrangement. In other cases, however, the tetrastichous arrangement is maintained, and only the *lie* of the leaves is altered. Anisophylly is then not infrequently observed, sometimes asymmetry of the leaves. This disposition of parts which in descriptive bryological works is commonly referred to as a distichous arrangement of the leaves, gives to the shoots a flat construction which, in the most cases, has to do with the utilization of feeble unilateral illumination, and it must not be forgotten that a sparingly-leaved shoot can much more easily retain water if its leaves take up a pseudo-distichous lie, than if they stand pointing in all directions upon a radial shoot. The following are some examples:—

Eriopus remotifolius, C. Müll. (Fig. 114, *I–V*). I collected this moss in Java[1]. It is of interest because the leaves which stand upon the upper side of the stem, and those which stand upon the under side of the stem are often only half as large as the lateral ones, and there are at the same time differences between the upper leaves and the under leaves. This case in some measure approaches that of Lycopodium complanatum[2], although the phyllotaxy is different.

Drepanophyllum (Fig. 114, *VI*). The sickle-like apparently distichous asymmetric leaves of this genus are remarkable. We have before now seen how oblique lie and asymmetric conformation go together in the moss-leaves, and in this genus we have a beautiful example of it. The under half of the leaf, that which is bent towards the base, is very much narrower than the other; the insertion of the leaf remains moreover, so far as I have investigated it, transverse, but the lamina soon bends into an oblique lie. The biological significance of this asymmetry is probably the same as that which was suggested in the case of Begonia[3], and it may have come about in the same way, but at present this is only hypothesis.

Schistostega[4]. It is only necessary to recall here that the bilateral construction in this genus is the result of displacement of the leaves out of the radial position and is found only in the vegetative shoots.

Fissidens. The formation of the leaves in the Fissidentaceae is remark-

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[1] Whether this is really Müller's species or a nearly allied one is not determined. If it be Müller's species then the figure of the habit given by Dozy and Molkenboer, Bryologia javanica, ed. by Bosch et Sande Lacoste, Lugduni Batavorum, 1855–70, tab. clviii, is hardly successful.

[2] See Part I, p. 103.

[3] See Part I, p. 119.

[4] See Part I, pp. 66 and 235, and Figs. 26 and 116.

able and formerly was incorrectly described. The primary leaves resemble in configuration those of other Musci. This is true of the subsequent leaves also in the first developmental stages; but soon there is formed upon the under side of the leaf-vein a wing-like outgrowth which afterwards becomes so large that it looks as if it were the leaf itself, whilst the true leaf appears as a sheathing portion of the wing. By this means the assimilating surface is markedly increased, and the leaf of Fissidens offers a remarkable parallel with that of Iris. The apical cell of the stem of Fissidens is two-sided, as has been stated above[1]. The young shoots, which bore through the soil, have, as Hofmeister first showed, a three-sided apical cell, and only at a later period do they acquire a two-sided one. The branches too, which arise in a distichous manner upon the stem, have at first a three-sided apical cell, and the position of their first leaves corresponds therewith, but the apical cell is gradually transformed into a two-sided one, and the leaves then become strongly distichous. The branches of Fissidens bryoides alone have from the first a two-sided apical cell. This transition from one kind of apical cell to another which leads to a different phyllotaxy cannot be hindered by absence of light, at least I could not hinder it in this way, although we may assume that it was primarily caused by the action of light.

c. DORSIVENTRAL SHOOTS.

Dorsiventrality, as has been shown, finds its expression especially in anisophylly, and of this there are many degrees[2]. Hypnum (Hylocomium) splendens, species of Thuidium, and others are not anisophyllous, but the direction of their terminal bud and the cross-section of the shoot (see Part I, Fig. 113) nevertheless show a dorsiventral construction. How Hypnum splendens, living in a shady wood, raises itself always above the detritus of the wood by its peculiar tiered growth, and contributes to the layering of humus, has been already shown[3].

2. *APPENDAGES.*

Most of the Musci possess, in addition to the leaves, structures in the form of cell-rows without chlorophyll, which, on account of their *external* similarity to many hairs of higher plants, have been termed 'hairs'; probably they are transformed protonema-branches. They are the homologues of the paraphyses, as will be shown below[4]. They stand usually in the axils of the leaves. The simplest forms of Musci, like Ephemerum, want them. They are also absent from the sterile shoots of Schistostega, whilst each of the envelope-leaves of the archegonia has one of them in its axil. The function of these 'hairs' is only known in Funaria hygrometrica and Diphyscium, in which I have shown that they secrete mucilage, and in Diphys-

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[1] See p. 131.

[2] See Part I, p. 100.

[3] See Part I, p. 69.

[4] See p. 151.

cium this takes place in a peculiar manner by the splitting of the cuticle of the hair-cells. These 'hairs' then conform in their function with the mucilage-papillae of the Hepaticae, and their mucilage serves for the protection of the young soft parts at the vegetative point. Whether this function is generally distributed requires investigation. Perhaps the 'hairs' produce a secretion in other cases, or they may take a share in the uptake of water; the latter function at any rate belongs to the paraphyllia[1] which will be described below, but these are readily distinguished both by their containing chlorophyll and by other characters from the 'hairs' we have under consideration.

III

ASEXUAL PROPAGATION IN MUSCI

The Musci have a much richer vegetative propagation than is found in the Hepaticae. Almost every living cell of a moss can grow out into *protonema*, and many produce *gemmae* of the most different kinds. I do not intend to describe these here. I shall only give a glance at the best-known ones along with a note of the special investigations of Correns[2]. We shall only consider how far the asexual propagation has led to a change in the *formation of organs*, and this is not clear in all the forms of gemmae.

We have to distinguish two things:—

(*a*) The application of parts of the leafy shoot to the formation of gemmae.

(*b*) The application of protonematous outgrowths to the formation of gemmae.

As propagative organs we have:—

1. **Entire shoots** provided with reserve-material which are thrown off,—either terminal portions of chief shoots and lateral shoots, as in Campylopus flexuosus, C. Schimperi, and others, or whole lateral shoots, as in Bryum argenteum. These shoots form rhizoids and grow subsequently. According to Correns, in some species of Webera the leaves of the gemma-shoot are reduced, and in Webera prolifera, for example, we find that the apical cell of the shoot no longer continues its normal growth, but instead there is the formation of protonema.

2. **Leaves.** The remarkable *gemma-leaves* of Aulacomnium palustre have been long known; they are formed upon special greatly elongated

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[1] See p. 146.

[2] Correns, Vorläufige Übersicht über die Vermehrungsweise der Laubmoose durch Brutorgane, in Berichte der deutschen botanischen Gesellschaft, xv (1897), p. 374; Id. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stocklinge, Jena, 1899.

shoots, are filled with reserve-material[1], and in germination they produce a protonema[2].

3. **Modified protonemata**, proceeding partly out of the leaves, partly out of the shoot-axes. These do not essentially differ from protonema in the manner of their multiplication. Sometimes they separate as filaments, sometimes as cell-masses. I may mention only one example. The Javanese moss Eriopus, represented in Fig. 114, has in the axils of its leaves numerous tufted, branched, brown protonema-threads, which form peculiar two-armed gemmae at their extremities (Fig. 114, *II*), and these gemmae are also distinguished from the brown threads by their uncoloured walls and probably also by their containing chlorophyll[3]. The gemma forms the end of a stem-borne protonema-thread. At the point of attachment of the gemma to the protonema-thread a short separation-cell is cut off, and as this cell dies a split, which is not produced merely mechanically, develops about the middle of its cell-wall. But before this occurs a branch which grows downwards issues out of the basal cell of the gemma. When the gemma has fallen off, the cell below the separation-cell grows out through the remains of the separation-cell into a new gemma, and this may be repeated often, with the result that there is visible on the outside of the cells the remains of cell-membranes like a ruffle (Fig. 114, *III*), recalling very much the features produced in the filament of Oedogonium in the process of interpolation of cell-membrane.

I may mention, as illustration of the formation of protonemata which have developed into cell-masses and which arise by suppression of the formation of leaves at the end of a shoot, the gemmae of Aulacomnium androgynum which stand upon leafless elongated portions of shoot comparable with the pseudopodia of Sphagnum and Andreaea, and those also of Tetraphis pellucida. In Aulacomnium androgynum they are not leaves and they show no transitions to leaves[4], as they do in the case of Aulacomnium palustre, yet they conform in their position with leaves. In Tetraphis the gemmae stand within a flat, cup-like envelope formed by widened leaves at the end of special shoots. These have a certain resemblance to the cup-like groups of antheridia of many Musci, and this led Schimper[5] to

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[1] The midrib has developed at the expense of the lamina as in the leaves of Leucobryum.

[2] For other cases see Correns, Vorläufige Übersicht über die Vermehrungsweise der Laubmoose durch Brutorgane, in Berichte der deutschen botanischen Gesellschaft, xv (1897), p. 374; Id. Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stocklinge, Jena, 1899.

[3] I examined material preserved in alcohol.

[4] Grevillius, Über den morphologischen Wert der Brutorgane bei Aulacomnium androgynum (L.), Schwaegr., in Berichte der deutschen botanischen Gesellschaft, xvi (1898), asserts that these exist, and would therefore regard the gemmae as transformed foliage-leaves. The arrangement of the gemmae is against this assumption. The 'transition-structure' might arise by the development of gemmae beginning at the apex of the leaves which are arrested in development, and thence invading the stem. This is what happens in many Hepaticae (see p. 49), only in them many gemmae arise upon the leaves not one only as here.

[5] Schimper, Bryologia europaea, Stuttgartiæ, vol. iii.

conjecture, although not upon solid grounds, that in these cups of gemmae we have a 'virescence of the antheridial groups.' The assumption of Correns, that the gemmae of Tetraphis are modified 'paraphyses,' is also untenable. When we speak of the sexual organs we shall learn about paraphyses which only occur with them. Gemmae, quite like those upon the shoots, may also occur upon the protonema of Tetraphis, as Correns has himself shown. How can paraphyses occur then upon the protonema? It is a 'contradictio in adiecto.' The facts clearly show that we have only to do with a special kind of formation of protonema in some measure like that which is found in paraphyllia[1].

IV

VEGETATIVE ADAPTATION IN THE MUSCI

I. RELATIONSHIP TO WATER.

It has been shown that in the Hepaticae the relationships to water exercise a dominant influence upon their configuration. In the Musci, although we have not such multifarious adaptations for the retention of water as are found in the Hepaticae, yet the relation to water affects their configuration in a profound degree. More than forty years ago Carl Schimper recognized the essentials of this relationship, although as a matter of fact his words evince a restricted appreciation of the uptake of water in the Musci[2]. That indeed a movement of water and of dissolved salts takes place in the stem of a moss-plant is suggested by the immense development of the rhizoid-system of many Musci, and we may surely conclude therefrom that this system is not simply an anchoring apparatus, but that its essen-

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[1] For an account of paraphyllia see p. 146.

[2] Carl Schimper, one of the founders of the Schimper-Braun hypothesis of phyllotaxy, must not be taken in this connexion for Wilhelm P. Schimper, the bryologist. In his 'Mooslob,' published in 1857, he says on p. 13:—

> Empfindlich für das Feuchte,
> Wie für des Ortes Leuchte,
> Was Wurz' und Stengel leisten,
> Gleich siehst du bei den meisten;
> Was die geheim auch mischen,
> Sie können nicht erfrischen
> Die kargen Wasserfasser —
> Moos welkt im Glase Wasser!
> Die Blätter sind die Leiter,
> Und aussen geht es weiter!

This, if wanting as verse, indicates good observation.

tial function is rather the uptake of dissolved salts from the soil. Haberlandt and others have also shown that there is in many Musci an internal movement of water. In the stalk of the sporogonium the water undoubtedly moves also, and its evaporation takes place from the assimilating tissue of the sporogonium. The outer walls of the sporogonium are cuticularized, and take in usually no water [1]; the water which is evaporated all comes from the leafy stem, from which it is drawn through the foot of the sporogonium. But in the leafy stem there is evidently no transpiration-stream [2] which could cover the loss of water from the leaves in somewhat dry air—as Schimper says 'moss wilts in a glass of water.' The leaves have, so far as they have been examined, no cuticularized walls; they rapidly flag and rapidly take up water again from outside, and the swelling of their cell-membranes evidently plays in this a different rôle from that which it does in the higher plants; even a dead moss-leaf may thereby immediately be made 'turgescent' again. The turgescence has, in my opinion, no importance in the living moss-plant also in relation to the imbibition of water through the membrane; the whole construction is quite different from that in the higher plants. With this is connected in the Musci as in the Hepaticae the fact that many xerophilous forms, for instance Andreaea, have in their leaves very strongly thickened membranes which can hold relatively much water.

The 'external' conduction [3] which is spoken of by Schimper is capillary. It is brought about partly by the close aggregation of the leaves and lateral shoots, partly by the weft of rhizoids, or by the paraphyllia which will be mentioned below. In Sphagnum there are entirely different devices for this purpose. Water-storage in the shoots of Musci, apart from that in their cell-membranes, is unknown, but there are contrivances for the retention of water and for the protection of the young parts especially against too great heating and consequent drying. Amongst the xerophilous forms there are moreover many which are well able to withstand periodic droughts, and I have not been able to keep alive Andreaea in a continuously

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[1] The stalk of the sporogonium in many Javanese Musci, for instance Eriopus, is beset with hairs which probably take up water (see Fig. 114, *IV* and *V*).

[2] See Oltmanns, Über die Wasserbewegung in den Moospflanzen und ihren Einfluss auf die Wasserbewegung im Boden, in Cohn's Beiträge, iv (1884); Haberlandt, Beiträge zur Anatomie und Physiologie der Laubmoose, in Pringsheim's Jahrbücher, xvii (1886); Vaizey, On the absorption of water and its relation to the constitution of the cell-wall in Mosses, in Annals of Botany, i (1887). The anatomical relationships which cannot be dealt with here are fully discussed in the works cited.

[3] Hedwig, Descriptio et adumbratio microscopico-analytica muscorum frondosorum, Lipsiae 1787, p. 109, describes this in the case of Hedwigia ciliata. He says 'Papillis nimirum, seu potius vesiculis diaphanis omne eorum exterius planum dense obsitum est, quae spongiae in modum, avide adeo attrahunt humiditatem, ut, si plantulam penitus siccam pollice et indice basi sua surrectam teneas, et minimam aquae guttulam ibi immittas, haec illico attracta, verticaliter adscendat de folio in folium, unde amoenissimo spectaculo sensim paulatimque unum post alterum ad cacumina usque erigatur, expandatur reflectaturque.' The 'vesicles' are really the solid thickenings of the membrane.

moist state; probably it is, like Metzgeria, adapted to conditions of periodic drought. Some of the chief adaptations will be now mentioned:—

1. *ARRANGEMENTS FOR THE RETENTION OF WATER.*

A. IN THE LEAF.

(*a*) In the Form of the Leaf.

There is wanting in the Musci the wealth of adaptation in the form of the leaf in relation to the retention of water that is so manifest in the Hepaticae. The leaves of the Musci are indeed often boat-shaped [1], and many are widened at the base like a spoon. In Phyllogonium speciosum, a beautiful moss hanging from the branches of trees in Venezuela, the edges of distichous leaves overlap at the point of insertion, so that a tube surrounding the stem is formed. In Phyllogonium fulgens, as in many Neckeraceae, there are at the basal portion of the leaf outgrowths of the leaves which recall in a measure the auricles of the Hepaticae, but only those of the most simple form. Further, the leaf-base in the Musci is often otherwise specially arranged for the uptake of water, as we shall see presently [2], but constructions which could be placed alongside of the complex auricles of the Hepaticae are unknown.

(*b*) In the Construction of the Leaf.

1. **By outgrowths of the leaf-surface:—**

(a) Mammillae. The simplest case is that where the cell-membrane protrudes outwards [3] and the leaf-surface becomes provided with *mammillae*, as in species of Timmia, Bartramia ityphylla, and others. This construction recalls that of Aneura hymenophylloides amongst the Hepaticae.

(b) Papillae. The formation of papillae, which in the matured condition appear as centrifugal thickenings of the cell-wall, has probably been derived from that of mammillae. In Hedwigia ciliata (Fig. 112, 1 and 2) there appears, as has been already mentioned [4], an extraordinarily effective capillary apparatus for water. In other Musci growing in sunny dry places, such as Encalypta, Barbula, Racomitrium, Grimmia, and Weissia, similar arrangements are found. They never occur, however, in hygrophilous forms. As many Musci which are commonly xerophilous become hygrophilous in moist conditions, the point should be investigated whether these

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[1] The undulations of the surface of the leaves of species of Neckera are also a means for the retention of water.

[2] See pp. 145, 147.

[3] See Lorch, Beiträge zur Anatomie und Biologie der Laubmoose, in Flora, lxxviii (1894).

[4] See p. 142, footnote 3.

papillae are formed or not in such hygrophilous states. The analogy of many Polytrichaceae, which will be mentioned below, makes it probable that these papillae would entirely disappear in cultivation under moist conditions as well as in the absence of light.

(c) LAMELLAE. More common than mammillae or papillae are outgrowths of the leaf-surface in the form of cell-rows or cell-plates containing chlorophyll. Formerly these were considered as merely increments to the apparatus for assimilation, but, as I have elsewhere shown[1], this is incorrect. Assimilation can only go on in the presence of water. The cell-rows or lamellae stand so close together that they hold water between them. A comparison of the relationships of the forms to the stations in which they grow leads also to the same result.

Polytrichaceae. We find the most beautifully developed lamellae upon the broad nerves of the species of Polytrichum which grow in exposed stations, but in the nearly allied Catharinea undulata which grows in moister and more shaded stations, the outgrowths are smaller and less numerous, mostly four to six. The surface of the leaf itself is in Catharinea still rich in chlorophyll, and its margins roll inwards over the lamellae in dry conditions; in Polytrichum the surface of the leaf is far behind its massively developed lamellae in importance as an assimilation-organ. It has recently been affirmed that the lamellae disappear under cultivation in moisture. This is not correct, they are reduced at the most in Catharinea, where they are without doubt the smallest. If Polytrichum be cultivated in water the old leaves die, becoming black, the new ones have lower lamellae, adapted to water-life.

Barbula. In some species of Barbula, for instance B. aloides, B. ambigua, and B. membranaefolia, there are close-set branched cell-rows, the terminal cell in each of which has often a peculiarly thickened membrane which is evidently protective. The one-layered leaf-surface is concave, bending over the portion provided with outgrowths, and thus an effective sponge-like apparatus is provided.

Pottia. Species of Pottia also there are which have lamellae, for example P. curvifolia, P. barbuloides.

Here then we have an adaptive character which has arisen independently in three cycles of affinity of the Musci—the Polytrichaceae, the Barbulaceae, and the Pottiaceae.

Campylopus polytrichoides. Campylopus polytrichoides also has lamellae-like outgrowths upon the *under side* of its leaves, they consist of somewhat thick-walled cells; their function requires further investigation. It is probable that they also serve for holding water.

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[1] Goebel, Archegoniatenstudien: V. Die Blattbildung der Lebermoose und ihre biologische Bedeutung, in Flora, lxxvii (1893), p. 430.

2. **By Empty Cells with Perforated Walls**:—

This arrangement is found in many different cycles of affinity, and in plants which grow in very different stations, both wet and dry.

Sphagnum. The species of Sphagnum are well-known examples of plants from a wet station. I do not require to describe the structure of the leaf and the stem, but only to recall that, as has already been shown [1], the meaning of the whole mechanism has not been recognized hitherto. It is most probable that its explanation lies in the fact that Sphagna grow in places where the water only contains a small amount of some of the mineral substances necessary for their nourishment, so that a profuse water-evaporation is necessary.

Leucobryaceae. The cushions of the Leucobryaceae are found in dry woods, not in wet marshy places. In them we find a many-layered leaf in which the chlorenchyma takes up only a small portion of the space as compared with that occupied by tissue containing no chlorophyll [2]. The conspicuous feature in the leaf of the Leucobryaceae is the presence of a strongly developed midrib with a peculiar construction. Its special characters stand out clearly when it is compared with the leaf of Dicranum albidum. The empty cells communicate with one another by numerous holes. On the outer walls there are relatively few pores, but they are found specially at the basal part of the leaf, whence the water can easily pass by capillarity into the upper part of the leaf. In the case of Leucobryaceae the water must not (to speak teleologically), as in Sphagnum, evaporate rapidly, but be retained for a long time for the chlorenchyma. The two apparently similar kinds of leaf-structure are thus specially adapted to different external conditions.

Dicranum albidum. The method of uptake of water in Dicranum albidum requires further experimental investigation. The plant shows a transition in the structure of its leaves from the ordinary leaf of the Dicranaceae to that of Leucobryum.

Pottiaceae. Perforated cells are also found in Calymperes, Syrrhopodon, and Encalypta, which are genera of the Pottiaceae, but in them always in one layer and usually only in the lower part of the leaf; they are also found upon all or nearly all of the outer walls and lateral walls.

Syrrhopodon revolutus. The extent to which the transformation of the function of the leaf tissue to that of absorbing water can go under suppression of the work of assimilation is shown by the case of Syrrhopodon revolutus, Dz. and Mb., which I investigated (see Fig. 115). The chlorophyll-cells, whose area is indicated by shading (Fig. 115, *I*), take but a small share in the structure of the leaf which is made up mainly of empty cells whose walls,

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[1] See Part I, p. 279.

[2] For the details of the structure and development I must refer to Lorch, Beiträge zur Anatomie und Biologie der Laubmoose, in Flora, lxviii (1894).

both the outer and the lateral ones, have pores. A transverse section through the lower part of the leaf (Fig. 115, *II*) shows but two kinds of tissue—the empty water-absorbing cells and the mechanical tissue of the midrib and margins which form the framework on which the thin-walled empty cells are stretched and which are necessary to them, for in themselves they have not sufficient firmness. The chlorophyllous cells possess moreover papillae, so that a most complete mechanism for the retention of water is provided in the plant. Then besides the above-mentioned anatomical features the leaf is also not flat but is strongly concave, and the stems grow thickly crowded together in tufts. Altogether the construction of a sponge in this moss is as good as is that in Sphagnum or one of the Leucobryaceae.

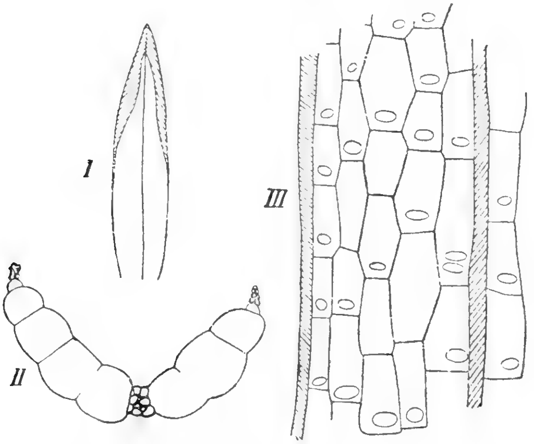

FIG. 115. Syrrhopodon revolutus. *I*, leaf. The position of the chlorenchyma is shaded. *II*, lower portion of a leaf in transverse section. *III*, part of the lower portion of a leaf in surface view. The mechanical tissue is indicated by shading, between the bands of this are the empty cells with pores. *I*, slightly magnified. *II* and *III*, more highly magnified than *I*.

B. IN THE STEM.

(*a*) PARAPHYLLIA.

The stems also of many Musci possess chlorophyllous outgrowths which may retain water and conduct it by capillarity. These are the so-called *paraphyllia*, which are found in some species of Thuidium and Hypnum. We have seen analogous structures in some of the Hepaticae. In the Musci they are remarkable in that they resemble somewhat leaves in their construction, and like leaves appear as cell-surfaces (Fig. 116). We have in them, however, in my view, structures which have sprung from *cell-threads* and which also have not the characteristic arrangement of leaves.

Hypnum splendens. In Hypnum splendens the paraphyllia cover with a thick weft the surface of the strong shoots. They are narrower or broader cell-surfaces and through their branching their long axes spread out in different directions. The history of the development of the paraphyllia being unknown, I examined it in Hypnum splendens, and found that they are laid down very early in the stem-bud. Their number increases in proportion as the surface of the segments increases, and new paraphyllia are laid down between the old ones. It is interesting that the arrangement of the cells in the paraphyllia resembles that of the leaves. There is a two-sided apical cell (Fig. 117, *I*, *II*), from whose segments, right and left, outgrowths proceed in rapid serial succession, and these repeat the cell-arrangement described; finally, the formation of the segment-walls ceases in the filiform end of the paraphyllium or its branches (Fig. 117, *III*, *IV*). The segment-walls are directed obliquely to the long axis of the thread in a characteristic fashion, reminding us of what occurs in the protonema. The paraphyllia are narrower and fewer on the lateral branches of higher order in Hypnum splendens.

Thuidium tamarascinum. In Thuidium tamarascinum, which I also investigated, the chief shoot alone has paraphyllia. These are usually only branched cell-rows (Fig. 117, *V*), provided with snag-like outgrowths like the papillae of the leaves, and such paraphyllia may take origin also out of the base of the *leaves*. Many of them are also developed as cell-surfaces whose origin differs, however, from that of the paraphyllia in Hypnum splendens. The origin of the cell-threads is not clear here, for there is no 'growth from an apical cell,' but simple anticlinal and periclinal chambering like that which is observed in the development of the leaves of Andreaea (see Fig. 110); the leaves of Thuidium have, however, the same disposition of cells as is found in the leaves of other Musci. The paraphyllia in Thuidium are therefore transitions to the protonema-threads of limited growth which spring from the stem-surface of other Musci. The protonema-threads, which arise upon the stem and bear the gemmae also aid in the uptake of water—those, for example, figured in Eriopus remotifolius (Fig. 114). In Drepanophyllum falcatum I found similar structures.

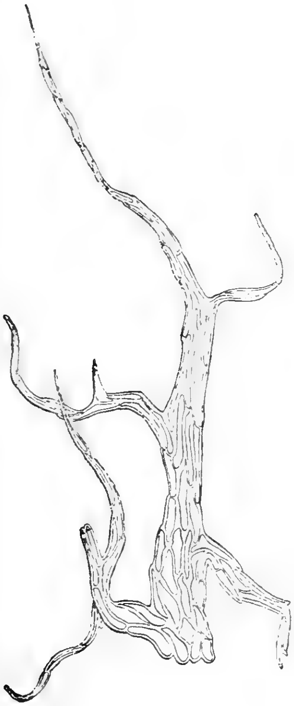

FIG. 116. Hypnum splendens. Paraphyllium. At the lower left side of the figure a recurved branch is shown. Magnified 210.

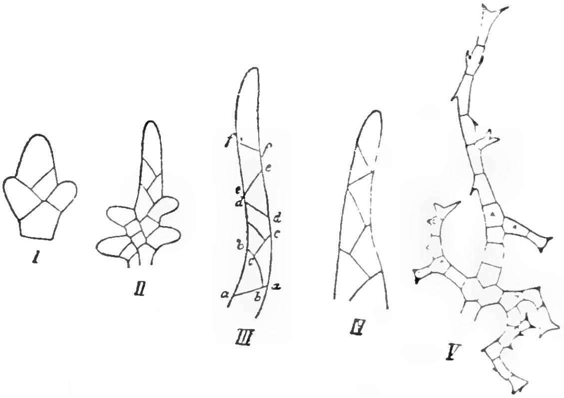

FIG. 117. Development of a paraphyllium. *I–IV*, Hypnum splendens. *V*, Thuidium tamarascinum. *I* and *II*, young paraphyllia. *III* and *IV*, apices of older paraphyllia not yet mature; the letters indicate successive segment-walls. *V*, mature paraphyllium.

Paraphyllia are then to be regarded as protonema-branches of limited growth which issue from the stem-surface, and which are partly developed into cell-surfaces and have in part attained to a growth and method of construction analogous with those of the leaves; their function is to take up water and at the same time to increase the surface for assimilation.

(*b*) OTHER ARRANGEMENTS FOR HOLDING OF WATER.

Special devices upon the axes of the shoots for the uptake or holding of water, apart from the paraphyllia, are known only in the Sphagna, but they possibly occur also elsewhere. Brizi [1] describes lens-like groups of cells with unthickened glistening walls on the surface of the shoot-axis in Cyathophorum pinnatum. When they are full-grown their content has disappeared. I think that these are cell-groups like those in other Musci indicating the place where protonema-filaments or lateral twigs take origin. It is possible, however, that these cells serve specially for the uptake of water. This can only be determined by experimental investigation.

2. *ARRANGEMENTS AGAINST DROUGHT.*

As I have already pointed out, xerophilous Musci experience long periods of drought without injury. Nevertheless, apart from the nature of the protoplasm, of which we have no knowledge, there are also in the Musci arrangements which are to be considered undoubtedly as protections against drought, partly also as protections against too great heat. This may perhaps be connected with the fact that, on the one hand, protection is required chiefly for parts that are not juvenile and enclosed in a bud, and on the other hand, it will not be a matter of equal importance whether the loss of water in drying follows slowly or quickly. A retardation of the loss of water will be the result of the movements which the leaves of many Musci experience in drying. Thus in Polytrichum the leaves lay themselves against the stem, others wind and twist themselves together, and in Leucobryaceae the same object is attained by the living cells becoming enveloped with a mantle of dead ones which contain air. We find the same thing in other cases where, however, the dead cells serve only as a protective mantle, and have nothing to do with the uptake of water.

Silver-glance. Bryum argenteum derives its name from the silver-glance of its shoots, and this is caused by the dying off of the cell-contents in the upper part of the leaf. These dead upper parts invest as with a mantle the bud of the stem and must check the outgo of water. It depends upon outside circumstances how far this process proceeds. If the plant be cultivated in shade and moisture the leaves remain green [2], but on dry places the silver-glance appears and the point of the leaf is drawn out into a hair.

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[1] Brizi, Sopra alcune particolarità istologiche e biologiche dei Cyathophorum, in Rendiconti della R. Accademia dei Lincei, ii (1893).

[2] Goebel, Über den Einfluss des Lichtes auf die Gestaltung der Kakteen und anderer Pflanzen, in Flora, lxxxii (1896), p. 10. Leucobryum glaucum, on the contrary, retains its tough leaf-structure even if cultivated under water.

Other similar cases are met with, for example Grimmia leucophaea, a moss growing upon sunny rocks, receives its name from the white apices of the leaves, and Hedwigia ciliata, mentioned above, forms in dry sunny places a variety leucophaea, whose leaves appear to be composed in the upper third of dead cells, as in Physcomitrium repens and others.

Hair-points. If we have in these cases to deal with a direct adaptation to external conditions, the same holds good for the *hair-points*, which are not uncommonly found in combination with them. Such diaphanous hair-like points are only seen in the inhabitants of dry stations. They are formed in the bud and their dense aggregation closes the end-bud to the outside, and their thickened cell-membranes sometimes act as water-reservoirs. Many of our Musci, like species of Racomitrium, Grimmia, Barbula, and others, which grow upon rocks and walls, show these diaphanous hair-like points, and it is characteristic that many of these Musci exhibit local forms when growing in moist localities or in water, which do *not* have diaphanous hair-like points upon the leaves. We see this, for example, in Racomitrium canescens with its form epilosum[1]. Musci which live in permanently moist conditions never produce these hair-points.

II. RELATIONSHIP TO LIGHT.

The relationships of the configuration of the Musci to light are manifold and have already been referred to. Let me only recall here that the dark colour of many Musci is evidently dependent on light, and the red colour of many species of Sphagnum is apparent on the plants exposed to the sun. These features can be homologated with what has been already said about the Hepaticae. The dense cushion-growth, which is characteristic of almost all high alpine Musci, enables the plant to maintain its heat better.

V

SEXUAL ORGANS OF MUSCI

1. *POSITION OF THE SEXUAL ORGANS.*

All the Musci are acrogynous. The archegonial-groups always form the end of the axis of a shoot, whether this be a main one, as in acrocarpous Musci, or a lateral one. The acrocarpous state is the more primitive condition[2]. Musci are also acrandrous in their primitive condition. The first antheridium proceeds from the apical cell: the following ones from the segment-cells. Only two exceptions to this are known, that of Sphagnum and that of Polytrichum.

Sphagnum. In Sphagnum the antheridium stands upon the anodic

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[1] See Limpricht, Die Laubmoose, in Rabenhorst, Kryptogamen-Flora von Deutschland, Ed. 2.

[2] See p. 129.

margin of the insertion of a leaf. Leitgeb shows that the antheridia take the position which otherwise the mother-cell of the lateral shoots would assume, and one might therefore suppose that the lateral twig passes over in the unicellular condition into the formation of antheridia, and it is noteworthy that the formation of leaves on the male twigs is often very small,—in Fontinalis, for example, we get minute reduced branches. Sphagnum, however, belongs to quite a different cycle of development from that of the Bryineae, and it appears questionable how far one can make the comparison, if there is one.

Polytrichaceae. The Polytrichaceae[1] have cup-like antheridial groups which are regularly transpierced by a vegetative shoot, that is to say, the apical cell of the chief axis remains, and later it elongates into a leafy shoot through the antheridial group. Within the group several antheridia stand clustered in transverse lines, there being two to three of them one above the other under a leaf. Mixed with the antheridia are the paraphyses. Hofmeister, and with him Leitgeb, has so interpreted this relationship, that 'every cluster of antheridia under a leaf represents a shortened lateral twig whose apex is developed into the first antheridium.' This explanation would bring the behaviour of Polytrichum into conformity with other Musci, and one might find an analogy with it in the species of Campylopus[2], in which many archegonial groups are united into 'heads' resembling the cup of Polytrichum in some measure. If I then give full weight to Hofmeister's interpretation I would point out that the *history of development* is yet wanting. Up till now no one has shown that originally in the place of a cluster of antheridia the apical cell of the twig is to be found which gives off segments. Also in the case of Mnium and other genera the developmental history of the antheridial groups is still unknown, and it is questionable whether all Musci must really be considered as *acrandrous*.

The monoecious Musci make no exception to the acrandry. In them the antheridia are found free in the axil of the stem-leaves, or of the perichaetial leaves. As Satter[3] has shown in the case of Phascum cuspidatum and Archidium, the foliage-shoot here ends with an antheridial group, and is then overtopped by one lateral female shoot or there may be two such shoots, and this may also take place in other Musci.

2. *DISTRIBUTION OF THE SEXUAL ORGANS.*

On this subject I shall say nothing more beyond this, that in dioecious

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[1] See Hofmeister, Über die Zellenfolge im Achsenscheitel der Laubmoose, in Botanische Zeitung, xxviii (1870), p. 465; Goebel, Über die Antheridienstände von Polytrichum, in Flora, lxv (1882), p. 323; Leitgeb, Die Antheridienstände der Laubmoose, ibid., p. 467.

[2] See figures in Dozy und Molkenboer, Bryologia javanica, ed. by Bosch et Sande Lacoste, Lugduni Batavorum, 1855–70; for example, Tab. lxviii.

[3] Satter, Zur Kenntniss der Antheridienstände einiger Laubmoose, in Berichte der deutschen botanischen Gesellschaft, ii (1884), p. 13.

Musci the male plants are frequently smaller and have a simpler organization than the female ones. A striking example of this is offered by Buxbaumia[1], whose extremely small male plant has only one leaf and no stem, whilst the female plant has a large number of leaves and a stem which is no doubt very small and has a simple construction. In Ephemerum also the male plants are smaller and have fewer leaves than the female (see Part I, Fig. 87), and in varying degree this is repeated in most dioecious Musci. Amongst the most striking examples are those *dwarf males* which are found along with larger male plants in Leucobryum and some species of Dicranum. Evidently in these Musci, as in the prothalli of the ferns, the male sexual organs can develop under external conditions that do not suffice for the formation of the female organs, and it is further clear that the female plant, which subsequently produces the embryo, must be better equipped than the male.

3. *THE ANTHERIDIAL GROUPS AND ARCHEGONIAL GROUPS*[2].

The sexual organs in Musci are protected on the one hand by the leaves which surround them, the *perichaetial* leaves, and on the other hand by the *paraphyses*.

Paraphyses. The paraphyses are cell-threads whose upper cells are frequently swollen into spheres, and contain chlorophyll. In Polytrichum the paraphyses end in small cell-surfaces[3]. With regard to their homology, there can be no doubt that they are nearly allied to hair-like structures which one meets with also on the vegetative shoot[4]. In many cases, as in Diphyscium, they cannot be distinguished from these; in other cases, as in Mnium and Polytrichum, I found all stages of transition between them. Their function has not been sufficiently dwelt upon. As I have elsewhere pointed out[5], they are in the first instance protective organs, especially against drought, and the spherical expansion of the cells that characterizes many paraphyses fits them better to cover the antheridia. Doubtless this is not their only function[6]. Excretion of mucilage by them is only known in Diphyscium. It is doubtful whether they also excrete water or slimy water such as Leitgeb has observed amongst the Hepaticae in Corsinia. The paraphyses can certainly retain water by capillarity, and this is specially the case in the disk-shaped or flat cup-like antheridial groups of Polytrichum, Mnium, and others, which are admirably suited by the disposition of their perichaetial leaves to retain water. If a drop of water be placed upon a dry

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[1] See also p. 127.

[2] These are not infrequently referred to as the 'flowers' of the Musci only on the ground of an external resemblance of the antheridial groups with the flowers of higher plants. Any other homology does not of course exist.

[3] See footnote on p. 132.

[4] See p. 138.

[5] Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882).

[6] See also Kienitz-Gerloff, Über die Bedeutung der Paraphysen, in Botanische Zeitung, xliv, (1886), p. 248.

antheridial group it is absorbed. The closely set paraphyses also furnish the ripe antheridia with an abutment by means of which the mucilage containing the spermatozoids is pressed out further from them.

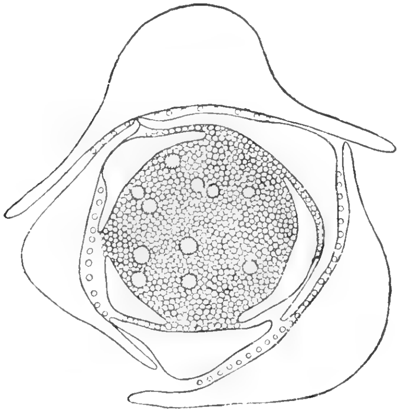

FIG. 118. Mnium undulatum. Immature archegonial group invested by its perichaetial leaves in transverse section. The archegonia and close-set paraphyses between them are seen. Magnified.

How the distribution of the spermatozoids is brought about, whether fortuitously through raindrops, or whether small animals are concerned in it, is as little known as it is in the case of the Hepaticae.

The archegonial groups are invested by one or more cycles of perichaetial leaves (Fig. 118), and have externally a bud-like aspect. We have already shown [1] that these perichaetial leaves are frequently distinguished from those of the stem by the possession of arrangements, such as *cilia* which can retain the water which is so necessary for fertilization.

VI

THE SPOROGONIUM OF MUSCI

1. *STRUCTURE AND DEVELOPMENT.*

The vegetative differentiation of the Musci is much more uniform than that of the Hepaticae, and the same may be said of the construction of their sporogonium. Different though the sporogonium of Splachnum rubrum, with its long stalk, its remarkable apophysis, and its peristome-apparatus for the distribution of the spores, appears to be from the unstalked sporogonium of Ephemerum which is filled at maturity with spores, and wants altogether arrangements for the distribution of the spores, it is nevertheless constructed upon the same 'plan'—only in one case we have an adaptation for the distribution of *many small spores,* whilst in the other only a *small number of large spores* is produced, and therefore a less size and simpler organization of the sporogonium is sufficient.

The calyptra. The archegonial venter does not behave in the same way in Musci as it does in the Hepaticae. Sphagnum is most like the Hepaticae in respect of it because its sporogonium remains enclosed almost until

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[1] See p. 135.

maturity within the archegonial venter which is only then ruptured by the stretching of the sporogonium. In the Phascaceae also we find primitive relationships. In Archidium the sporogonium, as in Sphagnum, comes out of the ruptured archegonial venter, and in Nanomitrium[1] (see Fig. 120, *II*) the capsular portion of the embryo presses together the cells of the archegonial venter until they are not recognizable; thereafter the capsule of Nanomitrium carries upon its apex the archegonial neck alone. The increase of the venter after fertilization provides a protective organ to the embryo, whose lower half bores more or less deeply into the moss-stem, and the ensheathing portion of the moss-stem—the *vaginula*—forms the continuation of the calyptra. In some Musci the venter forms at the same time a water-reservoir for the embryo. In Funaria hygrometrica and other Funariaceae, as well as in Encalypta vulgaris, the venter bulges out in its lower part and separates from the embryo, a behaviour that was quite unintelligible until I showed[2] that between the venter and the embryo there is fluid. The localities in which these Musci grow make it probable that the water thus excreted is made use of by the embryo at a later period, but an experimental research devised to settle this point gave no more result than it did in the analogous case of the exudation of water in the flower-buds of many Spermophyta.

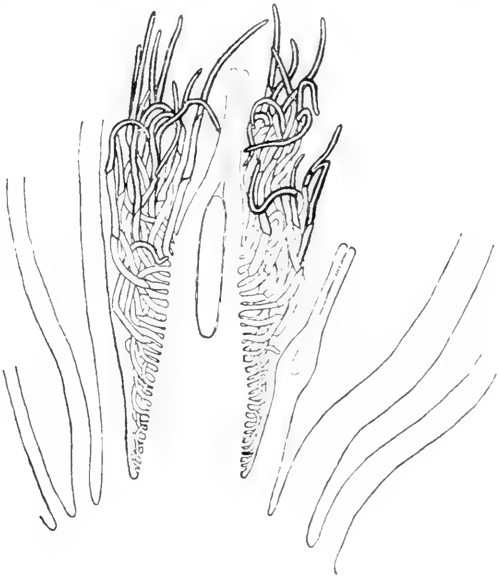

FIG. 119. Polytrichum. Shoot-apex in longitudinal section. Leaves are seen on the outside. A sterile archegonium on its stalk is on the right. At the summit one fertile archegonium enclosing an embryo. The embryo has grown down into the stalk of the archegonium, which stalk increased greatly in size after fertilization took place; how greatly may be seen by comparison with the stalk of the sterile archegonium. Out of the archegonial venter which is forming the calyptra many cell-rows have developed in basipetal succession. These are the 'hairs' of the calyptra. The upper ones are thick-walled and are protective; the lower are thin-walled and absorb water. Magnified 65.

In most Musci the elongated spindle-like embryo issues out of the archegonial venter at an early period. It lifts off the calyptra at its base where frequently a line of separation is early marked, and carries it up as a cap which invests the end of the sporogonium until shortly before maturity (Fig. 124, *c*). In Musci which live in dry places, like Polytrichum, Ortho-

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[1] Goebel, Archegoniatenstudien: VII. Über die Sporenausstreuung bei den Laubmoosen, in Flora, lxxx (1895), p. 463.

[2] Goebel, op. cit., p. 474. I there refer to the statements of Hedwig, which have been entirely overlooked.

trichum, and others, the calyptra is strengthened by '*hairs*'[1] which are merely protonema-threads of limited growth which have grown out of it after fertilization. These 'hairs' in Polytrichum are branched cell-rows which are closely interwoven with one another[2]. The cell-walls of the stronger threads are thick and cuticularized, clearly showing that they act as a protection against drought (Fig. 119).

The interpretation of these hair-like outgrowths upon the calyptra as protonema-threads may at first appear surprising, but a protonema out of which new plants arise is developed out of the calyptra in Conomitrium as I have before now shown[3]. In Polytrichum, Orthotrichum, and other Musci, these protonemata which are only formed after fertilization on the calyptra are very characteristic. They have oblique walls, for example in Polytrichum (Fig. 119). In this genus they evidently also serve for the absorption of water for the embryo so long as it is small and enclosed in the archegonial venter. The 'hairs' are developed in basipetal succession, and whilst the upper thick-walled ones retain air between them and protect from drought the archegonial venter enclosing the embryo, the lower, being still thin, absorb water, and it is through them that the store of water in the venter in Funaria and Encalypta is renewed.

In many Musci the embryo is surrounded by a *hyaline mucilage*[4] which, in my view, is a protection against the entrance of water, as the neck-portion of the archegonium is by no means always closed after fertilization.

Structure and development of the embryo. The cellular construction of the embryo in Sphagnum is like that in many Hepaticae. A transverse wall appears in the fertilized egg. The lower half then undergoes a few divisions; the upper divides into six to eight transverse disks, and each of these again into four quadrants whose further development will be mentioned below.

In all other Musci the method of division is different. After one or two transverse walls have appeared in the fertilized egg there arises in the upper cell, the one next the archegonial neck, an oblique wall to which a second wall, inclined to and opposite to it, follows. A two-sided apical cell is thus produced which gives rise to a number of segments (Fig. 120, *I*), but at a later period it sometimes becomes replaced by a network of cells, in the same manner as we find it in the apical cell of many prothalli of ferns, or of the strobilus of Equisetum.

In the cell-mass which constitutes the young embryo a relatively small number

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[1] The name Orthotrichum indicates that these 'hairs' are erect. They are narrow cell-surfaces of similar origin to the paraphyllia in Thuidium. Their cells remain alive for a long time, and may also share in the uptake of water.

[2] See Fritsch, Über einige mechanische Einrichtungen im anatomischen Bau von Polytrichum juniperinum, Willd., in Berichte der deutschen botanischen Gesellschaft, i (1883), p. 83, Plate 11.

[3] Goebel, Die Muscineen, in Schenk's Handbuch der Botanik, ii (1882).

[4] This is found in Andreaea and Sphagnum. See Waldner, Die Entwicklung der Sporogone von Andreaea und Sphagnum, Leipzig, 1887.

of the cells are devoted to the formation of spores. Most of them remain sterile and serve partly for the nutrition of the fertile ones, partly for the distribution of spores. We do not find amongst the Musci so primitive a sporogonium as that of Riccia amongst the Hepaticae, but, apart from Archidium, only such as correspond with the type represented by Anthoceros.

In the capsular portion of the moss-sporogonium there is differentiated at an early period a fertile cell-layer—the *archesporium*. Its evolution may be readily followed in transverse sections. If we make a transverse section through a young embryo only two cells can be seen at first, and these are separated by the segment-wall. Then follows a second wall at right angles to the first, and thus a *cylinder of quadrants* arises, but this is not formed in Archidium. In each quadrant there is formed an inner and an outer cell by the appearance of either an anticlinal or a periclinal wall (Fig. 122, 1), and thus we have four inner cells which may be called the *endothecium*, and a number of outer ones which may be called the *amphithecium* (Fig. 120, *II*, *III*). A primitive sporogonium would be one in which the amphithecium formed the wall of the sporogonium, whilst the endothecium gave rise to the spores. As a fact there are differences in the cell-contents between these layers in Nanomitrium, and the endothecium is much more rich in protoplasm. In Archidium the whole endothecium is an archesporium, but all its cells are not fertile; only a few, one to seven, become sporocytes; the others are nutritive cells [1] as in Riella. In the other Musci we always have an archesporium in the form of *one cell-layer* (Fig. 122, 2).

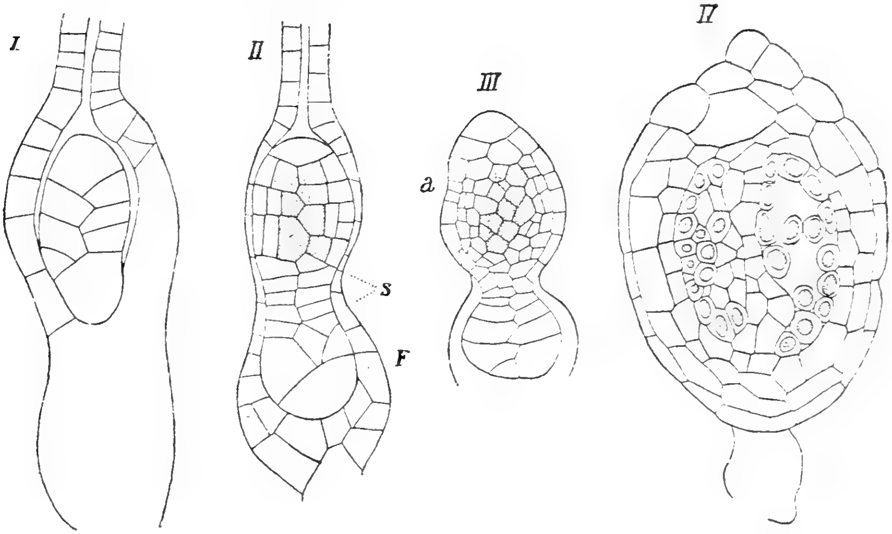

FIG. 120. Nanomitrium tenerum. Archegonium after fertilization and young sporogonium at different stages of development in longitudinal section. *I*, young embryo still within the archegonial venter. *II*, older embryo; the endothecium is shaded; the foot, *F*, has bored into the stalk of the archegonium: *S*, stalk of the sporogonium. *III*, still older embryo; *a*, amphithecium divided by periclinal walls. *IV*, sporogonium showing the sporocytes in great part separate around the columella. In most of the sporocytes the contents are indicated, in others they are absent, having fallen out in process of sectioning. All magnified; *I* the most highly magnified.

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[1] Nothing is known regarding the nature of their contents. Leitgeb speaks of them as 'clear as water,' so that possibly there is water-storage.

In Andreaea and Sphagnum this is dome-shaped (Fig. 121, *C*, *spo*); in the others it is pierced both above and below by sterile tissue, and thus has the form of a barrel open at both ends. The sterile tissue is very early laid down, and it is the *columella.* In Sphagnum the archesporium arises out of the amphithecium, the endothecium forms the columella alone. In all other Musci the endothecium divides by periclinal walls into an outer cell-layer, the archesporium, and a central sterile part, the columella. Both undergo further divisions; in the archesporium sporocytes are produced (Fig. 120, *IV*). The amphithecium undergoes cell-division by which it becomes many-layered even before the appearance of the archesporium. There is produced within the amphithecium an intercellular space which separates an outer many-layered capsular wall from two cell-layers lying against and enclosing the archesporium (Fig. 122, 3). These two cell-layers are termed the *outer spore-sac.* The outermost cell-layer of the columella abutting against the inside of the archesporium is the *inner spore-sac.* These cell-layers limiting the archesporium on the outer and the inner sides are distinguished by the richness of their cell-content, and it is clear that their function is to provide nourishment to

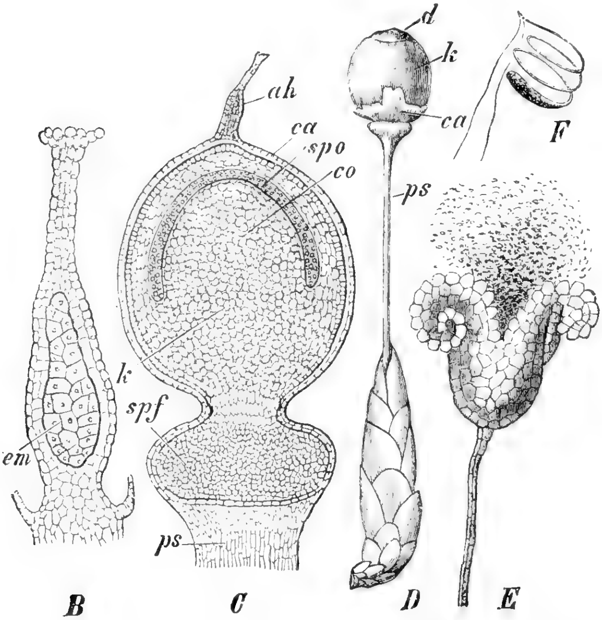

FIG. 121. *B*, *C*, *E*, *F*, Sphagnum acutifolium. *B*, archegonium with embryo, *em*, in longitudinal section; the representation of the arrangement of cells in the embryo is incorrect. *C*, young sporogonium in longitudinal section; *ah*, neck of archegonium; *ca*, calyptra; *k*, capsule; *spo*, spore-sac with spores; *co*, columella; *spf*, foot of the sporogonium; *ps*, pseudopodium. *E*, opened antheridium with escaping spermatozoids. *F*, single spermatozoid. *D*, Sphagnum squarrosum; mature sporogonium. *ps*, pseudopodium; *ca*, calyptra; *k*, capsule; *d*, operculum. All magnified. After W. P. Schimper. Lehrb.

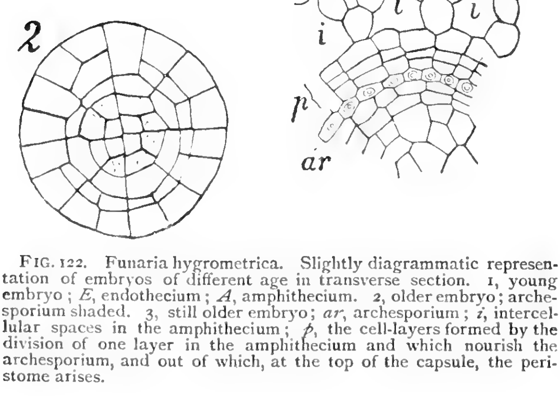

FIG. 122. Funaria hygrometrica. Slightly diagrammatic representation of embryos of different age in transverse section. 1, young embryo; *E*, endothecium; *A*, amphithecium. 2, older embryo; archesporium shaded. 3, still older embryo; *ar*, archesporium; *i*, intercellular spaces in the amphithecium; *p*, the cell-layers formed by the division of one layer in the amphithecium and which nourish the archesporium, and out of which, at the top of the capsule, the peristome arises.

the archesporium and its sporocytes. The construction of a copious sterile tissue —columella, wall-layer, and others—in the capsule, is evidently connected with the formation of the spores. In small capsules which form few spores there are few sterile cells. There is but a small demand for nutrition made by the fertile cells, and we find in ripe sporogonia, like those of Nanomitrium (Fig. 123) and Ephemerum, almost none left over. The cells of the columella serve only as nutritive cells, and before the spores are ripe they become used up. Ephemerum and Nanomitrium were regarded formerly, indeed up to quite recent times, as having no columella. Its existence in Ephemerum was pointed out long ago by J. N. C. Müller, and more recent investigations have shown me that it is present also in Nanomitrium, but in a very slightly developed condition. The more spores there are formed the larger is the columella. It serves as a *reservoir of water and of food-material* for the fertile cells, and it is commonly rich in starch.

In speaking further of the phenomena of life of the sporogonium, we must, first of all, notice its nutrition and then the manner in which the spores are scattered.

2. *RELATIONSHIPS OF NUTRITION OF THE SPOROGONIUM.*

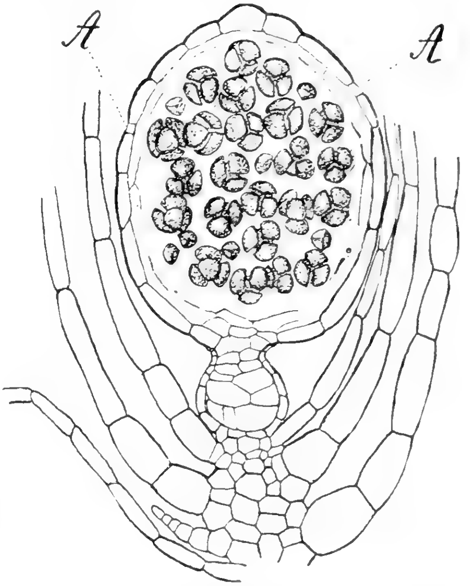

FIG. 123. Nanomitrium tenerum. Almost ripe sporogonium in transverse section; *A*, annulus. The spores are still in tetrads. The cells of the amphithecium have almost all disappeared excepting the wall-layer. The columella has entirely disappeared. Magnified 120.

The whole embryo of the moss is, in its earliest stages of development, a parasite upon the moss-plant. The lower, sometimes swollen, portion—the *foot*—serves as a haustorium, and is therefore in many cases, for example in Diphyscium [1] and Buxbaumia, provided with special tubular outgrowths which are chambered by cross-walls and may be so far branched that they are like rhizoids. With regard to the absorption of water the sporogonium in most Musci depends permanently upon the mother-plant [2], yet there are forms like Eriopus remotifolius which are able to take up water through the abundant hair-like outgrowths of the stalk of the sporogonium.

Rooting by rhizoids. Eriopus is also distinguished by this other

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[1] Goebel, Archegoniatenstudien: I. Die einfachste Form der Moose, in Flora, lxxvi (Ergänzungsband zum Jahrgang 1892), p. 103.

[2] There is frequently in the seta a ventral strand of thin-walled tissue wanting protoplasm, the *leptoxylem* of Vaizey, and it is the conducting channel; see Vaizey, The Transpiration of the Sporophore of the Musci, in Annals of Botany, i (1887), p. 73; id. On the Anatomy and Development of the Sporogonium of the Mosses, in Journal of the Linnean Society, Botany, xxiv (1888).

peculiarity, its sporogonium possesses rhizoids—the only example I know of a sporogonium rooting by rhizoids. The rhizoids are developed at the point where the sporogonium sits within the ruffle-like vaginula. They arise by the outgrowth of superficial cells and are cell-rows with partly oblique, partly transverse walls. They form a dense weft, and also in part grow downwards upon the outside of the vaginula. Rhizoids also force themselves into the vaginula from above, and they lay themselves upon the foot of the sporogonium, which is composed of large cells rich in cell-contents. Whether they also force themselves between these cells of the foot, I have been unable to determine from the small amount of material available for investigation. One might make these features in Eriopus the foundation of the most daring phyletic speculation. Such a rooting sporogonium requires only to grow out further at its apex and to branch and so forth in order to approach the behaviour of the sporophyte of the Pteridophyta. In my opinion such a conclusion would be absurd. We have here only what is indeed a remarkable adaptation, and it no doubt stands in connexion with the fact that at the point of junction of foot and seta of the sporogonium the cells become brown at a very early period and, as it appears, die off. By this the conduction of food-material is made difficult or interrupted. This interruption in the supply will be overcome by the development of rhizoids in the directions described; those to the outside will take up water, and those to the inside will lay claim to the material contained in the foot.

FIG. 124. Polytrichum commune. *rh*, a small portion of the part of the stem bearing rhizoids; *s*, seta; *c*, calyptra; *ap*, apophysis; *d*, operculum. Natural size. Lehrb.

Assimilation. The Apophysis. With regard to the nutrition of the sporogonium in other forms it has been definitely proved within recent times, especially by Haberlandt[1], that the sporogonia of many Musci are capable of independent assimilation. They are possessed of an assimilating chlorenchyma which is developed in very unequal quantity in the different forms, but in some cases approaches palisade-parenchyma. In a sporogonium organized so simply as that of Nanomitrium, the assimilation by the chlorophyllous wall-layer of the sporogonium can only be slight, and the same must be the case in other Musci, like Eriopus, with little capsules. But

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[1] Haberlandt, Physiologische Pflanzenanatomie, Ed. 2, Leipzig, 1896.

in others the assimilating tissue is present, partly in the wall of the capsule, partly in that portion of the sporogonium which lies below the capsule and at the top of the stalk, and is known as the *apophysis*[1]. Upon this apophysis in many Musci there are stomata of quite the same structure as those of the higher plants[2], and they place the numerous intercellular spaces of the tissue in communication with the outer air, and so make possible an exchange of gases and transpiration. Their different method of formation need not be dwelt on here. It may only be mentioned that they are rudimentary in Sphagnum, which shows that Sphagnum is derived from a form whose sporogonium projected out of the archegonial venter and displayed an assimilation-capacity like the sporogonia of the majority of other Musci, and that in this it was much nearer these other Musci than is the genus at the present time. Sphagnum, indeed, is evidently not a primitive but a greatly altered form, as we have already learned when considering its germination, and as the behaviour of its antheridia, if we accept the statement of Leitgeb, confirms. However this may be, at any rate it is remarkable that in the Bryophyta the formation of stomata repeatedly appears, as for example in Anthoceros and in the different series of the Musci, and they in every way correspond with the stomata of the Spermophyta.

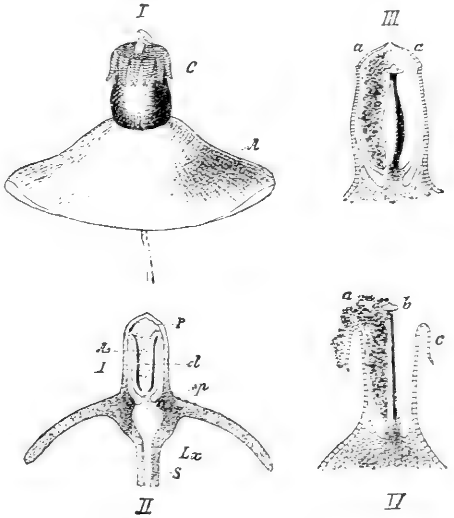

FIG. 125. Splachnum luteum. *I*, *c*, capsule open; *A*, apophysis. *II*, unopened capsule in longitudinal section; *S*, seta; *Lx*, leptoxylem; *sp*, stomata on apophysis; *cl*, columella; *p*, peristome; *As*, archesporium; *i*, intercellular space. *III* and *IV*, diagrams to illustrate the opening of the capsule in Splachnum; *aa*, peristome, incurved in *III*, recurved in *IV*; *b*, terminal disk of columella. *I*, magnified 3. After Hedwig. *II*, magnified. After Vaizey. *III* and *IV*, magnified. After Bryhn.

The development of the apophysis in many species of Splachnum is remarkable, especially in S. rubrum and S. luteum[3] (Fig. 125, *I*, *II*), in which the apophysis grows out into an umbrella-like fringe which in its structure resembles a dorsiventral leaf, and possesses stomata only upon the upper side. The apophysis also takes a share indirectly in the scattering of the spores as we shall see later. Other Splachnaceae also have the tendency to develop large apophyses—a character which has resulted in the most remarkable constructions.

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[1] I agree with Haberlandt in reckoning the apophysis as a portion of the seta, not of the capsule.

[2] See also Vuillemin, Sur les homologies des Mousses, Bulletin de la Société des sciences de Nancy, xix (1886); Bunger, Beiträge zur Anatomie der Laubmooskapsel, in Botanisches Centralblatt, xlii (1890).

[3] See Vaizey, On the Morphology of the Sporophyte of Splachnum luteum, in Annals of Botany, v (1890–1), p. 1.

3. ARRANGEMENTS FOR THE SHEDDING OF THE SPORES[1].

The whole configuration of the sporogonium has as its aim *formation of spores* and then *distribution of spores.* It has been already shown that the most simple constructions of the sporogonium are found where few and relatively large spores are contained in the sporogonium. Where many spores are formed there are often complex arrangements which have as their object the *gradual discharge* of the spores.

CLEISTOCARPOUS FORMS. In most Phascaceae arrangements for distribution of spores are not present. The sporogonium is *cleistocarpous*: it does not open; it rots[2]; as we see in the sporogonia of Ephemerum and others it can easily be broken off and carried away as a whole by rain. Whether the bright red colouring of the sporogonium of E. serratum has anything to do with attraction to animals requires investigation. It is remarkable that we have in Nanomitrium amongst the Phascaceae, a genus whose sporogonium opens by a lid and where there is an annulus, although indeed only a rudimentary one (Fig. 123, *A*). This shows us that a sharp distinction between cleistocarpous and stegocarpous Musci cannot be made. The majority of the Musci are stegocarpous.

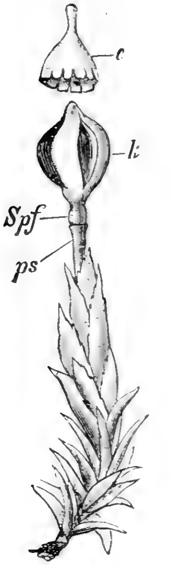

FIG. 126. Andreaea petrophila. *ps*, pseudopodium; *Spf*, foot of the sporogonium; *k*, capsule opening by four slits; *c*, calyptra. Magnified 12. Lehrb.

SCHIZOCARPOUS FORMS. Andreaea, however, is an exception, and its sporogonia are schizocarpous for no lid is produced, but four to six lines of dehiscence are laid down in the middle portion of the wall of the sporogonium and there it opens in dry air when mature (Fig. 126); if the capsule is moistened the valves close the slits. As the mass of spores in the capsule is moist it is glued to the valves and the spores as they dry are then *gradually* removed in clusters by currents of air.

STEGOCARPOUS FORMS. In the stegocarpous Musci the upper part of the capsule falls away as a lid. The line of separation is characteristically constructed. The processes which condition the separation have not been investigated from all sides, and they are somewhat different in the several groups[3]. In most cases there is an *annulus*, that is to say, a ring of one or more cell-layers lying over one another and distinguished by their

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[1] See Goebel, Archegoniatenstudien: VII. Über die Sporenausstreuung bei den Laubmoosen, in Flora, lxxx (1895), p. 459.

[2] Regarding Phascum subulatum and Physcomitrella patens, see Goebel, op. cit., p. 464. The division of the Musci into cleistocarpous and stegocarpous groups is entirely artificial. Cleistocarpous forms appear in different cycles of affinity.

[3] See Dihm, Untersuchungen über den Annulus der Laubmoose, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 286.

mucilaginous contents (Fig. 128). The mucilage acts as a store of water, and brings it about that the cells of the annulus, as they dry, crumple up less than the other parts of the capsule, and in this way tensions arise which result in the splitting of the wall of the capsule. The function of the annulus ends with this in many Musci. In the species of Hypnum it remains in connexion with the open capsule, or falls off in small pieces; but in other Musci it rolls itself off in one piece through the change in volume which its cells holding mucilage experience in their swelling in consequence of the moisture which has penetrated through the opening into the wall of the capsule. With reference to the many details, especially the remarkable behaviour of Tetraphis, Buxbaumia, and others, I must refer to the special treatises which are cited in the notes.

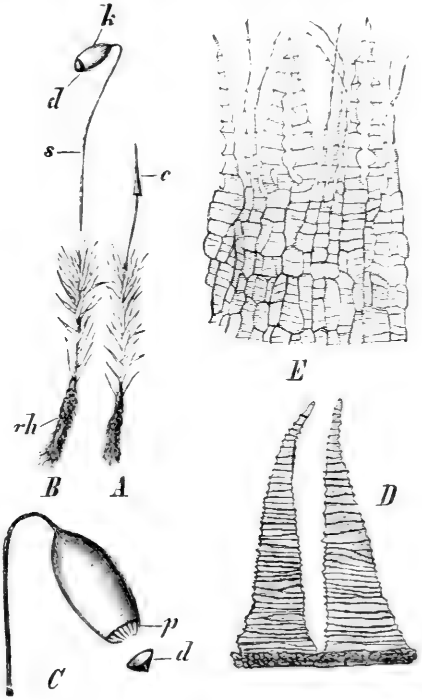

FIG. 127. Mnium hornum. *A*, plant with young sporogonium still bearing its calyptra, *c*. *B*, plant with ripe sporogonium; *rh*, rhizoids; *s*, seta; *k*, capsule; *d*, operculum. *C*, ripe capsule with operculum, *d*, removed; *p*, peristome. *D*, two teeth of the outer peristome. *E*, portion of the inner peristome with teeth and fine scattering threads. *A*, *B*, natural size; *C*, magnified 3; *D*, *E*, magnified 58. Lehrb.

The arrangements for shedding of spores, as they are met with in the stegocarpous Musci, are also multifarious. First of all let it be noted that the capsule is usually raised up above the stem by means of the stalk or *seta*, or it may be by the formation of a *pseudopodium*, as in Sphagnum (Fig. 121, *D*) and Andreaea (Fig. 126), that is to say, by a stalk-like elongation of the axis of the shoot immediately beneath the archegonium in which fertilization has been effected. In Musci which live on the stems of trees or on bare rocks, the seta is usually very short; they are exposed to relatively strong currents of air.

The character of the mouth of the capsule is of special significance in regard to the shedding of spores, whether it possesses a *peristome* (Fig. 127) or not. A great portion of the aperistomous Musci was formerly grouped together in a special genus, Gymnostomum, but it was subsequently recognized that forms without a peristome were found in the most different cycles of affinity. In the most of them we can scarcely express an opinion as to whether this want of peristome is a primary or a reduced character, and the phylogeny of the peristome of Musci is one of the most obscure parts of the natural history of the group [1]. We may regard

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[1] Phillibert, Études sur le péristome des Mousses, in Revue bryologique, 1884, 1890, does not clear up the question.

the want of a peristome in Nanomitrium, for example, as primary, but it may be a reduction in Orthotrichum gymnostomum, as its allied species are all provided with a peristome, and even in this species itself a rudimentary peristome exists[1]. The want of a peristome can be easily explained biologically. It is absent mostly in small capsules with narrow mouth, for example Schistostega, Hymenostomum, Pottia, and the spores are held together in one mass by means of thickenings of the spore-wall, so that they are only gradually thrown out.

An isolated case[2], so far as we know, is found in the distribution of the spores in Sphagnum[3]. When the ripe capsules of Sphagnum dry they explode with an audible sound, as indeed Bridel knew, and the cap and the spores are abjected for a considerable distance, as much as ten centimeters. This takes place on sunny days, and as the sun dries the capsule the columella is dried up and is replaced by air. In the process of drying the longitudinal diameter of the capsule is not changed, but the transverse diameter is considerably shortened, and thus the previously nearly spherical form of the capsule becomes more cylindric, and the air in the capsule underneath the spore-mass is consequently compressed. The lid of firmer texture does not shrink, or shrinks less than the capsule. In this way a difference in tension arises, which brings it about that the lid, at the position of the annulus, is broken off from the capsule and, together with the spores, is shot out by the compressed air like a bullet from an air-gun. The discharge of spores takes place here once and for all, and with considerable force, which makes perfectly certain the scattering of the spores—not in moist weather, however, because that hinders the drying of the capsule.

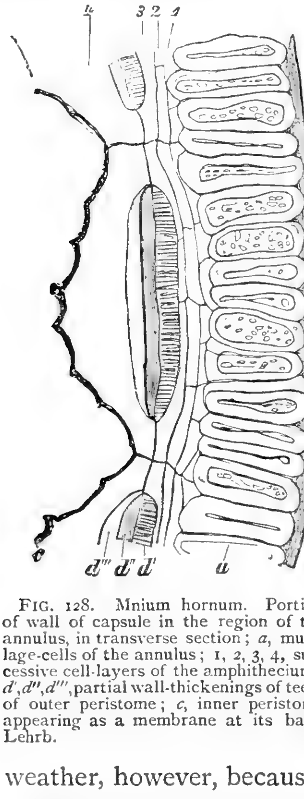

FIG. 128. Mnium hornum. Portion of wall of capsule in the region of the annulus, in transverse section; *a*, mucilage-cells of the annulus; 1, 2, 3, 4, successive cell-layers of the amphithecium; *d'*,*d''*,*d'''*, partial wall-thickenings of teeth of outer peristome; *c*, inner peristome appearing as a membrane at its base. Lehrb.

Where a peristome exists it prevents the entrance of moisture into the capsule, and it takes a share in the distribution of the spores. It arises always out of the amphithecium and consists, except in Tetraphis and the Polytrichaceae, always of fragments of cell-membrane, that is to say, the

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[1] See Goebel, Archegoniatenstudien: VII. Über die Sporenausstreuung bei den Laubmoosen, in Flora, lxxx (1895), p. 472.

[2] With regard to Phascum ephemeroïdes, see Hedwig, Descriptio et adumbratio microscopico-analytica muscorum frondosorum, Lipsiae, 1787.

[3] See Nawaschin, Über die Sporenausschleuderung bei den Torfmoosen, in Flora, lxxxiii (1897), p. 151.

thickened portions of the cell-membranes left after the thinner portions are destroyed. There are different types, of which the chief, from the biological standpoint, are mentioned here. It must be remembered, however, that the several groups are not sharply separated one from the other:—

(*A*) THE PERISTOME ALONE TAKES A PART IN THE SHEDDING OF THE SPORES.

I. THE PERISTOME SERVES ONLY AS A HYGROSCOPIC LID TO THE CAPSULE.

Type of Weissia. The teeth of the peristome, when moistened, bend over the mouth of the capsule and close it; when dry, they are bent backwards. The peristome is a simple one.

Barbula. In Barbula there is a slight modification of this type. The thirty-two teeth of the peristome are spirally twisted, and they fit closely to one another, and in many species, for example Barbula subulata, are united below by a membrane. As they dry the teeth twist into a brush; at the base they separate from one another, and there allow the exit of the spores.

Trichostomum. In the allied genus Trichostomum the hair-like teeth form a sieve which only allows of a gradual exit of the spores. This is a connecting link with the next.

II. THE PERISTOME SECURES BESIDES THE GRADUAL DISCHARGE OF THE SPORES.

1. PERISTOME SINGLE.

(*a*) *Trellis-work of Long Teeth.*

Dicranaceae, Fissidentaceae, Ceratodon. There is a development of long teeth which, in the dry state, remain bent over the mouth of the capsule, and so form a trellis-work. We find this in a number of Dicranaceae and Fissidentaceae, and in some the long teeth serve for the abjection of the spores; according to Steinbrinck this is also the case in Ceratodon purpureus. The teeth curve inwards when dry; the spores readily stick to the processes of the teeth as they primarily form one moist mass, and they are then easily thrown outwards as the teeth curve outwards.

(*b*) *Permanent Union of Teeth at the Tip.*

Type of Conostomum. In Conostomum the teeth form a cone which has sixteen long splits; moistened, these close; in dry air they open. I have often asked myself whether an arrangement of this kind, that is to say a membrane provided with holes, might not be a more primitive type of the peristome than that in which there are single teeth to the peristome. It occurs in different series of Musci.

2. PERISTOME DOUBLE. IN THIS CASE THE INNER IS USUALLY NOT HYGROSCOPIC.

(*a*) *The Inner Peristome narrows the Capsule-mouth; the Outer is only a Lid.*

Orthotrichum. The inner teeth bend in dry air over the mouth of the capsule; the outer bend backwards[1]. In Orthotrichum callistomum the teeth of the peristome hang together in the centre, and there is formed a caster.

Fontinalis and Cinclidium. A caster is also produced in Fontinalis, where the inner peristome makes a delicate trellis-work; also in Cinclidium, where it appears as a dome with sixteen holes at its base, which are closed in moist air by the teeth of the outer peristome.

Funaria. The teeth of the outer peristome in Funaria converge together at the tip, and they form a sieve there. The teeth of the inner peristome bend so that they narrow the position where the slits between the teeth of the outer peristome are the widest. In moist air the slits, through movement of the teeth of the outer peristome, are completely closed.

Type of Buxbaumia. The inner peristome is a funnel, composed of a folded membrane, and with a narrow mouth. This alone exists in Diphyscium and Buxbaumia aphylla. In Buxbaumia indusiata there are traces of an outer peristome (Fig. 129) in the form of small teeth whose function is unknown. The folded peristome of the Buxbaumiaceae arises through a special process of division in a ring-like cell-layer[2] which we must regard as the original position of the peristome. Probably in all Musci the origin of the peristome may be traced back to the innermost cell-layer of the amphithecium, which layer, however, may itself undergo divisions, as in the Buxbaumiaceae and Polytrichaceae. There would be then, if this were general, a certain analogy with the archesporium, which also is laid down in all Musci as *one cell-layer*. This point requires further investigation. At any rate the difference in the formation of the peristome within the genus Buxbaumia shows us again, what has been already suggested upon other grounds, that it is a very old type. The funnel of the peristome brings it about naturally that the spores only gradually escape, and they would be readily

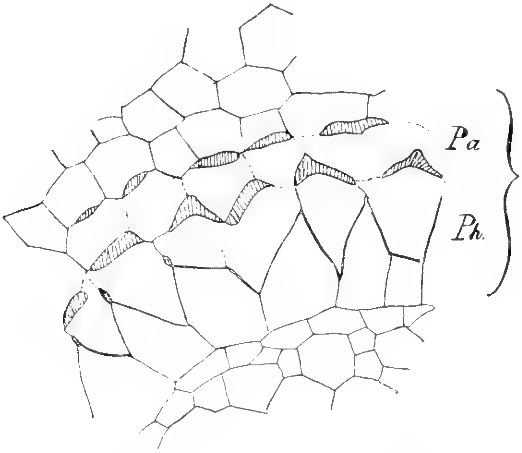

FIG. 129. Buxbaumia indusiata. Not quite mature peristome in transverse section; *Ph*, peristome-membrane; *Pa*, outer peristome-teeth.

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[1] With regard to abnormal species of Orthotrichum, see p. 162.

[2] It is indicated in Fig. 129 by the bracket.

washed away if a rain-drop should fall on the upper surface of the dorsiventral capsule f Diphyscium[1]. The separation of the thickened outer membranous layers in Buxbaumia indusiata, which have given it its name, may possibly provide parachutes.

(*b*) *The Inner Peristome serves also for the Abjection of the Spores.*

This is observed in a number of **Bryaceae**, **Hypnaceae**, and **Mniaceae** (Fig. 127). The mouth of the capsule is here mostly directed downwards; the spores reach the funnel of the peristome, but do not fall directly out of it; they are thrown out only by the threads of the inner peristome.

(*B*) THE COLUMELLA ALSO SHARES IN THE SHEDDING OF THE SPORES.

Type of Pottia truncata. This arrangement is found in many forms without a peristome, like Pottia truncata, in which the columella narrows the capsule-mouth and so prolongs the shedding of the spores.

Splachnaceae. The same arrangement occurs also in the species of Splachnum[2] (Fig. 125, *III* and *IV*). The columella in Splachnum has a disk-like expansion at the top. When the capsule shrinks the peristome curves outwards and downwards, the disk of the columella is projected beyond the mouth of the capsule, and at the same time the axis of the columella elongates, according to Bryhn, and this aids in pressing out the spores, which are here, as in many other mosses aggregated at first in a sticky mass. In moist air the capsule elongates again[3], and the peristome closes over it. It is now remarkable that the spores in Splachnum, according to Bryhn's observations, are spread by flies, which are attracted probably by the brilliant colour which distinguishes the apophysis, as the specific nomenclature in the genus indicates, for example in S. luteum and S. rubrum. We have in the visits of these insects an explanation of the peculiar habitats of the Splachnaceae—excrement and remains of animals. These stations are, as is known, visited by flies for oviposition, and they deposit at the same time the spores of the Splachnaceae. This is, so far as I know, the only case which has been established of spore-distribution by animals in the Musci, but it is probable that there are other cases.

Type of Tetraphis. The ripe capsules of Tetraphis pellucida and allied forms have a peristome of four teeth which have between them in dry air only relatively small slits. In moist air these slits are closed. The teeth are not portions of cell-membrane, but the whole upper part of the capsule, excepting the lid, splits into four pieces, and the columella therefore shares in the formation

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[1] See Goebel, Über Sporenverbreitung durch Regentropfen, in Flora, lxxxii (1896), p. 480.

[2] See Goebel, Archegoniatenstudien: VII. Über die Sporenausstreuung bei den Laubmoosen, in Flora, lxxx (1895), p. 481, where I give an account of the behaviour of Splachnum based upon my examination of dried material. Bryhn (Beobachtungen über das Ausstreuen der Sporen bei den Splachnaceen, in Biologisches Centralblatt, 1897, p. 48) confirms in essentials my observations; he was evidently unaware of my previous publication.

[3] The change of volume in the wall of the capsule is of importance in connexion with the shedding of the spores, and this requires further investigation.

of the peristome. But one finds here also[1] the characteristically thickened cell-layer, which elsewhere is alone used for the formation of the peristome, and it is as usual the innermost cell-layer of the amphithecium.

Type of Polytrichaceae. In all the Polytrichaceae the teeth of the peristome are formed out of entire dead cells, as has been mentioned above[2]. These cells arise from the mother-cells of the peristome by cell-division, which proceeds further than it does in the Buxbaumiaceae.

In Dawsonia, a genus very near Polytrichum in its vegetative characters, the peristome is a long brush of numerous bristles. These bristles are segmented by cross-walls, which are usually oblique. I had recently opportunity in Australia to examine two species of Dawsonia, the beautiful large Dawsonia superba and the smaller Dawsonia polytrichoides, and will here[3] only note the following:—The capsule is in both dorsiventral, as it is in Diphyscium. It possesses a flat side and a bulged side. It originally stands erect; then it bends so as to approach nearly the horizontal. The spores may become discharged by the same parachute-arrangement as occurs in Diphyscium, each shaking sufficing to bring out the spores through the slits of the pencil-like peristome. The spores are very small, and with this the construction

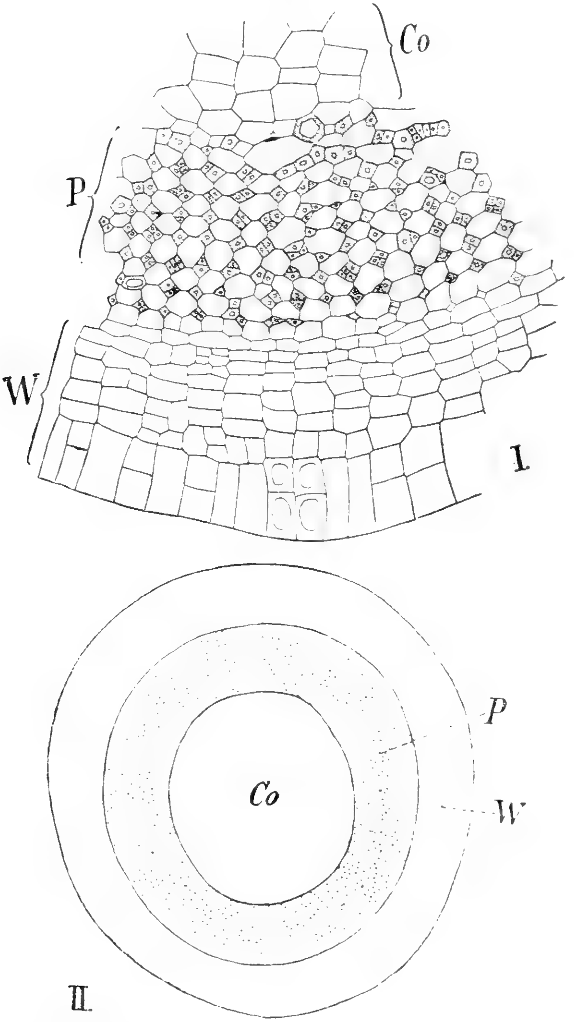

FIG. 130. Dawsonia superba. *I*, portion of the peripheral region of the upper part of the capsule in transverse section; *W*, wall-layer; *P*, peristome; *Co*, columella. *II*, outline of whole capsule in transverse section, lettering as in *I*. *II* less highly magnified than *I*.

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[1] Goebel, Archegoniatenstudien: VII. Über die Sporenausstreuung bei den Laubmoosen, in Flora, lxxx (1895), p. 482.

[2] See p. 162.

[3] With reference to the details I must refer to a communication which will soon appear.

of the peristome corresponds. Whilst it is possible, as is stated[1], that the columella in Dawsonia takes a share in the building of the peristome, I must against this point out that my earlier expressed doubt of this has been confirmed by examination of the history of development. Although an external *sharp* differentiation between peristome and columella does not exist, yet both can be readily recognized as separate tissues. The peristome proceeds from a ring-like mass of tissue (in Fig. 130, *II*, it is shaded), which, on its side, owes its origin evidently to the tangential splitting of *one* or a few cell-layers. From the originally similar cells smaller cells are cut off (Fig. 130, *I*), reminding one of the processes in Diphyscium and Buxbaumia, and these acquire a stronger thickening of their wall. These cells, placed over one another, form then the bristles of the peristome, which become isolated by the disappearance of the soft-walled cells.

In other Polytrichaceae we have the type of the pore-capsule. The mouth of the capsule is closed by an *epiphragm* which proceeds out of the columella, and is a thin membrane which is destroyed at a later period. The teeth of the peristome united with the epiphragm consist of bundles of mostly curved horse-shoe-shaped cells. The construction and origin of the peristome of the Polytrichaceae evidently point to their being far removed from the primitive type.

Reviewing what has been so shortly stated regarding the wonderfully multifarious arrangements for the distribution of spores, it is clear that we can now recognize on the whole the method of working of these arrangements, but we cannot explain how they have come to be in the several allied groups of the Musci, whose connexion is not yet very clear. Although this problem offers a better prospect of solution, it has stimulated less discussion than has that of the connexion between the Bryophyta and the next higher group, that of the Pteridophyta. We shall now proceed to consider, at least in part, the researches bearing upon this problem, although they have not led to positive results.

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[1] Hooker (Musci exotici, Tab. clxii) represents the bristles of the peristome as springing from the columella in Dawsonia polytrichoides. This I have never seen.

SECOND SECTION

PTERIDOPHYTA AND SPERMOPHYTA

PTERIDOPHYTA AND SPERMOPHYTA

THE Pteridophyta and Spermophyta, like the Bryophyta, exhibit in the course of their development a sexual generation, the *gametophyte*, alternating with an asexual generation, the *sporophyte*. In the Spermophyta the alternation of generations is concealed in the formation of the seed, which is a special further development of the megasporangium. Therefore the gametophyte of the Pteridophyta only will be described here ; description of the gametophyte of the Spermophyta is deferred until the development of the sporangium has been described.

THE GAMETOPHYTE IN THE PTERIDOPHYTA[1].

It has been shown that the gametophyte in the Bryophyta, starting from simple relationships, attains to a more complex configuration in different series, and that constructions outwardly alike, as for instance that of the leaf, may be arrived at in different series quite independently of one another. On the other hand, the structure of the sexual organs has moved along a common path, although even here there is no complete uniformity. Similar features recur in the Pteridophyta. The formation of the organs of their gametophyte, which in them is termed the *prothallus*, is by no means so multifarious as it is in the Bryophyta, and this is connected with the short duration of life of the gametophyte and with the reduction which it experiences. Before describing the relationships of configuration the structure of the sexual organs must be described.

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[1] References to the general literature are not given here; it is fully set out by Douglas Campbell, The Structure and Development of the Mosses and Ferns (Archegoniatae), London, 1895, and more recently by Sadebeck, Pteridophyta, Einleitung, in Engler and Prantl, Die natürlichen Pflanzenfamilien, 1898.

I

STRUCTURE AND DEVELOPMENT OF THE SEXUAL ORGANS

A. *THE ANTHERIDIUM.*

THE SPERMATOZOID.

The antheridium is the seat of formation of the spermatozoids, which in the Bryophyta have uniformly two cilia—they are biciliate[1]. The Pteridophyta, on the other hand, may be divided into two groups according to the structure of the spermatozoids:—

1. Pluriciliate Pteridophyta[2].
    - Filicineae.
    - Equisetaceae.
    - Isoetaceae.
2. Biciliate Pteridophyta[3].
    - Lycopodiaceae[4].
    - Selaginelleae[5].

The structure of the sexual cells is undoubtedly of great systematic value, for it is essentially constant within groups which we recognize as natural. We know indeed that the number of the cilia in the swarm-spores may be different in one and the same species of some Algae, for example Ulothrix, inasmuch as the megaspores have four cilia, whilst the microspores have only two, yet there the number is almost constant in each of the

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[1] See p. 9.

[2] Cycadaceae and Ginkgoaceae are pluriciliate.

[3] The male gametes of the Coniferae, and perhaps also of the Gnetaceae, which exhibit only passive movement, are evidently connected with this series.

[4] The spermatozoids are only known in Lycopodium, not in Phylloglossum and the Psilotaceae, but it is highly probable that in these latter they are biciliate.

[5] Isoetes is commonly placed among the Lycopodineae, with which in its sporophyte it has some common features, such as the early disappearance of the apical growth of the leaf, the position of the sporangia upon the upper surface of the leaf, the dichotomous branching of the root, the presence of a 'ligule.' But these are not critical points. The position of the sporangia varies in the Filicineae,

categories of megaspores and microspores[1]. As this is the case in so low a group we must regard the structure of the spermatozoid as a very old character and of much significance from a systematic standpoint. It is, however, probable that *different* developmental series are to be found within the pluriciliate Pteridophyta, yet we must regard the whole of them as having taken origin at an early period from biciliate forms.

The finer structure of the development of the spermatozoids cannot be described here; but I may point out that the spermatozoid of Lycopodium[2] appears to have the simplest construction, that is to say, it proceeds from a less fundamental transformation of the spermatocyte than is the case in the other groups. It has a conformation like that of the swarm-spore of many Algae—an elongated ovoid energid with a prominent nucleus within evident protoplasm and bearing two cilia slightly below its apex. It seems to include the whole plasm of the spermatocyte, whilst elsewhere in the formation of the spermatozoids a portion of the plasm of the spermatocyte remains behind unused, sometimes passing out with the spermatozoid as a vesicular body and then being cast off.

THE STRUCTURE OF THE ANTHERIDIUM.

The structure of the antheridium exhibits two types in the homosporous Pteridophyta, but these are not sharply differentiated:—

(*a*) *Embedded.* The antheridium is either entirely or in part sunk in tissue. This arrangement is found where the antheridia arise upon *cell-masses*, and this is the case in Lycopodiaceae, Equisetaceae[3], Marattiaceae, and Ophioglossaceae. This type also occurs in all the heterosporous Pteridophyta.

(*b*) *Free.* The antheridium stands free, and this is the case when it arises upon a cell-thread or cell-surface. It then usually projects as a somewhat spherical body upon the surface of the prothallus, or it may be

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for example. The 'ligule' does not occur in all Lycopodineae, and is also found elsewhere. Both the gametophyte and the sporophyte show such fundamental differences from those of the Selaginelleae that since I said (Outlines of Classification and Special Morphology, English edition, Oxford, 1887, p. 196), 'The groups which have been brought together under the name Ligulatae have scarcely anything in common but the presence of a ligule, and it would be better perhaps to make separate divisions of them,' the Isoetaceae have been placed by various authors amongst the Filicineae. I cannot but think that they would be better considered as a special group *near* the Filicineae showing at the same time relationships to the Lycopodineae.

[1] Variations in the number of the cilia do occur in Lycopodium, where there are occasionally three; see Bruchmann, Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien. Gotha, 1898, p. 32.

[2] Bruchmann, op. cit.

[3] In Equisetum the antheridium may also be formed upon a cell-thread or cell-surface, but there arises then in the formation of the antheridium a cell-mass (see p. 178).

seated on the cushion of tissue on the under side of the prothallus. Only in abnormal cases is the antheridium embedded. This type is met with in the leptosporangiate Filicineae.

EMBEDDED ANTHERIDIA. Where the antheridia are embedded we have to distinguish a limiting *opercular layer* to the outside, which serves, not only as a protection to the ripening spermatozoids, but also shares in the process of opening the antheridium. It consists of one layer in Equisetum (Fig. 131), and the Marattiaceae, of two layers in the Ophioglossaceae, whilst in Lycopodium there is an intermediate condition, for it is one-layered in the middle but two-layered or many-layered towards the periphery. In the Marattiaceae and Lycopodium this opercular layer, which originally starts from one cell, exhibits characteristic divisions resulting in the formation of a middle cell which is triangular in surface-view; in the Marattiaceae the pit around the antheridium is also surrounded by tabular cells cut off by periclinal walls from their neighbours, and these, like the tapetal cells of the sporangia or the 'lid-cells' of the archegonia of many Coniferae, regulate the transport of food-material to the spermatocytes. In other respects the embedded antheridia proceed, if we except the mantle just mentioned, just like the free antheridia from *one* mother-cell, and an accurate comparison of the history of development first made possible a discussion of the question of the correspondence of the two kinds in their whole construction. It may be mentioned here that the free antheridia are everywhere surrounded by a single layer of *wall-cells*, and that many possess a short stalk.

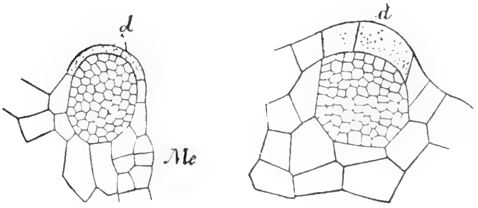

FIG. 131. Equisetum pratense. Antheridia in longitudinal section. The spermatocytes are not accurately shown. In the figure on the left the antheridium is half embedded, in the figure on the right it is completely embedded. *d*, opercular layer; *Me*, meristem. Magnified, the figure on the right more highly than the other.

OPENING OF THE EMBEDDED ANTHERIDIUM. It might be thought that structures which have been so often investigated as the antheridia of the Pteridophyta would be known in all the details of their structure and life-processes. I do not, however, think that this is the case. What, for example, is the work of the antheridial wall? We know that in the Bryophyta it not only serves as a protective envelope to the spermatocytes, but that it actively shares in the process of opening the antheridium. We know further that there is a difference in regard to it between Hepaticae and Musci[1], so far as we are acquainted with them, inasmuch as the process of opening in Musci is brought about by a narrowly limited group of cells, sometimes only one cell, of the antheridial wall which forms the *opening cap*,

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[1] See p. 10.

whereas in Hepaticae there is no such limitation, but many cells take a share in it. It is now commonly assumed that in the Pteridophyta the antheridial wall is burst by the swelling of the contents of the antheridium, the interpretation of the process of opening of the antheridium formerly regarded as the correct one in the case of the Bryophyta also. Any comparison of antheridia which is to be of value in its bearing on the question of the uniformity of their construction can only be undertaken when this point is cleared up. In my opinion, which, however, requires searching proof, it will be found that here also the wall-cells, or it may be only one of them, take an *active* part in the opening by the swelling of mucilage deposited in them or in it, or perhaps indeed in some other way. This appears to me to be most clear in Equisetaceae.

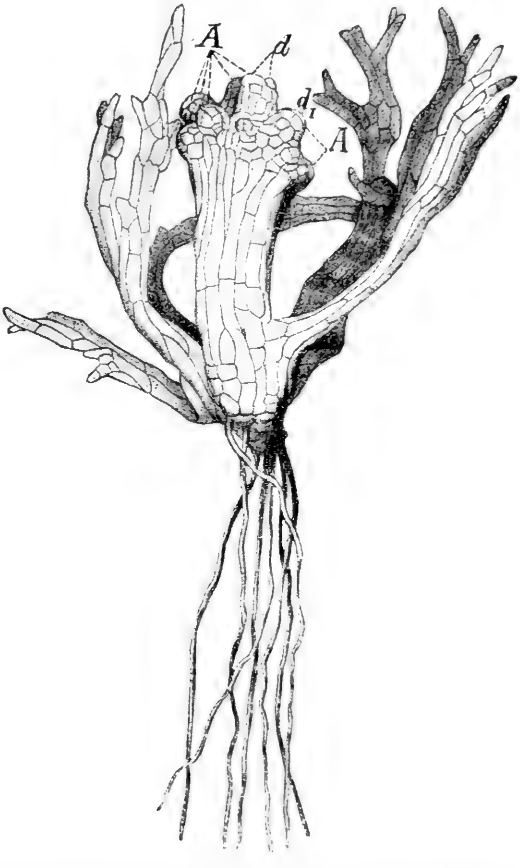

FIG. 132. Equisetum pratense. Male prothallus from below. *A*, antheridia; *d*, d_1, opercular cells. Between and below the antheridia there is no formation of lobes. Magnified 25.

Equisetaceae. The antheridia of Equisetaceae are, as in all other cases, invested by a cuticle which is ruptured afterwards. The cells of the opercular layer, marked by their bright colour, separate from one another, and thus leave a wide opening which in some species, for example Equisetum limosum[1], is encircled by the separated cells of the opercular layer arranged in the form of a 'coronet[2].' In other cases the formation of the coronet is less conspicuous, for instance in Equisetum pratense (Fig. 132). I find in this species that the opercular layer is usually divided into two cells only, which then separate from one another in the middle somewhat after the manner of the guard-cells in a stoma. In other species the opercular cell divides first of all into two, and the first partition-wall indicates the

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[1] See Thuret, Recherches sur les zoospores des Algues et les anthéridies des Cryptogames, in Annales des sciences naturelles, sér. 3, xvi (1851).

[2] This is beautifully shown in Thuret's figures.

position of the subsequent separation, but each of the two daughter-cells is again divided by anticlinal walls. It is evident that here all the cells share in the opening, and this notwithstanding statements to the contrary[1], and their curving outwards may take place as the result of causes similar to those which operate in the antheridia of the Hepaticae[2]. In relation to this we have learned in other examples, for instance amongst the sporangia of the Hepaticae, that the line of separation is from the first marked out clearly by the nature of the cell-membrane.

Lycopodium. In Lycopodium the construction of the mature antheridium is not everywhere the same. The antheridia are embedded in all known species, and but little weight is to be attached to the fact that in L. cernuum, L. inundatum, L. Phlegmaria, and others, the opercular layer consists of *one* cell-layer, whilst Bruchmann found in the species examined by him that it was many-layered towards the edge. In surface-view there appears in all species a small triangular cell in the middle of the opercular layer, and this is broken through, according to Treub, whilst Bruchmann says that some cells of the opercular layer become mucilaginous, and then the sporocytes absorbing water rupture the antheridium. It is possible that different species of Lycopodium behave differently; that in the first-mentioned case only one of the cells of the opercular layer is ruptured by the formation of mucilage, as in many Musci, whilst in the second case many cells are so ruptured, and this would be a primitive condition.

Marattiaceae. Among the Filicineae the Marattiaceae have antheridia which approach those of Lycopodium, especially through the structure of their opercular layer, which shows in the middle a special triangular cell which is 'thrown' off as an 'opercular cell[3].'

Ophioglossaceae. The antheridia of the Ophioglossaceae are distinguished by an opercular layer two cells thick; at least this is the case in the few members of the Ophioglossaceae whose gametophyte is known, namely, in Botrychium Lunaria, B. virginianum, and Ophioglossum pedunculosum. We have seen above that a periclinal rupture of the opercular layer of the antheridium occurs also in the Lycopodiaceae, although it is not complete, nor is it found in all the species. The construction of the wall which leads to the opening is, however, incompletely known also in the Ophioglossaceae. Mettenius[4] says, 'The cells of the inner of the two cell-layers which form the

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[1] Campbell (The Structure and Development of the Mosses and Ferns, London, 1895, p. 427) says of Equisetum Telmateja, 'There is often a triangular opercular cell, recalling the similar cell in these forms' (i.e. Marattia, Osmunda). To this I may say that the conformation of the cell is no indication of whether it is an opercular cell or not. *No such cell* has yet been found in Equisetum.

[2] See p. 12.

[3] Jonkman, De geschlachtsgeneratie den Marattiacceen, Utrecht; id., L'embryogénie de l'Angiopteris et du Marattia, in Archives Néerlandaises, xx (1896), p. 213; id., Üeber die Entwicklungsgeschichte des Prothalliums der Marattiaceen, in Botanische Zeitung, xxxvi (1878), p. 129.

[4] Mettenius, Filices horti botanici Lipsiensis, Leipzig, 1856, p. 119.

outer wall of the antheridium are pushed apart, and soon thereafter one cell of the outer layer is ruptured.' Jeffrey[1] says of Botrychium, 'The spermatozoids make their way out by means of an aperture formed by the disappearance of two superimposed cells of the outer wall of the antheridium.' What is the mechanism of the process is unknown, as it is in Ophioglossum.

FREE ANTHERIDIA. The leptosporangiate Filicineae normally possess antheridia which are free, not embedded. In Doodya caudata there are, besides the ordinary free antheridia, also embedded ones, but these must be considered as first indications of pathological changes of the sexual organs taking place in the prothalli of this fern as they age[2]. The structure of the antheridia is essentially the same everywhere, a one-layered wall surrounding the sporocytes.

OPENING OF THE FREE ANTHERIDIUM. The opening of the antheridium takes place in *one* cell of the one-layered wall, and this cell is designated the opercular cell. It lies usually at the apex of the antheridium, but in the Osmundaceae is somewhat to one side. The details of the working of the opening mechanism are here also unknown; all we know is that the opening may take place in two ways:—

(*a*) The opercular cell, after rupture of the cuticle, is raised up to allow of the escape of the spermatozoids. This is the case in the Hymenophyllaceae (so far as they have been examined), Osmundaceae, Cyatheaceae (in which the opercular cell is mostly divided into two), Gleicheniaceae, and amongst the Schizaeaceae in Lygodium.

(*b*) The opercular cell is broken through, and thus the spermatozoids gain exit. This occurs in the Polypodiaceae and in Aneimia and Mohria[3].

The method of opening of the antheridium is then, so far as investigation has shown, constant within a large cycle of affinity in the Filicineae, with the exception of the Schizaeaceae, among which, however, Lygodium differs from the other genera in this, as also in other features of its gametophyte and sporophyte.

DEVELOPMENT OF THE ANTHERIDIUM.

The history of development of the antheridium shows considerable variations, and the differences are specially marked between embedded and free forms. Careful comparison, however, as I shall endeavour to show, teaches us that the differences are not so great as they appear.

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[1] Jeffrey, The Gametophyte of Botrychium virginianum, in Studies from the University of Toronto, Biological Series, 1898, p. 15.

[2] Heim, Untersuchungen über Farnprothallien, in Flora, lxxxii (1896), p. 333. The marginal antheridia of Ceratopteris are half-embedded.

[3] It is characteristic that the cell-structure of the antheridium of these two genera diverges from that of Lygodium, which conforms with the type of Polypodiaceae.

HOMOSPOROUS PTERIDOPHYTA. In the first place, the spermatocytes always arise in *one* mother-cell in both the embedded and the free antheridia. In the embedded antheridia (Fig. 133, VI), the mother-cell of the antheridium divides by a periclinal wall into an outer cell, *d*, which forms the wall, and an inner cell, *M*, from which the spermatozoids are derived.

Equisetum. Now in Equisetum the formation of the antheridium may take place upon a cell-filament or cell-surface, although it commonly occurs upon a prothallus which has become a cell-mass. Where the former is the case a cell-mass must be first of all formed in some measure, and to this end frequently one cell divides in the manner diagrammatically shown in Fig. 133, IV, V, that is to say, division-walls are formed in three different directions so as to cut off a tetrahedral central cell with curved walls, and this is the mother-cell of the antheridium; this mother-cell then divides into the spermatocyte and the opercular cell, which undergoes further division. The cells cut off to the outside by the walls 1, 2, and 3, are not distinguished by any special features from other cells of the prothallus, whilst the opercular cells are so distinguished, markedly by their behaviour in the opening of the antheridium. We must therefore consider the first as belonging to the prothallus and not to the antheridium[1]. These divisions remind us

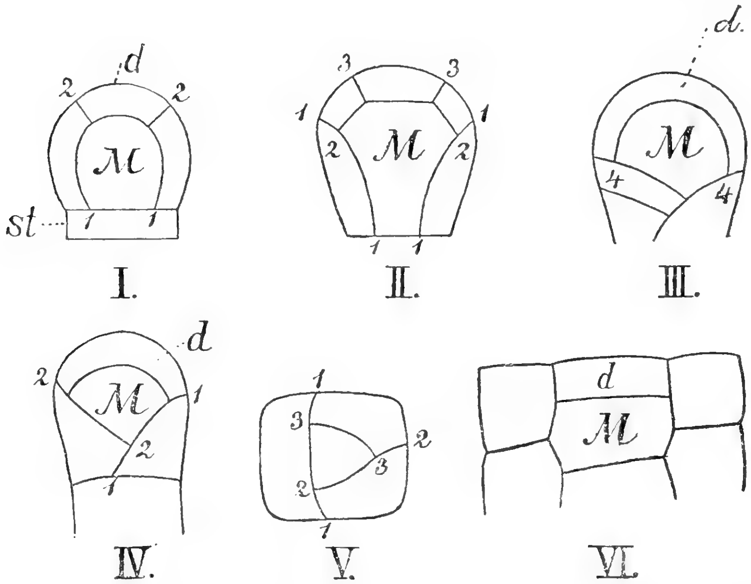

FIG. 133. Scheme of development of the antheridium. I, Aneimia. II, Polypodiaceae. III, Osmundaceae. IV, V, Equisetum. Development upon a cell-thread of which the end-cell is seen in IV in longitudinal section, in V from above. VI, Equisetum. Development upon a cell-mass. *M*, in all figures, the spermatocytes; *d*, the opercular cell; 1, 2, 3, 4, successive division-walls. Further explanation in the text.

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[1] This interpretation I put forward long ago, and Buchtien, Entwicklungsgeschichte des Prothallium von Equisetum, in Bibliotheca Botanica, viii (1887), discusses my views.

greatly of what we find in the primordium of the antheridium of the Osmundaceae (Figs. 133, III; 134).

Osmunda. In Osmunda (Fig. 134) many cell-walls arise, inclined in three directions in space, which lead to the formation of an antheridial stalk; then follows a wall curved in a cap-like manner which corresponds with that which in Marattia, Equisetum, and Lycopodium, separates the opercular layer from the cell within, and then, by further division of the outer cell thus cut off, the opercular cell of the antheridium is formed, as in Marattia.

Polypodiaceae. In the Polypodiaceae there is formed first of all within the mother-cell of the antheridium a funnel-like wall (Fig. 133, II, 1 1) which divides the cell into an outer one and an inner one; the inner one is the special antheridial mother-cell, from which, by a periclinal wall, there is cut off the wall-cell, and in this the opercular cell is then cut off by the ring-like wall 3 3. The ring-cell surrounding the mother-cell of the antheridium is quite different from the vegetative cells of the prothallus in conformity with the lie of the antheridium, for its function is to serve as a protection to the antheridium.

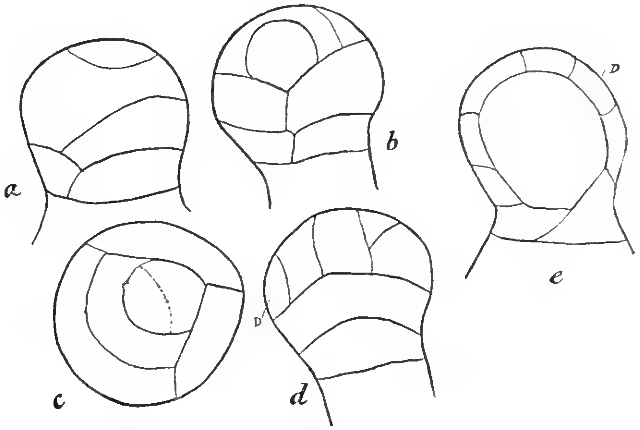

FIG. 134. Osmunda. *a*, *b*, *c*, *d*, *e*, several views of an antheridium; *D*, the opercular cell lying laterally. After Heim.

Aneimia. A further simplification is seen in Aneimia (Fig. 133, I) where first of all a wall, 1 1, curved in a cap-like manner appears, and then the ring-like one, 2 2, is developed.

If we were to construct a series we might say: It is a primitive character if the antheridium is laid down relatively late, when the prothallus is already a cell-mass; in this case it is *embedded*. If the antheridium is laid down earlier, when only a cell-thread or a cell-surface exists, then it is *free*. This type is also retained in the antheridia standing upon the cell-cushion which necessitates first of all the establishment of a cell-mass whereby variations in the direction of the walls take place, as we have seen them also in the Hepaticae. These appear to be constant within the natural groups, although the Hymenophyllaceae are insufficiently known in respect of this, but fundamentally the differences are really smaller than they appear to be at first sight, because everywhere we find the mother-cell of the antheridium dividing into mother-cell of the opercular cell and mother-cell of the spermatozoids. The cells derived from the former are either all, as in Equisetum, concerned in the opening of the antheridium, or only one of them—or it may be a few—takes part in this.

HETEROSPOROUS PTERIDOPHYTA. A knowledge of the history of development will also enable us to understand the formation of the antheridia of the heterosporous Pteridophyta. The antheridium of these is always sunk alike in the Filicineae and in the Lycopodineae. Its construction is like that in the other Pteridophyta; there are only some partial simplifications which may be connected with the reduction of the prothallus.

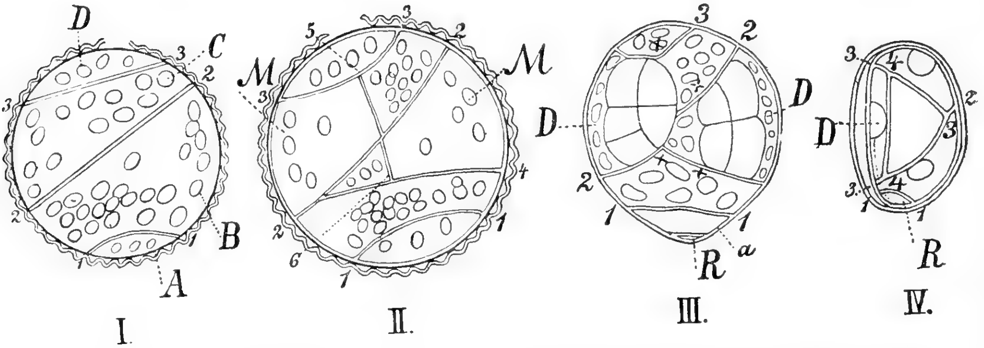

FIG. 135. Germinated microspores. I–III, Marsilia. IV, Isoetes Malinverniana. I, the prothallus consists of four cells *A*, *B*, *C*, *D*, separated by the walls 1, 2, 3. II, the mother-cells, *M*, of two antheridia have been cut off by the walls 5, 6. III, the mother-cell of each antheridium is divided into an opercular cell, *D*, and a pluricellular inner mass of mother-cells of the spermatozoids; *R*, rhizoid-cell cut off from *A*, showing cell *a*. IV, shows lid-cell, *D*, of the antheridium. After Belajeff. Highly magnified.

After I[1] had first suggested, in the case of Isoetes, that the two 'sterile cells' described by Millardet should be perhaps considered as the rudimentary *wall-layer* of the antheridium, the thorough investigations of Belajeff[2] furnished us with a sound basis for the explanation of the relationships.

(*a*) **Marsiliaceae.** These are first dealt with because they show the relationships which are least reduced. The microspore (Fig. 135, I) divides in germination first of all into three cells of a prothallus, *A*, *B*, *C*. From the uppermost of these the cell, *D*, is cut off. *D* and *A* remain sterile, and from the latter there is cut off at a later period the small lenticular cell *R* (Fig. 135, III), which Belajeff considers as a rudimentary rhizoid. In the

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 426, note 2.

[2] See Belajeff, Über die männlichen Prothallien der Wasserfarne (Hydropterides), in Botanische Zeitung, lvi (1898). The literature is cited here.

cells *B* and *C* the antheridial mother-cells *M* are cut out by the walls 5 and 6 (Fig. 135, II). Each of these mother-cells then, just as in the Marattiaceae, Equisetum, and others, divides into an opercular cell, *D* (Fig. 135, III), and the mother-cell from which the spermatozoids are formed; the opercular cell remains simple, the mother-cell of the spermatozoids produces sixteen spermatozoids. In other words we have a prothallus consisting of six sterile cells in which are sunk two antheridia, and it is noteworthy that the whole prothallus is dorsiventral; the antheridia stand towards one side.

(*b*) **Isoetes**[1]. There is only one antheridium (Fig. 135, IV). In the microspore a small cell, *R*, is cut off by the wall 1 1; the remainder and larger portion of the interior is divided by two oblique walls inclined towards the long axis of the spore into two flat cells, and a third which in optical longitudinal section is triangular. I consider this last one alone to be the antheridial mother-cell[2]. It divides by a periclinal wall into an outer cell, the opercular cell, *D*, and an inner cell, out of which the four mother-cells of the spermatozoids arise by division. We should have then a prothallus consisting of three sterile cells and one antheridium, and my explanation differs from that which I originally suggested, and which Belajeff and others have adopted, in that I do not consider all, but only one of the sterile cells, excepting *R*, as belonging to the antheridial wall. The ground for this is to be found in the comparative developmental history of the antheridia stated above, and besides, according to my thinking, the relationships in all the heterosporous forms are alike. That all the sterile cells, apart

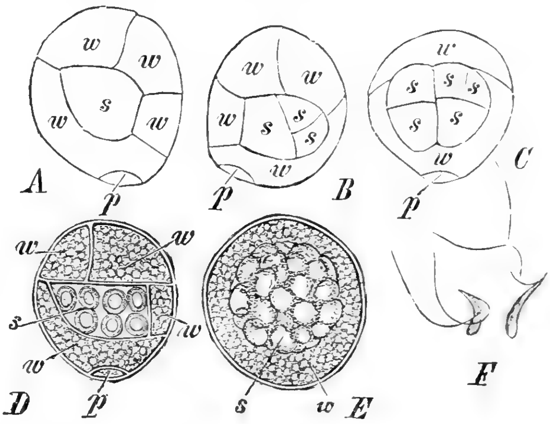

FIG. 136. *A-E*, Selaginella stolonifera. Successive stages in the germination of a microspore. *p*, cell of the prothallus; *w*, other sterile cells; *s*, spermatogenous cells. *A*, *B*, *D*, side views. *C*, dorsal view. In *E* all the sterile cells are disorganized. *F*, Selaginella cuspidata. Spermatozoids. After Belajeff. *A-E*, magnified 640. *F*, magnified 780. Lehrb.

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[1] Belajeff, Antheridien und Spermatozoiden der heterosporen Lycopodinen, in Botanische Zeitung, xliii (1885).

[2] According to Belajeff, it divides first by an anticlinal wall (which is not visible in Fig. 135, IV, as it falls in the plane of the paper) into two cells, and from these then by the wall 4 the two opercular cells are first cut off. This would be a deviation from the development of all other antheridia in the Pteridophyta, excepting those of Selaginella in which, according to Belajeff, the same process occurs. One might save the cause of uniformity by the somewhat forced assumption that two antheridial mother-cells lie close beside one another; moreover the formation of a separation-wall at a somewhat later period than usual, would be a primitive condition.

from *R*, take a share by the formation of mucilage in the *rupture of the exosporium* here, as is the case in Marsilia and others, cannot be brought forward as a reason for considering them as wall-cells. We have to deal here with an adaptation to *rapid germination within the endosporium*, and this brings it about that the sterile cells of the prothallus have quite other duties than is usual.

(*c*) **Selaginella.** In this genus a single antheridium is formed, and there is produced at first a small sterile cell (Fig. 136, *p*) which is considered by authors as a single cell of a prothallus. In my view, however, all the cells in Fig. 136, *A* and *D*, which are marked *w* are cells of the prothallus, with the exception of the one about the middle towards the right; it is the wall of the antheridium and forms the operculum. In this way, *mutatis mutandis*, there is obtained a tolerably complete conformity with the condition in the Marsiliaceae, a conformity which must rest essentially upon an analogy of the whole relationships under which the germination of the spore takes place.

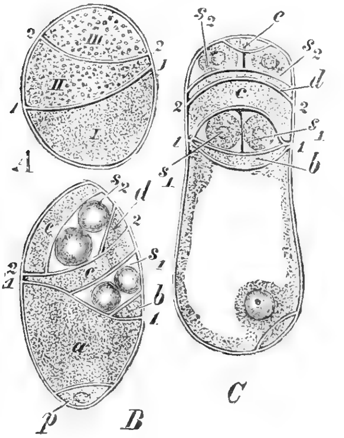

FIG. 137. Salvinia natans. Development of the male prothallus. *A*, division of the microspore into three cells *I*, *II*, *III*. *B*, mature prothallus from the side; *C*, mature prothallus from below. Cell *I* has divided into the cells of the prothallus *a* and *p*. Cell *II* has divided into the two sterile cells *b* and *c*, and the two spermatogenous cells s_1, each of which has formed two mother-cells of spermatozoids. Cell *III* has divided into the two sterile cells *d* and *e* and the two spermatogenous cells s_2. Each pair of cells s_1 s_1 and s_2 s_3 represent one antheridium. After Belajeff. *A*, magnified 860. *B*, and *C*, magnified 640. Lehrb.

(*d*) **Salviniaceae.** Salvinia alone is mentioned here as in it the reduction reaches an extreme, inasmuch as no opercular layer is formed. The microspore divides first of all into three cells of the prothallus, *I*, *II*, and *III* in Fig. 137, *A*. From cell *I* the small cell *p* is cut off; cells *II* and *III* produce each an antheridium, each of them divides by two anticlinal walls into the two sterile cells respectively *b* and *c*, *d* and *e*, Fig. 137, *B*, and the mother-cell of an antheridium out of which the two mother-cells of the spermatozoids are developed. The dorsiventrality of the prothallus is here very apparent. The cells *b*, *c*, *d*, *e*, which remain sterile, and which in my view are wrongly designated wall-cells, take no part in the opening of the antheridium. It is indeed clear that in so small antheridia the opening mechanism may be very simple. One might endeavour to interpret this simple structure as not a reduced, but a primitive rudimentary one, inasmuch as it conforms somewhat with that of the antheridia of Algae like Oedogonium. But general consideration of the reduction of prothalli makes the view of it as a reduction the more probable, as does also a comparison with what is found in the allied (although not very nearly so) Azolla, whose single antheridium possesses a lid. The proof of either view is wanting.

B. *THE ARCHEGONIUM.*

The term Archegoniatae used to embrace both the Pteridophyta and the Bryophyta shows that the structure of the archegonia in both groups is alike. The archegonium of the Pteridophyta has its venter embedded in the tissue of the prothallus. In Marattia and such heterosporous forms as Isoetes and Selaginella, the neck only slightly protrudes, and it thus approaches the condition of the archegonium in Anthoceroteae and in the Gymnospermae. The neck consists everywhere primarily of four cell-rows, and it invests the neck-canal-cells, in which is formed the mucilage which is concerned in the opening of the archegonium. A row of neck-canal-cells is always present in the Bryophyta, and we are therefore inclined to regard those archegonia which have a row of neck-canal-cells as the more primitive amongst the Pteridophyta. We find neck-canal-cells in some species of Lycopodium. L. clavatum and L. annotinum have six to ten of them, or there may be more, especially in L. annotinum[1]; L. Phlegmaria has three to five, according to Treub. The number may, however, be reduced to one, for example in L. cernuum and L. inundatum, although perhaps here there may be a nuclear division which is not followed by the formation of cell-wall. This at least is the case in the other Pteridophyta, which possess only one canal-cell, Marattiaceae, Botrychium, Equisetum, the Filices. Cell-walls are occasionally observed in the Marattiaceae, Osmunda, and Equisetum, and this supports the assumption that a reduction has taken place here. The reduction goes even further in the heterosporous forms. This neck-canal-cell is extremely small in the Marsiliaceae, and a nuclear division does not take place, and the same is true it appears in Selaginella. The nucleus of the single broad neck-canal-cell of Isoetes divides, at least sometimes, in a transverse direction. This reduction in the formation of the neck-canal-cells is of interest, inasmuch as the formation of neck-canal-cells does not generally take place in the archegonia of Gymnospermae.

OPENING OF THE ARCHEGONIUM. Our knowledge of the opening mechanism in the archegonium of the Pteridophyta is as imperfect as it is in the case of the antheridium. I have no doubt that the neck of the archegonium is not, as is commonly assumed, passively ruptured, but that it opens by an active opening movement of the cells at its apex. Equisetum furnishes us with a striking example in illustration of this. At the apex of the neck of the archegonium in this genus are four long large cells marked out by their hyaline, perhaps mucilaginous, content, and between these the neck-canal-cell is not forced. These cells bend outwards, and they undergo then a change in conformation which, excepting that they remain united with the other neck-cells, is exactly like that which I described in the wall-cell of

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[1] See Bruchmann, Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien, Gotha, 1898, p. 34.

the antheridia in Hepaticae (see Fig. 5, 5), and which, although less evidently, is also found in the opercular cells of the antheridia of Equisetum. In Selaginella spinulosa also[1], a strong outward curving of the four uppermost neck-cells takes place, and in the leptosporangiate Filicineae lower-lying cells in the neck take a share in the opening movement.

DEVELOPMENT OF THE ARCHEGONIUM.

The development of the archegonium in the Pteridophyta (Fig. 138) runs in all known cases on essentially the same lines. An epidermal cell divides by a transverse wall into an upper and a lower cell. The upper cell divides by cross-walls into four cells, and these continue to divide, and then project usually above the epidermal surface as the neck. In Marattia this projection is only very slight. In Selaginella (Fig. 138, *III*) the neck also projects but little, and the division-walls never reach the free surface, so that the neck of the archegonium appears many-layered, and this is noteworthy in comparison with the archegonium of many Coniferae which will be described later. The lowermost cell divides into two daughter-cells, the *neck-canal-cell* and the *central cell*. The former by subsequent divisions may produce daughter-cells, as has been shown above, or there is only a trace of these. The latter, after separation of the *ventral canal-cell*, forms the *egg*. In the Marattiaceae, the embedded portion of the archegonium is surrounded by tabular investing cells; in others, only that cell which limits the egg upon its under side is marked out by its form as a *basal cell*, and it may be assumed that this, like the cells investing the archegonium of the Gymnospermae, has, although in a minor degree, the function of conveying nutrition to the egg. The details of the relationships of cell-division in the neck are, as in the case of the Bryophyta, omitted here.

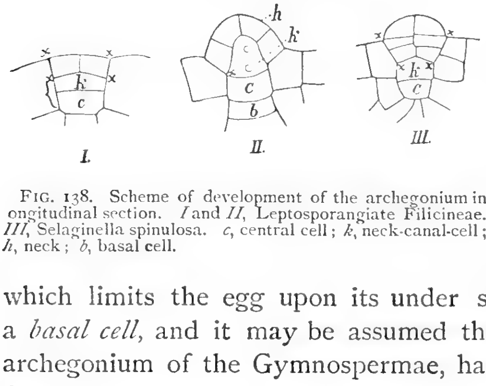

FIG. 138. Scheme of development of the archegonium in longitudinal section. *I* and *II*, Leptosporangiate Filicineae. *III*, Selaginella spinulosa. *c*, central cell; *k*, neck-canal-cell; *h*, neck; *b*, basal cell.

C. *COMPARISON OF THE DEVELOPMENT OF ANTHERIDIA AND ARCHEGONIA.*

WITHIN THE PTERIDOPHYTA.

A comparison of the development of the embedded antheridia with that of the archegonia brings to our notice a fairly far-reaching conformity to

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[1] See Bruchmann, Untersuchungen über Selaginella spinulosa, A. Br., Gotha, 1897.

which I directed attention some years ago[1]. We do not, however, know whether this is original or only accidental. Both in the young antheridium and the young archegonium a wall-layer is separated from an internal portion by a periclinal wall; the *neck-cells of the archegonium correspond to the strongly-grown wall-layer of the antheridium.* In the free antheridia the analogy apparently fails, but it yet can in some measure be followed as, for example, in Osmunda (Fig. 133, III) where an inner cell is separated from an outer cell by the wall 4 4. This corresponds in Fig. 133, II, to the wall 2 2, and in Fig. 133, I, to the wall 1 1, whose curved relationship is conditioned by the form of the mother-cell.

THE PTERIDOPHYTA AND THE BRYOPHYTA.

A comparison between these two groups is of importance in relation to the question of the connexion between the series, as will be evident from what has been said previously[2]. In such a comparison the Anthoceroteae have frequently been brought forward, and its best known and most widely spread member is the genus Anthoceros.

Anthoceros is certainly an exceptional type. Its cell-structure, showing a single chloroplast with pyrenoid, its anatomical construction with mucilage-cavities and mucilage-splits, the origin of its sexual organs, the structure and growth of its sporangium, all show deviations from other Hepaticae. But a careful examination does *not* show a resemblance with peculiarities found in the Pteridophyta. The mature antheridia are constructed like those of other Hepaticae with a wall-layer, stalk, and other parts, and its cellular construction is like what occurs elsewhere amongst Hepaticae, *but is known in none of the Pteridophyta.* To homologate the whole antheridial group, with a single antheridium of another liverwort, or of a fern, because it proceeds from one cell, I hold to be a purely formal, that is to say, only superficial, comparison. What can one not trace ultimately to a single cell? But the endogenetic origin is evidently a *secondary* phenomenon, that is to say, is a consequence of the widely spread feature of the sinking in a pit. That these pits are closed at the beginning finds an analogy in the origin of the air-chambers of Marchantia, which are not as they appear, though in Fegatella they really are, indentations of the surface, but from the beginning are spaces closed to the outside. When Campbell[3] endeavours to find an analogy between an antheridium of Marattia and an embedded antheridium of Anthoceros, which is covered on the outside by a double cell-layer, and to do so has to imagine the wall-layer and the stalk to be absent, the comparison seems to me to be bred of the wish to discover

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), pp. 425–6.

[2] See p. 8.

[3] Campbell, The Structure and Development of the Mosses and Ferns, London, 1895, p. 298.

points of relationship between the Bryophyta and Pteridophyta, and not to be founded on facts [1].

The development of the archegonium of Anthoceros differs also from that of the Pteridophyta. We recall that the archegonium in all Bryophyta is primarily laid down in the same manner; the mother-cell divides by three longitudinal walls into an inner cell and three outer cells which again are divided by longitudinal walls (Fig. 7). Anthoceros also shows the same character, only the mother-cell of the archegonium here does not project, but remains sunk, and the mother-cell of the neck is cut off from the opercular cell (Fig. 7, *d*). No archegonium in the Pteridophyta shows a development of this kind [2]. Even if we assume that the neck-cells of the archegonium in the Pteridophyta do not correspond with those of the archegonium of the Bryophyta, but only with the opercular cells (Fig. 7, *d*) which then have undergone a great further development, Anthoceros would, indeed in the matter of the development of its archegonia, be further separated from the Pteridophyta than other Hepaticae by the origin of its neck-canal-cells. The fact that notwithstanding the sinking of the antheridium in Anthoceros, its development coincides *not* with that of the Filicineae, but with that of the other Hepaticae, shows, as does also the development of the antheridium, that in Anthoceros we have to deal with a derived type which at any rate shows no near relationship to the Pteridophyta. The kinship of Anthoceros to the Pteridophyta is then, so far as the sexual organs are concerned, a mistaken one.

The result of our comparison then is: The structure of the sexual organs within the Pteridophyta is a systematic mark of great significance. That of the archegonium is more uniform than that of the antheridium, and it is essentially the number of the neck-canal-cells which is subject to variation, running from ten to one. The greater number is the more primitive relationship. The embedded type of antheridium is the more primitive. The developmental process in Equisetum furnishes valuable points for the comparative consideration of the formation of the free antheridium. The number of spermatozoids appears to be greater in the embedded antheridium than in the free, but free antheridia are more numerous than

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[1] Waldner, Die Entwicklung des Antheridiums von Anthoceros, in Sitzungsberichte der Wiener Akademie, lxxv (1887), p. 81, rightly says: 'The differentiation of a wall-layer so completely individualized in the antheridia of Anthoceros, and in a certain sense also in the archegonia, and the circumstance that the formation of this envelope-layer is quite like that of the other Hepaticae, makes the assumption probable that the sinking of the archegonia and the endogenetic origin of the antheridia are derived features.'

[2] The only cases which could be quoted are those of Isoetes and Marsilia, but there is wanting in them all proof of a *constant* arrangement of the cells in the origin of the archegonium resembling that of the Bryophyta. The mother-cells of the archegonium are cut out of single large cells of the prothallus and this is connected with the early origin. The process has much more resemblance with that which occurs when in Equisetum the antheridia are laid down upon a cell-thread, see p. 178.

embedded ones. The structure of the sexual organs is alike in its outlines in Bryophyta and Pteridophyta, but shows in the development and in the ultimate details so many differences that we have evidently here to deal with two phyletic series of which the higher has not been derived from the lower, but arising at an early period from simple similar primitive forms they have followed separate paths. Other considerations lead us to the same result.

D. *ABNORMAL SEXUAL ORGANS.*

Abnormal sexual organs are of interest upon many grounds, and may fittingly be considered here.

In ageing prothalli of Hemionitis palmata and Lygodium japonicum I have frequently found[1] a virescence of the neck-portion of the archegonium (Fig. 139). Whilst the neck of archegonia in which fertilization was not effected commonly died off, in many cases chlorophyll appeared, and the cells of the neck grew out into adventitious shoots which ultimately produced antheridia (Fig. 139, *A*), and also effected vegetative propagation. We may consider this condition as one of senescence. In young vigorous prothalli the meristem draws all the plastic material to itself, and distributes this proportionately amongst the primordia of the organs, but in old prothalli the meristem is enfeebled, the division of labour amongst the cells is less precise, and cells which otherwise have other functions may now take on a vegetative character.

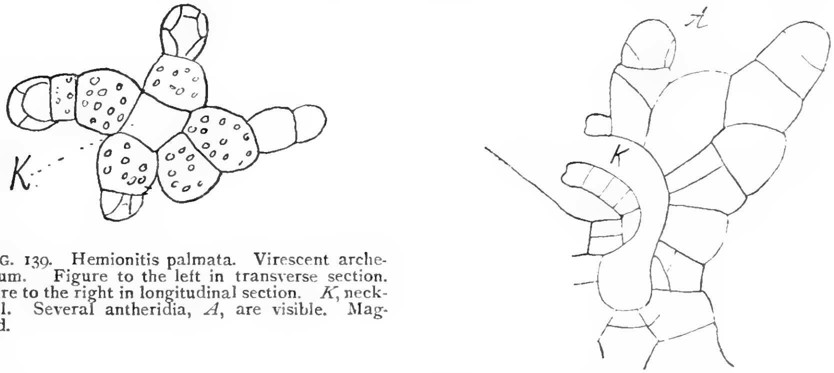

FIG. 139. Hemionitis palmata. Virescent archegonium. Figure to the left in transverse section. Figure to the right in longitudinal section. *K*, neck-canal. Several antheridia, *A*, are visible. Magnified.

Hofmeister[2] also mentions a case of abnormal sexual organs in Asplenium septentrionale, where the neck was entirely embedded in the prothallus.

That abnormal sexual organs are found on many prothalli which exhibit apogamous shoots appears to me to be a point of importance, and it is natural to assume that the two phenomena stand in causal connexion,

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[1] Goebel, Über Jugendformen von Pflanzen, und deren künstliche Wiederhervorrufung, in Sitzungsberichte der bayerischen Akademie, xxvi (1896), p. 475.

[2] Hofmeister, Vergleichende Untersuchungen, Leipzig, 1851, p. 83.

that the apogamous formation of new plants is a consequence of the sexual organs being functionless. It is not always the case that a functionless archegonium has the outward appearance of malformation, although this is the more striking condition. An apparently normal archegonium may be functionless. Heim[1] has shown that the prothalli of Doodya caudata produce first of all normal sexual organs, and that sexually produced embryos may also arise. But if there is suppression of this, *apogamy* takes place and the most varied malformations of the sexual organs appear, often mixed with normal antheridia. Abnormal archegonia are also found in the apogamous prothalli of Aspidium falcatum, where there may be three instead of four neck-cells, the neck-canal-cells may divide into many portions, the archegonium may not open, and so forth. In Osmunda the neck-cells divide by periclinal walls in archegonia which do not open, and thus form a papilla which encloses the archegonium. All these phenomena which in my opinion point to a degeneration, have as a consequence the asexual production of new plants on the prothallus. The condition of apogamous prothalli will, however, be referred to later[2].

II

THE CONFIGURATION OF THE PROTHALLUS

The gametophyte of the Pteridophyta has, as its name indicates, the configuration of a thallus. Where, as is the case in the prothallus of many species of Lycopodium and of Equisetum, lobes are developed which physiologically are in a certain degree comparable with the leaves of Hepaticae, we do not designate these as leaves because they have neither a determinate form nor a definite point of origin. A distant approach to the formation of leaf is only to be found in the formation of lobes upon old prothalli of Osmunda[3]. 'Hairs' of different kinds, and in some cases 'paraphyses' amongst the sexual organs are known as appendages to the prothallus just as they occur in thallose Hepaticae.

One-celled rhizoids act chiefly as the rooting-organs of the prothallus as in Hepaticae. But this is not always the case. Bauke[4] found rhizoids divided by cross-walls in the prothalli of Cyatheaceae, and they

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[1] Heim, Untersuchungen über Farnprothallien, in Flora, lxxxii (1896).

[2] See p. 220.

[3] Goebel, Entwicklungsgeschichte des Prothalliums von Gymnogramme leptophylla, Desv., in Botanische Zeitung, xxxv (1877), p. 705.

[4] Bauke, Entwicklungsgeschichte des Prothalliums bei den Cyatheaceen, verglichen mit derselben bei den anderen Farrenkräutern, in Pringsheim's Jahrbücher, x (1876), p. 64.

generally exist also in Danaea[1]. They are probably to be found elsewhere, and there can be little doubt that they are derived from unicellular ones. These pluri-cellular rhizoids have only slight resemblance to those of the Musci in which the walls are oblique[2]. Rhizoids are wanting in the male prothallus of the heterosporous forms[3], and also in the female prothallus of Salvinia and Azolla. As the macrospores germinate in these genera whilst floating in water, there is no fixing of them to the substratum, and further, as the development of the prothallus takes place exclusively at the cost of the reserve-material stored up in the macrospore, it is easy to understand how the rhizoids are wanting. In Marsilia and Pilularia the rhizoids arise relatively late, and serve only as temporary fixing-organs until the root of the embryo-plant has penetrated into the soil. In Isoetes rhizoids do occur upon the female prothalli, but they appear rarely, at least in the aquatic forms which have been investigated. We have here evidence of a reduction in the prothallus about which more will be said.

1. DURATION OF LIFE.

In the first place, however, the question of the duration of life of the prothallus must be discussed because the structural relationships are connected therewith. Amongst the Hepaticae only a few monocarpic forms are known, such for example as Sphaerocarpus terrestris. In it the thallus has a very simple configuration corresponding to its short duration of life. But in the gametophyte of the Pteridophyta the general feature is that it dies after producing an embryo. It is, as has been already explained, absorbed by the embryo. An exception in which repeated formation of an embryo takes place is *perhaps* to be found in the old band-like prothalli of Osmunda. It will be shown that the formation of the embryo may begin in many prothalli of Filicineae at so early a stage of development that the relationships of configuration which are possible to them may remain *latent*, as is the case in an Angiosperm which has been dwarfed through unfavourable nutrition, where all the forms of leaf which belong to a 'normal' plant before it flowers may not appear. Prothalli, upon which the act of fertilization has not been performed, may grow for a long time, but in them sooner or later phenomena of senescence appear, showing either in abnormal conformation or in the development of adventitious shoots[4]. It would perhaps be possible to obtain prothalli of Filices showing unlimited duration of development if they were cultivated under conditions which favoured active

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[1] Brebner, On the prothallus and embryo of Danaea simplicifolia, in Annals of Botany, x (1896), p. 109.

[2] See p. 117.

[3] With reference to the cells which perhaps act as substitutes, see p. 180.

[4] See Part I, Fig. 20, p. 49, and the facts there stated.

vegetative growth, but not the formation of sexual organs. Many prothalli may, in addition to multiplication by adventitious shoots, also form gemmae, and this feature has appeared independently in many series [1].

In the heterosporous Pteridophyta the shortly limited development of the prothallus is determined from the outset. The whole process may be passed through in the course of a few hours. The male prothalli are, from the beginning, incapable of vegetative development, but even the female, notwithstanding the supply of reserve-material in the megaspore which is at their service, show but feeble progress in the way of further development if the act of fertilization is not performed upon them; even the chlorophyllous prothalli of Salviniaceae and Marsiliaceae soon die off. They are in our experience, if one may use an old theological expression 'predestined,' their lot is once for all determined. As the megaspores and microspores are sown together, it is possible *directly* to hit upon the time of the formation of the embryo for which the megaspore possesses the necessary food-material. The homosporous Pteridophyta, on the other hand, can only slowly ripen their prothalli and the material which is required for the formation of the embryo is only acquired by their own effort. How independent of external factors are the prothalli of heterosporous forms is shown by the fact that the germination of the spores, the development of the prothalli, the fertilization, as well as the production of the embryo take place in the absence of light in Salvinia and Marsilia. But in the homosporous forms, except in some with chlorophyllous spores, light is an essential condition for germination, and the configuration and nutrition of the prothallus is profoundly influenced by it. As a consequence these prothalli are plastic; they can adapt themselves to their environment although in different degree. The most plastic are the prothalli of Filicineae, and we find that the leptosporangiate Filicineae at the present day, both in number of forms and in distribution, are at the head of the Pteridophyta. Less plastic are the prothalli of many Lycopodiaceae whose behaviour gives us the impression that they belong to an old family not up to date; the prothalli of the Equisetaceae also very easily succumb in nature to their enemies. The gametophyte also has a correlative significance in the maintenance of forms. This is most prominent in the Filices where one finds prothalli and germ-plants in abundance, and some forms, such as Anogramme chaerophylla and A. leptophylla, Salvinia natans, and many tree-ferns, are exclusively maintained by their gametophyte. Equisetaceae and Lycopodiaceae have long-lived sporophytes capable of vegetative multiplication, and the sexual reproduction is, although greater than was formerly believed, *relatively* subordinate, and these forms would not disappear from the earth even if their gametophyte were entirely suppressed.

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[1] See p. 213.

2. RELATIONSHIPS OF SYMMETRY.

Radial construction of the prothalli only seldom occurs, and in this the Pteridophyta resemble the Hepaticae. It is found in Lycopodium, Ophioglossum pedunculosum, and in the archegoniophore of some species of Trichomanes. The prothalli of Filicineae and Equisetaceae are markedly *dorsiventral.* The relationships to light of the dorsiventrality of the prothalli of Filicineae has been already explained[1]; but dorsiventral construction is also known in cases where there can be no effect of light, for example in the male prothalli of Salvinia, Isoetes, Marsilia, and in hypogeous prothalli of Botrychium virginianum. We cannot say whether in such cases we have to deal with an 'inherited' character from a primitive chlorophyllous prothallus or with a condition produced by 'internal causes.'

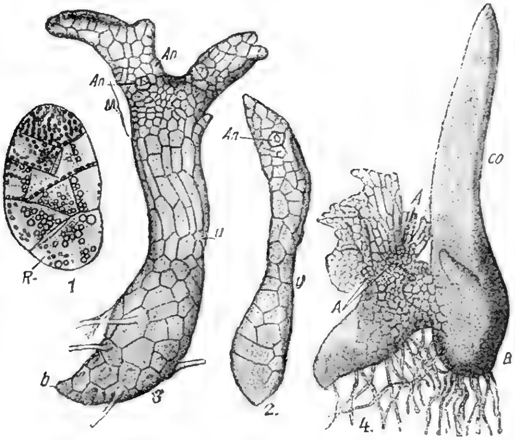

FIG. 140. Lycopodium inundatum. 1, few-celled prothallus; *R*, basilar cell. 2, prothallus with antheridium, *An*; *U*, injured cell. 3, older prothallus with antheridia, *An*, and meristem, *M*; *U*, injured cell; *b*, basilar cell. 4, prothallus with archegonia, *A*, and an embryo showing cotyledon, *Co*, and 'protocorm,' *B*. All magnified; after De Bary.

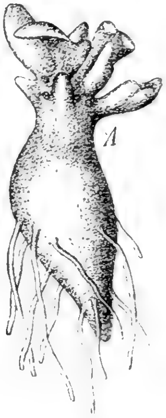

FIG. 141. Lycopodium inundatum. Prothallus with archegonia, *A*. Magnified.

3. THE GAMETOPHYTE IN THE SEVERAL GROUPS OF PTERIDOPHYTA.

We must now shortly describe the formation of the prothallus in the several groups in order that we may discuss how far we can recognize or construct relationships between them. We shall begin with the Lycopodineae because here the sexual organs show a relatively primitive construction as has been already indicated:—

A. *GAMETOPHYTE OF THE LYCOPODINEAE.*

Lycopodium[2]. In recent years the formation of the prothalli in

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[1] See Part I, p. 229.

[2] Literature: De Bary, Über die Keimung der Lycopodien, in Berichte der naturforschenden Gesellschaft zu Freiburg i. Br., 1858; Fankhauser, Über den Vorkeim von Lycopodium, in Botanische Zeitung, xxxi (1873), p. 1; Treub, Études sur les Lycopodiacées, in Annales du Jardin botanique de

a number of the species of this genus has been made known. Some of the prothalli are chlorophyllous, others have no chlorophyll and are saprophytic. It is, however, probable that even in the chlorophyllous forms there is a *partial* absorption of organic substance through symbiosis with a fungus[1]. The configuration of the prothallus varies somewhat in the several species.

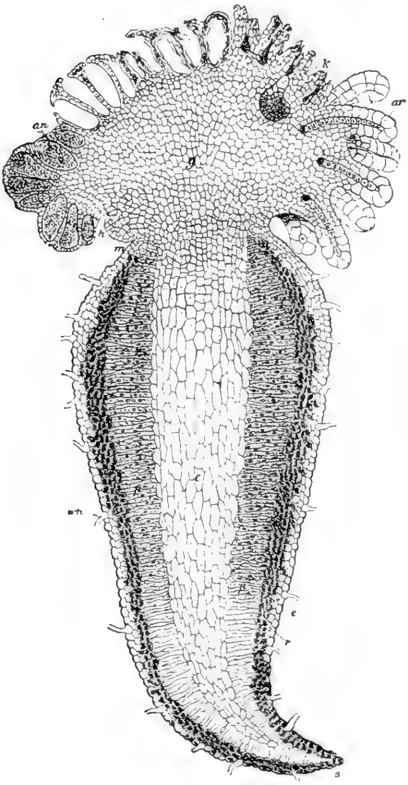

FIG. 142. Lycopodium complanatum. Prothallus in longitudinal section. *s*, base, in oldest part; *e*, epidermis; *r*, cortical layer; *p*, palisade-layer; *c*, central tissue; *m*, meristem; *g*, 'generative tissue'; *an*, antheridia; *ar*, archegonia; *k*, young embryo. Magnified 26. After Bruchmann.

Chlorophyllous prothalli. Starting from the chlorophyllous prothalli such as we find in Lycopodium inundatum and L. cernuum we find a body which is erect in the soil, comparable in form with a miniature beetroot. It bears a crown of lobes above and below this there is a meristem which encircles the prothallus and from which new lobes may proceed. The portion in the soil is poor in chlorophyll and bears rhizoids. Both antheridia and archegonia occur together upon the prothallus, and as in most Pteridophyta the antheridia appear earlier (Figs. 140, *An*; 141, *A*) than the archegonia, and as regards their point of origin are less restricted than the archegonia, being found both upon the lobes and upon the body of the prothallus. The archegonia are confined to the meristem immediately under the crown of lobes.

The prothallus of Lycopodium salakense is similarly chlorophyllous, but has no crown of lobes or only an indication of these, and perhaps this is connected with the fact that the basal tuberous portion of the prothallus is richly *branched*, and these branches are the biological representatives of the lobes.

Saprophytic prothalli. In the saprophytic forms the crown of lobes is absent from the prothallus, and this should not be unexpected, for in the Spermophyta it is common to find a reduction of the organs of assimilation where there is saprophytism.

Bruchmann has shown that the prothalli of Lycopodium Selago which

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Buitenzorg, iv (1884), v (1886), vii (1888); Goebel, Über Prothallien und Keimpflanzen von Lycopodium inundatum, in Botanische Zeitung, xlv (1887), p. 161; Bruchmann, Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien, Gotha, 1898.

[1] See p. 219.

are commonly hypogeous and colourless, may also be epigeous and are then green. This alternation can be artificially brought about, although in less degree, in Lycopodium clavatum, L. annotinum, and L. complanatum. Mettenius showed that the hypogeous prothalli of Ophioglossum pedunculosum are in like manner capable of the same modification.

Fig. 142 represents a longitudinal section through a prothallus of Lycopodium complanatum. It conforms, excepting in its remarkable anatomical structure, with the prothallus of Lycopodium inundatum and L. cernuum, only the lobes fall off and the sexual organs stand upon the swollen upper portion of the prothallus, below which there is also a meristem.

The prothallus of Lycopodium clavatum is similar in essentials, its upper part being only relatively broader and more hollowed. The same may be said of the prothallus of L. annotinum.

Dorsiventral prothallus. If one conceives that in such a prothallus a portion of the marginal zone were to grow out strongly and become separate from the others, the appearance of a *dorsiventral* prothallus would be produced. This takes place not infrequently in Lycopodium Selago. The relationships of configuration are here somewhat manifold, yet are connected with the forms mentioned above, and the prothallus is markedly characterized by the presence of segmented hairs (paraphyses) between the sexual organs. In general it is radial, and may by symmetrical growth assume a cup-form. Usually, however, single portions of the meristem grow out into elongated prothalli which then, in consequence of their origin, bear the sexual organs only upon *one* side, whilst the rhizoids are distributed radially at the base. Such forms arise, according to Bruchmann, where the prothalli, owing to the firmness of the soil, become aggregated on its surface.

Phlegmaria-type of prothallus. With these dorsiventral forms, which can be traced back to the ordinary prothallus, I connect those of the Phlegmaria-type. Here is included, according to Treub, both Lycopodium Phlegmaria and L. carinatum, and in the main features also L. Hippuris and L. nummulariaefolium. These species have filiform thin prothalli, unlimited in their apical growth, and without chlorophyll, and the sexual organs are borne on *one side*, and this appears to me to be an important fact. They have, like the prothallus of Lycopodium Selago, paraphyses, and produce remarkable gemmae which will be described below. The early stage of the development is not known, but I derive them as unilateral outgrowths from radial prothalli like those which occur in Lycopodium Selago. Whether this derivation, and indeed whether the whole concatenation of the different forms of prothalli as I have stated them, is correct, is open to discussion. It appears to me, however, in the present state of our knowledge, to be natural, and I can see no valid ground for regarding the gap between the several forms of prothalli of the Lycopodia to be so great, as Treub and Bruchmann will have it [1].

Development of the prothallus. The development of the prothallus of Lycopodium from its germinating in the spore is well known in a few species only. In Lycopodium inundatum the germinating spore divides first of all by a cross-wall into a basilar cell (Fig. 140, 1, *R*) and an upper cell in which two series of segments arise by inclined walls formed alternately right and left; later there develops the body of the prothallus, upon whose apex at first the prothalli-lobes grow out (Fig. 140, 2). Treub found that in Lycopodium cernuum and L. inundatum a small cell-body, the 'tubercule primaire,' develops out of the spore quite like what is shown in Fig. 140, 1. An arrest in the development then ensues, and the apical cell grows out into a cell-row which then is transformed by division into a cell-mass. These cell-rows become very long in the absence of light, and as in the prothalli of Filices, this formation may be again caused to develop in feeble light upon young prothalli, and perhaps also upon enfeebled old ones. They can produce secondary tubercles if they come in contact with the soil.

In the saprophytic prothalli, where the relationship to light is wanting, a similar cell-body may grow out from the spore. In Lycopodium salakense, and occasionally also in L. cernuum, many branches spring out from the 'tubercule primaire,' and this probably accounts for the fact that the differentiation of members is less rich than in Lycopodium inundatum. Features that are analogous in some measure will be described presently in the case of Anogramme leptophylla.

Selaginella. The formation of the male prothallus has been described above [2], and we have therefore only to refer to the female prothallus. In it there is little to remark of organographic interest. A cell-mass fills the megaspore and subsequently ruptures its apex. It bears some archegonia, and forms also rhizoids, but is incapable of further vegetative development.

In most species of Selaginella which have been examined, the *development* of the prothallus begins whilst the spore is still within the megasporangium, and proceeds so far that the primordia of the archegonia are laid down. This is found for instance in Selaginella Mertensii, S. lepidophylla, S. erythropus, S. serpens, and others—all anisophyllous forms [3]. In the only isophyllous species which has been examined, Selaginella spinulosa [4], the development of prothallus begins only after the scattering of the spores.

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[1] W. H. Lang, The prothallus of Lycopodium clavatum, Linn., in Annals of Botany, xiii (1899), p. 278, has recently arrived at similar conclusions. His paper only became known to me after my manuscript was completed. The facts stated by Lang confirm those of Bruchmann.

[2] See p. 182.

[3] See Part I, p. 105.

[4] Bruchmann, Untersuchungen über Selaginella spinosa, A. Br., Gotha, 1897, p. 42.

The procedure in the formation of the prothallus[1] corresponds in nuclear division, free cell-formation, and so forth, with that in Isoetes, and the formation of a cell-mass in the apical portion of the spore is rapidly promoted, because here only are the archegonia laid down. But the sharp limit by means of a 'diaphragm' which earlier investigators like Hofmeister and Pfeffer described as existing between the first-formed and the later-formed portions of the prothallus has no existence. The 'rupture-tubercles' which Bruchmann has discovered in the prothallus of Selaginella spinulosa are remarkable structures. There are three of these cellular tubercles, one lying under each of the sutures of the spore, and by their increase in volume they bring about the rupture of its thick envelope. Upon them arise also the 'trichomes' which here occur as long unicellular tubes, and which we must regard as somewhat modified rhizoids serving the purpose of taking up water, although they do not enter the soil.

B. *THE GAMETOPHYTE OF EQUISETACEAE.*

The prothalli of all species of Equisetum which have been investigated, all of them species confined to Europe, agree in being usually dioecious. The dioecism is, however, not a peculiarity of the spore. Poorly nourished prothalli are male, well-nourished ones are female, and it is possible, as Buchtien[2] has shown, to induce a female prothallus to develop antheridia instead of archegonia by starving it. The male prothalli are not essentially different from the female; they are with reference to the female ones arrested formations and, as elsewhere, the arrest may take place earlier or later. I have found, moreover, occasionally monoecious prothalli in Equisetum pratense; one had formed an embryo between the lobes; another was female in one longitudinal half, and the meristem was interrupted by an ameristic zone, after which came the male half. It is noteworthy that in Equisetum the female prothalli do not *first of all* produce antheridia[3].

The female prothallus. This has some resemblance with a prothallus of Lycopodium cernuum on account of the coronet of lobes which it possesses and the meristem which lies underneath the lobes. But there is a fundamental difference in symmetry. The prothallus is *not radial but dorsiventral*, and, as in the prothallus of Filices, we have an illuminated and a shaded side. Upon the shaded side there is a meristem beneath the lobes from

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[1] See Arnoldi, Die Entwicklung des weiblichen Vorkeimes bei den heterosporen Lycopodiaceen, in Botanische Zeitung, liv (1896), p. 159.

[2] Buchtien, Entwicklungsgeschichte des Prothallium von Equisetum, in Bibliotheca Botanica, viii (1887).

[3] In most homosporous Pteridophyta the prothallus produces first of all antheridia. It is probable that in Equisetum it would be possible by feeding to cause the male prothallus to develop into the female. It is, however, scarcely to be expected even if one sowed the spores singly in apparently quite similar conditions that they would all furnish female prothalli, as the reaction to stimuli of the spores is never quite the same. As to the scattering of the spores, see p. 575.

which new cells are developed both anteriorly and posteriorly. On the side of the meristem towards the lobes archegonia and new lobes arise, and thus the archegonia come to lie between the lobes and appear pushed towards the upper side of the prothallus. Towards the base of the prothallus new rhizoids appear. The meristem, as Fig. 143 shows, is not uninterrupted. The lobes serve partly as organs of assimilation, and partly as organs for holding drops of water, and thus facilitate fertilization. The body of the prothallus stores up, as in Lycopodium and Filices, a reserve-material which is used by the growing embryo at a later period.

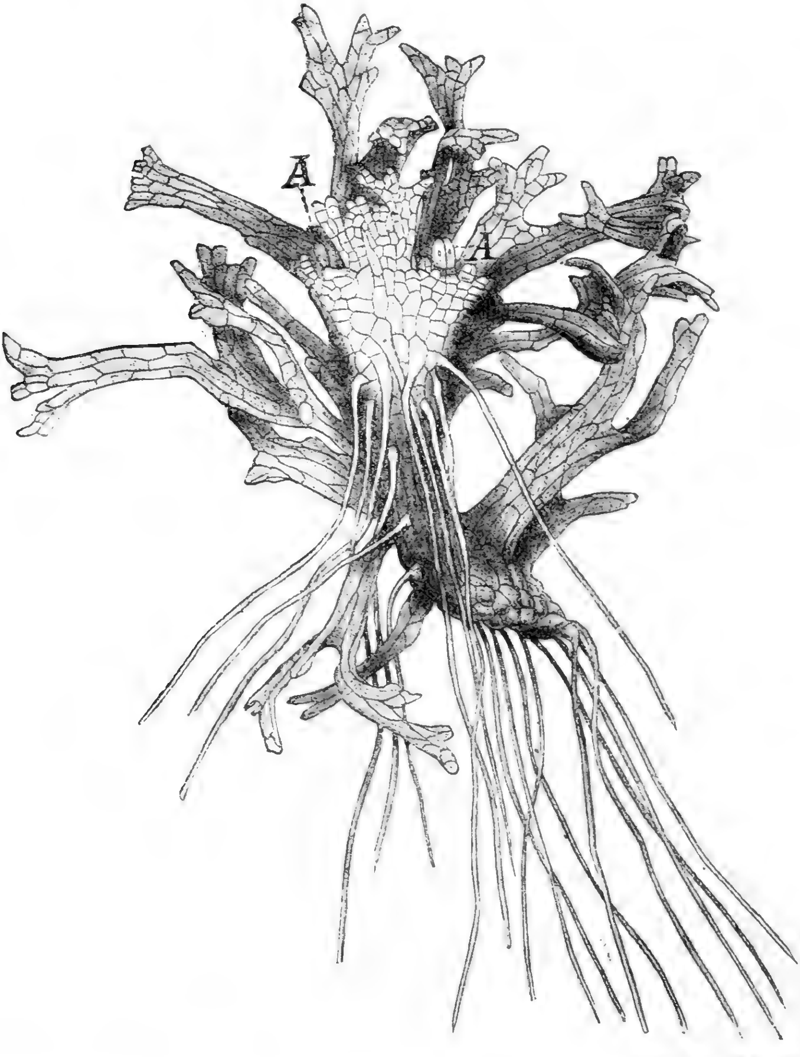

FIG. 143. Equisetum pratense. Female prothallus seen from below; *A*, *A*, archegonia. Magnified 35.

The male prothallus. This is smaller and is provided with smaller and fewer lobes (Fig. 132), it is also less rich in chlorophyll than the female. It varies, however, in bulk according to the environment and to the period of its development at which the formation of the antheridia sets in, and this moment depends also upon the environment. If the antheridia are formed relatively late, the male prothallus is very like the female ; it has a meristem which produces new antheridia anteriorly, but the formation of lobes from the meristem does not take place, and this is specially striking where female prothalli have been transformed into male ones. If, on the other hand, formation of antheridia takes place early, we commonly find that the prothalli are *ameristic*, and then they bear the antheridia at the points of their lobes. It is manifestly an advantage in the distribution of the spermatozoids when the antheridia are not interspersed amongst lobes.

Development of the prothallus. The earliest stages of germination of the spores of Equisetum are strongly influenced by external conditions. As they contain chlorophyll they are able to germinate right away. The mother-cell of the rhizoid is first of all cut off from the spore, and the rhizoids are negatively heliotropic in strong light, but if the atmosphere is moist they do not pierce the soil, being evidently affected by hydrotropism. In feebler illumination within a moist chamber, the rhizoids are positively heliotropic, a phenomenon which can scarcely have much significance for their life under normal conditions. In favourable conditions of illumination a cell-row proceeds from the mother-cell of the prothallus, and this row is developed into a surface which branches by the growing out of single cells. Upon the shaded side of the prothallus, which is already many cells thick, there appears then a meristem, and from it new lobes and archegonia are formed. Strong illumination brings about an earlier formation of a cell-surface, and where there is a copious supply of food-material a cell-mass may be formed, but this is not the common course of development. We shall find quite analogous cases of such plasticity amongst the Filicineae.

C. *THE GAMETOPHYTE OF THE FILICINEAE.*

The relationships of configuration of the prothalli of Filicineae have been the subject of many investigations, nevertheless our knowledge of them is not wanting in gaps, and as yet the prothallus is only known in about a tenth part of the species. For a long time it was supposed that the prothallus of the Filicineae was very uniformly constructed, and its type is figured in all text-books in what is indeed a very commonly occurring form, namely, a small thallus of heart-like outline which bears upon the under side behind the apical indentation the sexual organs—although the antheridia may also occur upon the one-layered lateral wings—and rhizoids. It is clear that even if all the prothalli of Filices appeared alike, this would only show the incompleteness of our method of investigation, because the prothallus of Gleichenia must have *inwardly* quite a different nature from that of Aspidium, otherwise its fertilized egg could not produce so very different a plant. The egg-cell is only a specially formed cell of prothallus, and is not fundamentally different from the other cells. There are, however, in the external relationships of configuration many more differences than has been supposed, as I have endeavoured to show in a series of publications. The prothallus with heart-like outline, far from being typical, is only a single case, no doubt widely spread, but hardly to be considered as the primary.

1. THE EUSPORANGIATE FILICINEAE.

Marattiaceae[1]. In the Marattiaceae where the prothallus is known it appears in the form which has been referred to above as that long considered 'typical.' It is distinguished amongst prothalli of like outline by its dark-green colour and by its fleshiness, and this extends to the margins which are here many-layered. The whole prothallus is usually from the first a cell-mass. It is also distinguished by the structure of the sexual organs which have been already described. The prothallus of Danaea has pluricellular rhizoids[2].

Ophioglossaceae. The prothalli of the Ophioglossaceae are still incompletely known, but they have this in common that they are hypogeous and saprophytic like those of some of the Lycopodia :—

Ophioglossum. In the genus Ophioglossum the prothallus has only been found in O. pedunculosum, and this by Mettenius[3]. The youngest prothalli are tubers from which a conical projection proceeds and this elongates considerably, exhibiting unlimited growth at its *apex*. This cylindric prothallus may become green and split into two or three small lobes in the light. Can this be an indication of a coronet of lobes? Mettenius appears to regard the distribution of the sexual organs on these prothalli as radial. Doubtless the prothalli are inhabited by a fungus. The prothallus has a certain resemblance to the prothallus of the Phlegmaria-type of Lycopodium, but the resemblance is entirely superficial.

Botrychium. With regard to Botrychium we have the older observations of Hofmeister[4] on Botrychium Lunaria and the more recent ones of Jeffrey[5] on B. virginianum. The tuberous prothallus of B. virginianum is dorsiventral and bears the sexual organs upon its upper side, and the

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[1] Jonkman, in Archives Néerlandaises, xx (1896); id., Über die Entwicklungsgeschichte des Prothallium der Marattiacieen, in Botanische Zeitung, xxxvi (1878), p. 129.

[2] Brebner, On the Prothallus and Embryo of Danaea simplicifolia, in Annals of Botany, x (1896). The first root of the embryo-plant has pluricellular root-hairs, a circumstance which appears to me to favour the view that we are dealing with a derived character.

[3] Mettenius, Filices horti botanici Lipsiensis, Leipzig, 1856, p. 119.

[4] Hofmeister, The Higher Cryptogamia. English Edition, Ray Society, London, 1862, p. 307.

[5] Jeffrey, The Gametophyte of Botrychium virginianum, in Studies from the University of Toronto, Biological Series, 1898.

meristem of the prothallus is also pushed upwards. Antheridia first of all arise on a ridge-like projection, on both sides of which the archegonia appear. The rhizoids are often pluricellular, especially those upon the ridge or upon the flanks of the prothallus[1], but those at the base of the prothallus are unicellular tubes. The prothallus is always inhabited by an endophytic fungus. Botrychium Lunaria probably resembles this in its main features, but from Hofmeister's observations we learn nothing about the position of the sexual organs and meristem. In both cases the earliest developmental stages are unknown and therefore we do not know whether or no the dorsiventral prothallus of Botrychium arises by a unilateral outgrowth from a primary radial body. The position of the sexual organs upon the upper side is manifestly more advantageous for fertilization in these hypogeous prothalli, than would be their position upon the under side[2], as in the Marattiaceae and others; and that the prothallus is not spread out as a surface is doubtless connected with the fact that it does not assimilate.

2. THE HOMOSPOROUS LEPTOSPORANGIATE FILICINEAE.

Hypogeous prothalli are, so far, unknown in this group. Chlorophyll is always present, except in the male prothalli of Salviniaceae and Marsiliaceae. There is one circumstance in their relationships of configuration that deserves notice as being of general interest, namely, that *growth of the prothallus is often arrested by the production of an embryo at an early period and before its characteristic peculiarities appear.* Two examples may illustrate this.

Osmunda. The prothallus of Osmunda is evidently heart-like in outline like that of the Polypodiaceae. If it is not arrested in its growth by the early formation of an embryo, it takes on its peculiar and characteristic growth-form: it grows into a band-like thallus extremely like that of many Hepaticae, attaining a length of over four centimeters and often perennating for many years[3]. The cushion of tissue on the under side which usually serves for the storing up of food-material is developed as a midrib and the archegonia are arranged to right and left of it, lobes occasionally shoot out only at the growing point, and these may be considered a rudimentary leaf-formation as in Dendroceros[4]. Formation of 'hairs' does not occur in the prothallus of the Osmundaceae.

Cyatheaceae. The Cyatheaceae furnish a second example. If the prothallus is arrested in its growth in consequence of the formation of

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[1] May these not rather be paraphyses?

[2] Compare also a like condition in the tuberous archegoniophore of Anogramme.

[3] Goebel, Entwicklungsgeschichte des Prothalliums von Gymnogramme leptophylla, Desv., in Botanische Zeitung, xxxv (1877), p. 704.

[4] See pp. 36, 56.

embryos at a time when it has not yet formed its peculiar 'hairs,' these hairs appear as bristle-like cell-surfaces on both sides of the prothallus, and also upon the edge in Balantium antarcticum.

I may conclude this notice of these facts by mentioning some other peculiarities of the Cyatheaceae, particularly the regular and sometimes very early branching of the prothallus in some forms. This occurs occasionally also in Osmunda (see Fig. 20, Part I), and in the old prothalli of Polypodiaceae, but in Cyatheaceae the prothallus may at a very early period become forked, as in Hemitelia (Amphicosmia) Walkerae (Fig. 144), or many vegetative points may be developed through branching, as in Hemitelia gigantea. These phenomena[1] are of interest because they furnish an indication of how the reduction of the prothallus may be brought about by the shifting of the inception of the sexual organs to an earlier period in the development of the prothallus. Such reduction appears in a very striking manner in the male prothalli of the heterosporous Filicineae, and in badly-nourished prothalli of Filicineae antheridia may appear when only two cells have been formed.

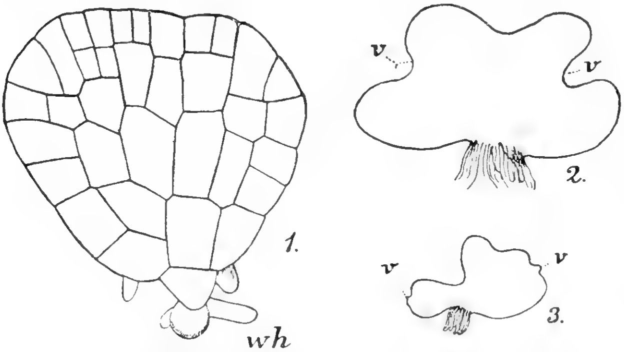

FIG. 144. Hemitelia (Amphicosmia) Walkerae. Development of prothallus. 1, young prothallus; *wh*, rhizoid. 2 and 3, older prothalli, each with two vegetative points, *v*, *v*. Magnified; 1 more highly so than 2 and 3.

Polypodiaceae. In the Polypodiaceae the prothallus has always unicellular 'hairs' if hairs are present. Some of them are 'glandular hairs,' some of them are 'bristle-hairs' (Figs. 145, 146); both are protective organs against the gnawing of animals. The Dicksonieae furnish a transition to the hair-formations of the Cyatheaceae. In them, both upon the upper and under side, as well as upon the edge of the prothallus, there are gland-hairs which have a basal foot-cell out of which a cell-row, sometimes branched, develops. Exceptions to the usual heart-like outline of the prothallus are found in some epiphytic Polypodiaceae, as well as in the Vittariaceae[2] and species of Anogramme. These epiphytic forms have long band-like prothalli with no cushion of tissue upon the under side, and the prothallus has many layers only at the positions where the archegonia arise (Fig. 145). This condition may be connected with the epiphytic method of life, inas-

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[1] The analogous condition is found in some heart-like prothalli of the Polypodiaceae and Aneimia, where, if an archegonium is fertilized at an early period, there is unequal development of the wings of the prothallus, and one of them may be entirely suppressed.

[2] See p. 206.

much as such epiphytic prothalli evidently can only develop archegonia in special favourable conditions, and they live vegetatively between times; their free propagation by gemmae which will be presently mentioned[1], may also be connected with this epiphytism.

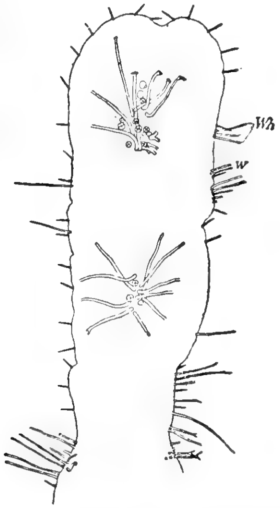

FIG. 145. Polypodium obliquatum. Prothallus seen from below. On the margin are 'bristle hairs' and rhizoids, *Wh*. On the surface two groups of archegonia surrounded by rhizoids. It is only at the points where these groups are that the prothallus is many-layered. Magnified.

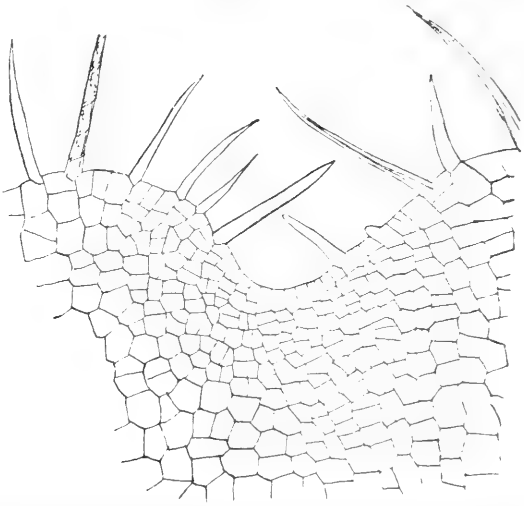

FIG. 146. Apex of a band-like prothallus with 'bristle hairs.' One of these bristle hairs shows a spiral line of rupture the result of swelling in potash solution. Highly magnified.

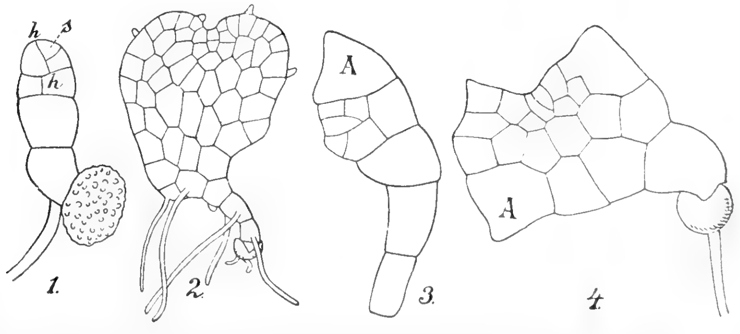

FIG. 147. Prothalli of Filicineae at different stages of development. 1, Hymenolepis spicata. Young prothallus. Below the ruptured wall of the spore. *s*, two-sided apical cell cut off by the oblique walls, *h*, *h*. 2, an older prothallus of a species undetermined. The two-sided apical cell is divided by a periclinal wall which initiates marginal growth. 3 and 4, Asplenium Nidus. *A*, end-cell of the prothallus, the meristem arises laterally. All magnified.

PROTHALLI OF POLYPODIACEAE WITH HEART-LIKE OUTLINE.

The prothallus, with heart-like outline, of the majority of the Polypodiaceae does not always develop in the same manner. In germination the cell-filament is first formed from the spore. Its length depends upon

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[1] See p. 214.

external factors. I have already pointed out when speaking of the Hepaticae that the form of the germ-plant depends upon external conditions, and that the filamentous form is always able to arrive at favourable conditions of illumination, in the same way as these are attained to often by the seedlings of Spermophyta through the elongation of the hypocotyl. Now in the Polypodiaceae this filamentous stage is not, or only rarely, missed out even in the most favourable conditions[1]. If the spores germinate closely together this stage persists longer (Fig. 150, *V*), and not infrequently a branching of the thread may take place; where the spores germinate isolated in most favourable conditions of illumination, surface-growth may begin in the second cell of the thread[2]. I found this to be the case in all the germ-plants of Pteris longifolia which were germinated singly upon mud. There can be little doubt that it would be possible to retain the germ-plant longer in the filamentous condition by subjecting it to other conditions than that of feeble illumination[3], and it is further possible that this stage could be again called forth at a later period. Young germ-plants

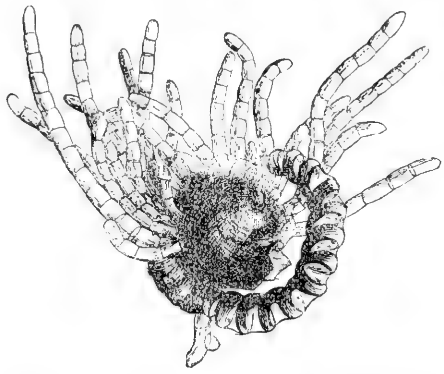

FIG. 148. Acrostichum peltatum. Sporangium in which spores have germinated while it was still attached to the sporophyte. The spores have formed only cell-rows. Magnified.

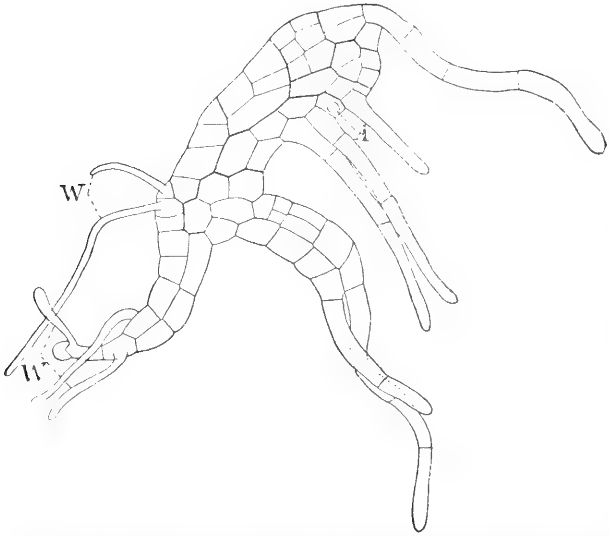

FIG. 149. Alsophila australis. Prothallus which has reverted to the formation of cell-threads in consequence of unfavourable nutritive conditions. The two-sided apical cell, the segments from which are indicated by stronger lines in the figure, has also grown out into a cell-thread; *W*, rhizoids; *A*, antheridium. Magnified.

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[1] There can be little doubt, however, that just as in Equisetum this can be artificially achieved by special conditions of cultivation.

[2] The first cell also may sometimes undergo division by a longitudinal wall, and it is probable that by definite methods of culture it would be possible to cause a cell-mass to form directly out of the spore after the fashion which is sometimes normal in the Marattiaceae.

[3] In Fig. 148 we have a representation of a sporangium of Acrostichum peltatum in which the

which have not yet formed typical meristem easily pass over again into the filamentous stage in feeble illumination (Fig. 149), in the same way as I have shown this to be the case in Preissia[1]. In older prothalli this only takes place if they have lost their meristem[2] and are enfeebled by an unfavourable environment. Commonly these conditions result in the production of pluricellular adventitious shoots[3]. The 'light-optimum' for the filamentous formation is lower than that for surface-growth[4]. Surface-growth is initiated in

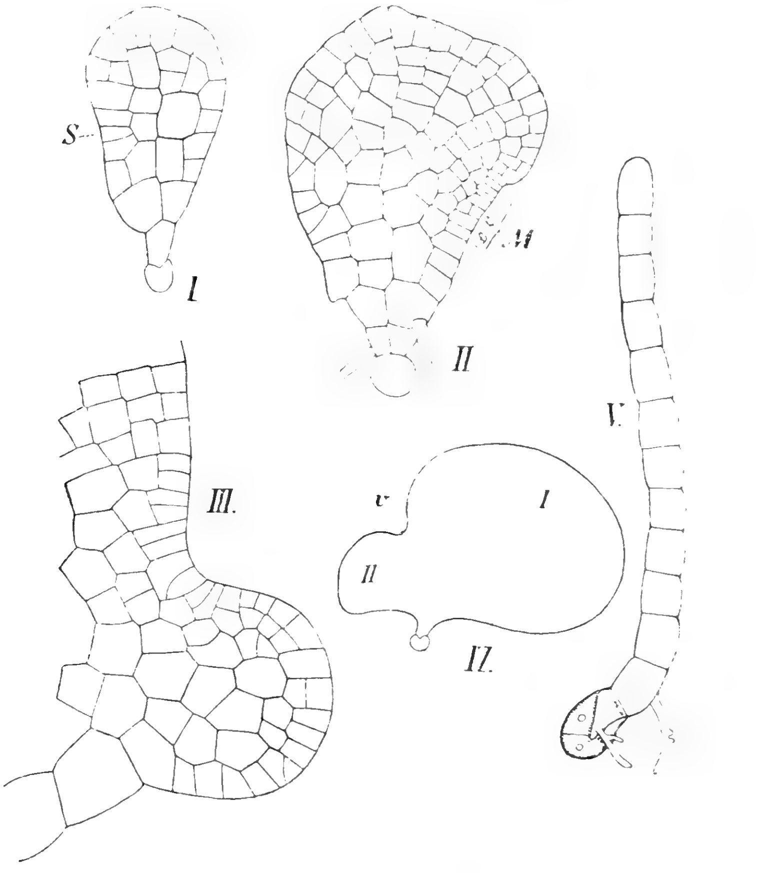

FIG. 150. *I–IV*, Pteris longifolia. Development of prothalli. In *II* the first cell of the filamentous part of the prothallus is concealed in the spore. *S*, apical cell; *M*, apical meristem; *v*, vegetative point. *V*, Acrostichum peltatum; a filamentous prothallus from the germination of a spore within the sporangium, as shown in Fig. 148. All magnified. Further description will be found in the text.

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spores have germinated whilst the sporangium is still fastened to the sporophyll. They have all grown out into dark-green cell-rows, and naturally contain only a very small amount of ash-elements.

[1] See Part I, p. 239.

[2] Goebel, Über Jugendformen von Pflanzen und deren künstliche Wiederhervorrufung, in Sitzungsberichte der bayerischen Akademie, 1896.

[3] See pp. 213, 216.

[4] Longitudinal divisions may take place in prothalli which under special conditions have developed in the dark.

the germ-thread by longitudinal division, usually before—and often very early—the first rhizoid has gone out from the position on the thread limited by the spore-membrane. Numerous other rhizoids follow the first one at a later period, and these issue from prothalli growing on the soil in the normal position always on their under side, but in epiphytic prothalli the rhizoids grow also from the margin (Fig. 145). It is not my intention here to depict the relationships of the cell-arrangement; I may merely point out that at the end of the young cell-surface a two-sided apical cell is found commonly, but this is subsequently divided by a periclinal wall[1], and thus *marginal growth* sets in (Fig. 147, 2). The two wings of the prothallus are developed right and left of the vegetative point, the heart-like outline is attained to, and then begins the formation of the many-layered cell-cushion. To this often-described construction I must merely add that the two wings of the prothallus are *not of the same age*. The surface of the prothallus which first develops from the germ-thread becomes at once the one wing, and the meristem which forms the vegetative point of the prothallus comes thereby to occupy a lateral position, and underneath it the second wing of the prothallus shoots out. Fig. 150 exhibits this process in Pteris longifolia. Here it will be seen that a one-layered cell-surface is formed first of all from the germ-thread without the aid of an apical cell, and the anticlinal walls diverge at the apex. It shows also the method in which the cells become chambered in the older stages (Fig. 150, *II*). The intensity of the cell-multiplication remains strongest at a *lateral* position on this cell-surface, and there is the meristem in which often a two-sided apical cell is visible. Below this meristem then shoots out the second prothallus-lobe which is at first, naturally, much smaller than the older one, but gradually reaches its size. In this case the cell-surface which first arises forms the greater part of the first lobe of the prothallus—in other cases it forms only a small portion of it. In Fig. 147, 4, for example, the young prothallus of Asplenium Nidus is represented, in which the meristem lies laterally in an earlier stage of development than that shown in Pteris longifolia (Fig. 150). If we compare Fig. 147, 3, we shall see that the meristem proceeds from the second cell from the apex of the cell-filament which ends with a papilla. In Platycerium[2] the meristem proceeds from one half of the end-cell.

I have here shortly referred to these relationships, not because they are of any great significance, but because they show us:—

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[1] In Lygodium the two-sided apical cell persists.

[2] The same is the case often in Aspidium Filix-mas and others. In Platycerium the meristem may sometimes be terminal, and one could also say, in cases in which a two-sided apical cell arises at the point of a cell-filament, that it only proceeds out of one half of the terminal cell. Such considerations, however, carry us no further, although analogous assertions, such as that the embryo of Musci corresponds only to one half of the embryo of Hepaticae, are even now repeatedly made.

(*a*) That *every gradation exists between a terminal and lateral primordium of a meristem.*

(*b*) That *in different sections of the Filicineae both conditions occur.*

Thus all Gymnogrammeae, so far as we know the development of their prothalli, are characterized by the lateral position of the primordium of their meristem, and by the late appearance of the two wings of the prothallus. Among the Schizaeaceae, Lygodium terminale has terminal, Schizaea and Mohria have lateral meristem. If the formation of *one* of the two wings be suppressed we pass then to the form of prothallus like that of Anogramme and Vittaria described below. I do not believe that one can construct a phyletic relationship between apical and lateral position of meristem. It seems to me that we have rather before us an instructive example of *two possible developments* between which one and the same species may oscillate, and of which, so far as our present knowledge permits us to judge, sometimes one sometimes the other is become dominant in more than one cycle of affinity, although, at the same time, it is a matter of indifference from the point of view of the manner of life which of them obtains. That the heart-like outline of the prothallus is always finally attained to, although by different ways in these forms, may find its explanation in this, it is a beneficial configuration. The wings lie loose, seeing that they develop no rhizoids, upon the surface of the soil, and under them drops of water collect[1] (Fig. 151), which then can be readily absorbed by the middle portion of the prothallus with its numerous rhizoids. The prothallus of Osmunda, shown in Fig. 151, was the result of a prolonged culture upon a substratum very poor in nutriment. It was weakly, the wing-formation was almost entirely suppressed, no archegonia appeared, antheridia were numerous and mostly upon the edge. After feeding it well the wing-formation began and also archegonia were formed. The prothalli of Osmundaceae revert to the filamentous form much less easily than do those of other ferns.

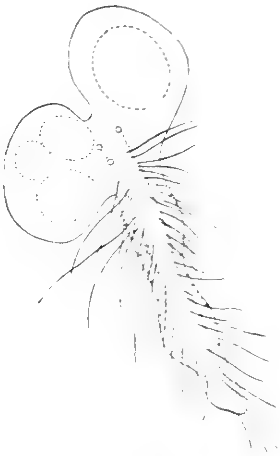

FIG. 151. Osmunda regalis. Prothallus which was at first badly fed, and therefore was almost wingless and with marginal antheridia. This is seen in the lower part of the figure. The upper part of the figure shows the prothallus, after being better fed, where broad wings have developed, beneath which drops of water (indicated by dots) collect.

PROTHALLI OF POLYPODIACEAE WANTING THE HEART-LIKE OUTLINE.

Anogramme. The prothallus of the genus Anogramme connects with the forms in which the formation of the two wings takes place at different

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[1] How they arise we shall not stop to inquire.

times. On account of its noteworthy adaptations it will be mentioned particularly below[1]. It produces only, if one may so say, one wing with lateral meristem, behind which there is formed a peculiar tuberous archegoniophore. The prothallus with heart-like outline is here never reached.

Vittariaceae. The Vittariaceae also have not prothalli with heart-like outline in the cases which have been accurately investigated. There arises in the first instance a simple cell-surface with marginal growth. This divides into lobes (Fig. 152), through isolated portions of the meristic margin passing into a permanent condition, and thus there is developed a highly irregular lobed body in some ways resembling the flat protonema of Sphagnum, and it forms marginal groups of archegonia which, primarily arising in the meristem, are separated from it at a later time by the portions which have passed into the permanent condition.

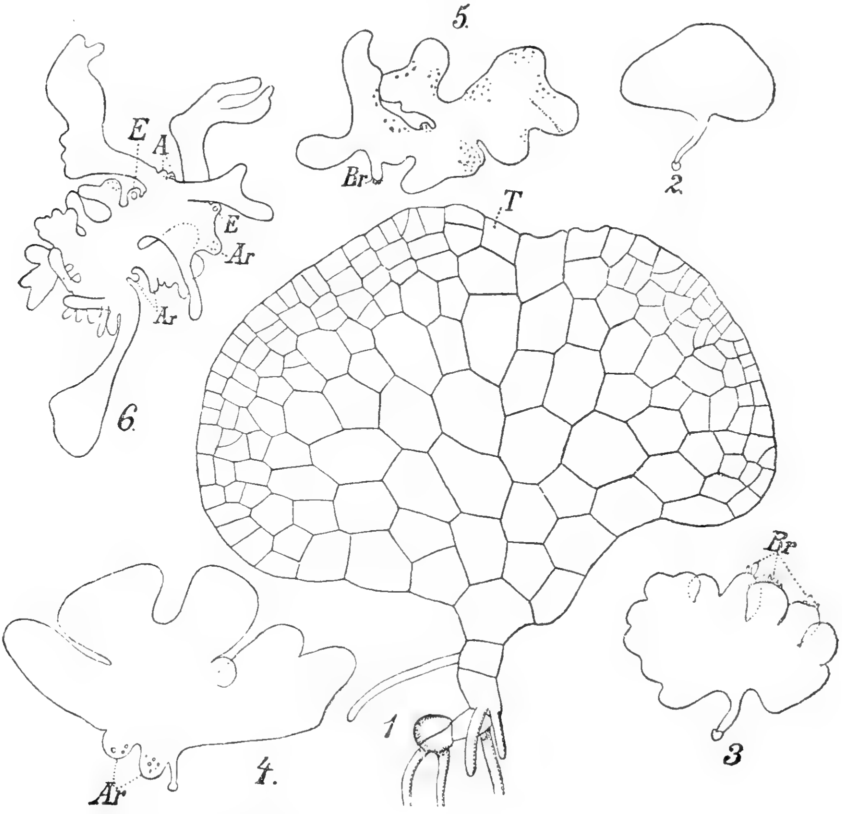

FIG. 152. Vittaria. 1–6, Formation of prothallus; *Ar*, archegonia; *E*, embryo; *Br*, gemmae. 1, highly magnified. The others slightly magnified.

Hymenophyllum. The form of prothallus of Vittariaceae leads us to that of Hymenophyllum. Here we have also to do with a richly-branched,

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[1] See p. 216.

one-layered prothallus, upon which in most cases only the many cushions bearing archegonia are many-layered. The meristem is mainly limited to the points of the lobes of the prothallus, and the lobes are more band-like than in Vittaria. The rhizoids arise upon the margin. A portion of a prothallus of Hymenophyllum axillare is represented in Fig. 153. Cell-cushions bearing archegonia, *A*, are formed at five positions on the margin of the one-layered prothallus. These cushions are originally in connexion with the apical meristem, as is shown at the top of the figure to the right, and as the tissue of the cushion retains for a long time its meristic quality, the cushion often projects lobe-like beyond the margin of the prothallus. The prothalli may multiply vegetatively by dying off behind, thus isolating the twigs; but the prothalli of many species of Hymenophyllaceae possess special propagative organs besides, as will be shown below[1]. The configuration of the prothallus is alike in all the species of Hymenophyllum which have been examined up to this time—not many it is true.

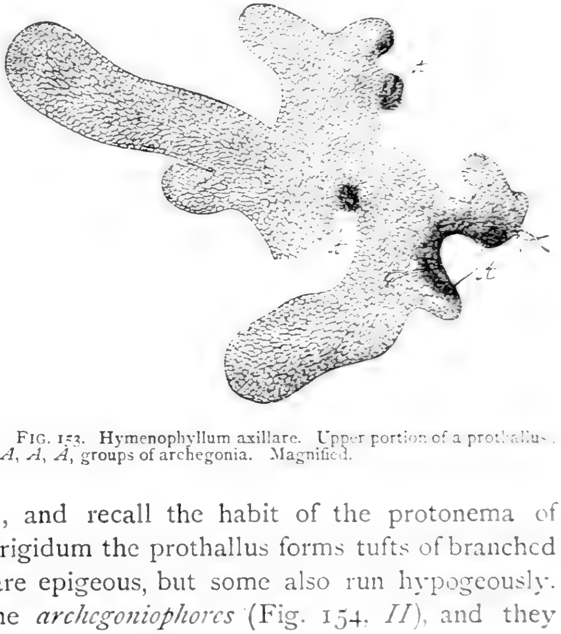

FIG. 153. Hymenophyllum axillare. Upper portion of a prothallus. *A*, *A*, *A*, groups of archegonia. Magnified.

Trichomanes. We do not find this similarity, however, in Trichomanes. The prothalli in some forms of this genus, such as T. rigidum, T. diffusum (Fig. 154, *I*), and others, diverge markedly from those which have been already described, and recall the habit of the protonema of the Musci. In Trichomanes rigidum the prothallus forms tufts of branched cell-threads, most of which are epigeous, but some also run hypogeously. Single short branches become *archegoniophores* (Fig. 154, *II*), and they develop as cell-masses, whilst the antheridia stand upon the ordinary cells of the filament, a difference which is easily understandable from the biological side, and is repeated in essentials in the prothalli of other Filicineae. The archegoniophores are cell-bodies of limited growth and the archegonia are distributed radially upon them. Species of Trichomanes, like T. sinuosum, in which the prothallus is not merely a cell-filament, but also a cell-surface which has only limited growth, like the organs of assimilation in the protonema of Tetraphis and allied Musci[2], afford a transition from the filamentous prothallus of Trichomanes to

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[1] See p. 214.

[2] See p. 121.

the surface-prothallus of Hymenophyllum. The groundwork of the whole prothallus, its skeleton so to speak, is formed by the threads, and these also spring out in numbers from the cell-surface (Fig. 154, *III*)[1]. The cell-surface here must be considered as a transformation of the cell-filaments, and the distribution of the sexual organs also confirms this view. The antheridia stand on the cell-filament, more rarely on the margin of the cell-surface; the archegonia stand upon the archegoniophores, which are formed as cell-masses at the end of short filaments, just as in Trichomanes rigidum, only here frequently, but not always, the archegonia have a dorsiventral distribution. The archegoniophores can grow out into cell-surfaces if the formation of the embryo is suppressed; the cushion of the archegonia then stands on the margin of the under side of this cell-surface, and the whole reminds one of the behaviour of the prothallus of Hymenophyllum. If the transition from cell-filaments to cell-surfaces in the prothallus of Trichomanes sinuosum takes place at an early period in the germination, the cell-filament will appear as a juvenile stage rapidly passed through; the cell-masses which are to be designated archegoniophores with unlimited growth are formed then directly and without any intervention of a cell-thread on the margin of the cell-surface. The first stages of germination suggest such a derivation. These show that from the spore there usually arise many cell-filaments, frequently three, which I have observed at an early period becoming branched, although this is not the case in Trichomanes maximum and T. radicans which germinate like other leptosporangiate Filicineae. Of the three cell-filaments thus initiated all may develop as cell-filaments in Trichomanes, but in Hymenophyllum one quickly passes over into a cell-surface, the others are arrested.

SUMMARY.

When we review the facts which have just been cited regarding the development of the prothallus in the Filicineae, different questions force themselves upon us; one is, Is there any connecting-thread between all these varieties of configuration? Can they be arranged in connected series which would also link on to the gametophyte of the Musci? I have before now endeavoured to answer this question, and I have pointed out that if we seek for such a hypothetical link it is essential to keep in view the configuration of the gametophyte of the Musci as it appears in the mature stage, that is to say, at the time of the formation of the sexual organs, as this is, when we regard it from the standpoint of the theory of descent, also the result of a long development which started from simple relationships of configuration. We may, from our knowledge of the configuration of the vegetative body produced in germination in many Bryophyta, conceive these simple primitive forms to have had a configuration of

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[1] Compare the analogous case of the leaves of Buxbaumia, p. 127.

branched threads upon which the sexual organs sat[1]. The portion of the filaments which bore the archegonia achieved a more massive development in correspondence with its 'need' of a better nutrition, and it became a cell-mass as we find it in Trichomanes rigidum—an archegoniophore. In Trichomanes sinuosum we see this grow out into a surface, and thus the configuration of the prothalli of other Filicineae is approached. If we suppose that this assumption of vegetative activity of the archegoniophore, which renders possible a rapid nutrition of the embryo, was begun at an early period of development, the filamentous phase of development of the prothallus would be shortened. It would appear, as in most of the leptosporangiate Filicineae, only in the first steps of development, and might be entirely lost. And thus a cell-body might arise in the germination at once similar to that which is found in many examples both of the Hepaticae and of the Musci. Finally we see that the different forms of surface-formation—terminal and lateral meristem, heart-like and simple surface-formation—are

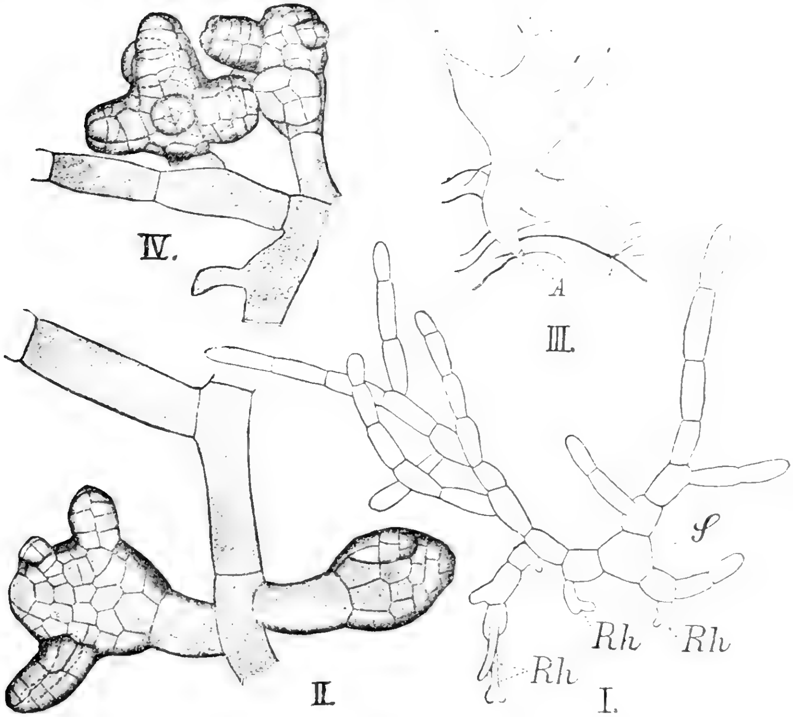

FIG. 154. Trichomanes. Formation of prothallus. , T. diffusum. Young filamentous prothallus; *S*, spore which has developed cell-filaments in three directions; *Rh*, rhizoids. *II*, T. rigidum. Portion of filamentous prothallus with two archegoniophores. *III*, T. sinuosum. Prothallus showing habit. From the cell-surface filaments pass out which give origin to new cell-surfaces; *A*, position of an archegoniophore. *IV*, T. sinuosum. Portion of a filamentous prothallus bearing two archegoniophores which pass over into cell-surfaces. *I* and *III*, slightly magnified. *II* and *IV*, highly magnified.

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[1] Compare Buxbaumia, p. 127.

connected with one another by transition. We observe then *the connexion* between the forms, but whether this corresponds with a *phyletic series* is altogether uncertain. We can also here, as has been already pointed out in the case of the Musci, invert the series, and may start from forms which begin with massive prothalli, like those of Lycopodium, and which then from a radial construction pass over into the dorsiventral, as we have observed it in Lycopodium Selago, and we may consider the formation of cell-filaments as merely an adaptation to the environment. There is indeed at the present time nothing to indicate why within the Hymenophyllaceae, which are so wide-spread yet occur under similar conditions of life, the species of Trichomanes should have mainly a filamentous prothallus, whilst species of Hymenophyllum[1] have a surface-prothallus. In the present state of our knowledge we must not reckon upon discovering any certain phyletic indication in the prothallus; we must simply content ourselves with recognizing the connexions whose genetic significance remains uncertain. It has already been shown that the structure of the spermatozoids makes improbable a monophyletic origin of the Pteridophyta, and the similarities which exist, for example, between the prothallus of Ophioglossum and that of Lycopodium, do not require us to ascribe to these a *genetic* relationship. It is much more probable that these resemblances have come about like those of the formation of the thallus of many Hepaticae[2], in which we can certainly trace *parallel lines of formation* which, starting *from different simple forms*, have arrived at *similar conformations*. Within single natural groups also one may well recognize a conformity in the formation of the prothallus which is expressed in the possibility of arranging them in series, as we have endeavoured to do for the Hymenophyllaceae and other Filicineae, but as soon as we pass beyond this we always reach uncertain ground which indeed offers a favourable field for hypotheses, but is not one upon which to raise a surely founded superstructure.

3. THE HETEROSPOROUS LEPTOSPORANGIATE FILICINEAE.

We must now say something regarding the heterosporous leptosporangiate Filicineae. It is only necessary to deal with the female prothallus[3].

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[1] If the configuration of the prothallus of the Hymenophyllaceae, especially that of Trichomanes, were an adaptation, one would expect similar phenomena in other forms under similar life-conditions, and we find in the sporophyte of some of the Polypodiaceae, for example Asplenium obtusatum f. aquatica, of the Osmundaceae species of Todea, and others, adaptations quite like those in the leaves of the Hymenophyllaceae. Up till now, however, no case has become known of the prothalli of any of the above-mentioned forms conforming with those of the Hymenophyllaceae. They all resemble those of *allied* forms. This does not mean that such cases may not exist, but the position of the archegonial cushion in Hymenophyllum could scarcely be considered as an adaptive character, and it appears to me very doubtful whether adaptation can be proved in the other peculiar features of the prothallus.

[2] See p. 25.

[3] See p. 180.

SALVINIACEAE. The female prothallus of Salviniaceae resembles that of Marsiliaceae in so far as it is only formed at the apex of the megaspore (Fig. 156); the greater portion of the internal space of the megaspore remains as a reservoir of reserve-material. The prothallus is chlorophyllous and in varying degree, that of Salvinia has much, that of Azolla caroliniana very little chlorophyll.

Salvinia. The prothallus of Salvinia possesses *meristem*, and thus approaches also most nearly that of the other ferns. In Fig. 155, *II*, is shown a prothallus of Salvinia natans viewed from the upper side. It has the shape of an equilateral triangle with blunt angles[1]. The portion ending in the angle turned towards the lower part of the figure remains sterile, whilst three archegonia are produced towards the opposite subtending side. If fertilization is affected in one of these archegonia no more are developed, but otherwise new archegonia arise out of the meristem, *sk*. We may say that the whole prothallus corresponds somewhat with the cushion of tissue of the prothallus of one of the Polypodiaceae, only that the archegonia arise here upon the upper side. Two wings arise at a later period out of the meristem, but they do not extend forwards but backwards. It is scarcely likely that these wings correspond with those of the prothallus of the Polypodiaceae; they probably serve to increase the absorptive surface of the prothallus, and

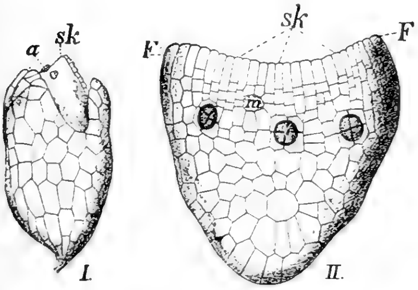

FIG. 155. Salvinia natans. *I*, megaspore germinating; *a*, archegonium; *sk*, apical ridge. *II*, prothallus isolated seen from above; three archegonia and the mother-cell, *m*, of a fourth are visible; *sk*, apical ridge of meristem; *F*, position whence the wings are developed. Magnified. *I* After Pringsheim. *II* After Bauke.

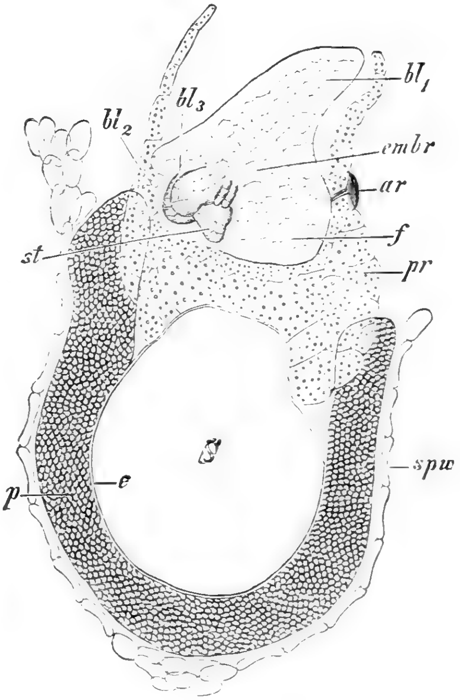

FIG. 156. Salvinia natans. Germinated megaspore; prothallus and embryo in longitudinal section in the median line of the prothallus. *spw*, portion of wall of sporangium; *p*, perinium; *c*, exine; *s*, cavity of the spore; *pr*, prothallus; *ar*, neck of archegonium; *embr*, embryo; *st*, apex of stem; *f*, foot; bl_1, bl_2, bl_3, the first three leaves. Magnified 100. After Pringsheim. Lehrb.

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[1] The whole prothallus is, however, curved like a saddle (see Fig. 155, *I*).

take a share in adding to the ash-constituents of the embryo. The capacity for growth of the apex of the prothallus is limited, just as it is in the Polypodiaceae. There are formed from it a great number of archegonia, but there is no vegetative development, although this were perhaps possible if the formation of archegonia were suppressed [1].

Azolla. The female prothallus of Azolla [2] is smaller and more reduced than is that of Salvinia, and there appears to be no formation of meristem in it. It produces first of all one archegonium, and if fertilization is effected in this one no more are produced; if fertilization does not take place more archegonia arise up to about ten [3].

MARSILIACEAE. In the Marsiliaceae but one archegonium is produced. The prothallus here develops rhizoids, and if no fertilization takes place upon it, it exhibits an exuberant growth; but it does not form new archegonia nor adventitious shoots, and soon withers. The reason for the reduction in the number of the archegonia may in some measure be understood, I think, when we look at it from the biological standpoint. In Marsilia and Pilularia the megaspores and microspores are always distributed together. That an archegonium should remain unfertilized is here an occurrence which is rare relatively when compared with the case of homosporous ferns. In Salvinia fertilization is less certain, but it is made more probable by the longer duration of active archegonia through their formation anew. In Azolla the frothy masses in which the microspores are aggregated possess the remarkable hooks (*glochidia*) through which they become anchored, so to speak, to the megaspores [4], and therefore fewer archegonia appear to be necessary here. We may say then generally that *the number of archegonia varies inversely with the certainty of fertilization.* Where fertilization appears to be certain few archegonia are produced. If, on the other hand, there is a risk of its failure, many archegonia are produced.

4. ISOETACEAE.

I may conclude this account of the formation of the prothallus by a short description of that in Isoetes, which occupies so isolated a position. The very simple formation of the male prothallus I have already mentioned [5]. The female prothallus fills as a cell-tissue the whole interior of the megaspore, but it forms no chlorophyll, and projects only slightly out

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[1] This would be very difficult to bring about because the megaspore contains food-material sufficient to make the prothallus independent of light.

[2] The megaspores of Azolla germinate under water, and subsequently rise to the surface of the water. I observed the same in Marsilia Drummondi; it is only with the development of the intercellular spaces in the embryo-plant that the whole structure is able to float to the surface. Megaspores within which no fertilization has taken place remain submerged; see Goebel, Pflanzenbiologische Schilderungen, iii (1893), p. 272.

[3] In Salvinia there may be four times this number.

[4] See p. 218.

[5] See p. 181.

of the ruptured wall of the megaspore. The course of its development accords with that in the megaspore of Selaginella [1], and also with the formation of the prothallus in the megaspore of the Gymnospermae. As in Selaginella, the prothallus shows to a certain extent a polar differentiation as its formation begins at the apex of the spore, and there alone the archegonia are formed in limited number. So far as we know the prothallus is incapable of becoming green or of developing further. There is no doubt that the female prothallus of Isoetes resembles much more that of the Lycopodiaceae than that of the heterosporous Filicineae, but we know only the heterosporous forms of leptosporangiate Filicineae, and with these Isoetes has but little in common.

III

ASEXUAL PROPAGATION OF THE PROTHALLUS

ADVENTITIOUS SHOOTS.

It has been already pointed out that the prothallus may propagate itself vegetatively and perennate; that from the old cells that have already passed into a permanent condition new formations may start, and these may grow out into prothalli. These are the so-called *adventitious shoots*. All prothalli, however, have not this capacity. Adventitious shoots are unknown in Lycopodium annotinum, L. clavatum, L. complanatum, whilst from broken-off portions of the coronet of lobes in Lycopodium inundatum new prothalli may proceed. Bruchmann also found adventitious shoots on prothalli of Lycopodium Selago [2] which were either old or had an injured apex, conditions which, as I have previously shown, have to be considered in connexion with the prothalli of Filicineae [3]. The question of the capacity for regeneration in the Equisetaceae requires new investigation. Buchtien [4] denies the possibilities, yet I see no reason why it should not occur. In the homosporous Filicineae the formation of adventitious shoots is extraordinarily common, but I do not require to mention the details.

GEMMAE.

The formation of special asexual organs of propagation which are designated *gemmae* or *brood-buds*, occurs in the prothalli of some species

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[1] See Arnoldi, Die Entwicklungsgeschichte des weiblichen Vorkeimes bei den heterosporen Lycopodiaceen, in Botanische Zeitung, liv (1896), p. 160.

[2] Adventitious shoots also appear in Lycopodium Phlegmaria.

[3] See Part I, p. 49.

[4] Buchtien, Entwicklungsgeschichte des Prothallium von Equisetum, in Bibliotheca Botanica, viii (1887), p. 24.

of Lycopodium, and also in many Hymenophyllaceae and Vittariaceae, and thus, as in the Hepaticae, formation of gemmae has arisen frequently and independently in different series of the Pteridophyta, as a 'character of adaptation.'

Lycopodium Phlegmaria. Treub found in Lycopodium Phlegmaria two kinds of gemmae, ordinary ones, and those with thickened outer wall. The former are ovoid cell-bodies seated upon a short stalk[1], and they grow out directly into the new cylindric prothallus. Thick-walled gemmae arise from the prothallus when it finds itself under unfavourable conditions for vegetation, and they consist of few cells, each of which has a thick outer wall. These gemmae are essentially resting buds, and they secure the perennation of the prothallus when the conditions are unfavourable.

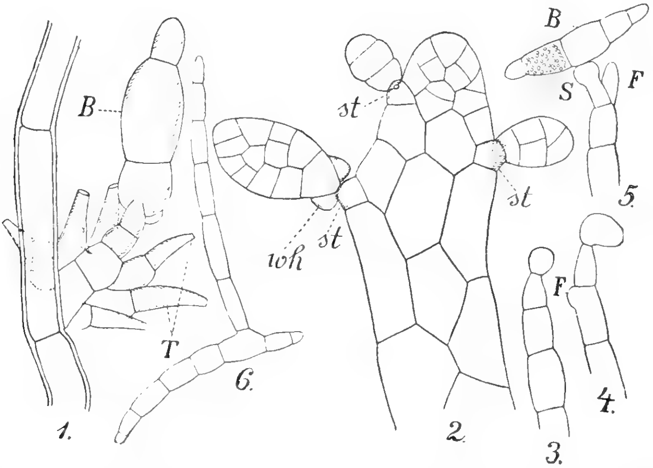

FIG. 157. Hymenophyllaceae. Formation of gemmae on the prothallus. 1, Trichomanes rigidum; *B*, gemma; *T*, sterigma. From a specimen collected in Venezuela. 2, Hymenophyllum sp.; *st*, sterigma; *wh*, primordium of rhizoid. From a specimen collected in Java. 3, 4, 5, Trichomanes venosum; *B*, gemma; *S*, sterigma; *F*, developing stalk for a gemma. From a specimen collected on the Black Spur Mountains, Australia. 6, Germination of gemma.

Hymenophyllaceae. Gemmae are known in the species both of Trichomanes and Hymenophyllum. I have already carried back the gemmae of many Hepaticae 'to the formation of brood-cells, which frequently develop further even upon the mother-plant,' and this holds also for the gemmae of the prothalli of Filicineae. It is sufficient to refer to Fig. 157 in order to make clear the relationships.

Vittariaceae. In Vittariaceae[2] gemmae are known in Vittaria, Monogramme, Hecistopteris, where they appear in the form of cell-rows. The two end-cells are distinguished from the others which contain chlorophyll

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[1] Gemmae may also proceed from the paraphyses of the sexual organs.

[2] Goebel, Morphologische und biologische Studien: II. Zur Keimungsgeschichte einiger Farne, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 78; id., Hecistopteris eine verkannte Farngattung, in Flora, lxxxii (1896), p. 67.

and starch by their smaller size, and by the absence of chlorophyll, or by its small quantity. One of them shows an almost circular brown fleck, the position at which the gemma was attached to its stalk-cell. These stalk-cells are, just like those of Trichomanes shown in Fig. 157, not ordinary cells of the prothallus, but special outgrowths upon the prothallus, and they may be designated *sterigmata.* Many sterigmata may arise upon one cell of a prothallus, and many gemmae may be formed from each sterigma, consequently the number of buds produced is immense. The gemmae arise upon the sterigmata originally as narrow outgrowths which are subsequently constricted at their base, at which point they become separated from the sterigma by a wall, and each outgrowth is the mother-cell of a gemma. This mother-cell divides then by cross-walls, and the gemma finally separates and forms a new surface-prothallus. Large gemmae may give rise to two prothalli.

It appears to me probable that the formation of gemmae has originated, especially in these prothalli of the Pteridophyta, because the *formation of the embryo is often hindered for a long time by the conditions of life.* At any rate the formation of gemmae furnishes a means for unlimited propagation of the prothallus independently of the germination of the spore.

IV

PHENOMENA OF ADAPTATION OF THE PROTHALLUS

The reason why we should expect fewer striking and less numerous phenomena of adaptation in the prothalli of Pteridophyta than in the Hepaticae has been already stated [1].

Relationships to Water.

There are no special contrivances for the holding of water—if we except the formation of lobes in the prothalli of Lycopodium inundatum and L. cernuum as well as in the female prothallus of Equisetum [2]—and up till now arrangements for the tiding over of a period of drought have been found only in two species of the genus Anogramme, and these take the form of the production of tubers which, as we know, occur also in many Hepaticae [3].

Anogramme chaerophylla. It has been already pointed out that

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[1] See p. 189.

[2] See p. 195.

[3] It appears to me probable that analogous conditions occur in other Filicineae, as the formation of sclerotia occurs in different cycles of affinity in the Hepaticae. See p. 66.

Anogramme belongs to that group of Filicineae in which the prothallus with heart-like outline does not appear, and indeed we might regard the prothallus of Anogramme chaerophylla[1], as it is shown in Fig. 158, as quite that of Gymnogramme or of Pteris longifolia, on which the second wing had not yet been developed, and the meristem was lateral. Old prothalli are funnel-shaped, not flattened as is usually the case elsewhere, and a tubercular archegoniophore[2] arises behind the meristem instead of the usual flat cell-cushion bearing archegonia. This archegoniophore pierces the soil. Its hinder portion elongates mostly into a stalk, the front portion bears a roundish tubercle within which is much starch and other reserve-food. The tubercle is thus very like tubercles which we have seen in many Hepaticae and is in a condition to persist through dry periods, and if it bears an embryo this is in a position to develop rapidly with the advent of more favourable vegetative conditions. Should the formation of the embryo be suppressed, there is formed from the tuber a new lobe of a prothallus which then later will form a tuberous archegoniophore (Fig. 158, 3, 4). Adventitious shoots may sometimes develop into similar tubers in other positions upon the prothallus, and these are then simply resting vegetative sclerotia, and they appear only when the conditions of nutrition are bad. It is probably the external conditions which determine whether an adventitious shoot of the ordinary kind or one in the form of a sclerotium shall arise, just as these determine the development of the resting gemmae in Lycopodium Phlegmaria.

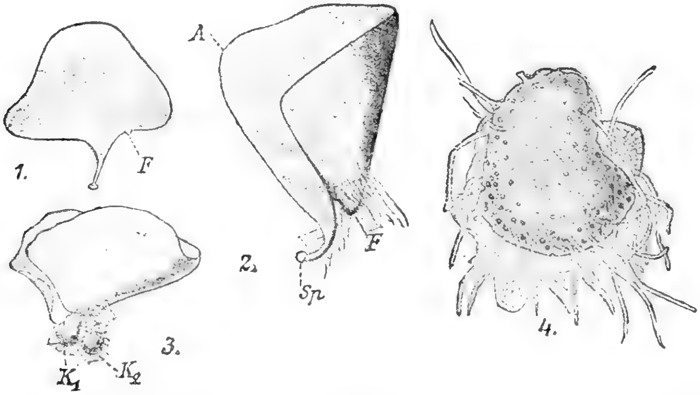

FIG. 158. Anogramme chaerophylla. 1, young prothallus spread out upon which an archegoniophore, *F*, is already laid down. 2, a somewhat older prothallus in profile view; *A*, probably original apex of prothallus; *sp*, exosporium still sticking to the base of the prothallus; *F*, archegoniophore. 3, prothallus issuing from a tuber, K_1; a new tuber is seen at K_2. 4, tuber from which a new prothallus is shooting. All magnified.

Anogramme leptophylla. The relationships in the widely-spread

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[1] See Goebel, Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 21.

[2] This term of Bower's is preferable to 'fruit-shoot,' the one I used earlier.

Anogramme leptophylla[1] are somewhat more complex. Its sporophyte is annual, as is that of A. chaerophylla. The prothallus, like that of A. chaerophylla, is a spathulate cell-surface which is funnel-shaped and not flat (Fig. 159), and which can branch and form lobes somewhat after the fashion of that in Vittaria. The tuber-like archegoniophore, however, does not arise upon the lobes, or does so only in a few exceptional cases; but the base of the cell-surface which is many-layered produces a new cell-surface of limited growth[2], and this forms upon its under side a tuberous archegoniophore, or at its base brings forth a new cell-surface, and so on. From one spore there proceed therefore a great number of surface-prothalli which are connected at their base, and the youngest of these produces the archegoniophore. Their great assimilating surface enables them to produce larger tubercles than is the case in A. chaerophylla, and as in that species these form, when no embryo arises, two or it may be three surface-prothalli. The prothallus in this species is then pre-eminently fitted to withstand a period of drought.

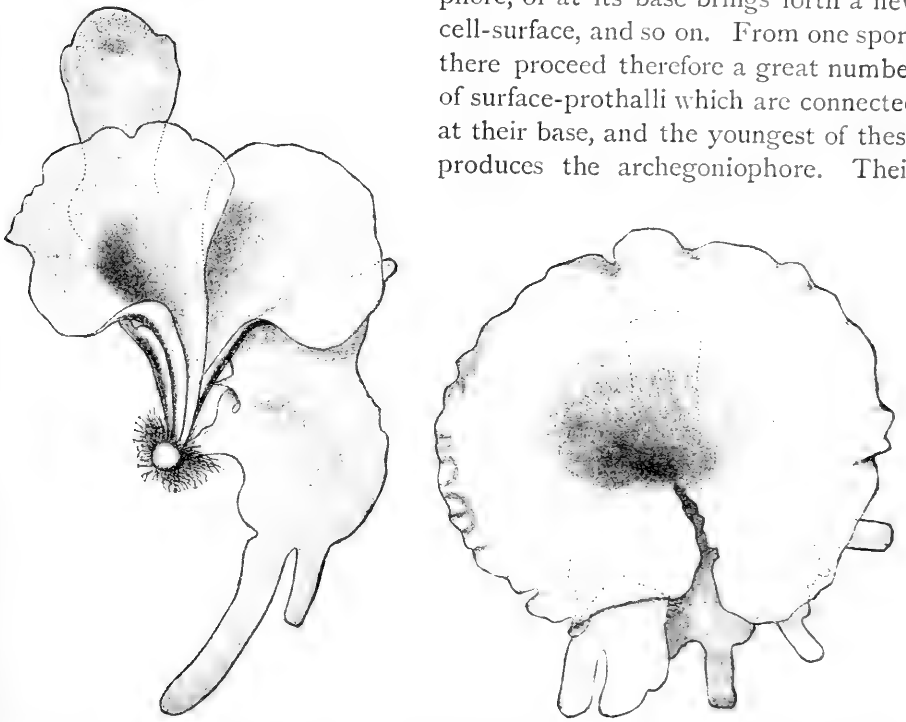

FIG. 159. Anogramme (Gymnogramme) leptophylla. Two prothalli to show habit. To the left a prothallus with tuber in profile view. To the right a prothallus seen from above. Magnified about 4.

Aquatic prothalli. In prothalli which are adapted to a water-life we

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[1] See Goebel, Entwicklungsgeschichte des Prothalliums von Gymnogramme leptophylla, Desv., in Botanische Zeitung, xxxv (1877), p. 697; id., Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 25.

[2] This recalls the behaviour—*mutatis mutandis*—of Lycopodium salakense, where many prothalli shoot out from the 'tubercule primaire.' In both cases we have to deal with a derived phenomenon. I have recently found like appearances in Mohria caffrorum.

find, as we might expect, arrangements which stand in relation to their method of life. These will be in part mentioned when dealing with the sporangia[1]. Here I merely point out that the microspores of the Salviniaceae are not scattered singly, they would be very easily swept away if this were the case[2]. In Salvinia they remain as a frothy mass embedded within the microsporangium, and burst through the sporangial wall in germination. In Azolla their relationships are still more remarkable, for there is formed within the microsporangium, not one mass enclosing the microspores, but many, the so-called *massulae*, and these reach the water by the rotting of the sporangial wall. They have numerous stalked hooks (*glochidia*) by means of which they are able to anchor to the rough envelope of a megaspore—one of the most remarkable arrangements for securing fertilization[3].

SYMBIOSIS WITH FUNGI.

We have already referred to the remarkable symbiosis of Cyanophyceae and some Hepaticae[4], regarding the biological significance of which it is only possible to put forward conjectures. In the gametophyte of the Pteridophyta a symbiosis such as that in the Hepaticae which presupposes the existence of mucilage-chambers is excluded. It turns up, however, in the most remarkable manner in the sporophyte of Azolla. On the other hand, the gametophyte of many Pteridophyta harbours fungi, and there is not the slightest doubt that they live in a number of cases in a state of reciprocal symbiosis, and not as simple parasites in the prothallus. Probably they bring about decomposition of organic remains in the substratum and thereby contribute to the saprophytic nutrition of the prothallus. They are found particularly in all prothalli which have no chlorophyll, those, for example, of the Ophioglossaceae[5], and of many species of Lycopodium in which a remarkable formation of tissue is part of the consequence of the presence of the fungus. There are probably gradations between cases in which the fungus inhabits the prothallus as a harmless parasite, and those in which it is of use to the prothallus. Experimental investigation can alone clear up this point. In what follows I state shortly the most important morphological facts, beginning with the simplest cases:—

Polypodiaceae. The prothalli of Polypodium obliquatum[6] and some undetermined allies have the rhizoids almost always infected with fungi, and the mycelium is found also in the cell from which the rhizoids spring as

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[1] See p. 494.

[2] We may compare the bundles of floating pollen in Zostera.

[3] See p. 212.

[4] See p. 78.

[5] The existence of the fungus in Ophioglossum pedunculosum is not mentioned by Mettenius, but there can be little doubt that it is present there.

[6] See Goebel, Morphologische und biologische Studien: II. Zur Keimungsgeschichte einiger Farne, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 76.

a fine coil of hyphae. The fungus here gives the impression of being a harmless parasite.

Hymenophyllaceae. Infection by fungi through the rhizoids takes place in the prothallus of Trichomanes. All the tufts of prothalli of Trichomanes rigidum[1] which I examined showed the fungus, but always limited to a relatively small number of the cells near the soil, which were frequently swollen and poor in contents.

Ophioglossaceae. In Botrychium a considerable number of the cells of the prothallus are inhabited by an unsegmented mycelium which enters through the rhizoids, the hyphae swell between the cells and frequently become vesicular. Jeffrey[2] found in older prothalli which had produced embryos that the fungus was dead and shrivelled, but this does not prove that it was digested by the cells of the prothallus.

Lycopodiaceae. The relationships are not everywhere alike in the prothalli of species of Lycopodium. Endophytic fungi are found in all, with the exception of L. nummulariaefolium, Bl.[3] I, however, can refer here only to one most interesting case as an illustration. The one I take is that of L. complanatum, for the knowledge of which we have to thank Bruchmann. The fungus in this species has an intimate connexion with the anatomical construction (see Fig. 142). We can recognize beneath the meristem in the beetroot-like portion of the prothallus the following tissues: the central tissue, palisade-like cells surrounding it, and the tissue of the rind, the cells of which inhabited by the fungus have a darker content. The cells are filled with fine hyphae-coils which are in contact with the outer world through individual rhizoids, the fungus in some cases passing throughout the whole length of a rhizoid. The rhizoids are, as in other prothalli of Lycopodium, relatively few in number. The fungus is not able to pierce the palisade-cells, but only runs between them, and as plastic material is stored up in them it is highly probable that the fungus shares in the process of storage. The central tissue serves for the transport of food-material and perhaps also for water-storage. This highly differentiated anatomical structure gives us, however, no ground for considering that the prothallus is really a stem reduced by its saprophytic mode of life. We have seen in the Hepaticae that the thallus of many forms, for instance the Marchantieae, has a much more differentiated construction than the shoot of the foliaged forms.

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[1] See Goebel, Archegoniatenstudien: I. in Flora, lxxvi (Ergänzungsband zum Jahrgang 1892), p. 106.

[2] Jeffrey, The Gametophyte of Botrychium virginianum, in Studies from the University of Toronto, Biological Series, 1898.

[3] Treub, Études sur les Lycopodiacées, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 147, says nothing about an endophytic fungus in Lycopodium salakense, but as the prothallus conforms in every way with that of L. cernuum and L. inundatum I think we may assume it exists.

DISTRIBUTION OF THE SEXUAL ORGANS.

This subject has been often referred to in the preceding pages, and here it is only necessary to refer shortly to its biological interest. The prothalli in most of the Pteridophyta produce first of all antheridia and then archegonia, and then at a later period antheridia again. The formation of male prothalli is easily induced by unfavourable environment. Such prothalli are frequently *ameristic*. There are, however, amongst the Filicineae cases in which well-nourished prothalli produce only archegonia, for example in Lygodium and Mohria caffrorum according to Bauke, in Onoclea Struthiopthoris according to Douglas Campbell, and in Gleicheniaceae according to Rauwenhoff, who calls such prothalli *apandrous*. But it is questionable how far we have here to deal with a constant relationship; it is much more probable that in most cases definite external conditions yet unrecognized bring about the passing over of the stage of formation of antheridia. I have always found both antheridia and archegonia upon the prothallus of Mohria. Heim's investigation of Lygodium give different results from those of Bauke, for he showed that in this genus the antheridia appeared after the archegonia. In Equisetum also the prothalli are, as has been shown above, dioecious, but the dioecism is cancelled by external factors.

The position of the sexual organs and the rare occurrence amongst them of 'paraphyses,' to which we can ascribe the same function as in the Bryophyta, do not call for detailed treatment here.

APOGAMY.

Farlow was the first to show that the embryo-plant in Pteris cretica arose by vegetative sprouting, and not from the fertilized egg. De Bary, Leitgeb, Heim, W. H. Lang, and others have investigated this remarkable condition, and have proved its occurrence in a great number of Filicineae. I do not intend to treat this subject with any fullness here[1], I wish only to state some fundamental points.

In the first place one must remember that the egg, while certainly different from the other cells of the prothallus, is only a special construction-form of these. Then it has been already shown[2] that in many apogamous prothalli normal sexual organs in the first instance appear, and these are followed by abnormal ones, and that a change in the constitution of the sexual organs may be considered as probably the cause of the appearance of apogamous shoots. In Doodya caudata, for example (Fig. 160)[3], papillae are frequently produced from malformed sexual organs upon the under side

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[1] See, for a comprehensive statement, Sadebeck, Pteridophyta, Einleitung, in Engler and Prantl, Die natürlichen Pflanzenfamilien, 1898.

[2] See p. 188.

[3] Heim, Untersuchungen über Farnprothallien, in Flora, lxxxii (1896).

of the prothallus, and on these young plants then arise. It is remarkable that in the formation of these young plants, the single organs—first leaf, vegetative point of the shoot, root—are laid down independently of one another as in the true embryo, and it is the rule that the individual parts of the sporophyte appear independently of one another. W. H. Lang has recently observed sporangia upon apogamous prothalli, and if we must assume that these are placed upon an extremely rudimentary sporophyte we have a very remarkable shortening of the development which is of extreme interest for the theory of inheritance and development. We might find in these facts a support to the assumption that for each organ or complex of organs there exists a definite material carrying the inheritance, which usually appearing late, may, under abnormal relationships, appear early. The same may be said in a certain sense also of the anatomical relationships. Tracheids, for example, which normally belong only to the sporophyte, may appear also in the apogamous prothalli of Filicineae, although the formation of the organs of the sporophyte is not reached. It even appears in apogamy that there is a jumbling together of the different organs such as has been shown to occur in other malformations[1].

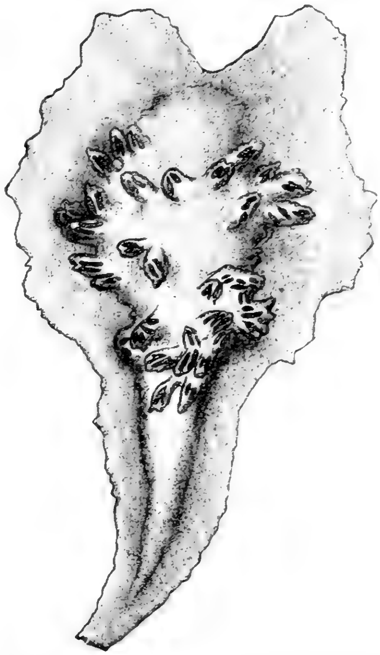

FIG. 160. Doodya caudata. Apogamy in a prothallus. Papillae are seen, and upon these young plants arise. After Heim.

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[1] See Part I, p. 196.

THE SPOROPHYTE IN THE PTERIDOPHYTA AND SPERMOPHYTA

THERE is so great a resemblance in the formation of the organs of the sporophyte in the Pteridophyta and in the Spermophyta that we may take the two groups together. In the 'typical' cases we find that the vegetative organs are roots and leafy shoots, and the reproductive organs are sporangia[1] in both groups or aggregate of groups, and whilst there are many differences, both in the external configuration and in the inner structure of these organs in the two groups, yet in essentials they are alike.

THE ORGANS OF VEGETATION

I

INTRODUCTION

In the first part of this book I have pointed out the general features of the vegetative organs. If we distinguish root and shoot as fundamental organs this is only based upon the fact that they are the most important and are the most generally distributed. I have also shown[2] that all organs cannot be referred back to transformations of root, shoot-axis, and foliage-leaf. Anchoring-organs, such as we find in many Podostemaceae, furnish us with an illustration. They serve to fix to their substratum these plants which grow in flowing water. In Fig. 161 is shown a portion of the root of Weddelina squamulosa which has produced on the left a leafy 'adventitious' shoot. The root is beset upon both sides by outgrowths which serve as anchoring-organs, and may be designated by Warming's term *haptera*. These haptera resemble in some degree short roots, but they differ from roots in their structure and origin. They are new formations developed in response to the requirements of the habitat. Many similar organs are to be found and formal morphology has grouped them together as *emergencies*. There is no reason why such new formations should not, under certain conditions, attain considerable size.

Tendrils of Smilax. For example, the tendrils which appear upon

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[1] The fact that the microsporangia of the Angiospermae are frequently not sharply distinguished from the microsporophyll has up to recent times led to much confusion.

[2] See Part I, p. 13.

the leaf of Smilax (Fig. 162) probably take origin in a way quite similar to that of the haptera of the Podostemaceae, at least no satisfactory reference of them to parts of the leaf out of which they may have arisen by a change of function has as yet been advanced.

That they cannot be transformed stipules, as has been often assumed, can be shown upon various grounds but specially by this—that in some species the upper end of the sheath of the leaf can be recognized beneath the tendril, but if the tendril was, like a stipule, an outgrowth from the base of the leaf it must spring from this sheath. Čelakovsky's opinion, recently expressed[1], that these tendrils are metamorphosed separate lobes of the lamina of the leaf does not, in my opinion,

FIG. 161. Weddelina squamulosa. One of the Podostemaceae. Portion of a root. To the left above is an adventitous shoot. Right and left below are haptera. Slightly magnified.

FIG. 162. Smilax Sarsaparilla. End of a shoot. The lamina of the leaf is here arrested, it becomes developed in later-formed leaves. The tendrils are well developed. Natural size.

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[1] Čelakovsky, L. T., Über die Homologien des Grasembryos, in Botanische Zeitung, lv (1897), p. 171.

give us any advance. There is no known species of Smilax which really shows such 'lobes.' If the tendrils develop from the beginning as *tendrils* upon the primordium of the blade, they can be *no transformations* but *new formations*. The question seems to me to be one in which change of function is predominant, it is not the purely formal one of whether the tendril springs from the base of the leaf or from the lamina of the leaf[1].

Haustoria of Parasites. The haustoria of parasites may also be considered as organs *sui generis*[2]. Parasites are of course derived from non-parasitic plants. There are two ways in which this may have come about :—

(*a*) Either organs which previously existed became devoted to the service of a parasitic life; for instance, a root-primordium might obtain the capacity to bore into a host-plant ;

(*b*) Or the plant had recourse to new formations in order to bring it into union with its host. This appears to me to be that which has been actually followed.

It has been customary to consider the haustoria of Cuscuta, for example, as partly transformed roots, and this mainly because they are endogenetic ; but no really convincing proof in support of this has been brought forward, and certainly such an assumption finds no application in relation to the haustoria of the Rhinantheae, Orobanchaceae, Balanophoreae, and others. The haustoria which arise usually in consequence of a chemical or mechanical stimulus are indeed not fundamentally different from those which we shall have to notice in the embryo-sac of many Angiospermae[3]. In Orobanche[4], for example, the form of the haustorium which is produced on its root is different according as this is in touch with the root of the host-plant at one small point or over an extended area. In the first case a single superficial cell may grow out and penetrate the root of the host as a filiform haustorium, just like the mycelium of a fungus ; in the second case the suctorial process is a cell-mass which has a much higher anatomical construction, containing both vessels and sieve-tubes, and these enter into union with similar elements of the host-plant. It is the same in other cases. We have to deal with new formations in these haustoria which arise in consequence of a stimulus as does the anchoring-disk on the tendril of an Ampelopsis[5].

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[1] See, for a *résumé* of the different views, Delpino, Contribuzioni alla storia dello sviluppo nel regno vegetale: I. Smilacee.

[2] The older literature about parasites is brought together in my Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884). The limits of the present book allow only of a citation of some of the more general and important relationships, but f no details.

[3] See p. 638.

[4] See Hovelacque, Recherches sur l'appareil végétatif des Bignoniacées, Rhinanthacées, Orobanchées, et Utriculariées, Paris, 1888, p. 598. The literature is cited in this work.

[5] See Part I, p. 268.

It is remarkable that the haustoria of many parasites can exhibit unlimited growth within the host-plant, whilst the portion of the parasite outside the host-plant suffers so great a reduction that sometimes only the flower-shoots remain, and the haustoria then alone represent the vegetative body. Such a case is that in Fig. 163, which is an illustration of a species of Pilostyles[1].

Pilostyles Ulei. Upon the surface of the shoot of the host-plant only the small flower of the parasite appears. The vegetative body of this member of the Rafflesiaceae appears to have the same nature as that of Pilostyles aethiopica described by Solms, a plant which lives as a parasite upon the twigs of the caesalpineous Berlinia paniculata. In the secondary rind of the host run strands which have no definite form, and from which small, plate-like branches pass off, and these grow radially against the wood and gradually become enclosed by this as *sinkers*. Foliage-shoots are wanting here as in all Rafflesiaceae. The several shoots which develop as 'adventitious buds' within the 'thalloid vegetative body,' and burst through the rind of the twigs of the host, are flower-buds. The arrangement is therefore like that of the mycelium of an endophytic fungus—Peronospora, for example, the conidiophores of which burst through the host and appear above the surface.

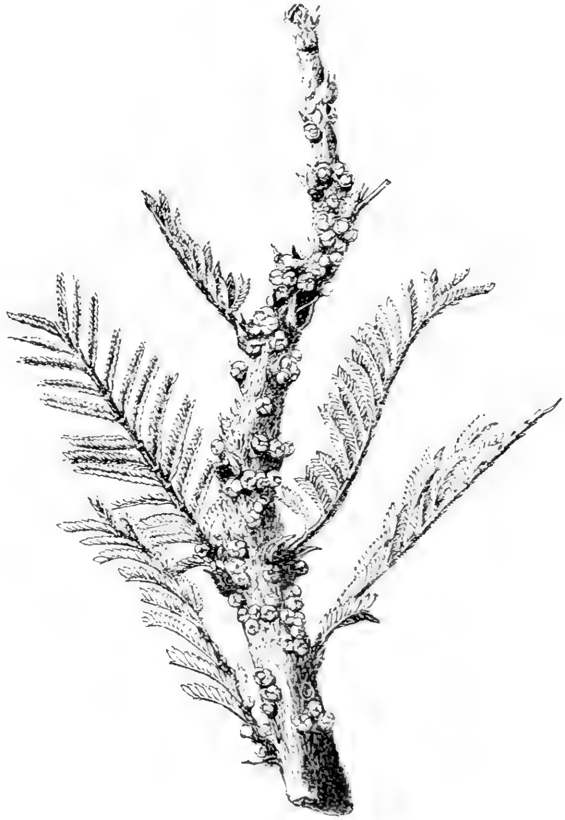

FIG. 163. Pilostyles Ulei, Solms. Only the small flowers of this parasite are visible upon the shoot-axis and leaves of an Astragalus, which is the host-plant.

Pilostyles Haussknechtii. In another species of Pilostyles, P. Haussknechtii[2], the reduction of the intramatrical vegetative body is carried still further. The plant lives as a parasite upon species of Astragalus, and the flower-shoots appear

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[1] The plant was sent to me through the kindness of Dr. Ule, and it has been determined by Count Solms-Laubach to be a new species. See Endriss, Monographie von Pilostyles ingae, Kant. (P. Ulei, Solms), in Flora, xci (Ergänzungsband zum Jahrgang 1902), p. 209.

[2] Solms-Laubach, Über den Thallus von Pilostyles Haussknechtii, in Botanische Zeitung, xxxii (1874), p. 49.

upon the basal portions of the leaves. Young stages of development show that the flower-buds sit upon a cushion-like irregularly limited mass of tissue of the parasite termed the *flower-cushion* which is in firm union with the tissue of the leaf of the Astragalus. Two such flower-cushions are regularly found in the leaf of the host when it has reached its development. After the flowering time these die away. The intramatrical body of the parasite which produces this flower-cushion consists of simple cell-strands, which Solms designates mycelium on account of their resemblance to the mycelium of a fungus. It is chiefly spread in the pith of the shoot of the Astragalus, but its branches force themselves also into the vascular bundles, penetrate the medullary rays, and spread in the form of irregular tangled filaments in the rind and end finally in the young flower-cushions. It is easy to follow this vegetative body right up into the vegetative point —into a region where there is scarcely yet a differentiation of rind and pith— and there it is richly developed. Solms has definitely traced it to the ultimate cell-layers of the apex[1]. The flower-cushion arises from the mycelium which penetrates into a leaf, immediately after the primordium of the leaf is laid down. This mycelium swells up in the base of the primordium, and then the ends of its filaments divide and form a net of irregular polyhedral cells which later swell up into the flower-cushion. The flower-bud is endogenetic in this cushion.

These examples must suffice to show that besides 'root and shoot,' as defined above, other organs are formed with special aims, to use a teleological expression, and these are not transformations of others, and cannot be referred back to previously existing ones. Keeping in view the relationships of configuration of root and shoot we must remember that the plasticity of the vegetative organs is very great, and that consequently it is impossible to find general far-reaching differences between the single categories of them. The cases where passage-forms occur between the categories are of special interest, and they require here fuller description than could be given to them in the general part of this work.

II

ROOT AND SHOOT

I do not propose to give here a general account of the characteristics of root and shoot. My object will be much better accomplished by an exposition of individual cases, but I must discuss here the question: Can roots pass over into shoots, and does the converse also happen?

A. *TRANSFORMATION OF UNDOUBTED ROOTS INTO SHOOTS.*

Both in Pteridophyta and in Spermophyta there are a number of cases in which, sometimes regularly sometimes occasionally, roots become trans-

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[1] Solms-Laubach, Über den Thallus von Pilostyles Haussknechtii, in Botanische Zeitung, xxxii (1874), p. 68.

formed into shoots at the apex by throwing off their root-cap and forming leaves.

Filicineae. The transformation has been observed with certainty in Diplazium (Asplenium) esculentum[1], and in many species of Platycerium, such as P. alcicorne, P. Willinkii, P. Stemmaria, P. Hilli. These are plants which in their manner of life behave very differently. The species of Platycerium are epiphytes, and produce spores which germinate freely; nevertheless, vegetative propagation by shoots from the roots is profuse in them. Diplazium esculentum, on the other hand, is a tree-like geophyte which in cultivation apparently seldom produces sporangia, but in its natural habitat does so abundantly. The formation of root-shoots cannot then be considered as a substitution for the usual propagation by spores. Transformation of the tip of the root into a shoot may take place in short roots or in long roots, and indeed every root appears to have the capacity to become a shoot, for one can almost always observe the transformation in healthy separated tips of roots. The transformation seems to be favoured in the plant by the position of the root near the surface of the soil. It is easy to follow the process by which the apical cell of the root becomes the apical cell of the shoot.

Spermophyta. The transformation of roots into shoots has been observed as yet only amongst the Monocotyledones in, for example, Listera cordata[2], Neottia Nidus-avis[3], Anthurium longifolium[4]. The observations which have been made in Dicotyledones are altogether wanting in accuracy[5].

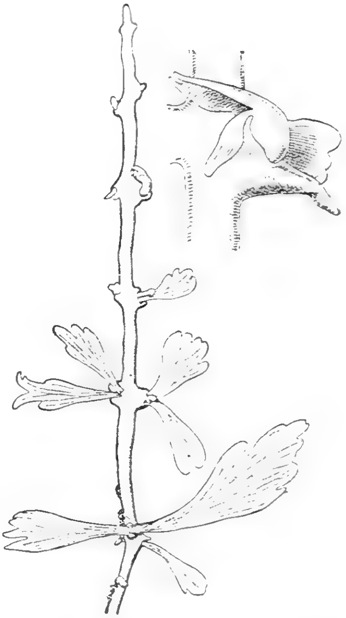

FIG. 164. Marathrum utile. Root with two rows of adventitious shoots. To the right above a young adventitious shoot. The root forms at its base a lobed anchoring-disk. Magnified.

The transformation of roots into shoots is, in my opinion, only an

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[1] See Lachmann, Contributions à l'histoire naturelle de la racine des Fougères, in Annales de la Société botanique de Lyon, xvi (1889), p. 159. They are more accurately described by Rostowzew, Beiträge zur Kenntniss der Gefässkryptogamen, in Flora, lxxiii (1890), p. 155.

[2] Brundin, Über Wurzelsprosse bei Listera cordata, L., in Bihang till k. Svenska Vetenskap Akademie Handlingar xxi. 3 (1895).

[3] Warming, Om rødderne hos Neottia Nidus-avis, L., in Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn, 1874. The literature is cited in this work.

[4] Goebel, Über Wurzelsprosse bei Anthurium longifolium, in Botanische Zeitung, xxxvi (1878), p. 645.

[5] With regard to this see the literature quoted by Rostowzew.

individual case of the general phenomenon that shoots arise upon roots. Root-borne shoots occur quite regularly in many plants, the shoots are laid down endogenetically in serial succession towards the growing point of the root; their endogenetic origin gives their vegetative point, like that of the lateral roots, the protection which they could not otherwise get upon the leafless root. This is very strikingly shown in many Podostemaceae[1]. In Fig. 164 there is a portion of a root of Marathrum, a podostemaceous plant which I collected some years ago in the Rio Boconó in Venezuela. It will be seen that there are two rows of shoot-primordia upon it, and the youngest of these primordia are evident upon that portion of the root which is still covered by the root-cap. Suppose now that the formation of the shoots approaches more nearly the tip of the root. Such a case is found in Ophioglossum vulgatum, whose multiplication, so far as we know, takes place exclusively by shoots upon the root, and in it the primordia of the shoots arise out of the youngest segments of the apical cell of the root, whilst the tip of the root itself continues its growth[2]. It is but a short step from this to the transformation of the tip of the root itself into the tip of the shoot, in which case the primordium of the shoot would be terminal. We shall have occasion to describe presently a similar pushing of the formation of shoot to the apex in the leaves of Filicineae[3].

B. *ORGANS WHICH ARE NOT TYPICAL ROOTS.*

THE RHIZOPHORE OF SELAGINELLA.

Many authors have considered as roots the *rhizophores*, which are found in a number of species of Selaginella, and which are confined exclusively to plagiotropous dorsiventral forms such as Selaginella Martensii and S. cuspidata. The upper portions of the plagiotropous but not creeping shoots in such species, where they are at some distance from the ground, are enabled to get into connexion with the soil by means of the rhizophores, just as in Mastigobryum[4], one of the foliose Hepaticae, the *flagella*, which are branches provided with reduced leaves and numerous rhizoids, bring the plant into connexion with the soil.

The rhizophores of Selaginella (Fig. 165) are leafless. They arise usually in pairs, one above and one below the fork, which is formed by the branching of the axis of the shoot. They are exogenetic[5], and near their

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[1] Warming, Familien Podostemaceae: I–V in Skrifter af det kgl. danske Videnskabernes Selskab, 1881, 1882, 1888, 1891, 1898, has described this in great detail.

[2] See Rostowzew, Beiträge zur Kenntniss der Gefässkryptogamen, in Flora, lxxiii (1890), p. 155. I had expressed my doubts of the accuracy of Van Tieghem's statement that the tip of the root was transformed into the tip of the shoot; see Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 344.

[3] See p. 241.

[4] See p. 43.

[5] See Treub, Recherches sur les organes de la végétation du Selaginella Martensii, Spring., in Musée botanique de Leide, ii (1877), p. 11.

tip they form endogenetically the primordia of one or many roots. The rhizophores may branch dichotomously, and they attain in many forms a considerable length which is not brought about, as is sometimes wrongly supposed, by intercalary growth, but by prolonged apical growth. The formation or extrusion of roots is caused by moisture. Usually it takes place in the soil, occasionally also in moist air. Pfeffer has shown that these rhizophores may be transformed into leafy shoots[1], and he pointed out that cutting through the two shoot-branches above the fork where the rhizophores arise, appeared to favour the transformation of the rhizophores into shoots. We can certainly cause the transformation in young rhizophores if we treat the parent-shoot as a cutting, and make the apex of the rhizophore the vegetative point[2]. A case of the kind is illustrated in Fig. 167. Two rhizophores, WT_1 upon the upper side, and WT_2 on the lower side, are shown here at the point of forking of the shoot. WT_2 has developed into a leafy shoot which, after

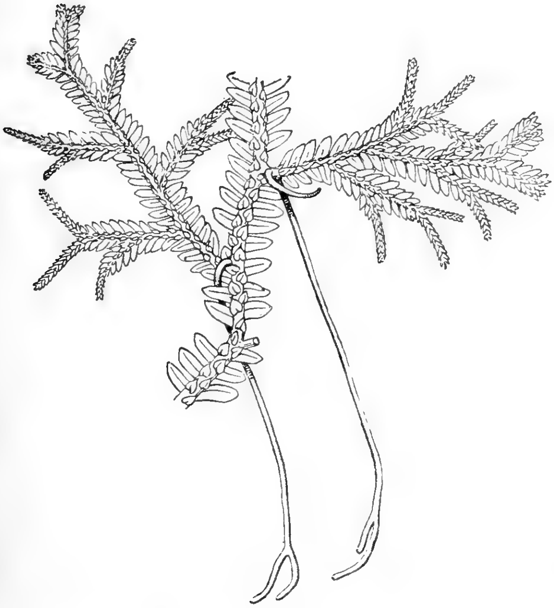

FIG. 165. Selaginella Martensii. Portion of a shoot with rhizophores. Natural size.

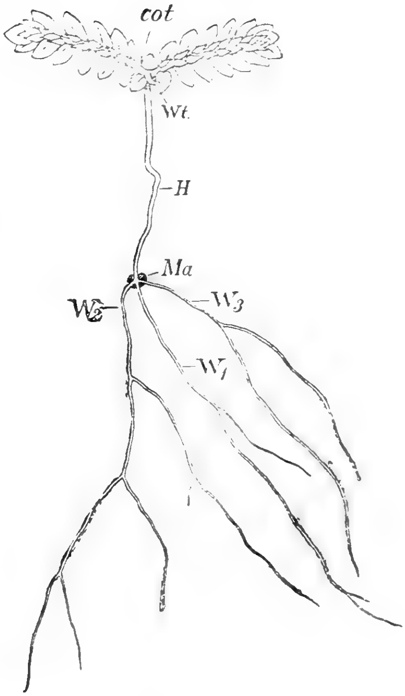

FIG. 166. Selaginella. Seedling. *Cot*, cotyledon; *Wt*, young rhizophore; *H*, hypocotyl; *Ma*, megaspore; W_1, chief root; W_2, W_3, roots springing from the hypocotyl. Magnified 2.

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[1] Pfeffer, Die Entwicklung des Keimes der Gattung Selaginella, in Hanstein's Abhandlungen, i (1871).

[2] Behrens, Über Regeneration bei den Selaginellen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897), p. 159; Beijerinck, Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln, in Natuurkundige Verhandelingen der koningklijke Akademie van Wetenschappen in Amsterdam xxv (1886), p. 16.

producing some deformed leaves, bears those of normal Selaginella. A root, *W*, or it may be a rhizophore, is already seen upon it. This simple experiment is one of the most instructive and most easily carried out that we know of for the purpose of showing change of function.

The question now is: What is the rhizophore? There are three possibilities. It may be a leafless shoot; it may be a capless root; it may be neither of these, but an organ *sui generis*.

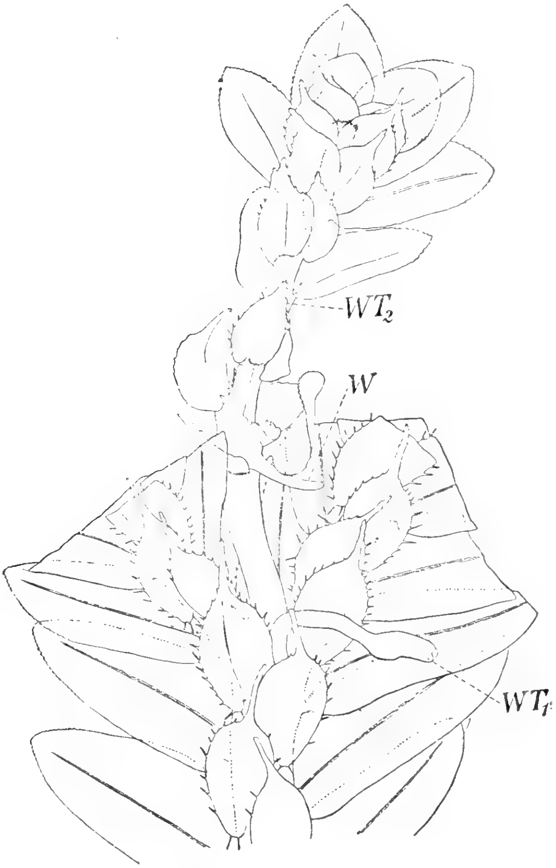

FIG. 167. Selaginella cuspidata. The apices of the two shoots of a forked branching were cut off. One of the two rhizophores of the fork, *WT*$_2$, became transformed into a leafy shoot, the other, *WT*$_1$, did not develop further; *W* root. Magnified 9.

In favour of its being a shoot there may be advanced its easy transformation into a leafy shoot, as well as the method of its origin. But we do not know any transition-form between a rhizophore and a leafy shoot. Even in the germ-plant the rhizophore appears with the same configuration as it has upon the mature plant. Fig. 166 shows a germ-plant which has developed the first rhizophore above the two cotyledons.

In favour of its being a root the anatomical considerations have been specially advanced, but these do not appear to be critical.

More recently Bruchmann[1] has pointed out that in Selaginella spinulosa, a species of radial configuration which does not produce rhizophores, the roots do not arise immediately from the stem, but are produced endogenetically in a cell-body of exogenetic origin. This body appears in this species as if it were a very short 'stalk' to the root, and it is found also in other species. The rhizophores of dorsiventral species of Selaginella may then be only a further development of this 'stalk' in correlation with their life-relationships, and we may compare

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[1] Bruchmann, Untersuchungen über Selaginella spinulosa, A. Br., Gotha, 1897.

this stalk with the 'protocorm' of other Lycopodineae. If this be so, the rhizophore of Selaginella is neither the result of the transformation of a shoot nor of that of a root, but is the result of a prolonged growth of an outgrowth of tissue, which appears in all species, but in the radial forms exists only in a rudimentary condition. Further investigation of the formation of the roots of Selaginella is needed before we can say that this explanation is founded upon a right basis. It has, however, the advantage that it is supported by the comparative consideration of the organs within the genus itself, and not upon any forced general scheme.

THE PROTOCORM.

The organ which Treub[1] has designated *protocorm* is found in the germination of some species of Lycopodium. It is also known in Phylloglossum, the germination of which has not yet been observed.

Lycopodium. Fig. 140, 4, shows a germ-plant of Lycopodium inundatum, which still holds on to its prothallus by means of its foot (haustorium). In addition to the cotyledon, *Co*, the second leaf has developed, and at its base there is not, as in other germ-plants, the hypocotyl with the root, but instead a tuber-like body provided with rhizoids, and it corresponds morphologically with a hypocotylous segment of a stem in which the primordium of a root is suppressed[2]. The plant as it grows further becomes dorsiventral, forms some new leaves, and only at a relatively late period does the first root arise as an endogenetic structure, and then also is developed for the first time a more complex anatomical construction, evidenced in the presence of vascular bundles. We can recognize thus in the germ-plant two stages of development; the first gives us a parenchymatous tuber which bears a few leaves; in the second the internal and external differentiation of the plant appears for the first time. Similar tubers arise also upon the roots in Lycopodium cernuum, and they may bear leaves and become each of them a new plant should they be isolated. Treub considered that the tuber of the germ-plant in the species of Lycopodium mentioned above was not a reduced organ, but a rudimentary one, and that it was the forerunner of the leafy shoot of the Pteridophyta of the present day; he therefore named it the *protocorm*. I must own that this phyletic conception does not appeal to me.

We find very similar formations in Spermophyta, both amongst the

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[1] Treub, Études sur les Lycopodiacées: VIII. Considérations théoriques, in Annales du Jardin botanique de Buitenzorg, viii (1890), p. 30. Bruchmann adopts the earlier view of Treub that the protocorm is a foot which has become free. I cannot agree with him. The function of the foot (haustorium) is, in the cases referred to, usurped by the strongly developed suspensor.

[2] See Goebel, Über Prothallium und Keimpflanzen von Lycopodium inundatum, in Botanische Zeitung, xlv (1887), p. 184.

Monocotyledones and the Dicotyledones, if the formation of root is suppressed temporarily or entirely in the seedling.

Monocotyledones. The Orchideae furnish examples of these 'protocorms.' I have described them in the germination of the epiphytic species Taeniophyllum Zollingeri[1], and Račiborski[2] found the same relationships in a number of other epiphytic orchids. The germ-plant is an elongated green body with a rudimentary cotyledon in front, and below this the vegetative point of the stem. The chief mass of the seedling is formed of the 'protocorm,' that is to say, of a rudimentary hypocotylous segment which is not prolonged as the primordium of a root, and which is fastened to the surface of the tree by numerous anchoring-hairs. Račiborski observed adventitious shoots upon this 'protocorm' in Aerides pusillum. In the seedlings of orchids growing in the soil the 'protocorm' is commonly tuberous.

Dicotyledones. Streptocarpus polyanthus may be mentioned as an illustration amongst dicotylous plants of this formation of the 'protocorm.' Its rootless hypocotylous segment, which is the 'protocorm,' is fastened by anchoring-hairs to the soil, according to Hielscher[3]. On the embryos of species of Utricularia[4], the hypocotylous segment is commonly an undifferentiated cell-body serving as a reservoir of food-material. The same is the case in some rootless species of Podostemaceae.

Phylloglossum. Phylloglossum is an Australian lycopodineous plant which bears at the base of its leafy stem two parenchymatous tubers, and these are able to perennate in the same way as do those of many Ophrydeae. These tubers, which show no infection by fungi in the examples I examined, are generally regarded as being comparable with the 'protocorms' of the germ-plants just mentioned. They are swellings of the axis of the shoot upon which no root is laid down; the root arises exogenetically on the plant above the new tubers[5].

The appearance of a protocorm in very different cycles of affinity appears to me to be unfavourable to the hypothesis of its having a phyletic significance; I can only see in the protocorm an organ which corresponds in its development, especially in its formation of roots, to an arrested hypocotylous segment; its appearance is probably connected with external conditions of life. That in plants which generally have given up the forming of roots, like the Utriculariae, there should be no formation of

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[1] Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 195.

[2] Račiborski, Biologische Mittheilungen aus Java, in Flora, lxxxv (1898), p. 337. The literature is cited here.

[3] Hielscher, Anatomie und Biologie der Gattung Streptocarpus, in Cohn's Beiträge zur Biologie der Pflanzen, iii (1883).

[4] Compare the figure of Genlisea (Fig. 169, 1), which in this respect resembles Utricularia.

[5] See Bower, On the Development and Morphology of Phylloglossum Drummondii, in Phil. Trans., 1885.

roots in the seedling, is easily understandable. In other plants, like the species of Lycopodium and Orchideae mentioned above, the suppression of the formation of roots may be connected with the prolonged development of the germ-plant; perhaps also with the symbiosis with fungi which takes place in these plants[1]. At the present time, however, we have no clear view of these relationships.

C. *TRANSFORMATION OF SHOOTS INTO ROOTS.*

Shoot-axes which have the form of roots have already been described in the Hepaticae[2]. They are found also in the Pteridophyta, for example in the Psilotaceae, and also in the Spermophyta, but an actual transformation of a shoot into a root has, as yet, not been shown. Beijerinck has described its occurrence in Rumex Acetosella, but I cannot accept his statement as conclusive[3].

III

FREE-LIVING ROOTS AND LEAVES. TRANSITION BETWEEN LEAF AND SHOOT

We are accustomed to think of the several organs of the plant-body always as they occur in connexion one with the other, because this is the most common condition, corresponding as it does with the ordinary requirements of the life of the plant, and we regard it consequently as the 'normal.' We see in the vegetative organs the root and the shoot joined to one another, and the phenomena of regeneration have shown us that the taking away of the root-system or of the shoot results frequently in a new formation of the lost parts. But there is another way of looking at these facts. Under *special life-conditions* the organs may also live alone, at least for a time.

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[1] At isolated places in the stem of Lycopodium inundatum, cushion-tissue develops which becomes infected with fungus-hyphae. In the vicinity of this the new formation of roots is promoted, and upon the protocorm of Lycopodium inundatum similar cushions of tissue are found. In both cases, and in the root-tubers of Lycopodium cernuum also, the fungus-infection appears to promote an increase of plastic material.

[2] See p. 45.

[3] Beijerinck, Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln, in Natuurkundige Verhandelingen der koningklijke Akademie van Wetenschappen in Amsterdam, xxv (1886), p. 41. Beijerinck found at the base of newly formed roots one or two leaflets, and concluded therefrom that a shoot continued its growth as a root after the primordia of one or two leaves had been laid down. Neither in the text nor in the figures is it, however, shown that these leaves had vascular bundles, and therefore there is the possibility that these leaf-like structures were only portions of the ruptured rind-tissue.

ROOTLESS SHOOTS.

The existence of *rootless shoots* is generally known. They occur in some free aquatic plants, for instance in Salvinia, Ceratophyllum, species of Utricularia ; also in terrestrial plants in which the function of the root has been taken on by the axis of the shoot, as in Psilotum, Epipogon, Corallorrhiza, or by the leaves, as in Genlisea, Polypompholyx, and species of Utricularia.

FREE-LIVING ROOTS.

Less known, however, is the occurrence of *free-living roots*, that is to say of roots which do not spring from a shoot. They occur in some saprophytes and parasites. In the former the saprophytic mode of life of the roots is made possible by symbiosis with fungi. They are rendered thereby independent to a certain degree of the assimilating shoots, and as a matter of fact the assimilating shoots no longer exist in many saprophytes, for example Monotropa.

Pyrola uniflora. If we examine, for example, the growth of Pyrola (Monesis) uniflora[1], we find that the leafy shoots spring from a root-system in the soil. They are quite dependent upon this because they themselves develop no roots, and form also no lateral shoots[2]. There are also root-systems which evidently exhibit younger stages, and have not developed any shoot. The germination is unfortunately unknown, but probably there arises from the unsegmented embryo in the germinating seed, not as elsewhere a leafy and rooting shoot[3], but, the shoot being arrested, only a saprophytic root-system upon which shoots subsequently appear as endogenetic structures.

Monotropa. The condition is quite similar in the allied Monotropa, which, however, does not produce foliage-leaves. Whilst shoots aboveground die down after the flowering period, the root-system perennates and develops new flower-shoots again in the next vegetative period.

I do not consider it necessary to distinguish this root-system, which thus lives independently, by a special name[4] as we have doubtless here to do with a condition correlated with the saprophytic mode of life, and derived from the normal in which frequently we meet with roots that produce shoots, but they are *not independent* roots being always connected with chlorophyllous shoots.

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[1] See Irmisch, Bemerkungen über einige Pflanzen der deutschen Flora, in Flora, xxxviii (1855), p. 628.

[2] In the neighbourhood of the shoot a lateral root commonly arises from the root-system.

[3] We may of course suppose, with Irmisch, that in the germination a shoot arises whose chief root, or one of its lateral branches, then develops into the root-system producing shoots, but the analogy with the germination of Orobanche leads me to think that the assumption I have made in the text is the more probable, and that the chief shoot is entirely suppressed in germination.

[4] As does Velenovsky, Über die Biologie und Morphologie der Gattung Monesis, in Rozprávy české Akademie, Prag, 1892.

FREE-LIVING LEAVES.

Streptocarpus. The cotyledons of Streptocarpus polyanthus and S. Wendlandii can scarcely be considered as of this category, although they frequently are regarded as of this nature. In the germination of the seeds of these species two cotyledons unfold as in other species of Streptocarpus. One cotyledon is soon outstripped in size by the other, and disappears altogether at a later period; the other grows into a large foliage-leaf out of whose base the inflorescence springs subsequently. Hielscher[1] considered these inflorescences as adventitious formations. It is, however, more probable—although an unprejudiced investigation of the developmental history has not been carried out—that the inflorescence proceeds from the end of the primary axis, which elongates into an internode between the two cotyledons, and appears later as the stalk of the large cotyledon.

Lemnaceae. But we can reckon in this category the vegetative body of the Lemnaceae. The flat members which spring one from the other in this plant have been considered sometimes as segments of a thallus, sometimes—and this has been far the commonest view—as leafless shoots in most species. These leaf-like structures are, however, *really leaves*, as I have stated elsewhere[2]. The general conclusion in favour of their shoot-nature was arrived at because one (in Wolffia) or two new members (Fig. 168) shoot out from the base of each old member, and morphological dogma maintained that a leaf could never arise out of another leaf but only out of the vegetative point of a shoot. This dogma, however, has been overthrown by the condition in Utricularia and in the embryos of many Monocotyledones, conditions which will be described below[3]. The first leaves arise in many monocotylous embryos *without any vegetative point being visible,* and there is no necessity to suppose that it is existent although not visible. The cotyledon, the first leaf, is a portion of the embryo, and is not formed out of a vegetative body. Subsequent leaves may develop in like manner out of embryonal tissue remaining over at the base of other leaves. This is what happens in Lemna and its allies, and in support of this view the following points may be advanced:—

1. Plants with leafless shoots are found elsewhere amongst those which 'aim at' reduction of the transpiration. Such a condition in plants like the Lemnaceae, which live partly on, and partly in the water, is quite impossible.

2. In germination the cotyledon of Lemna develops into the first

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[1] Hielscher, Anatomie und Biologie der Gattung Streptocarpus, in Cohn's Beiträge zur Biologie der Pflanzen, iii (1883). Against this put Fritsch, Über die Entwicklung der Gesneriaceen, in Berichte der deutschen botanischen Gesellschaft (General-Versammlung), xii (1894), p. 96.

[2] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 276.

[3] See pp. 236, 253.

'member' of the plant, and all the *following members essentially resemble it*; but the cotyledon is the first leaf, and consequently the following 'members' must also be leaves if we are to accept the comparative method as of any value.

3. The structure which has hitherto been regarded, for example in Spirodela, as a leaf-organ, has scarcely any resemblance to a foliage-leaf, and can without difficulty be arranged amongst the 'ligular formations.'

The morphology of these remarkable plants cannot be treated of in detail here. I will only point out that the new 'members' of Lemna appear in pairs upon the upper side of the old ones, and are enclosed in pocket-like outgrowths (Fig. 168). A zone of embryonal tissue persists at the base of each leaf and out of it the new formations proceed. A special vegetative point is never differentiated. If now we were to regard as leaf that part of the member of a Lemna which stands above the position of formation of the lateral members and roots (*F* in Fig. 168), and as shoot-axis the portion which lies behind this (*S* in Fig. 168), we should not get rid of the fact that the two are not differentiated one from the other. According to my view, the Lemnaceae retain a condition which is otherwise found only in seedling-plants, just as Phylloglossum retains in the formation of its tubers a feature of formation of organs that is limited to the germ-plant in Lycopodium inundatum and L. cernuum, and to the 'adventitious shoots' resembling those in L. inundatum. This view appears to me to be at the present time the most natural one, even though it may appear a heresy to the older morphology.

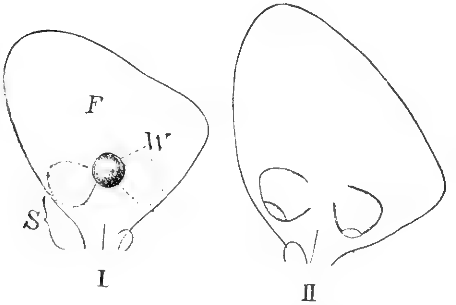

FIG. 168. Lemna trisulca. I, segment separated and seen from below; *W*, root. II, a like segment seen from above. For the explanation see the text. Magnified.

TRANSITION BETWEEN LEAF AND SHOOT.

I have frequently said that the behaviour of Utricularia is of special interest in the general consideration of the formation of organs, and I must now say something about it:—

Lentibulariaceae. Utricularia belongs to the family of the Lentibulariaceae, all the genera of which are insectivorous. Pinguicula shows the normal differentiation of the vegetative body of Spermophyta, namely, root and leafy shoot. The other genera are rootless. The function of the root in Genlisea[1] has been usurped by the highly remarkable tubes which at the

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[1] Goebel, Pflanzenbiologische Schilderungen, ii (1893); id., Zur Biologie von Genlisea, in Flora, lxxvii (1893), p. 208.

same time serve as insect-traps, and they pierce the substratum just like roots (Fig. 169). There can be no doubt that these tubes are transformed leaves. In Polypompholyx, and some few of the species of Utricularia which live on land, we find the following formation of organs:—

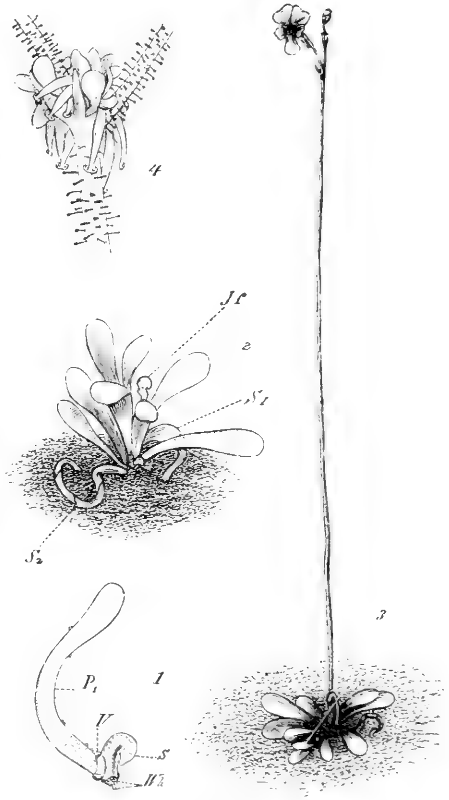

FIG. 169. Genlisea violacea. 1, seedling with three leaves; P_1, first foliage-leaf; S, incipient tubular leaf; V, vegetative point; Wh, root-hair. 2, older seedling which has formed a number of foliage-leaves, and two tubular leaves, S_1 S_2, which have pierced the soil; Jf, terminal inflorescence. 3, the same seedling older. A second inflorescence is developing at the base of the first one. 4, portion of an inflorescence with vegetative shoot, the young two-armed tubular leaves point downwards. 3, natural size. The others magnified.

Utricularia Hookeri. As an example I shall take the West Australian Utricularia Hookeri[1] (Fig. 170). A radial shoot proceeds from the seed and ends in an inflorescence. This shoot, apart from the leaf-structures of the flowers and the bracts, bears the following organs:—

(*a*) *foliage-leaves*,

(*b*) *tubes* (tubular leaves) which end in insect-traps (bladders),

(*c*) elongated, but unbranched and non-tubular, thin structures resembling roots, which we shall call *leaf-roots* or *rhizoids*.

The leaf-roots enter the moist soil like the tubes; the foliage-leaves raise themselves above this. Here then the double function of trapping animals and of anchoring and absorbing water for the plant, which is performed by the tubular leaves of Genlisea, is distributed between two organs, the tubes and the leaf-roots. These stand near one another; they are both transformed leaves. The stalk-portion of the tubular leaf resembles very much the leaf-root, and not infrequently there is found at the end of the stalk an elongated leaf-structure, which one might at first mistake for a leaf-root instead of a tube[2] (Fig. 170). Now the transformation of leaves into tubes is known elsewhere, it is therefore not specially

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[1] For the relationships of configuration in Utricularia, see Goebel, Der Aufbau von Utricularia, in Flora, lxxii (1889); id., Morphologische und biologische Studien: V. Utricularia, in Annales du Jardin botanique de Buitenzorg, ix (1891); id., Pflanzenbiologische Schilderungen, ii (1893). The simply organized Utricularia Hookeri was unknown to me at the time of my earlier investigations.

[2] In Utricularia vulgaris also the tube occasionally appears at the end of the first leaf in the seedling. See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 141, Fig. 43.

remarkable here. Leaf-roots are, however, unknown outside the genus Utricularia, but they do not always differ very markedly from the *leaves* of Utricularia Hookeri; they retain for a much longer period the apical growth which is present at first in the leaves although only for a short time, and they remain smaller than the foliage-leaves, and in this exhibit a character seen elsewhere in organs which do not come to the light. But in other species of Utricularia we find the organs which correspond to the leaf-roots in Utricularia Hookeri developing into stolons with unlimited growth, upon which are produced the bladders, the foliage-leaves [1], the inflorescence, and other lateral shoots; —they thus lose entirely the leaf-character.

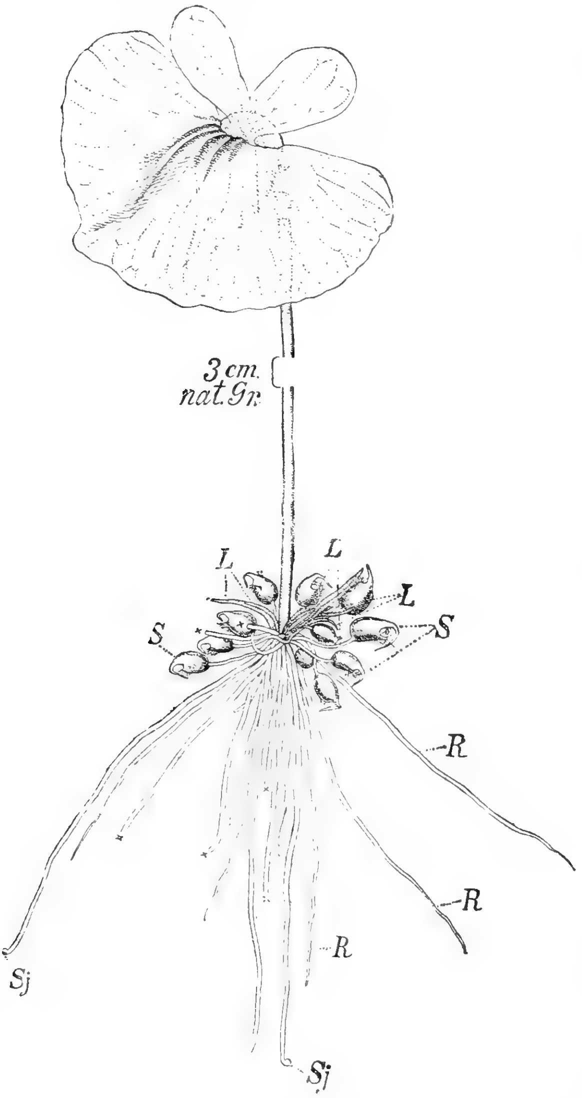

FIG. 170. Utricularia Hookeri. Flowering-plant showing the subterranean parts dissected out; *L*, foliage-leaves, all shaded for the sake of distinction; *S*, tubes; *R*, leaf-roots; *Sj*, young tube at the end of a leaf-root; x marks where the ends of these have been cut off. Magnified 3. A portion, three centimeters long, has been cut out of the scape.

Utricularia coerulea. In Fig. 171, *II*, we have an illustration of this in Utricularia coerulea. At the base of the inflorescence there are no foliage-leaves, but only organs, *K*, corresponding to leaf-roots, and with them are branched stolons which bear leaves, *b*. The leaf-roots may pass over into stolons, and again between these stolons and the foliage-leaves there are found in many species all transitions, of which I have before now given many examples.

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[1] These turn their under-surface to the apex of the stolon, and, consequently, axillary shoots

The leaves in many species are marked by an extraordinary power of reproduction; stolons, even new leaves, may spring from the leaves (Fig. 171, *I*). The stolons themselves may become claw-like anchoring-organs, as in Utricularia neottioides, or tuberous water-reservoirs. In brief, we may say that the ordinary scheme of formation of organs is jumbled here.

Examination of the germination and a comparison of the history of development have given us the starting-point of all these marvellously varied relationships. The seedling-plants[1] in most of the investigated species have retained the behaviour which Utricularia Hookeri shows throughout its life, that is to say, the tubes stand as transformed entire leaves on the chief axis, while we find them also in many other species on the leaves. Further, the stolons which arise on the seedling-plant resemble at first the leaf-roots, but afterwards they branch in the way described above.

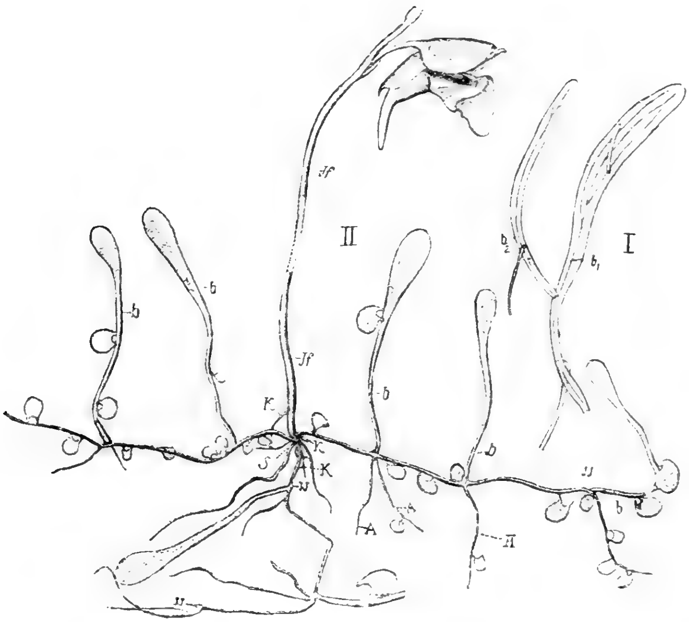

FIG. 171. *I*, Utricularia affinis. b_1, a leaf which has shot out a stolon and also a second leaf, b_2. *II*, Utricularia coerulea. Habit of a flowering-plant, the flower somewhat withered. *S*, remains of seed-coat; foliage-leaves, *b*, are not found now at the base of the scape of the inflorescence, *Jf*, but only leafy stolons, *A*, and leaf-roots, *K*. Magnified.

The reasons for our regarding as leaves these organs which have such different configuration in the terrestrial species of Utricularia are briefly as follows:—

1. The bladders. The leaf-nature of the bladders is determined by

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of these leaves arise upon the side away from the apex of the stolon, and this is a feature which is altogether opposed to an interpretation of them as being shoots.

[1] We shall return to these when speaking of the cotyledons, see p. 254.

comparison with Genlisea, as well as by the history of development and by the germination, and there are occasionally forms of transition between bladders and primary leaves[1].

2. We saw that the stolons appear at different stages. We find all transitions between foliage-leaves and stolons, for instance in Utricularia longifolia, U. bryophila, U. coerulea, and others.

3. Leaves and stolons are alike in their position on the shoot of the seedling, and we see, further, that stolons may also appear instead of the prophylls of the flower and the bracts of the inflorescence.

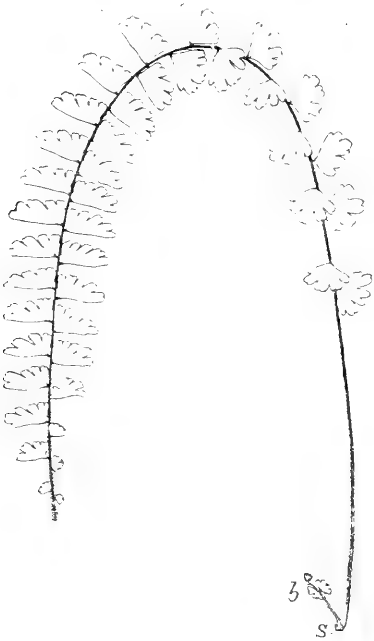

FIG. 172. Adiantum Edgeworthi. Habit of bud-forming leaf; *b*, first leaf of bud, *s*, arising at the tip of a leaf far removed from the apex of the stem. One-half natural size.

It is therefore evident that the way in which the formation of organs in these species of Utricularia has come to pass leaves no room for doubt.

The species of Utricularia which have been hitherto spoken about are not found in the European Flora. In it we only know of forms which live in water and have long, floating, distichously-leaved 'shoots.' Comparative consideration leads to the conclusion that these aquatic species are derived forms in which the shoot of the embryo does not develop[2], whilst a stolon grows into the 'shoot' of the plant and produces inflorescences, lateral shoots, and other parts, that is to say the same structures as we have seen to be formed out of the leaf-roots or leaves in the terrestrial species. The aquatic species of Utricularia therefore furnish us with the most striking example of a free-living leaf, although it has entirely thrown off the features of the ordinary leaf.

The remarkable protean organ which we find in Utricularia appears to me to

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[1] If we start from Genlisea and compare therewith forms, such as Polypompholyx as well as Utricularia Hookeri, where transitions between bladders and stolons are to be found, we might come to the conclusion that the steps of the transformation were as follows:—

1. Leafy plants with roots as in Pinguicula.
2. Parts of the leaves are formed as tubes to penetrate the soil. The roots become reduced as useless organs.
3. The stalk of the tube is partly formed into leaf-root, with arrest of the formation of tube, as in Utricularia Hookeri and Polypompholyx.
4. The leaf-roots become stolons which form the leaves and tubes.

[2] In the terrestrial form it makes an inflorescence.

be connected with the relationships of nutrition of the plant. I do not mean to say that the manifold variations of the formation of the organ are *directly* conditioned by the relationships of nutrition, but Utricularia is, by its carnivorous habit, made independent of the substratum, and it can therefore, if the expression may be allowed, indulge its fancy in the same way as a rich man does. The fate of the poor is just like that of the ordinary plant—to be kept strictly to the iron fate of the requirements of life. On a former occasion[1] I said that the Podostemaceae is a group of water-plants whose manifold configuration of vegetative organs cannot be referred back as an adaptation, but that living as they do in places whence plant-competitors and many animal-enemies are excluded, they can retain in great measure the forms that may arise through 'sports of configuration.' In Utricularia it has not been the habitat but the relationships of nutrition which have given rein to the 'sports of configuration,' and adjuvant thereto are naturally the 'inner' factors, especially the prolonged apical growth of the large leaves of Utricularia which favoured their further development.

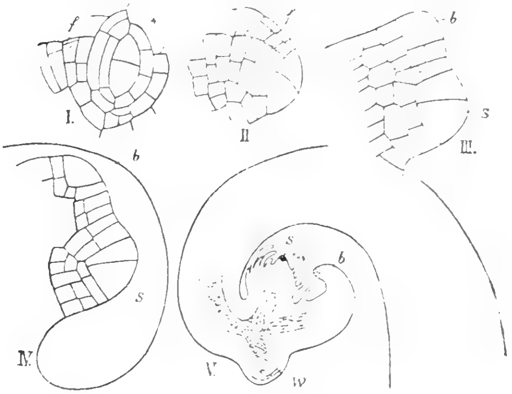

FIG. 173. Adiantum Edgeworthi. Origin of leaf-borne buds. *I*, apex of leaf seen from above; the apical cell has divided by a cross-wall; x, position at which the first leaf of the bud arises; *f*, position of origin of the lateral leaf-series whence usually in a leaf the pinnules develop. *II*, apex of leaf seen from the side; lettering the same. *III*, apex of leaf in optical longitudinal section; *s*, divided apical cell; *b*, first leaf of the bud. *IV*, somewhat older stage than *III*. *V*, apex of leaf in longitudinal section; *s*, apex of the bud surrounded by scales; *b*, first leaf looking like the continuation of the mother-leaf; *w*, incipient root. *I-IV*, highly magnified; *V*, less highly magnified.

Filicineae. The transformation of leaves into shoots, as we find it in some ferns whose leaves are characterized by prolonged apical growth, must be added to the cases which have just been described. This transformation is by no means infrequent. I first showed it in Adiantum Edgeworthi (Fig. 172), where, as in some species of Aneimia, for example Aneimia rotundifolia, also species of Asplenium and other genera, we find the upper portion of the leaf prolonged into a flagellum, and at the end of this a new fern-plantlet (Fig. 173). It is clear that by this elongation of the leaf the plantlet produced upon it is widely separated from the mother-plant, in the same way as happens in the runner of a strawberry, and in the fern the young plantlet at the tip of the 'flagellum' is, as in the strawberry, already provided with the primordia of roots. The question now is, Does the new plantlet really grow *out of the tip of the leaf*? The formation of buds upon the leaves of ferns is a wide-spread phenomenon, and therefore we may

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[1] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 227. Reinke has recently expressed similar views regarding the interesting relations of configuration in Caulerpa.

have here as elsewhere a bud laid down *near the tip*[1]. My investigations enable me to answer the question in the affirmative. The leaves of Adiantum Edgeworthi show at their apex a two-sided apical cell, like the leaves of other leptosporangiate Filicineae[2], and from it two rows of segments are formed. Preparations of the tip of the leaf repeatedly showed a stage in which this apical cell was divided by a wall at right angles to its bent side-walls (Fig. 173, *I*, *II*), and thus two apical cells were produced, each of which approached in form that of the three-sided pyramid as it is found in the apical cell of the stem of many ferns, and one of them became the apical cell of the bud arising at the tip of the leaf (Fig. 173, *III*, *IV*, *V*). The first leaf of the bud, however, does not proceed from the new vegetative point produced out of the tip of the leaf, but from a position near it upon the convex side of the mother-leaf[1]—an unexpected phenomenon, but one with which we can find a parallel in the formation of the embryo, and in the apogamous origin of a fern-plant. The young plant soon forms endogenetically the primordium of a root and then many leaf-primordia, and so it develops further; as its leaves repeat the process through which it arose there is created quite a small colony of plants through these 'wandering leaves.' It is noteworthy that the elongation of the parent-leaf into a flagellum begins only after the formation of the bud. The case is analogous with that of the roots of the Filices, in which, as we have already seen[4], the transformation into a shoot may be supposed to take place, speaking theoretically, by the pushing up of the otherwise lateral formation of the bud to the tip of the root; there would be here also not a *transformation* but a *terminal new formation*.

IV

CONFORMATION OF THE VEGETATIVE ORGANS IN THE EMBRYO

MORPHOLOGICAL DIFFERENTIATION OF THE EMBRYO.

The egg is originally a simple cell. It becomes the embryo by dividing into a cell-body. Numerous investigations during the last ten years have made known the connexion between the arrangement of the division-walls

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[1] A consideration of the matured condition gives no clue to the point of origin of the bud.

[2] See p. 316.

[3] The early inception of this leaf which precedes all those borne upon the bud itself may be explained biologically: it is developed early because it is required to bring food-material to the bud. An examination of the older stages (Fig. 173, *V*) might lead one to consider it as a continuation of the leaf upon which the bud sits; it is formed, however, undoubtedly to the side of the original leaf-tip.

[4] See p. 228.

and the primordia of organs, and the differentiation of tissues. We may well say that the results of these investigations have not been proportionate to the trouble that has been expended upon them, in so far as only little of general significance has come out of them. On this ground therefore a discussion of the details will not be attempted here; I shall only try to state shortly some general considerations.

In the first place two cases must be distinguished:—

1. Where the whole of the cell-body which is derived from the egg becomes devoted to the formation of the embryo.

2. Where only a portion of this cell-body is used for the embryo, another portion serves either as the *foot* or the *suspensor* to bring the embryo into the most favourable conditions for nutrition, and after it has done its work dies off[1]. We shall discuss the relationship of the nutrition of the embryo of the Spermophyta in a special chapter, we shall deal at present only with the morphological features.

A. PTERIDOPHYTA.

Filicineae. One is often inclined to consider the development of the embryo in Filicineae as 'typical' of the other Pteridophyta; it is, however, not 'typical.' In judging of the embryo of Filicineae one must not forget what is, however, often neglected, namely the biological relationship. In the prothallus there is but a small amount of reserve-material laid down relatively to what is the case in the Ophioglossaceae and most species of Lycopodium, and the capacity for assimilation of the prothallus cannot be very great on account of its small size. The young fern-plant must therefore become independent at an early period. In correspondence with this the several organs are differentiated from one another at an *early* period. It is characteristic of the embryo that there arise *independently* of one another: (1) stem-bud, (2) one cotyledon—so called because it does not arise like the later leaves out of the stem-bud, (3) first root, and (4) foot—a suctorial organ or haustorium, by means of which the embryo, when it has burst through the archegonium, can absorb the food-material that is in the prothallus, and which also serves to fix the embryo before the root has bored into the soil. The position in the embryo where these organs are formed may be early discerned. The embryo (see the scheme in Fig. 175, *I*) divides into octants, of which one furnishes the stem-bud, two others the cotyledon—or a third may give a second cotyledon—one the root, and the rest are devoted to the foot. It would be an error to assume that with the first divisions a material differentiation proceeds in the embryo. The regular sequence of cell-division permits us only to trace relatively far back the positions occupied *later* by the primordia of the organs. The embryo is

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[1] Both *foot* and *suspensor* may occur in one and the same plant, for example in Selaginella.

at first, even after formation of the octants, still composed of essentially similar cells in which then *gradually* a difference in construction appears. All Filicineae, as it appears, are alike in essentials, but in the Marattiaceae it is difficult to trace back the single organs even to the octants, and it has not been achieved yet in Botrychium.

Isoetes. In this genus a vegetative point to the stem is not recognizable after the differentiation of the root and the cotyledon; it only becomes conspicuous later, and the feeble formation of leaves in the embryo-plant is probably connected with this.

Equisetum. The development of the embryo is in essentials like that of the Filicineae, but the formation of the leaves in the embryo is delayed. It takes place, as in some Lycopodia which germinate underground, only to form a protection to the apex of the shoot.

Lycopodineae. We have in this class both monocotylous and dicotylous embryos. The former are found in Lycopodium Selago, L. inundatum (Fig. 140, 3), and L. cernuum, as well as in allied forms. The latter are found in L. clavatum and L. annotinum. The difference may perhaps be connected with the life-relationships, as hypogeous germ-plants require to have the apex of their stem more protected by the formation of leaves than do the epigeous. Selaginella (Fig. 174, *B*) has two cotyledons. The embryo of Selaginella spinulosa has no haustorium (foot) according to Bruchmann. The embryos of the Lycopodineae which have been examined, have a suspensor (Fig. 175, *IV*, *Et*), and recall in this the features of Spermophyta. The reference of the organs back to single cells in the young embryo is, in most cases, impossible here.

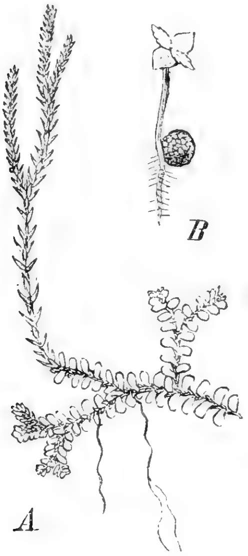

FIG. 174. Selaginella denticulata. *A*, mature plant. *B*, germ-plant attached to the megaspore and showing two foliage leaves above the two cotyledons. Magnified. After Bischoff. Lehrb.

B. SPERMOPHYTA.

It is not my intention to review in this book the well-known facts of embryogeny. I did this some years ago[1], and there is the less necessity to repeat here what I then said, as there is nothing *fundamentally* new to add to it. I shall therefore only shortly touch upon the most important phenomena:—

1. The embryo of the Spermophyta consists in typical cases of a root

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884).

and shoot. The shoot having one or more cotyledons is divided into the vegetative point of the shoot, and the hypocotylous segment of the stem prolonged into the first root. The inception of the root may take place in some cases, for example in Gramineae, in such a way that practically there is no hypocotylous segment of the stem.

2. These organs are laid down independently one of the other, and the cotyledons do not arise at the vegetative point of the shoot. The vegetative point of the shoot is not visible in many embryos within the seed, nor is it yet visible in the formation of the first leaves in many of the Monocotyledones[1].

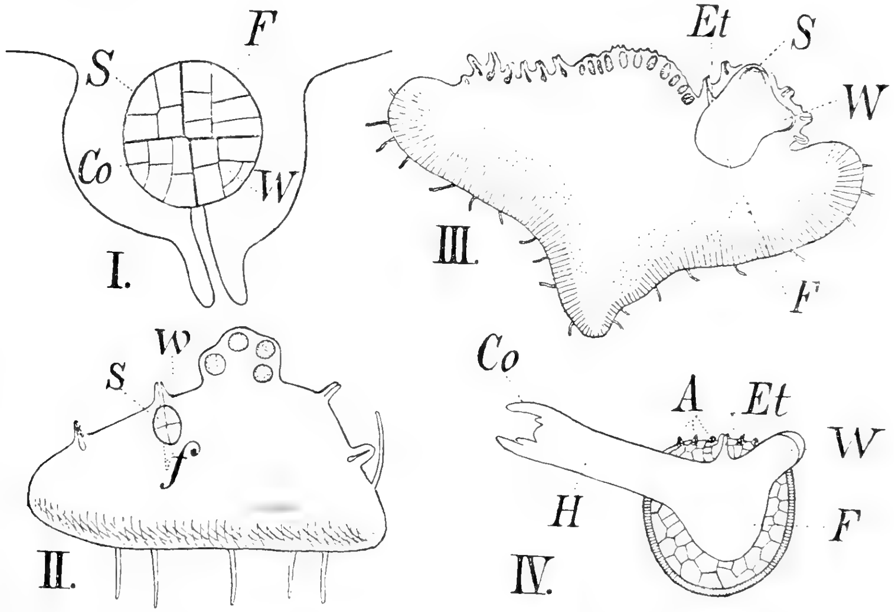

FIG. 175. Schemes of orientation of organs in the embryo of Pteridophyta. In the figures: *S*, apex of stem; *F*, and *f*, haustorium (foot); *Co*, cotyledon; *w*, root; *Et*, suspensor; *A*, archegonium; *H*, hypocotyl. *I*, Homosporous leptosporangiate Filicineae. Young embryo within the archegonial venter. *II*, Botrychium virginianum. The whole lower portion of the embryo becomes haustorium, the stem and the root proceed from the upper half. *III*, Lycopodium clavatum. *IV*, Selaginella. The schemes have been constructed by the help of figures by Jeffrey in the case of *II*, by Bruchmann for *III*, and by Pfeffer for *IV*.

3. The differentiation of the organs may at most in some cases be carried back to definite cell-divisions in the embryo, but here we must remember what I have already said regarding the Filicineae that the actual *separation* of the organs begins only late, even although the arrangement of the cells allows of the *position* upon the embryo where they will arise being recognized at an early period. 'We know no more than this, that one portion of the embryo which is turned to the micropyle will become the

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[1] We may, as I have already said (Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884)), consider it indeed as existing, and of a few cells not visible externally. The necessity, however, of such an assumption does not seem to exist. See p. 235.

root, whilst the cotyledons in the Dicotyledones and the Gymnospermae are lateral sproutings of the embryo, and in Monocotyledones the cotyledon is apical, although not always so[1].' This tallies with what I have so often said, that a differentiation of the primarily similar cells of the embryo takes place only *gradually*.

ORIENTATION OF THE ORGANS IN THE EMBRYO.

The arrangement of the organs in the embryo, especially the relationships in space of the root, the cotyledon or cotyledons, and apex of the shoot are not the same in all vascular plants. The question what causes, external or internal, determine these positions, has often been asked, but not so far as I can see, the question of how far the arrangements stand in connexion with the relationships of life. In the first part of this book I have explained[2] that *external* forces do not come into consideration in the arrangement in space of the parts of the embryos, therefore we have here only to consider *internal* factors, and we may say generally, *root, shoot, and haustorium are laid down in the positions that are the most beneficial for their function.*

A. PTERIDOPHYTA.

Amongst the Pteridophyta we have to consider separately the forms in which there is no suspensor in the embryo, and the forms in which one exists. When the suspensor is developed there is in consequence of it a polar differentiation, and the end of the embryo which is turned away from the suspensor is the shoot-pole.

(*a*) FORMS WITHOUT A SUSPENSOR. **Filicineae.** A scheme of the lie of the parts in the embryo of Filicineae is given in Fig. 175, *I*. We find the following organs:—primordium of the vegetative point of the shoot, *S*, the haustorium, *F*, the cotyledon, *Co*, the root, *W*. The archegonium in which the embryo is formed, stands upon the under side of the prothallus: it is clear then that the haustorium, *F*, which takes the nutrition from the prothallus, must be turned towards the prothallus; the root, *W*, will most easily pierce the venter of the archegonium when it lies towards the downwardly directed side of the embryo; the vegetative point of the stem, *S*, if it were not already upon the upper side, must reach this position by curvature; the cotyledon, *Co*, aids in the breaking through of the accrescent venter and adjacent tissue of the archegonium, and therefore its position must be over against the root. How in

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 171.

[2] See Part I, p. 219.

the horizontal floating megaspores of the Marsiliaceae these positions are reached by the 'torsion' of the first division-walls of the embryo has been explained before[1]. If we compare now the formation of the embryo of Botrychium[2] (Fig. 175, *II*), we find that in it the shoot and root both proceed from the upper part of the embryo. Were the root to originate below in this case, it must either undergo curving, or pierce through the tuberous body of the prothallus.

Isoetes. In Isoetes, whose megaspore germinates, not in the horizontal, but in the upright position, that is to say with the neck of the archegonium upwards, the root and shoot are laid down in the upper part of the embryo as in Botrychium.

(*b*) FORMS WITH A SUSPENSOR. **Lycopodium.** Lycopodium clavatum (Fig. 175, *III*) and L. annotinum[3] may be taken as examples. The embryo is provided with a suspensor, *Et*, which gives it therefore a *polar* differentiation. The suspensor submits at an early period to a curvature which brings the apex of the embryo upwards (see also Selaginella). In an old embryo we find on the lower side a massive haustorium, *F*, around which lies the nutritive material. On the upper side we find the apex of the stem, *S*, and laterally the root, *W*. The bud of the stem, which must rise up out of the earth, is here covered by the primordia of many leaves. The inception of the root takes place relatively late, because the tuberous prothallus which is rich in reserve-material permits of the embryo remaining independent for a relatively long time.

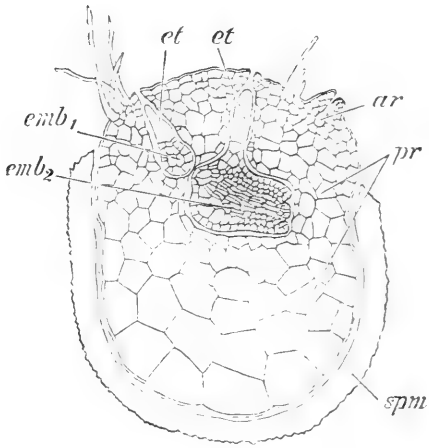

FIG. 176. Selaginella Martensii. Female prothallus, *pr*, projecting from the ruptured wall, *spm*, of the megaspore; *ar*, sterile archegonium; *emb*$_1$, *emb*$_2$, two embryos embedded in the tissue of the prothallus; *et*, *et*, suspensors. Magnified 124. Adjusted after Pfeffer. Lehrb.

Selaginella. Fig. 175, *IV*, shows a germ-plant which has broken through the thick wall of the megaspore surrounding the prothallus, both by its hypocotylous segment, *H*, and by its root, *W*. This has taken place at the position where the thick episporium has been ruptured by the prothallus. The arrangement resembles somewhat that of Isoetes, but is

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[1] See Part I, p. 220.

[2] See Jeffrey, The Gametophyte of Botrychium virginianum, Studies from the University of Toronto, Biological Series, 1898.

[3] See Bruchmann, Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien. Gotha, 1898.

brought about really in quite a different way. As Fig. 176 shows, the embryo is pushed into the prothallus by the suspensor, *et*. The apex of the embryo forms the shoot-portion which curves, *emb*$_2$, so that the point at which the thick megaspore, *spm*, is ruptured, is reached. The root, *W* (Fig. 175, *IV*), is laid down relatively late when the embryo is already bent at nearly a right angle to the suspensor, and then in such a way that it at once is in the most favourable position *for reaching the ruptured portion of the wall* of the megaspore, that is to say, it is laid down in a nearly horizontal position. Selaginella is also of interest, inasmuch as in it the root, at least subsequently, falls fairly accurately in the long axis of the hypocotylous segment of the stem[1] (Fig. 174, *B*), a feature in which it differs from all other Pteridophyta, and which gives it a striking resemblance in habit to the seedling of the Dicotyledones.

B. SPERMOPHYTA.

In this group the *polar differentiation* of the embryo is established from the beginning, as it is in the Lycopodineae, because the fertilized egg is fixed in the embryo-sac on one side and usually by a suspensor[2]. The end of the embryo-sac to which the embryo is fixed, is that next the micropyle, and the side turned away from this becomes the *shoot-pole* of the embryo. The root arises on the micropylar side. This is of advantage, as in most Spermophyta the root (including the hypocotyl) passes out through the micropyle. Water is necessary for this, and the micropyle serves as one of the points of the seed-coat through which the entrance of water can be most rapidly effected. The arrangements for the nutrition of the embryo in the seed will, as I have said, be discussed along with the details of the formation of the seed, in this place I shall only describe the configuration of the embryo in the seed.

In the Pteridophyta the development of the fertilized egg proceeds uninterruptedly ; there is no resting period interposed. But in the Spermophyta the embryo, with only a few exceptions, which will be presently mentioned, experiences either sooner or later an interruption of its development which is only resumed in germination. The degree of development which the embryo has attained at the moment when the seed is ripe varies, and has relation both to the amount of differentiation, that is to say, to the kind and number of the organs in general, and to the transformations which are associated with the deposition of the reserve-material in the embryo.

I. DIFFERENTIATION OF THE EMBRYO.

A 'normal' embryo consists of root and shoot, the shoot exhibiting

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[1] It is really laid down laterally.

[2] See Part I, p. 220, footnote.

a cotyledon or cotyledons, an axis, and a vegetative point upon which there may often be found primordia of leaves. In this form the embryo is ready for germination. But deviations from this naturally raise the question—Why should these be?

I. Incomplete Embryos. In a number of plants the embryo is an undifferentiated cell-mass at the moment when the seed falls from the mother-plant. We must regard it in this state as a retarded formation, and it is correspondingly small. We may recognize two groups amongst these incomplete embryos:—

1. That in which the retardation lasts for a relatively short time and the embryo *develops further in the seed after its fall.* We have here a kind of *after-ripening* such as takes place when seeds are artificially plucked from the mother-plant.

2. That in which the incomplete formation of the embryo persists during the whole period of quiescence of the seed up to the moment of germination. To this group belong a number of saprophytes and parasites, as well as a number of other plants.

(*a*) *Embryos temporarily retarded within the seed.* In order that we may see how far this is a biological group we must consider a number of individual cases:—

A. DICOTYLEDONES.

Eranthis hyemalis. Baillon[1] has briefly said regarding this embryo 'it has long been known that the mature seeds do not contain an embryo.' How then does the plant maintain itself? That no visible embryo exists in a ripe seed is, however, improbable, and as a matter of fact the embryo in the ripe seed of Eranthis hyemalis is a cell-mass like that which we know in other Ranunculaceae and elsewhere amongst dicotylous plants at the stage of development preceding the laying down of the cotyledons; that is to say, the embryo is no longer quite spherical but somewhat flattened at its anterior end. It is so small that it may be easily overlooked in a casual examination.

Ranunculus Ficaria. Ranunculus Ficaria behaves in exactly the same manner. It would be superfluous to describe here the embryo of this plant, for this has been already so well done by Hofmeister[2] and Hegelmaier[3]. Hofmeister says that the embryo in the matured seed has a spherical form, whilst Hegelmaier states that it is arrested in the stage preceding the laying down of the cotyledons.

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[1] Baillon, Sur l'embryon et la germination des graines de l'Eranthis hiemalis, in Bulletin de la Société Linnéenne de Paris, No. 2, séance du 3 juin 1874, p. 14.

[2] Hofmeister, Neuere Beobachtungen über Embryobildung der Phanerogamen, in Pringsheim's Jahrbücher, i (1858), p. 83.

[3] Hegelmaier, Vergleichende Untersuchung über Entwicklung dikotyledoner Keime, Stuttgart, 1878.

He did not succeed in causing seeds to develop further in a chamber, but this takes place not infrequently in nature[1].

Anemone. The features exhibited in the genus Anemone[2] are interesting. The embryo is sometimes dicotylous, sometimes acotylous, as in the sections Sylvia and Hepatica. The size and degree of development of the embryo varies even in one and the same plant. In Anemone trifolia the cotyledons are occasionally developed; usually the embryo is a spherical unsegmented body, as for example in Anemone nemorosa, A. ranunculoides, and A. Hepatica; the Pulsatilleae have a small dicotylous embryo. Germination takes place in them only in the year following the formation of seed, although the root breaks through the pericarp commonly in the autumn of the preceding year.

Fumariaceae. In Corydalis cava[3] and C. solida[4] it is known[5] that the embryo which is only a small undifferentiated cell-body in the seed at the time of its fall develops further in the course of the summer and autumn, and when germination takes place the seedling bears, as in the case of Ranunculus Ficaria and Anemone apennina[6], only one cotyledon.

Stylidiaceae. The species of Stylidium[7] which have been examined have an undifferentiated embryo without any indication of cotyledons and root.

B. MONOCOTYLEDONES.

That an undifferentiated embryo without any indication of cotyledons and root may occur in Monocotyledones was pointed out fifty years ago by Hofmeister[8], but his observation appears to have been overlooked. Speaking of

Gagea arvensis he says:—'The embryo forms an ovoid cell-mass. When its formation has proceeded so far that it shows in the direction of its longitudinal axis twenty-four cells and in its small axis twelve cells, the walls of the cells of the endosperm which for some time have closely invested it . . . begin to show a thickening, the cells of the embryo become filled with granular material and lose sap—the period of ripening of the seed is entered upon. Gagea therefore furnishes

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[1] See Irmisch, Beiträge zur vergleichenden Morphologie der Pflanzen: I. Ranunculus Ficaria, Halle, 1854.

[2] Janczewski, Études morphologiques sur le genre Anemone, in Revue de Botanique, iv (1892), p. 241.

[3] Bischoff, Beobachtungen über den eigenthümlichen Gang des Keimens und der Entwicklung der Knollen bei Corydalis-Arten, in Tiedemann et Treviranus, Zeitschrift für Physiologie, iv (1831). Bischoff could not find an embryo in the ripe seed, it only became evident towards the end of August.

[4] Irmisch, Über einige Fumariaceen, in Abhandlungen der naturforschenden Gesellschaft zu Halle, iv (1860); Hegelmaier, Vergleichende Untersuchungen über Entwicklung dikotyledoner Keime, Stuttgart, 1878.

[5] Hofmeister, Neuere Beobachtungen über Embryobildung der Phanerogamen, in Pringsheim's Jahrbücher, i (1858), p. 83.

[6] See Janczewski, op. cit., p. 296.

[7] Burns, Beiträge zur Kenntniss der Stylidiaceen, in Flora, lxxxvii (1900), p. 354.

[8] Hofmeister, Die Entstehung des Embryo der Phanerogamen, Leipzig, 1849, p. 43.

the interesting example of a plant of which we can scarcely say that it is nourished only from organic material . . . and whose embryo—like that of Orchis although composed of more cells, not to mention the embryo of Monotropa which is never more than 1/100‴ in diameter—consists of a homogeneous cell-mass and at the period of ripening of the seed possesses none of the vegetative organs (terminal bud, rootlet, and cotyledon) which we meet with in the majority of Phanerogams.' The seeds of Gagea lutea which I examined ripened at the end of May, at which time the leaves had passed out of the condition of active life. The embryo to which the upper portion of the suspensor is attached is an ovoid body, which in one carefully examined case had a length of 0·26 mm. and a breadth of 0·17 mm. In its lower third a shallow pit was visible marking the position of the vegetative point of the shoot or that of the very slightly conspicuous cotylar sheath. The formation of the root was scarcely visible. The embryo was altogether more differentiated than was to be expected after Hofmeister's statement, but it was still incomplete. I did not examine into the question of when its further development began.

Of other Monocotyledones I may mention :—

Paris quadrifolia. The embryo of this plant is figured by Gaertner as a small undifferentiated body, but at germination it is normally developed.

Erythronium Dens-canis. The embryo of Erythronium Dens-canis is said by Irmisch[1] to be a spherical body pointed at the root-end.

Hymenocallis speciosa. A. Braun[2] describes the embryo of the amaryllidaceous Hymenocallis speciosa as spherical and scarcely a third of a millimeter in diameter.

Crocus vernus. In Crocus vernus I found complete embryos, and in the cotylar pit was developed the primordium of a second leaf.

Scilla sibirica. Scilla sibirica has an embryo which is further developed than that of Gagea, and possesses a deeper pit of the cotylar sheath.

There are, as will be seen, all stages of transition from complete to incomplete embryos, and in the former before the germination a further development of the organs that are laid down is initiated.

C. GYMNOSPERMAE.

I will only mention here the cases of Ginkgo biloba and Gnetum.

Ginkgo biloba. In Ginkgo fertilization, and consequently the development of the embryo, takes place in fallen seeds.

Gnetum Gnemon. In Gnetum Gnemon[3] the primordium of the embryo has been formed at the time when the seed falls, but it only develops further at a later period.

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[1] Irmisch, Beiträge zur vergleichenden Morphologie der Pflanzen: IV. 2. Erythronium Dens-canis. Halle, 1863.

[2] A. Braun, Über Polyembryonie und Keimung von Coelebogyne, in Archiv der Berliner Akademie, 1860, p. 172.

[3] Lotsy, Contributions to the life-history of Gnetum Gnemon, in Annales du Jardin botanique de Buitenzorg, xvi (1899), p. 46. Literature is cited in this paper.

I mention these two cases here but remark at the same time that I would urge care in the consideration of what is said regarding them, because the proper relationships of the formation of the embryo to the life-conditions can only be obtained in the natural home of the plants.

From the examples which have been cited it may be gathered that the behaviour of the embryos of which I am speaking is no exceptional one.

About the *causes* which bring it about we know really nothing, although various conjectures may be advanced. The most evident is that the optimum of temperature for the development of the embryo is higher than that for the formation of endosperm, and that between the two there is a consequent correlation. One might also suggest that there was some correlation in the relationship between the formation of seeds and the deposition of reserve-material in tubers, bulbs, and rhizomes, and this has been established in some plants[1]. But as the seeds are provided in the endosperm with all the necessary material which is subsequently required for the complete formation of the embryo such a relationship is less probable.

Another question that arises is, Can we give a *biological* explanation of this embryogeny?

I have elsewhere[2] pointed out that perhaps a relationship to external factors may be recognized. Most of the plants exhibiting the features in question are 'spring-plants which have but a short period of development[3], and this occurs at a time when very few plants are strongly developed and the foliation of the trees in the wood is not yet thick; it therefore must give them an advantage over other plants. Teleologically considered it is of importance for them that the duration of the development of seed upon the mother-plant should also be shortened. The mother-plant provides the seed indeed with endosperm, but the further development which usually goes on upon the mother-plant during a long period takes place here in the seed after it has fallen.' That the slow development of such seeds with incomplete embryos brings it about that they germinate only at a late period, and at a time which falls in with the normal period of development of the plant, favours their obtaining proper conditions for germination and must not be overlooked[4]. The seeds of Eranthis, for example, always germinate, favourable conditions being supposed, in February or

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[1] See the literature cited in Part I, on p. 213.

[2] Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 118.

[3] Spring plants which vegetate far into the summer, like Chrysosplenium alternifolium, Symphytum bulbosum, Pulmonaria, and others, and form also their seeds slowly, have complete embryos so far as I know.

[4] Haberlandt, Schutzeinrichtung der Keimpflanzen, Wien, 1877, p. 50, expresses himself in a like sense regarding Eranthis.

March, and therefore it must happen that the stage of development in which they are capable of germination is reached only after sowing and during the process of ripening of the seed. The like may be said of the species of Anemone, the complete embryos of which germinate after some weeks, but the incomplete ones only in the spring after sowing. I think, however, that the shortening of the development in relation to evolution of the plant in spring is the more important. On the one hand we see in not a few plants that the development of the embryo takes more time really than does that of the endosperm. On the other hand it is questionable if any injury would accrue to a plant of Hepatica or of Leucojum if its seeds, in this case provided with complete embryos, were to germinate in the summer after their formation.

The Stylidiaceae also have only a short vegetation period before the dry period in which they rest, and perhaps in other plants of their habitat and other physiologically analogous districts similar relationships might be found.

(*b*) *Embryos incomplete up to the Time of Germination.*—In this category we include a number of plants which so far as I can see possess only one common biological character—they have small seeds:—

Juncus glaucus. Juncus glaucus and perhaps other species of the genus are illustrations[1]. Embryos removed by pressure from the ripe seeds show that the stage of development reached by them, especially with regard to the primordium of the root, is not the same in every case. The cotylar end is easily distinguished by its larger cells and greater thickness from the other. A definitely limited vegetative point of the shoot is not visible, yet the embryo which has already reached its full length is more developed than is that of most of the Orchideae.

Orchideae. Amongst our endemic Orchideae the embryo is an ovoid cell-mass in which there is no differentiation of cotyledon, of bud of the stem, or of root, and the meristem is only present to this extent that a layer of dermatogen which is not always sharply limited covers the embryo. On the other hand Treub has found in Sobralia macrantha both the cotyledon and the bud of the stem at least indicated in the embryo. The primordium of a chief root is never found in the embryo nor does it appear even in germination[2], the lower portion of the embryo which is not differentiated into hypocotyl and root swells up into a tuber and becomes fastened to the soil by a number of root-hairs, whilst from the apical part the cotyledon proceeds. Epiphytic Orchideae which have been examined show like features, and divergent statements regarding the vegetation of terrestrial Orchideae appear to me to be untrustworthy, because when the apical cotyledon is relatively small

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[1] Cladium Mariscus behaves in an analogous way, see Didrichsen, Om Cyperaceerns Kim, ii, in Botanisk Tidsskrift, xxi (1897–8). Schoenus nigricans has a similar embryo.

[2] See p. 232.

and the lower end of the embryo large and swollen, the appearance may readily suggest that the origin of the bud of the stem is terminal, as has been often asserted. The embryo of the Orchideae is then to be regarded as a simple retarded form of the ordinary monocotylous embryo whose apical portion develops subsequently into the cotyledon.

Dicotylous saprophytes. Most of the Orchideae are humus-plants, and it is noteworthy that dicotylous saprophytes, such as the Pyrolaceae, the gentianaceous Voyria, and others, show a reduction of the embryo like that of the Orchideae. In Monotropa the embryo has but nine cells[1]. The germination of the seeds of these dicotylous saprophytes is unknown. It takes place only in the presence of very special surroundings. Probably the fungi which are found in the roots in symbiosis are essential. The smallness of the seeds allows of a large number being formed, and thus the probability that one of the seeds at least will reach favourable conditions for germination is increased.

Parasites. Many parasites show exactly the same condition. Incompleteness in the construction of the embryo is not necessarily associated with parasitism. The mistletoe, which is a chlorophyllous parasite, develops a large and well-constructed embryo, and the same is true of Lathraea which has no chlorophyll. In the parasitic Cuscuta the embryo is not only somewhat large and long, but the chief root is incompletely formed. It wants a certain portion of the tip of the root together with the root-cap, so that it appears as if it were unclosed. It does not require a greater differentiation, as in germination it functions for a short time only until the embryo-plant has been able to reach the host on which it fastens itself by means of its haustoria. The root then dies along with the whole lower portion of the embryo-plant, and the plant then becomes entirely parasitic upon the host. The embryo of Orobanche[2] is even less formed. It is laid down like an ordinary dicotylous embryo, but it remains stationary at an early stage of development, and is represented in the ripe seed by an undifferentiated cell-mass. The same is true of other parasites, such as those of the Balanophoreae and Rafflesiaceae.

Utricularia. Of non-saprophytic plants Utricularia has yet to be mentioned. The connexion of the differentiation of the embryo in this genus with the relationships of life of the plants is still unknown. We only know that the equipment of the embryo in the ripe seed is strikingly different in the different species. Utricularia reniformis[3] and U. Humboldti have green leaf-organs developed within the seed, and the embryo appears to pass through no period of rest in the seed and approaches in that way the case of the viviparous plants which are mentioned below. The other extreme is shown by, for instance, Utricularia montana, the embryo of which has no leaf-primordia within the seed. In others again, like Utricularia orbiculata[4], these leaf-primordia are in the form of very small papillae which develop further in

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[1] Koch, Die Entwicklung des Samens von Monotropa Hypopitys, Linn., in Pringsheim's Jahrbücher, xiii (1882).

[2] Koch, Über die Entwicklung des Samens der Orobanchen, in Pringsheim's Jahrbücher, xi (1878).

[3] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 142.

[4] Goebel, op. cit., p. 146.

germination, and the embryo resembles so far that of other dicotylous plants in having only two such papillae; in some of the aquatic species of Utricularia a large number of these papillae appear. Utricularia amongst Dicotyledones exhibits this exceptional feature in its embryo that the cotyledons, if one may speak of them by this name, differ from the primary leaves only by their position.

II. Embryos of Viviparous Plants[1]. In those plants which have been designated viviparous the relationship between the differentiation which the embryo attains to within the seed and the external conditions of life is very clear. Strictly speaking we understand by viviparous plants only those in which the embryo germinates without any period of rest, and indeed within the fruit as it is attached to the mother-plant:—

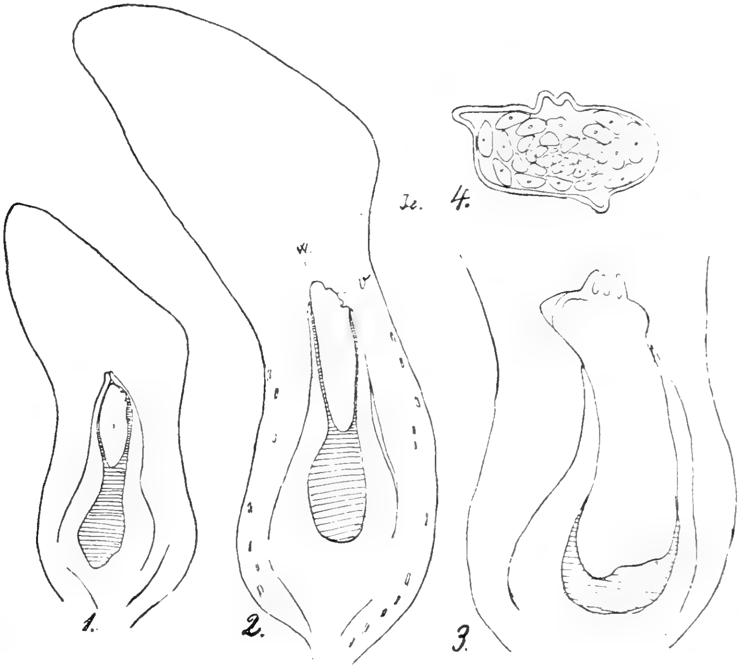

FIG. 177. Cryptocoryne ciliata. Development of the seed. 1, ovule with young embryo in longitudinal section. The outer integument has formed a spongy body, the embryo is still within the embryo-sac which is shaded in the figure. 2, an older stage of the same. The embryo has now issued from the inner integument by its root, *w*, and the vegetative point, *v*; *Je*, outer integument. 3, somewhat older stage similarly seen. 4, seed in transverse section. The embryo has many leaves.

Mangroves. This is the case in mangroves, especially species of the genus Rhizophora, Bruguiera, and Ceriops. The embryo of these Rhizophoreae is

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[1] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 113, where the older literature is cited. Karsten, Über die Mangrove-Vegetation im malayischen Archipel, in Bibliotheca botanica, xxii (1891), gives the result of a thorough investigation of the subject.

distinguished by the great development of a club-like or pole-like hypocotyl, reaching in many a length of over half a meter, whilst the embryo is still attached to the mother-plant. The cotyledons serve only as haustoria, absorbing for the embryo the plastic material supplied by the mother-plant. The embryo acquires by its configuration the capacity of fastening itself into the muddy substratum more rapidly than it could do were it to grow in this from the first, and, as Karsten rightly says[1], this is of special importance for plants of relatively slow development. Seeds of the species of mangrove which are marked by rapid development, for example Sonneratia acida, do not show vivipary, and the rapid development is favoured by the rich deposit of reserve-material[2]. The seedling of the mangrove falls with the tip of the root foremost into the mud[3], and there roots very rapidly by means of a root-system, which spreads out laterally in accordance with the requirements of the environment, and does not produce a chief root. Avicennia forms, as it were, the transition amongst mangroves to the viviparous plants in which the fruit-wall is not bored through on the mother-plant; its seedlings are set loose, sometimes invested by the fruit-wall, at other times without it. They have stiff upwardly curved hairs upon their hypocotyl, and these serve for the first fixation in the mud. The embryos of Aegiceras grow out of the seed within the curved horn-like fruit, and fill the internal cavity of the fruit with their large hypocotyl[4].

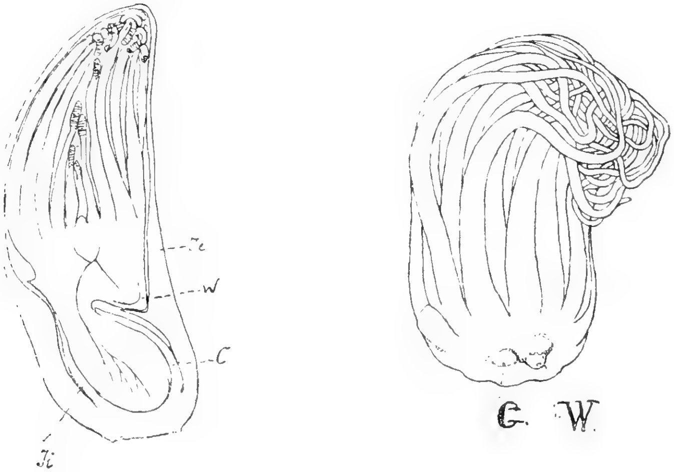

FIG. 178. Cryptocoryne ciliata. Figure to the left: seed, not quite ripe, in longitudinal section. The cotyledon, *C*, of the embryo lies within the embryo-sac, the primary root, *W*, and the bud of the stem have developed outside it; *Je*, outer integument; *Ji*, inner integument. Figure to the right: older embryo which has broken off from the cotyledon; *C*, point of attachment of cotyledon; *W* root.

Cryptocoryne ciliata. Amongst Monocotyledones analogous phenomena

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[1] Karsten, Über die Mangrove-Vegetation im malayischen Archipel, in Bibliotheca botanica, xxii (1891), p. 38.

[2] Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 135.

[3] Many also reach the water by which they are carried away and some of them may develop later.

[4] Goebel, op. cit., Plate V; Karsten, op. cit.

are observable, for example in Cryptocoryne[1], leaving out of consideration Crinum. The ovule of this aroid has two integuments, of which the outer grows, after fertilization has been affected, into a spongy mass of tissue (Fig. 177, 1, 2); and the further development of the embryo takes place in it. The under part of the embryo, that is to say bud of the stem, hypocotyl, and root, grows out of the inner integument, and only the cotyledon remains as a haustorium in the endosperm (Fig. 178). The bud of the stem grows into a large body that produces many leaves, and is invested by only an extremely thin seed-coat; the embryo separates itself readily from the cotyledon (Fig. 178, to the right), and is now rapidly equipped for further development.

Vivipary in its different states is, as I have before now endeavoured to show, only a special form of the widely spread feature observable in the inhabitants of moist localities of the germ proceeding to further development without a resting period. We have seen this in the Hepaticae, whose spores germinate even within the sporangium[2], and in the two analogous cases of the Musci[3]. Also in the Filicineae, which inhabit moist localities, the spores are arranged for continuous germination and, as in the Hymenophyllaceae, the first stages of germination may take place partly within the sporangium; on the other hand spores of the inhabitants of dry regions have always a resting period. The nutrition of the embryo of viviparous plants is facilitated from the side of the mother-plant by the presence of water. The peculiar form which the hypocotyl of the Rhizophoreae possesses, the arrangements for anchoring of the embryos of Avicennia and others, are, as we have seen, special adaptations to locality, and particularly for securing rapid fixation in the substratum.

2. CHANGE OF CONFIGURATION OF THE EMBRYO THROUGH THE DEPOSITION OF RESERVE-MATERIAL.

Characteristic changes take place in the embryo when large masses of material are stored up in it during the resting of the seed.

A. DICOTYLEDONES.

In dicotylous plants the storage takes place commonly *in the cotyledons*, and the massive development of these relatively to the construction of the root and shoot is well known in the Papilionaceae, Cupuliferae, and other families. Both cotyledons are commonly used for the storage, but in Trapa[4] only one is so used, and it swells up to a considerable size, whilst the other remains small. It is of interest to notice that this difference is expressed too in the inception of the two cotyledons[5]. The larger one arises as a

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[1] See Goebel, Morphologische und biologische Bemerkungen: 5. Cryptocoryne, eine 'lebendig gebärende' Aroidee, in Flora, lxxxiii (1897), p. 426.

[2] See pp. 106, 108.

[3] See p. 124.

[4] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), Plate XXIV.

[5] See Gibelli e Ferrero, Ricerche di anatomia e di morfologia. Intorno allo sviluppo dell' ovolo e seme della Trapa natans, in Malpighia, v (1891), p. 156.

terminal structure upon the embryo; the smaller is lateral to the stem-bud. As I have previously said[1], I can only see in this the expression of the fact that an organ that is earlier used is also earlier laid down—and in this case also in another position—than is one that remains rudimentary.

In many dicotylous plants *the hypocotyl is also used* for the storage of reserve-material, and in such cases the cotyledons may remain so small that in some cases they appear almost to be wanting. I may quote some examples, but without mentioning species of Utricularia, which might have been quoted as illustrations, as I have spoken of them elsewhere.

Our first example is from the family of the Guttiferae:—

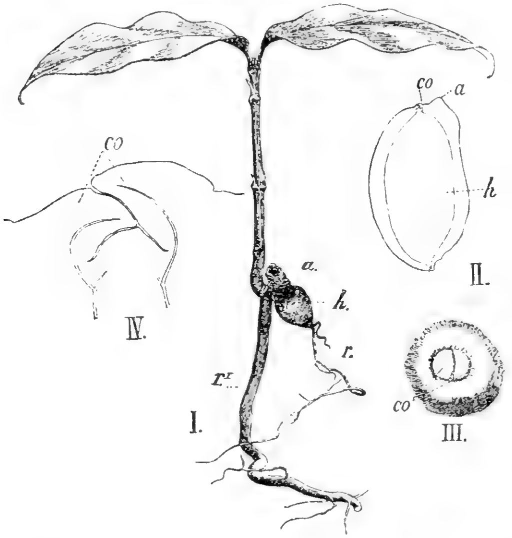

FIG. 179. Xanthochymus pictorius, Roxb. I, seedling; the shoot directed upwards has produced a pair of foliage-leaves after some scale-leaves; *h*, tuberous hypocotyl; *a*, outgrowth from hypocotyl; *r*, primary root; r^1, adventitious root. II, embryo isolated from a ripe seed and in longitudinal section; *Co*, cotyledons; *h*, hypocotyl; *a*, outgrowth from hypocotyl becoming subsequently epigeous and green. III, embryo isolated, the two cotyledons, *Co*, in surface view. IV, upper part of embryo in longitudinal section, not quite median; *Co*, cotyledons. I, one-third natural size. II, two-thirds natural size.

Xanthochymus pictorius. In Fig. 179 the configuration of the embryo and the germination of Xanthochymus pictorius, Roxb., is illustrated[2]. The longitudinal section (Fig. 179, II) shows the two very small cotyledons, *Co*, but upon the surface-view (Fig. 179, III) they are more conspicuous. They do not appear right at the point of the embryo but are pushed to the side by an outgrowth (Fig. 179, I, II, *a*) of the hypocotyl[3], which in germination rises above the ground and becomes green but dries up later. The primordium of the root is small but develops further in germination. The primary root is surpassed in its development by an adventitious root formed at the base of the shoot of the embryo, and this elongates with the elongation of the shoot of the seedling and gives origin to the permanent root-system. In this way a more direct and

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[1] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 374.

[2] See Planchon et Triana, Mémoire sur la famille des Guttifères, in Annales des sciences naturelles, sér. 4, xvi (1861). The older literature will be found in this paper.

[3] This appears even more strikingly in the Lecythidaceae. See the figure of the seedling of Eschweilera obtecta given by Miers, On the Lecythidaceae, in Transactions of the Linnaean Society, xxx (1875), where the axis of the shoot springs evidently out of the middle of the side of the hypocotyl.

more simple connexion of the shoot with the soil is established than would be the case if the path of transport through the hypocotyl, which serves as a reservoir of food-material and which is later pushed aside, were to persist.

In the family of the Lecythidaceae there are relationships which are analogous with those of the Guttiferae, and the following are illustrations:—

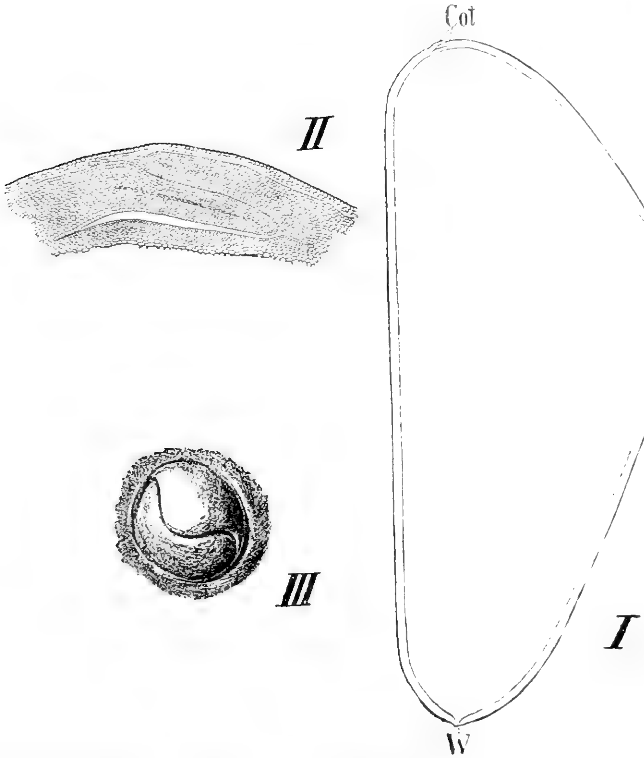

FIG. 180. Bertholletia excelsa. *I*, embryo in longitudinal section; *Cot*, cotyledons; *w*, root-end. *II*, apical portion of an embryo in longitudinal section. The cotyledons are still covered by a thin layer of endosperm. *III*, the overlapping cotyledons seen from above. *I*, magnified 3½. *II* and *III*, more highly magnified.

Barringtonia Vriesei. Treub has investigated carefully the forms of the embryo in Barringtonia Vriesei[1]. Barringtonia differs in its embryo from Xanthochymus chiefly in this, that not only is the hypocotyl thick and fleshy but also its continuation upwards, which is, however, elongated in germination. This portion of the axis of the shoot bears some irregularly placed scales[2], the lowermost two of which are not opposite one another, so

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[1] Treub, Notes sur l'embryon, le sac embryonnaire et l'ovule: 5. L'embryon du Barringtonia Vriesei, T. et B., in Annales du Jardin botanique de Buitenzorg, iv (1884), p. 101.

[2] I have found in another species of Barringtonia axillary shoots to these scales when the end of the shoot of the embryo was injured.

that we could scarcely call them cotyledons; they are neither by their position nor in other respects different from the other scales. According to Treub the chief root does not develop. As in Xanthochymus the reserve-food-material is deposited in the strongly swollen central portion of the axis of the shoot of the embryo-plant.

Bertholletia excelsa. The embryo of Bertholletia excelsa is 'undifferentiated,' according to the most recent observations upon the Lecythidaceae[1], and this probably means the same as the description of that of Lecythis, of which it is said that it consists only of stem, that is to say it is a leafless body whose vegetative point only later elongates into the axis of a shoot. Investigation of the embryo shows, however, that it possesses primordia of leaves which cover the vegetative point. They are indeed very small and have hitherto been overlooked, but in the longitudinal section they are clear enough (Fig. 180)[2]. There are two small scales (*Cot*, Fig. 180, *I*) which closely cover the vegetative point of the embryo; whether they are placed directly opposite one another or not I cannot say. Other primordia of leaves were not found, apart from small papillae at the vegetative point. The massive hypocotyl stores the food-material in the pith which is separated from the rind by a tissue[3] which is composed of small elongated cells in which conducting bundles are subsequently differentiated. The primordium of the root, *W*, is but little developed but is recognizable by the arrangement of the cells according to the figures. It develops afterwards in germination into a chief root.

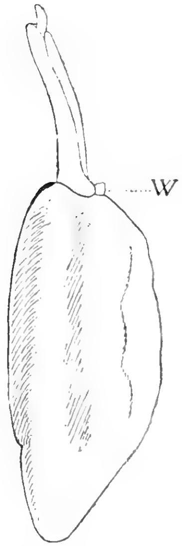

FIG. 181. Posidonia sp. Embryo; *W*, primary root. Magnified about 3.

In the embryos which have been mentioned there exists a relationship, a correlation, between the small development of the cotyledons and the massive development of the hypocotyl, a relation which appears also in many Cacteae[4], whose hypocotyl is specially developed as a seat of water-storage.

B. MONOCOTYLEDONES.

The deposition of reserve-material in the embryos of monocotylous plants is marked in those forms which have macropodous embryos:—

Zannichellia. Amongst them we have specially the Potamogetonaceae, and

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[1] See Niedenzu, Lecythidaceae, in Engler und Prantl, Die natürlichen Pflanzenfamilien, iii, 7 (1892).

[2] The embryo lies in a thin layer of endosperm two cells thick.

[3] The limit is indicated in the figure by the line running parallel with the contour line.

[4] Goebel, Pflanzenbiologische Schilderungen, i (1889).

of these Zannichellia shows a thickened hypocotyl at the end of which the primordium of the chief root is commonly visible.

Posidonia. Fig. 181 shows another case in the embryo of a Posidonia, whose fruit I have found in quantity on the shores of West Australia. The lower end of the massive swollen hypocotyl does not develop a root; the root is a lateral one at the base of the cotyledon (*IV*, Fig. 181). One would be inclined to consider it as an adventitious root, and that the chief root was wanting, but it is much more probable that the chief root has been pushed aside by a lateral growth of the hypocotyl. Bornet's account of the history of development of the embryo of Phucagrostis, and the behaviour of Zostera which I have described below, support this view.

Ruppia. The question which arose in connexion with Posidonia recurs in Ruppia[1] where, according to Wille, the primordium of the chief root is indicated at the lower end of the hypocotyl by a few cell-divisions, whilst at the base of the cotyledonary sheath there is laid down at a later period a lateral root which Ascherson[2] held to be the chief root shoved to one side.

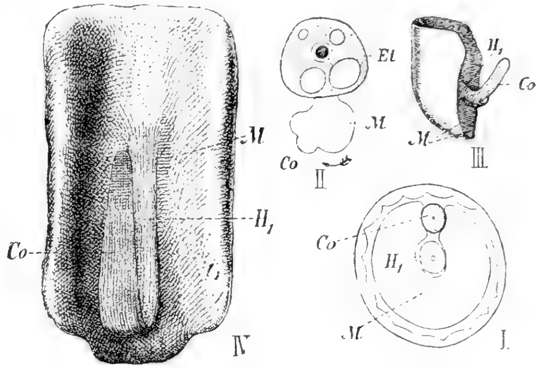

FIG. 182. [Zostera marina. I, fruit in transverse section. II, young embryo in optical longitudinal section. The arrow indicates the direction in which the apex of the embryo is displaced. III, older but not mature embryo in profile. IV, embryo seen from in front. In all figures; *Co*, cotyledon; H_1 hypocotyl; *M* mantle-like outgrowth of hypocotyl; *Et*, unicellular vesicular suspensor.

Zostera. That lateral outgrowths of the hypocotyl[3] occur in macropodous embryos is shown in the remarkable construction of the embryo in the genus Zostera. Here the portion of the embryo which exhibits further development in germination apparently springs out of a shield-like body which is folded in the fruit and encloses the upper portion of the embryo (Fig. 182, III). This makes a strong S-shaped curvature, the lower leg of which is formed by the cotyledons, *Co*; the upper, lying against the shield, corresponds to the upper portion of the hypocotyl (H_1, Fig. 182, I), whose lower part has developed into the shield-like growth above mentioned, in which the reserve-material is stored. There takes place in the embryo at a very early period through the development of the outgrowth, a torsion of the hypocotyl like that which has been described above in Lycopodium and others. In Fig. 182, II, a curvature of the point of the embryo by the outgrowth, *M*, through about 90° has taken place, and the cotyledon no longer appears to be terminal. Hofmeister[4], who was the first to investigate the developmental history of the

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[1] Wille, Om Kimens Udviklingshistorie hos Ruppia rostellata og Zannichellia palustris, in Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjøbenhavn, 1882.

[2] Ascherson, Potamogetonaceae, in Engler und Prantl, Die natürlichen Pflanzenfamilien, ii, 1 (1889), p. 199. Subsequent investigations did not bear out the correctness of Ascherson's views.

[3] These occur also in dicotylous embryos. See p. 258.

[4] Hofmeister, Zur Entwicklungsgeschichte der Zostera, in Botanische Zeitung, x (1852), p. 121.

embryo of Zostera, interpreted the embryo somewhat differently. What we call the shield-like outgrowth of the hypocotyl he considered the 'axis of the embryo of the first order.' In this no one now will follow him, but it is much to be wished that one of the modern microtomists would follow accurately the development of the embryo of Zostera[1]. In Hofmeister's Fig. 28, the curvature of the embryonal axis is probably shown.

These examples will suffice to show how far-reaching are the changes in form which are brought about in the embryos of different plants by the deposition of reserve-food-material. Fundamentally nothing else takes place but what is found in many shoots at a later period of development. The deposition of reserve-material in cotyledons corresponds to that in the leaves of a bulb; the deposition in the hypocotyl to that in the axis of a tuber; the deposition in a lateral outgrowth of the hypocotyl finds its parallel in the axes of many shoots.

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[1] Since the above was written this has been done by Rosenberg, Über die Embryologie von Zostera marina, Linn., in Bihang till kongl. svenska Vetenskaps Akademien, Handlingar, 27, iii (1901). Rosenberg confirms the view given in the text about the 'mantle' of the embryo of Zostera. Of special interest is the embryo of Halophila, whose close relation to the embryo of Zostera was pointed out long ago by Balfour, On the genus Halophila, in Transactions of the Botanical Society, Edinburgh, xiii (1879).

SPECIAL CHARACTERS OF THE ORGANS OF VEGETATION

THE ROOT

Originally all subterranean parts of plants were termed 'root.' As our knowledge increased comparisons showed that under this collective name organs of different structure and different function were grouped together. As 'typical' roots, that is to say, those which are the most common because they correspond with the most widely distributed conditions of life, we may recognize the *soil-roots*, which act as nutritive organs and as anchoring-organs. Organs with analogous function, in which, however, the anchoring function tends to predominate, occur also in the lower plants [1], but they are essentially of more simple configuration, a difference of which we shall have an explanation if we remember that vascular plants alone appear as the typical *land-plants* of any significant size. In the vascular plants therefore the subterranean organs have to satisfy quite different claims from those which are laid upon the rhizoids of one of the Musci, for these have not to support a transpiration-current, and have not reached beyond the stage of development of branched threads [2]. At the same time we must remember that in the vascular plants the functions we have mentioned may be taken over by organs other than the roots [3], and then we find generally that the roots are not developed. A few illustrative cases may be cited here:—

I

ROOTLESS PLANTS

A. *PTERIDOPHYTA.*

Filices. In a number of small epiphytic Hymenophyllaceae, whose embryogeny we do not yet know, roots are not to be found. They are forms which are distinguished almost always by their small size. The species represented in Fig. 183 is much less complex than many of the Musci, and the work which its vegetative body has to do is correspondingly

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[1] See Part I, p. 38 and Fig. 14, also pp. 26, 119 of this Part.

[2] Compare the rhizoid-strands in Polytrichum and elsewhere.

[3] See p. 237.

inconsiderable. The uptake of water is maintained by the one-layered leaves. 'Hair-roots,' which are unicellular tubes on the axis of the shoot and frequently also on the leaves, serve as anchoring-organs. Where the leaves of rootless forms attain to relatively large size, as in Trichomanes Hildebrandti[1], there are special arrangements—in this case the apposition of the leaves to the substratum—on account of which the formation of the roots can be easily spared. Many forms, for example T. membranaceum, have developed instead of roots leafless shoots, which perform the function of roots. Mettenius[2] gives a list of the rootless species of Trichomanes which he had found, and to it I may refer the reader. There are probably other rootless forms amongst the small species of Hymenophyllum, and there can be little doubt from a comparison of the behaviour of a number of species that we have before us in them not primary, but *reduced* forms. The larger ground-species of Trichomanes have a well-developed root-system. Some which live epiphytically among the Musci of tree-stems have relatively few roots. Mettenius states that he only once found an adventitious root amongst hundreds of examples which he examined of T. pedicellatum, T. Ankersii, and T. muscoides. Whether the germ-plants of the rootless species of Trichomanes possess a root or not we do not know. Perhaps the different species behave differently in this respect.

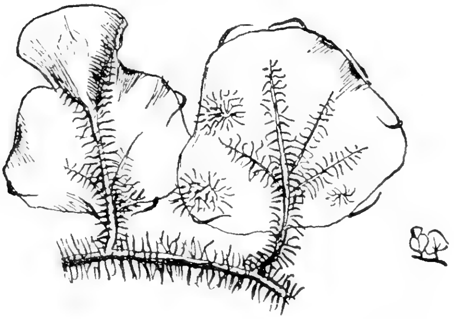

FIG. 183. Trichomanes Goebelianum, Giesenhagen. The plant is rootless and has unicellular hair-roots developed from the stem, leaf-nerves, and also from the leaf-surface, as anchoring-organs. Figure to right natural size. After Giesenhagen.

Salvinia. All the species of Salvinia which have been examined are rootless, and the primordium of the root is suppressed in the embryo. What for a long time were considered as the roots of these floating species of water-plants are peculiarly formed submerged water-leaves, which are divided into numerous segments, and in this respect contrast with the entire floating leaves.

Lycopodineae. Psilotum and Tmesipteris are both rootless. The function of the root is performed by a leafless rhizome. In both genera the superficial development and manifestly the area of transpiration of the shoot are very small. In Tmesipteris, which possesses the larger leaves of the two, these are vertical.

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[1] See Giesenhagen, Die Hymenophyllaceen, in Flora, lxxiii (1890), Plate XIV.

[2] Mettenius, Über die Hymenophyllaceae, in Abhandlungen der königlich-sächsischen Gesellschaft der Wissenschaften, xi (1864).

B. *SPERMOPHYTA.*

Dicotyledones. We have already seen some examples of rootless forms of Spermophyta amongst the Lentibulariaceae. The genera Genlisea, Polypompholyx, Utricularia, are entirely rootless. The position of roots is occupied in the land-form of these genera by peculiar transformed leaf-organs; in the submerged free-swimming water-form the absence of roots is easily understandable, inasmuch as the uptake of dissolved food-material can take place through the whole plant-body, and the function of anchoring-organs is of course done away with. Other water-plants living under similar conditions have no roots, for example species of Ceratophyllum and Aldrovanda[1], as well as the submerged lemnaceous plant Wolffia Welwitschii[2]. Some small floating species of Wolffia, such as W. arrhiza, have also no roots. It is remarkable that in some fixed water-plants the roots are wanting. We find this, for example, in some though not in all the Podostemaceae[3], especially those of considerable size like Rhyncholacis macrocarpa. The arrest of the roots is here made possible by the development of other anchoring-organs—the haptera[4]. Where roots are present on forms of Podostemaceae, which possess haptera, they are devoted partly to purposes other than those of the typical root—to asexual propagation for example, and to other purposes which will be mentioned below[5].

Monocotyledones. Two rootless saprophytic orchids are known—Corallorhiza innata and Epipogon Gmelini. They possess only scale-leaves, and the intake of water is effected by the rhizome-shoot. The reduction of the assimilating and transpiring leaf-surface characteristic of saprophytic life has made possible here the reduction also of the roots. Examples of rootless plants amongst the epiphytes are known—Tillandsia usneoides takes up water, and with it dissolved food-material through the surface of the shoot, and fixes itself by twisting its base round the branch of a tree; roots are therefore not required. They appear, however, in the germination, but soon die off.

II

CHARACTERS OF THE ROOT

There are four organographical regions in a typical soil-root:—

1. The apex, that is to say, the vegetative point covered by the root-cap.

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[1] The statement, frequently repeated, that Myriophyllum is rootless, is erroneous. The winter-buds, when they shoot out, form long roots.

[2] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 279.

[3] See Goebel, op. cit., p. 331; Warming, Familien Podostemaceae (Afhandl. I (1881), II (1882), III (1888), IV (1891), V (1899), VI (1901), in Skrifter af det kongelige danske videnskabernes Selskab, Række 6, ii (1881–6), iv (1886–8), vii (1890–94), ix (1898–1901), xi (1901).

[4] See p. 222.

[5] See p. 280.

2. The very short region of growth.
3. The region covered by root-hairs.
4. The region in which the short-lived hairs are dead.

This holds for the single nearly cylindric root-threads. The construction of the root-system will be mentioned below. I shall now pass in review these several regions.

I. THE APEX OF THE ROOT.

The biological significance of the root-cap requires no explanation here. Every one knows that it protects the soft tissue of the vegetative point in its passage through the soil, and that it makes this passage easier by the mucilaginous degradation of its outer cell-membranes[1]. It is also clear that the possession of the root-cap makes up for absence of leaves upon the root. Hypogeous shoots protect their vegetative point almost exclusively by scale-leaves, and they are often markedly developed as boring-organs, as in Equisetum and Triticum repens. Where this is not the case, as for example in the rhizomes of Psilotum and Tmesipteris, the shoot lives under special life-conditions: the plants are epiphytes, whose rhizomes are not growing in firm soil but between the aerial-roots of tree-ferns, or are living a half-saprophytic life in loose pulpy humus[2]. It is noteworthy that in the two known cases where the vegetative point of the primordium of a shoot is provided with a cap of tissue which serves as a boring- and protecting-organ, and which we can compare in function with a root-cap, this happens before the appearance of the leaves. Strasburger has shown that in Cephalotaxus Fortuni and Araucaria brasiliensis the apex of the primordium of the embryo is not developed into the vegetative point of the embryo. The vegetative point is formed within the primordium of the embryo whilst the original apex which served only as a boring- and protecting-organ is thrown off. Cases which might lead up to these of leafless shoots provided with root-caps have been described, but their anatomical differentiation has not been made clear. The significance of the root-cap is also shown by the behaviour of some water-plants, in which the roots hang free in the water. The root-cap can then no longer be considered as a protective organ, although one must not forget that we have to deal in such cases with roots of limited growth whose apex soon loses the embryonal character. A root-cap constantly regenerating itself by the formation of new cells must be more or less superfluous in a case of this kind, and therefore it submits to a reduction of a varying degree, and such roots

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[1] Concerning the significance otherwise of this mucilage, see Goebel, Pflanzenbiologische Schilderungen, ii (1893).

[2] Solms-Laubach has shown that in Psilotum triquetrum when the apex of a rhizome-shoot has suffered injury, either a lateral primordium grows out or new shoot-primordia are formed in the periphery of the apical meristem. See Annales du Jardin botanique de Buitenzorg, iv (1884), p. 160.

are so intimately adapted to the life in water that they have frequently lost their power of normal growth in the soil. The roots of Lemna minor and L. trisulca, Azolla filiculoides and Hydrocharis Morsus-ranae, all swimming water-plants, show for example in a normally moist garden-soil hardly any growth[1]. Other water-plants, which are not so exclusively adapted to a swimming life, are probably more plastic. In conformity with this are the morphological states, which supply a transition to the cases of complete suppression mentioned above[2]. I must now mention some examples:—

Azolla. In contrast with the allied Salvinia this genus possesses two rows of roots upon the under side of its stem. The apical growth of these roots is limited. The apical cell of the root produces but *one* cap-segment instead of many, as in other Pteridophyta. If the root grows out the cap is thrown off. The superficial cells, including the apical cell, grow out into hairs so that the root resembles the hairy lobes of the water-leaf of Salvinia.

Lemnaceae. Other swimming water-plants like the Lemnaceae possess an evident root-cap, but it is distinguished by the history of its development from a true root-cap, inasmuch as it does not arise like the ordinary root-cap of monocotylous plants from the epidermis of the root, and it does not show periodic renovation. This cap, in form like the finger of a glove, protects the root-apex against the attacks of small animals, the effect of currents of water, and the like. But it does not correspond to a root-cap, but to the envelope which in other roots only exists for a short time, and which has been called by Van Tieghem[3] 'la poche digestive' (Fig. 185).

Hydrocharis, probably also the allied **Trianea bogotensis,** and **Pistia Stratiotes** show similar features. The root-envelope is in them, as in Azolla, lost if the roots continue their growth. In these plants also the differentiation of epidermis from rind is not visible, and their roots are in the narrower sense of the idea quite capless.

Aesculus Hippocastanum. The roots of land-plants are only capless in rare cases. Aesculus Hippocastanum furnishes an example[4]. There arise periodically upon the roots of this plant, in addition to the ordinary lateral rootlets, small tuber-like roots, about 2 mm. long, which have no root-cap; these are in addition to the normally formed lateral roots. These rootlets, whose function is unknown, we may designate arrested formations,

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[1] See Wakker, Die Beeinflussung des Wachsthums der Wurzeln durch das umgebende Medium. in Pringsheim's Jahrbücher, xxxii (1898), p. 71.

[2] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 280. The literature is cited here.

[3] Van Tieghem et Douliot, Recherches comparatives sur l'origine des membres endogènes dans les plantes vasculaires, in Annales des sciences naturelles, sér. 7, viii (1888).

[4] See Klein und Szabó, Zur Kenntniss der Wurzeln von Aesculus Hippocastanum, L., in Flora, lxiii (1880), p. 146.

whose loss of root-cap stands in relation to their short existence and their small size. This explanation is rendered probable by the fact that there are transition-stages between the capless and the normal rootlets.

Bromeliaceae. A peculiar condition which requires further investigation has been shown by Jørgensen[1] to occur in the roots produced by the shoots of the Bromeliaceae. These commonly grow for a long period in the tissue of the shoot-axis, and there they have a well-developed cap. But when the root-tip has bored through the surface of the axis the cap consists of only a thin layer of dead, more or less compressed, cells. Perhaps we have to deal here with roots of limited growth—merely anchoring-roots.

Cuscuta. The chief root of the seedling of the parasite Cuscuta[2], which discharges its function for only a very short time, is capless throughout its life. It has only the duty of fixing the seedling-plant in the soil, and of taking up water for it during its first developmental stages. Two days after germination has taken place it usually begins to wither, and with it naturally the whole plant also, unless it has found a host-plant through which it can be nourished[3].

Like other organs which have become useless under definite life-conditions the root-cap in some cases is thrown off in course of the development; in others it shows no further development. That the root-cap is lost when transformation of the root takes place has already been pointed out[4]. Other cases will be mentioned hereafter.

2. THE REGION OF GROWTH OF THE ROOT.

The distribution of growth in the root will not be spoken of in detail here, but it may be pointed out that as Sachs has shown it is an advantage for the penetration of the root-tip into the soil that the growing region lies immediately behind the root-tip and is relatively very short—only two to ten millimeters; the shorter in relation to its cross-section the axis of a nail is, the less easily does the nail bend when one drives it into a board. In this connexion we may also note that in air-roots the growth-relationships are altogether different. That otherwise the growth of the root is best under the conditions in which it normally grows, and to which it is 'attuned' need not surprise us. The roots of some land-plants, Vicia Faba, Lupinus albus and others, when they were cultivated in water, showed, as might be expected, a retardation of their growth in length[5].

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[1] Jørgensen, Bidrag til Rodens Naturhistorie, in Botanisk Tidsskrift, Række 3, ii (1877–9), p. 144.

[2] Koch, Untersuchungen über die Entwicklung der Cuscuteen, in Hanstein's Botanische Abhandlungen, ii, 3 (1874). The roots of Orobanche have at first no cap, a feeble one develops at a subsequent period. See Koch, Die Entwicklungsgeschichte der Orobanchen, Heidelberg, 1887.

[3] See p. 254.

[4] See p. 227.

[5] See Wakker, Die Beeinflussung des Wachsthums der Wurzeln durch das umgebende Medium, in Pringsheim's Jahrbücher, xxxii (1898).

3. THE REGION OF THE ROOT-HAIRS.

The root-hairs[1] arise as outgrowths of the superficial cells of the root. They have a great significance because by their appearance the absorbing surface of the root is very greatly increased, and besides in land-plants they grow firmly around the particles of soil, and so not only strengthen the hold of the roots in the soil, but also are able to make use of the water-envelope which adheres to each particle of soil. They are not, however, present in all plants. They are markedly absent from a number of water-plants and marsh-plants, as for example Butomus umbellatus, Hippuris vulgaris, species of Lemna, Menyanthes trifoliata, Pistia Stratiotes, and also from a number of Coniferae, for example Picea excelsa, Pinus sylvestris, Biota orientalis, Thuja occidentalis. From some monocotylous plants which produce tubers like Crocus sativus, and from some parasites and humus-plants like Monotropa, Neottia, and Orobanche ramosa, they are also absent. The plants just mentioned are all of a kind which either have water in quantity at their disposal, as is the case with water-plants and marsh-plants; or they do not exhibit intense transpiration from their epigeous parts, as the Coniferae which have leathery leaves—although others like Taxus have numerous root-hairs; or they have roots which are inhabited by fungi, as Monotropa and Coniferae; or the epigeous parts are only slightly developed and have a short life, as in Crocus; or the leaves are mostly reduced to small scales, as in the parasites and humus-plants. In the greater number of plants which produce hairs normally their formation is suppressed if the roots are grown in water. We see this in Allium Cepa, Hyacinthus orientalis, Zea Mais, Cucurbita Pepo, Phaseolus communis, Pisum sativum, and others. This is, however, not the case in all plants, and many swimming water-plants like Trianea bogotensis possess very large root-hairs. The possession of root-hairs by Azolla, Hydrocharis, and other plants, has been already mentioned. The case of air-roots will be discussed hereafter[2].

4. THE REGION IN WHICH THE SHORT-LIVED HAIRS ARE DEAD.

The inner character of that portion of the root which is no longer concerned with the taking up of nutrition lies in the domain of anatomy. The point of organographical and biological interest in it is the *shortening* which takes place in many roots subsequently to the cessation of growth in length. There are formed in many plants roots which differ from the others in their configuration, and whose chief significance consists in their contractility. Rimbach[3] has fittingly termed them *pull-roots.* They are

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[1] See Schwarz, Die Wurzelhaare der Pflanzen, in Untersuchungen aus dem botanischen Institut zu Tübingen, i (1881–5), p. 135.

[2] See p. 283.

[3] Rimbach, Die kontraktilen Wurzeln und ihre Thätigkeit, in Fünfstück's Beiträge zur wissenschaftlichen Botanik, ii (1898), p. 1. The literature is cited here.

distinguished by the relatively strong development of their thin-walled cortical parenchyma, whilst the thick-walled cells of the mechanical system of tissue are entirely, or almost entirely, wanting. These pull-roots have often the subsidiary function of storing reserve-material, but their chief work is that of shortening, and in so doing they exercise a pull upon the portion of the plant out of which they arise. When we consider the use of this arrangement we must distinguish cases in which the pull-roots *draw down the shoot into the soil* from those in which they do not do so.

In the latter, for example in Polygonatum multiflorum, Canna indica, and Asparagus officinalis, the shortening of the root only brings about a firmer anchoring of the plant in the soil, and this is of great importance in plants with richly developed epigeous organs seeing that they expose to the wind and other agencies a relatively large surface.

In other plants the shortening of the root is one of the means by which the hypogeous shoots are brought to a definite depth. The following example will illustrate this:—

Arum maculatum. In the germination of Arum maculatum the elongating cotyledon, which is negatively geotropic, pushes the bud of the seedling vertically downwards into the soil to a depth of fifteen millimeters. The tuber which develops out of this bud lies therefore at first about two centimeters from the surface. Full-grown tubers of Arum lie, however, at a depth of about ten centimeters, and this change in position is brought about by the power of the pull-roots. The roots arise in a zone which surrounds the terminal bud of the tuber like a somewhat obliquely lying ring. Those upon the under side are thick and very contractile, those upon the upper side are thin and only slightly or not contractile. As a consequence of this the tuber is pulled downward at its apex usually about one centimeter in each vegetative period, but only during about two or three months from September to November. Once the *normal depth* is attained the contractility of the roots is diminished, and they grow no longer directly downwards, but horizontally outwards. If one takes such a tuber and plants it higher strong contractile roots are again developed. We know nothing of the causes which bring about this remarkable regulation which recurs in the growth of many rhizomes.

Pull-roots are widely spread and are best developed among perennial and herbaceous Spermophyta. In cryptogamous plants and phanerogamous woody plants they have not yet been observed. The shortening is sometimes very considerable. Rimbach found that for a stretch of root five millimeters long the contraction in some Amaryllideae, for example Phaedranassa chloracea and in Oxalis elegans, was seventy per cent., in Agave americana and Arum maculatum fifty per cent., in Allium ursinum thirty per cent., in Asparagus officinalis ten per cent. These high figures are only applicable to one portion of the shortening stretch of root. Taking the root as a whole the percentages are somewhat smaller. For Phaedranassa chloracea, for example, the shortening was only thirty to forty per cent. In many persistent roots, for example the chief roots and lateral roots of Taraxacum, Heracleum, Phyteuma, the contraction goes on throughout the whole year. In other short-lived roots, as in the example of Arum quoted above, the shortening takes place only during a limited period. In many plants all the roots of one order are contractile, in others there is distribution of labour, as has been already mentioned in the case of Arum, and this is seen more strikingly in many other Monocotyledones and some Dicotyledones. Thus it has been long known that Tigridia, Gladiolus, Crocus, and Scilla possess two kinds of roots which arise in different positions and at different times. Crocus longiflorus, for example (Fig. 184, I), produces at the beginning of the vegetative period on the under side of its tuber numerous thin filiform non-contractile roots, but later upon one side of the new tuber there are produced a few—in the figure only two are shown—thick roots which are strongly contractile and which draw down into the soil the tuber to which they belong, After doing this they soon die. These roots are considered by Daniel[1], who has overlooked the shortening, as a transitory compensating system which develops with the need of the plant when from any cause, internal or external, the general nutrition is hindered. This conclusion is supported by the fact that the tubers in Gladiolus, from which evident buds were removed, produced these roots specially strong, and after two months they were reabsorbed, they were built anew as well as the new tuber, and they contained large masses of glucose which disappeared afterwards. It is not impossible that these fleshy roots at the same time serve as short-lived reservoirs of food-material and also

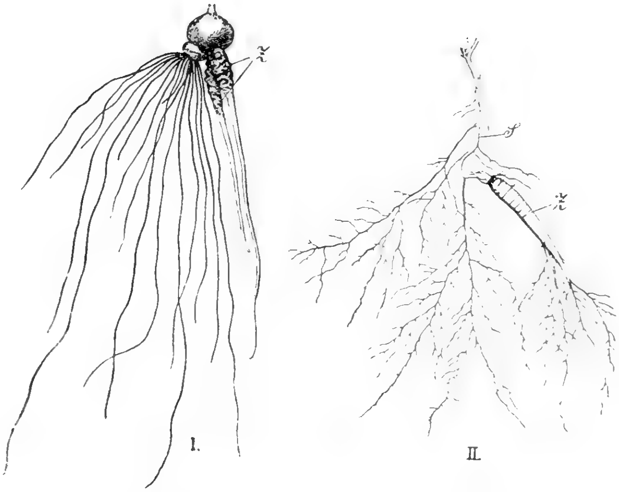

FIG. 184. I, Crocus longiflorus. II, Oxalis sp. (marked as pentaphylla). *Z*, pull-roots; *S*, stem. Half natural size.

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[1] Daniel, Sur les racines napiformes transitoires des Monocotylédones, in Revue générale de Botanique, iii (1891), p. 455.

for water. Their substance can then be taken up by the permanent reservoirs, tubers, and the like; at the same time their significance as pull-roots is none the less evident.

In Dicotyledones analogous cases are known. We have one represented in Fig. 184, II, which shows a species of Oxalis.

III

THE ROOT-SYSTEM

The seedling possesses in most cases at first only a simple unbranched root. Later a root-system develops which is formed either exclusively from the chief root or by the new formation of roots on the shoot-axis. If the latter is the case the primary root soon dies. It is well known that this takes place commonly in the Monocotyledones, but a number of Dicotyledones show it also, and it may be asked if this different behaviour in the formation of the root-system has biological relationships. Inner structural relationships are first of all concerned, and then the conditions of life come into consideration.

Monocotyledones. Monocotyledones show, with few exceptions, no secondary growth in thickness. This means that the primitive conducting-channels for water and other plastic material as they lie in the vascular cylinder of the chief root must remain the same. The demands which the epigeous parts of the plant make upon the roots are, however, always becoming greater with the increasing development in their surface by the multiplication in the number and size of the leaves, and the capacity of the chief root, even if it were ever so much branched, would no longer suffice, therefore it is replaced by the formation of new roots on the shoot-axis, and these appear in great numbers, and in many quickly developing plants, as, for example, a number of grasses, are developed even upon the embryo.

Dicotyledones. We have already learnt, when considering the germination of the plants of the mangroves[1], of a case amongst the Dicotyledones in which the development of a root-system proceeding from the chief root was so evidently unsatisfactory in the sticky mud, poor in oxygen, that it has become suppressed[2]. Were I to describe here the relationships of the duration of development of the chief root to the manner of life of its plant, I should exceed the limits imposed upon this book, for the many-sided subject of the 'succession of shoots[3]' would have to be dealt with. It must

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[1] Some swamp-plants with superficial root-system probably behave in like manner, for instance Taxodium distichum.

[2] See p. 256.

[3] See Warming, Om Skudbygning, Overvintring og Foryngelse. Den naturhistoriske Forenings Festskrift, Kjøbenhavn, 1884.

suffice that I have indicated merely that it depends on the whole economy of the plant. The relationships in individual cases frequently still require explanation.

Methods of Origin of Secondary Roots. New roots are usually endogenetic. They have to burst through the peripheral tissue of the mother-organ, and this only happens if the young root which is laid down under the protection of the older tissue is sufficiently strong. The endogenetic formation is, however, not without exception. Exogenetic roots are formed, according to Bower, in Phylloglossum Drummondii; Treub says that the first roots of the germ-plants of some species of Lycopodium are endogenetic; and according to Warming[1] this is the case in the roots upon the stem of Neottia Nidus-avis. They are laid down in the third and fourth periblem-layer whilst the first and second layers form the root-cap. The epidermis functions for some time as the outermost layer of this and then dies off[2]. According to Hansen[3] the roots at the base of the adventitious shoots and the adventitious roots in the leaf-axils of Cardamine pratensis, Nasturtium officinale, and N. sylvestre are also exogenetic, whilst the adventitious roots of other water-plants and marsh-plants, for example Veronica Beccabunga, Polygonum amphibium, and Ranunculus fluitans, are commonly laid down as endogenetic structures.

Place of origin of the Lateral Roots on the Chief Roots. This is definite. If we leave out of consideration the dichotomy of roots as it occurs in Lycopodiaceae the primordia of lateral roots are always found at the circumference of the axil vascular bundle-cylinder of the root, the so-called 'plerome.' This is surrounded by a simple layer of tissue, the pericycle, which is limited on the outside by the innermost layer of the rind usually designated the endodermis and which has a peculiar structure. In Spermophyta the lateral roots are laid down in the pericycle, in the Pteridophyta in the endodermis. In the Pteridophyta the root-primordium proceeds from a single cell, whilst in Spermophyta several cells always share in the formation of the lateral root. This cell-group of the pericycle lies opposite one of the xylem-groups of the axil-strand in plants which have more than two groups of vasa (Fig. 185), hence the lateral roots are commonly found arranged in as many longitudinal rows as the vascular cylinder of the root has got xylem-groups. In roots with diarch bundles there are four rows of lateral roots according to Van Tieghem, and they arise in the intervals which separate the xylem-bundles from the two adjacent sieve-groups. I must pass over here the history of the origin, and merely state that the lateral roots burst through the rind-layers of the chief root at a relatively late period. The roots of Nuphar for example, leave a stretch of ten or more centimeters above the tip free from lateral roots. The first formation of the primordia of the roots

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[1] Warming, Om Rødderne hos Neottia Nidus-avis, L., in Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjøbenhavn, 1874.

[2] This takes place so early, as is shown in Warming's figures, see Plate IV, Fig. 9 and others, that it occurs when the root is still only a papilla, and one might here assume an endogenetic origin of the root by holding that the epidermis takes no share in the formation of the root, but is only stretched by the root-primordium until it dies or is broken through.

[3] Hansen, Vergleichende Untersuchungen über Adventivbildungen bei Pflanzen, in Abhandlungen der Senckenbergischen naturforschenden Gesellschaft, xii (1881), p. 159.

was found by Nägeli and Leitgeb, in the cases which were examined, close to the apical region of the root at a point where the first vasa were not yet differentiated from the surrounding cells. Janczewski says that in Polygonum Fagopyrum the lateral roots are laid down in the tissue of the vegetative point which is still covered by the root-cap, and which has not yet lignified vessels; also in Pistia these lateral roots arise opposite vessels which have not yet become lignified. Still at the time when the primordia of these lateral roots are laid down the cells of the rind of the root have already in many cases passed into the permanent condition and intercellular spaces already exist between them. The cells which give origin to the lateral roots are evidently derived from the terminal embryonal tissue.

The late appearance of the lateral roots has from my point of view to be considered as a phenomenon standing in relation to the conditions of life. The early formation of lateral roots must hinder the passage of the primary root into the soil. The chief root makes first of all the path and fastens itself with its root-hairs, and only when the normal further development of the root-system is required do the lateral roots burst forth. In many plants, especially those which grow in moist soil or whose roots function for a relatively short time, the branching may be altogether suppressed. We see this in Ophioglossum and especially in a number of Monocotyledones, for example Arum maculatum, Colchicum autumnale, Gagea lutea, Leucojum vernum, Ophrydeae[1]; similarly the 'anchoring-roots' which will be described below are usually unbranched.

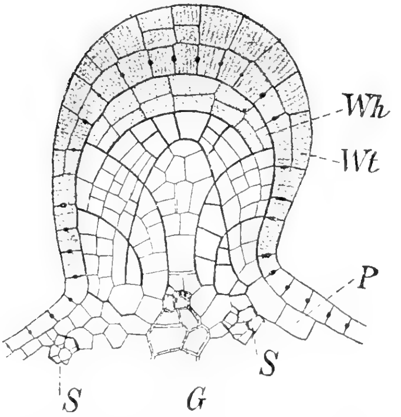

FIG. 185. Young lateral root of a monocotylous plant in diagrammatic longitudinal section. *G*, xylem of chief root; *S*, phloem of chief root; *P*, pericycle of chief root; *Wh*, root-cap of lateral root; *Wt*, digestive pocket formed from the endodermis of chief root.

The Origin of Roots upon Shoots. Adventitious Roots. The behaviour of shoots in the matter of the capacity to bring forth roots is extremely varied. Many annual herbaceous species of Spermophyta do not possess the capacity at all, whilst others, which have creeping as well as upright shoots, lay down roots quite close to the vegetative point. According to Van Tieghem and Douliot the roots which are developed on the shoots in the Spermophyta arise in the pericycle, and thus the relationships observed in the branching of the root are repeated; but where the roots are exogenetic this is not the case. The tissue of the rind contributes nothing to their formation; it surrounds them with a root-pocket (Fig. 185) which is of use to them in boring through the tissue, although there is not everywhere a 'digestion' of its tissue. There are differences according as primordia appear earlier or later, but these have little organographical interest. All the primordia of the roots which

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[1] See Rimbach Beiträge zur Physiologie der Wurzeln, in Berichte der deutschen botanischen Gesellschaft, xvii (1899), p. 29.

are formed upon shoots do not develop into roots, but many may remain for a long time, or indeed always, as 'latent' primordia. We can scarcely reckon amongst these the arrested developments of normal root-primordia which take place under unfavourable external conditions, for instance in Hedera, when the plant is cultivated without any substratum for its shoots. On the other hand we find in Salix latent root-primordia under the cortex, either singly on both sides of the axillary bud or in numbers as in Salix vitellina, S. pruinosa, and others. These primordia of roots develop on cuttings of Salix whilst in the normal vegetation they do so only seldom. Nothing is known about the time of their appearance, but they probably arise pretty early, at least Vöchting mentions them upon the twigs of Salix viminalis, S. pruinosa, and others, which were only three to four months old. No doubt they exist also in other woody plants, and they are also found in Equisetum where an adventitious root is laid down upon every lateral bud, but these do not develop usually in the epigeous parts. They can, however, be forced into development in moisture and darkness.

IV

DIFFERENT CONSTRUCTION OF THE MEMBERS OF THE NORMAL ROOT-SYSTEM OF THE SOIL[1]

The construction of the members of the root-system and their relationship to external factors vary according to their position in the system. The morphological differences are like those which have been already mentioned as occurring in the long and short shoots of the lower plants. If we turned downwards the apex of the shoot represented in Fig. 12 of Part I, and imagine the cell-walls removed, we should obtain a picture corresponding in some measure with a root-system in which, however, as we know, branching would not come quite so close to the apex. The members are usually less strong the higher their order, and this finds explanation in their anatomical structure, in perennial plants also in the shorter duration of life[2] of the 'absorbing rootlets' about which, however, we have few exact investigations.

The classical investigations of Sachs have shown us that the regular spreading of the root-system in the soil is conditioned by the different capacity of reaction to gravity in the roots of different orders. The primary roots are positively geotropic; the lateral roots of the first order possess a 'special geotropic angle[3],' which is different according to their point of origin. In the upper roots which stand nearest the root-base it is commonly a right angle, but in those standing below this it is smaller. The lateral

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[1] See Sachs, Über das Wachsthum der Haupt- und Nebenwurzeln, Gesammelte Abhandlungen, ii (1893), xxxi and xxxii.

[2] All the roots of the first order do not have a long life, for instance those on a chief root of Taraxacum. A number of them die off. But I know of no investigation of this phenomenon.

[3] Sachs investigated the roots of seedling-plants. The relationships of matured roots deeper in the soil may be different.

roots of the second order which spring from those of the first order are, on the other hand, not geotropic. They grow from their mother-roots in a straight line and show no geotropic curvature. That a number of them under usual conditions do not grow out on the surface of the soil is the result of the fact that the air is too dry for them. If the air is artificially kept moist many thin rootlets, especially in the Monocotyledones, will grow out on the surface of the soil[1], a fact which is of special interest in connexion with the development of the breathing-roots, of which mention will be made below, when it will be shown that under definite conditions negatively geotropic roots are formed, and also roots which have entirely lost their geotropic sensitiveness. I may add that such negatively geotropic roots are not yet known amongst soil-roots, yet possibly normal negatively geotropic roots occur also amongst them, but their existence has not yet been brought to light. At any rate we see in the soil-roots that geotropic sensitiveness is, to speak teleologically, regulated by the need of it, and this is also the case in transformed roots. The roots which spring out of the base of the shoot in Monocotyledones appear to behave like lateral roots of the first order, but their geotropic sensitiveness is very small in many monocotylous water-plants. The lateral roots of these roots grow in Pontederia, Pistia, and others in every direction, and are plainly not geotropic. It is important, when considering the 'transformed' non-geotropic roots, to remember the fact pointed out by Sachs that geotropic roots if they grow *in the air* without being wetted lose their geotropism either entirely or in part.

The negative heliotropism and positive hydrotropism which are observed in many soil-roots play a great part evidently in the formation of the air-roots, which will be subsequently mentioned, and the same may be said of contact-stimuli, to which also air-roots, like soil-roots, appear to be sensitive. To what extent 'exotropy' is concerned in the direction of the lateral roots requires further investigation. According to Noll[2] the lateral roots which radiate in the direction of the four points of the compass from the primary root in Lupinus or Vicia Faba, if they are artificially moved out of their position, assume again the radial position to the primary root when the distorting force is removed, making a sharp bend to do so. This power may be of considerable significance for their uniform distribution in the soil.

The Production of Shoots by Roots. Adventitious Shoots. This appears to be a subsidiary function of many roots, but in some cases, as, for example, in the Podostemaceae, it has become the chief function. Amongst Dicotyledones particularly we find a large number of plants whose

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[1] See Sachs, Physiologische Notizen: V. Über latente Reizbarkeiten, in Flora, lxxvii (1893), p. 1.

[2] Noll, Über eine neue entdeckte Eigenschaft des Wurzelsystems (Exotropie), in Sitzungsberichte der Niederrheinischen Gesellschaft für Natur- und Heilkunde zu Bonn, 1894.

roots produce shoots, and these normally arise as endogenetic structures at the positions whence the lateral roots take origin. Frequently the position of the lateral shoots has some relationship to that of the lateral roots. They arise sometimes in the vicinity of the point of origin of a lateral root[1], as in Linaria vulgaris, Solanum Dulcamara, Pyrola, and Dioscorea, and this position secures that the shoot shall obtain water from the soil by the shortest way, just as the position of the bud in the axil of the foliage-leaf of a shoot secures not only its protection but also gives it the advantage of the materials formed by the assimilation of its axillant leaf. In other cases the adventitious roots are formed at least in the vicinity of lateral roots. They arise independently of these, however, when they appear upon older root-parts which have already developed a woody character. In Pyrus japonica, Rubus, Prunus, and others, their seat of origin is in the primary medullary rays; in Ailanthus they are distributed over the general surface of the mother-root. The exact point of origin too is not constant. In Aristolochia Clematitis[2] this is not in the pericycle but in the outer layers of the primary rind, as it is in the Podostemaceae, only in the somewhat deeper layers. The root-buds of Linaria[3] are moreover exogenetic structures. It appears then that the method of origin of the primordia of root-shoots is as various as is that of the root itself.

V

ROOTS ADAPTED TO SPECIAL FUNCTIONS

In a number of plants a portion of the root-system, or it may be the whole of one of the ordinary soil-roots, is adapted to a special function, and consequently exhibits a more or less marked change in its inner and outer configuration. A series of transitions, for example, leads us from the soil-roots to those which spring from the base of the stem of many Monocotyledones, and which soon entering the soil serve as *prop-roots*. They appear in slight degree in, for example, Zea Mais. They are more conspicuous in the Pandaneae and in many Palmae, for example Iriartea and others. But their most remarkable formation is found in the Rhizophoreae and many species of Ficus, in which they have been frequently confounded with stems.

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[1] Beijerinck, Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln, in Natuurkundige Verhandelingen der Koningklijke Akademie van Wetenschappen in Amsterdam, xxv (1886).

[2] Beijerinck, op. cit., p. 109, says the epidermis of the root is usually bored through by the bud, but in the buds laid down very early the epidermis of the rind of the mother-root is an integral part of the new formation. There is here a transition from endogenetic to exogenetic inception.

[3] Beijerinck gives no certain developmental account of this, and his story of the inception of the lateral roots does not conform with that of Van Tieghem and Douliot for other species of Linaria.

A classification of *transformed roots* according to their function is difficult, inasmuch as a root which is constructed as an assimilation-organ may at the same time serve as an anchoring one. It will therefore be better to deal with the several forms in the biological groups of plants in which they occur:—

(*a*) PNEUMATOPHORES OR BREATHING-ROOTS OF MARSH-PLANTS.

It has been already pointed out that the roots of marsh-plants live in a substratum which is poor in oxygen and unfavourable to their respiration[1], and it is through the intercellular spaces of the epigeous parts that they obtain their oxygen[2]. Some marsh-plants have, however, special arrangements for drawing in air.

Mangroves. Fig. 186 is a portion of Laguncularia racemosa, one of the plants of the mangrove of South America. All round it upon the muddy ground washed by the sea there rise hundreds of asparagus-like breathing-roots or *pneumatophores*. We find the same in species of Avicennia and Sonneratia. These negatively geotropic roots are commonly unbranched, but if their tip is injured they may branch and then arise two or more negatively geotropic roots. The pneumatophores have their internal structure, which I cannot describe here, arranged specially for intense gas-exchange. They spring from the roots which are horizontally stretched in the mud. Similar roots appear in other plants, for example sugar-cane and some palms, if they are grown in wet soil. The features of Laguncularia, Avicennia, and Sonneratia, are only an exaggerated condition of a feature that is found elsewhere.

Westermaier[3] has recently thrown doubt upon the generally accepted morphological nature of the pneumatophores. He considers that they are organs, *sui generis* on account of their anatomical relationship. The vegetative point also is not covered by a special root-cap, but is protected by a cork-mantle which has come about evidently as an adaptation to their life in air. This mode of life possibly may have brought about also the anatomical differences from the normal root-structure[4]. We do not, however, know anything about the primordia of these pneumatophores, and until we do know this we can say little certainly about their 'morphological significance.' It is quite possible that the pneumatophores have arisen in quite the same way as, only probably earlier than, the structures which we find in Carapa moluccensis doing the work of pneumatophores. In this species

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[1] See Part I, p. 260.

[2] Goebel, Pflanzenbiologische Schilderungen, ii (1893). Prior to this these intercellular spaces were regarded as reservoirs of air which hardly explained their occurrence in the epigeous parts of marsh-plants.

[3] Westermaier, Zur Kenntniss der Pneumatophoren; Botanische Untersuchungen im Anschluss an eine Tropenreise, Heft 1; Freiburg, Schweiz, 1900.

[4] Besides, there is no far-reaching anatomical difference between root and shoot. The usual scheme of shoot-structure is, for instance, in abeyance in many species of Utricularia and Stylidium.

horn-like or finger-like outgrowths arise[1] by inequalities in the secondary growth in thickness in the upper part of the roots which creep near the surface of the mud.

Fig. 186. Laguncularia racemosa with pneumatophores rising above the water. From a photograph I took in October, 1890, in the island of Curaçao.

In my view it is most probable that these pneumatophores are roots. In Bruguiera knee-like curved portions of the root rising above the mud perform the same

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[1] See Karsten, Über die Mangrove-Vegetation im Malayischen Archipel, in Bibliotheca Botanica, xxii (1891), p. 51.

function. In Lumnitzera numerous lateral roots ascend in a negatively geotropic manner from the horizontal roots and then bend downwards with a sharp curvature. At the point of bending special large lenticels are developed, often a centimeter in diameter, and these perform the work of gas-exchange.

Taxodium. I can do no more than mention here the 'root-knees' of Taxodium which discharge a similar function.

The biological significance of the air-roots first of all suggested upon the ground of their anatomical relationships, and the localities in which they were found[1], was experimentally supported by Karsten and Greschoff. Westermaier's hypothesis that they act as 'pumps' is very improbable, and has no experimental foundation.

Jussieuea. The peculiar roots which are developed in some species of Jussieuea belong to this category[2]. These roots have large intercellular spaces, and their apex is directed upwards. They were formerly considered as swimming-organs, an explanation which it is easy to see is inappropriate. They have limited growth, are usually unbranched, and may reach twenty centimeters in length, as in the case of J. salicifolia. They evidently serve the purpose of gas-exchange.

Sesbania aculeata, one of the Papilionaceae, possesses similar roots[3].

(*b*) ASSIMILATION-ROOTS AND SHOOT-FORMING ROOTS OF THE PODOSTEMACEAE[4].

The Podostemaceae is a group of water-plants distinguished by many remarkable adaptations. They grow upon stones in rapidly flowing water. The roots, when these are present, cannot therefore enter into a substratum, and therefore they have been adapted to many other functions. Owing to their position the roots are exposed to light and contain chlorophyll. The formation of chlorophyll may take place in many roots which are usually not green if they grow in the light, for example in those of Menyanthes trifoliata, Mirabilis Jalapa, whilst at the same time other roots of the plant are not in a position in which this can occur. The roots of the Podostemaceae are, however, all chlorophyllous, and many are constructed as assimilation-organs. I quote the following examples from Warming:—

Dicraea elongata and D. algaeformis. Dicraea elongata and D. algaeformis have two kinds of roots. One of these spreads itself over the substratum to which it

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[1] See Goebel, Über die Rhizophorenvegetation, in Sitzungsberichte der naturforschenden Gesellschaft zu Rostock, 1886; id., Über die Luftwurzeln von Sonneratia, in Berichte der deutschen botanischen Gesellschaft, iv (1886), p. 249; id., Pflanzenbiologische Schilderungen, i (1889), p. 113.

[2] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 259, where the literature is cited.

[3] See Scott and Wager, On the floating-roots of Sesbania aculeata, Pers., in Annals of Botany, i (1887), p. 307. In this plant the roots are, in my view, not swimming-roots but breathing-roots.

[4] See Warming, Familien Podostemaceae: I–V, in Skrifter af det kgl. danske videnskaberne Selskab, 1881, 1882, 1888, 1891, 1899; Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 331. The literature is cited in the last-mentioned work. Also Willis, Studies in the Morphology and Geology of the Podostemaceae of Ceylon and India, in Annals of the Royal Botanic Gardens, Peradeniya, 1901.

is fastened by root-hairs[1] and haptera[2]. The other kind floats free in the water like so many algae anchored at their base. There is evidently no geotropic sensitiveness in them, and this may be noted in most algae. These free-floating roots produce in progressive acropetal succession the primordia of foliage-shoots which are endogenetic, but are laid down far from the central cylinder of the root with which they only come into connexion at a later period, and they attain to only a slight construction and are far behind the roots which are rich in chlorophyll in their power of assimilation. The free roots evidently have a limited growth, and in this they contrast with the non-metamorphosed roots which are spread out over the substratum. In D. elongata they are round, in D. algaeformis they are band-like and have the appearance of a foliage-leaf. The root-cap is but little developed and rudimentary. The likeness to a leaf of these remarkable roots of D. algaeformis is heightened sometimes by the fact that on one side of them there is developed a palisade-like parenchyma, and in this they exhibit, indeed, an analogy with phylloclades. The roots of these plants diverge then in conformation, direction of growth, and function altogether from the common condition, and this deviation is evidently brought about under the influence of light.

We find also elsewhere amongst the Podostemaceae that roots are flattened sometimes upon the side to the light and sometimes upon the side to the substratum.

Oenone leptophylla. In the root of Oenone leptophylla, the transverse section of which is represented in Fig. 122 of Part I, its dorsiventral character is well shown, and we observe how here, as in the aerial roots of the orchids which will be mentioned presently, a form may be only indicated in one plant while it appears as a conspicuous feature in a nearly allied one.

Hydrobryum. The flattening reaches its extreme in Hydrobryum, a small podostemaceous plant in which the roots form a flat crust upon the stones and the shoots spring out from its upper side—a most remarkable construction in which we naturally do not find any special root-cap. In this plant the roots are anchoring-organs, but they are also of importance for assimilation and for the production of shoots. This latter function is met with also in other Podostemaceae in which the transformation of the roots has not gone so far (see Fig. 164). Altogether the roots of the Podostemaceae give us one of the most striking examples of how change of configuration goes hand in hand with change of function.

(*c*) AIR-ROOTS OF THE CYCADACEAE.

Remarkable root-formations which require further investigation are found in many, perhaps all, Cycadaceae:—

These are roots which appear above the soil or near its surface, and by repeated forkings give rise to coral-like structures. They are shown in Fig. 187, II, where in Macrozamia Fraseri from each side of the thick beetroot-like hypocotyl there spring near the surface of the soil some roots which grow upwards and perhaps may be negatively geotropic. The swelling at their points indicates the beginning of

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[1] These arise only on the side next the substratum. Whether light hinders their formation on the exposed side and contact-stimulus induces them on the other is unknown.

[2] See pp. 222, 265.

branching. The lateral roots are much shorter, and branch earlier. They are represented in Fig. 187, I, in a rootlet of Ceratozamia robusta. In this plant the coral-roots appear, as in Cycas, often in great numbers. They differ from the ordinary soil-roots by their forked branching. As we find a like abnormal construction of the roots following upon an infection of lower organisms in other plants, for instance in the mycorrhiza of many Coniferae and the mycodomatia of Alnus, it is possible that micro-organisms are also the cause of the condition in Cycadaceae. Janczewski [1] considers the dichotomy in Cycas as a 'pathological process,' brought about by an 'endophytic' Nostoc. Reinke [2] was the first who showed that in the cortex of the roots of such Cycadaceae an Anabaena is found. That these Cyanophyceae cannot be the cause of the forking in the roots, as Janczewski would have it, and is still less the cause of the appearance of the remarkable breathing-roots[3], is evident inasmuch as the presence of the Anabaena is by no means a constant occurrence. Other lower organisms, such as fungi and bacteria, are *not constant* inhabitants—according to some slight investigations which I myself made—and inducers of the air-roots of the Cycadaceae. I must therefore assume that we have here to deal with normal vegetative organs, whose peculiarity consists in this that they come in contact with the atmosphere, and that they are probably to be considered as pneumatophores. At any rate we gain nothing by supposing, as some authors do, that they are 'atavistic.' The Cycadaceae are allied to the Filicineae, but dichotomous branching of the root is unknown in the Filicineae, if we do not reckon Isoetes with them. We shall only gain a knowledge regarding the significance of the air-roots of Cycadaceae by experimental investigation. It must be remembered that the air-roots need not always have to do with the absorption of oxygen.

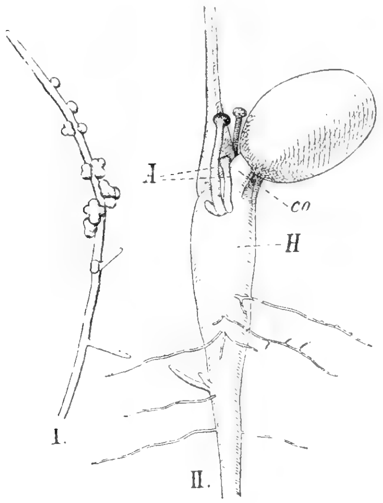

FIG. 187. I, Ceratozamia robusta. Root with normal lateral roots below and coral-like branched air-roots. II, Macrozamia Fraseri. Seedling with erect air-roots, *A*, springing from the hypocotyl, *H*, close to the insertion of the cotyledons, *co*. I, natural size. II, half natural size.

(*d*) ROOTS OF EPIPHYTES.

The assemblage of epiphytes which is so richly developed in the tropics finds itself in the matter of nutrition and anchoring frequently under conditions altogether different from those of plants rooting in the soil,

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[1] Janczewski, Das Spitzenwachsthum der Phanerogamenwurzeln, in Botanische Zeitung, xxxii (1874), p. 116.

[2] Reinke, Über die anatomischen Verhältnisse einiger Arten von Gunnera, Linn., in Göttinger gelehrte Nachrichten, 1872, p. 107; id., Zwei parasitische Algen, in Botanische Zeitung, xxvii (1879), p. 473.

[3] A. Schneider, Mutualistic Symbiosis of Algae and Bacteria with Cycas revoluta, in Botanical

and this has led to a divergence in the anatomical and morphological construction of the root-system in many cases. Epiphytes have been repeatedly and comprehensively described in botanical literature in recent times[1], and I need therefore give here only a short exposition of their most important relationships of an organographical character.

With reference to the anatomical structure the remarkable apparatus for the uptake of water which is visible in the *velamen* of the air-roots of many orchids and of some aroids may be recalled. Further it may be pointed out that the root-hairs have in many cases taken on qualities other than those found in soil-roots. The root-hairs of soil-roots are extremely sensitive to dryness. Many of the root-hairs of epiphytes are by no means so sensitive. The older root-hairs, especially in many epiphytic Filicineae, have a brown colour; their walls behind the point are 'encrusted' with a substance which resists the action of sulphuric acid and boiling potash, and this makes them very resistent to drying. The root-hairs also partly serve here to fix water by capillarity. In Antrophyum cayennense[2], for example, the shoot-axis is entirely enveloped by a dense reddish root-felt which is formed by the numerous exposed root-hairs, and it forms a kind of root-sponge for the taking up of water. In many epiphytic orchids also the root-hairs are peculiarly constructed[3].

The geotropic behaviour of these roots is interesting. Many aerial roots of orchids have lost their geotropic sensitiveness in great measure, in others it appears in a peculiar form. Some of the more remarkable constructions are these:—

a. NEST-ROOTS OF EPIPHYTES.

By this name we designate negatively geotropic roots which grow up out of the substratum and form nest-like masses within which humus accumulates. They are found in some species of Aroideae, for example Anthurium Hugelii and others, and amongst Orchideae in Grammatophyllum speciosum, species of Cymbidium, Aeriopsis javanica[4], and others.

Gazette, xix (1894), p. 25, found bacteria in the outer cells of the coral-roots of Cycas revoluta, but it does not follow that this is either a 'symbiosis' or a cause of the appearance of the roots.

[1] See Schimper, Die epiphytische Vegetation Amerikas, in Botanische Mittheilungen aus den Tropen, i, Jena, 1888; Goebel, Pflanzenbiologische Schilderungen, i (1889).

[2] Goebel, Archegoniatenstudien: VIII. Hecistopteris, eine verkannte Farngattung, in Flora, lxxxii (1896), p. 73.

[3] They may be 'lignified,' according to Molisch, Über Wurzelausscheidungen und deren Einwirkung auf organische Substanzen, in Sitzungsberichte der Wiener Akademie, xcvi, 1 (1887), p. 107, footnote. Free hanging aerial roots of orchids form usually no root-hairs, but this is not always so. They appear in moist air upon the air-roots, usually adherent, of Vanilla, Phalaenopsis, and others, even if these do not touch a substratum.

[4] The numerous close-set, negatively geotropic, thin roots are covered with short, spreading, lateral rootlets. All water flowing down from the upper surface of the tree will filter through this weft of roots, but it cannot retain large objects. See Račiborski, Biologische Mittheilungen aus Java, in Flora, lxxxv (1898), p. 352.

b. ASSIMILATION-ROOTS OF EPIPHYTES.

The roots of epiphytes which are exposed to the light usually contain chlorophyll, but where there are numerous and well-developed leaves then chlorophyll is only present in relatively small amount. In some Orchideae, however, the roots are essentially the assimilation-organs and even may be the exclusive ones, and then they show corresponding changes in their anatomical structure and their configuration—they are conspicuously dorsiventral[1].

Phalaenopsis. I shall first of all speak shortly of the formation of the roots in the genus Phalaenopsis. In Fig. 188 there are portions, in transverse section, of the root of three species. Ph. Esmeralda (Fig. 188, I) has roots which we cannot designate as dorsiventral, but they function only to a small extent as assimilation-organs; they are rather to be regarded, apart from their capacity to absorb water, as seats of water-storage in the dry period during which the plant has lost its leaves. Ph. Lueddemanniana (Fig. 188, II) shows conspicuously flattened and dorsiventral roots. The root-hairs are produced upon the under side and only along the middle line of the roots which lie close upon the branch of the tree[2]. The long roots, often a meter long, of Ph. Schilleriana (Fig. 188, III) show this flattening in an extreme degree. These roots are firmly adherent to the stem of the tree (Fig. 189). The tissue of the cortex on both sides of the central cylinder is massively developed—an arrangement which may be of advantage by enabling the root to retain by capillarity the water upon the under side. The flattening begins very early; probably the transverse section of the vegetative point of the root is not circular but elliptic[3]. The uptake of water chiefly takes place by the under side whilst the upper side is constructed to protect the root against strong transpiration. The anatomical structure (Fig. 190) shows this clearly. On both sides there is a two-layered *velamen*, under which lies the *exodermis*. The outer walls of the cells of the exodermis are greatly thickened in those of the upper side, but only slightly thickened in those of the under side. The velamen is developed upon the upper side only as

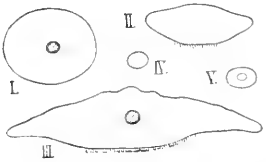

FIG. 188. Phalaenopsis. Roots in transverse section. I, Ph. Esmeralda. II, Ph. Lueddemanniana. III, IV, V, Ph. Schilleriana. Mature root in III; young root, that is to say close behind vegetative point in IV and V. Shaded central cylinder shown in I and III. All of same slight magnification.

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[1] See Janczewski, Organisation dorsiventrale dans les racines des Orchidées, in Annales des sciences naturelles, sér. 7, ii (1885); also Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 197, and ii (1893), p. 344.

[2] The factors which determine the localization of the root-hairs upon the under side require investigation. The substratum is not the effective influence because *free* roots in moist air have hairs only upon the under side. Possibly the dorsiventrality originally induced by light is the critical factor.

[3] I have only examined one root-tip. Fig. 188, IV, represents a transverse section near the tip.

an apparatus for taking up water, and is composed of empty thin-walled cells with fibre-thickening. The outer thin-walled layer of the velamen is hardly visible upon the upper side, but the inner is transformed into thick-walled cells. In correspondence with this the characteristic 'aeration-striae' of the velamen of the aerial roots of the Orchideae are to be found here only upon the under side. It has been already pointed out[1] that the flattening of the aerial roots of many Orchideae is brought about by light[2], whilst in other cases it is 'fixed by inheritance.' Phalaenopsis Schilleriana furnishes us with a case where the flattening is not due to light. A portion of the root many centimeters long which was grown in a non-translucent tube was quite devoid of chlorophyll, and yet as flat as a portion which was developed in light. On the other hand, thickening of the walls of the cells, especially of the exodermis, was markedly less[3]. In many species of Phalaenopsis the leaves die away in the annual dry season, and only the green roots, which are well protected against loss of water, and the vegetative point of the shoot persist.

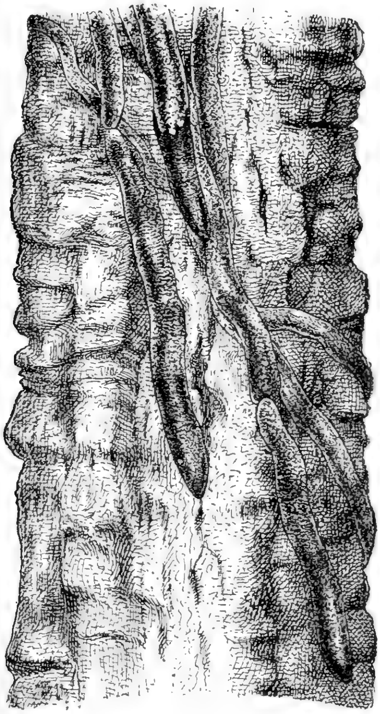

FIG. 189. Phalaenopsis Schilleriana. Roots flattened and adpressed to bark of a tree. The notches on two of the roots are a consequence of interruption of growth. One-half natural size.

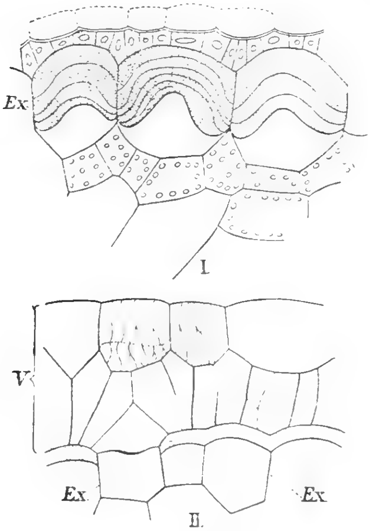

FIG. 190. Phalaenopsis Schilleriana. Portion of root in transverse section. I, through the upper side. II, through the under side. *Ex*, exodermis; *v*, velamen.

Taeniophyllum. This behaviour leads us on to the cases in which the

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[1] See Part I, p. 246.

[2] The anatomical structure also through transpiration-relationships.

[3] I pass over other anatomical differences.

leaves are reduced to scales without chlorophyll, and in which the roots are the special assimilation-organs. We find this in species of Taeniophyllum, and also in Angraecum fasciola and others; foliage-leaves do not arise even in the germination in Taeniophyllum[1], and as the roots are frequently adapted to living in light the foliage-leaves do not appear, according to Wiesner, even if Taeniophyllum be grown in the absence of light.

c. ANCHORING-ROOTS OF EPIPHYTES.

In some epiphytic plants which are able to take up through their leaves large quantities of water, with the substances that are dissolved in it, the roots serve only as anchoring-organs. They cannot take up water to cover the needs of the plant, their conducting channels are small, and their mechanical tissues are strongly developed. Such anchoring-roots are found in some species of Tillandsia, for example T. bulbosa and others, and in some (not all!) other epiphytic Bromeliaceae. That Tillandsia usneoides has lost its roots has been stated above[2].

(*e*) ANCHORING-ROOTS OF CLIMBING PLANTS.

Root-climbers possess anchoring-roots, and are not sharply distinguished from the epiphytes. We frequently find in them a division of labour in the roots such as has been so long known in the case of Hedera—we have anchoring-roots and nourishing-roots. As anchoring-roots we understand here those which serve *purely* as anchoring-organs; their function as nourishing-roots having been given up either entirely or in great measure. One can easily satisfy oneself in the case of Hedera, for example, anchored to a wall by means of its anchoring-roots, that if its connexion with the nourishing-roots which are in the soil is cut through the plant withers. The nourishing-roots on the other hand are only for the purpose of acquiring and bringing nutrition. Anchoring-roots[3] are distinguished from nourishing-roots not only by their shorter length and thickness, their shorter duration of life and different anatomical structure, but also by different physiological peculiarities. They have lost entirely or in great measure geotropic sensitiveness, and therefore their negative heliotropism and their sensitiveness to contact-stimuli are often much stronger than in soil-roots[4].

As regards relationship to contact-stimulus we may specially bring under notice the roots which Von Mohl[5] designated *root-tendrils* because

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[1] With regard to the relationships of configuration see Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 194; the species of Taeniophyllum figured there (Fig. 86) is not T. Zollingeri, but a mountain form in which the assimilation-roots are only partially pendent.

[2] See p. 265.

[3] See Went, Über Haft- und Nährwurzeln bei Kletterpflanzen und Epiphyten, in Annales du Jardin botanique de Buitenzorg, xii (1895).

[4] How far positive hydrotropism has to be considered as I formerly supposed it was, demands experimental inquiry. See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 160.

[5] Mohl, Über den Bau und das Winden der Ranken- und Schlingpflanzen, Tübingen, 1827, p. 49;

they can twine round thin supports just like a tendril. These root-tendrils, however, are not always only anchoring-roots. Von Mohl specially observed them in Vanilla aromatica, in which species they hang straight towards the soil if the twig from which they spring hangs free in the air, but force themselves into the splits on the surface of a tree-stem should they reach it, and twine round any thin support with which they come in contact, in the same manner as do tendrils. The melastomaceous plants Medinilla radicans, Dissochaeta, and others, show the same features, but in them the root-tendrils are exclusively anchoring-organs.

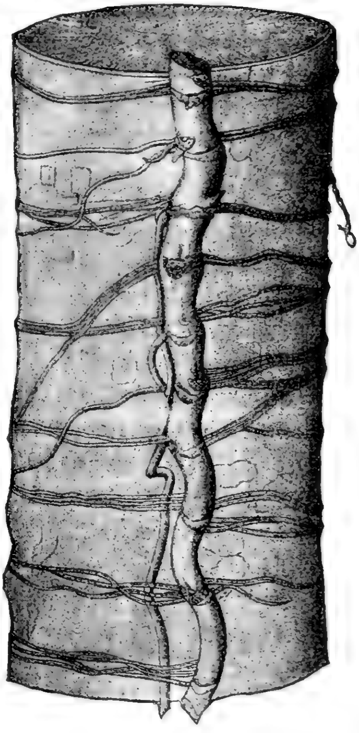

FIG. 191. Philodendron melanochrysum. Stem with vertical nourishing-roots and horizontal anchoring-roots. Half natural size. After Schimper.

The difference in behaviour between anchoring-roots and nourishing-roots may be depicted in one single example. The anchoring-roots of Philodendron melanochrysum (Fig. 191) twine round thick tree-stems like horizontal thongs; they are not geotropic, but they are negatively heliotropic and extremely sensitive to contact-stimuli, the cylinder of conducting bundles has few and narrow vasa and much sclerenchyma. The nourishing-roots are thicker than the anchoring-roots; they do not arise like them from the side of the shoot-axis of Philodendron which is turned to the substratum, but upon the opposite side; they grow downwards towards the ground, and usually in contact with the support on which the plant is climbing, but in other Aroideae they pass down freely through the air; the cylinder of conducting bundles is larger, and has many vasa and little sclerenchyma. It is clear that the nourishing-roots can only be formed after the plant has reached a certain size and has already obtained material for the formation of these roots, and development of the nourishing-roots is rendered necessary because so many of these climbing plants reach so great a size. In climbing plants which soon lose their connexion with the ground and thus throw off their original root-system, or which from the beginning grow upon the trees and not in the soil, it may be assumed that anchoring-

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also Treub, Sur une nouvelle catégorie de plantes grimpantes, in Annales du Jardin botanique de Buitenzorg, iii (1883); Went, Über Haft- und Nährwurzeln bei Kletterpflanzen und Epiphyten, in Annales du Jardin botanique de Buitenzorg, xii (1895).

roots first of all develop out of soil-roots, and then nourishing-roots form from these—an explanation which is supported by the interesting occurrence in the Aroideae of intermediate transition-forms between anchoring-roots and nourishing-roots[1].

What has been said applies equally well to other climbing plants. Freycinetia imbricata, one of the Pandaneae, has no nourishing-roots but only anchoring-roots, but in Fr. javanica anchoring-roots may develop into nourishing-roots. Fr. Bennettii has well-developed nourishing-roots. Anchoring-roots are elsewhere known in a large number of climbing plants of the Clusiaceae, Artocarpeae, Bignoniaceae, Asclepiadaceae, and other families.

(*f*) Roots as Mechanical Organs of Protection. Thorn-Roots.

Roots may develop into thorns just as do leaves and shoots. Examples are known both amongst the Monocotyledones and Dicotyledones.

MONOCOTYLEDONES.

Amongst Monocotyledones the case of the palms Acanthorhiza[2] and Iriartea have been long known:—

Acanthorhiza aculeata. Acanthorhiza aculeata possesses in its lower stem-region normal soil-roots, but in the upper region there are formed feebler roots which lose their root-cap, whilst the cell-membranes, with the exception of the sieve-tubes, become lignified, and the cells of the outer cortex take on a strongly sclerenchymatous character.

Iriartea. In Iriartea it is the lateral roots which become small thorns.

Dioscorea prehensilis. Dioscorea prehensilis[3] furnishes a further example. This remarkable plant possesses tubers which are enclosed in a sheath of thorn-roots. These are in the soil not above it as in the case just mentioned. There can be little doubt that these thorns are an effective mechanical protection against animals, perhaps also against the pressure of the dried-up soil. Similar relationships are found perhaps in D. spinosa.

Moraea. A South American species of Moraea[3], one of the Irideae, has at the base of its stem a dense net-work of thorn-roots which recalls the skin of a hedgehog. The thorn-root-system is here hypogeous.

DICOTYLEDONES.

Myrmecodia. Only one case of thorn-roots is known, that of the remarkable rubiaceous genus Myrmecodia, which Treub[4] has investigated. The thorns which appear upon the outer side of the tuber and the

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[1] See Went, Über Haft- und Nährwurzeln bei Kletterpflanzen und Epiphyten, in Annales du Jardin botanique de Buitenzorg, xii (1895).

[2] Friedrich, Über eine Eigenthümlichkeit der Luftwurzeln von Acanthorhiza aculeata, Wendl., in Acta Horti Petropolitani, vii (1880), p. 537; see also Russow, Über Pandanus odoratissimus, Untersuchungen, p. 537.

[3] Scott, On Two New Instances of Spinous Roots, in Annals of Botany, xi (1897), p. 327.

[4] Treub, Sur le Myrmecodia echinata, Gaud., in Annales du Jardin botanique de Buitenzorg, iii (1883), p. 129. The literature is cited here.

shield-like projections of the stem bearing the leaves are metamorphosed roots which have lost their root-caps.

(*g*) STORAGE-ROOTS.

These are roots which are used for the storage of reserve-material. According to the amount of this they diverge more or less from the configuration of the ordinary soil-root. Where considerable masses of reserve-material have to be deposited they develop parenchyma for its reception, and frequently therefore become fleshy. The whole root may thus become a *tuber*, or only portions of it, and these are then separated from one another by regions showing the common root-character. We find this in the cucurbitaceous Thladiantha dubia, and in it the tuberous portions of the root persist whilst the intermediate portions die away. Where the whole root forms one tuber the root-cap usually disappears, as for example in the tubers of Ranunculus Ficaria and of the Ophrydeae. A description of these tuberous roots belongs, however, more to the province of anatomy. All fleshy roots do not, however, serve as storage-roots; at least this does not appear to be the case [1], or is so only in a slight degree, in the fleshy roots of Oxalis tetraphylla previously mentioned as pull-roots [2].

(*h*) MYCORRHIZA.

I pass over here the formation of mycorrhiza, as any account of this would involve the description of a number of details of an anatomical and physiological experimental character, which is beyond the scope of this book. The examples which I have already given will show how in a number of cases function and the formation of organs hang together.

VI

PERIOD OF DEVELOPMENT OF THE ROOT

In plants whose vegetation is periodically interrupted the development of the root naturally shares in this, and we may say generally that the development of the root precedes in time the epigeous parts, a fact which is easily observable in most seedlings, and the biological significance of which requires no explanation. The periodicity of root-development is very sharply marked in bulbous and tuberous plants, because in them the formation of the root is limited to a very short period. Supposing that the moisture and other conditions are favourable the development of the roots takes place in Ranunculus Ficaria at the end of June, in the bulbs of Fritillaria imperialis in August, whilst the majority of other bulbous plants develop their roots commonly in the autumn before the bud begins to

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[1] See Rimbach, Beiträge zur Physiologie der Wurzeln, in Berichte der deutschen botanischen Gesellschaft, xvii (1899), p. 28.

[2] See p. 272.

shoot. Tulipa sylvestris, for example[1], forms in September twenty to thirty thread-like roots without root-hairs, and these die in June as well as the epigeous parts. A longer duration of the roots in bulbous plants may, however, take place; for example in Leucojum vernum, which inhabits moist places, the roots live from two to three years. Roots which have different functions in these bulbous and tuberous plants develop at different times[2]. Thus the nutritive roots of Crocus longiflorus (Fig. 184, I) arise in the autumn, the pull-roots in the spring when the new tuber is ready.

In trees[3] we can as a rule distinguish two periods of development of roots, one in autumn, the other in spring before the shooting out of the leaves. These periods are separated by the winter's rest, which is here not, as in the case of the shoots, a resting period caused directly by external factors, but must be regarded as only a retardation caused by the sinking of the temperature. In a mild winter development and growth of the roots takes place in the winter. In Tilia europaea, for example, a copious formation of the root-system occurs in August, September, and October, and this the cold interrupts. In one special case in a mild winter the new roots were formed again in December; the period of greatest growth fell in April before the shooting out of the buds. All trees do not, however, behave alike in this respect. Quercus, for example, has no strong root-growth in spring. Its new rootlets only begin to show in June, and the period of greatest growth falls in October. The differences, so far as they may be considered constant, evidently have the closest connexion with the whole economy of each plant. We are, however, very incompletely acquainted with the co-operation between the several organs.

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[1] See Rimbach, Beiträge zur Physiologie der Wurzeln, in Berichte der deutschen botanischen Gesellschaft, xvii (1899), p. 28.

[2] See p. 270.

[3] See Resa, Über die Periode der Wurzelbildung. Inaug. Dissertation, Bonn, 1877.

THE SHOOT

The general features of shoot-formation have been described already [1]. The conformation of the leaves is in most cases so important for the configuration of the shoot, that it appears advisable first of all to speak of the leaves and then to pass on to consider the different forms of the shoot.

A. THE LEAF

I

INTRODUCTION

The characteristics of leaves have been already described [2], and it has been shown [3] also that in the Bryophyta, starting from leafless forms, the formation of leaves has been frequently repeated along different paths. We do not know how the formation of leaves in the Pteridophyta and Spermophyta has phyletically come about. The leaves in these groups have nothing whatever to do with the formation of the leaves in the Musci, for there the leaves belong to the sexual generation, and we have no room here to discuss the purely hypothetic view which derives the leafy plant of the Pteridophyta and Spermophyta from the sporogonium of a moss. The recently repeated attempts also which have been made to explain the leaves of ferns as shoots are based upon entirely false suppositions, and have no longer even a historical interest, and therefore we shall say nothing about them.

That the chlorophyllous assimilating foliage-leaf, whose capacity alone renders possible further development in the autotrophic plants, is the leaf-form out of which the others have been derived by change of function, follows from what has been already said [4]. Moreover there is scarcely one foliage-leaf which has not some other function in addition to assimilation. Apart from transpiration, we may point out the importance of the leaves as protective organs to the buds, whether these be terminal or axillary—a work which is sometimes taken up by different parts of the leaf. In Aristolochia Sipho, for example, the leaf-lamina is folded about the end-bud, the leaf-base encloses the axillary buds. Analogous relationships are found in other plants with small leaves placed in many rows.

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[1] See Part I, section I, chap. ii.

[2] See Part I, p. 13.

[3] See p. 35.

[4] See Part I, p. 6.

No organ of the plant-body appears in so many forms as does the leaf, and this is so because the relationships of the leaf to the outer world are by far the most manifold. In correspondence with this there are great differences in the *anatomic and symmetric construction* of the leaf.

ANATOMIC CONSTRUCTION.

Vascular Bundles. We must specially mention the behaviour of the vascular bundle, as it has been used partly for solution of the question whether the organ is a leaf or not.

The majority of leaves are traversed by one or many vascular bundles which are often copiously branched, and are arranged, as will be shown hereafter[1], in definite relation to the growth of the leaves, whose function we must suppose to be known. There are, however, leaves without vascular bundles, and this simplification of structure must be regarded as a *reduction*. Leaving out of consideration the numerous cases in which the primordium of the leaf remains stationary at an early period of its development and differentiation[2], as well as those of the outer bud-scales of many plants which show a *rudimentary* primordium of a vascular bundle, we find leaves without vascular bundles in the bracts of the flower of Utricularia orbiculata[3]; in the scale-leaves on the rhizome of the saprophytic orchid Epipogon Gmelini where there is no chlorophyll, and according to Schacht[4] the leaves consist of three cell-layers, possess neither vascular bundle nor stomata, serve only as protective organs of the vegetative point, and have evidently only a short existence; in the scale-like leaves also of the parasitic Cuscuta there is only a trace of vascular bundles, and similar cases can readily be found in other saprophytes and parasites[5].

That leaf-structures without vascular bundles occur in the flower-region should not surprise us. Thus they are wanting, for example, in the sepals of Gaiadendron punctatum (Loranthaceae), the stamens of some Arceuthobiaceae, the carpels of Balanophoreae. In all these cases we have to deal with a small delicate leaf-structure whose differentiation is correspondingly simplified.

Hymenophyllaceae furnish also a striking proof of this. The small sterile leaves of Trichomanes Motleyi[6] have no trace of a vascular bundle in their leaf-nerves, the reduction of the conducting channels for water being possible here because the leaves can take up water directly from the outside, as is the case

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[1] See p. 338.

[2] Not proceeding beyond the stage of a papilla.

[3] Goebel, Morphologische und biologische Studien: V. Utricularia, in Annales du Jardin botanique de Buitenzorg, ix (1891), p. 55.

[4] Schacht, Beiträge zur Anatomie und Physiologie der Gewächse, Berlin, 1854, p. 115.

[5] It appears to me not superfluous to refer to these details here, although they are mentioned in Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884). Van Tieghem, Sur l'existence de feuilles sans méristèles dans la fleur de certaines Phanérogames, in Revue de botanique, viii (1896), p. 482, has asserted: 'Happily such roots, stems, or leaves [that is without vascular bundles] have not yet been met with in the vegetative apparatus of Phanerogams.'

[6] G. Karsten, Morphologische und biologische Untersuchungen über einige Epiphytenformen der Molukken, in Annales du Jardin botanique de Buitenzorg, xii (1895), p. 135.

amongst Musci. The fertile leaves, however, have in the leaf-nerves a bundle provided with tracheids—usually only with one.

Similarly the water-channels in the submerged Ceratophyllum are entirely reduced.

The same holds for the leaves of the podostemaceous Terniola longipes, Tristicha trifaria, and Tr. hypnoides[1]. Weddellina squamulosa has leaves upon the lateral twigs, in which all trace of even the most rudimentary vascular bundle is wanting.

The possession of vascular bundles cannot therefore be considered as a general feature of the leaves in Pteridophyta and Spermophyta.

Chlorenchyma. The formation of chlorophyllous leaf-tissue is in the same position. As will be shown briefly in the following pages, chlorenchyma is extremely variable as a tissue in the leaves themselves, and is found also in phylloclades, which are shoot-axes, in the same state as has been considered to be typical of the leaves.

SYMMETRY OF CONSTRUCTION.

We are accustomed to consider as typical leaves those which are *dorsiventral* (bifacial), and which possess usually a leaf-lamina in the form of a thin plate of tissue. Had botany started in West Australia instead of in Europe, this leaf-form would have been considered as a not altogether rare, but yet by no means typical form.

LEAF-FORM IN AUSTRALIA.

Radial and bilateral leaves are very common in Australia, and are found in the most different families, and there are also transitions between dorsiventral and bilateral leaves[2]. The bilateral leaves are usually not spread out horizontally like dorsiventral ones; much more commonly they adopt a 'profile-position' like the sickle-leaves of the Eucalypti, the phyllodes of the Acaciae, the leaves of many Proteaceae, or possess entirely or nearly vertically placed surfaces, or diverge in their form from the usual.

Cylindric leaves are not uncommon. Fig. 192 represents a twig of Hakea trifurcata, one of the Proteaceae, which at the beginning of the vegetative period produces simple flat leaves, but the leaves which are produced later on are branched, and have nearly a circular outline on transverse section[3].

The *flat leaves* have the upper and under sides essentially differently constructed, but they are less strongly protected against loss of water.

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[1] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 340, where there are figures.

[2] See the facts stated by Reinke, Untersuchungen über die Assimilationsorgane der Leguminoseen, in Pringsheim's Jahrbücher, xxx (1897).

[3] The palisade-parenchyma here goes entirely round the leaf, but is interrupted by many rod-cells; it is also characterized by smaller cells for a short distance upon the under side, and thereby there is always a slight difference visible between the upper and under side.

Their epidermis is not so thick as in the cylindric leaves, and the stomata are not sunk in pits. The surface which is exposed to light in the horizontal leaves is larger than the whole surface of the cylindric branched leaves. It is well known, however, that light increases transpiration.

Whilst I have not observed in Hakea trifurcata any transition between entire and divided leaves, such gradations are found in abundance in other species of Hakea, for example H. pectinata. It is not possible, however, to bring all the manifold leaf-forms of the Proteaceae *severally* into relationship with their life-conditions; to do this would require not only full knowledge of the conditions of life, but also of the whole organization of the plants in question. Under the same external conditions the leaf of one plant, which through the activity of its root-system obtains less water, may be xerophilous, that of another, which through the activity of its similar organs receives more water, is not xerophilous. I specially draw attention to this because in recent times questions of adaptations have been frequently treated in a one-sided manner on the basis of an investigation of a *single* organ.

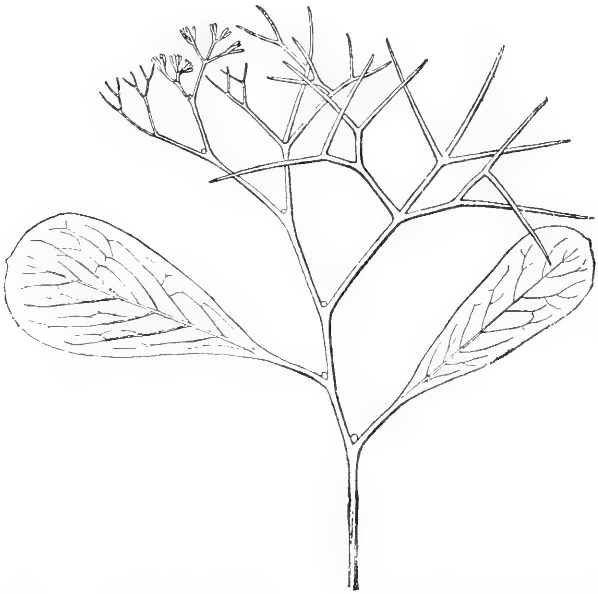

FIG. 192. Hakea trifurcata, R.Br. Lower leaves simple flat; upper leaves branched cylindric.

LEAF-FORM IN EUROPE.

In Europe comparatively few plants possess bilateral or radial leaves.

Amongst plants with *bilateral ones*, however, we must notice the so-called 'compass-plants [1],' which bring their leaves, which have a similar leaf-construction on both sides, into the profile-position under intense insolation, and also a number of marsh-plants—the sword-like leaves of Iris, whose different species, but by no means all, live in wet places, and those of Acorus

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[1] See Stahl, Über sogenannte Kompasspflanzen, in Jenaische Zeitschrift für Naturwissenschaften, xv (1881); Heinricher, Über isolateralen Blattbau mit besonderer Berücksichtigung der europäischen, speciell der deutschen Flora, in Pringsheim's Jahrbücher, xv (1884). Further literature is cited by Haberlandt, Physiologische Pflanzenanatomie, ed. 2, Leipzig, 1896, p. 260.

Calamus, have markedly from the outset a profile-position[1]; in Typha this position is attained by a slight torsion of the blade.

Amongst plants with *radial leaves* we have our species of Juncus, in which the leaf has a circular transverse section, and internally is a tubular leaf, that is to say, it contains numerous air-canals which conduct oxygen to the subterranean parts. It is clear that such leaves, which we only meet with in plants growing in the light and therefore freely exposed to the wind and rain, offer a very small surface to mechanical influences. The leaf-form of Juncus finds a parallel in the cylindric leaves of Pilularia which too grows in moist places, and in those of Crantzia and Ottoa two genera of Umbelliferae in which the leaves are quite like those of the species of Juncus that are partitioned by diaphragms. In these Umbelliferae probably we have to do with a leaf-form which has arisen by reduction from compound leaves. In an investigation of Crantzia linearis (Fig. 193), a plant which I collected in New Zealand, I noticed on the young leaves the primordia of lateral organs which one might indeed consider as arrested pinnules, although they only appeared to be in *one* row, and not, as one would expect, in two rows. The features of Oenanthe fistulosa support this conclusion. On its tube-like leaf-spindle the leaflets appear in reduced form. In Ottoa[2] I found at the end of the leaves only a small depression or flattening which perhaps corresponds to the remains of a rudimentary blade.

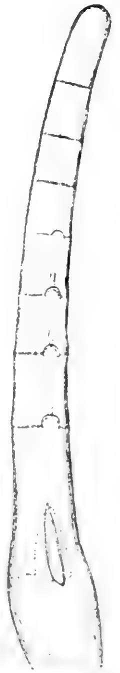

FIG. 193. Crantzia linearis. Young leaf. At the base, the narrow slit of the open vagina. Above, the dotted transverse lines indicate the diaphragms, and the series of papillae are probably arrested primordia of leaf-pinnules. Magnified about 20.

In the same biological category I would also place the leaves of some species of Eryngium which are so like those of Monocotyledones. They are not phyllodes, as is shown by the transition-forms and by the history of development, but consist of leaves whose blade has become greatly elongated, whilst there has been reduction or suppression of the leaflets and of the leaf-stalk. I find in species of Eryngium, for instance E. bromeliaefolium, E. pandanifolium, and others, which are such beautiful marsh-plants, that the narrow grass-like leaves undergo the torsion of the blade that is characteristic of Typha and Sparganium, and thereby they take up the profile-position. By this means they are protected from great transpiration as fitly as a number of marsh-plants are by their xerophilous character[3]. We need not be surprised that in those plants, growing as they do in

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[1] See p. 328.

[2] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 45.

[3] See what is said later, p. 447, about the shoot-formation of some Cyperaceae and Restiaceae.

positions openly exposed to the wind, the earlier differentiation of the leaf-blade has been lost, and the torsion of the leaf-blade is of advantage from a mechanical point of view.

We are justified by the facts which have just been stated in saying that in the ordinary plagiotropous leaves their *dorsiventral* construction is caused by their lie, although so far as we know it has become usually an inherited character; and in support of this it may also be pointed out that a similar dorsiventral construction is marked in shoot-axes and roots which have become leaf-like. The behaviour of a number of scale-like leaves bears also upon the causal relationship of lie to leaf-structure. In the xerophilous Compositae Lepidophyllum quadrangulare and Phoenocoma prolifera [1] the leaves lie with their upper side closely pressed against the axis of the shoot; the under side, which is turned outwards, is the most important for assimilation, and it has palisade-parenchyma, whilst the upper side has spongy parenchyma. We thus have the normal conditions of leaf-structure reversed. As here a *change* of the anatomical structure has come about in connexion with the change from the usual lie, it follows that the dorsiventral differentiation in the ordinary leaf was originally caused by the lie.

INVERSION OF THE LEAF.

The cases just mentioned lead us on to speak of the special phenomenon that in some plants the morphologically upper side of the leaf has the structure of the under side, and the reverse is also the case. In plants which exhibit this, a torsion takes place after the unfolding of the leaves which brings the anatomically upper side upwards, and the anatomically under side downwards. A number of Monocotyledones show this, for example Alstroemeria [2], Allium ursinum, Pharus brasiliensis, and some other grasses. Amongst Dicotyledones analogous cases are found, for instance, in the composite genus Metalesia, and in Stylidium.

A. MONOCOTYLEDONES.

Pharus brasiliensis. In this plant I find the following. The morphologically upper side of the leaf is brighter green than is the under side. This comes about in this way: the epidermal cells of the upper side are higher than those of the under side, and the chlorophyllous cells, which in the greenhouse-plant I examined were in two layers, one under the upper side and one under the lower side, are higher upon the under side than upon the upper side. The upper

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[1] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 32, Plate XXIII, Fig. 12. Passerina hirsuta, one of the Thymelaeaceae, resembles those Compositae. On the seedling-plant the decussate leaves have essentially the ordinary structure, but later, where the alternate leaf-position occurs, the leaves stand pressed to the stem, and upon the very hairy upper side there is spongy parenchyma and stomata, whilst the under side does not possess these but has palisade-parenchyma. See Caruel, Struttura delle foglie della Passerina hirsuta, in Nuovo giornale botanico italiano, i (1869), p. 194.

[2] Czapek, Studien über die Wirkung äusserer Reizkräfte auf die Pflanzengestalt, 1, in Flora, lxxxv (1898), p. 429. The literature is cited here.

side is by a torsion of the leaf-base directed downwards. In the leaf standing immediately below the inflorescence the torsion is only through 90°.

Alstroemeria. Czapek[1] has carefully examined the process in Alstroemeria. The leaves after the first ones submit as they unfold to a torsion through 180° (Fig. 194) which may take place, although tardily, in darkness. Czapek comes to the same conclusion regarding the origin of this peculiar inversion of the leaf-surfaces as I have done. He holds that the inverted leaves of Alstroemeria have arisen in the course of the phyletic development of the genus out of leaves which first of all took up a profile-position, and in consequence of this had a similar construction on *both* sides. Such leaves occur in some species of Alstroemeria, and in species also which have leaves exhibiting torsion the first leaves of the shoot have a profile-position[2]. This profile-position which has to be regarded as a protection against intense insolation and transpiration, was changed again under altered external conditions into a horizontal position, not by a reversion of the torsion through 90°, but by a further torsion through 90°, and thus the leaf came to have an inverted dorsiventral construction in correspondence with its changed lie. I think, however, it is probable that the inversion of the leaf-surface took place in different ways in different groups.

FIG. 194. Alstroemeria psittacina. Leaf. Torsion of the stalk-like lower portion through 180° inverts the lamina. Natural size.

Melica nutans. Among endemic grasses Melica nutans shows inversion of the leaf-lamina[3]. The basal leaves show no torsion usually, and turn therefore the brighter green upper side upwards. On the leaves which stand higher up on the shoot the lamina becomes either vertical with a bending over of its upper part or it undergoes a torsion whereby the under side is brought upwards. As now xerophilous forms such as Melica ciliata are found with rolled leaves, we may suppose that the changes proceeded as follows:—Starting from a leaf having the ordinary lie, there followed first of all either an erect leaf lying against the haulm or a rolled leaf whose under side took on the structure of the upper side[4], as in the scale-leaves mentioned above. If such forms again adapt themselves to moister conditions the structural changes which have been induced cannot be made to revert. The leaf indeed becomes again horizontal, and exhibits now the movements which result in its lie as described above. That the lower smaller leaves which are situated in a moister environment do not share in this, is from the biological standpoint readily understood.

Stahl[5] has advanced another explanation which does not appear to me to be a fertile one, and he has given no experimental proof. He finds in the inversion

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[1] See Czapek, Studien über die Wirkung äusserer Reizkräfte auf die Pflanzengestalt. I, in Flora, lxxxv (1898), p. 429.

[2] With reference to their behaviour on the clinostat, see Czapek, op. cit.

[3] The stomata are found only upon the upper side which bears also hairs. The 'unfolding cells' lie as usual upon the upper side.

[4] Especially limitation of the stomata to the upper side, as this is the rule in this kind of leaf.

[5] Stahl, Regenfall und Blattgestalt, in Annales du Jardin botanique de Buitenzorg, xi (1893), p. 151.

of the leaf-lamina 'a means for lessening the effect of the impact of rain.' The leaf-blade according to him is made less stiff by the torsion. But the plants in question, at least our endemic ones, do not grow under conditions which would render a special protection against raindrops as of much importance, and the leaves are by their conformation no more set out for protection against raindrops than are those of other monocotylous plants growing in the same locality, for example Convallaria majalis. The leaf-lamina of Melica nutans is moreover no broader than that of many other grasses with leaves which are not inverted. Pharus brasiliensis possesses a stalk-like narrowed portion of the leaf-surface which can throw off the raindrops from the leaf without any inversion of it. We find further in other grasses that the leaf-blade is often only vertical or, as is often the case in Brachypodium pinnatum, is only twisted in its upper part. According to Stahl's hypothesis it would be difficult to understand how these leaves can change their structure. That in Alstroemeria, for example, the flat leaf-stalk, which is nothing else than the lower narrowed portion of the blade, should attain by the torsion a greater mechanical capacity cannot be denied.

B. Dicotyledones.

Among Dicotyledones, apart from the above-mentioned Compositae, I know of a torsion of the leaves only in some Australian species of Stylidium—S. pilosum and S. reduplicatum[1].

Stylidium. The stomata here lie upon the morphologically upper side, the lower side is covered by a many-layered thick-walled epidermis, a construction which is favourable to the protection of the bud. After unfolding a torsion takes place somewhat early in S. reduplicatum, later in S. pilosum. There are species of Stylidium with bilateral as well as with rolled leaves, and the explanation advanced above for the grasses would appear here also to be the most natural. Stahl's hypothesis is evidently inapplicable to this case.

II

OUTER DIFFERENTIATION OF THE LEAF

The configuration of small scale-like leaves is very simple; the leaf exhibits no segmentation, and there may be only a leaf-surface. Usually, however, we find the leaf is composed of a *leaf-blade*—the lamina, a *leaf-stalk*—the petiole, and a *leaf-base*. In the leaf of Juncus there is only the cylindric leaf-lamina and the short sheath-like leaf-base which serves as a protection to the bud.

The Leaf-base.

In Monocotyledones, such as grasses, which have a long persistent intercalary growth of their internodes, the leaf-base is developed into a long *sheath* investing the internode of the shoot-axis, and giving the

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[1] Burns, Beiträge zur Kenntniss der Stylidiaceen, in Flora, lxxxvii (1900), p. 337.

necessary support to the still soft plastic tissue of the internode which has not yet grown out. In Dicotyledones also we find the leaf-base is the more developed the more it has a protective function. We may recall here the massive development of the leaf-sheath which covers the dense inflorescence-buds of such Umbelliferae as species of Archangelica, Heracleum, and others which possess large umbels. When hypsophylls and stipules are described this subject will be referred to again. In this place I shall only mention one case which shows an apparent exception.

Leucojum. Narcissus. The leaves of Leucojum, Narcissus, and other like genera have a closed leaf-sheath, that is to say, it completely surrounds the shoot-axis; only the leaf in whose axil the flower develops possesses an open one—a behaviour quite different from that which one would expect. Any transverse section of a bulb (Fig. 195), however, shows that the construction of the foliage-leaf, which is axillant to a flower, is conditioned by *considerations of space*. The bulb consists of leaves which are packed extremely closely one upon the other. In order to provide room for the flower-bud, the base of its axillant leaf is not amplexicaul; if, however, no flower-bud comes to development, then the leaf forms a closed sheath. Between the formation of the axillary bud and this diverse conformation of its axillant leaf[1], there is evidently a causal connexion. Whether it is caused *only* by a mechanical relationship of space[2], or in other ways, can only be settled by experiments, but the processes which go on inside the bulb are very difficult to test.

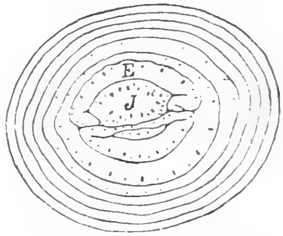

FIG. 195. Narcissus poeticus. Bulb in transverse section; *J*, axis of inflorescence; *E*, axillant leaf of inflorescence-axis having an open leaf-base. Magnified 2.

THE LEAF-STALK.

The *leaf-stalk* is an arrangement for bringing the leaf into the most favourable lie in regard to light, besides it enables the leaf-lamina to lessen the effect of the impact of wind and rain. The function which in many plants is assigned to the *cushion*, which is formed at the base of the leaflets, is so fully treated of in physiological textbooks, that I may pass over it here.

The origin of the leaf-stalk out of the basal portion of the leaf-lamina, by the narrowing of its surface-development, is easily followed in monocotylous plants.

A leaf-stalk is a feature in only a few families of Monocotyledones—Palmae, Aroideae, Scitamineae, and Dioscoreaceae. In other families it

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[1] Otherwise developed as a foliage-leaf.

[2] In that the early development of the axillary bud hinders the primordium of the axillant leaf from developing itself round about the shoot-axis.

occurs only in individual forms. In not a few, however, we can recognize that the *base of the lamina* is differently organized from its upper part, and in many grasses this is strikingly seen, for the ear-like base of the lamina evidently offers stronger mechanical resistance than it would do were it flat [1], and its anatomical construction also appears to be different.

Xerotes longifolia. In Xerotes longifolia, one of the Liliaceae, the lower portion of the leaf-lamina is bent into the form of a channel (Fig. 196, 4, 5), the upper portion is flat. In this way there arises a kind of stalk without the form-change essential to the stalk, and it is easy to satisfy oneself that this stalk-like portion is stiffer than the upper portion of leaf-lamina to which it serves as a stalk.

Phormium tenax. The leaves of Phormium tenax and other species of the genus have a much nearer approach to the formation of leaf-stalk (Fig. 196, 1–3). The lamina is in the upper portion flat, lower down it is narrowed and retains as a stiffening aid a keel-like projection (Fig. 196, 2, *F*), which is scarcely visible in the upper part (Fig. 196, 1, *F*), and in the portion of the leaf close to the leaf-base the keel diminishes again (Fig. 196, 3, *F*).

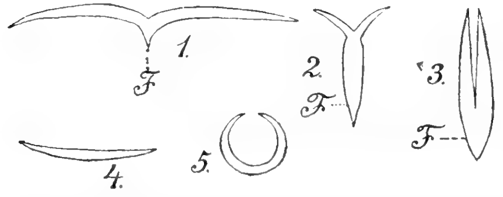

FIG. 196. 1–3, Phormium tenax. 4, 5, Xerotes longifolia. Leaves in transverse section. *F*, wing-like growth on the under side of the leaf. Explanation in the text. Natural size.

Numerous other examples link on with these :—

In Alstroemeria psittacina (Fig. 194), Funkia (Fig. 220), and others, the leaf-stalk appears as the narrowed leaf-base, and in correspondence with the claims of greater mechanical resistance is thicker than the lamina, and also has a slightly different arrangement of its tissue.

Amongst Dicotyledones analogous examples may be mentioned, for example, in species of Plantago.

The existence of a leaf-stalk and the length which it reaches has always a relationship to the structure and size of the leaves [2], and also to external factors. When hypsophylls are discussed it will be shown that in many plants the length of the leaf-stalk in the upper regions of the stem is very much diminished, and when we consider the behaviour of the species within one genus, we shall not infrequently find that those which grow in shady localities are provided with leaves having leaf-stalks, whilst those which occur in sunny localities have no leaf-stalks. The relationships of size,

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[1] In Bambusa the base of the lamina is so narrowed that it can easily twist. In Pharus, Anomochloa, and others, there is formation of a conspicuous stalk.

[2] A very thick leathery leaf of a considerable size can do without a stalk better than a soft one, for example in Coccoloba pubescens.

however, must always be borne in mind; a small leaf can do without a leaf-stalk better than a large one—compare for example Saxifraga rotundifolia and S. granulata, both of which have stalked leaves, with S. Aizoon and S. longifolia which have unstalked leaves; or the rock-species of Edraianthus, which have unstalked leaves, with Campanula rotundifolia, C. latifolia, and others which have stalked leaves. One must not expect to find here strong far-reaching relationships, because that unknown quantity—the 'specific constitution'—always enters into the problem. Aposeris foetida, for example, although a very marked shade-plant, has unstalked or very shortly stalked leaves; the pinnatifid lamina is narrowed downwards, and one might consider this lower portion of the leaf-lamina as a kind of expanded stalk, but in general it appears to me that the leaf-stalk is 'attuned' to a less light-intensity than is the lamina [1], as it always tends to elongate considerably in etiolated plants. In such etiolated plants the formation of a stalk takes place, and the several lobes of the lamina are separated by the elongation of the intermediate portions, and thus the leaf takes altogether a different habit (Fig. 197).

If now we consider the leaf-rosettes of Trapa and other plants which swim on the surface of the water, we shall see that the formation of leaf-stalk in the inner strongly illuminated leaves is restricted, but in the older ones, which are shaded by the others, formation of leaf-stalk is favoured, so that the relationship of the formation of leaf-stalk to light becomes very clear.

In the larger leaf-surfaces of land-plants the greater mechanical demands made upon the leaf-stalk bring about its stronger construction, and therewith comes a greater deviation from the configuration of the leaf-lamina.

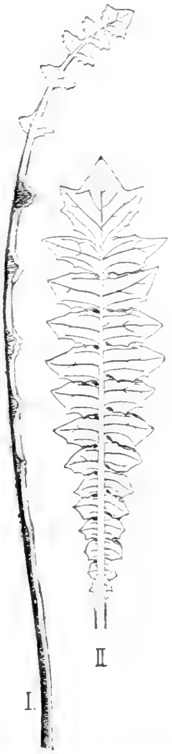

FIG. 197. Aposeris foetida. I, etiolated leaf in which the basal part is greatly elongated, and the leaf has become 'stalked' whilst the several lobes of the lamina are separated. II, normal leaf. Half natural size.

For the view that the leaf-stalk of the leaves of Spermophyta is nothing else than a narrowed and greatly elongated portion of the leaf-lamina, we have not only the support of the cases amongst the Monocotyledones described above and the fact that the formation of leaf-stalks sometimes also takes place in the leaflets of a compound leaf, and they then arise as lateral outgrowths of the leaf-lamina, but also this,

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[1] See Part I, p. 238.

that the leaf-stalk attains its significant thickness, and thereby the form by which it differs markedly from the lamina in most cases only by the longer duration of secondary cell-divisions in its ground-tissue[1]. The arrangement of the vascular bundles in the leaf-stalk is closely connected with this divergent conformation. This point is involved in the consideration of the development of the whole leaf, and will therefore be referred to on a subsequent page[2].

III

DEVELOPMENT OF THE LEAF

A. *HISTORY.*

So early as in the pages of Malpighi (1686)[3] we find some account of the history of development of the leaf. After depicting in characteristic fashion the form-changes exhibited by the bud-scales which follow one another in an opening bud—the 'folia caduca,'—he examines the development of the foliage-leaves—the 'folia stabilia.' He does not distinguish the vegetative point from the youngest primordium of a leaf[4].

The investigations of Kaspar Friedrich Wolff (1759) were more far-reaching. He recognized that the leaves arise upon the projecting point of the stem above the youngest primordium, and that on this point there is no differentiation of tissue visible. Here at the vegetative point[5], the leaves arise by the exudation of the 'succus nutritivus' whose outflow is not restrained by the epidermis or rind. He recognized the 'acropetal' arrangement of the leaves, distinguished between primordial stages and stages of permanent construction, and knew further that divided leaves arise through the branching of originally simple primordia. The midrib according to him appears first. Upon it there arises by exudation a clear margin, the leaf-lamina, on which then by further exudation the foliola spring.

The investigators who followed Wolff at a much later time occupied themselves primarily with the question whether the growth of the leaf was from above downwards, basipetal, or from below upwards, acropetal. At first, however, no sharp distinction was drawn between the different phases of growth as they were later established by Sachs, especially between the embryonal phase, in which the tissue is meristic but increases little in volume, and the phase of elongation. Amongst the older works upon this subject—putting aside speculation unsupported by

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[1] See Deinega, Beiträge zur Kenntniss der Entwicklungsgeschichte des Blattes und der Anlage der Gefässbündel, in Flora, lxxxv (1898), p. 439.

[2] See p. 338.

[3] Malpighi, Opera omnia, Londini, 1686.

[4] He sums up his investigations thus:—'Naturae pariter methodus in producendis stabilibus foliis mirabilis est. Primo enim costula seu petiolus, carinae instar humore turgidus cum appensis fibrulis manifestatur e quibus probabiliter sacculorum seu utriculorum transversalium membranulae pendent (i. e. the secondary veins with the leaf-lamina) ut in animalium primaeva delineatione observatur. Patent autem deducto novo alimento, quia complicata sacculorum moles, subintrante succo, turget et ita folii latitudinem et laxitatem conciliat.' Malpighi, op. cit., p. 30.

[5] 'Ne omni momento opus sit largam descriptionem instituere, liceat vocare haec loca generatim puncta vegetationis vel superficies vegetationis.' K. F. Wolff, Theoria generationis, Halae, 1759.

investigation such as that of de Candolle[1] and others—we find those of Steinheil, Mercklin, Schleiden, Trécul, and others.

Steinheil (1837)[2] found that the leaf grows from above downwards. The point is then the oldest part but in the compound leaf the upper leaflets are the youngest.

Schleiden (1843)[3] maintained that the leaf shoots out as it were from the axis, that the point is the oldest, and the base the youngest, and this led to a lively discussion.

Mercklin (1846)[4] supported Schleiden's view by a series of investigations.

Nägeli (1846)[5] took up the opposite side, and in order to realize Schleiden's idea of tracing the history of the formation of the leaf in that of its single cells he commenced his investigations into the lower plants, the Algae and the Musci, whose simple organization allowed of an examination of the succession of cells. That the leaf is here not thrust out of the axis, but arises from a single superficial cell, showed Schleiden's theory, at least for the cases which had been examined, to be untenable. Nägeli proved:—

'(1) that the peripheral cell-formation, that is to say formation at the apex and at the margin, proceeds from above downwards, and that the base of the leaf is laid down first, the apex last.

'(2) that the intercalary cell-formation which follows upon the peripheral cell-formation ceases sometimes first at the base, sometimes first at the apex, sometimes all at once throughout the whole leaf.

'(3) that the elongation of the cells may proceed either from above downwards, or from below upwards, or may take place equally all over.'

Amongst Phanerogamae the leaves of Utricularia, Astragalus, and Myriophyllum were examined, and it was shown that in Astragalus and Myriophyllum the lateral leaflets are laid down in *basipetal* succession. According to this the leaf then possesses originally an apical vegetative point (embryonal tissue), but it may be the first to pass over into permanent tissue, whilst at the base of the leaf cell-formation takes place freely, inasmuch as the tissue there retains its embryonal character (vegetative point-tissue). In a later work upon Aralia spinosa[6] Nägeli explained in detail the leaf-growth of the Phanerogamae.

Trécul (1853)[7] by his extended investigations, although they did not concern

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[1] De Candolle, Organographie végétale, i, Paris, 1854, p. 354. 2nd English edition by Kingdon, London, 1841.

[2] Steinheil, Observations sur le mode d'accroissement des feuilles, in Annales des sciences naturelles, sér. 2, viii (1837), p. 289.

[3] Schleiden, Principles of Scientific Botany, English edition by Lankester, London, 1849, p. 261. In a special form we find the same thought expressed by Naudin, Résumé de quelques observations sur le développement des organes appendiculaires, in Annales des sciences naturelles, sér. 2, xviii (1842), p. 360.

[4] C. E. von Mercklin, Zur Entwickelungsgeschichte der Blattgestalten, Jena, 1846.

[5] Nägeli, Über Wachsthum und Begriff des Blattes, in Zeitschrift für wissenschaftliche Botanik, Hefte 3 and 4 (1846), p. 153.

[6] Nägeli, Wachsthumsgeschichte des Blattes von Aralia spinosa, in Pflanzenphysiologische Untersuchungen, i (1855), p. 88.

[7] Trécul, Mémoire sur la formation des feuilles, in Annales des sciences naturelles, sér. 3, xx (1853), p. 235.

this cell-formation, brought to light a large number of valuable facts, of which we may note here that the process of leaf-formation in different plants, even those nearly allied, may be very different. That, for example, the development of the lateral members takes place sometimes in acropetal manner, sometimes in basipetal manner, or from the middle both upwards and downwards. His error in considering that the leaf-sheath was the first to arise was later corrected by Eichler. The leaf-sheath is only differentiated at a late period from the leaf-primordium, as one can readily see in the leaf of any grass; the base of the leaf does not at once take on the character of the leaf-sheath, but the leaf-sheath is only formed by intercalary growth out of the basal portion of the leaf.

Eichler (1861)[1] gave a clear account of these relationships, along with a correction and an extension of Trécul's investigations.

Hofmeister (1868)[2] explained in detail the distribution of growth in the leaf, and also gave a summary of the development, although this is not very far-reaching.

At a later date I applied the facts of historical development to the general morphology of the leaf, and especially to its metamorphoses[3]. I showed that *a genetic connexion exists between the different leaves—foliage-leaves in different forms, hypsophylls, kataphylls—which in the matured condition diverge very widely from one another*, in other words, the path of development is originally the same for all leaves, but in many leaves at an earlier or later period the development may proceed along different paths. If we start from the highest differentiated form of leaves the less differentiated appear as retarded formation. With the retardation there may also be associated a transformation[4], which is all the more far-reaching the earlier in the stage of development it appears.

An outline of the development of leaves will be found exhibited in the works I have referred to, and I shall only further cite here some of the more recent investigations.

With regard to terminology it may be pointed out that Bower[5] has proposed a different terminology from that of Eichler which is made use of in the following pages. He calls the whole chief axis of the leaf excluding its branches *phyllopodium*. This phyllopodium may be differentiated by the varying distribution of growth, alike in the transverse and in the longitudinal direction, into different parts which behave differently, namely into *hypopodium* which corresponds with Eichler's leaf-base, a middle elongated portion *mesopodium* which corresponds with the leaf-stalk, and an upper portion *epipodium*.

The history of development of the leaf is of course conditioned by the form of the mature leaf, as has been said already:—'What we call

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[1] Eichler, Zur Entwickelungsgeschichte des Blattes, mit besonderer Berücksichtigung der Nebenblattbildungen. Inaug. Dissertation, Marburg, 1861.

[2] Hofmeister, Allgemeine Morphologie der Gewächse, Leipzig, 1868, p. 519.

[3] Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880), p. 753; id., Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884).

[4] See Part I, p. 6.

[5] Bower, On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms, in Phil. Trans., 1884.

the *mature* condition is only the terminal one of a series of stages of development which follow one on the other[1].' We may say in general that parts which have the earlier functions to perform appear the earliest, and in connexion with this we must remember that the foliage-leaves are not only organs of assimilation, transpiration, and so forth, but have also to act as protective organs for the bud.

Massart[2] has stated that those parts of a compound leaf which in the expanded condition are smallest, are also the last to appear. This is frequently true, but not always. Thus in Acer platanoides (Part I, Fig. 1) the lowermost of the five lobes of the leaf are the smallest, and as the development of the leaf is basipetal they arise last; but in Fraxinus excelsior the lowermost pair of leaflets, which are smaller than the others, arise first. Retardation relatively to the growth of the rest of the leaf-stalk may indeed appear at all stages of development.

B. *GROWTH OF THE LEAF IN GENERAL.*

The primordia of the leaves arise as *lateral outgrowths* on the vegetative point of a shoot-axis, an arrangement which ensures the *rapid development of numerous* leaf-primordia. We have already seen exceptions to this rule in the behaviour of some monocotylous embryos where the leaf-development is relatively slow, and of the embryo in Lemnaceae where one leaf only is developed, and where the origin of the cotyledon itself[3] might be cited in illustration, for it arises independently of a vegetative point. We shall see hereafter, when discussing the development of the flower, that its vegetative point is frequently used up entirely for the flower-leaves[4], and if there be but one of these we arrive at *terminal leaves*[5]. If, then, the statement 'that the leaves always arise as lateral outgrowths on a vegetative point' is not altogether true, yet this is true that the leaf-primordia always proceed from embryonal tissue. There is no case known in which a leaf-primordium has proceeded from permanent tissue, although vegetative points of a shoot may arise from this in regeneration[6]. So far as we know also there are no such things as *adventitious leaves*[7] *or parts of leaves*, although many authors speak of them, for example, in Filicineae. In the Musci the leaf-primordia proceed from one cell which is a segment of the apical cell. In the Pteridophyta this is the case in the Filicineae alone[8]. In all the other groups

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[1] See Part I, p. 9.

[2] Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société royale de botanique de Belgique, xxiii (1894).

[3] The first leaves of the fern-embryos which arise apogamously and are formed independently of the vegetative point of the shoot are also examples.

[4] This probably holds also for the development of the tendrils of some Cucurbitaceae. See p. 426.

[5] See Part I, p. 41.

[6] See Part I, p. 43.

[7] See Part I, p. 42. Regarding adventitious leaves see Goebel, Über Regeneration im Pflanzenreich, in Biologisches Centralblatt, xxii (1902).

[8] At least in the leptosporangiate Filicineae where, however, a leaf does not proceed from every

of Pteridophyta, as well as in the Spermophyta, the leaf-primordium grows out always from a group of cells. These primordia only gradually attain their full size, and there arises at first usually only the primordium of that portion of the leaf which will later become the apex, and after this the leaf-primordium broadens out laterally because further portions of the vegetative point are drawn into its formation, and this may proceed so far that the leaf-primordium finally extends completely round the vegetative point like a ring. This happens, for example, in the grasses which have a closed leaf-sheath and in other cases (Fig. 198).

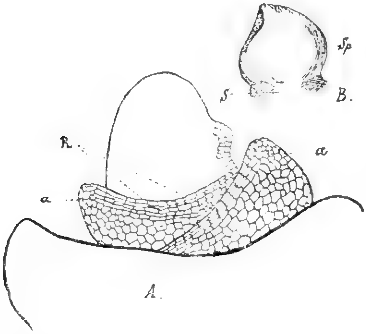

FIG. 198. Dactylis glomerata. *A*, vegetative point with leaf primordia; *a*, *a*, apices of primordia; *R*, margin of leaf-primordium around the vegetation-point. *B*, young leaf differentiated into leaf-lamina, *Sp*, and leaf-base, *s*. After Deinega.

As to the longitudinal extension of the primordium of the leaf, we find, in vegetative points with close-set primordia of leaves, that not infrequently there is no free surface of the vegetative point left over between them, and in such cases the lower portion of the leaf-primordium remains frequently united with the surface of the shoot, and appears in the mature shoot as a leaf-cushion. This process is important for the understanding of the inferior ovary, and the same process is found also amongst lower plants, for example in Chara.

C. *DISTRIBUTION OF GROWTH IN THE LEAF.*

(*a*) APICAL GROWTH AND INTERCALARY GROWTH.

The primordia of leaves, whether they spring from a single cell or from a group of cells, are primarily composed throughout of embryonal tissue. Soon, however, there appears within this a differentiation which in different plants runs a different course. Let us, in the first place, recall what takes place in the Musci.

Leaf-tip in Musci. In them the leaf[1], apart from many exceptions, is composed at its apex at first of a two-sided apical cell, from which right and left two rows of segments are cut off[2], and thus the foundation is laid for the construction of the primordium of the leaf. The capacity of this apical cell is, however, limited. In Schistostega (Part I, Fig. 26) its capacity

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segment, nor is the whole surface of the segment, as in the Musci, devoted to the formation of the primordium of the leaf. In the eusporangiate Filicineae pluricellular origin of the leaf-primordium must take place.

[1] See p. 131.

[2] We must remember that the leaves of all Musci primarily consist of *one* cell-layer, and that where many layers are present, as is the case when nerves and the like are laid down, these are *subsequent* formations.

disappears early, but the cell itself retains its form for some time. We see in Fig. 26 of Part I, on the right, that already the apical cell of the leaf-primordium, which consists of thirteen cells, has grown out to some extent—an indication that it has expended its capacity for *division*, and that its phase of *elongation* has now set in; but in the basal portion of the primordium, which is still small, as we may see by a comparison with the figure standing on the left, the cell-division and growth are still in progress. The growth and the differentiation of tissue which is very simple in Schistostega is ended sooner at the apex than the base. Is this a meaningless phenomenon? In my view this phenomenon, which as we shall see is widely spread elsewhere, is connected with the fact that the leaf-apices have first to serve as *protection to the bud*, because they reach furthest outwards, and we have seen in the Musci that the leaf-tips in plants inhabiting dry places are prolonged into diaphanous

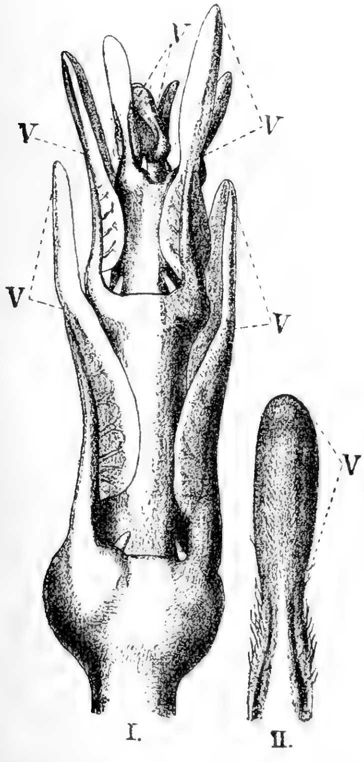

FIG. 199. Gonolobus sp. I, end of a shoot. II, young leaf. *V*, *V*, forerunner-tips. I, magnified 5. II, magnified 10.

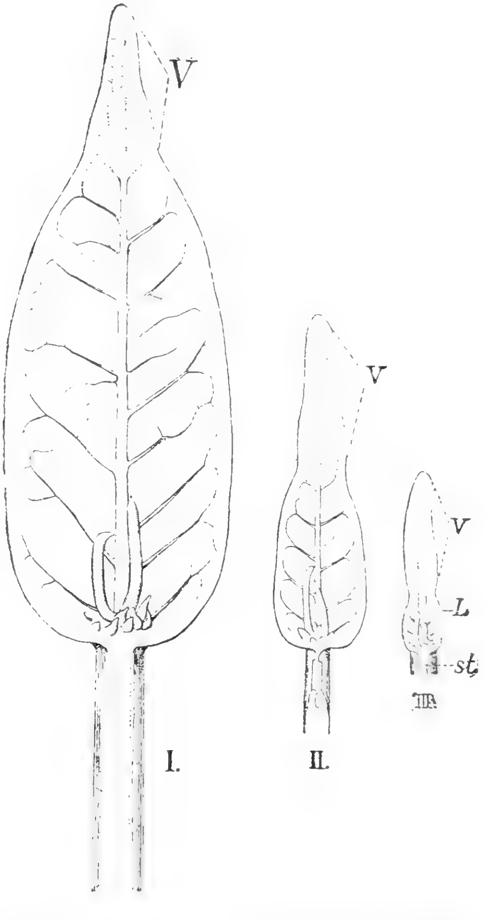

FIG. 200. Gonolobus sp. Leaves of different age in opposite sequence of numbers I, II, III. *V*, forerunner-tip; *L*, lamina with mucilage-hairs at base; *st*, leaf-stalk. The venation indicated in the forerunner-tip in I and II is not seen in fresh leaves. Magnified 2½.

hair-points, which form a little tuft above the stem-bud. The growing portions are, however, covered over and protected within the bud.

Forerunner-tips. This precedence of the leaf-apex appears specially prominent in a number of climbing plants, and Račiborski[1] has recently shown the biological significance of it to them. It lightens at first the weight of the shoot, which is in search of a support in its revolving nutation, and consequently makes possible a much stronger growth in length of this shoot out of an equal amount of available material. Račiborski designates the early developed apical portion of the leaf the *forerunner-tip* (Figs. 199, 200, *V*). On the young leaf (Fig. 200, III) the forerunner-tip is essentially complete in development, and is almost twice as long as the primordium of the leaf-lamina *L*, which is still very small, but this, as a comparison with the older leaves shows, grows afterwards, whilst the forerunner-tip exhibits only an insignificant elongation at its base. The leaf-apex in a compound leaf shows the same features. In Fig. 201, which illustrates the development of the leaf in Benincasa cerifera the precedence in development of the leaf-apex over the leaf-surface is very strikingly shown, and by this the leaf in its young condition has quite a different appearance from that which it has when mature. Rhodochiton volubile shows similar features.

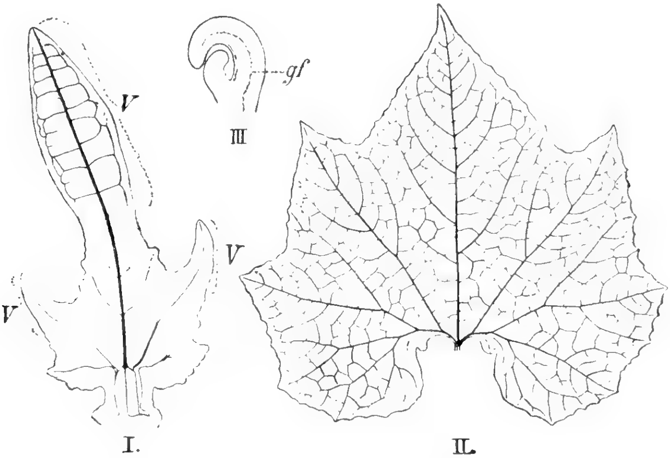

FIG. 201. Benincasa cerifera. I, young leaf: the orerunner-tip, *V*, precedes markedly the development of the lamina. II, mature leaf: the distinction of the forerunner-tip hardly visible. III, branched tendril in juvenile state: no vegetative point of a shoot is visible between the two tendrils, even at the apex of the larger tendril the tissue is still embryonal; *gf*, vascular bundle. I, magnified 9. II, natural size.

We must look for the significance of the forerunner-tip in the protection of the vegetative point apart from considerations of the importance of reduction of the leaf-development for the rotating shoots of climbers; and

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[1] Račiborski, Über die Vorläuferspitze, in Flora, lxxxvii (1900), p. 1. The statements of Crüger and others are dealt with here.

then when the forerunner-tip contains chlorophyll it can carry on the function of assimilation as well as those of respiration and of transpiration until the leaf-surface has attained a sufficient extent to take up the work.

Plug-tips. The rapidly drying-up leaf-apices of the unfolded leaves of Musa which may sometimes be as much as ten centimeters long, and which were formerly erroneously described as a kind of tendril, as well as the smaller similar structures which are to be found in the Zingiberaceae, in some Aroideae, and elsewhere, are in my view structures which serve to *close the bud*, and which may be termed *plug-tips*. With them we may reckon the stipules and ligules which will be mentioned below[1]. The leaves of all these Monocotyledones have a lamina which is convolute in the bud. The somewhat cylindric apical prolongation on the one hand closes each convolute lamina above, and on the other hand fills up the space formed by the convolution of the leaf which stands immediately above it, and in this way there is produced a long thin plug which, growing proportionately with the space, pushes itself upwards. In correspondence with this we find in Hedychium Gardnerianum, for example, that this closing body is provided with somewhat long hairs, and in some Aroideae, for example Colocasia, there are at the leaf-apex water-slits from which drops of water exude. Where the apices of the leaf-tips in toothed or otherwise segmented leaves pour out a secretion within the bud[2], it is open to us to suppose that this is not merely the excretion of superfluous by-products, but that there is here a provision of a special protection for the young parts. The precedence in growth of the leaf-apex becomes frequently evident also through the fact that the first hairs appear upon it, and these have evidently to do with its protective function.

Measurements. Sonntag[3] has given some measurements from which I extract a few figures. They give the length which the primordium of the leaf has reached when the apex has completed its growth, whilst embryonal tissue is still visible at the base:—

Amongst *Gymnospermae* we have—

Taxodium distichum	0·2 mm.
Picea excelsa	0·29 mm.
Abies pectinata	0·32 mm.
Pinus silvestris	0·35 mm.

Similar figures have been obtained from a number of *Monocotyledones*. In Phragmitis communis, whose leaves reach a length of as much as half a meter, the primordium of the leaf at the end of its apical growth is only half a millimeter long,

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[1] See p. 359. For illustrations of plug-tips see Goebel, in Flora, lxxxviii (1901), p. 470.

[2] See Reinke, Beiträge zur Anatomie der an Laubblättern, besonders an den Zähnen derselben vorkommenden Sekretionsorgane, in Pringsheim's Jahrbücher, x (1876), p. 119.

[3] Sonntag, Über Dauer des Scheitelwachsthums und Entwicklungsgeschichte des Blattes, in Pringsheim's Jahrbücher, xviii (1887).

and from this we may conclude that the leaf attains its size mainly through intercalary growth and stretching of the cells.

Amongst *Dicotyledones* the relationships are more manifold, as is also the construction of the leaves. The following figures are instructive—

Ruta graveolens	0·58 mm.
Juglans cinerea	0·6 mm.
Geranium Robertianum . . .	1·75 mm.
Ailanthus glandulosa	2·91 mm.
Anthriscus silvestris	4·5 mm.
Archangelica officinalis . . .	15·0 mm.

Still larger numbers could be obtained if the Droseraceae, about which we shall speak presently, were taken into consideration.

Guarea. We shall hereafter deal with the sequence of origin of the lateral members of the leaf. The peculiar features of Guarea, one of the Meliaceae, which was formerly considered to be in a line with many ferns, will only be mentioned here. Its pinnate leaf unfolds at first only a portion of its pinnae—the lower ones; in the next vegetative period new pinnae appear at the leaf-apex. According to Sonntag this is not a case of long-lasting apical growth of the leaf. The leaf, as in other cases, is laid down *in toto*, and its capacity for development is closed therewith. It is only the time of unfolding which is periodic. The basal three to four pairs of pinnae unfold in the first vegetative period, whilst the rest unfold in the succeeding one. How far these peculiarities are connected with the conditions of the life of the plant is at present unknown.

The behaviour of the leaves of the Spermophyta [1], about which we have just spoken, is in marked contrast with that of the leaves of Filicineae in which the embryonal tissue occupies the apex during the whole duration of the development of the leaf, and only *in the end* passes over into permanent tissue. It would be an error, however, were one to ascribe apical growth to the leaves in Filicineae alone.

Apical growth in Spermophyta. In some Spermophyta the leaf is marked by its apical growth, inasmuch as the apical portion during the whole period of the building up of the leaf retains its embryonal character. In such cases we find, just as in the Filices, a ptyxis different from that which is otherwise usual in the Spermophyta. The leaf is circinate, and the embryonal portions are thus brought into a position in which they are protected by the older and more resistant parts. We see this in Drosophyllum (Fig. 202), in which genus the leaf is revolute, and also in some other Droseraceae, for instance Drosera binata and D. dichotoma [2], in which the leaf-apex is involute. The like may be observed in a number of Utricularieae. That the distribution of the growth-area is not

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[1] As well as of the Lycopodineae and Equisetaceae.

[2] In other Droseraceae the duration of apical growth is much shorter. In the Filices also like cases are found.

determinant of the leaf-form is shown for example by the fact that in Byblis gigantea—which has hitherto been erroneously reckoned by the systematists amongst the Droseraceae—the leaves are quite like those of Drosophyllum, but possess a very marked intercalary growth, and in correspondence therewith have no circinate ptyxis[1]. The ptyxis of the leaves depends in my view partly upon the distribution of the growth in the leaf-development, and partly upon the amount of space available in the bud. A superficial examination of some leaves which have laterally involute ptyxis shows that they are always leaves which retain for a long time embryonal tissue and grow at the margin—*mutatis mutandis*—we have here the same relationships as are found in leaves which are involute at the apex. But the influence of space-relationships appears in this, that a leaf in whose axil at a very early period a bud arises is hindered by the bud from assuming the ptyxis which it would otherwise do by its growth. The ordinary foliage-leaves of Caltha palustris, for example, are in the bud laterally involute; those, however, which subtend a flower-bud are spread out flat[2].

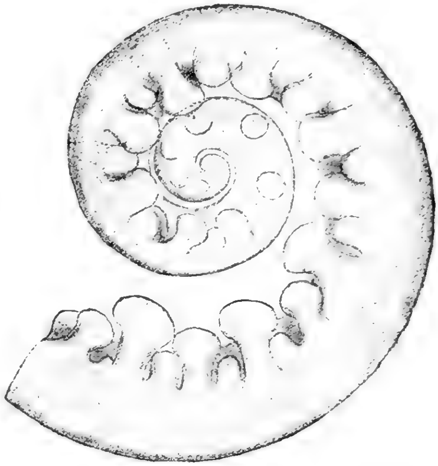

FIG. 202. Drosophyllum lusitanicum. Leaf showing circinate ptyxis. The tentacular glands are laid down in serial succession, but later ones are also intercalated. Magnified.

(*b*) THE INCEPTION OF THE LEAF-SURFACE IN SPERMOPHYTA.

In what we have said above we have dealt with the distribution of growth in the primordium of the leaf in general. We must now briefly deal with the laying down of the leaf-surface. The process is relatively simple where the leaf is from the first laid down as a flat structure which attains its mature configuration by a uniform stretching of the embryonal tissue in the transverse direction. Where, however, at a very early period a portion thickens into a midrib, and is thus separated from a thinner part which is devoted to the making of the lamina, most complex relationships ensue between embryonal growth and stretching. The types which have been created around which to group the forms that are exhibited show

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[1] By this character young plants of Byblis gigantea can be readily recognized at first sight from those of Drosophyllum. See F. X. Lang, Untersuchungen über Morphologie, Anatomie und Samenentwicklung von Polypompholyx und Byblis gigantea, in Flora, lxxxviii (1901), p. 149.

[2] See Arnoldi, Über die Ursache der Knospenlage der Blätter, in Flora, lxxxvii (1900), p. 453.

many transitions, and their limitation is consequently more or less arbitrary. The categories framed by Prantl[1] are quoted here in illustration.

He distinguishes:—

(1) **Basiplastic type.** The stretching takes place at the apex of the primarily uniform embryonal primordium, and proceeds downwards therein until nearly the whole of the active meristem disappears. This is found in the Musci, Lycopodineae, Coniferae, with the exception of the genus Ginkgo[2], most Monocotyledones, a number of Dicotyledones with simple leaves, such as Sempervivum, Erica Tetralix, Gentiana asclepiadea, and the Asclepiadeae. Where, as in Dicotyledones, feathered veins occur, a strong midrib is first of all differentiated, and this is accompanied (Fig. 199, II) both right and left by meristic tissue, which passes over into stretching-tissue successively in a basipetal direction, and at the same time simultaneously in a transverse direction. In other leaves which may be assigned to this type there appear basipetally in the meristem branchings which become leaf-teeth as in Salix, Celtis, and Prunus avium, or pinnules as in Cephalaria leucantha, or lobes as in Bryonia and others (see also Fig. 201).

(2) **Pleuroplastic type.** Where the meristem is marginal the leaf-apex does not pass into the permanent condition so rapidly as it does in the basiplastic type. Of simple leaves may be mentioned those of Aristolochia tomentosa, Rhamnus Frangula, and Syringa vulgaris. The transition into the stretching-tissue takes place in the whole tissue arising out of the meristem at nearly the same moment, only at the margin some cells remain for a longer time in the meristic condition. Where branchings take place these proceed in acropetal succession as in Quercus, Corylus, Tilia, and others, but in Ulmus from the middle upwards and downwards.

(3) **Eucladous type.** The branchings here do not proceed, as in the two former types, only when a portion of the meristem has begun to stretch, but appear at a time when the leaf is still one uniform mass of embryonal tissue. This is seen in Ginkgo, Juglans, Papilionaceae.

A sharp limit is not to be drawn between these types, especially between the first and second, and the advantage of such a grouping appears to me very doubtful. Upon the question of the distribution of the growth more will be said in subsequent pages when the leaf-formation in the several large groups receives special consideration, and when the relationship of the development of the leaf to the course of the leaf-nerves is discussed.

We find in other parts of plants with *limited* growth, for example in placentas, quite similar differences in the distribution of the growth[3], and far too much weight has been attached to these processes of growth in the leaves.

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[1] Prantl, Studien über Wachsthum, Verzweigung und Nervatur der Laubblätter, insbesondere der Dikotylen, in Berichte der deutschen botanischen Gesellschaft, i (1883), p. 280.

[2] Now no longer to be reckoned amongst Coniferae.

[3] See also Part I, p. 41.

D. *FORMATION AND DEVELOPMENT OF THE LEAF IN THE CHIEF PLANT-GROUPS.*

(*a*) PTERIDOPHYTA.

1. EQUISETACEAE AND LYCOPODINEAE.

The simple relationships of the formation of the leaf in the Equisetaceae and Lycopodineae, where all the leaves are basiplastic, require no further mention here. But the formation of the leaf of the Filicineae demands notice as it is marked by many characteristic features, although none of them, apart from the arrangement of the cells, is limited to the class.

2. FILICINEAE.

The formation of the leaf is in the different forms of this class externally very different. One need only recall the contrast between the small leaves of some Hymenophyllaceae, where they are less in size than those of some Hepaticae and Musci (compare, for example, Fig. 183), and the massive leaves of Angiopteris with their stout leaf-stalks. Nevertheless we cannot ignore the fact that there is a common path in their development, and this appears particularly when we compare not the fully formed but the primary leaves of the different forms with one another, and with the pinnate leaves. On these primary leaves we see a conspicuous *marginal growth*, that is to say, the meristic tissue occupies the margin of the leaf, and in association therewith a forked branching of the leaf-nerves appears—this only being possible where there is marginal growth. Another extreme is seen where the primordium of the leaf appears as a structure with conspicuous *apical growth*, and on it, when branching takes place, the lateral pinnules arise in monopodial series. There are not wanting transition-stages between these two, especially do we find, for example in Botrychium, that the apex of the primordium of the leaf frequently, after it has produced pinnules, passes over by lateral shooting into marginal growth and dichotomous branching, and in many leptosporangiate ferns we find the dichotomously branched leaf is built up sympodially[1]. This latter process is often considered as typical of the ferns, but as opposed to this it may be pointed out that within the series of the ferns is to be found a type of leaf-development with lateral origination of the leaf-pinnules like that which is observed in the fern-like Archegoniatae—the Cycadaceae; and when this occurs, as we shall presently see, it is associated with a gradual reduction of the apical growth of the leaf-primordium.

It is evident then that alike in the distribution of the growth and in the branching, the development is determined here by the configuration

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[1] See p. 316.

which, to speak teleologically, *must* be reached in the mature condition, and we find the same in the relationship between the leaf-spindle or midrib and the lamina. The more massively developed the leaf-spindle is, the *earlier* is it in general laid down, and therefore the more does the lamina appear upon it as a wing-like outgrowth originating at a *later* period. Bower[1] has attached special importance to the fact that the fern-leaf is typically provided with a wing even where, as in the almost cylindrical leaf-stalk of Angiopteris and others, this does not appear externally. The wings on the lower region of the stalk-like portion of the leaves are shorter and thicker than they are above, and may in Osmunda, the Marattiaceae, and others, broaden at the base into a sheath-like form. If now, as indeed cannot be denied, most of these wing-formations appear in correspondence with the dorsiventral character and the flattening of the fern-leaf, yet we must not forget that all transitions may be formed from the cylindric wingless leaves of Pilularia right up to the leaves of the Hymenophyllaceae, which are from the very first laid down as flat structures. In Pteris serrulata, for example (Fig. 207, II), the primordium of the leaf is somewhat flattened at the apex, but it is almost cylindric. On each side there shoots out upon the rhachis, which is first of all laid down, a lamina which is provided with wedge-like marginal cells, and these divide by walls inclined alternately upwards and downwards. At first the cells, which proceed from this division of the marginal apical cells, are devoted to the construction of the rhachis, and only at a later period does the further growth of the thinner lamina proceed. A leaf which had a thin rhachis would allow the marginal cells to pass over *earlier* to the formation of a lamina. In the Hymenophyllaceae, where the lamina is only one-layered[2], the marginal growth of the lamina is naturally somewhat different, and the same may be said of the thicker, more massive leaf-lamina of the Osmundaceae[3] and of the Marattiaceae. In the relationships of the arrangement of cells, however, we find, just as in the case of the thallus of the Hepaticae[4], the expression of the working of inner factors which have no direct connexion with the grosser relationships. We have also seen when examining the Hepaticae that in the thallose forms the thallus has a thinner lateral surface and a thicker middle part, and that in the larger forms of Aneura, for example, the wing-formation may be practically suppressed in the chief axis. Fig. 22 in its lower part might, *mutatis mutandis*, correspond to a transverse section through a young leaf of Hymenophyllum; the upper portion of the figure

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[1] Bower, On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms, in Phil. Trans., 1884; id., The Comparative Examination of the Meristems of Ferns as a Phylogenetic Study, in Annals of Botany, iii (1889), p. 305.

[2] Where the lamina is many-layered, as in Trichomanes reniforme, it is not so from the beginning, but the layers are the result of subsequent division parallel with the surfaces.

[3] With the exception of the species which resemble some of the Hymenophyllaceae.

[4] See p. 21.

might be the transverse section of a thick fern-leaf. In the development of the fern-leaf we meet with the two factors which everywhere confront us: on the one hand the relationships to *outer* factors which find their expression, especially in the size which the leaves reach, and this supposes again definite relationships of organization which determine the developmental history; and on the other hand incidents which spring out of an *inner* influence on configuration, and which, if we consider the end-result, might be brought about equally well in other ways. Thus the leaves of the tree-fern Amphicosmia Walkerae have just as good a two-sided apical cell [1] as the small leaves of the Hymenophyllaceae up to a certain stage in their development; they have not, as has been supposed. a three-sided apical cell like the Osmundaceae.

Marattiaceae. The leaves of the Marattiaceae [2] are relatively massive, at least in the case of Marattia and Angiopteris. The development of the leaf has only been examined in these two genera, but we may assume that its course is the same in the other genera. At the base of the leaf of the Marattiaceae as is well known there are stipular formations [3], which are met with elsewhere amongst the ferns in Todea only where one 'axillary stipule' occurs. The primordium of the leaf is circinate at the apex [4] as in other ferns, and the lateral pinnules arise in acropetal succession. The laying down of the leaf-surface is from the first more massive than in the leptosporangiate forms, and the leaf-apex is in Angiopteris frequently, perhaps always, not involved in the leaf-formation.

Osmundaceae. The Osmundaceae conform with this type in so far as all the parts of their leaf appear in acropetal succession, and the marginal growth, so characteristic of the leaves of other ferns, appears only relatively late at the apex of the leaf and of the pinnules which are further divided. The presence of a three-sided pyramidal apical cell may, as in the case of the thallose Hepaticae,[5] be connected with the more massive construction of the leaf. But as the leaves of the tree-fern Amphicosmia Walkerae have a two-sided apical cell and those of Todea superba, which are not very large and are of delicate construction, have a three-sided one, the character is evidently racial.

Leptosporangiate Filicineae. In the leptosporangiate ferns [6] which have

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[1] Bower, The Comparative Examination of the Meristem of Ferns as a Phylogenetic Study, in Annals of Botany, iii (1889), p. 305.

[2] Bower, On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms, in Phil. Trans., 1884.

[3] The 'stipular scales' which occur one upon each side of the leaf-base in Ceratopteris thalictroides are really scale-hairs of special construction, and are found also upon the stalk and lamina of older leaves. See Kny, Die Entwicklung der Parkeriaceae, in Nova acta der kaiserl. Leop.-Carol. deutschen Akademie der Naturforscher, xxxvii (1875), p. 29.

[4] The arrangement of the cells at the apex is like that at the apex of the root of the Marattiaceae, that is to say, there are many initials, but in Marattia there is often, although not always, a three-sided apical cell. For further details see Bower, op. cit.

[5] See p. 21.

[6] The works of Hofmeister, Kny, Sadebeck, and Prantl, which are mentioned in all textbooks,

been carefully examined, we find that the leaf-primordia which proceed from one cell, have at first a two-sided apical cell (see Fig. 173), which, in ferns like Pilularia, remains for a somewhat long period because the leaf has a cylindric configuration and is unsegmented. Pilularia has leaves which are traversed by only *one* conducting bundle. In ferns whose leaves are developed as flat expansions the course of the nerves of the leaf, and the branching of the leaf itself which is connected with these are of special interest. When speaking of the primary leaves of the ferns[1] it was shown that the nerves of the leaf are dichotomously branched and Fig. 92, 5, Part I, which represents the leaf of Asplenium viride, shows clearly that its pinnules are the result of repeated dichotomous branching. In the leaf represented in Fig. 92, 4, Part I, on the other hand, only one dichotomy has taken place. Fig. 203, which represents a leaflet of Allosorus crispus, shows clearly also the dichotomous branching. This dichotomous branching may likewise be found by careful developmental investigation in many cases. The meristem is on the margin, and retains its embryonal character over the cells arranged in longitudinal rows which are to give rise to the leaf-nerves, whilst the cells which lie between these pass over at an early period into permanent tissue. We do not, however, find this in every case. Where we have to deal with *elongated* leaves *provided with numerous lateral parts* there is developed a uniform, continuously growing apical meristem. Fig. 204 shows the leaf-tip of Adiantum Edgeworthi. At the apex is a two-sided apical cell which is not visible in the figure owing to its small size. The leaflets are laid down as *lateral* outgrowths beneath the apex which continues its growth. They branch dichotomously and finally in feeble leaves the leaf-apex itself passes over into the same conformation as that exhibited by the pinnules. We observe, then, that in this characteristic marginal growth we have, as in many prothalli of ferns, the wedge-shaped apical cell replaced later by a group of meristic marginal cells. If we conclude[2] from these and from other facts -- for instance the frequently 'abnormal' forked division of the leaf of different ferns which do not show the 'normal' features—that the branching of the fern-leaf

FIG. 203. Allosorus crispus. Outline of a leaflet. The branching is clearly dichotomous. The apex has divided into lobes 1 and 2 of which 1 is the stronger and continues the growth, 2 forms a lateral lobe. Below we have lobes 3 and 4 which have been similarly formed. The leaf-spindle (rhachis), *S*, is only a slightly broader portion of the lamina which is subsequently mechanically strengthened. Magnified.

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give particulars of these, as do also the memoirs of Bower. Here the details of the arrangement of the cells cannot be discussed.

[1] See Part I, p. 151.

[2] Goebel, Über die Jugendzustände der Pflanzen, in Flora, lxxii (1889), p. 26.

exhibits the primary and now partly lost type we must remember that this is in the meanwhile nothing more than a hypothesis against which many other facts might be quoted. What appears to be more important is that we have the relationship above mentioned between lateral branching and dichotomy, from which we learn that in all ferns the *lateral primordia of the pinnae appear on the primordium of the leaf, and that if the leaf is a greatly elongated one the lateral parts are laid down in rapid succession, but where surface-growth predominates then there is dichotomous branching, and there is no formation of a strong leaf-spindle or midrib.* In some cases, as, for example, the Gleicheniaceae where dichotomy has been assumed, it is in error.

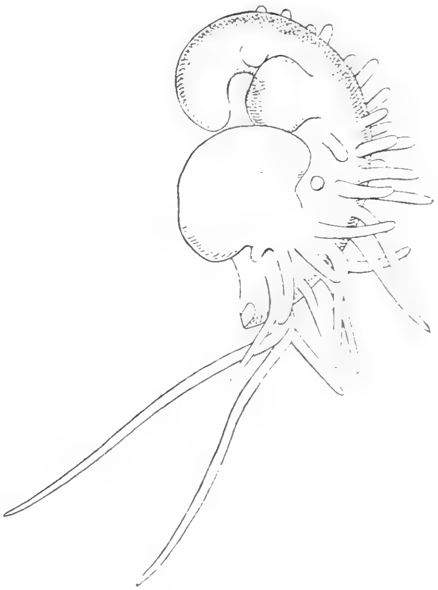

FIG. 204. Adiantum Edgeworthi. Leaf-apex exposed. Lateral primordia of pinnules are visible. Long hairs seen on the outer side. The several pinnules branch dichotomously at the margin at a later period. Magnified.

In ferns where the leaves show a strong rhachis developing for a long time by monopodial growth the lateral leaflets frequently have a relation in their configuration to the circinate ptyxis of the apex of the bud. This is the case in Nephrolepis exaltata (Fig. 205). Each pinnule of the simply pinnate leaf has here at its base a lobe-like outgrowth which is directed towards the leaf-apex. A consideration of the leaf-tip will easily convince one that it is these lobes which at first cover, on the outside, the circinate apex, whilst the tip of the young pinnule itself is concealed beneath the next older pinnule. By the early development of these lobes[1] a better protection to the young parts is made possible, as is the case in many Spermophyta where the stipules perform a like function[2]. We may say the same for the special configuration of the leaflets of many species of Adiantum, for example A. trapeziforme. It will be shown below that even more peculiar relationships are observed in many of the Gleicheniaceae, relationships which have been erroneously interpreted, through want of consideration, to the standpoint of function.

Apical Growth in the Leaves of Filices. The apical growth of the leaves of many ferns is prolonged over several periods of vegetation. The growth of the apex is periodically arrested, and then again resumed at a later period.

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[1] In the mature leaf each lobe is in great part covered by the base of the one above it, and they are therefore of little moment in assimilation.

[2] See Part I, p. 125.

Nephrolepis. Some but not all species of Nephrolepis[1] show this, but it is not observable in their primary leaves. In at least many species, as I have satisfied myself is the case in Nephrolepis exaltata, it is possible to recognize the limits of the several yearly growths by the diminution in size of the pinnules. In old leaves I found the leaf-apex, which is still circinate, finally dried up.

Hymenophyllum. Many species of Hymenophyllum, for example H. interruptum, H. Karstenianum, and H. plumosum, show similar features.

Gleicheniaceae. The Gleicheniaceae behave strikingly in a like manner, and their circinate leaf-tips which are found in the successive resting periods have been confounded with adventitious buds. The Gleicheniaceae also exhibit some remarkable adaptations which have hitherto not received the attention they deserve. Of these the most remarkable is the adjustment of several pinnules as a *protection to the resting apex of the leaf* so as to form a kind of bud-scales. These pinnules have been quite superfluously named 'adventitious' and 'aphleboid'[2] formations, and Potonié[3] has conjectured that they are 'vestiges of the originally laminar expansion of the chief spindle of the leaf.' But we have here neither 'adventitious' structures nor 'vestiges,' but only pinnules which, standing next to the resting leaf-apex, are constructed as protective organs to it. As is shown in Fig. 206, they lie primarily like two mussel-shells over it. They are, at least in the relatively small leaf which is represented, scarcely divided, but in other species of Gleichenia they are lobed or cut. The larger the resting-apex which they have to protect the larger are these protecting pinnules, and they may be absent if it is very small, whilst many species of Gleichenia, especially those with a dense covering of scales or hairs, want them altogether. The figure shows that the portion of the leaf which is directed outwards is furthered[4]. Where, as in Gleichenia bifida, leaflets appear upon the primary axis of the leaf, at first only upon the inner side, we have perhaps to deal with pinnules which are effective as protective structures during the period of unfolding[5]. We do not know

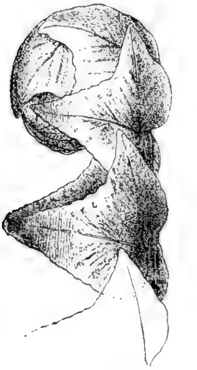

FIG. 205. Nephrolepis exaltata. Leaf-tip. Every pinnule has developed an upwardly directed 'covering lobe.' Magnified 2.

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[1] Mettenius, Filices horti botanici Lipsiensis, Leipzig, pp. 99 and 101. With regard to the Hymenophyllaceae, see Mettenius, Über die Hymenophyllaceae, Leipzig, 1864.

[2] For instance by Sadebeck, Pteridophyten, Einleitung, in Engler and Prantl, Die natürlichen Pflanzenfamilien, 1898.

[3] Potonié, Lehrbuch der Pflanzenpalaeontologie, Berlin, 1899, p. 119.

[4] See Part I, p. 124.

[5] In one example which I have before me the chief pinnule begins with five lateral pinnules standing only upon the inner side, and thereafter follows the usual formation of pinnules upon both sides.

what is the connexion between the periodic growth[1] of these leaves of ferns and their relationships of life, yet we may conjecture that the further development proceeds in moist periods of the year, and that the arrest takes place in the dry periods.

Lygodieae. The leaves of species of the Lygodieae are those which exhibit the most prolonged growth in length, and they twine around supports. Further investigation is required before we can say that we have an 'unlimited' growth here, and that the leaf only dies down finally by, as it were, an accident through, it may be, unfavourable external conditions, difficulties of water-transport, and so forth[2].

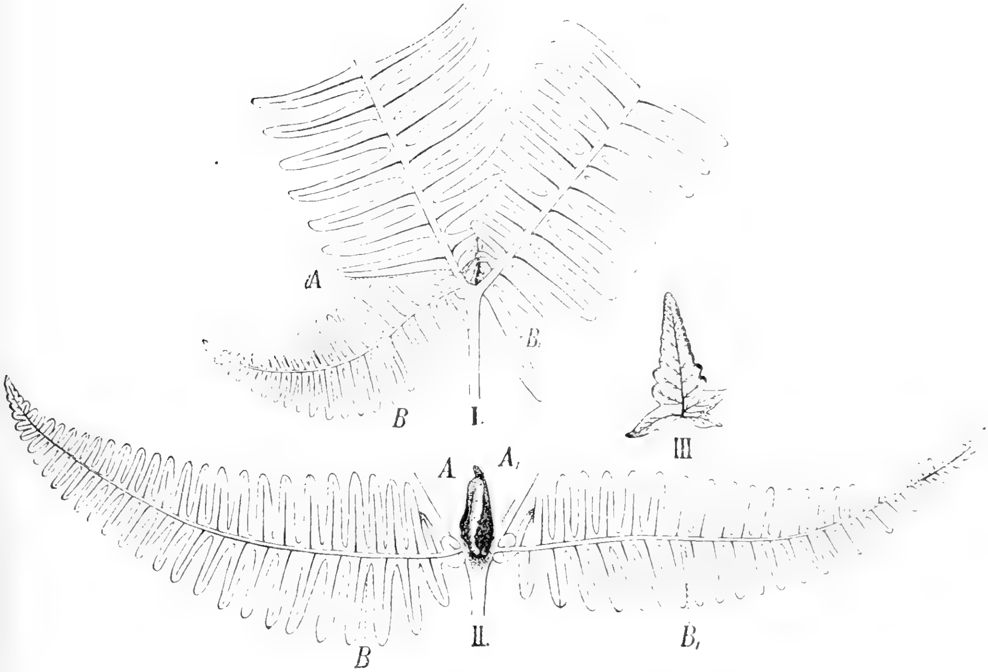

FIG. 206. Gleichenia dichotoma. I, fork of leaf in which is a 'bud' covered by the protecting pinna; *A* and *B*, A_1 and B_1, pairs of pinnae of very unequal size; *A* and A_1, smaller protecting pinnae; *B* and B_1, pinnae turned outwards, larger and more segmented. II, the same. III, protecting pinnae. I and II, two-thirds natural size. III, natural size.

From what has been said we can recognize in the Filicineae the following stages:—

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[1] The formation of the leaves is incorrectly described in the most recent account of the Gleicheniaceae by Diels, in Engler and Prantl, Die natürlichen Pflanzenfamilien, 1898—'adventitious shoots' do not exist in the 'forkings' of the leaf-axis. The structure found in these positions is the continuously growing leaf-apex. The 'forking' is the consequence of the two pinnules below the circinate persistent leaf-tip developing equally. No species of Gleichenia has a dichotomous leaf.

[2] The primary leaves, like those of other ferns, have limited growth.

(1) The germ-plant begins with a cotyledon, which has marginal growth from the outset, and it as well as the primary leaves—which only for a short time have apical growth from a two-sided apical cell—show dichotomous branching or evident dichotomous venation.

(2) The leaf-apex grows at first monopodially, but after a shorter or longer time it passes over into marginal growth, and dichotomous branching follows.

(3) The apical growth persists during many periods of vegetation. The leaf forms to a certain extent long growths and short growths, and these latter are the branchings of the higher order, which from the outset have limited growth.

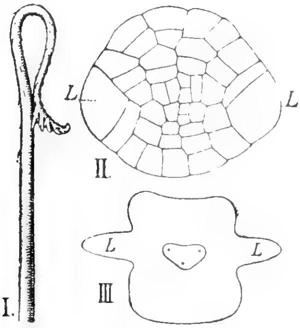

FIG. 207. Pteris serrulata. I, young leaf. The leaf-stalk is incurved, the lamina is already divided but is not incurved. II, young leaf in transverse section near the tip of a leaflet. It is almost circular. The lamina arises later from the marginal cells, *L*, *L*. The upper side, in correspondence with its lie in the bud, is turned downwards. III, older leaflet in transverse section. The precedence in development of the thick rhachis over the lamina, *L*, *L*, is shown. The upper side is in this figure turned upwards. I, natural size. II and III, magnified.

Whether this series forms an ascending or descending one, or whether we must recognize it as simply one construction cannot certainly be determined. What is certain is that the configuration of the primordium of the leaf is connected with that of the mature condition in the manner that has been indicated above.

The relationship that has been pointed out[1] between apical growth of the leaves of the ferns and their circinate ptyxis is not altogether without exception. The apical growth of the leaf is also not *necessarily* bound up with circinate ptyxis. In Pteris serrulata (Fig. 207), P. cretica, and P. umbrosa I found the laminar portion of the leaf to be *straight* from the beginning, the stalk alone showed a sharp curvature so that the leaf-apices of the leaflets were all directed downwards[2]. Nevertheless the normal apical growth exists here. I must confess that I was astonished to find this, but I believe that we may obtain the biological explanation in the consideration of two facts—first of all there are a number of segmented hairs developed at a very early period, and these cover over the leaf-apex and protect it, and secondly the leaf-spindle precedes in development the lamina to a very great extent, and the lamina attains even later no very marked breadth;

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[1] See p. 310.

[2] It is remarkable that no one has mentioned the facts, although they appear in the cultivation of one of the commonest ferns, but I may add that Leszcyc-Suminski says of the leaves of Pteris serrulata that the primary leaves appear to be circinate. His figures, however, show there is only an incurving of the stalk, not of the lamina, and the statement of Kaulfuss that there is no circinate ptyxis in Pteris serrulata is correct, although Leszcyc-Suminski endeavoured to controvert it. See Leszcyc-Suminski, Zur Entwicklungsgeschichte der Farrnkräuter, Berlin, 1848, p. 16.

it shoots out to both sides of the almost cylindric leaf-stalk, and retains for a relatively long period its embryonal character throughout (Fig. 207), and to its protection the hairs are devoted. A leaf-bud of this kind appears only in ferns which grow in specially moist shaded stations, as is the case with these species; possibly also the character is of importance from a systematic standpoint.

The case is different in ferns which at an early period lose their apical growth, and in which therefore the circinate ptyxis is wanting. We see this in some small-leaved species of Hymenophyllaceae, as, for example, the species of Trichomanes represented in Fig. 183, and some other forms with similar leaves. We also find it in T. peltatum and T. Motleyi, which have small peltate leaves that pass over at an early period into marginal growth[1]. The leaves of Ophioglossum and Botrychium also have no circinate ptyxis[2].

These examples amongst the Pteridophyta, as well as those amongst the Dicotyledones[3], show that circinate ptyxis is not a systematic character, but is one connected with apical growth, although not necessarily so, and that it may be constant, more or less, in one series.

(*b*) SPERMOPHYTA.

In simply constructed leaves, especially those which have no leaf-stalk, there appears to be no segmentation of the leaf-primordium as it develops. It is different, however, in more highly membered leaves. The first thing that strikes us here is that the leaf-stalk arises relatively late, with which corresponds the fact that its work has to be done during and after the unfolding of the leaf. The primordium of the leaf appears at first with the configuration of a ridge or papilla, and in this condition it is designated a *primordial leaf*. The primordial leaf next segments into two portions which, however, are not separated sharply one from the other, but are only distinguished by the share which they take in the further growth of the primordium. That portion which sits upon the vegetative point of the shoot, the *leaf-base*, takes no share in the further differentiation of the leaf-primordium, or at least only in so far as in many plants an outgrowth develops at each side of the primordium, and these outgrowths of the leaf-base are designated *stipules*. In many cases the leaf-base acquires a sheath-like form, *leaf-sheath*, especially in the grasses and the Umbelliferae. The portion of the leaf-primordium which lies above the leaf-base is the *upper leaf*, and it is from this that the leaf-lamina proceeds. If in the mature condition the lamina is segmented, pinnate for example, or otherwise

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[1] Compare what is said under peltate leaves, p. 335.

[2] The example of some species of Pteris mentioned above shows that even where there is prolonged apical growth circinate ptyxis of the bud is not necessary.

[3] See p. 310.

divided, the divisions come about, apart from the case of palms, by branching of the upper leaf. The leaf-stalk is everywhere of late origin, and it is intercalated between leaf-base and upper leaf, that is to say, it arises from that portion of the leaf-primordium which lies between these two, and which retains the peculiarity of an embryonal tissue for a longer time. That a leaf-stalk is absent in many cases requires as little explanation as the fact that there is no sharp limit between the leaf-stalk and the leaf-sheath. In what follows the development of the leaf of the larger systematic groups will be described :—

1. GYMNOSPERMAE.

Cycadaceae[1]. The leaves of the Cycadaceae externally resemble in their pinnation those of many Filices, especially in the fact that the pinnules are circinate in the bud; but the whole leaf is not circinate because the leaf-apex passes at a relatively early period into the permanent condition, sometimes even before the appearance of the pinnules. The pinnules proceed from two wing-like growths of the primordium which remains embryonal, and in this we have a difference in the development of the leaf as compared with that of the Marattiaceae. The available statements do not, however, give us a satisfactory view of the duration of the apical growth. Sonntag[2] observed a leaf of Cycas Thouarsii which had a length of about fifty centimeters and possessed a circinate leaf-apex with completely embryonal apex, whilst in the cases examined by Bower[3] this apical growth which was never very marked ceased with the appearance of the pinnules. The pinnules appear in acropetal succession in C. Seemanni, but in other species they appear almost simultaneously, or those in the middle regions of the leaf appear before the upper and the under ones, as in C. Jenkinsiana, whilst in Macrozamia Miqueli and Encephalartos Barteri the succession of development is basipetal.

Ginkgoaceae. The apical growth in Ginkgo persists longer than it does in the Cycadaceae. The division of the leaves takes place by actual branching, and there is an apical marginal meristem, as in the leaves of many Filices, and the branching is clearly dichotomous.

Coniferae. The simple configuration of the leaves of the Coniferae makes it unnecessary to discuss here the development of the leaf.

Gnetaceae. The apical growth of the leaf-primordium ceases very early amongst the Gnetaceae. This is specially evident in the remarkable Welwitschia mirabilis which possesses during its life only two leaves, placed at right angles to the cotyledons, and these grow perennially by means of a persistent basal zone[4].

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[1] See Warming, Undersøgelser og Betragtninger over Cycaderne, in Oversigt over det kongelige danske videnskabernes Selskabs Forhandlinger, 1877; Bower, On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms, in Phil. Trans., 1884.

[2] Sonntag, Über Dauer des Scheitelwachsthums und Entwicklungsgeschichte des Blattes, in Pringsheim's Jahrbücher, xviii (1887), p. 241.

[3] In part seedlings; perhaps older plants behave differently.

[4] Bower, op. cit., p. 600.

2. MONOCOTYLEDONES.

DORSIVENTRAL LEAVES.

The simple construction and the predominance of intercalary growth in the leaves of most Monocotyledones has been already mentioned[1], but we may here take as an illustration the formation of the leaf of Dactylis glomerata (Fig. 198).

Dactylis glomerata. The leaf is composed of a *closed* sheath and a lamina. At the point where these join is the membranous ligule. The function of the leaf-sheath is to support the internode which has long intercalary growth. If one holds horizontally the haulm of a grass which is still in a condition of growth, and from which the leaf-sheath has been removed, it is unable to support its own weight. The ring-like swelling upon the leaf-sheath above its point of attachment may at first serve to give a firmer support to the haulm, because it is formed at the point where the tissue of the internode is softest. The importance of these nodes for the erecting of the haulm is well known and need not be further spoken of here.

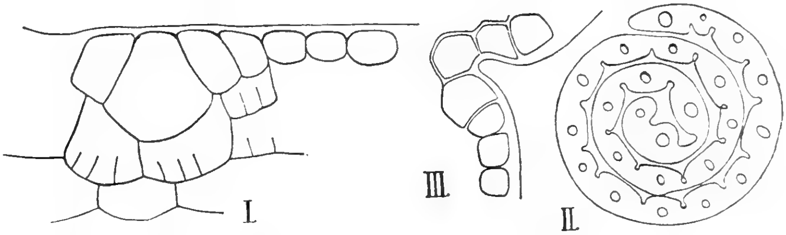

FIG. 208. Bambusa verticillata. Leaf in transverse section; I, hinge-cell. II, convolute lamina. III, hinge-cell after unfolding of leaf. All magnified.

The youngest primordium of a leaf on the massive vegetative cone has the form of a ridge which does not entirely surround the vegetative point. It is only in the second youngest leaf that the primordium takes on the form of a circular wall from one side of which the lamina springs, and this side is marked out from the first by being somewhat higher than the adjacent part. This side grows more strongly, whilst the amplexicaul leaf-base, which at first is very small, develops by intercalary growth gradually into the leaf-sheath. The laminar portion only appears as sharply separated from the leaf-base after the appearance of the ligule. It is clear that this development cannot be crisply interpreted as Trécul would have it—that the leaf-sheath is first formed. The primordium of the leaf at the beginning shows rather neither lamina nor sheath. The former does not grow out of the latter, but both differentiate only in the further course of development. As to the leaf-sheath which subsequently becomes the tube, we cannot say that this results from the 'concrescence' of the margins of an originally open primordium of a sheath, as was

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[1] See p. 298.

formerly supposed, but only that a ring-like zone of the vegetative point of the shoot takes a share in the formation of the leaf.

Hinge-cells in grasses. A peculiarity of the leaves of grasses may be mentioned here because often it is interpreted incorrectly. The lamina in Bambusa has convolute ptyxis (Fig. 208), and it remains in this condition for a relatively long time until the tissue-formation in the leaf is nearly completed. The expansion of the leaf is provided for by special *hinge-cells*—epidermal cells which remain at first small, but in the process of unfolding of the leaf grow rapidly and attain a volume which is considerably larger than that of the other epidermal cells. These hinge-cells are found also in some other Monocotyledones[1].

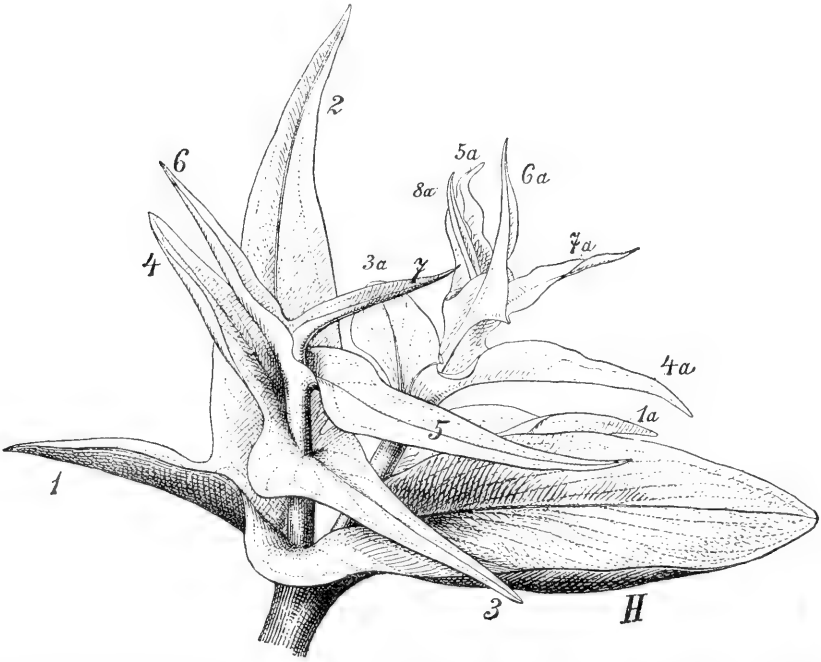

FIG. 209. Helicodiceros muscivorus. Leaf seen obliquely from above; *H*, the leaf surface; 1 and 1*a*, two sagittate lobes which branch sympodially in the respective series 2, 3, 4, 5, 6, 7 and 2*a*, 3*a*, 4*a*, 5*a*, 6*a*, 7*a*, 8*a*. Reduced.

BASAL LAMINAR GROWTH. The leaves of some Monocotyledones have a lamina in which growth persists at its lower end. In this way there arises a *sagittate* leaf, such as we find in Sagittaria and some Aroideae. This growth is particularly striking in cases where a branching appears, as it does in Helicodiceros, Helicophyllum, Dracunculus, Sauromatum, and others. In Fig. 209 we have a representation of the remarkable formation of the leaf in Helicodiceros. At first sight it would appear as if two radial leafy shoots were springing from the base of the leaf. In reality the leaf-lamina has

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[1] Their significance was first recognized by Duval-Jouve, Histotaxie des familles des Graminées, in Annales des sciences naturelles, sér. 6, i (1875).

two lobes, 1 and 1*a*, which would make it a sagittate leaf, as in many other Aroideae, were they to remain simple. But they branch sympodially, that is to say a branch, 2, arises out of the base of branch 1, branch 3 arises out of branch 2, and so on. But these branches are not spread out, as in Sauromatum, in one plane, but are twisted in a ladder-like spiral, so that the leaf-lobes appear as if they were arranged around a central axis. But this apparent axis is only the thickened outer margin of the base of the successive lobes—an interesting example of how definite parts of the leaf become more strongly constructed in proportion as they have stronger mechanical claims made upon them. There can be little doubt that such a special leaf-configuration has some biological significance if we could only discover it. This much is clear, that the whole leaf-surface occupies a smaller area than would be the case if the leaf-branches were spread out in one plane, and that the spiral arrangement prevents shading by the leaf-lobes as they rise above the original leaf-surface. The small space which the leaf-surface occupies may be connected with the denser arrangement of the leaves and the shorter length of the leaf-stalk compared with other forms like Sauromatum. At least I have found that other Aroideae with a sympodially branching leaf form only one or few leaves, which are raised free upon long leaf-stalks, whilst in Helicodiceros the leaves stand close together and have relatively short stalks.

PERFORATE AND SPLIT LEAVES OF AROIDEAE. Many other Aroideae are distinguished by remarkable formation of their leaves. The leaves of Anadendrum medium (Part I, Fig. 97) are distinguished by the formation of holes in the lamina, and also by the development of lobes which are like pinnules. The construction of the leaf here may be reached in much the same way as in Monstera deliciosa[1] and its allies, where the tissue lying between the nerves lags behind in growth and dries up. If this dying-off tissue lies near the laminar margin, and this be thin, it splits outwards into limited strips of tissue, and thus arises a feather-like lobed leaf; if the splits take place further within the laminar margin there is a hole. The biological significance of this splitting of the leaf-lamina will be noticed below. In the pinnatifid or pinnate leaves of species of Philodendron there is no formation of holes, but only of lobes through the stronger growth of single marginal portions of the lamina, and in those species of Anthurium which, like A. digitatum, have compound digitate leaves, the leaflets arise as branchings from the leaf-primordium in basipetal succession.

LEAVES OF PALMS. The leaves of palms require special notice. Many of them are the largest leaves which we know of. The segmentation of the leaves is no doubt connected with their size, and so also is their possession of a strong leaf-stalk, and in many cases of a massive midrib.

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[1] See Engler, Araceae, in Engler and Prantl, Die natürlichen Pflanzenfamilien, ii. 3, p. 104.

Where the leaf-lamina is membered this is not the result, as is usual, of the branching of an originally simple primordium, but is a consequence of the splitting of an originally entire leaf-surface. We have cases analogous with this amongst other Monocotyledones, for example in Musa, whose leaves are easily torn into isolated lobes fastened to the thick midrib. In Musa external factors, especially the wind, bring about the partition, but in other Monocotyledones, as, for example, Cyclanthus bipartitus, the splitting is a consequence of the tensions arising in the process of the unfolding of the leaf. Formerly the division of the palm-leaves also was considered to be the consequence of mechanical splitting, but investigation of the history ot development has shown that this is incorrect. The splitting in the palm-leaves is due to the death, at a more or less early period, always *before* the unfolding of the leaf, of definite portions of the tissue, or it may be that it is mucilaginous degeneration of the cell-walls of the tissue which brings about the separation. The splitting of the leaf-surface is therefore from the first prepared for. Two types of palm are commonly distinguished by the form of the leaf, the *fan-palms* and the *feather-palms*; in both the leaf diverges from the usual type of Monocotyledones, and it is easily shown that the deviation stands in relation to the increase in size.

LEAF OF FAN-PALMS. Let us start with the leaf in fan-palms, because it is much nearer the primary form of leaf in the Monocotyledones. The fan-like folding of the leaves has the same mechanical significance as the folded paper of a fan, that is to say, the leaf-surface is kept expanded without much expenditure of material[1]. Were it flat it would be ruptured by its weight, or very strong ribs would be required. The same principle of construction is repeated in the pinnules of the feather-palms, which, at least at their base, are often folded into channels. The folding of the leaf-lamina begins at a very early period in the leaf-primordium, and this has led to some misunderstanding[2].

If a fan-leaf is to reach a considerable size, the several rays of the fan must diverge from one another at their apex; at the base this is not well possible on mechanical grounds. The construction is reached thus:—The upper portion of the primordium of the leaf which has not taken a share in the folding dies off; thereby room is provided for the divergence of the folds, and the points of the several rays also separate from one another more or less far. The separation takes place at a varyingly early period in different palms. In Pritchardia filifera the upper angles of the folds which

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[1] The same, although less noticed, is the case in the liliaceous Curculigo, which has thin not flatly expanded leaves.

[2] Naumann's statements, in Beiträge zur Entwickelungsgeschichte der Palmenblätter, in Flora, lxx (1887), are for example erroneous. See Deinega, Beiträge zur Kenntniss der Entwicklungsgeschichte der Blätter und der Anlage der Gefässbündel, in Flora, lxxxv (1898). The literature is cited here.

are already provided with vascular bundles die off, and one can see the ruptured strips of tissue as long brown threads hanging on the unfolded leaves. In Chamaerops the separation takes place much earlier, whilst the tissue of the leaf has still somewhat of an embryonal character, and it is brought about by the mucilaginous degeneration of the cell-walls just as it is in Rhaphis and the feather-leaved Cocos. Archontophoenix which has feather-leaves furnishes, as it were, a transition between these two methods of separation, for in it the strips of leaf-tissue, which die off in the process of unfolding of the leaf, are from the first laid down as thinner layers than the rest of the leaf-tissue. The seedlings of almost all fan-palms[1] have the ordinary leaf-form of monocotylous plants, the veins running with a curved course and not diverging at the tip (Fig. 210).

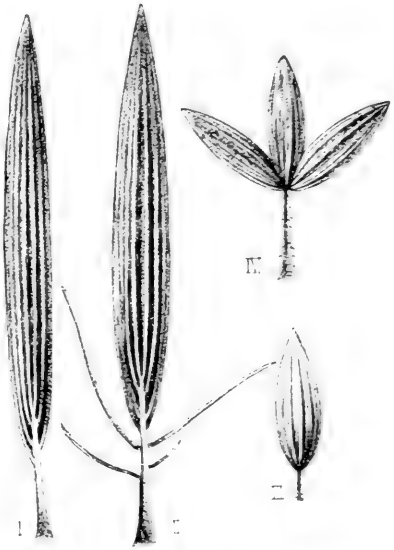

FIG. 210. I and II, Phoenix canariensis. Primary leaves. III and IV. Chamaerops excelsa. Primary leaves. One-sixth natural size.

LEAF OF FEATHER-PALMS. We must next speak of the feather-palms. The pinnation here is likewise the result of a splitting, not of a branching, of the leaf-surface. Let us consider first of all the primary leaves of Phoenix. Here we find leaves which resemble the ordinary ones of Monocotyledones, except in having slightly expressed folding of the lamina (Fig. 210). At the base, and at first limited to the base, of the leaf there is formed a stronger middle portion, which gradually involves a larger portion of the primordium of the leaf and becomes a strong midrib. The leaf-surface separates then into single segments. That this procedure begins at the base of the primary leaves is a consequence of the intercalary growth of the leaf (Fig. 210).

Thus, starting from the ordinary leaf of Monocotyledones, we obtain an altogether different form of leaf, and we may recognize the following stages of development which lead from an entire leaf-surface to a divided one :—

(1) The splitting takes place in expanded leaves under the influence of external factors, such as wind and rain. We find this in Musa, and the function of the leaf is not interfered with by the splitting. In Heliconia

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[1] In many palms the first leaf is divided. See Pfitzer, Über Früchte, Keimung, und Jugendzustände einiger Palmen, in Berichte der deutschen botanischen Gesellschaft, iii (1885), p. 32. The literature is cited here.

dasyantha Karsten[1] found that there is a special arrangement which brings about a splitting of the leaf-lamina under the influence of raindrops. A marginal strip of the leaf-tissue dies away before the middle portion has reached its complete growth, and in this way tensions arise which cause the splitting of the lamina when rain falls upon it.

(2) The splitting takes place during the unfolding of the leaf by tensions within it, as in Cyclanthus bipartitus.

(3) The points of separation are prepared in the bud by the dying-off or by the mucilaginous degeneration of cells. This is found in palms.

RADIAL AND BILATERAL LEAVES.

In the preceding cases we have dealt with the leaves of monocotylous plants in which the ordinary horizontal expansion is observed. A number of leaves, however, in Monocotyledones, have a profile or vertical position, and they are then either radial or bilateral. Species of Juncus, for example, have radial leaves which were formerly considered to be shoots because of their external resemblance to shoots, and because their internal structure is like that of shoots[2]. We find radial leaves also in some species of Allium. Iris supplies a specially good illustration of bilateral leaves, yet they have frequently given rise to controversy, and even in works of the most recent date we may read that 'the leaves of the Iris have taken their present form by concrescence of the two leaf-surfaces upwards[3],'— and this on the ground of anatomical investigation.

Leaf of Iris. The developmental history of the sword-like leaves of Iris is as follows:—

The primordium of the leaf has the normal form, and when it first appears does not embrace the stem (Fig. 211, *A*, b_1); but this it soon does (Fig. 211, *A*, b_2). The primordial leaf grows now like an ordinary primordium. Its apex (Fig. 211, *A*, *a*) should become the apex of the leaf-lamina, but it is found to be subsequently at the position where the leaf-lamina passes over into the leaf-sheath (Fig. 211, *B*, *a*). This 'displacement' is explained by the developmental history. The primordium acquires soon a growth in surface, and retains therefore a cap-like configuration (Fig. 211, *A*, b_3). Upon its back the growth in surface is the strongest, and here at one position the character of the vegetative point is retained (Fig. 211, *A*, *s* in the fourth unnumbered primordium), and the keel of the leaf-primordium grows out into the primordium of its 'sword-like' lamina. This lamina is hollow only where it passes into the sheath, in its other part it is from the beginning a solid plate of tissue. There are on the primordium of the leaf then now two apices—the

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[1] Mentioned by Stahl, Regenfall und Blattgestalt, in Annales du Jardin botanique de Buitenzorg, xi (1893).

[2] They have an evident, although small, leaf-sheath, and arise laterally on the vegetative point.

[3] Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société Royale de Botanique de Belgique, xxiii (1894), p. 252: 'La feuille d'Iris . . . doit être considérée phylogéniquement comme le produit de la soudure des deux moitiés de la feuille par leur face supérieure.' I hold this to be an impossible view.

original one, *a*, and the new one, *s*. The laminar primordium, *s*, soon acquires an actual terminal position, and the transition to this is shown in the larger leaf represented in Fig. 211, *B*, where the leaf-base which develops later into the leaf-sheath is marked off from the laminar primordium by a dotted line. The laminar primordium has indeed still a lateral position, but its middle line is raised up already about 45°, and the original apex, *a*, has assumed a lateral position.

This kind of leaf-development finds an interesting parallel in that of the genus Fissidens amongst the Musci[1]. In this genus the leaf-lamina arises also as a wing-like outgrowth of the original leaf-primordium, and as in Iris this formation of wing[2] proceeds in Fissidens from the back of the keel of the leaf-primordium. The two sides of the leaf-primordium share equally in this from the first, so that we need not wonder that in the anatomical structure, especially in the course of the vascular bundles, these sides are both indicated. Neither in the ontogenetic nor phylogenetic sense can we speak of the 'concrescence' of two leaf-surfaces here, as a comparison with the radial leaves of Juncus and Allium will readily show, for their origin resembles in all essentials that of the leaves of Iris.

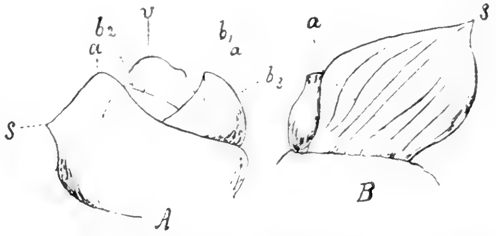

FIG. 211. Iris variegata. Development of leaf. *A*, vegetative point, *v*, dissected out, showing four leaf-primordia; b_1, b_2, and b_3 are numbered; b_1 is the youngest. The point marked *a* is the highest point in the primordia, but it becomes the apex of the leaf-sheath. The point *s* becomes the tip of the lamina. *B*, an older leaf; lettering as before. Magnified.

The few cases of peltate leaves in Monocotyledones will be spoken of when other peltate leaves are discussed below.

3. DICOTYLEDONES.

BRANCHING OF THE LEAF.

In Dicotyledones the segmentation of the leaf always depends upon a branching of the primordium, and this always starts from its margins, which, however, are often bent upwards, so that it looks as if the inception of the lateral members was upon the upper side. The origin of lateral members takes place after the following chief types:—

1. **Dichotomy**:—*A division of the vegetative point* of the leaf, such as we find in Filices, relatively seldom takes place, but is found in Utricularia[3], Ceratophyllum demersum[4], and also in Drosera binata and D. pedata, which have dichotomously

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[1] See p. 137.

[2] See also what is said about the formation of a wing on the back of the leaf of Phormium (p. 300). If these wing-like growths arise *very early* we should get the form of Iris. Perhaps there are transitions between the form of Iris and of Phormium.

[3] Goebel, Morphologische und biologische Studien: V. Utricularia, in Annales du Jardin botanique de Buitenzorg, ix (1891).

[4] Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société Royale de Botanique de Belgique, xxiii (1894).

branched leaves. This method of branching is only possible in leaves with prolonged apical growth.

2. **Monopodium** :—Lateral branching occurs after the following types :—

(*a*) *Acropetal Development.* All the branches of the leaves arise in serial acropetal succession, as in the Umbelliferae, Papilionaceae, Mimoseae, Caesalpinieae, Sambucus Ebulus, and others. The leaf-apex itself passes at an early period into the permanent condition, but below this there remains an embryonal zone on which in acropetal succession the lateral parts appear. On this account Sonntag reckons them as belonging to an intercalary type, but as a matter of fact the several types are not sharply limited.

(*b*) *Basipetal Development.* The youngest leaf-segments are the lowermost, as in Myriophyllum, Hottonia, Rosa, Potentilla anserina, Sambucus nigra of pinnate forms, Helleborus foetidus and all digitate forms.

(*c*) *Divergent Development.* The branching here proceeds from one position of the primordium upwards and downwards, as in Achillea Millefolium, the leaf-teeth of Ulmus, and others.

The course of development in nearly allied plants varies, for example in pinnate leaves it is sometimes acropetal, sometimes basipetal, so that this difference is not of very great importance.

The question of Sympodium :—In some Dicotyledones a partially sympodial construction of the leaf has been assumed, of the same character as that which we have observed in the Aroideae, but most of these cases are 'palmatifid' leaves, with basipetal evolution of the leaf-lobes. In the leaf of Acer platanoides, which is shown in Fig. 212, *C*, there are, for example, five chief lobes present, one in the middle and two at each side. Fig. 212, *A*, shows how the lobes arise in basipetal succession, but one may interpret the procedure as that only two lateral lobes exist, from which then the two lower ones shoot out as

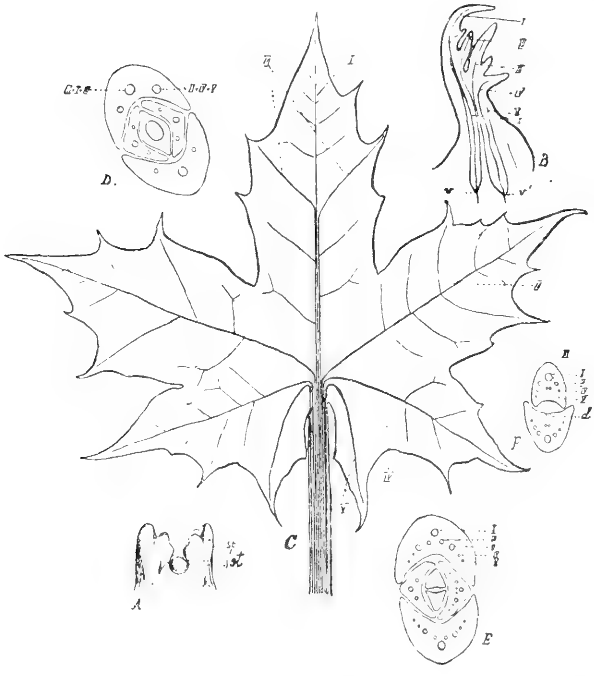

FIG. 212. Acer platanoides. *A*, bud dissected out, showing two young leaves; *st*, stem; *sp*, lamina with five segments. *B*, older leaf from the side, showing the course of the conducting bundles. *C*, scheme of the course of the conducting bundles in the mature leaf. *D*, basal portion of a bud in transverse section. Each leaf has three conducting bundles. *E*, the same higher up. *F*, leaf-stalk in transverse section. The figures *I*, *II*, *III*, *IV*, *V*, *VI*, in all the figures indicate the bundles of successive age. After Deinega.

members of the second order[1]. It is extremely difficult to follow here the history of development, and to say whether these lobes arise directly out of the leaf-primordium as members of the first order or not. That leaf-lobes branch frequently only upon their outer side is very common. If the leaf of Chelidonium, shown in Part I, Fig. 73, were cut through beneath the upper pinnule a five-lobed leaf would result, but its two lower lobes are outgrowths of the lateral ones. I do not see, however, why one should call such a leaf cymose, because the several members of the leaves are not at all separated from one another and the notion of 'cymose branching' is, therefore, not really applicable. The whole question may be of importance if we are dealing with the *derivation of the leaf-forms within one cycle of affinity*. For the *general organography* it appears to me to be of little importance. Prantl certainly goes too far when he says[2] of Achillea Millefolium that the segments arising basipetally in the leaf may be regarded as 'shooting from one another,' and that the leaf in its under portion is cymose. Here the history of development shows that the pinnules arising basipetally shoot out from a marginal zone which remains meristic, whilst in the inner portion of the leaf differentiation of the tissue has already begun as the appearance of intercellular spaces first indicates. The pinnules are as elsewhere outgrowths of the margin of the leaf bent somewhat upwards. I have found no indication that would suggest a genetic relationship of these one to another.

INTERRUPTEDLY PINNATE LEAVES. Interruptedly pinnate leaves, that is to say, leaves in which the pinnules are alternately of a very different size, may also be considered to be sympodial. Examples of these we find amongst the Solanaceae, as in Solanum tuberosum, Rosaceae, as in Spiraea Filipendula, species of Geum, Potentilla anserina, and others[3]. It has been shown[4] that the small pinnules fill up the spaces between the larger, and an analogy may be found within the class of Algae. Here we have only to notice the origin of these small pinnules. They might be regarded as lateral leaflets of the leaflets of the first order which have been displaced upon the leaf-spindle. But the history of the development, so far as it is known, is in the direction of showing that they are independent formations. Their inception takes place *later* than that of the larger leaflets, and in this we have an interesting parallel case with that of the alga Euptilota Harveyi (Part I, Figs. 46, 80). It is easy to convince oneself that the larger pinnules also arise earlier than the small ones standing oppo-

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[1] In support of this one might appeal to the course of the vascular bundles. Three chief veins enter the leaf; one, *I*, in the middle, and one upon each side of it, *II* and *III*. The vascular bundles *IV* and *V* unite in the leaf-base with *II* into one strand, and we may suppose that the leaf-lobes behave likewise.

[2] Prantl, Studien über Wachsthum, Verzweigung und Nervatur der Laubblätter, insbesondere der Dicotylen, in Berichte der deutschen botanischen Gesellschaft, i (1883), p. 280.

[3] Also Reseda alba according to Sonntag, Über Dauer des Scheitelwachsthums und Entwicklungsgeschichte des Blattes, in Pringsheim's Jahrbücher, xviii (1887), p. 247.

[4] See Part I, p. 127.

site to them. I regard the small pinnules as *reduced* leaflets of the first order, probably the result of correlation, but not as *intercalated new formations* as has been assumed. For this interpretation[1] we have support in the fact that these interposed leaflets may be entirely absent in feebly developed leaves, for example those of the potato.

RELATION OF THE PINNATE TO THE DIGITATE LEAF. Relatively small differences in the distribution of the growth upon one and the same primordium may bring about leaf-forms which are outwardly very different. Let us suppose, for example, that on one leaf-primordium there are produced upon each side five lateral primordia. From this would develop a leaf with five marginal projections if the lamina itself is strong in growth and the lateral primordia grow less strongly. If now the laminar portion between the lateral primordia grows strongly in length and less in breadth[2], and the base of each lateral primordium grows similarly, a pinnate leaf will result, but if the laminar portion scarcely grows further between the lateral primordia then the leaf will be digitate. As a matter of fact pinnate and digitate leaves do not differ essentially one from the other. In Aesculus Hippocastanum, for example, we usually find digitate leaves, but occasionally they are pinnate.

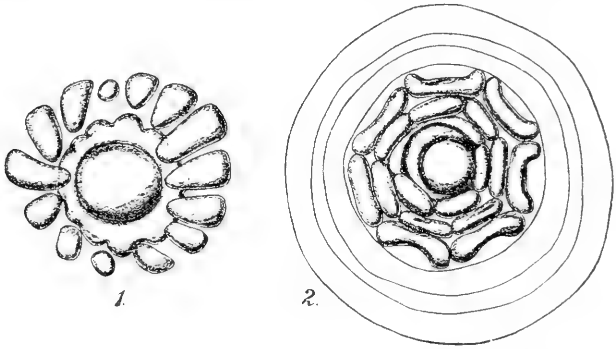

FIG. 213. 1, Limnophila heterophylla. Apex of shoot seen from above. 2, Alchemilla nivalis. Apex of shoot seen from above; a young primordium of a leaf seen to the left upper side of apex, the older leaves are deeply divided into leaflets, in the outer two the ring-like sheath-portion is formed. Magnified.

SINGLE BRANCHED LEAVES AS APPARENT WHORLS. Segmented leaves which have no stalks and are deeply divided have a somewhat peculiar aspect. The single leaf-lobes then take on the appearance of independent leaves and are partly also described as such. These cases have some biological interest and therefore two examples are referred to here:—

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[1] It has to be proved whether in cases like Spiraea Filipendula the first view—that these small leaflets are displaced lateral leaflets—which seems to me to have been hitherto lost sight of, is correct. A drawing by Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société Royale de Botanique de Belgique, Pl. II, Fig. 33, supports it. Possibly both cases occur.

[2] The transition-forms between toothed and pinnatifid and pinnate leaves as they occur, for instance, in Scabiosa Columbaria, tell the same story (Fig. 228).

Alchemilla nivalis. Alchemilla nivalis is a plant of the high Andes. It possesses apparently whorled leaves which are concrescent below into a sheath. In reality the whorl of leaves is a single leaf, as may be concluded from the fact that the leaves of the false whorl do not alternate (Fig. 213, 2). Each leaf-primordium is at first laid down singly on the side of the vegetative point, which it soon surrounds as a ring. This primordial ring itself remains in an arrested state, while the leaf-lobes which shoot out of it appear in descending serial succession, and these all attaining to about the same size they appear as a false leaf-whorl. The foliage-leaves of this species of Alchemilla are produced in quite the same way as the hypsophylls of other species of Alchemilla which have stalked leaves with usually a well-formed leaf-lamina[1]. The stalk remains unformed, the sheath is strongly developed, and it grasps round the vegetative point. We may understand the biological significance of this leaf-formation in some measure if we reflect that the young portions of the shoot are perfectly protected by the leaf-sheaths, which are inserted one into the other, and the small leaf-pinnules are in response to the physiologically xerophilous station.

Limnophila heterophylla. The second example is that of a marsh-plant, Limnophila heterophylla. Its *submerged* shoot-portions bear leaves in an apparent whorl (Fig. 214), whilst the ends of the shoots above water have the leaves arranged in decussate dimerous whorls. The history of development (Fig. 213, 1) shows that the water-leaves also appear in dimerous whorls, the leaves in each whorl soon uniting together into a ring-wall. Each leaf forms in descending succession numerous leaf-lobes which again may branch. As we pass upwards on the shoot the middle lobe of each leaf is at first larger than the lateral ones, and then the formation of the lateral ones is gradually entirely suppressed or reduced to mere marginal leaf-teeth in the aerial leaves. We shall refer to this plant again when speaking of the biological significance of leaf-forms.

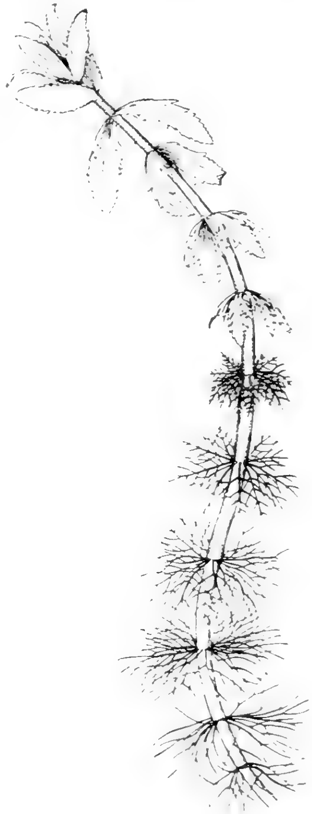

FIG. 214. Limnophila heterophylla. Water-leaves and air-leaves and transition-forms. One-half natural size.

PELTATE LEAVES[2].

By peltate leaves we understand those in which the lamina does not expand directly out of and in line with the leaf-stalk, but grows out over the stalk. Where this form is developed we always find upon the *upper*

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[1] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 33. Alchemilla is figured.

[2] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 234. A picture of the peltate leaves, without reference to the recent

(dorsal) side of the leaf, close to the position where the stalk is originally fixed to the lamina, a zone of the young leaf, which shares in the formation of the lamina. It is only in cotyledons and some kataphylls, hypsophylls, and stamens[1] that we find upon the *under* (ventral) side of the leaf an outgrowth which prolongs the lamina. De Candolle has in accordance with these facts divided such leaves into *epipeltate* and *hypopeltate* forms. In the hypopeltate forms the construction is mainly (leaving out of account the case of 'versatile' anthers) directed to the provision of means of protection.

FIG. 215. Asparagus comorensis. Turio with peltate kataphylls; the lower part of each kataphyll stands out later from the shoot, hardens, and becomes a climbing-thorn.

PELTATE KATAPHYLLS. The kataphylls of some species of Asparagus are peltate, and furnish an efficient protection to the shoot-bud. In most cases of this kind these kataphylls fall away later; they are merely protective organs. But in Asparagus comorensis (Fig. 215), the outgrowth of the under side of the leaf becomes a hard thorn or hook projecting from the shoot-axis, and is used as a climbing-organ.

PELTATE STAMENS. The pollen-sacs of Juniperus are protected by an outgrowth of the scale-like lamina of the covering leaf, and this I have compared with an indusium[2].

PELTATE COTYLEDONS. Where we find peltate cotyledons, as in the grasses, the object is to provide a contact-surface with the endosperm. The short 'radicle' of the oak is invested by the cotyledons, which grow out below and protect it.

PELTATE FOLIAGE-LEAVES. The biological significance of the peltate foliage-leaves is less clear. We have first of all to recognize two groups—the short-stalked and the long-stalked:—

Short-stalked peltate foliage-leaves. I only know of such leaves in some epiphytic species of Trichomanes, T. Hildebrandtii[3], T. peltatum, and T. Motleyi[4], but in the last-named all the leaves are not always peltate. When we recollect that in other species of Trichomanes, for

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literature of development, is given by C. de Candolle, Sur les feuilles peltées, in Bulletin des travaux de la Société botanique de Genève, 1898–99.

[1] I have pointed out, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), that stamens with versatile anthers conform with peltate leaves in their method of formation.

[2] Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien, in Botanische Zeitung, xxxix (1881), p. 703; C. de Candolle, Sur les phyllomes hypopeltées, in Bulletin des travaux de la Société botanique de Genève, 1895–7.

[3] See Giesenhagen, Die Hymenophyllaceen, in Flora, lxxiii (1890), p. 452.

[4] G. Karsten, Morphologische und biologische Untersuchungen über einige Epiphytenformen der

example T. brachypus, the leaves are closely adpressed to the tree-bark, to which they are fastened by rhizoids, and that many of the Acrosticheae have the same kind of leaves, we may assume that the peltate form is of special advantage in a given size of leaf-surface, both for the retention of water and for the protection of the delicate stem, which in the cases under notice is rootless.

Long-stalked peltate foliage-leaves. In the case of these leaves other considerations have to be looked to. In the first place the size of the peltate lamina is very different. The 'ideal' peltate leaf would be one with a stalk attached in the middle of an almost circular leaf-surface. This is approached in, for example, Nelumbium. In others, like many species of Caladium, the anterior portion of the leaf-surface, which has grown out over the stalk, is much smaller than the posterior. Possibly the peltate form has appeared in these later than it has done in cases like Nelumbium.

CONDITIONS UNDER WHICH PELTATE LEAVES OCCUR. Peltate leaves appear in plants which occur under very different conditions of life, in both water-plants and land-plants, and amongst the latter in succulents like Umbilicus, climbers like Tropaeolum majus, trees like Sterculia platanifolia. These leaves are sometimes small, as in Utricularia peltata where they are only half a centimeter in diameter, sometimes relatively very large, as in Victoria regia where they may attain a diameter of two-and-a-half meters. They are almost exclusively found in plants with alternate phyllotaxy, only in a few plants with opposite leaves are they known. It is easy to understand this from the biological standpoint. The peltate lamina requires in its unfolding more room than others; frequently the laminae are supported upon orthotropous stalks, and would cover one another if they were to stand close together[1]. In plants with creeping rhizomes, or in climbing plants, the peltate leaf appears to be a particularly advantageous method of placing the leaf-surface by the shortest way in a transverse position to the light, and of shading the adjacent plants which appear as competitors for the light-supply. But although this explanation fits many peltate leaves, it is not possible to give any plausible causal explanation of their origin. We can only say that the factors mentioned above favour their origin. Further, a leaf like that of Geum bulgaricum (Fig. 81, Part I), whose lower part is far overshadowed by the terminal lobe, is biologically like a peltate one. A relationship of the peltate form of the lamina to the length of the stalk and to the position of the leaves, may be recognized in many cases. Whilst, as in Utricularia peltata, the peltate leaves are relatively small and have not

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Molukken, in Annales du Jardin botanique de Buitenzorg, xii (1895), p. 127. The developmental history of the leaves is given, and it is shown that as the apical growth of these species ceases early they never have circinate ptyxis.

[1] See Part I, p. 114.

very long stalks, we find allied forms, such as Utricularia nelumbifolia, with long-stalked larger peltate leaves, and we may conclude that the former are perhaps derived from originally long-stalked forms. The relation between the length of the leaf-stalk and the peltate form of lamina appears also in the individual development of many plants. In Umbilicus (Fig. 216) the basal leaves are long-stalked and peltate and somewhat concave above, whilst those upon the flowering shoot, especially the bracts, are not peltate, and appear usually as ordinary leaves with short stalks. We find the like in the berberidaceous Diphylleia cymosa, where the upper short-stalked leaves have frequently, but not always, lost, or nearly lost, the peltate form. In seedlings also the peltate form appears usually in the primary leaves, for example in Tropaeolum majus, T. minus, and Nelumbium, yet I have found frequently the primary leaves in Umbilicus pendulinus to have the usual form, and in species of Drosera with peltate leaves, there is always developed first of all a rosette of leaves of the ordinary droseraceous form.

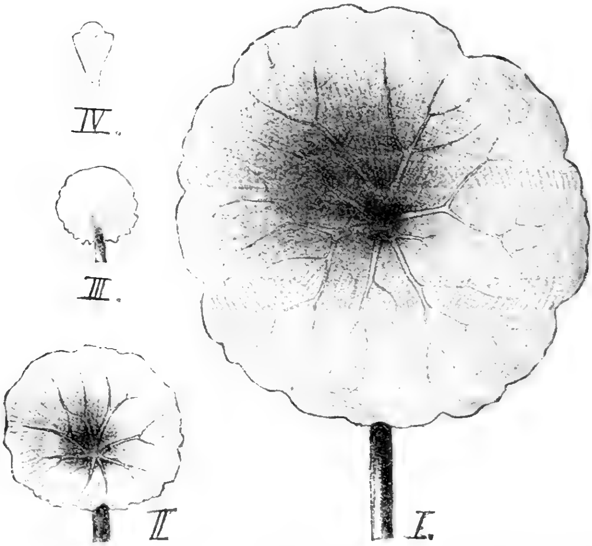

FIG. 216. Umbilicus pendulinus. *I*, basal foliage-leaf. *II*, foliage-leaf higher up. *III* and *IV*, hypsophylls. Natural size.

It is characteristic of the history of development of peltate leaves that they all belong to the basipetal type. We may find an explanation of this in that the peltate form owes its origin to a process of development at the base of the leaf-lamina. Moreover, the history of development of the peltate leaves shows fundamentally no other growth-processes than are to be observed in the peltate hairs, which occur, for example, in ferns, in the Elaeagnaceae, and elsewhere. The old explanation that the peltate leaves were the result of a concrescence of the leaf-edges projecting above the leaf-stalk is erroneous. Only in the biological sense has it any pretensions to correctness in so far as peltate leaves conform essentially in their behaviour with cordate leaves and other forms in which the lower leaf-edge projects over the point of insertion of the leaf-stalk.

Many peltate leaves are evidently derived from ordinary leaves which originally possessed a richer segmentation of the leaf-lamina. Segmentation is more conspicuous in the leaves of Hydrocotyle vulgaris when they are in a juvenile state than when they are adult[1], and the same is the case in Tropaeolum majus and T. minus whose leaves in the unfolded condition are apparently entire, whilst in their juvenile stages they recall the cut leaves of Tropaeolum aduncum and others. To this Massart[2] raises the objection that these facts are found also in Umbilicus, whilst its allied genera possess leaves which in all stages of their development are entire. He overlooks, however, that Bryophyllum possesses *segmented leaves* and that one species of Bryophyllum has passed over to the formation of peltate leaves. This species is the Bryophyllum crenatum of Baker which only forms leaves that are indented at the edge high up on the shoot-axis[3], and possesses at the base of this somewhat short-lived outgrowths which are directed upwards, and whose biological significance requires investigation.

TUBULAR LEAVES.

Tubular leaves conform with the peltate leaves in the history of their development up to a certain stage. These tubular leaves are found in a number of insectivorous plants. I do not mean that phyletically they are derived from peltate leaves, at any rate I know of no facts in support of such a view. In Cephalotus follicularis alone, outside the Utricularieae, are there, besides the tubular leaves, others of a different form, and these are not peltate but of the normal flat-form. Occasionally intermediate states are produced between these leaf-forms (Fig. 217). They are leaves with an excavation upon the upper side, but they do not approach the peltate form and are easily explained, when one knows the history of development of the tubular leaves, as *retarded formations*, without the necessity of looking upon them as *atavistic*. We meet with tubular leaves also especially amongst the Hepaticae[4], where no peltate leaves are known. If we follow the history of development[5], we find that an indentation appears upon the upper side of the leaf, and it gradually deepens (Fig. 218). The lower edge of the depression (Fig. 218, *d*)—this edge corresponds to the new formation in a peltate leaf—is in its upper part made into a lid, and at the same time forms a portion of the collar-like thickened entrance. The upper portion of the leaf-primordium forms the special

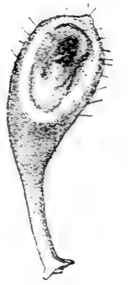

Fig. 217. Cephalotus follicularis. Leaf showing a stage between a tubular leaf and an ordinary leaf. On the upper side of the leaf is a depression, the leaf having apparently reached the stage shown in Fig. 218, 1, has continued its growth without further change in conformation.

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 234.

[2] Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société royale de botanique de Belgique, xxiii (1894), p. 81.

[3] At least in the single living example before me.

[4] See p. 58.

[5] See Eichler, Über die Schlauchblätter von Cephalotus follicularis, Labill., in Jahrbuch des königlichen botanischen Gartens zu Berlin, i (1881), p. 193.

tube which is later so bent back upon the stalk that the lid comes to lie on the top.

If we compare with these the tubular leaves in Nepenthes, Sarracenia, Utricularia and its allies, all of which genera are carnivorous like Cephalotus, we find that the history of the development is very similar, only the resulting configuration is somewhat different. I have elsewhere[1] given so full a description of these that I shall here only briefly refer to them. The portion marked with *d*, in Fig. 218, and which, as has been shown, is devoted in Cephalotus to the formation of the lid, serves in these other genera for the construction of a portion of the wall of the tube. The upper portion of the tube-wall corresponding to the leaf-apex forms the lid in Sarracenia, it grows out in Utricularia and Polypompholyx to the remarkable valve which closes the entrance of the tube, and in Genlisea two lateral portions of the margin of the mouth of the tube grow out into long arms which subsequently become twisted. In Nepenthes the lid arises as an outgrowth underneath the leaf-apex[2], and the leaves are here further remarkable in that the leaf-base develops later into a laminar surface, whilst between it and the pitcher a stalk-like portion, which frequently acts as a tendril, is intercalated.

Tubular leaves are only known outside insectivorous plants, passing over of course abnormal formations, in the epiphytic Dischidia Rafflesiana[3], and in the bracts of the Margraviaceae. In Dischidia Rafflesiana the inner side of the tube corresponds to the under side of the leaf, not to the upper side as in the cases first mentioned, and leaves which are concave upon the under side of another asclepiadaceous plant, Conchophyllum imbricatum, form a kind of transition to the tubular leaves of Dischidia. In the bracts also of many Margraviaceae the inner side of the tubular leaf corresponds to the under side of the leaf.

IV

RELATIONSHIPS BETWEEN VENATION AND DEVELOPMENT OF LEAF[4]

The relationships between the venation of the leaf and the growth of the leaf already described in the case of the Filicineae, are found also amongst the Angiospermae, although in somewhat different form.

The function of the veins of the leaf is two-fold, mechanical and nutritive.

It is well known that between the leaves of Monocotyledones with *striate venation*, and those of Dicotyledones with *reticulate venation*, there are differences which, however, are not very far-reaching. On the one hand there are amongst Monocotyledones not a few, especially of the Aroideae,

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[1] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 53.

[2] Goebel, op. cit., Plate XXI.

[3] Treub, Sur les urnes du Dischidia Raffesiana, Wall., in Annales du Jardin botanique de Buitenzorg, iii (1883), p. 13.

[4] See Deinega, Beiträge zur Kenntniss der Entwicklungsgeschichte des Blattes und der Anlage der Gefässbündel, in Flora, lxxxv (1898).

which have the venation common in Dicotyledones, and on the other hand there are amongst the Dicotyledones many in which the venation of the leaves is that most commonly observed in Monocotyledones, for example Eryngium pandanifolium, E. agavaefolium, Plantago media, and others.

We find too, in one and the same plant, differences in the venation in the different leaf-forms, and this is a point which is apt to be overlooked. The hypsophylls, sepals, petals, and so on, when they diverge considerably in form from the foliage-leaves, have a venation different from that of the foliage-leaves, and this raises therefore the question:—*What is the relationship between conformation of leaf and course of the veins?*

The investigations which have hitherto been made on the subject of venations, have dealt mainly with the relationships of the veins in the matured leaf, when the original arrangement of the conducting bundles is frequently no longer correctly recognizable, because branching, anastomosis, formation of strong midrib, and so forth, conceal the primary arrangement. Besides, such simple technical terms as 'striate' and 'reticulate,' give us no information regarding the connexion between venation and growth of leaf in a large cycle of affinity.

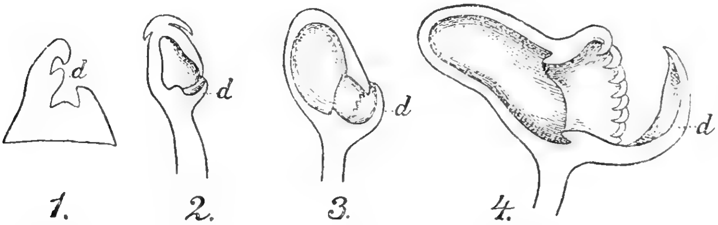

FIG. 218. Cephalotus follicularis. Development of the pitcher-leaves. The numbers show the succession. The pitchers formed by a growing out of the upper side of the leaf, whose lower margin becomes the lid *d*. After Eichler, but modified.

We shall deal first of all with this connexion, as it is seen in Monocotyledones, for there it can be proved that the apparently great differences which the venation exhibits, are all modifications of one 'type,' just as we can refer the flowers of all Monocotyledones to one type.

VENATION OF MONOCOTYLEDONES. The typical venation of Monocotyledones arises when a primordium of a leaf, attached by a broad base to the stem, grows nearly uniformly in length and breadth in all its parts (but at different times!). The conducting bundles which enter the leaf, and out of which the median is formed, traverse its whole length nearly uniformly from the base to the apex. The veins do not project, or only slightly, upon the leaf-surface. This type occurs in the foliage-leaves of the grasses, and amongst the Dicotyledones in the species of Eryngium, which have leaves like Monocotyledones; and it also occurs, but with some marked deviations however, in many hypsophylls.

When the upper portion of the primordium of the leaf spreads out by growth in diameter into a leaf-surface, it receives, from the not very different leaf-stalk, veins with a more curved course, and we get but a slight modification of the preceding venation. This happens in Eichhornia crassipes (Fig. 219). In the stalk, that is the portion of the leaf-lamina which is narrow, the conducting bundles retain their parallel arrangement, but in the lamina they are strongly curved. A like arrangement is found in the later primary leaves of Sagittaria and other plants.

A lamina constructed after this method cannot, without considerable demand upon the building-material to make it firmer, or without special arrangements, such as the folding which has been mentioned in the case of Curculigo[1] and other plants, attain any considerable development of surface, and the method is limited therefore to the relatively small primary leaves of plants, which produce adult leaves that are large or are adapted to special purposes. An instructive illustration of this is afforded by the seedling-plants of Phoenix and other palms mentioned above[2] (Fig. 210).

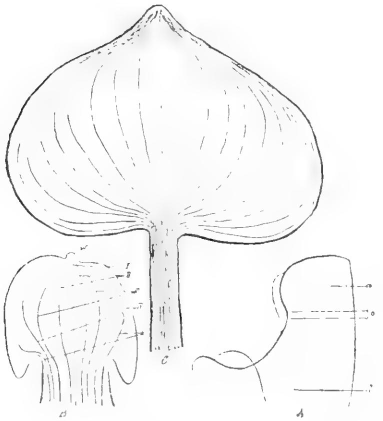

FIG. 219. Eichhornia crassipes. *A*, young leaf. *a*, leaf-lamina; *b*, leaf-base; *c*, zone out of which the leaf-stalk is developed later. *B*, upper part of an older leaf showing the course of the conducting bundles which are numbered successively *I*, *II*, *III*, *IV*, *V*; *w*, apical water-absorbing organ. *C*, scheme of the course of the nerves in the fully formed leaf. After Deinega.

In other Monocotyledones we find that the enlargement of the leaf-surface is made possible[3] by the formation of a thick middle portion, on which the thin lateral parts are, as it were, suspended. It is interesting to observe by what varying gradations this comes about, until the extreme is reached, in the species of Musa, where there is a lamina many meters long, and a thick midrib. This form is, however, only a terminal member of a series which we see beginning in, for example, Funkia ovata (Fig. 220).

Funkia ovata. In this plant the leaf-lamina has nearly an oval outline and is continued into a channelled leaf-stalk—the portion of the primordium which has been only slightly widened, and which differs from the leaf-lamina, in respect of the course of its vascular bundles, only to the slight extent of having them arranged in one row. In the lower part of the leaf-lamina we

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[1] See p. 326.

[2] See p. 327.

[3] I use this expression intentionally. I do not base this upon the fact that we find large leaf-surfaces, for instance, in the Aroideae, and that they have the 'venation' about to be described, but I say:—This venation *makes possible* the acquisition of a more significant size of leaf, but we may meet with it also in small leaves brought about there by the internal peculiarities of the family which beget the *possibility of development* of larger leaf-surfaces.

see already an indication of a 'mid-vein,' and at this point the bundles appear to be clustered together, for they run at first parallel, and then bend out into the leaf-surface which is thicker also at this position than it is higher up and at the sides. Let us assume now that the vascular bundles are originally all nearly parallel in the leaf-primordium, and that the growth in surface of the leaf proceeds from above downwards, first of all nearly uniformly and then chiefly at the margins because it is in the lower part that the thicker middle portion is first formed; then the course of the bundles in the upper part must be that which is diagrammatically represented in Fig. 220, *B*. The first bundles laid down have the ordinary course, and further downwards in the leaf, progressively, more bundles were present in the middle leaf-portion before the growth in breadth began which caused them to bend out into the younger portion of the leaf. This appearance of a mid-vein[1] at the leaf-base is related to the intercalary growth of the leaf and the strong mechanical claims of the leaf-base, as in the case of the palms.

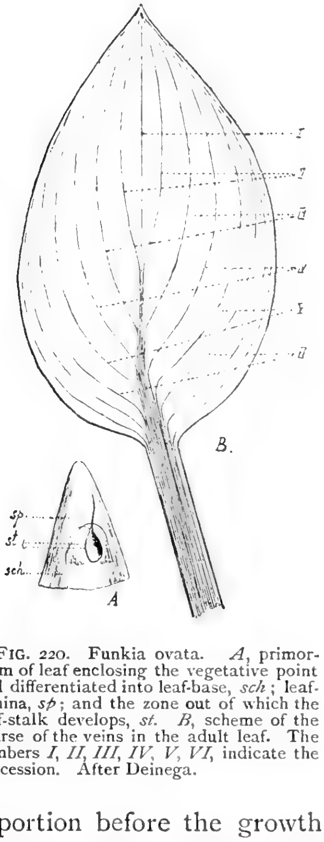

FIG. 220. Funkia ovata. *A*, primordium of leaf enclosing the vegetative point and differentiated into leaf-base, *sch*; leaf-lamina, *sp*; and the zone out of which the leaf-stalk develops, *st*. *B*, scheme of the course of the veins in the adult leaf. The numbers *I*, *II*, *III*, *IV*, *V*, *VI*, indicate the succession. After Deinega.

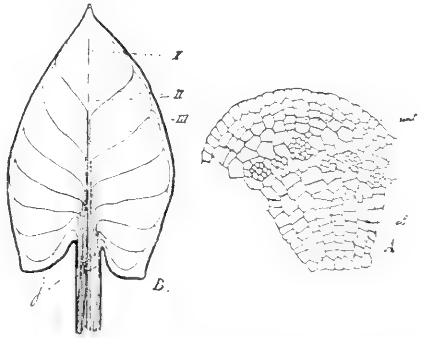

FIG. 221. Xanthosoma belophyllum, one of the Aroideae. *A*, leaf-stalk in transverse section the upper side turned downwards, and showing at *ob* stronger 'secondary growth in thickness'; *unt*, under side with less marked secondary growth. *B*, scheme of the course of the vascular bundles in the leaf; they apparently diverge from the monocotylous type. *I*, *II*, *III* indicate successive bundles; *j*, the youngest vascular bundles which bend out into the lower part of the leaf. After Deinega.

Xanthosoma belophyllum. Aroids show exactly the same relationship. In Fig. 221 we have the scheme of Xanthosoma, and the only difference from Funkia ovata is that there is a much stronger 'midrib' traversed by numerous bundles, and disappearing towards the apex. Here also the oldest bundles, that is to say those which are most early differentiated,

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[1] Which is, however, only the result of the clustering together of the ordinary veins.

reach the highest point in the leaf. The bundles bend out from the midrib in the leaf-surface in correspondence with the fact that this grows out, if one may so say, *as a wing from each side of the thick middle portion.* This growth takes place, however, earlier *above* than *below*, and the course of the bundles conforms with this. The bundles are not disposed in one row in the leaf-stalk as they are in the Monocotyledones in which lamina and stalk are only relatively slightly differentiated from one another, but they are distributed over the transverse section, and this may be explained by the fact that the stalk has acquired more of a cylindric form in response to greater mechanical claims, and exhibits a subsequent increase of growth in the ground-tissue (Fig. 221, *A*). The arrangement of the bundles is also different; the younger ones, which on account of their origin are found in the lateral portion of the leaf-sheath, bend upwards in the leaf-stalk, and they it is which bend out in the lower portion of the leaf-surface. The hypsophyll of the Aroideae, which corresponds to the vagina of a foliage-leaf, has on the other hand the ordinary monocotylous venation, and there is from the beginning, except at the tip, a uniformly distributed growth, as in the case of grasses.

In this account of the venation in Monocotyledones, I have endeavoured to show two things:

1. That morphologically, as well as in the distribution of its vascular bundles, the leaf of Aroideae—and the same holds also for the Scitamineae, Musacae, Cannacae[1], and others—can be derived from a grass-leaf, and that the vascular distribution has relation to the whole leaf-growth.

2. That the organization of the leaf—especially the appearance of a midrib—stands in relation to the leaf-size.

VENATION OF DICOTYLEDONES. From what has been said it will be gathered that there is no specific venation which can be called dicotylous, but the distribution of the conducting bundles in the leaves of the Dicotyledones also is determined by the relationships of growth. The following will serve as illustrations:—

Acer platanoides. In the leaves of Acer platanoides (Fig. 212) the divergent course of the veins is a consequence of the basipetal development of the leaf, by which the single leaf-lobes are not produced one from another but the leaf in all its parts is tolerably uniformly expanded. The middle nerve arises first and then the veins for the two upper leaf-lobes, and so forth. Finally the chief veins appear to radiate from one point[2].

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[1] Canna indica is very instructive. The large foliage-leaves have a mid-nerve, and whilst the upper hypsophylls have no lamina the reduced small laminae of the lower hypsophylls show the normal monocotylous venation such as is found only at the tops of the foliage-leaves. The conformation of the lamina in these hypsophylls is very varied; sometimes it is like that in Funkia (Fig. 220, *B*), at other times it is that of the fully developed leaf of Canna.

[2] See the details in Deinega, Beiträge zur Kenntniss der Entwicklungsgeschichte des Blattes und der Anlage der Gefässbündel, in Flora, lxxxv (1898).

Caltha palustris. We may compare with the case of Acer platanoides that of the unsegmented leaf of Caltha palustris. The chief veins radiate outwards here also from the base of the lamina (Fig. 222), and on the margin of the lamina there are insignificant projections. These arise relatively much later than the lobes in the leaves of Acer. The course of the veins depends upon the fact that the lamina which comes off from the thick leaf-stalk at a very early period develops, uniformly and without preference for any definite direction of growth, into a surface with its margins inrolled. In Fig. 246 the leaf is still entirely embryonal, only at the position which corresponds to the base of the lamina intercellular spaces appear. Its configuration, however, has in essentials been reached. The veins appear relatively late and radiate from the leaf-base in correspondence with the nearly uniform growth of the surface[1].

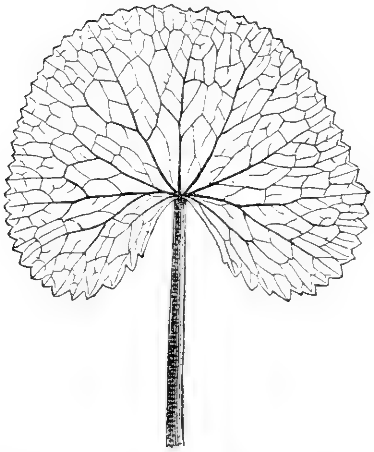

FIG. 222. Caltha palustris. Leaf. One-half natural size.

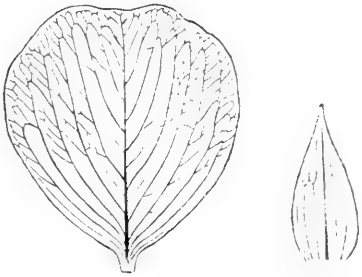

FIG. 223. Jussieuea salicifolia. Petal to the left. Sepal to the right. Magnified 1½.

If an undivided leaf with 'feather-venation' had arisen from such a primordium, all that would have happened further would have been that the primordium would have elongated; the middle part would have developed strongly; the leaf-lamina would have appeared as a lateral outgrowth on each side of this; and thus a middle nerve would have been formed from which the lateral veins would have proceeded. Of course there are here also all transitions between the forms of growth and the corresponding distribution of the veins.

Asarum europaeum. In Asarum europaeum, whose leaf resembles that of Caltha in all essentials, the elongation is not uniform, is more basipetal, and the middle nerve is stronger.

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[1] The margin remains longer meristic and produces then the leaf-teeth, and the apex of the leaf appears in the process of elongation to precede the base. These details cannot, however, be discussed here. It may be pointed out only that the mid-nerve develops somewhat more strongly than the others and also precedes them somewhat in inception. A monocotylous venation does not come about here on account of the early inception of a massive cylindric leaf-stalk (see Fig. 246, to the left).

Jussieuea salicifolia. The relationships in the formation of the leaves of the flower are very instructive. Fig. 223, for example, shows a petal of Jussieuea salicifolia upon the left and a sepal to the right. The sepal has monocotylous venation. From the first its base is broader and it is elongated with uniform growth in surface. The petal arises as a much smaller papilla, which then widens out in the direction indicated by the course of the nerves.

Fraxinus excelsior. Fraxinus gives us an example of a pinnate leaf (Fig. 224). The pinnules are laid down in acropetal succession, and there appears in the broad base of the leaf-primordium a large number of conducting bundles (Fig. 224, *C*), which radiate from one another in correspondence with the growth of the pinnules. As the pinnules separate from one another at a later period, there is formed from a portion of the upper leaf between each pair a stalk-like leaf-spindle or rhachis, and the original arrangement of the bundles is lost. The leaf-stalk here exhibits also a growth in thickness, and the bundles are arranged nearly in a circle.

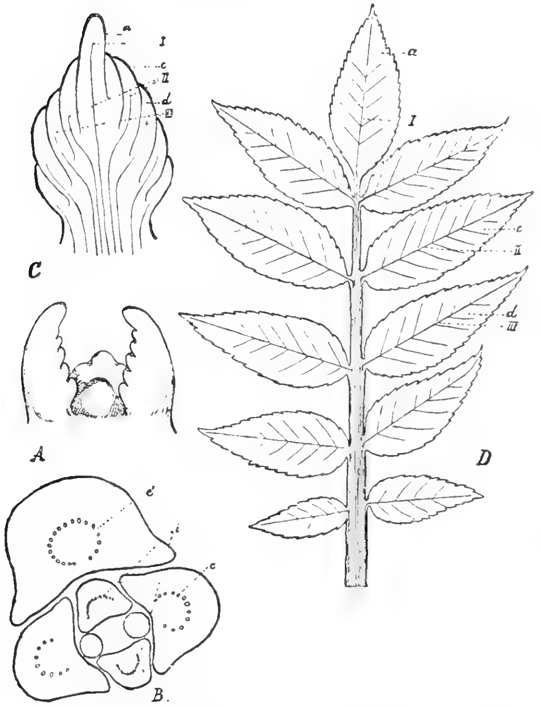

FIG. 224. Fraxinus excelsior. *A*, tip of the shoot from the outside. Right and left of the apex the primordia of pinnate leaves already show the acropetal pinnules. *B*, bud in transverse section. *i*, initial strand in base of young leaves; *c*, vascular bundle in basal part of leaf-stalk of next older leaf; *c'*, vascular bundle in upper part of leaf-stalk. *C*, young leaf showing the pinnules *a*, *c*, *d*, and the conducting bundles *I*, *II*, *III*. *D*, scheme of the course of the conducting bundles in the adult leaf, lettering as in *C*. After Deinega.

Amongst the Dicotyledones there are also cases where the leaf-stalk is distinguished from the lamina only by its small size. It arises then relatively late and has the vascular bundles arranged in one row, as, for example, in Plantago media, whose leaf-lamina has the primary veins arranged quite like that of the 'type' of Monocotyledones.

V

CONNEXION BETWEEN CONFIGURATION OF LEAF AND RELATIONSHIPS OF LIFE. HETEROPHYLLY

Frequent reference has been made to the connexion between configuration of leaves and the relationships of life, and a comprehensive treatment of this subject is scarcely possible without a pretty full account of anatomical structure, and this is beyond the scheme of this book. We know, too, in many cases nothing at all about the meaning of the configuration of the leaves, and I do not think that the configuration of the leaf is everywhere to be regarded as a direct adaptation. It is quite clear in xerophilous plants, in which so often there is reduction of the leaf-surface, that when rolled leaves appear in the most different families they have relation to the external conditions. Similarly the divided leaf-surface which occurs in submerged water-plants of most different cycles of affinity, whether it arise by branching, as is usual, or by the formation of holes, as in Ouvirandra [1], has clearly a relationship to the conditions of life, just as have the gills in animals. The long drawn-out tips of the leaves of many plants which grow in wet regions serve as drip-tips [2], and are therefore adapted to the rapid drying of the leaf-surface. On the other hand, we find that many forms of leaves appear through 'variation' and stand only in very indirect relationship [3], and cannot at any rate be regarded as direct adaptations, to environment [4]. The fern-leaved 'varieties' of beech and other plants and the remarkable crested and other so-called 'monstrous' leaves in ferns are of this character (Fig. 225).

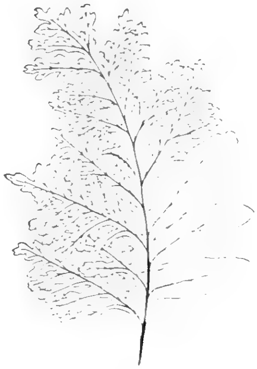

FIG. 225. Polypodium vulgare. Leaf which, in some pinnules, shows more copious branching than usual.

In these circumstances it will be more satisfactory in dealing with this part of the subject if a few examples be described, drawn from plants in which the configuration of the *foliage-leaves* is strikingly different at different periods of their life.

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[1] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 320.

[2] Jungner, Anpassungen der Pflanzen an das Klima in den Gegenden der regenreichen Kamerungebirge, in Botanisches Centralblatt, xlvii (1891), p. 353; Stahl, Regenfall und Blattgestalt, in Annales du Jardin botanique de Buitenzorg, xi (1893), p. 100.

[3] See Goebel, op. cit., ii (1893), p. 320, where I show that the Podostemaceae may under *like* external conditions exhibit *manifold* relationships of configuration. See also Goebel, op. cit., i (1889), Introduction; id., Über Studium und Auffassung der Anpassungserscheinungen bei Pflanzen, Akademie-Rede, München, 1898.

[4] See Part I, p. 185.

(1) *PTERIDOPHYTA.*

Where the configuration of the leaf is so simple, as it is in the Lycopodineae and Equisetaceae[1], it is hardly to be expected that there will be any or, at least, any considerable division of labour between the leaves.

Lycopodium. The difference in the conformation of the leaves in the dorsiventral shoots of Lycopodium has been already explained[2]. Exceptional cases like the formation of hooks on the leaves of the chief shoots of Lycopodium volubile are evidently modifications for the purpose of climbing.

Filicineae. The Filicineae, as is well known, show a marvellously varied configuration in leaf. The great division of the leaf-lamina renders it more resistant to the effect of wind and rain, an effect which can only be overcome in an undivided leaf by greater strength of construction. The Hymenophyllaceae are particularly instructive in this respect. One of the few forms with *large* undivided leaves is Trichomanes reniforme, and it is provided with kidney-shaped leaves. It grows on tree-stems on the wet west coast of New Zealand[3]. Its leaf-lamina is many-layered, in contrast with the case of other Hymenophyllaceae, where the lamina is almost without exception one-layered. A similar comparison may be instituted between the construction of the leaves in Adiantum reniforme, where they are entire and kidney-shaped, and those in other species of Adiantum, where they are greatly divided and have delicate leaflets. These examples show that external form and internal structure are most intimately connected.

Of this anatomical construction I can say but little here. The leaves of most Filicineae have essentially the same structure as the leaves of other land-plants, that is to say they possess an epidermis which is often very little different from the tissue immediately below it; there are stomata upon the epidermis ; the mesophyll is traversed by conducting bundles and intercellular spaces, and the whole structure is such that the leaf is not able to take up water in any quantity from the outside. But there are a number of ferns which live in moist shady localities whose leaf-structure is simplified in much the same way as we find it in the leaves of many water-plants ; they have no stomata, and in the physiological sense no epidermis ; of intercellular spaces there are none ; the leaf-surface, apart from the veins, is frequently one-layered, and the whole differentiation of tissue is quite like that in one of the Musci. This modification appears in different groups of the Filicineae and independently in each, a fact of so much interest that a few examples will be given in illustration :—

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[1] The leaves are here essentially protective organs, in hypogeous shoots also boring organs. The concrescent sheath-like leaves of the fertile shoots are more strongly developed than those of the sterile shoots because the bud of the fertile shoot is more massive. See Goebel, Über die Fruchtsprosse der Equiseten, in Berichte der deutschen botanischen Gesellschaft, iv (1886), p. 184.

[2] See Part I, pp. 103 and 252.

[3] On rainless days the leaves are rolled up, and if the drought does not last long they expand again when moistened and continue active life.

Asplenium obtusifolium. Asplenium obtusifolium, Linn.[1], is a fern which grows in moist shady localities. The leaves have no stomata and no intercellular spaces, and can take water directly from outside. That we have here to deal with a reduced form is evident, inasmuch as forms so nearly allied as to be regarded as belonging to the same 'species' have both stomata and intercellular spaces.

Todea. Amongst the Osmundaceae some species of the genus Todea—T. pellucida, T. superba, and their allies which form the section Leptopteris, often isolated as a special genus—have been long known by their thin translucent leaves and their life in moist shady localities. T. superba is, however, as I have satisfied myself in New Zealand, much less sensitive than one would suppose to drought that is not too prolonged.

Teratophyllum aculeatum, var. inermis, Mett. Amongst the Acrosticheae Karsten[2] has noticed some remarkable examples of analogous adaptation. Teratophyllum aculeatum, var. inermis, Mett., is a climbing fern with two kinds of leaves, those which lie against the tree-stem and those which stand off from it. The latter are the special assimilation-organs and have the ordinary structure of the leaves of ferns. The former have an anatomical structure which recalls by its translucency and colour the leaves of the Hymenophyllaceae, but they have upon their under side stomata, they can be wetted, and they serve to retain water, and probably also take up water. It is much to be wished that we knew the configuration of the leaves of the germ-plant.

Hemitelia capensis. In this category we may place those remarkable formations upon the leaf-stalk of Hemitelia capensis, which were of old regarded as Hymenophylleae[3], and have in literature the senseless name of 'adventitious pinnules.' Judging from their appearance and the anatomical structure of dried material[4] they are merely formations of the basal pinnules of the leaf adapted to the absorption of water. The plant grows in moist hollows in the vicinity of waterfalls; and as in the Hymenophyllaceae and in Dumortiera amongst Hepaticae, a change has been brought about in the plant by the conditions of the locality, but it is limited to a portion only of the leaf. The basal pinnules are finely divided, and the lamina is much less developed than it is in the 'normal' leaf-pinnules and is only unilateral along the veins. It is thin, probably wettable, and resembles the leaves of Teratophyllum in having stomata only upon one side. The intercellular spaces are very small.

Hymenophyllaceae. In the Hymenophyllaceae adaptations like those just mentioned are very common. We know of no species of Hymenophyllum provided

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[1] See Giesenhagen, Über hygrophile Farne, in Flora, lxxvi (Ergänzungsband zum Jahrgang 1892), p. 157.

[2] Karsten, Morphologische und biologische Untersuchungen über einige Epiphytenformen der Molukken, in Annales du Jardin botanique de Buitenzorg, xii (1895), p. 117. Christ, Die Farnkräuter der Erde, p. 39, unites this fern with Acrostichum (Lomariopsis) sorbifolium, an identification that appears to me *very* doubtful. I cannot discuss systematic questions here, and will only remark further that Christ's term 'adventitious leaves,' for water-absorbing leaves, is an impossible one, as there are no adventitious leaves here.

[3] In the Munich Herbarium some pinnules are named Trichomanes incisum, Th.; another had the equally erroneous label 'palearum Hemiteliae ripariae, R. Br., metamorphosis.'

[4] I unfortunately had no fresh material.

with stomata. In many of them—for instance Trichomanes brachypus whose leaves, lying close upon the stem of the tree, give the impression of a gigantic richly branched thallose liverwort, T. Hildebrandti, and others—the leaves are fastened to the substratum by hair-roots evidently in order that they may retain the water which runs down the stem.

Giesenhagen has shown that arrangements for holding water similar to those found in some thallose Hepaticae are also known amongst the Filices.

Salvinia. Salvinia possesses leaves which are adapted to a life in water. Every text-book explains that this plant has two kinds of leaves, float-leaves and water-leaves, the former are simple, the latter, apparently branched in a tufted manner[1], hang in the water and have no stomata. A peculiar divergent form of construction is described for the float-leaves. Whilst the float-leaves of S. natans are in the unfolded condition flat those of S. auriculata have a peculiar canoe-form (Fig. 226). This upfolding of the lamina protects the plant from too strong illumination, but it particularly affords the leaf-surface protection against wetting, for it bears many stalked tuftedly branched hairs which do not allow water-drops to reach the leaf-surface, and even if the leaf be submerged the air between the hairs is held so firmly that the water cannot touch the leaf-surface. Other float-leaves are rendered unwettable by the nature of their surface and not by hairs.

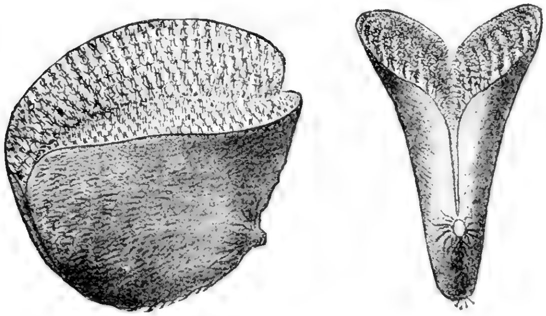

FIG. 226. Salvinia auriculata. On the left: leaf seen obliquely from above. On the right: leaf seen from point of insertion. Magnified 3.

Azolla. In Azolla there is only one kind of leaf. The leaves which stand upon one leaf-axis have a similar construction, but there is a different construction in the parts of one and the same leaf, and in this way biological relationships like those in Salvinia are established. The remarkable construction of the leaf of this floating water-fern has been described, so far as I know, from the purely morphological side only, not from that of its biological significance[2]. Each leaf consists of two lobes, an upper and an under, and these both in structure and function are very different. The upper and upwardly directed leaf-lobe serves as an assimilation-organ, its morphologically lower side is directed upwards, and has an arrangement of the tissue in correspondence thereto—there are palisade-like cells (Fig. 227, II, o_1, o_2) and numerous papillae which contribute to making this side unwettable. Upon the morphologically upper side, here turned downwards, of the upper lobe, there occur the peculiar pits secreting mucilage[3] which are inhabited by one of the Nostocaceae,

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[1] See for the history of development, Glück, Die Sporophyllmetamorphose, in Flora, lxxx (1895), p. 368.

[2] See Strasburger, Über Azolla, Jena, 1873.

[3] I pointed out many years ago that these pits are organs for the secretion of mucilage. The significance of the symbiosis with Anabaena can only be understood when the metabolism within the Cyanophyceae is better known.

and which are the feature in the leaf of Azolla that commonly attracts notice. The under lobe is constructed in an altogether different way (Fig. 227, II, u_1, u_2). It consists throughout its greater part of *one* cell-layer, only a middle portion lying somewhat towards the top is many-layered. In this many-layered area some chlorenchyma and stomata are present upon the upper side, and it is evidently the position which, as the transverse section shows, is least covered by the upper lobe and receives the most light. What is the meaning of this remarkable leaf-structure? It is clear that the juvenile portions are aptly protected in this infolding, formation of lobes, and covering, and investigation shows that the lower leaf-lobe is wettable on its outer side and takes up water [1]. If one lays rootless portions upon the surface of a weak solution of methyl-blue, the cell-contents soon become partly coloured blue. The uptake of water occurs not only through the roots but also through the lower lobe of the leaf, which therefore has the double function of protection of the bud and uptake of water, besides that of assimilation which seems to me to be only secondary. The upper lobe, rich in chlorophyll, is on the other hand essentially an assimilation-organ, and as it nowhere comes in contact with the water, stomata are formed on both sides, instead of on the upper side only as in float-leaves generally, whilst its oblique position protects it, as is the case in Salvinia auriculata, against too strong insolation. Further, the leaves of Azolla by their peculiar configuration and position form many air-spaces between their lobes, and these are of service not merely in the gas-exchange of the plant but also in enabling the plant to float. Azolla is thus an instructive plant because it shows how the formation of the leaf is influenced by its *lie*—it has palisade-parenchyma upon the under side, and a different construction of the upper and under lobes—and also how the conformation of the leaf is bound up with the manner of life.

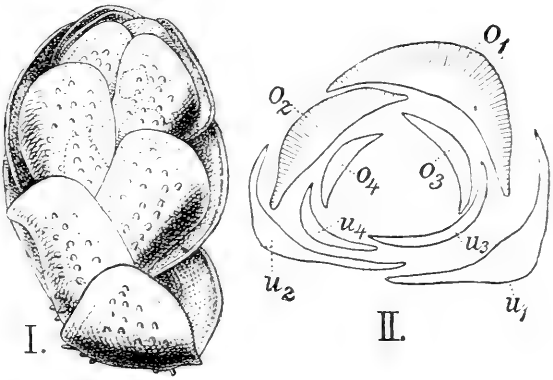

FIG. 227. Azolla filiculoides. I, habit of a shoot, seen from above. The pits inhabited by Anabaena are indicated by circles of dots. II, bud in transverse section. o_1 u_1, o_2 u_2, o_3 u_3, o_4 u_4 are respectively the upper and under lobes of four leaves. The shading lines on o_1 and o_2 indicate the palisade-parenchyma. Magnified.

Epiphytic Filices. Remarkable heterophylly also is found in many epiphytic ferns [2], and this was formerly confounded with the differences in configuration of sterile and fertile leaves which occur in many ferns:—

Polypodium (section Drynaria). In Polypodium quercifolium, P. propin-

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[1] This is also the case in a land-plant, Pinguicula.

[2] See Goebel, Morphologische und biologische Studien: I. Über epiphytische Farne und Muscineen, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 1; id., Pflanzenbiologische Schilderungen, i (1889), p. 216.

quum, and other species of the section Drynaria, there are stalked pinnate foliage-leaves which serve as assimilation-organs and also bear the sporangia; but besides there are unstalked *nest-leaves*, possessing broad heart-like bases which soon lose their chlorenchyma, and being provided with thick ribs act as accumulators of humus which the fern then uses as a 'soil.' Both leaf-forms appear in regular alternation, at least in the cultivated examples which I have observed for many years; they are not mixed up irregularly one with the other. The formation of the leaves as it is described in the germ-plants, as well as a comparison with allied forms, for example P. Heracleum, make it probable that the species which have nest-leaves have been derived from those possessing at first stalked-leaves, all of which were assimilation-organs only; then, a shortening of the stalk and a broadening of the base of the lamina having taken place, only one kind of foliage-leaf with broad base was produced, serving both for assimilation and for the accumulation of humus; following this a division of labour occurred, and one leaf lost almost entirely the function of assimilation, whilst another became constructed as an assimilation-organ alone.

Platycerium. Like features are to be found in the genus Platycerium[1]. This fern has two kinds of leaves: one is that of the *mantle-leaf*, wholly spread out close upon the substratum, or with its posterior part erect, and thus able to act as a nest-leaf; the other is that of the ordinary foliage-leaf. The mantle-leaves form layers closely placed one above the other, and as they die their humus is taken up by the roots. The erect portion collects humus just like the nest-leaves of the species of Polypodium mentioned above. The relationship between size and organization appears in these ferns very markedly; only by the construction of a special adaptation are they able to reach the giant size often attained by Platycerium grande and P. biforme, and which makes them amongst the most bizarre constructions in the plant kingdom.

KATAPHYLLS IN PTERIDOPHYTA. The formation of kataphylls will be treated of in a special section, but I may mention here their occurrence in the Pteridophyta. They are known in only a few species of Filices, for instance in Onoclea Struthiopteris and some species of Osmunda, O. regalis and O. cinnamomea. In Cystopteris bulbifera they occur as storage-organs on the bulb-like leaf-borne 'adventitious shoots[2].' They arise in this way: the leaf-lamina at a relatively late stage of development—a stage quite visible to the naked eye—becomes arrested, whilst the leaf-base acts as a protection to the bud. In O. Struthiopteris, moreover, there are transitions also from the foliage-leaves to the kataphylls, they are leaves with a reduced lamina. The following remark of Stenzel[3] upon the kataphylls of O. Struthiopteris illustrates well the earlier dominant idealistic morpho-

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[1] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 224.

[2] Also in the first leaves of the adventitious buds which arise upon the fleshy *stipules* of the Marattiaceae the lamina is usually arrested.

[3] Stenzel, Untersuchungen über Bau und Wachsthum der Farne, in Nova Acta der Kaiserl. Leop.-Carol. Akademie der Naturforscher, xxviii (1861).

logy which is even now not without influence. 'Their apex bears a circinate leaf-lamina which, although it is very reduced, prevents me from recognizing them as kataphylls.' This remark shows very clearly how the genetic relationship of the foliage-leaves to the kataphylls[1] was ignored in idealistic morphology. Characteristic kataphylls are found in the species of Isoetes which grow upon land and whose stem during the resting period is covered by a sheath of hard brown scales. These are the basal portions of leaves whose arrested lamina is still visible as a small point.

(2) *SPERMOPHYTA.*

We leave out of consideration for the moment the cotyledons, hypsophylls, and kataphylls, although we shall see that there is no sharp limit between them and the foliage-leaves, and we shall pass over also the primary leaves, which have been already treated of, and only deal with a few examples which may show how the appearance of different forms of leaf in one and the same plant can be explained from the biological standpoint.

(*a*) LAND-PLANTS.

Campanula rotundifolia and other Campanulaceae. It has been already shown[2] that these plants possess two leaf-forms which are connected with one another by transitions. On the basal part of the plant there occur stalked leaves with roundish reniform laminae, the so-called *round leaves* (Fig. 121, Part I). Further up there are leaves which are either unstalked or shortly stalked, and have long narrower leaf-laminae. These are the *long leaves.* The absence of the stalk in the long leaves can be so far explained by the position of these leaves upon an elongated shoot-axis, which rises up over the adjacent parts. The narrowing of the leaf-laminae may make them more resistant to mechanical injuries in their more exposed position. The round leaves also, as has been shown, are 'attuned' to a less light-intensity than are the long leaves, and this may also explain why such species of Campanula as C. latifolia, C. Trachelium, and others, which grow in stations of a different degree of shadiness, for instance in shrubberies, on the margin of woods, have no long leaves in their upper part, but leaves which are distinguished from the lower ones only by the absence of leaf-stalk and their smaller size. In such localities the leaves are also more protected against wind and rain than they are in the open. On the other hand we find in species of Edraianthus, for example E. Pumilio, which grows on sunny rocks, alike in the upper and in the basal part, leaves which correspond *only* with the long leaves of C. rotundifolia.

Scabiosa Columbaria and allies. We have a similar relationship in many Dipsaceae. In Scabiosa Columbaria there is a striking difference between the lower and the upper leaves (Fig. 228). The lower are stalked and have a simple leaf-lamina with toothed margin. As we pass upwards the stalk disappears and the leaf becomes pinnatipartite, at first at its base and then later above, and in the

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[1] See Part I, p. 7.

[2] See Part I, p. 242.

upper leaves branches are formed upon each lobe. The plant grows in sunny stations and the basal leaves are more fitted to contend with the environment[1] as entire leaves than as divided ones, whilst divided leaves on the other hand, by their division, are better able to withstand wind and rain[2]. Putting aside this teleological explanation it would appear that these undivided leaves are 'attuned' to a smaller light-intensity than are the divided ones, just as are the round leaves of Campanula rotundifolia. At least I have found that plants growing in shady places produce more undivided leaves than do plants in the sun, and Knautia sylvatica which naturally grows in the shade, has all its leaves, in the neighbourhood of Munich, undivided. Knautia arvensis has pinnatifid leaves, but there is a 'variety'—integrifolia—in which the leaves are not pinnatifid, and I conjecture that the variety is merely a shade-form. Culture experiments are indeed necessary for the solution of this question, but that in plants which first of all bring forth undivided leaves, and then later leaves which are more or less divided, we can *hinder* the formation of the less divided leaves by external conditions is shown by the behaviour of many arctic plants. Regarding them Pansch[3] says, 'Some plants, which in the temperate zone possess mostly divided or cut leaves, for example Saxifraga caespitosa, Linn., and Taraxacum, produce in the far north chiefly simple leaves.' This, however, does not enable us to decide how far the difference is the result of *direct* influence of external factors. That the segmentation of the leaf in Taraxacum is much richer in well-nourished examples can be easily established by the comparison of the starved form of our meadow-moors—the Taraxacum palustre, DC.—with the well-nourished examples of our glens; and it is likewise known that in Symphoricarpus racemosus segmented leaves appear upon the luxuriant water-shoots whilst they are undivided commonly. A *direct* connexion of the segmentation of the leaf with the external conditions of life is not perceptible.

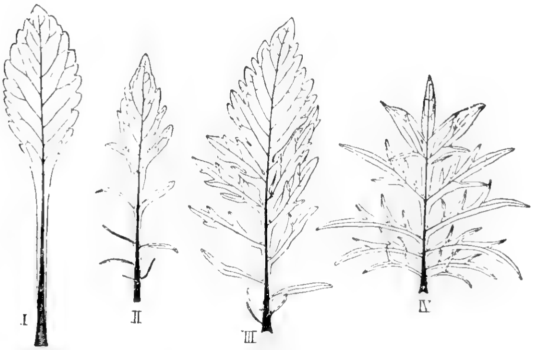

FIG. 228. Scabiosa Columbaria. Leaves, in the succession I, II, III, IV from below upwards, from different regions of the shoot. One third natural size.

Cases which are the converse of those which have just been described in which then the differentiation of the foliage-leaves in course of development

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[1] Which suppresses them through withdrawal of light like the leaves pressed to the ground of Plantago media.

[2] See Stahl, Regenfall und Blattgestalt, in Annales du Jardin botanique de Buitenzorg, xi (1893), p. 168.

[3] Pansch, Klima und Pflanzenleben in Ostgrönland, in Zweite deutsche Nordpolfahrt, Botanik, p. 18. See also what is said about nanism in Part I, p. 259.

may become simpler than it was at the beginning, are met with especially in many plants with xerophilous adaptations[1].

SCALE-LIKE LEAVES. So far as morphology is concerned I may mention here, because of the analogy they show with many kataphylls, that the scale-like leaves of the chief axis, for instance, of Veronica lycopodioides (Fig. 106, Part I), correspond to the *leaf-base* of the more highly segmented leaves which appear in germination, and occasionally also later as reversions. The lamina is only indicated by a short point. In this category we may also include—

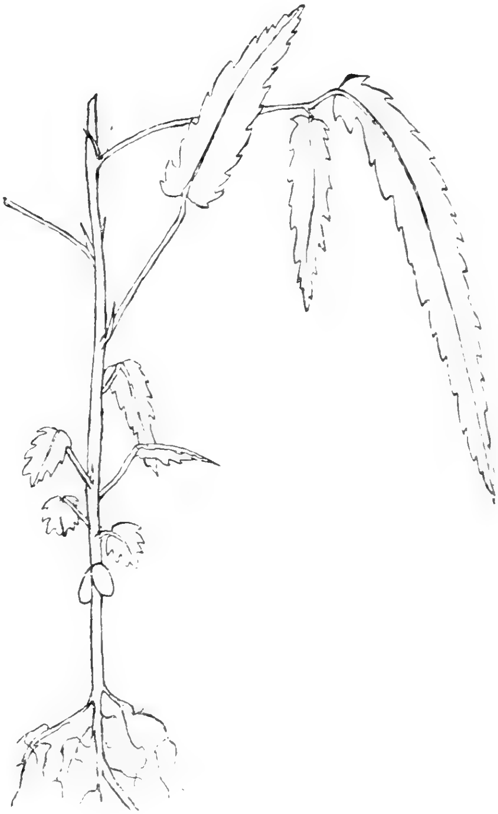

FIG. 229. Rubus australis var. cissoides. Seedling-plant. The foliage-leaves have well-developed laminae. After A. Mann.

PHYLLODIA. Here there is an alternation of function between the parts of *one* leaf-primordium. The leaf-stalk, in many cases also the leaf-spindle or rhachis, is constructed as an assimilation-organ, whilst the leaf-lamina is more or less reduced. The expression phyllodium has been frequently used, in an indefinite and wrong manner, for leaves which diverge from the forms in their alliance by being simple and unsegmented; for example, for the leaves of the species of Eryngium which are like Monocotyledones, the leaves of Ranunculus Lingua and R. Flammula, and the riband-like primary leaves of Sagittaria, and the leaves of some species of Lathyrus[2]. As we have learnt from the account of the history of development of the leaf above given, the notion of phyllodium involves that *an arrested primordium of a lamina* is present, although the arrest may take place at a very early period. But in those cases where the term phyllodium has been wrongly used, a leaf-stalk has not generally been laid down, and we must keep the two cases entirely separate, as they have nothing whatever to do with one another.

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[1] See what is said regarding juvenile stages, Part I, p. 165.

[2] See Part I, p. 162.

The arrest of the leaf-lamina may take place at various ages, and there are therefore transitions between phyllodia and foliage-leaves.

Rubus australis. The first example to be quoted is of a plant whose leaf-stalk serves as an assimilation-organ, but without suffering any striking change in its outer conformation, whilst the size of the lamina is reduced. It is Rubus australis. This plant occurs in different forms, which are particularly marked by the different degree of development of the leaf-surface. The plant depicted in Fig. 230 has branched leaves with very small lamina, and the long stalks of the leaflets serve as assimilation-organs. The seedling (Fig. 229), on the other hand, bears leaves with well-developed lamina. We can hardly speak here of phyllodia because the leaf-stalk has not the flattened form which is characteristic of most leaves. Such a limit is, however, scarcely to be drawn, as we know of cylindric leaves.

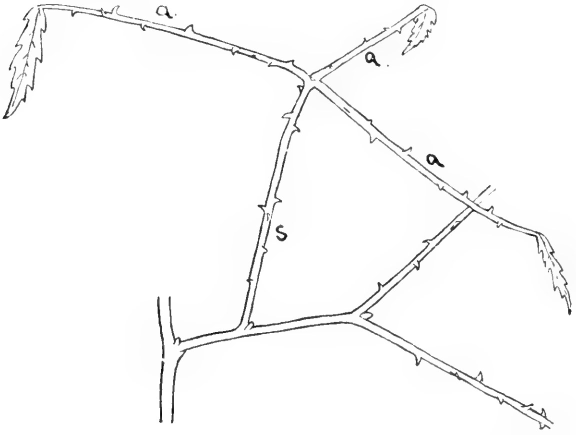

FIG. 230. Rubus australis var. cissoides. Portion of an older leaf. Laminae of the leaflets reduced. The stalk serves as an assimilating and scrambling-organ. After A. Mann.

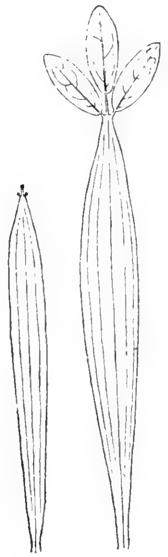

FIG. 231. Oxalis ruscifolia. Two leaves. That to the right has a well-developed ternate lamina. That to the left shows only the three points from which the leaflets, which were early arrested, have fallen off. Natural size.

Viminaria denudata. Viminaria denudata, one of the Leguminosae, behaves like Rubus australis. The phyllodia are cylindric, and whilst no apparent leaf-lamina is present, yet in a careful investigation of the history of development it could easily be shown. On seedling-plants it is regularly present.

Oxalis ruscifolia. Fortuitous formation of the leaf-lamina, at least in the plants cultivated in greenhouses, appears in Oxalis ruscifolia (Fig. 231). Here the leaves have a leaf-stalk which is broadened out like a lamina. The leaf-lamina consists of three delicate leaflets, and is in many leaves fully developed and falls away later, whilst in others it never unfolds. We have then here *from the beginning* a typical phyllode with arrested lamina. The event would be quite the same if it took place at a still earlier period[1], at a stage when the primordia of the three leaflets of the lamina are visible as small rudiments, or at a stage when the leaf-lamina is still undifferentiated. When speaking of leaf-tendrils hereafter we shall see what a stumbling-block the notion of a 'transition' has always been to many authors. Such cases as that above explained are therefore worthy of mention here.

Parkinsonia aculeata. Parkinsonia aculeata behaves in a similar manner in so far as the leaf-spindle is here widened, and the leaflets sitting upon it fall away later.

Before discussing other examples it must be mentioned that in the formation of phyllodes we have always an adaptation against loss through intense transpiration. We may assume that in the cases which have been described, the tissue of the leaf-lamina was not in a condition in which it could change in response to the requirements of the environment, whilst the leaf-stalk, which arises as we know at a *later* period in the course of the development, remains more plastic. That we must regard the outer conditions as a *stimulus* only, which brings about a varying reaction according to the peculiarity of the individual species, does not require any further exposition[2].

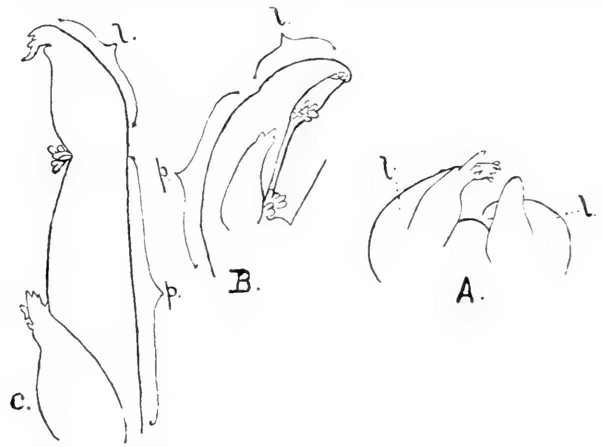

FIG. 232. Acacia calamifolia. *A*, *B*, *C*, stages in the development of a phyllode. *l*, the laminar primordium in process of arrest; *p*, the leaf-base developing into the phyllode. Beside each leaf one of its two stipules is seen. Magnified. After A. Mann.

Acacia. The best known examples of the formation of phyllodes are to be found in a number of Australian species of Acacia. It is usually said that in the phyllode of Acacia the lamina is entirely wanting[3]. This is incorrect, for the lamina can always be seen upon the primordium[4].

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[1] The behaviour of the Australian species of Cassia is instructive. Cassia eremophila has a leaf-stalk expanded vertically, but which bears pinnules in pinnate fashion; in C. phyllodina those pinnules are suppressed.

[2] See Part I, p. 217.

[3] Hildebrand, Über die Jugendzustände solcher Pflanzen, welche im Alter vom vegetativen Character ihrer Verwandten abweichen, in Flora, lviii (1875), p. 322; Frank, Lehrbuch der Botanik, ii. p. 260.

[4] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 241. A. Mann, Was bedeutet 'Metamorphose' in der Botanik? Inaug. Dissertation, München, 1894.

The lamina is relatively large in Acacia calamifolia (Fig. 232, *l*), and the whole history of development of the phyllode conforms throughout to the normal development of a leaf, only the lamina soon becomes stationary and arrested, the leaf-stalk develops into the phyllode. A study of the history of germination leads to the same result (Fig. 102, Part I). The lamina is visible in Fig. 233 representing a shoot of Acacia alata.

In some species of Acacia, for example A. floribunda, A. melanoxylon, and A. uncinata, there are transition-forms which show that the rhachis may have a share in the formation of the phyllode.

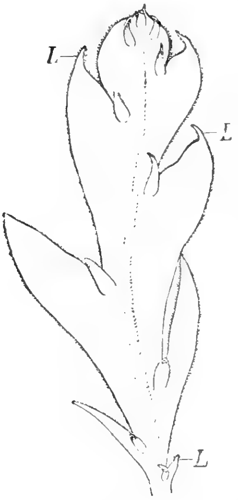

FIG. 233. Acacia alata. Apex of shoot winged by phyllodes. Beside each phyllode one of the two stipules of the leaf is seen. *L*, the arrested lamina of the phyllode.

The configuration of the phyllodes varies greatly in the genus Acacia[1]. We may consider as 'typical' the phyllode which is developed in a vertical direction and has a leathery texture, but the phyllodes may be needle-like, as in A. juniperina and A. verticillata, or cylindric and stalk-like, as in A. teretifolia, A. juncifolia, A. scirpifolia, and others. We do not know what is the relation between the configuration of the phyllode and the habitat in individual cases, and we must therefore, in framing an explanation of the forms, draw upon the whole behaviour of the plants. It is clear that, in one and the same place, a plant which possesses a deep widely spread root-system requires the formation of its leaves to be less adapted to the lessening of transpiration than does one in which the root-formation is less developed[2]. It is also scarcely open to doubt that the profile position of the leaves which is so common in Australian plants, and which is also observed in the formation of phyllodes, is an arrangement for the lessening of transpiration. The degree to which this control is developed varies greatly in the different species of Acacia which have phyllodes. Many have their phyllodes constructed as relatively thin plates of tissue of considerable size, resembling in their configuration very markedly the leaves of many species of Eucalyptus, and these will naturally transpire more than the forms with small needle-like phyllodes. Of species possessing such needle-like forms A. verticillata (Fig. 245) is worthy of mention

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[1] See Reinke, Untersuchungen über die Assimilationsorgane der Leguminoseen: VI. Mimosaceen, in Pringsheim's Jahrbücher, xxx (1897), p. 563.

[2] The relationships of the root-system to the epigeous part, especially to the leaf-formation, is generally little regarded. These relationships are evidently different in the seedling and in the adult; and that in good soil many thorny plants do not have their twigs developing into thorns is essentially connected with the development of the root-system. The effect of the relationship must be more marked in bad soil than in good soil, and must be specially influenced by the water-supply.

because in it we find a division of labour amongst the leaves. Only a few of its phyllodes have axillary shoots, and it is such phyllodes only which commonly are provided with stipules[1] and they precede the others in development. This has given rise to the *incorrect* hypothesis that the phenomena here are similar to those observable in the Stellatae, that is to say, that the phyllodes which have no stipules and no axillary shoots are not independent leaves, but the stipules of the others.

In some species of Acacia we find an alternation between the formation of phyllodes and of foliage-leaves, even after the plant has long passed the seedling state. This happens in A. heterophylla, A. melanoxylon, and others. We have here possibly a case like that which has been described above in Hakea trifurcata[2], and which is also known elsewhere, namely, that the several shoots which develop periodically repeat the alternation of the configuration of the leaf which is found in the seedling, and that at the beginning of the vegetative period, when water is abundant, the juvenile form of leaf is formed, and then later the formation of phyllodes sets in. In plants grown in the botanic garden such a periodicity is unrecognizable, but then such plants are not under natural conditions. It is easy to see that the formation of phyllodes is no longer under the direct influence of outer conditions, for seedling-plants of Acacia which I examined formed phyllodes even though they were cultivated in a very moist chamber. On the other hand it has happened[3] in young plants of A. verticillata, which had reached the stage of the formation of phyllodes, that when they were retained for a very long time in a very dry chamber and were thus 'enfeebled,' the formation of phyllodes was again called forth by cultivation in a moist chamber. All these phenomena will find their explanation if we remember the important fact of development, that the primordium of the lamina is always present in the phyllode, although in most cases its capacity for development is limited only to the seedling-plant.

(*b*) MARSH AND AQUATIC PLANTS.

Differences in the leaf-forms are frequently met with in plants in which the vegetative organs are placed partly under, partly above the surface of the water. We shall pass over the differences in anatomical structure and consider only the differences of form[4]. There are two groups of phenomena to be noticed here.

MONOCOTYLEDONES. In monocotylous aquatic and marsh plants the submerged leaves are essentially more simple than are those above the water. The submerged leaves have frequently a *riband-form*, the aerial leaves have frequently a segmentation into lamina, stalk, and sheath. That

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[1] Other species occasionally have stipules.

[2] See p. 294.

[3] See Part I, p. 172.

[4] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 217, for details.

this latter conformation will be more advantageous in enabling the leaves to rise above the water or to float upon its surface requires no demonstration, and it is also clear that leaves living submerged in water do not require segmentation into stalk and lamina[1].

DICOTYLEDONES. A second kind of heterophylly, which resembles that in Salvinia mentioned above, is found in a number of dicotylous plants which possess leaves appearing above the water-surface and leaves remaining submerged. The leaves appearing above the water-surface have either entire margins, for instance the float-leaves of Cabomba, or have a surface which is only slightly divided at the margin as in Ranunculus aquatilis, Bidens Beckii, and Limnophila heterophylla[2]. The submerged leaves, on the other hand, are divided into numerous filaments, so that they expose a relatively large surface to the water out of which they take the material for their food. The biological utility of the difference in the form of leaf is also clear, although as has been already stated[3], there are but few cases where a direct influence of the water-life upon the leaf-form can be established.

Limnophila heterophylla. I had expected to find an illustration of this influence in Limnophila heterophylla[4] because in this plant all transitions may be readily observed from the much cut apparently verticillate water-leaves to the undivided leaves which stand upon the shoot above the surface of the water. The observations which I was able to make on living plants[5] showed, however, that no such direct influence occurs. The seedling produces divided leaves whether germination takes place in water or upon the land, although in water the leaves are more elongated and show a different anatomical structure. Cuttings also from the upper portion of the plant, where the leaves are undivided, if cultivated as *land-plants*, produce not only side shoots with divided leaves, but themselves grow partly at the tip into shoots producing this form of leaf.

Cabomba. The relationships in Cabomba where the water-leaves are divided are similar. The simple peltate float-leaves are only produced at the flowering period. Although it is natural to assume that the form of the water-leaves is the result of a direct adaptation, there is no proof of it up to the present.

Ranunculus multifidus. Ranunculus multifidus which is a form only slightly adapted to life in water[6], shows when growing in the water a much richer branching of the leaf-lamina (Fig. 128, Part I), and it is very probable that a similar direct influence took place originally in other similar leaves, although it cannot now be proved.

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[1] See also Part I, p. 165.

[2] In Bidens Beckii and Limnophila heterophylla there are no float-leaves.

[3] See Part I, p. 260.

[4] See p. 333.

[5] Plants I brought from Ceylon grew easily and luxuriantly under cultivation.

[6] See Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 313.

VI

STIPULES, LIGULES, STIPELS

1. ORIGIN AND FUNCTION OF THE STIPULES.

The expression stipule was made use of by the older authors in no very sharply limited sense. They understood by it any small leaves or leaf-parts, as for example hypsophylls, or prophylls, or the intravaginal squamules in the axil of the leaf-base of many water-plants[1]. As stipules, however, we can only designate appendages of the leaf-base, which spring right and left from the leaf-base, as do the pinnules and leaf-teeth from the upper part of the primordium of the leaf. Phenomena of growth appear later, and in many cases conceal the original features.

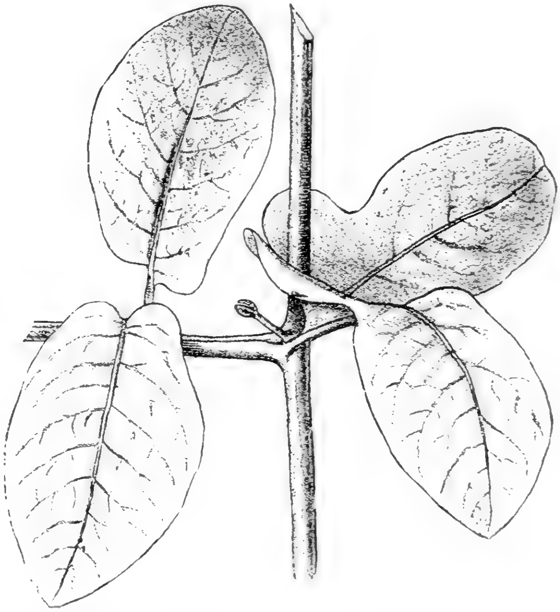

FIG. 234. Cobaea scandens. Portion of a shoot seen obliquely from the side. The lowermost pair of pinnules of the leaf that is shown cut off to the left have each an auricled base, and these cover the axillary bud.

In the simplest case the leaf-base continues to elongate after the laying down of the stipules and raises the stipules somewhat. These are then 'adnate stipules.' Frequently more far-reaching changes ensue which, however, as will be shown, can be elucidated by a comparison with allied forms and by the history of the development—take, for example, the axillary stipule of Ficus and other plants. The recognition of this frequently led also to the derivation of other outgrowths of the leaf-base from the formation of free stipules. Free stipules were taken as the 'type' because they occur in a number of plants and suffer definite modifications, and to it even structures, like the ligule of grasses, were referred by the assumption of

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[1] See Caspary, Die Hydrilleen (Anacharideen, Endl.), in Pringsheim's Jahrbücher, i (1858), p. 394. The intravaginal squamules are organs which secrete mucilage for the protection of the bud, as I showed, and as was confirmed by Schilling, Anatomisch-biologische Untersuchungen über die Schleimbildung der Wasserpflanzen, in Flora, lxxviii (1894), p. 280.

a 'concrescence' or other change. This retracing assumption, which up to the most recent times has been dominant, I hold and shall endeavour in what follows to show is altogether an incorrect generalization. Outgrowths of the leaf-base, even of the leaf-surface—in the form of the ligule of Selaginella and Isoetes which secretes slime, as well as of stipels or of transformations of the basal parts of the leaf-lamina—are developed in different families 'for the purpose' of protecting the bud. That this frequently takes place to the right and left of the leaf-base is easily understandable because here the axillary bud is chiefly exposed. I must, in the first instance, bring forward a few examples about which there has been some doubt as to whether they are really stipules, or only the lowermost leaf-pinnules.

FIG. 235. Cobaea scandens. Leaf seen from above. A portion only of the terminal tendril is shown. Each pinnule of the lowermost pair has an auricular outgrowth directed upward.

Cobaea scandens. In Cobaea scandens the lowermost pinnules of the foliage-leaf have a different configuration from the others (Figs. 234, 235). Whilst the upper pinnules, as is usual[1], are asymmetric with their basiscopic half the larger, in the lowermost leaf-pair the acroscopic half, that is to say the side turned away from the shoot-axis, is the broader, and at its base is provided with an ear-like excrescence. Careful examination shows that the axillary bud is formed beneath the 'auricles' of the lowermost pinnules which form a roof over it and so protect it against rain and sun. The position here is quite different from the usual one that is found when the stipules protect a bud, because commonly the stipules have their upper side turned to the bud, whilst these lowermost pinnules of Cobaea turn their *under side* towards it. In the light of these observations we can, however, readily understand what is the teleological meaning of this divergent configuration of the pinnules. It is possible that something else has to be considered, but one can scarcely ascribe a special significance to the circumstance that raindrops can collect in the narrow depression formed by the

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[1] See Part I, p. 122.

lowermost pinnules, although of course one may suppose that this might also prevent the access of 'unbidden guests' to the flowers. The case shows us at any rate how leaf-pinnules can be transformed into protective organs *resembling stipules*, and one might conjecture that elsewhere—but not everywhere!—stipules have taken origin in a similar way.

Guilandina. A striking example of the employment of the lower pinnules as stipules is supplied by a species of Guilandina from Ceram, which is cultivated in the garden at Buitenzorg (Fig. 236). The leaf is bipinnate; the lowermost pinnules have a peculiar form and are developed to serve as stipules. Possibly we have the same thing in other Leguminosae.

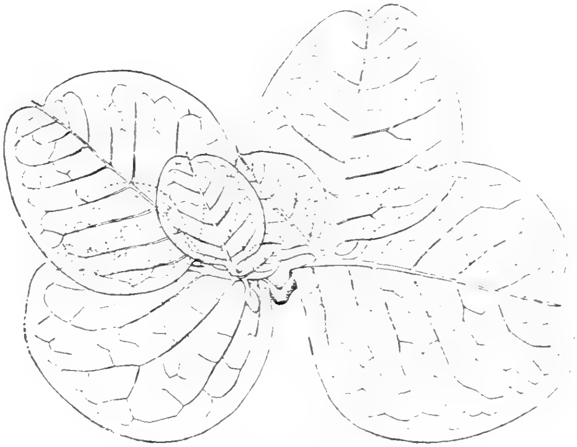

FIG. 236. Guilandina sp. (Ceram). Stipules.

Lotus corniculatus. The leaves, again, of Lotus corniculatus are ternate and have two persistent stipules, but below these there is found on each side a small tooth which by many is considered the proper stipule. If this is right, which can only be determined by comparative investigation, the lowermost pinnules here are developed in the place of the arrested stipules, and have taken on quite a stipular form.

Tetragonolobus siliquosus. In this plant we have the same features as in Lotus corniculatus.

AURICLES. It is not possible in many cases to separate sharply the pinnules from the stipules, and we find in many plants outgrowths at the base of the leaf-lamina which are described as *auricles*, and these have grown out into stipular formations. One example of this will suffice.

Adenostyles albifrons. The leaves on the under portion of the stem of Adenostyles albifrons have a sheath-like leaf-base (Fig. 237, *I*). This appears in the leaves which stand higher up as two lobe-like expansions, and these, in the stage represented in Fig. 237, *III*, have become quite stipule-like structures. The only reason why they are not called stipules is that they are not present on the lower leaves; but we can easily find a biological reason for this. The lower leaves have only the stem-bud to protect, whilst the upper leaves have to protect the massive primordium of the inflorescence, and the wing-like expansion of the leaf-base, which has led to the formation of the stipules, corresponds to this duty.

In most of the other plants which have got stipules these have arisen in much the same way only they are present in all leaves. In many cases, however, their origin has been different.

Viburnum. Lubbock[1] has in connexion with this pointed out that in the genus Viburnum only V. Opulus possesses stipules, and he supposes that these 'stipules' are so placed in the intervals between the leaf-bases that they protect the stem-bud. It must be noted, however, that the stipules here bear almost always glands at their apex, and further that they appear often in pairs at the base of a leaf (Fig. 238)[2]. Now below the lamina there appear a number of disk-like glands—which are much sought after by ants, and their secretion may also take a share in the *protection of the bud*, a point to which Lubbock gives too little attention—and there are transitions between these sessile glands and the stipules. These 'stipules,' then, are nothing more than stalked leaf-glands; on account of their position they may be named 'stipules' because, as I have endeavoured to show above, stipules have no uniformity in origin.

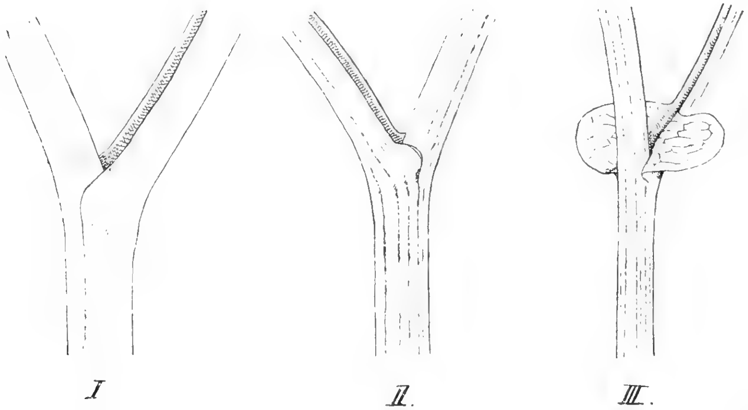

FIG. 237. Adenostyles albifrons. Appearance of the leaf-sheath. *I*, a lower leaf; *II* and *III*, from higher up the shoot.

In deciding, then, the question what parts that occur at the base

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[1] Lubbock, On Buds and Stipules, London, 1899.

[2] Impatiens glandulosa behaves in a like manner. The lower teeth of the leaves are transformed into glands. Such stalked glands are found also in pairs or in greater number upon the expansion which unites the bases of the opposite leaves. One may regard them as 'stipules.' Sambucus nigra also shows on strong shoots formations corresponding to those of Viburnum Opulus. Between its two opposite pinnate leaves there occur two or three nearly cylindric or somewhat flattened 'stipules,' bearing at their apex a gland. Similar structures are found also singly at the base of each of the leaves of the lowermost two pairs of pinnules, and they are often constructed like leaves, and indeed considered as lateral leaflets of the second degree. They often, however, are not developed. In many plants the capacity for a higher leaf-development remains latent. The lowermost pinnules of the potato, for example, also show frequently an indication of the formation of pinnules of the second order, and in very strong examples these may be fully developed.

of a leaf are to be considered as stipules, *function* must be taken into consideration. That this function, in the first place, is that of protecting the bud has been already stated, and it is performed in two ways:—

(*a*) Some stipules protect the lamina of the leaf upon which they spring, along with the portion of the shoot which lies above it, for example in Cunonia capensis, Castanea vesca, Amicia Zygomeris, and others;

(*b*) Other stipules protect the next higher leaves, for example in species of Cinchona, Magnolia, Ficus, Liriodendron, and others.

PROTECTIVE FUNCTION OF STIPULES. Frequently the work of protection is the only function of stipules. In trees with marked periodic development as, for example, Quercus and Fagus, the stipules fall after the unfolding of the winter-bud. They are *caducous*. In the buds of these plants the lamina of the outermost leaves is arrested at an early period, and then the stipules alone discharge the function of protection; in the inner leaves, however, the primordium of the foliage-leaf attains its normal size. An arrest of the lamina on the leaves whose stipules serve as protective organs *during the resting period* is exhibited in very unequal degree, as other plants show. Sometimes the arrest is early, sometimes it is late. In Liriodendron tulipifera at the end of the vegetative period the outermost leaf is already laid down in a complete condition with lamina, stalk, and two stipules, but only the stipules remain as bud-scales, the lamina and stalk—the leaf itself—are arrested and fall away; on the next leaf also, which will be the first to unfold in the spring, the stipules alone develop further. In this case the primordium of the leaf becomes arrested only at a late stage of development, yet the process is fundamentally the same as that which is found in Quercus and Fagus and like plants. The tendency thereto is undoubtedly transmitted by the shoot-axis, whose internodes remain extremely short between the bud-scales.

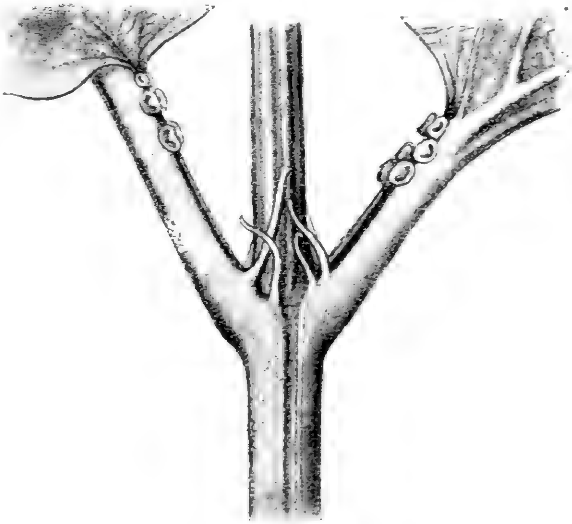

FIG. 238. Viburnum Opulus. Portion of a shoot. Two pairs of 'stipules' at the base of each leaf of the pair. Glands on the petioles below the lamina. Magnified 2.

ASSIMILATIVE FUNCTION OF STIPULES. In other cases the stipules take a share in the assimilation-work of the foliage-leaves and live as long as these do. Such stipules are *persistent.*

NUMBER OF STIPULES. As to the number of the stipules we commonly find that there is one stipule upon each side of the leaf-base, apart from concrescences and splittings. In Viburnum Opulus (Fig. 238) we have not infrequently a pair, as is the case also in Sambucus Ebulus, in which plant the number and construction of the stipules is very variable—sometimes there are two structures completely formed like pinnate leaves, sometimes there are four, and especially upon the upper leaves and on the first strong lateral shoots the stipules are much smaller and reduced to stalked glands like those in Sambucus nigra[1].

VASCULAR SUPPLY OF STIPULES. That the stipules are basal outgrowths of the primordium of the leaf is also shown by the course of the vascular bundles, although I do not think that this is a point of great importance in the notion of 'stipule.' As is pointed out by De Bary[2], the bundles which enter into the stipules are mostly branches from the leaf-bundles. Colomb[3] found this to be the case in all the plants he investigated. I would, however, call an organ a stipule which had otherwise all the characters of a stipule, even if it had independent vascular bundles, and Colomb's derivation of the stipules from ligular formations I hold to be quite unsupported and I shall advance further proof of this presently.

2. DEVELOPMENT OF STIPULES.

It has been shown above that the stipules are outgrowths of the leaf-base. The time of their origin is not fixed. In general it may be said with Massart[4] that the *stipules arise the earlier, the earlier their work as protective organs begins.* In Hydrocotyle, for example, where they enclose the leaf upon which they arise, they appear very early before the indication of any segmentation of the primordium of the leaf[5]. But most stipules have only to protect the younger leaves of the bud, and then they arise after or before[6] the appearance of the differentiation of the upper leaf; if their function is an insignificant one or they are inclined to arrest then they arise relatively late.

ARREST OF STIPULES. Such an arrest of the stipules takes place

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[1] See footnote 2 on p. 362.

[2] De Bary, Comparative Anatomy of the Vegetative Organs in the Phanerogams and Ferns (English Edition), Oxford, 1884, p. 297.

[3] Colomb, Recherches sur les stipules, in Annales des sciences naturelles, sér. 7, vi (1887).

[4] Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société Royale de Botanique de Belgique, xxiii (1894).

[5] Massart's figure is very unsatisfactory.

[6] According to Massart they arise, in Cunonia capensis, before the primordium of the lamina appears. This exception to an otherwise general rule requires further investigation.

frequently, so that the stipules may appear as small teeth or may be entirely wanting. Their absence is teleologically explained when the protection of the bud is otherwise provided for. Such a case has already been described[1] in the leaves of Lathyrus Clymenum, which have extremely reduced stipules, sometimes invisible. The increase in breadth of the whole leaf-primordium has made superfluous the development of the stipules as protective organs. We find the same in other cases, for example in Tropaeolum majus, where the stipules arise only upon the first two leaves as small pointlets and the broadened leaf-stalk itself protects the axillary bud. The case of Helianthemum described by Lubbock[2] is instructive. A number of species like H. vulgare and H. tomentosum have stipules; others like H. oelandicum and H. lasianthum have none. The former possess a narrow leaf-stalk, the latter have a broadened sheath-like leaf-stalk, and in the former the stipules act as a protection to the bud, in the latter the leaf-sheath. In H. guttatum the leaves in the lower part of the shoot have no stipules; stipules appear in the vicinity of the flower-region, occasionally one of them is more or less arrested. A comparison with the case of Adenostyles[3] gives us a biological explanation of this.

DISTRIBUTION OF STIPULES IN THE PLANT KINGDOM. It would carry me too far here to give the story of the distribution of stipules in the different families, and the few illustrations I have mentioned show that the appearance of these organs within the genera, even within the course of development of one plant, may vary. I will only say:—

Pteridophyta. Stipules are found in the Marattiaceae of the group of the Pteridophyta, and their thick fleshy appearance is extremely characteristic[4]. The structures which were frequently considered to be stipules in the Ophioglossaceae are not of this nature.

Monocotyledones. In Monocotyledones, whose ligular formations will be presently mentioned, typical stipules are unknown, and this is connected with the wide-spread existence of the strongly developed leaf-sheath in this group. The interpretation of the structures which stand in the axil of the leaves of Tamus europaeus and of the tendrils of Smilax as stipules is certainly incorrect[5].

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[1] See Part I, p. 162.

[2] Lubbock, On Buds and Stipules, London, 1899, p. 203, thinks that the time of origin of stipules distinguishes them from pinnules, and that in a compound leaf with basipetal development they appear not last but relatively first. But this entirely overlooks the biological point that early origin is connected with earliness of functional activity.

[3] See p. 361.

[4] These are axillary stipules. They appear in the same manner in Todea.

[5] With regard to Smilax see p. 223.

3. RELATIONSHIPS OF CONFIGURATION OF THE STIPULES AND THEIR TRANSFORMATION.

Stipules do not stand in such varied relationships to the outer world as do the leaves, and therefore their configuration is simpler than is that of leaves. The size and form of the stipules is closely connected with their function as protections to the bud. Where, as in Vicia Cracca (Part I, Fig. 78), they have only to fill the space between the leaf-pinnules in the bud, they are naturally smaller than where they have to cover the whole bud, as in Bauhinia and Lathyrus Aphaca (Part I, Figs. 72 and 77). The form and size of the stipules often change in the course of the individual development, during which of course the size of the bud which is being protected increases, and it is clear that buds of an inflorescence require more room than a vegetative bud. The primary leaves of Viola tricolor have, for example, no stipules, then follow leaves with simple stipules, and further up the stem come leaves with large pinnatifid stipules. The lobes of these stipules bear glands which secrete mucilage and serve markedly in this relationship for the protection of the bud. Whether this is the case in all fringed stipules requires further investigation.

INEQUALITY IN SIZE. Not infrequently the two stipules of a leaf differ from one another. In the dorsiventral shoots of many Leguminosae [1] the stipule which stands upon the illuminated side is greater than that upon the shaded side, and in Ervum monanthos the smaller stipule is simple whilst the larger has its margin divided into lobes. Perhaps this is connected with the fact that the axillary shoot of the Leguminosae is displaced towards the illuminated [2] side and requires here more perfect protection.

RELATIONSHIPS OF SYMMETRY. With regard to the symmetry-relationships of the stipules nothing will be said here as the subject has been already discussed [3]. Their peculiar construction in many Leguminosae only requires here a short notice:—

Stipular Appendages in Leguminosae. We have here to deal with appendages which are found at the base of many stipules and which make these sagittate or half-sagittate. The relationships are not so simple as might appear from Lubbock's description [4], because the significance of the stipular lobe is evidently not the same in all cases. In Aeschynomene indica the stipules are unilaterally prolonged outwards at the base, and this prolongation invests the outer side of the young internode whilst the stipule itself covers the bud. The meaning of the appendage is here quite clear. Lathyrus pratensis has usually two stipular lobes of which one

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[1] See Part I, p. 121.

[2] See Part I, pp. 121 and 126.

[3] See Part I, p. 125.

[4] Lubbock, On Buds and Stipules, London, 1899, p. 175.

is not infrequently arrested or only indicated by a small tooth, whilst the larger lobe is on the outside. In the primordium of the bud these stipular lobes cover, as in some other species of Lathyrus, only so small a portion of the surface of the internode that they can scarcely be considered as protective organs to this as they are in Aeschynomene, rather might one say that, where they lie nearly horizontally against the stem-surface (Fig. 239, to the left), they serve to hold the stipules in their right position. After their exit from the bud-condition they enlarge considerably, and this would seem to indicate that they have in the unfolded condition a definite function to perform. In Lathyrus latifolius (Fig. 239, to the right) they appear to serve the function of 'drip-tips.' The unilateral elongation of the stipule is here very great, and the appendages are not flat but so bent that rain must run out easily along them from the leaf-axils, instead of trickling down from one leaf to another as it would otherwise do.

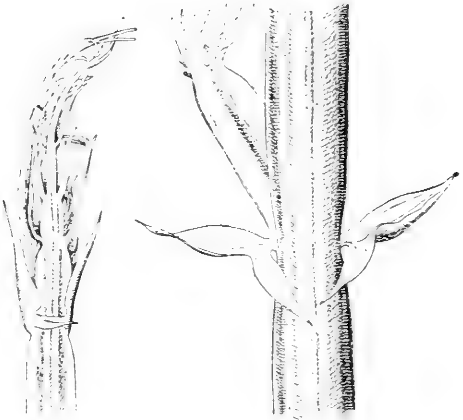

FIG. 239. To the left: Lathyrus heterophyllus: end of a shoot. To the right: Lathyrus latifolius: node. The unilateral stipular outgrowths are horizontal in the young shoot of L. heterophyllus, are directed downwards at the older node of Lathyrus latifolius. Natural size.

CONCRESCENCE OF STIPULES. 'Concrescence' of stipules appears regularly in many plants and there are two cases:—

(*a*) Concrescence of stipules of one and the same leaf;

(*b*) Concrescence of stipules of adjacent leaves. This can only take place, of course, where there is a cyclic phyllotaxy, and it occurs especially where there are dimerous whorls[1].

Concrescence of stipules of one leaf. Fig. 241 shows an example of the concrescence of the stipules of one and the same leaf. Here instead of two separate stipules we find one scale-like structure[2] which is the result of the union of two stipules, as the apical division in two indicates. How effective is the protection of the bud thus provided is shown in the transverse section (Fig. 242). In Dipterocarpus alatus (Fig. 240) the stipules join across the upper side of the leaf-stalk, forming in this way a sheath enveloping the bud, and the formation of the sheath by the concrescence of two stipules can be easily recognized by the presence of two stipular apices.

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[1] The opposite primary leaves of Phaseolus multiflorus furnish an example. The subsequent leaves are alternate, and there is naturally no concrescence.

[2] In Onobrychis the concrescent stipules form a dry membranous structure.

Concrescence of stipules of adjacent leaves. Concrescence of stipules belonging to two separate leaves is frequently observable in the opposite-leaved species of Urticaceae, for example in Humulus Lupulus and in a less degree also in Urtica dioica. Here I have found the two neighbouring stipules of one leaf-pair sometimes quite free, sometimes united more or less, and they may form an apparent single leaflet whose nature, however, is made clear by the two lobes at the apex. The whole arrangement suggests that instead of four only two stipules are present which enclose like mussel-shells the bud. In this way protection of the bud is provided for by the expenditure of less material than would be the case were the stipules to remain free. Such stipules formed by the concrescence of two belonging to different leaves are called *interpetiolar stipules*, and they are specially characteristic of the Rubiaceae. Fig. 243 shows a bud of Cinchona with this construction. There can be no doubt we have here to do with the 'concrescence' of two pairs of stipules, even although this is not to be traced in the history of development, that is to say, the interpetiolar stipule appears from the first as a single primordium. It is clear that such a concrescence in whorled and opposite leaves could readily ensue.

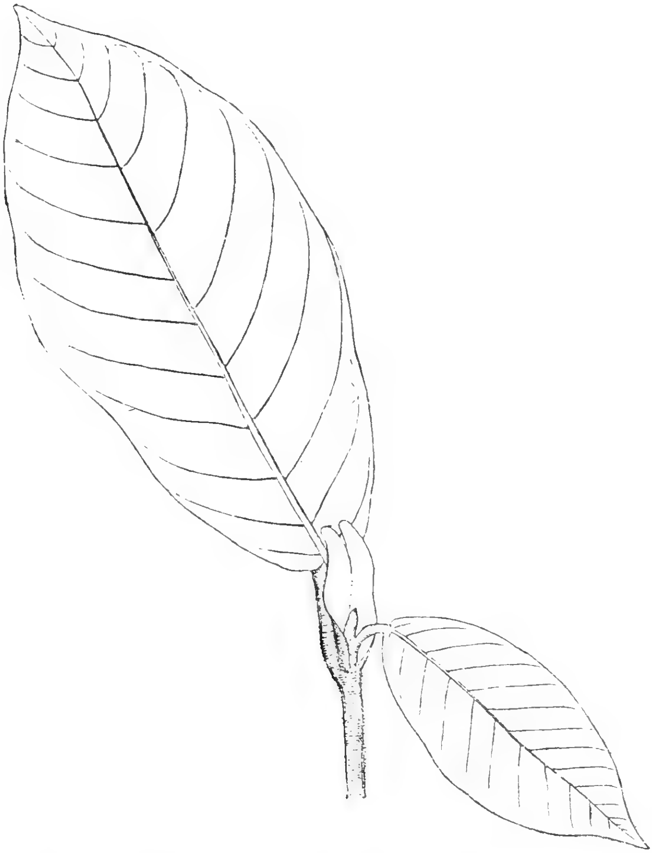

FIG. 240. Dipterocarpus alatus. Apex of the shoot of a young plant. The stipules of the erect leaf are concrescent over the face of the leaf and originally formed a sheath enclosing the bud of the stem.

Stipules of the Stellatae. Much attention has been given to the development of the leaf in the Stellatae, a tribe of the Rubiaceae. The leaves are apparently arranged in four to eight-membered whorls, but these leaves are not of equal value as is shown by the fact that in every leaf-whorl at most two leaves, which stand opposite one another, have an axillary shoot. These axillant leaves were considered by de Candolle[1] to be the true leaves, the others were regarded as stipules which have become leaf-like and which have undergone a 'chorisis' if there be more than six leaves present in the whorl, or a 'concrescence' if there be less than six. The history of development supports this interpretation. In Fig. 244 an axillary shoot of the leaf *fl* is shown in surface-view. It has two leaves b_1 and b_2, each of which has a primordium of an axillary shoot *A*, and each has two stipules S_1S_1 and S_2S_2. At the vegetative point the primordium of a 'leaf-whorl' appears as a ring-wall whose growth at two opposite points is taking place and these points mark the apices of the two chief leaves of the whorl. The stipules appear after the primordium of the leaves and they arise from the margin of the ring-like primordium between the foliage-leaves and then gradually grow out into a form and size like that of the proper leaf-primordium. Sometimes, and this regularly takes place in certain species, there arise between the two primordia of the leaves more than two stipules so that the 'whorl' is then more than six-membered. On the other hand there sometimes occurs a less number. In Galium palustre, for example, we find in the false whorl four similarly constructed one-nerved leaves which are distinguished only from one another by the fact that

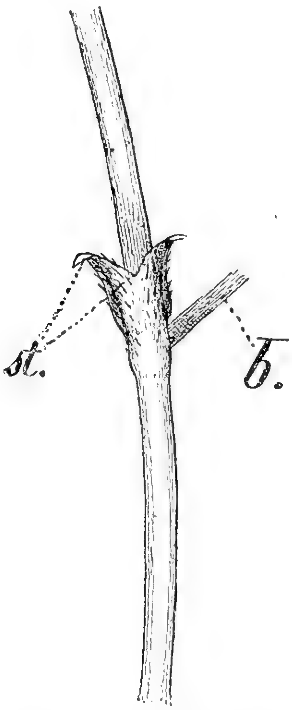

FIG. 241. Astragalus adscendens. *b*, stalk of a leaf, the stipules of which have become concrescent around the axis into a sheath *st*, at the top of which its composition out of the two stipules is indicated.

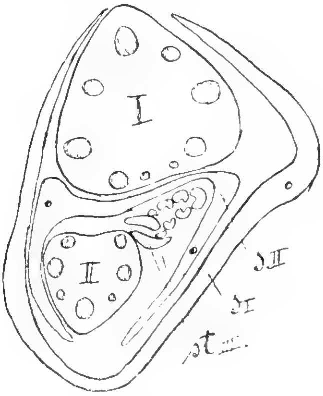

FIG. 242. Hedysarum obscurum. Bud in transverse section. *I*, oldest leaf with its stipular sheath *sI*; *II*, second leaf with its stipular sheath *sII*; *stIII*, free upper parts of the stipule of the third leaf. Magnified.

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[1] De Candolle, Vegetable Organography. English Edition by Kingdon, London, 1841, ii. p. 286; also M. Franke, Beiträge zur Morphologie und Entwicklungsgeschichte der Stellaten, in Botanische Zeitung, liv (1896), p. 33. The literature is cited by Franke.

two of them, which are opposite to one another, have axillary shoots. According to Eichler we have here a *true* concrescence of originally separate members, each of the two stipules being formed out of originally separate primordia. I have found, however, that in Galium palustre this is not or only seldom the case, but that sometimes the margin of the primordium of the stipule is swollen up or at least expanded or obliquely projected[1], and certainly we may consider this to be an indication of the primordia of two stipules; more often, however, I found no such indication, but the stipular primordium appeared uniformly single. There is as a fact, in the position of the two stipular primordia here, a new formation which presents the appearance of one single leaflet. Comparative morphology would here speak of a 'congenital concrescence,' which is only a clumsy way of stating the fact that where other species of Galium have two stipules here there is only one present from the beginning. Massart says that in Sherardia arvensis all the leaves of a whorl arise at the same time. One may bring forward in further support of the interpretation adopted above, which is also borne out by comparison with other Rubiaceae, that in most of the species of Galium the primary leaves do not differ from those which follow, but in Sherardia arvensis and Galium peregrinum the 'stipules' in the first leaf-whorl are narrower and somewhat shorter than the 'leaves'[2]. From the standpoint of the history of development there is possible, however, another interpretation which would bring the facts into conformity with those of the formation of the leaf of Limnophila heterophylla[3]:—That we have here leaves which stand in a two-membered whorl but are very

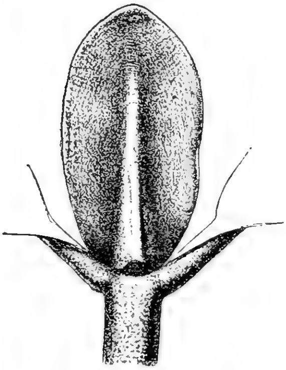

FIG. 243. Cinchona succirubra. Terminal bud enclosed by the mussel-like interpetiolar stipules of the pair of leaves of which the stalks only are shown.

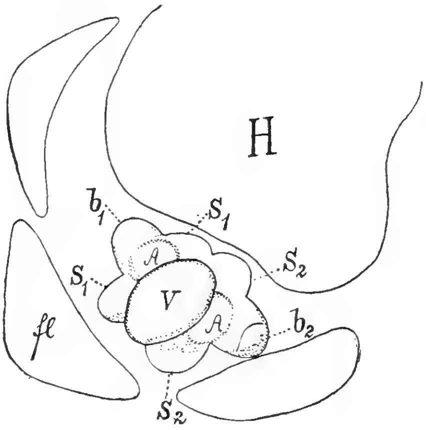

FIG. 244. Galium Mollugo. Axis of the shoot H in transverse section; *fl*, axillant leaf of a bud, which has laid down the first leaf-primordia of a 'whorl'; V, vegetative point of the axiallry bud; b_1, b_2, the first leaves with stipules S_1S_1, S_2S_2; A, A, axillary shoots of these leaves. The stipules are less developed upon the side next the axis.

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[1] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 231, Fig. 48 B. Franke has confirmed my observations. Occasionally the number of the leaves in following whorls changes. In a species of Galium growing as a weed in a plant-house I found successive numbers to be 4, 5, 4, 6.

[2] Massart, La récapitulation et l'innovation en embryogénie végétale, in Bulletins de la Société royale de botanique de Belgique, xxiii (1894), p. 200.

[3] See pp. 333, 358.

deeply divided and perhaps have never possessed stipules. To such an interpretation, however, the frequent occurrence of four-membered whorls is altogether unfavourable. The question here, as in all other like cases, is what weight should we attach to the comparison with allied forms in framing our explanation. Amongst the Stellatae there is a form, Didymaea mexicana, which possesses opposite leaves with two or three small interpetiolar stipules that are not like foliage-leaves. The plant conforms in all respects with the other Rubiaceae and may be considered as standing near the original type[1]. In the flower-region of the Stellatae simple leaves without stipules appear and the same is the case in the vegetative region of some species of Asperula[2]. Asperula scutellaris has upon the seedling-plant above the cotyledon first of all a four-membered 'false whorl,' but the stipules in it alternating with the chief leaves appear to be already reduced and in the following whorls gradually they disappear almost entirely.

Alchemilla galioides. Whilst in the Stellatae the manner in which the peculiar formation of the leaf has come about does not appear to be quite certain from the phyletic side, the derivation of an analogous configuration of leaf in another cycle of affinity is quite clear[3]. The leaf-whorl of Alchemilla galioides[4] consists of six almost equal leaves which are united with one another below into a sheath. Really we have here to do not with a dimerous leaf-whorl as in the Stellatae, but with a single leaf whose lamina is deeply divided and to such an extent that the single segments are constructed quite like stipules. A similar feature is found in allied species[5] which, in the region of the hypsophylls, are provided with stalkless leaf-laminae markedly different from the stipules. Not only is the formation of the stalk suppressed, but the size of the leaf is diminished, and the several equally large leaf-segments spring apparently directly from the leaf-sheath.

It was previously stated[6] that in species of Alchemilla, which have apparently whorled leaves, we might recognize in some measure a use for the configuration of the leaf. We cannot do so yet in the case of the Stellatae. We might suggest that, the Stellatae being plants with mostly long, thin shoot-axes, a nearly equal distribution of leaf-substance in a ring about the node involves, for the production of an equal surface of assimilation, a less expenditure of material in the strengthening of leaf and stem than would be the case if there were only two opposite leaf-surfaces, which would need of course to be provided each with its own ribs, stalks, and so forth. It seems to me that with this suggestion in one's mind it is of interest to note that Didymaea mexicana mentioned above is a climbing plant and uses as climbing hooks the recurved stipules and that its shoot-internodes have experienced no strengthening although the leaves are *stalked*.

Acacia verticillata. Hofmeister[7] supposed that he discovered in Acacia

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[1] See Schumann, Rubiaceae, in Engler and Prantl, Die natürlichen Pflanzenfamilien, p. 147, Fig. 47 N, O.

[2] M. Franke, Beiträge zur Morphologie und Entwicklungsgeschichte der Stellaten, in Botanische Zeitung, liv (1896), p. 33.

[3] Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 32.

[4] See Goebel, op. cit., p. 35, Fig. 9.

[5] See p. 333.

[6] See p. 333.

[7] Hofmeister, Allgemeine Morphologie der Gewächse, Leipzig, 1868, i. p. 525. See p. 356.

verticillata a case like that of the Stellatae because in the apparently whorled phyllodes only single ones have axillary shoots—the others therefore he took to be leaf-like stipules (Fig. 245). A. Mann and I have shown that Hofmeister's supposition was incorrect because at the base of the phyllodes, which have axillary shoots, there always occur very reduced stipules and these also occasionally occur upon the other phyllodes. The axillant phyllodes precede the others in the development. We have here then only a case of peculiar division of labour amongst the leaves, and it has only a superficial resemblance to the relationships in the Stellatae.

4. AXILLARY STIPULES.

We designate as *axillary stipules*, structures which stand in the leaf-axil, and sometimes are attached to the leaf-base over a longer or shorter extent. In some cases we find that the axillary stipules have proceeded from lateral stipules, which have become united to one another by a new formation across the upper side of the primordium of the leaf. In Melianthus, for example, there is formed at the upper limit of the leaf-base, a transverse cushion which unites the two lateral expansions of the leaf-base with one another, and then grows along with them, so that one may say that the stipular formation here encroaches over the upper surface of the leaf. In species of Ficus, many transitions are observable between free stipules and a stipular sheath, which appears as an independent leaf investing the bud, and which may be considered as a giant axillary stipule deciduous from its base. This deciduous axillary stipular sheath is found in Ficus elastica. In Ficus Pseudo-Carica there are free stipules, whose insertion, however, extends so far upon each side along the upper side of the leaf-base, that if we imagine this zone-insertion to be raised up upon a common base, we should have an axillary stipule with free upper ends, and open upon the outer side as is the case in Artocarpus; in seedlings of Artocarpus integrifolia I found, moreover, an incision upon the sheath above, showing its composition out of two stipules. The earlier the union by the transverse cushion takes place, the more will the axillary stipule appear as a single structure, and if the stipules become united also upon the side opposite to the point of insertion of the leaf, a closed sheath must be formed. Whilst in many cases axillary stipules are derived in this way from free lateral ones, I do not think that this is the case

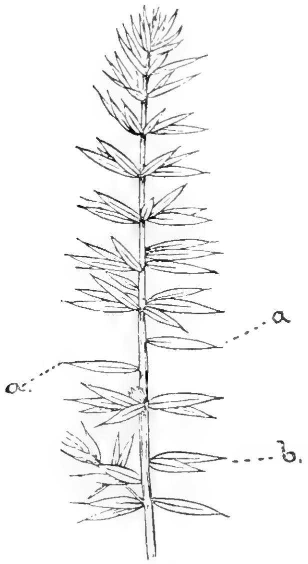

FIG. 245. Acacia verticillata. End of a shoot. Few of the needle-like phyllodes, *a*, *b*, have axillary shoots. Natural size. After A. Mann.

always. An axillary stipule may appear where there were never any free lateral stipules laid down, and where we have no ground for assuming them.

DICOTYLEDONES.

Caltha palustris. As an example I take Caltha palustris, of which Fig. 246 shows in the figure to the left, a dissected-out bud. This bud (turned to the left) is surrounded by a structure, which is somewhat conical and open at the top. This is the axillary stipule of the foliage-leaf on its right. In the figure to the right, which is a bud (turned to the right) developing into an inflorescence, the axillary stipule which served as a protection to the bud is developed more massively, corresponding to the more massive construction of the bud. In older conditions we find the upper part produced as a kind of horn, or the one margin of the mouth is cap-like, projecting over the other, and thus the mouth is closed to the outside. The leaf arises primarily as a ridge-like projection of the vegetative point. At an early period there appears on the upper side at the base of the leaf, an outgrowth which is united with the lateral parts of the leaf-base. The leaf-base itself extends round sometimes the whole shoot-axis, and grows out with the outgrowth of the upper leaf-surface over the vegetative point, and so forms the axillary stipule. How can we see in this two stipules? These are not even present in other Ranunculaceae.

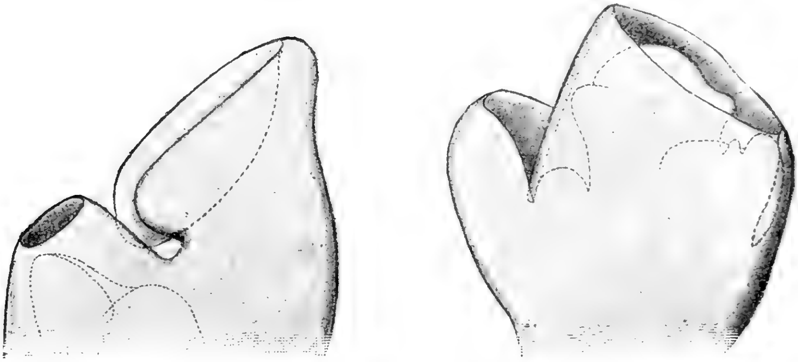

FIG. 246. Caltha palustris. Young leaves dissected out. To the left: leaf with axillary stipule which invests the bud. To the right: leaf with axillary stipule investing a young inflorescence.

Polygonaceae. The *ochrea* of the Polygonaceae arises in the same manner. Here the derivation of the axillary stipule from lateral ones is not probable, although at first in Rumex there appears to the right and left on the leaf an enlargement of the leaf-sheath, which one might regard as an indication of stipules[1], but one does not require to consider it as such,

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[1] The free lateral stipules which I described in the flower region of Rheum undulatum (see Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 232) are apparently the result of the splitting of the ochrea into two lobes.

for it is easy to understand that the formation of the protecting organs of the bud is direct in this case. There appears upon the upper side of the leaf an outgrowth, which connects the lateral parts. The ochrea also protects the bud by the mucilage-glands which it possesses.

Gaertnera. Such axillary stipules may also appear combined with interpetiolar stipules, and then there is a very peculiar construction, because the interpetiolar stipules unite with one another to form a sheath-like body, which then serves as a protection to the bud. We find this in a species of Gaertnera which I collected in Ceylon (Fig. 247). The origin of the construction is shown in Fig. 247, I, where between the leaves of the youngest leaf-pair, the interpetiolar stipules are visible. If now we suppose that the upper side of the base of each leaf shares in the stipular formation, the interpetiolar stipules would in a certain degree be united across the surface of their leaves, and thus would arise the peculiar condition which we have in this plant. The stipular sheaths are provided with numerous glands, and these it may be assumed aid in the protection of the bud.

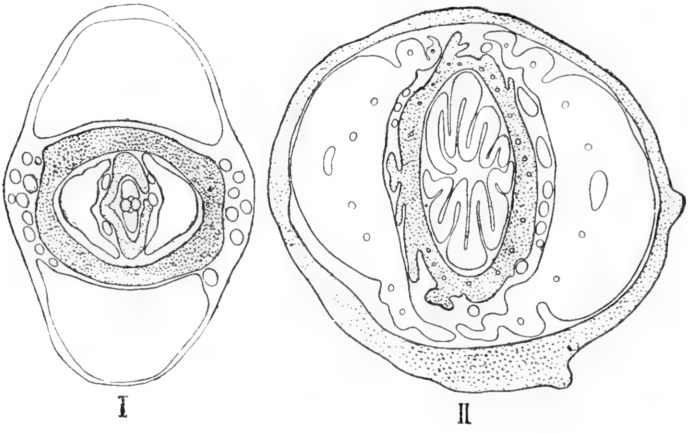

FIG. 247. Gaertnera sp. (Ceylon). Bud in transverse section. I, higher up; II, lower down. The stipules are shaded.

Gunnera. Some species of Gunnera possess remarkable axillary stipules. This genus contains forms of very different dimensions, and the axillary stipules are only found in those which possess a thick tuberous stem, and whose terminal bud is therefore very massive. For its protection, organs are developed which are absent in the species with more slender stem, like G. macrophylla and the small New Zealand species. We have in this one of the most striking relationships between size and formation of organs within one genus. The axillary stipules which are found in Gunnera chilensis[1],

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[1] See Reinke, Untersuchungen über die Morphologie der Vegetationsorgane von Gunnera, in Morphologische Abhandlungen, Leipzig, 1873, p. 78.

and G. manicata are of considerable size, as much as six or seven centimeters long. They are traversed by conducting bundles, and serve to store up food-material as well as to protect the bud in the resting period. The protection which they offer is increased by the fact that they are glued together by a mucilage. One may perhaps best derive them from mucilage-glands which appear as outgrowths of the leaf-base as well as elsewhere, but are here adapted to other functions and have reached a giant size.

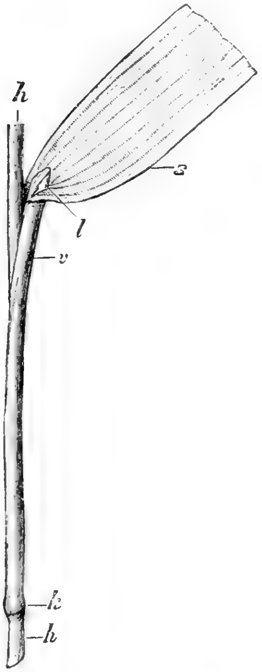

FIG. 248. A grass. Stem and portion of leaf: *h*, haulm; *v*, leaf-sheath; *k*, swelling of the leaf-sheath above the node; *s*, portion of lamina; *l*, ligule. Natural size. Lehrb.

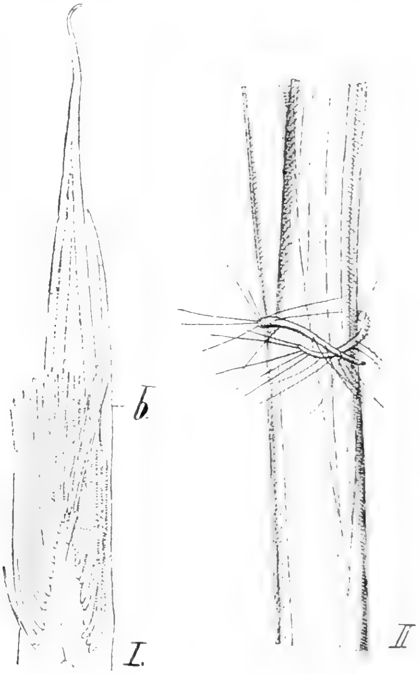

FIG. 249. Oryza sativa. *I*, ligule in the bud-condition dissected out. *b*, portion of the leaf to which it belongs. The ligule closes up the bud, the two hairy 'sickles of the leaf' act as aids in strengthening this closure by the ligule; they are erect, one outside, one inside. *II*, 'sickles of the leaf' are expanded, the ligule has been grown through by the next younger leaf.

MONOCOTYLEDONES[1].

Axillary stipules like those of Caltha are found in a number of Monocotyledones:—

Potamogeton. The leaf in Potamogeton possesses at first only a leaf-sheath sharply marked off from the lamina and very nearly amplexicaul. Subsequently an outgrowth appears upon the inner side of the leaf, at the point where the margins of the leaf-sheath meet, and this grows inwards from both sides of the leaf-sheath and unites them together. The sheath which is thus built up, and which afterwards grows out to

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[1] See Glück, Die Stipulargebilde der Monocotyledonen, Heidelberg, 1901.

a considerable extent, acts as a protection to the bud, and it is distinguished from that of the Polygonaceae, in all cases which have been examined, only by being open on one side.

5. LIGULES.

The Ligule of Grasses. The ligule of grasses appears in the form of a membranous outgrowth at the limit between the leaf-sheath and the leaf-lamina (Fig. 248). It usually contains no chlorophyll. Its size varies greatly in different grasses. In Psamma arenaria it may be as long as four centimeters, and in this species it is traversed by veins which are accompanied by tissue containing chlorophyll, and provided with stomata. In other species with a well-developed ligule, such as Oryza sativa and Arundinaria japonica, a conducting bundle is present[1], but the ligule usually consists of parenchymatous tissue alone.

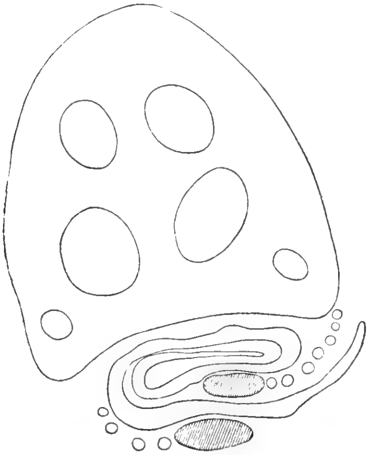

Fig. 250. Oryza sativa. Leaf in transverse section above the point of origin of the ligule; this is still convolute and closes the bud, and is strengthened by the erect 'sickles' and their hairs. The 'sickles' are shaded in the figure.

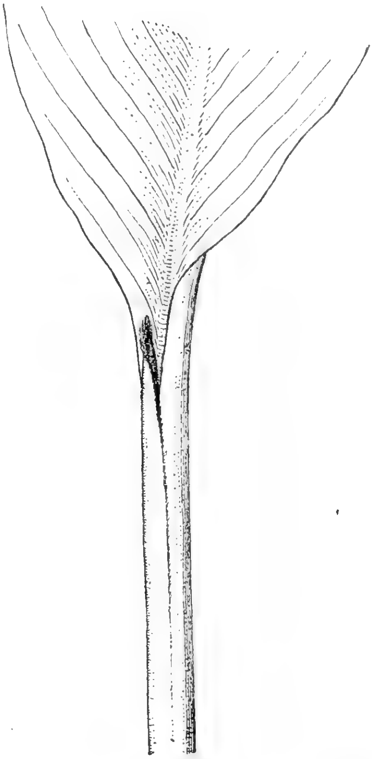

Fig. 251. Alpinia nutans. Portion of a leaf. The leaf-sheath ends above in a convolute ligule which closes the bud. Natural size.

Function of the Ligule of Grasses. Widely spread though the ligule is, we know as yet little about its meaning; the only conjecture regarding it which has been put forward is, that it prevents rain-water from

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[1] Regarding the course of this, see Colomb, Recherches sur les stipules, in Annales des sciences naturelles, sér. 7, vi (1887).

penetrating into the space between the leaf-sheath and the stem. This interpretation of the function of the ligule, first propounded by Schlechtendahl, does not appear to me to be very illuminating. It is easy to prove that the well-developed ligule in Oryza does not hinder the entrance of water in the way suggested, for water-drops which reach the leaf-surface do not roll towards the ligule, but fall to the ground from the tip of the unwettable, downwardly curved leaf.

The ligule has unquestionably the function of *protecting the bud.* The terminal bud is invested by the leaf-sheath, and in its further growth only gradually projects from the sheath, and if one removes the unfolded leaves, one comes to a point where the bud is closed over by the ligule. As Fig. 249, *I* shows, the ligule is rolled up into a conical point, through which the bud subsequently penetrates. This view is strengthened by the fact that, at the base of the leaf-lamina, there are found two sickle-like outgrowths, which in the unfolded leaf stand nearly horizontally (Fig. 249, *II*), but in the bud are directed upwards and in such a way that one of the 'sickles' lies outside and the other inside, as is shown in Figs. 249, *I*, 250. The long stiff hairs, which clothe the outer edge of the sickle, are in the bud similarly directed upwards, and contribute to the strengthening of the protective cap, which is formed above the bud by the convolute ligule.

Even more easily seen, that is to say no removal of the older parts is necessary, is the significance of the ligule in the uppermost leaf which invests the inflorescence of Dactylis glomerata and of many Zingiberaceae, for example Hedychium Gardnerianum and Alpinia nutans (Fig. 251). In these also the sheath elongates as a ligule beyond the point of insertion of the lamina, and the ligule of the uppermost foliage-leaf serves as a cover to close the bud on the top, and it remains as an outgrowth at the base of the lamina in just the same way as does the ligule in a grass after the bud has grown through it. It contains many conducting bundles.

In grass-spikelets, where through the formation of the ligule the *awn*, which corresponds to a lamina, is often apparently dorsal, we cannot speak of a protection against the entrance of water; but the ligular outgrowth at the base of the awn, brings about a close overlapping of the glumes covering the spikelet, and this is intensified in Bromus and other cases where the sheathing portion of the glume is elongated right and left into an outgrowth which may be designated a stipule by those who find pleasure in giving names to things.

The ligule of grasses is not always as it is in Oryza, an organ which closes in the terminal bud. It may act elsewhere as a temporary protective organ. Fig. 252 shows a transverse section through a bud of Alopecurus pratensis. The ligule is found as usual at the point where the leaf-sheath passes into the leaf-lamina. As the leaf-lamina subsequently spreads out as a *flat* structure and the leaf-sheath remains as a hollow *cylinder*, there is formed at this point of union an open space. The free margins of the ligule overlap in front as the figure shows, cover the open space, and surround the next younger leaf at its base. This younger leaf gradually pushes itself by intercalary growth out of the ligule, and its tissues have time *gradually* to change in response to the claims of the outer world. In other words, I consider the ligule here as an organ which is also able to give a certain amount of cover to the bud, during the elongation of the next youngest leaf through the ligule. In Hordeum, Lolium, and others, the protective function of the ligule is increased by the sickle-like outgrowth on both sides of the base of the lamina.

According to my view, the ligule in grasses only performs its function at a somewhat late period, whether it serves as a 'bud-cap' or in some other way aids in the protection of the bud. The time of its origin corresponds to this, for it is only formed at the limit of the leaf-sheath and the leaf-lamina as an outgrowth on the upper side of the leaf when the sheath has been already differentiated, whilst axillary stipules, whose function is performed much earlier, are laid down at the leaf-base near its insertion. It would, however, be a mistake to consider, as was formerly done[1], that the ligule of the grasses was derived from an axillary stipule, which is *concrescent* by its outer side with the leaf-sheath. There is no concrescence here, but only a later inception in correspondence with the later claims made upon the organ, and this conforms with what we have seen in the axillary stipule of Caltha and elsewhere. The relatively short time during which the ligule has to perform its function, explains also its usually delicate construction, about which, however, we cannot say much here. Whether besides this one function in relation to the bud the ligule has some other function *after* unfolding, I cannot say. It must suffice that I have shown the conjecture hitherto accepted regarding the function of the ligule to be certainly incorrect in the case of Oryza, and in the case of other grasses, at least to be not proved, and this without reference to the consideration that it may be more 'harmful' if the water-drops remain lying upon the base of the lamina, rather than at the bottom of the sheath—a position indeed, in most grasses, that could be reached by them only in a very limited amount.

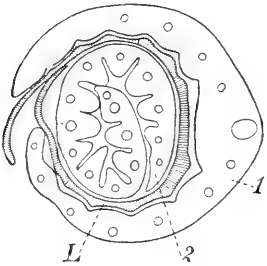

FIG. 252. Alopecurus pratensis. 1, leaf in transverse section above the insertion of the ligule, *L*, which is shaded; 2, an enclosed second leaf. Slightly magnified.

THE LIGULE OF PALMS. Ligular formations are formed also in the palms. The leaf of Chamaerops[2], and of Rhaphis, is in the juvenile

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[1] See A. de St-Hilaire, Leçons de botanique, comprenant principalement la morphologie végétale, Paris, 1840, p. 193, and other later writers.

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der

condition covered by an envelope composed of many layers of cells. This envelope (Fig. 253) proceeds from a scale which is formed at the limit between the leaf-stalk and the leaf-lamina, and grows up over the *anterior* side of the leaf, and from two scales, or it may be one which is bulged in the middle, which develop out of the *posterior* side of the leaf-primordium. In the matured leaf, this structure appears as a brown membrane, but in the young condition it forms a very effective protection to the bud. In accordance with this function, it develops somewhat early, and the ligule serves at first as a protection to the leaf-surface which it covers, but later it is bent forward and forms with the leaf-sheath, which is now developed, an almost closed cylinder, in which the next younger leaf is found. These ligular formations are undoubtedly *new formations* upon the leaf-surface, and serve as protections to the bud. At the same time, it is clear that in a case like that of Chamaerops, where these outgrowths are formed upon the anterior *and* upon the posterior side, they cannot be reckoned as similar to the lateral stipules of other plants. There is as little ground also for such an opinion in the case of the ligule of grasses.

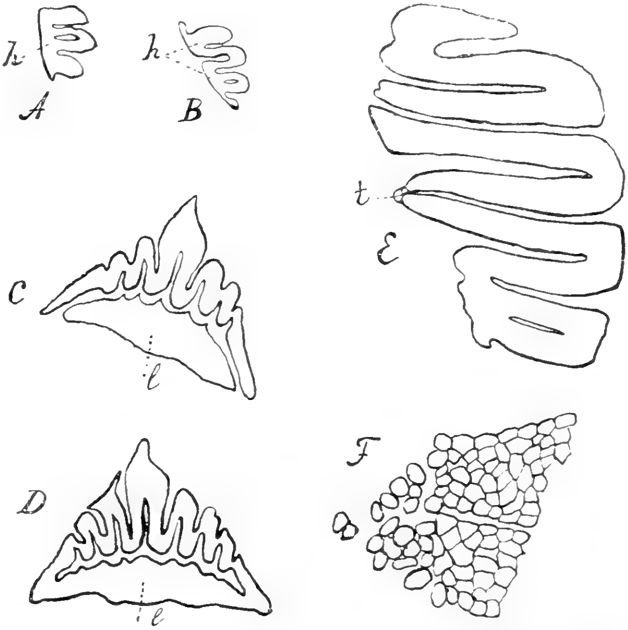

FIG. 253. Chamaerops humilis. Development of leaf in a series of transverse sections. *A*, upper part of the young leaf; *h*, membrane. *B*, the same lower down. The middle apical fold no longer covered by the membrane *h*. *C*, middle part of leaf-lamina; *l*, ligule. *D*, basal part of leaf-lamina, the ligule, *l*, runs into the lamina. *E*, leaf-lamina of older leaf; *t*, separation cells. *F*, cells of upper angles in mucilaginous degeneration bringing about the separation. After Deinega.

6. STIPELS.

The ligular formations of these palms lead us on to the stipels of some Dicotyledones.

Under the term *stipel* formal morphology has brought together

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Botanik, iii (1884), p. 221. Deinega, Beiträge zur Kenntniss der Entwicklungsgeschichte des Blattes und der Anlage der Gefässbündel, in Flora, lxxxv (1898), p. 488. Deinega gives the literature.

structures of very different origin[1]. On the one hand we have independent outgrowths, which, as will now be pointed out, may serve as protections to the bud, on the other hand we have reduced pinnules.

The best known example of independent outgrowths is seen in a number of (although not all) species of Thalictrum. In Thalictrum the leaf is composed of ternately branched leaflets, and the stipels arise in pairs, one upon the dorsal side, and one upon the ventral side of the leaf, at the point where the lateral leaflets of the first order proceed from the rhachis (Fig. 254). As the leaflets stand nearly opposite one another, there are four stipels at the points of branching, and not infrequently they unite with one another. These stipels cover the leaf-parts in the bud, as is shown in Fig. 255, and this is their meaning; they have nothing to do with the retention of drops of water. What value could a pair of rain-drops be to a large leaf of Thalictrum?

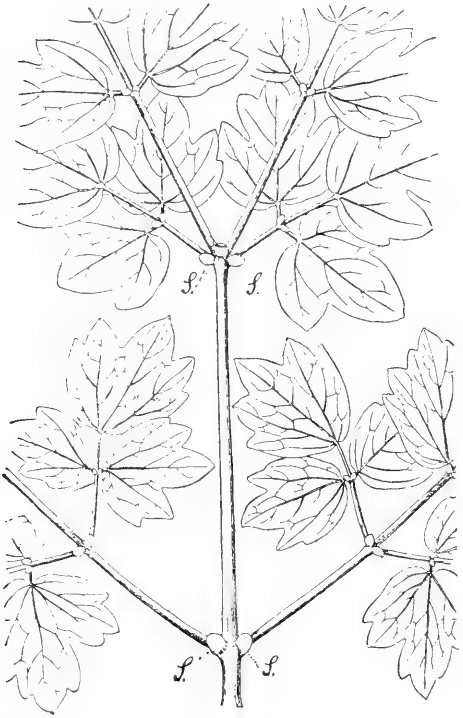

FIG. 254. Thalictrum aquilegiaefolium. Portion of a foliage-leaf. *S*, *S*, the stipels which are also visible upon the stalk of the leaflets of higher order. Reduced.

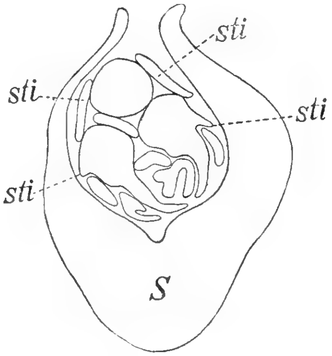

FIG. 255. Thalictrum aquilegiaefolium. *S*, young leaf-sheath in transverse section, showing an enclosed young leaf with stipels, *sti*.

The stipels which occur in species of Phaseolus, Robinia, Desmodium, and other Leguminosae, are found at the base of the leaflets, and are rudimentary pinnules. They appear usually in the form of small teeth, but occasionally they are developed as leaves upon sucker-shoots, for example in Robinia. That we have here to do with reduced organs, is not very probable, nevertheless, not infrequently we have arrested structures in leaves

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 233.

of other Leguminosae to which stipels are not assigned. For example, in Acacia lophantha, I find that the lowermost pair of pinnules standing close to the pulvinus, are either entirely aborted or appear in the form of one or two small pointlets. It is open to question whether these reduced structures in Leguminosae ever discharge a function. They arise at a relatively late period, as is frequently the case with reduced organs.

7. TRANSFORMED STIPULES.

The chief function of the stipules is the protection of the bud, and it has been shown that in this work organs which secrete mucilage may take a share, so that the stipules may be considered also as organs of secretion.

Honey-glands also are found upon the stipules in many plants, for example in species of Vicia, and in some cases, as in Sambucus nigra, the whole stipule according to the common interpretation is devoted to the formation of glands and appears only in its original form upon luxuriant shoots. The converse is, however, also possible, as the case of Viburnum Opulus shows[1], for there the stipules have developed out of glands of the leaf-margin. Only by a careful comparison of all the relationships concerned, can we make a distinction.

Račiborski[2] found one of the two stipules in Pterospermum javanicum, transformed into a small cup standing upon the under side of the twig with its inner surface covered by pearl-glands. These were eagerly sought after by ants which removed them.

The stipules are transformed into thorns in Robinia Pseudacacia, the succulent species of Euphorbia, Paliurus australis, and others.

SUMMARY.

Comparison of the different formations of stipules, from the two standpoints of how they arise and of what is the relationship in them between configuration and function, shows many gaps in our knowledge. Nevertheless it is clear that we have to do with structures which serve as protection to the bud, a function otherwise accomplished by the broadening out of the leaf-base, by the sinking of the bud in the tissue of the shoot, and in other ways. We see that in correspondence with this function there appears frequently to right and left of the leaf-base an outgrowth, but other parts of the leaf also can produce analogous protecting organs, and therefore formal morphology, which everywhere assumes two *free* stipules as a starting-point, has arrived very often at untenable constructions.

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[1] See p. 362.

[2] Račiborski, Über myrmecophile Pflanzen, in Flora, lxxxvii (1900), p. 40.

VII

TRANSFORMED LEAVES

By transformed leaves we mean leaves which have taken on a function different from that of ordinary foliage-leaves, and have therefore experienced a more or less far-reaching change in conformation. There is of course no limit between normal foliage-leaves and transformed leaves as the transformations appear in different degrees and have set in at very different stages of the development of the leaf. The earlier the transformation sets in the greater is the change. The treatment of the subject here is not consistent; sometimes it is approached from the formal side, that is to say that of positions, sometimes from that of function. I have, however, selected the examples as far as possible to give illustrations from different directions of the manifold relationships between form and function. This seems to me to be more instructive than would be the treatment from a single point of view. We limit ourselves just now entirely to the vegetative region. Sporophylls will be discussed when the flowers are spoken of.

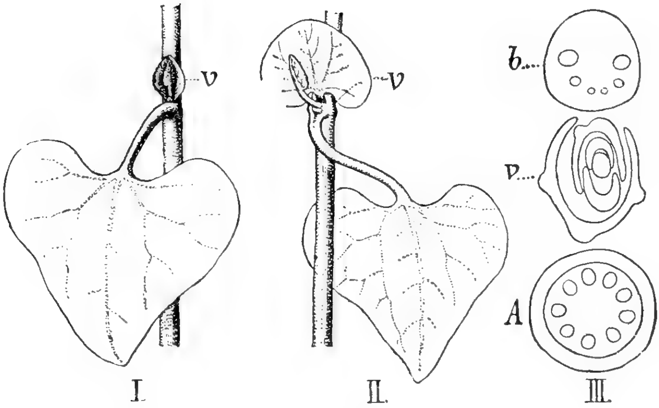

FIG. 256. Aristolochia elegans. I and II, portions of shoot with leaves and axillary shoots; *v*, prophyll which has reached a considerable size. III, shoot in transverse section: *A*, stem of mother-axis; *v*, prophyll of lateral axillary bud; *b*, bract.

1. PROPHYLLS.

Prophylls are characterized first of all by their position. We find them where they occur in the Dicotyledones usually in pairs at the base of the lateral shoots. In Monocotyledones there is commonly only one which is placed upon the side of the daughter-shoot next the mother-axis. There is no doubt, however, in many Monocotyledones that the prophyll is formed by the concrescence of two leaves[1], whilst in others the prophyll is 'reckoned' to be only a single leaf, as the appearance of one axillary shoot opposite its median indicates. In relation to their position prophylls, except in cases where they are adapted to special functions, are usually small and simple, so that frequently, even in recent times[2], they have been confounded with stipules, from which, however, they are distinguished at once by their origin. Their function, is, however, like that of stipules, the protection to the bud.

Aristolochia elegans. Aristolochia elegans (Fig. 256) gives us a simple case. *One* prophyll only is present here, and it at first surrounds the bud of the axillary shoot, and is distinguished from the later leaves by its small size, the less intense green colour of its lamina, and the almost complete suppression of its stalk—an interesting example of a feature which has already been mentioned, and will be illustrated again[3] as appearing in many hypsophylls, namely, that the stalk is suppressed in leaves whose function is specially that of protecting a bud. Superficial examination here might readily lead to the confusion of this prophyll with an axillary stipule of the subtending leaf[4]. Where there are two prophylls their position filling up the gap between the mother-axis and the stalk of the subtending leaf is particularly favourable for the protection of the young bud in its first stages of development.

Winter-buds. In overwintering buds the prophylls are usually indistinguishable from the other bud-scales. Sometimes the whole 'bud-covering' is furnished by the prophylls alone, as in species of Salix, where they are 'concrescent' into a thick scale. In other plants they are distinguished by their early development, which precedes that of the rest of the axillary bud. This is seen in Solanum tuberosum, where the prophylls are asymmetric and their posterior half is scarcely developed, and consequently they are bent in the direction towards the axis of the chief shoot.

Tilia. Of prophylls which are adapted to special functions the wing-leaf of the inflorescence of Tilia may be mentioned. It first of all acts as a protective covering to the downwardly bent inflorescence during the unfolding of this, and thereafter when full grown forms a kind of parachute, although not a very complete one to the fruits. It has moreover, during the ripening of the fruit, a physiological significance which will be described when the formation of the fruit is dealt with.

Cyperus. The prophylls of some species of Cyperus play a part which has been until now overlooked. They act as expanding bodies which force

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[1] See Goebel, Morphologische und biologische Studien : III. Über den Bau der Ährchen und Blüten einiger javanischer Cyperaceen, in Annales du Jardin botanique de Buitenzorg, vii (1888), p. 120; id., Ein Beitrag zur Morphologie der Gräser, in Flora, lxxxi (Ergänzungsband zum Jahrgang 1895), p. 28.

[2] By Lubbock, On Buds and Stipules, London, 1899.

[3] See p. 392.

[4] In species of Aristolochia in which the axillary bud is protected by the base of the subtending leaf, the formation of the prophyll is suppressed.

the leaves after their unfolding to stand away horizontally from the axis. This is most clearly seen in shoots of Cyperus alternifolius, which do not attain to the formation of flower (Fig. 299). In the axil of the foliage-leaves fleshy bodies pointed at the top are visible, and these have brought the leaf into its horizontal position. In the formation of these swollen bodies the fleshy prophyll of the axillary shoot has taken almost the whole part (see Fig. 299, *III*), at the same time the base of the foliage-leaf is swollen somewhat and becomes fleshy at both sides, but this is not clearly shown in the figure.

Cucurbitaceae. In the Cucurbitaceae the prophylls are transformed into tendrils, and these will be described when the tendrils are spoken of.

2. KATAPHYLLS.

The expression kataphyll, as first used by C. F. Schimper, referred to the formation of leaves on hypogeous shoots. On such shoots the leaves, where they cannot function as assimilation-organs, are more simply constructed than they are on epigeous parts, and appear mostly in the form of simple scales, whose function it is to protect the vegetative point. In many plants they are used for the storing up of reserve-material, and of this something will be said later[1]. To these leaf-formations, both in their construction and function, all those epigeous parts which have been called bud-scales (tegmenta) conform, and so closely that they have received the same name, which is not altogether wrong, inasmuch as these leaf-formations upon an upright growing shoot stand upon the 'lower' region of the shoot and are followed by the foliage-leaves.

That the kataphylls arise from a transformation of the primordia of foliage-leaves can be certainly proved[2] by the history of development, by transition-forms, and by experiment, and therefore the formation of these kataphylls has been made use of in this book as a simple example of the transformation of the primordium of an organ[3]. This transformation may take place in three ways :—

(A) The primordium as a whole becomes a kataphyll, undergoing more or less far-reaching changes.

(B) The lamina is arrested and the stipules form kataphylls.

(C) The leaf-base develops into the kataphyll, the primordium of the leaf-lamina is arrested, and the leaf-stalk is not developed.

A. KATAPHYLLS FORMED BY THE WHOLE LEAF-PRIMORDIUM. A very instructive example of this is furnished by Talisia princeps, Oliv. (Fig. 257), because in it the kataphylls are but little different from the

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[1] See p. 398.

[2] Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880). See also Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 243.

[3] See Part I, p. 6.

foliage-leaves. The foliage-leaves are pinnate, and we find the same segmentation also in the kataphylls, but these, before they reach the size of ordinary foliage-leaves and before they develop in breadth, dry up, and so form an envelope to the bud. The protection afforded by this envelope is not very great. In plants whose buds are more liable to the danger of drying and freezing we find that the protection to the bud is correspondingly increased, as, for example, in Syringa and some other Oleaceae, such as Ligustrum and Forsythia; one might also reckon here Salix, whose bud-cover is formed by the concrescence of two prophylls.

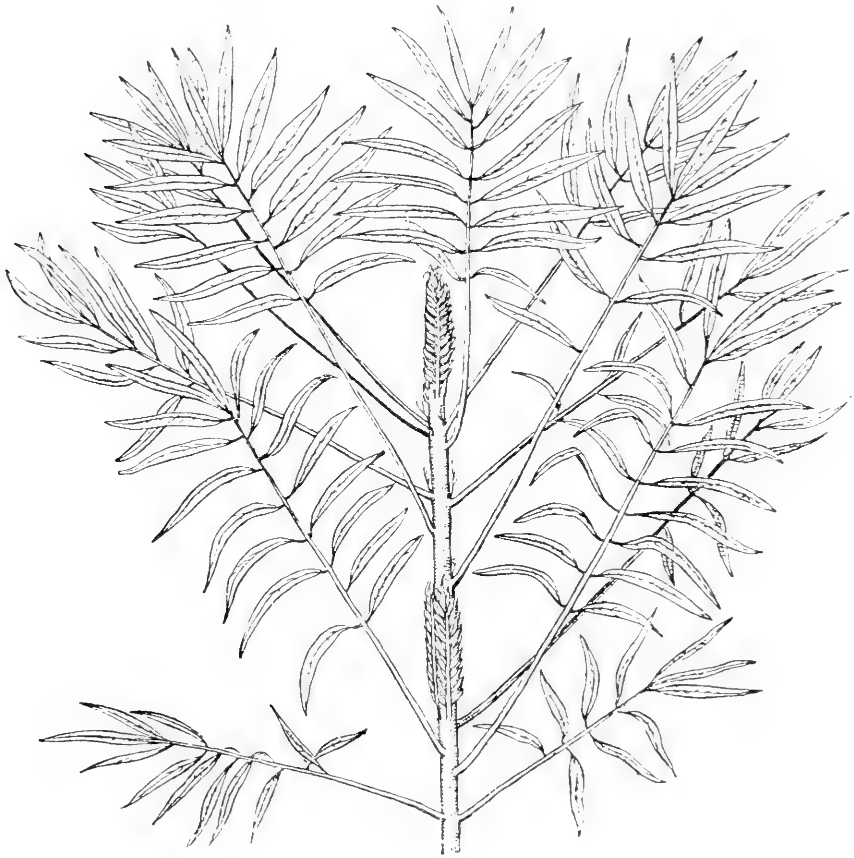

FIG. 257. Talisia princeps, Oliv. End of a shoot with foliage-leaves and erect pinnate kataphylls. Reduced.

B. KATAPHYLLS FORMED BY THE STIPULES. Here also we find transitions to the ordinary condition. In Alnus the protection of the bud is commonly[1] furnished by three scales. These are stipules, two belonging

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[1] Occasionally on the outside a still folded foliage-leaf is formed.

to the outermost leaf of the bud and one to the second. The primordia of the foliage-leaves to which these stipules belong are well developed and unfold later. In Magnolia the different species behave differently. The buds are always protected by stipules. In Magnolia fuscata the leaf itself to which the stipules belong is arrested usually, but sometimes it is developed; in other species, such as Magnolia Campbelli[1] and M. Umbrella, the protective stipules belong to a leaf which discharges its function. In other woody plants, especially in Quercus and Fagus, the buds are protected by pairs of stipules, according to the statements of the descriptive botanists, but the laminar primordia of these are not developed in the outer ones. I have shown[2] that the history of development is opposed to this, and that as a fact the laminar primordium stands as a small unstalked pointlet between the two stipules which belong to it, and only the first two leaves of the bud, the prophylls, are simple structures. Beijerinck[3] subsequently confirmed this, whilst E. Schmidt[4] could not find the rudiment of the leaf probably because it had fallen away at the time of his examination. I have recently by a series of microtome-sections confirmed my old statement, and we see therefore that in these genera there is an arrest of the primordium of the foliage-leaf and a somewhat divergent formation of the stipules. Analogous processes are found also in herbaceous plants, for example in the hypogeous shoots of Humulus Lupulus.

C. KATAPHYLLS FORMED BY THE LEAF-BASE. The kataphylls of the third category show but little fundamental divergence from those last described, and I repeat here the account of them I have given elsewhere, in which the evidence in support of their relation to foliage-leaves is discussed[5]:—

EVIDENCE FROM DEVELOPMENT. If an expanding bud of **Acer Pseudoplatanus** be examined in the spring, it will be found that the lowest kataphylls are small bodies with a broad base narrowing upwards and bearing at the tip a small black pointlet (Fig. 258, 7 *A*, *L*), which appears upon investigation to be an arrested leaf-lamina (Fig. 258, 7 *B*, *L*). These leathery scales are traversed by feebly developed vascular bundles. The bud-scales immediately above them are larger, sappy, and sometimes have at their apex a small leaf-lamina. If we compare the bud-scales

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[1] Hooker, J. D., and Thomson, T., Flora Indica, London, 1855, p. 77.

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 244.

[3] Beijerinck, Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen, in Natuurkundige Verhandelingen der Koninklijke Akademie van Wetenschappen in Amsterdam, xxii (1883), p. 17.

[4] E. Schmidt, Beitrag zur Kenntniss der Hochblätter, as Wissenschaftliche Beilage zum Programm der Friedrichs-Werder'schen Oberrealschule in Berlin, Ostern 1889. Also Lubbock, On Buds and Stipules, London, 1899, p. 138, says of the stipules 'there are sometimes more than forty, or twenty pairs, before those containing the first leaf.' In these pairs the laminar primordium is early arrested.

[5] Goebel, op. cit., p. 246.

shown in Fig. 258, 7 with a young primordium of a foliage-leaf immediately before the formation of the stalk, the resemblance between the two structures is evident. The bud-scale is evidently the leaf-base which is more strongly developed than it is in the foliage-leaf, whilst the leaf-lamina is arrested; it has, however, produced two lateral segments (Fig. 258, 7 *B*) whose development in the foliage-leaf is in basipetal succession. If the primordium of the foliage-leaf should develop further into a foliage-leaf, the laying down of the lateral members of the leaf-lamina proceeds further, and between the lamina and the leaf-base there is also intercalated a leaf-stalk by elongation of the upper part of the leaf-base. The transition from the kataphylls or bud-scales to the foliage-leaves is sudden; the first foliage-leaf follows directly the last large kataphyll.

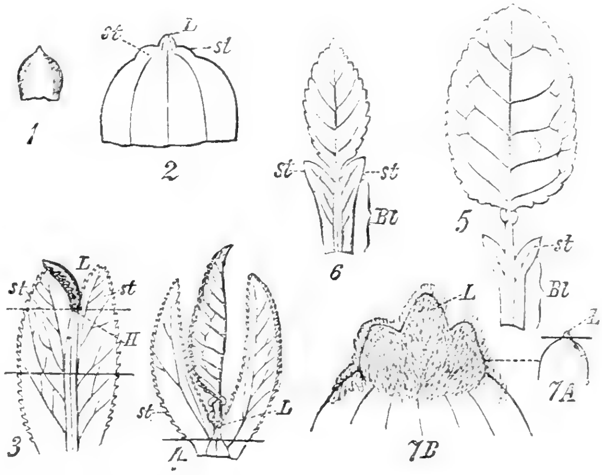

FIG. 258. 1–6, Prunus Padus. 1 and 2, bud-scales formed of the broadened leaf-base; *L*, arrested primordium of the lamina; *st*, primordia of the stipules seated on the leaf-base. 3, one of the uppermost scales of an unfolding bud, the three vascular bundles traversing the leaf-base have branched; *st*, stipules; *L*, lamina; *H*, gland at base of lamina. The central portion between the cross-strokes becomes the petiole, the portion below the lower stroke is that represented in the bud-scale. 4, young leaf; *st*, stipules; *L*, lamina. The cross-stroke marks the limit of the leaf-sheath represented in the bud-scale. 5 and 6, middle stages between bud-scale and foliage-leaf; *Bl*, leaf-base; *st*, stipules. See the text for further explanation. 7 *A* and 7 *B*, Acer Pseudoplatanus. Bud-scales; *L*, lamina. The arrested lamina in 7 *A* is shown natural size.

Prunus Padus. Prunus Padus possesses stipules like other members of the cycle of affinity of the Rosaceae, but these are not, as has been erroneously supposed, constructed as bud-scales in the bud. The bud-scales are here formed out of the leaf-base. It is interesting to notice the gradual transition from the outer small bud-scales in the lateral buds to the inner larger ones. The middle line of the scale is traversed by a strand of elongated cells in which there are neither vasa nor tracheids. These are only found, small and few in number, in the scales higher up, forming three strands, a middle and two lateral ones (Fig. 258, 2, 3). The scales end as do those of Acer in a pointlet, *L*, which is the arrested primordium of the lamina. In scales such as those shown in Fig. 258, 2 there is observed to right and left of the pointlet a projection, and this is the first indication of the stipules. These are absent from the lowest scale-leaves because they proceeded from the transformation of the primordia of foliage-leaves whose leaf-base had not yet laid down stipules. The later formed primordia standing higher up undergo the transformation only at a later stage, when the stipules are already laid down and more or less developed. Fig. 258, 3 shows a bud-scale in which this is the case. The leaf-base which forms the bud-scale is here well developed, and branches proceed into the widened leaf-base from the three vascular bundles traversing it. These branches are not found in the slightly developed leaf-base of the foliage-leaf, a fact which is of fundamental importance as it shows that the appearance of vascular bundles is always of secondary importance in morphological questions. Where an organ is developed so as to have a somewhat extensive outline vascular bundles appear in it in correspondence therewith. It would be a mistake, yet it is often made, to endeavour to base a conclusion regarding the nature of an organ upon its vascular bundles. In Fig. 258, 4 a young foliage-leaf whose stalk is still short is shown for the sake of comparison with the bud-scale. Three vascular bundles are observed passing into the leaf-base from the stem and from each of the lateral ones a branch passes over into the stipules; the cross-stroke indicates the limit of the portion which is represented in the bud-scale.

Evidence from Transition-forms. In those woody plants which possess terminal buds the transition from the foliage-leaves to the kataphylls (bud-scales) is commonly a gradual one. In Aesculus Hippocastanum, for example, the lamina of the last leaf before the scaly bud is often reduced to one leaflet and the rudiments of two others. The same is the case in Juglans regia [1], and in species of Acer. In Prunus Padus also the laminar primordium is greater, the leaf-base smaller, in the first bud-scales than in those which follow. I mention these circumstances here because they appear in like manner in plants which have no bud-scales, such as species of Lycopodium, Juniperus, and Araucaria. Also in the broad-leaved trees which have been mentioned the leaves which are formed towards the end of the vegetative period are smaller, and resemble in this way the middle form between foliage leaves and bud-scales. We may assert that originally all plants possessed no bud-scales, but arrested or degraded foliage-leaves only appeared as the vigour of vegetation decreased, and that by a very simple process of growth the bud-scales took origin from these arrested forms. As a matter of fact we have seen a thoroughly illustrative case in Talisia princeps [2].

Evidence from Experiment. That the bud-scales have proceeded from the primordia of foliage-leaves is proved not only by a comparison of the history of development but also by experiment. It is possible to cause the primordia which in the normal course of development would develop into bud-scales to grow into foliage-leaves. This takes place if one causes a bud which has been laid down and which would normally shoot in a succeeding year, to develop in the same year as that in which it is formed, at the time when the bud-scales are still at the stage of inception. This may be done by removing the leaves of the apex from a young shoot. The lateral buds are then induced to shoot out and do not form scale-leaves but only foliage-leaves with complete well-developed lamina and leaf-stalk as well as a leaf-base which is exactly like that of the ordinary foliage-leaf [3].

Middle stages between foliage-leaves and kataphylls are not wanting. They are shown in Fig. 258, 5 and 6. Fig. 258, 6 shows a broad leaf-base with

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[1] See for further details Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880), p. 775.

[2] See p. 385, Fig. 257.

[3] See Goebel, op. cit., for details.

small stipules, *st*, no leaf-stalk, and a normal although very small leaf-lamina. Fig. 258, 5 approaches much more a normal foliage-leaf, from which it differs mainly by the great development of the leaf-base. These two leaves would in undisturbed vegetation have formed small bud-scales as in Fig. 258, 1. They were caused to develop into foliage-leaves at a time when the primordium of the foliage-leaf had only begun to develop and to form itself into a bud-scale by widening of its leaf-base; a relationship which if once started cannot be reversed but through the increased addition of food-material which the shooting-out of the bud brings about, must go on still increasing. The same is the case in the leaf shown in Fig. 258, 6, where the leaf-base resembles entirely the bud-scale in Fig. 258, 3, although this was one of the *uppermost* bud-scales of a normally elongated shoot, whilst the leaf in Fig. 258, 6 was the *lowermost* leaf of a bud which had been artificially forced into elongation. The causes of the configuration must indeed be considered to be the same in both cases. The first bud-scales are laid down very early, about the beginning of April, at a time when the reserve-material is chiefly required for processes of growth which find their expression in the shooting-out of the bud completely laid down in the preceding year. The bud-scales which arise later and the foliage-leaves which they invest are laid down at a time when the unfolded foliage-leaves of the shoot to which they belong are still doing assimilation-work. Of course this circumstance is only *one* fact of importance which has to be considered in the investigation of the configuration-relationships in question. It is no explanation of them.

The features which have been described in the case of Prunus Padus are observable also in other plants, for example in Aesculus and Acer, and also in plants whose bud-scales are formed from the stipules of arrested foliage-leaves, such as Quercus, Fagus, and others.

Monocotyledones. In Monocotyledones also we find frequently kataphylls and transitions from them to foliage-leaves. On such intermediate forms we observe the lamina reduced and the leaf-base developed—the leaf-base being very strong on the chief shoots of the Bambuseae which send up giant epigeous turios upon which kataphylls alone are produced at first. In many cases the lamina is altogether wanting. The kataphyll has developed into a sheath before any differentiation of the lamina and the leaf-base had taken place. This subject will be referred to again, when speaking of the hypsophylls, which arise in the same way as do the kataphylls, indeed the only distinction between the two is their place in the plant's construction.

3. HYPSOPHYLLS.

We owe the term hypsophyll to Schimper. Originally[1] he distinguished, besides the foliage-leaves of the plant, the forms of sheathing-leaves in which

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[1] Schimper, C. F., Description du Symphytum Zeyheri, et de deux espèces voisines précédemment connues, in Bull. Sci. Nat. Férussac, xxi (1830), p. 442; id., in Verhandlungen der schweizerischen naturforschenden Gesellschaft zu Solothurn, 1836, p. 113.

there is no leaf-lamina, and which are found upon the lower regions of the shoots of a plant and upon the upper regions. The latter leaves he subsequently[1] called the *hypsophylls*; the former are the *kataphylls*. Schimper's terms were established mainly through the influence of A. Braun, who gives the following account of the hypsophylls[2]. 'To the formation of the hypsophylls belong the leaves of the involucre and the common calyx of the inflorescence, the bracts, the bracteoles or prophylls, the glumes and paleae which accompany the flowers. They are like kataphylls in that the stalk and lamina as well as the green colour are almost or entirely absent. They are distinguished from kataphylls chiefly by the narrowness of their base, their more delicate structure, their rapid formation and equally rapid decay.'

This explanation does not fit a very large number of the structures which belong to this category. It is based like that of the kataphylls upon the conception of construction founded by the idealistic morphology and not upon the real processes of development, and it leaves out of consideration entirely the relationships of the hypsophylls to the foliage-leaves. I have shown[3] that the hypsophylls, like the kataphylls, are developed out of the primordia of foliage-leaves, and that they may come into existence *in different ways*, and of this some examples will be mentioned below.

It may be asked, is there any advantage in retaining Schimper's terminology? The leaves have only this in common, that they occur in the flower-region, whilst in respect of their function they have very different significance. Sometimes they are still assimilation-organs; usually they are protective organs for the flower-buds or inflorescence; not infrequently they act as a flag, or they may combine this with protection; sometimes their service is claimed for the distribution of the seeds or of the fruits, as in Tilia; whilst again they may be greatly reduced or even aborted. It has always appeared to me of use to have a common name for the leaves which occur in the flower-region, and which do not belong to the flower itself, although the only common link between them may be that of their position. It is also probable that between the formation of the flower and the configuration of the hypsophylls, which deviates from the typical form of the foliage-leaf, there exists a correlative connexion, because often, although not

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[1] See also Wydler, Morphologische Mittheilungen, in Botanische Zeitung, ii (1844), p. 626.

[2] A. Braun, On the Phenomenon of Rejuvenescence in Nature. English Translation by A. Henfrey, published by the Ray Society, 1853, p. 63.

[3] Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880); id., Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 250. The objections which E. Schmidt, Beitrag zur Kenntniss der Hochblätter, as Wissenschaftliche Beilage zum Programm der Friedrichs-Werder'schen Oberrealschule in Berlin, Ostern 1889, has raised against single points in my explanation are only of a formal nature. Schmidt starts from the assumption that I have declared the differentiation of the primordial leaf into leaf-base and upper leaf to be a *universal* phenomenon. This is an error. I have shown that in *unsegmented* leaves also the development is simplified. See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 215.

always, if the inflorescence grows further vegetatively the ordinary leaf-form again appears. The configuration of the hypsophylls therefore has a causal connexion with the place of their occurrence, and the name, upon this ground, should be maintained. The causal relationships are here, as in most other cases, at the present time obscure.

There are, however, two questions which we can answer:—

How do the hypsophylls arise? Does the law hold for them that the course of development of all leaves of a plant is originally the same, but that at different stages of development different paths may be assumed?

In what relation do configuration and function stand in them?

A. THE DEVELOPMENT OF HYPSOPHYLLS.

We may first of all note that on the one hand graded transitions are found in many plants between foliage-leaves and hypsophylls, and also it is impossible to draw any sharp limit between foliage-leaves and hypsophylls in many cases, although the hypsophylls are very different from the foliage-leaves. On the other hand, the difference between foliage-leaves and hypsophylls may sometimes be very great, whilst in other cases it sinks to nothing. This is the more the case the less segmented the typical leaves are. In Epilobium parvifolium and in Edraianthus Pumilio, a campanulaceous plant with linear leaves, the hypsophylls differ little from the foliage-leaves; they are only smaller, and those which stand further up upon the stem and have to protect the flowers in their bud-state have a somewhat broader leaf-base. In many Monocotyledones also, for example Cypripedium Calceolus, the bracts of the flowers are only distinguished from the foliage-leaves by being shorter and smaller. But even in simple leaf-forms amongst the hypsophylls there may be far-reaching transformation. Thus in Rhinanthus major the foliage-leaves show no evident distinction between leaf-base and lamina externally, nevertheless such differences exist in the course of the vascular bundles. The leaf has three vascular bundles, and the middle one runs as a strong mid-vein from which the lateral nerves pass out into the depressions between the leaf-teeth (Fig. 259, *I*). The two lateral bundles extend only into the lower third of the foliage-leaf, bend then into one of the marginal depressions (Fig. 259, *I*, *a*), and send off twigs which pass out into the other marginal depressions. If we designate the upper portion of the leaf, that, namely, which lies above *a* in Fig. 259, as the lamina, although it is only distinguished from the lower part by this distribution of the vascular bundles, and if we call the lower portion the leaf-sheath, then we should find that amongst the hypsophylls the lamina becomes shortened and the sheath becomes wider (Fig. 259, *II* and *III*), evidently because it is required for the better protection of the flower-bud. In Fig. 259, *IV* and *V*, the lamina is reduced to a very small portion, barely one-fifth or one-sixth of the whole length of the leaf, the sheath which serves specially as a flag-apparatus has a white colour, and upon it the lamina appears at last as only a small green tip.

On plants with stalked and branched, that is to say, segmented leaves, we observe the following differences usually in the formation of the hypsophylls as compared with the foliage-leaves:

(*a*) *Diminution and final disappearance of the leaf-stalks.* Teleologically this is easily understandable because:—

1. The hypsophylls are developed in the upper region of the shoot above all the other leaves.

2. Owing to the diminution of the leaf-surface which will be presently described, the necessity of a leaf-stalk either as a mechanical support or for the placing of the leaf in a favourable lie in relation to light is less than in the typical foliage-leaf.

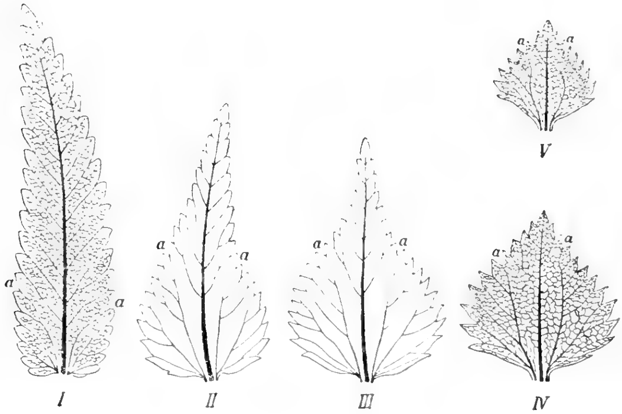

Fig. 259. Rhinanthus major. Transition, in the sequence *I* to *V*, from foliage-leaf to hypsophyll. *a* indicates the upper limit of the leaf-base.

3. The suppression of the leaf-stalk enables the leaf-lamina more readily to protect the axillary bud.

(*b*) *Diminution of the leaf-surface along with a simplification of its segmentation.* The work of assimilation is but slightly or not at all performed by hypsophylls.

(*c*) *The widening and often elongation of the leaf-base.* This takes place because its protective function is the chief one.

We find in the development of hypsophylls the same variety of processes as in the formation of the kataphylls:—

A. Hypsophylls formed by the whole Leaf-primordium. The hypsophylls are produced by transformation of the leaf-lamina or of the whole primordium of the leaf in leaves where there is no marked difference between lamina and sheath. We find illustrations of this in cases where the hypsophylls are but little different from the foliage-leaves. In Caltha palustris, for example, the hypsophylls have usually a shorter stalk than have the foliage-leaves, and in the uppermost hypsophylls the stalk may be wanting altogether. Apart from the fact that the lamina is smaller than is that of foliage-leaves, such hypsophylls resemble foliage-leaves in every respect. From a simplification of this kind there are all transitions to the most characteristic hypsophylls. In Epilobium angustifolium, for example, the lowermost flowers of the inflorescence stand in the axils of ordinary foliage-leaves, and the higher one goes the smaller become the bract-leaves, their breadth sinking to about half a millimeter, and they consist then only of a midrib and a narrow green wing upon each side of it. Circaea intermedia, a member of the same family, has all its bracts in the form of delicate scales which have no vascular bundle, and they form a transition to the complete arrest of the hypsophylls which will be mentioned below.

In the origin of the hypsophylls we have to deal with an *arrest* in the development of the primordium of the foliage-leaf; the extent of this varies, reaching sometimes complete suppression, and it always begins with a simplification of the configuration of the leaf.

In some plants, for example Ranunculus acris, Saxifraga rotundifolia, Heuchera Menziesii, and others, there is a peculiarity, the biological significance of which appears to me to be still doubtful:—The hypsophylls, at least a portion of them, are relatively more divided than are the foliage-leaves, whilst commonly the converse occurs. The recognized features of the formation of hypsophylls are visible in these cases, namely, shortening or suppression of the leaf-stalk, diminution of the leaf-surface, and to this end deeper division of the leaf-surface, but the causes of this divergent configuration are unknown, although a functional as well as a developmental relationship appears to exist. So far as I know, the occurrence of such divided hypsophylls is limited to many-flowered inflorescences, which even in the bud-condition have a somewhat elongated conformation. The long lobes of the lower hypsophylls lie against the outside of the inflorescence, and thus form an envelope about it which resembles an envelope formed out of many narrow separate hypsophylls of which we have an illustration in the involucre of the Compositae. The formation of these lobes would be in harmony with the explanation of the hypsophylls as arrested states of the foliage-leaves if, in the development of the foliage-leaves, the formation of the lobes preceded the development of the lamina. We have already seen some cases of this kind. If, for example, the young leaf of Benincasa cerifera (Fig. 201, *I*) remained at this developmental stage, with elongation of the three upper leaf-lobes, and no further development of the lamina took place, a deeply 'divided' hypsophyll would be formed which apparently would deviate far from the foliage-leaf, but would be only, after all, a product of the arrest of this. Whether this is true of all cases of hypsophylls which are more deeply divided than are the foliage-leaves of the same plant requires further investigation. In Heuchera Menziesii the leaf-development conforms with the theoretical derivation above given. In its hypsophylls there are fewer lobes laid down than in the foliage-leaves, but these experience a greater enlargement, especially elongation.

B. Hypsophylls formed by the Stipules. Hypsophylls may consist of stipules whose leaf-lamina is arrested. We find these in the inflorescence of Humulus Lupulus for example. The leaves in the axil of which the catkins of female flowers arise, show from below upwards a gradual diminution of the lamina, until in the uppermost portion of the inflorescence this is arrested at so early a period that it apparently no longer exists. We may, however, cause its evolution artificially by removing, for example, the leaves from the shoot, and occasionally it may develop without such external interference because its primordium is always visible between the stipules. A corresponding case is only known to me in the inflorescence of Amicia Zygomeris where the stipules of the bract-leaves of the flowers are developed as protective organs whilst the lamina itself is arrested.

C. Hypsophylls formed by the Leaf-base or mainly so. Where this happens the segmentation of the leaf-primordium into leaf-base and upper leaf proceeds gradually, and finally the leaf-primordium without reaching the stage of expansion as a leaf-lamina becomes shèath-like. This process is found especially in plants with well-developed leaf-base. In Rhinanthus we have, as has been above shown, an analogous example in the case of leaves which are very slightly segmented. A few examples from plants with highly segmented leaves must now be cited :—

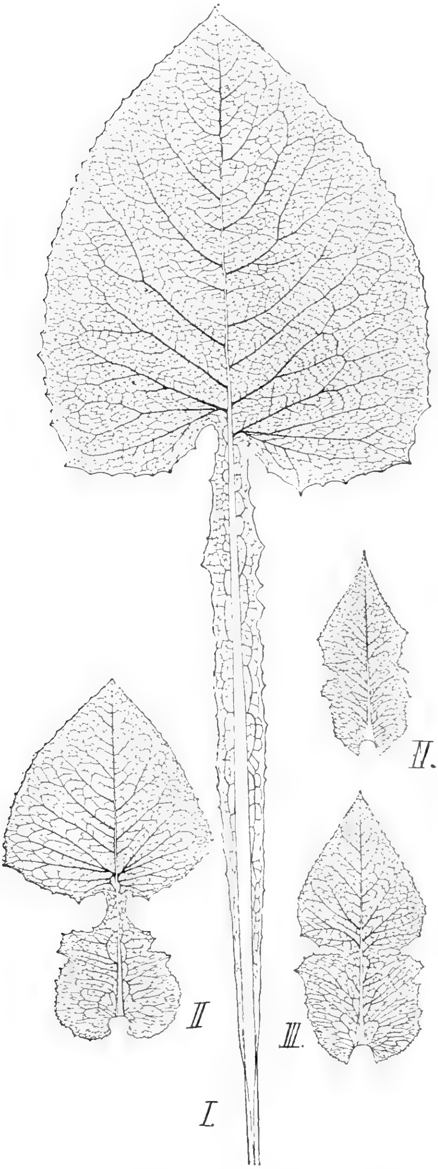

Fig. 260. Mulgedium macrophyllum. Transition, in the sequence *I* to *IV*, from foliage-leaf to hypsophyll. Reduced.

Mulgedium macrophyllum. Mulgedium macrophyllum, represented in Fig. 260, *I*, possesses at first a foliage-leaf whose lamina is plainly delimited from the leaf-stalk, and the latter is 'winged' in its upper part.

The leaf in Fig. 260, *II* is one from the lower region of the hypsophylls, and in it the leaf-stalk is scarcely indicated, but the leaf-base is enlarged evidently in correspondence with its function of protecting the inflorescence-bud which is thicker than an ordinary foliage-leaf-bud. The leaf in Fig. 260, *III* has the limit between leaf-lamina and leaf-base still marked by a deep constriction. No leaf-stalk is present. Fig. 260, *IV* shows a leaf in which the limit between lamina and leaf-base is scarcely at all shown, and in leaves standing higher up the distinction disappears altogether. This transformation is easily understandable when the history of the development of the leaf is followed. All these leaf-forms resemble one another in their primordial stage, and the hypsophylls arise by the arrest of the primordium of the foliage-leaf accompanied by an increase of its leaf-base at an earlier or later stage of its development.

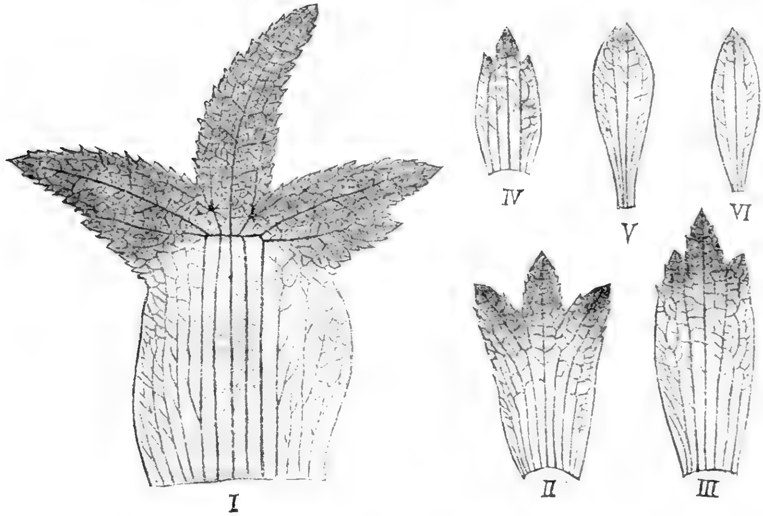

FIG. 261. Astrantia major. Hypsophylls of different degrees of configuration, showing a reduction series from *I* to *VI*. Chlorophyllous parts are shaded darker.

Astrantia major. Astrantia major shows similar features (Fig. 261). If we pass upwards from the region of the stalked foliage-leaves we observe that the leaf-stalk and the leaf-surface gradually become smaller. The leaf-stalk gradually vanishes and the leaf-lamina sits directly upon a widened leaf-base (Fig. 261, *I*). The sheathing leaf-base retains at first at the margin a whitish colour, and the differentiation of the lamina decreases step by step (Fig. 261, *II*, *III*). The white colour of the leaf-base becomes more conspicuous as we pass upwards, and the lamina can ultimately only be recognized as a dark green tip upon the top of the otherwise undifferentiated hypsophyll (Fig. 261, *IV*). The hypsophylls (Fig. 261, *VI*) which form the *involucre* have in contrast with the preceding ones a narrow base, and this is connected with their ring-like arrangement around the axis : here the protective function is taken over by numerous small leaves, whilst it is elsewhere performed by single relatively large leaves.

The processes in the history of development which led to the formation of hypsophylls can be readily understood from what we know of the development of kataphylls from foliage-leaves, and therefore I do not require here to set them forth in detail. We have to deal with an external *transformation* of the primordium of the foliage-leaf; it is often marked by transition-forms, and it may begin sometimes later and sometimes earlier, even before the appearance of any differentiation of the leaf-primordium, and then we obtain a sheath-like structure without any indication of a lamina. That we have really to deal with a structure homologous with the leaf-sheath is shown by its whole nature, especially often by the course of the vascular bundles, and by comparison with transition-forms. The course of the bundles in the hypsophylls of Dicotyledones recalls frequently that in the ordinary monocotylous leaves (see Fig. 261, *III*). That the whole as yet unsegmented leaf-primordium can be made use of in a construction to which otherwise only a part is devoted, need not surprise us when we assume Sach's hypothesis of 'material and form.' The difference between lamina and sheath then appears to depend upon definite material processes—upon the appearance of definite 'growth-enzymes,' or whatever one chooses to call the unknown material used in the formation of the organs. Let us name the material which is necessary for the formation of the lamina x, and that for the leaf-sheath (leaf-base) y, then in the primordium of the foliage-leaf $x+y$ must appear, and the same will happen in many hypsophylls, but in many only y will be present.

HYPSOPHYLLS IN MONOCOTYLEDONES. The hypsophylls in many Monocotyledones may be specially mentioned here, for they also show transition-forms. In Carludovica plicata the spadix is surrounded by a number of hypsophylls. In one case which was investigated the outermost of these had still an evident lamina, smaller indeed than that of the foliage-leaf, but it possessed a stalk, and this was shorter than that of the foliage-leaf. The following hypsophyll had no stalk but only the rudiment of a lamina, with the ptyxis characteristic of the genus. In the third the lamina was still more reduced, and finally the hypsophylls showed only a sheath without any laminar portion. The paleae and glumes of the grasses belong also here, and the awn which occurs in many of them has for long been considered rightly as a rudimentary lamina.

B. RELATIONSHIPS BETWEEN CONFIGURATION AND FUNCTION IN HYPSOPHYLLS.

It has been already shown several times that we can recognize, usually very easily, the relationships between the form and the function of the hypsophyll, because the leaf-base from which it is developed serves habitually as a protection to the bud, and thus directly points to the chief function of the hypsophyll.

The recognition of the relationships is no less easy in cases of the arrest of hypsophylls[1]. Let us in the first place confine our attention to the bracts. We may say of them that wherever these are arrested the flowers have some other method of protection, either by being placed close together or by special protective arrangements. We need only recall here the behaviour of most Cruciferae, many Umbelliferae and Compositae, in which the bracts of the flowers are arrested, because the whole inflorescence is protected otherwise in the bud-condition, either by special envelopes of hypsophylls, by the sheathing portion of the foliage-leaves, or in other ways.

Many arrested hypsophylls exhibit the peculiar phenomenon of division about which I have before spoken[2]. Some examples, however, may be mentioned :—

Lolium. The grass-spikelets are enveloped by two glumes. In Lolium these are developed upon the terminal free spikelet, but in the lateral spikelets, which lie with one side in a depression of the axis of inflorescence, the glume next this axis is absent, because it would be superfluous as a protective organ[3]. In Lolium temulentum, especially in the lower flowers of the inflorescence, it is frequently developed, seldom as an entire leaf but usually replaced by two small leaflets, which are separated from one another by a broad intervening space. These are connected with the undivided glume by transitional forms of glumes with a deep indentation. The like is found upon the axis of inflorescence of Typha.

Xeranthemum macrophyllum. Division of the hypsophylls is also seen in the Compositae. Thus in Xeranthemum macrophyllum[4] the hypsophylls of the involucre pass, as in other cases, quite gradually into the bracts of the flowers, the outer bracts are undivided, those further in show a tendency to divide into two, many being split almost to the middle, whilst others are split nearly to the base, so that two apparently completely independent leaves stand before each flower. Each one of these may again divide, and so instead of one bract there may be a number of small linear, frequently almost bristle-like, leaf-lobes.

We have here, as it appears to me, the beginning of a new formation. In the *position* of the hypsophylls in process of arrest appear bristles which subsequently act as substitutes for the pappus in the scattering of the fruit,

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[1] See Nauhaus, Die Verkümmerung der Hochblätter. Inaug. Dissertation, Göttingen, 1870.

[2] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 299.

[3] See Part I, p. 57.

[4] See Warming, Die Blüthe der Compositen, in Hanstein's Botanische Abhandlungen, iii, 2 (1876).

and these bristles, as in other Cynareae, such as Cirsium, Carduus, and Centaurea, cover the receptacle in great number and without transition to bracts. I put the process thus:—In hypsophylls in process of arrest there is uniform growth, and to a certain extent a 'discipline' amongst the cells no longer exists; therefore single parts grow out and these may appear very early, even on the shoot-axis itself single cell-groups may shoot out instead of the whole primordium of the hypsophyll. Where now instead of single parts of a hypsophyll we see 'bristle-scales,' a *qualitative* change has taken place which may have begun with a *transformation* of the single parts of the hypsophyll, but I see no ground even then, if the hypsophyll no longer exists, for keeping its ghost hovering above, or rather below, these bristle-scales; to assume that it still exists is an 'idea,' and this 'idea' is stuck somewhere in the axis and only allows the bristle-scales to appear. Such 'ideas,' however, are to be found in botanical literature even recent!

4. STORAGE-LEAVES.

The function of storing reserve-material can be undertaken along with the ordinary function of the foliage-leaves. We find this, for example, in the leaves of succulent plants which store water as reserve-material in their foliage-leaves. Other reserve-materials may be similarly stored. Androsace sarmentosa (Fig. 305) forms towards the end of the vegetative period leaf-rosettes of which the single leaves are thicker and shorter than the foliage-leaves of the active period of vegetation. Pinguicula caudata and others behave in like manner. They have green epigeous leaf-tubers. In the winter-buds of Utricularia and Myriophyllum processes which are fundamentally the same are to be observed. These leaves do little work as assimilating organs, and do not develop further in the shooting out of the bud, but give up their reserve-material into the new shoot.

The two functions of assimilation and storage may also be taken on at different times by a leaf. Dicentra Cucullaria[1] forms tubers on its rhizome. These are the bases of leaves which are swollen as reservoirs of reserve-food, and transformation takes place partly *at the base of ordinary foliage-leaves*, partly at the base of leaves whose lamina is arrested and which we can consider as kataphylls acting as reservoirs of reserve-food. Here we have a case showing that change of function and also change of form may take place sometimes at a relatively late period of development, sometimes at an early period[2]. Similar cases are found amongst Monocotyledones. For example, the outer scale-leaves of a bulb of Lilium candidum are the basal

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[1] See Holm, Notes upon Uvularia, Oakeria, Diclytra, and Krigia, in Bulletin of the Torrey Botanical Club, xviii (1891), p. 5.

[2] See also Part I, p. 9, and the case of Oxalis rusciformis described on p. 354.

portions of *foliage-leaves* whose lamina has fallen off, the inner ones are *kataphylls* such as are found elsewhere commonly in scaly bulbs, and they are leaf-structures in which the transformation has taken place at a much earlier period.

There is no necessity to describe here the different features of storage-leaves, which from an organographical standpoint are usually very simple. There is, however, one case of special interest to which I must refer :—

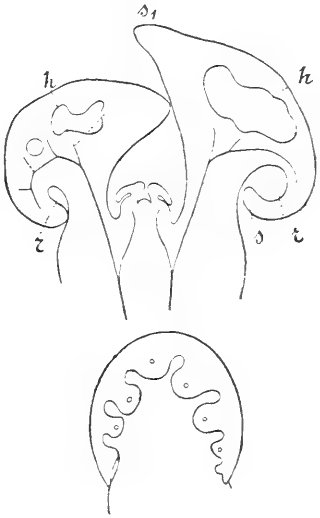

FIG. 262. Lathraea Squamaria. Upper figure: apex of a shoot in longitudinal section; *s*. incurved apex of kataphyll; s_1, apparent tip; *r*, entrance to leaf-pit *h*. Lower figure: young kataphyll in surface-section showing the pits. Magnified.

Lathraea Squamaria. Lathraea Squamaria is a root-parasite, hypogeous except in its inflorescence. Its rhizomes are provided with thick fleshy decussate scales, which serve as reservoirs of reserve-material and have a peculiar structure[1] (Fig. 262). Externally they appear as simple scales, but really the margin of the scale is not the true leaf-margin, nor is its point the true leaf-tip. The upper side of the leaf is so curved downwards that a cavity is formed which only communicates with the outside by a narrow slit at its base, and from it canal-like extensions extend deeper into the fleshy leaf-tissue.

Tozzia alpina. The allied genus Tozzia has simpler scale-leaves; besides it possesses foliage-leaves. Its scale-leaves are therefore of special interest because they show to a certain extent the structure of those of Lathraea in a more rudimentary form. In its scale-leaves the leaf-margin alone is bent over, and only in the protective cavity which is thus made are water-glands found (Figs. 263, 264, 265). We can easily imagine how the special form of leaf of Lathraea has sprung from the simple structure of Tozzia, and if this conformation is the result of a biological need the case in Lathraea where scale-leaves *alone* are present, satisfies higher claims than that of Tozzia, which subsequently sends a shoot bearing foliage-leaves above the soil. What now is the meaning of this peculiar formation of leaves? The object is the protection of the water-glands which are found in large numbers in these hypogeous leaf-organs, and the activity of which replaces partially that of transpiration. These water-glands are by the form of the

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[1] It has been frequently described, but I do not cite the literature, as the plant is so widely spread. I will only say that Irmisch, Zur Morphologie der monokotylischen Knollen- und Zwiebelgewächse, Berlin, 1850, p. 188, was the first who rightly described the morphology of the leaf of Lathraea, and refer to Stenzel, Über die Blätter des Schuppenwurz (Lathraea Squamaria), in Botanische Zeitung, xxix (1871), p. 241.

leaf brought into protected cavities. It is possible that, especially in the juvenile stages, these cavities serve also for aeration [1].

5. COTYLEDONS [2].

The cotyledons demand a special description here, as in more than one way they exhibit peculiarities which go so far as to have led some authors to doubt their leaf-nature. They are distinguished by their position. We designate as cotyledon the first leaf or the first leaves which appear upon the embryo, and they do not, as do the later leaves [3], proceed out of the vegetative point of a shoot, but proceed from the unsegmented primordium of the embryo. Leitgeb has established the use of the term 'cotyledon' also for the one or two leaves of the embryo of Pteridophyta, which arise independently of the vegetative point of the shoot.

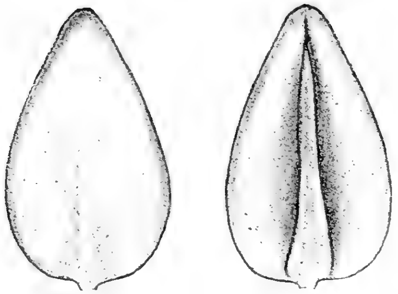

FIG. 263. Tozzia alpina. Storage-kataphyll of the rhizome. To the left: seen from above. To the right: seen from below so as to exhibit the revolute margin of the leaf.

A. PTERIDOPHYTA.

The cotyledons of the Pteridophyta require hardly any special description. They are so like the primary leaves [4] that they really may be considered as the first members of these. They are without exception *arrested forms of foliage-leaves*, and they show this more clearly than do the cotyledons of Spermophyta, inasmuch as they do not discharge the function which is so common in the Spermophyta of suctorial organs. This work is in the Pteridophyta taken on by the 'foot' of the embryo. They also do not act as storage-organs. Their

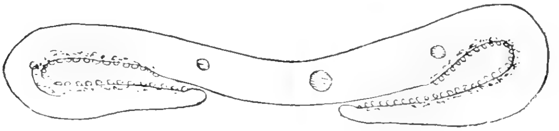

FIG. 264. Tozzia alpina. Kataphyll in transverse section. Water-glands are seen within the revolute margins of the leaf.

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[1] See Goebel, Morphologische und biologische Bemerkungen: 7. Über die biologische Bedeutung der Blatthöhlen bei Tozzia und Lathraea, in Flora, lxxxiii (1897), p. 444; Haberlandt, Zur Kenntniss der Hydathoden, in Pringsheim's Jahrbücher, xxx (1897), p. 511. Darwin observed the exudation of water in Lathraea.

[2] Du Petit Thouars proposed many years ago to replace the inexpressive term 'cotyledon' by the term 'protophyll.' No one seems to have supported him in this excepting Turpin (see Annales des sciences naturelles, sér. 1, xxiii (1831), p. 10 footnote). The name therefore remains, and is crystallized in the group-names 'Monocotyledones' and 'Dicotyledones.' The leafy cotyledons developed in germination have also been called 'feuilles seminales' by, for instance, A. P. De Candolle.

[3] See, however, the development of the embryo in Monocotyledones.

[4] See Part I, p. 152, Fig. 93.

resemblance to the other foliage-leaves is therefore very evident, because they have no other function but that of these. Only in the floating forms of Salvinia and Azolla has the cotyledon different conformation from the first foliage-leaves. It is peltate in Salvinia and turbinate in Azolla, so that an air-bubble can be retained upon the deepened upper side[1], and the construction of the cotyledon makes more certain the normal floating position of the embryo upon the surface of the water.

B. SPERMOPHYTA.

The embryo of the Spermophyta occupies quite a different position from that of the Pteridophyta. It submits in the seed to an interruption in its development, except in the case of viviparous plants, and is during this invested by stout envelopes. The divergence in form of the cotyledon from that of the foliage-leaves is usually very great. The question is, how can we explain morphologically and biologically this divergence? Can we furnish utilitarian explanations and satisfactory causes? With respect to explanations we must not forget that even in the foliage-leaves the connexion between configuration and life-relationships are still obscure, and therefore in the case of the cotyledons also we must use teleological considerations with caution. As regards the causes, it is evident that there are many factors which have to be considered beyond those which affect the foliage-leaves, and this, apart from what is involved in inclusion within the seed and the probably consequent relationships of correlation.

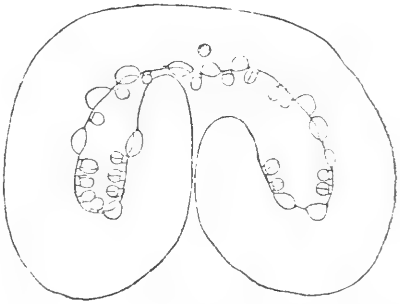

FIG. 265. Tozzia alpina. Upper part of a kataphyll in transverse section. The water-glands are shown. Magnified.

Cotyledons may serve as—

1. *Protective Structures.* They act in this way to the stem-bud, not only during its rest in the bud but frequently also during the germination (Fig. 266). In this connexion we have in many dicotylous plants the formation of a long cotylar sheath, at the base of which sits a stem-bud; regarding this we shall say no more here, but the many remarkable and somewhat similar relationships of monocotylous embryos will be discussed below.

2. *Reservoirs of Reserve-material.* In many cases.

3. *Haustoria*—for the absorption of the endosperm. In this connexion it may be noted that there are only two genera of Spermophyta—Gnetum

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[1] See Goebel, Pflanzenbiologische Schilderungen, i (1889) and ii (1893).

and Welwitschia—in which the suctorial organ is developed as an outgrowth of the hypocotylar segment, independently of the cotyledons. In other cases where we have a suctorial organ the cotyledons act as this, and in most cases *within* the seed-coat, yet it sometimes happens that, in germination after the embryo has left the seed-coat, a portion of the endosperm is taken along with it and is used *outside* the seed. I found this, for example, in a species of Sterculia (Fig. 267) in Java, whose cotyledons are usually separated by an internode.

4. *Pistons*—to push the seedling deeper into the soil in germination. This occurs especially in some Monocotyledones, for example Phoenix, whose cotyledons are positively geotropic.

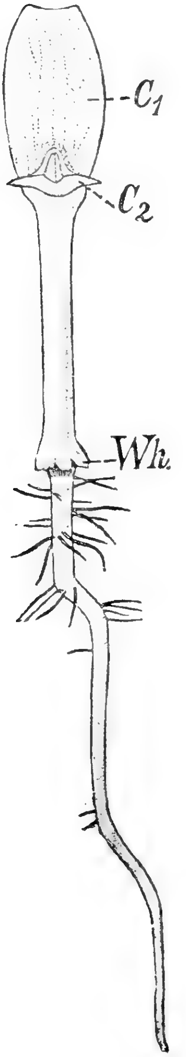

FIG. 266. Leucodendron argenteum. Seedling plant. C_1, cotyledon, the other cotyledon has been removed at line C_2. The bud of the stem is seen in a depression of the base of the cotyledon. *Wh*, root-collar, limit between hypocotyl and root.

(1) **Dicotyledones.**

MORPHOLOGY OF THE COTYLEDONS. I shall suppose that the external relationships of configuration which are usually very simple are known; some of the more interesting cases only will be noticed. The first general question that arises is—Are the cotyledons to be considered as structures *sui generis*, or are they only developmental forms of foliage-leaves? The answer is affirmative to the last question, and for the following reasons:—

(*a*) *Analogy with the Pteridophyta* whose cotyledons, apart from their inception, resemble the primary leaves.

(*b*) The fact that *in many Spermophyta the cotyledons resemble the foliage-leaves.* Thus the single cotyledon of Cyclamen resembles in form the foliage-leaves (Fig. 268). Utricularia, Pinguicula, Viscum, Spergula, all show the same features as do the exalbuminous Monocotyledones hereafter mentioned. In many plants which possess tubers, such as species of Corydalis, Carum Bulbocastanum, Bunium petraeum, Aconitum Anthora, and others, the cotyledons in the first year of the seedling are the only assimilation-organs, but usually they quickly die away—lasting only for a few weeks in many plants, as in Claytonia perfoliata, Nolana atriplicifolia, and others. We can easily understand that such short-lived leaves will be more simply constructed than will be the 'typical' foliage-leaves. In some annual plants[1] the cotyledons may persist until flowering, as in Adonis aestivalis, Fumaria officinalis, Veronica hederaefolia, Melampyrum pratense, Urtica urens, Euphorbia helioscopia; but, owing to their position at the base of the plant, they are unfavourably placed for assimilation and can do little in this way. The small size of the cotyledons, compared with the foliage-leaves, is a matter of correlation[2]. We observe that the cotyledons are largest in plants like Streptocarpus, in which the chief shoot which commonly arises between the cotyledons is suppressed, and we may express this otherwise by saying that where the cotyledons are specially constructed to be like foliage-leaves, they precede in development the stem-bud. In many cases also, if the stem-bud be removed, the cotyledons exhibit an increase in size beyond the usual.

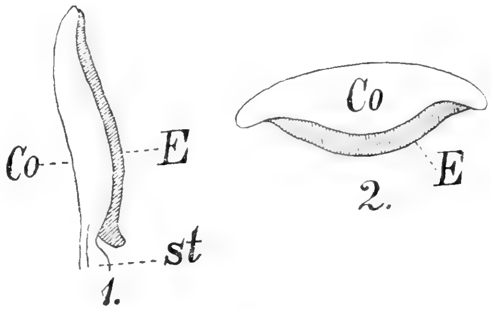

FIG. 267. Sterculia sp. in Buitenzorg Garden. 1, portion of embryo and endosperm in longitudinal section; *Co*, cotyledon; *st*, stalk of cotyledon; *E*, the endosperm, shaded in the figure. 2, the same in transverse section. Lettering the same.

The simpler configuration of epigeous cotyledons is thus easily understandable from the biological side. There are transitions, however, between epigeous and hypogeous cotyledons, and the fact that different species of one genus may have epigeous and hypogeous cotyledons, for example Rhamnus Frangula and R. cathartica, Mercurialis perennis and M. annua, shows that in the hypogeous cotyledons the functioning as assimilation-organs has only been given up at a late period in connexion with the deposition within them of reserve-material, and that in consequence of this they no longer reach the light.

The simplicity of the configuration of the cotyledons, compared with the foliage-leaves, we may consider as a phenomenon of arrest, as it is in the Pteridophyta. This arrest is usually persistent, but in many cases, as a few examples will show, it is only temporary. These temporary cases are especially interesting, because they throw light upon the persistent forms, and establish directly the transition of the cotyledons to the foliage-leaves.

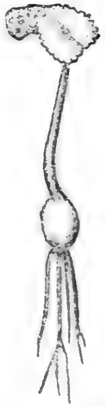

FIG. 268. Cyclamen persicum. Seedling plant. The apex of the cotyledon is a haustorium, the hypocotyl is swollen into a tuber. Magnified.

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[1] See Winkler, Über die Keimblätter der deutschen Dicotylen, in Verhandlungen des botanischen Vereins der Provinz Brandenburg, xvi (1874), p. 16.

[2] See Part I, p. 206.

(*c*) The existence of *all stages of transition-forms between cotyledons and foliage-leaves.* Many cotyledons experience in the process of germination only an increase in size[1]. Others exhibit a *change in configuration*, which in extreme cases like that of Streptocarpus polyanthus[2] and other species, and also in Monophyllea, results in the formation of a massive foliage-leaf, often over thirty centimeters long, whilst in the embryo it only possessed a length of about half a millimeter. It need hardly be mentioned that this takes place by 'intercalary' growth, and we have here, as in the case of Oenothera mentioned below, only an extreme illustration of the fact[3] that the leaf-apex in most Dicotyledones passes over into the permanent condition at an early period, whilst at its base continued growth proceeds—it is the apex which appears first as the cotyledon. This remarkable condition in Streptocarpus and other plants is connected with the fact that in them the cotyledon is the *only* foliage-leaf, and therefore it has a much longer period of life than usually is the case where the cotyledons *rapidly die away* and are replaced by foliage-leaves.

Even, however, in plants in which foliage-leaves appear later there are not wanting examples of post-embryonal further development of the cotyledons. The Onagrarieae furnish some very instructive examples of this. In this family[4] we find a varying behaviour of the cotyledons. In some plants the cotyledons show the ordinary construction, they are small, with entire margins and a feeble venation, for example in Epilobium angustifolium, Oenothera pumila, O. glauca, O. rosea. In others the cotyledons show after germination further intercalary growth as it is seen in Streptocarpus, and a portion of foliage-leaf is, as it were, intercalated in the cotyledon, and carries at its end the original cotyledon; we find this, and naturally in various degrees, in Clarkia pulchella, Oenothera stricta, O. bistorta, O. macrantha, and others.

Oenothera bistorta. Let us take Oenothera bistorta as an example. After the germination the cotyledons are sessile, and they have only a few long glandular hairs especially at their base. Six days afterwards this base is elongated into the form of a stalk. Fig. 269, I, shows a seedling eight days old, and the cotyledons are seen in their surface-view but otherwise unchanged. The new intercalated portion visible beneath them grows subsequently into a narrow leaf-surface, provided with a mid-rib and a short leaf-stalk (Fig. 269, II). In this condition it differs from the primary leaves only by having at its tip the original cotyledon.

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[1] Compare, for example, Ampelopsis, Part I, p. 145.

[2] See Hielscher, Anatomie und Biologie der Gattung Streptocarpus, in Cohn's Beiträge, iii (1879), p. 1. As regards the cotyledons in germination, see specially Klebs, Beiträge zur Morphologie und Biologie der Keimung, in Untersuchungen aus dem botanischen Institut zu Tübingen, i (1881–5), p. 536.

[3] See p. 308.

[4] See Lubbock, A Contribution to our Knowledge of Seedlings, London, 1892, i. p. 553.

Oenothera shows that in one genus we may have partly *persistent* partly *temporary* arrest of the development of the cotyledon, and we cannot doubt from this as to the way in which the simpler construction of the cotyledons, compared with the foliage-leaves, has come about.

THE FACTORS CAUSING THE CONFIGURATION OF COTYLEDONS. It has been already shown that we must in the first instance consider in respect of this the enclosure of the cotyledons in the seed; further, it is probable that relationships of correlation operate here as they do so often. A limit is put to the growth of the embryo by that of the embryo-sac in which it is enclosed, and the history of the development of the seed shows that the growth of the embryo-sac is primary, that of the embryo itself is secondary, and therefore we come to the question :—*How far is the form of the cotyledon dependent upon the relationships of space within the seed?*

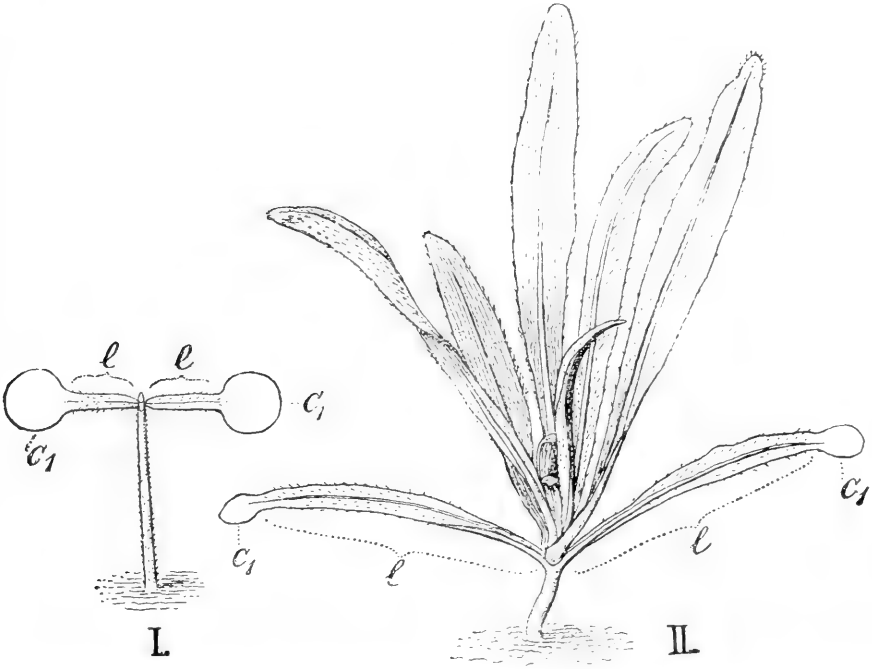

FIG. 269. Oenothera bistorta. I, younger, II, older seedling-plant. C_1, the original cotyledon; *l*, the intercalated portion. After Lubbock.

We have relatively few investigations bearing upon this point. Hofmeister[1] was the first who took up the question of the relationship of the *lie* of the embryo to the space available for it in the embryo-sac. Lubbock[2], starting from the relationships in the matured seed, has endeavoured to

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[1] Hofmeister, Allgemeine Morphologie der Gewächse, Leipzig, 1868, i. p. 620.

[2] Lubbock, A Contribution to our Knowledge of Seedlings, London, 1892, i. p. 8.

bring the form of the cotyledons into relationship with the conditions of space, and he has thereby arrived at certain suggestive interpretations which, however, can only be placed upon a sound basis by investigation of the history of development, because he has, for example in the Caryophylleae, altogether overlooked the difference between endosperm and perisperm, and it is clear that the conformation of the latter can exercise no influence upon that of the embryo. The most important of Lubbock's statements will be noticed below, but here I may only remark that a consideration of the mature seed shows that the space-relationships do not operate everywhere directly in determining the form—for example, in embryos which nowhere come into contact with the seed-coat. We should expect to find the influence of such relationships therefore especially in seeds which have no endosperm. Also if the history of development should show that the space-relationships are not the *direct* causal factors of the configuration of the cotyledons, one might nevertheless maintain that a relation exists between them, as it might be that an original causal connexion existed, but that in course of time its effects have become hereditary and therefore we have no longer to deal with direct causal phenomena [1]. The results of investigations of the history of development bearing upon this question have been published by Hegelmaier alone [2]. They show, for example, that in the Geraniaceae, whose cotyledons are convolute [3] and from an early period asymmetric the ptyxis begins in them at a time when the embryo lies still *free* within the embryo-sac, and therefore when no considerations of pressure are operative, and the asymmetric construction of the cotyledons cannot be regarded as the effect of pressure. I must refer for details on the subject to Hegelmaier's exposition of it, and here I only quote some of Lubbock's results amongst the Dicotyledones :—

1. **Narrow and broad cotyledons.** In many cases the narrow cotyledons correspond exactly with the form of the embryo-sac, for instance in Platanus and the Chenopodiaceae [4]. The broad ones may do the same, for example, in Ruellia, Phaseolus, Quercus. This is not the case however, everywhere and Lubbock, in speaking of the narrowness of the cotyledons in Galium saccharatum, says that their form enables them to be more easily withdrawn from the hard testa.

2. **Asymmetric cotyledons.** These are found in a number of Geraniaceae, for example, Geranium pratense, G. cicutarium, G. Robertianum, species of Erodium, in the Leguminosae, and in the Polygonaceae, for example Polygonum

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[1] See what is said Part I, p. 217.

[2] Hegelmaier, Über Orientirung des Keimes im Angiospermensamen, in Botanische Zeitung, liii (1895), p. 143; id., Über convolutive Cotyledonen, in Berichte der deutschen botanischen Gesellschaft, xvii (1899), p. 121.

[3] See Part I, Fig. 67.

[4] Lubbock does not recognize the presence of perisperm in this family.

Fagopyrum, P. emarginatum, and others. Lubbock refers the asymmetry of the Geraniaceae to the folding within one another of the cotyledons. The smaller half of each cotyledon is the inner one. But Hegelmaier's investigations quoted above show that the influence here is not a direct one. In Polygonum Fagopyrum[1], also, the asymmetry of the cotyledons begins early at a time when their margins are still far away from the seed-coat and the furthered lateral half, which may either be the right or the left—using these words in a like sense for each cotyledon—one is always involute and over-lapping whilst the smaller is always revolute and overlapped. What takes place in the Leguminosae requires further investigation, at any rate the asymmetric form of the cotyledon corresponds here with that of the seed.

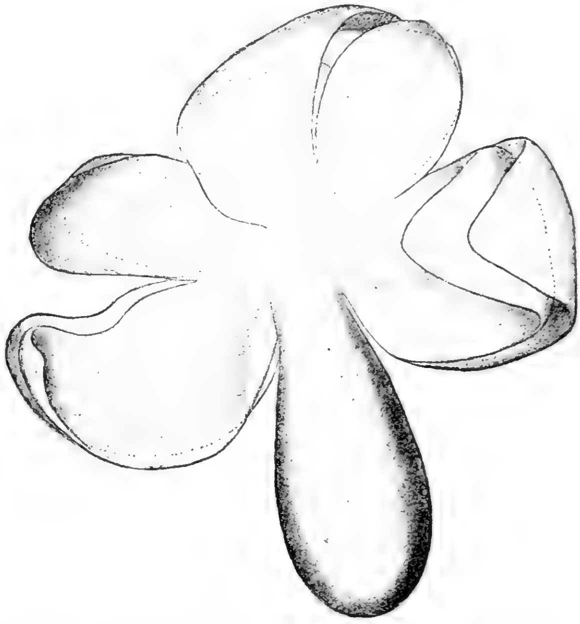

FIG. 270. Tilia parvifolia. Embryo dissected out of the seed. Magnified 15.

3. **Lobed and emarginate cotyledons.** The emargination of the cotyledons at their anterior end corresponds in many cases to the thickening of the seed-coat, or it may be of the fruit-wall, for instance, in Quercus, Impatiens, Urtica. In many Cruciferae, such as Raphanus and Sinapis, the terminal depression of the cotyledon facilitates their ptyxis[2], and so also may the lobing of the cotyledons of Tilia (Fig. 270) facilitate their packing in the seed, as Lubbock explains. But in my view we must also consider here that by the development of the lobes the absorptive power of the cotyledons as *haustoria* is increased. They have the somewhat hard endosperm to dissolve and to bring the material it contains into the embryo. The case of Myristica fragrans shows that as a matter of fact the division of cotyledons stands in relation to their haustorial function[3]. In this plant the endosperm is, as is well known, *ruminate*, that is to say infoldings of the seed-coat produce a brown marbling in it. The cotyledons of the somewhat small embryo increase in germination considerably, divide in correspondence with the infoldings of the seed-coat, and when dissected out appear to be lobed like a coronet. The single lobes which have apical growth force themselves into the endosperm. It

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[1] Lubbock, A Contribution to our Knowledge of Seedlings, London, 1892, i. p. 134.

[2] With regard to Convolvulus and others, see Lubbock, op. cit.

[3] See Tschirch, Physiologische Studien über die Samen, insbesondere die Saugorgane derselben, in Annales du Jardin botanique de Buitenzorg, ix (1891), p. 143.

is quite evident that here the lobes, which are only formed in germination, have a relation to their function as suctorial organs. Similar cases will be described in Monocotyledones.

(2) Monocotyledones[1].

STAGES OF DIFFERENTIATION OF COTYLEDON. The *simplest case* of the cotylar configuration is to be found in the embryos of exalbuminous Monocotyledones. It has been stated above[2] that the leaf of Monocotyledones is usually only differentiated into lamina and sheath, and this we find also in the cotyledon, for example in the Juncagineae, Butomeae, Alismaceae, and elsewhere. The cotyledon becomes green, and does not differ in form and structure essentially from the first foliage-leaves, although its anatomical differentiation is usually somewhat simpler[3]. The lamina as in ordinary leaves appears as the direct continuation of the sheath. This degree of differentiation of the cotyledon we may designate as the first and most primitive[4]. We distinguish in the cotyledon the *lamina* and the *sheath* which invests the but slightly developed stem-bud.

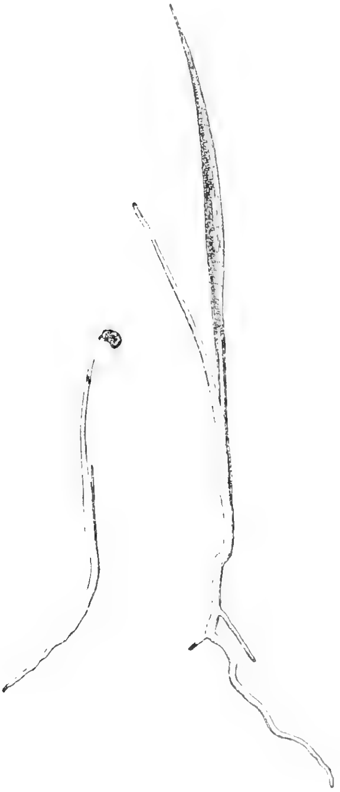

FIG. 271. Dracaena indivisa. Seedling plant. The cotylar tip, which acts as a haustorium, and is enclosed in the seed in the figure to the left, is marked by a dotted line in the figure to the right of an older seedling. It becomes more or less green. Natural size.

From the first stage a *second* is distinguished by the further development of the sheath. There is now developed not only the *lateral* parts of the lamina, but more particularly there is also an outgrowth upon the upper side of the primordium of the leaf, such as we have seen in the development of many axillary stipules and ligules; and further the completely ensheathing sheath has grown up at its base as an outgrowth, so that the stem-bud is surrounded by an oblique upwardly directed ringwall formed by the cotyledon.

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[1] See Klebs, Beiträge zur Morphologie und Biologie der Keimung, in Untersuchungen aus dem botanischen Institut zu Tübingen, i (1881–5), p. 536.

[2] See p. 299.

[3] Anatomical details are given by Schlickum, Morphologischer und anatomischer Vergleich der Kotyledonen und ersten Laubblätter der Keimpflanzen der Monokotylen, in Bibliotheca Botanica, xxxv (1896).

[4] See Klebs, op. cit.; Tschirch, Physiologische Studien über die Samen, insbesondere die Saugorgane derselben, in Annales du Jardin botanique de Buitenzorg, ix (1891); Čelakovský, Über die Homologien des Grasembryos, in Botanische Zeitung, lv (1897), p. 141.

In the *next stage* we see the sheath still more developed and further separated from the upper part of the cotyledon which in some degree appears as its appendage.

These three stages are connected, on the one hand, with the size which the stem-bud reaches before or during the germination, and, on the other hand, with the changes which the cotyledon passes through in losing gradually its leaf-nature and finally becoming entirely a haustorium, functionally, but not morphologically, resembling the suctorial organ of the embryo of Gnetum and Welwitschia. The stronger development which the cotyledon as a haustorium has already attained in the seed is connected, on the one hand, with the richness of development of the endosperm, and, on the other, with the relative rapidity with which the process of germination has to be passed through. That the cotylar sheath may take on, besides its protective work, other functions also, will be shown in the examples cited below. It must be remembered, however, that there are many transitions between the different types, and they are especially conditioned by the varying strength of the claims upon the cotyledon as a haustorium in endospermous seeds.

FIG. 272. Seedling of unknown monocotylous plant (Allium sp.?). The cotyledon is the only part above ground, and is divided in two parts—the lower persistent thicker green part, that to the left in the figure, and the upper thinner part (on the right of the figure) which apparently is lateral.

EPIGEOUS COTYLEDONS.

We shall consider in the first instance cases in which the epigeous cotyledon becomes green. It then behaves as it does in seeds which have got no endosperm, only that its tip serves as a suctorial organ in varying degree, either temporary or permanent. In Dracaena (Fig. 271) the end of the cotyledon remains enclosed in the seed as a haustorium. If it is set free from the seed-coat it becomes green less intensively, no doubt, than the rest of the cotyledon, from which it also differs in anatomical structure. Other Liliaceae, like Allium and Hyacinthus, also Agave and other plants, behave in this manner.

The seedling represented in Fig. 272, which belonged to an unknown monocotylous plant, probably a species of Allium, shows an interesting case[1]:—The whole cotyledon is not devoted to the formation of a foliage-leaf; its upper part, the thin portion on the right of the figure, the tip of which functions as a suctorial organ, remains thin and thread-like and dies away later, whilst the lower portion, the thicker portion on the left of the figure, becomes an almost cylindric foliage-leaf, whose relatively short sheath invests the stem-bud. It is very striking to note that the persistent part of

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[1] The seedlings appeared in a pot in which Australian seeds were growing, but they all died off early, and a certain determination of their affinity could not be made.

the cotyledon has grown out slightly beyond the thread-like transitory portion from the point where they are joined in a knee-like bend. This outgrown portion, directed downwards in the figure, forms subsequently the 'tip' of the cotyledon, and acts as a boring-organ; the thread-like portion, the real upper part, appears in consequence to be lateral.

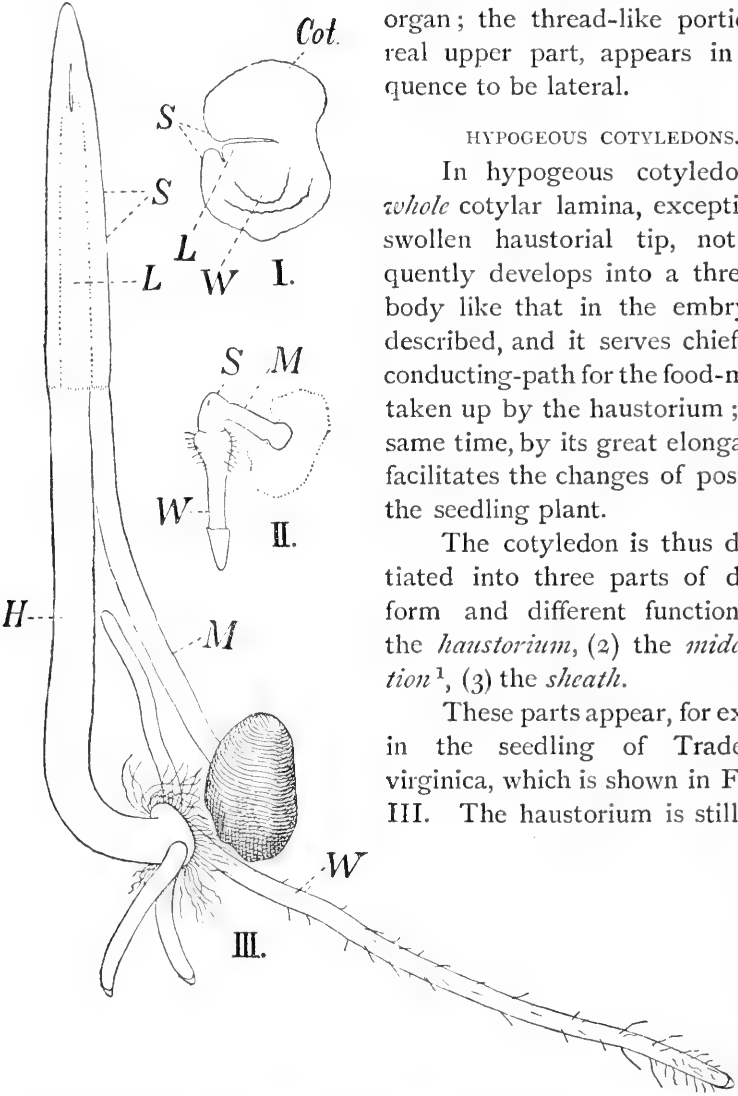

Fig. 273. Tradescantia virginica. Seedling plant in three stages I, II, III. *Cot*, cotyledon; *S*, cotylar sheath; *M*, middle portion; *L*, first foliage-leaf; *W*, first root; *H*, hypocotyl. In II the endosperm is enclosed in a dotted line. Magnified 6. I and II after Gravis.

HYPOGEOUS COTYLEDONS.

In hypogeous cotyledons the *whole* cotylar lamina, excepting the swollen haustorial tip, not infrequently develops into a thread-like body like that in the embryo just described, and it serves chiefly as a conducting-path for the food-material taken up by the haustorium; at the same time, by its great elongation, it facilitates the changes of position of the seedling plant.

The cotyledon is thus differentiated into three parts of different form and different function:—(1) the *haustorium*, (2) the *middle portion*[1], (3) the *sheath*.

These parts appear, for example, in the seedling of Tradescantia virginica, which is shown in Fig. 273, III. The haustorium is still within the seed-coat, *M* is the middle portion, and *S* is the sheath. The sheath has, *during the germination*, grown out to a considerable extent, and has elongated above its point of attachment to the middle portion; it protects

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[1] Klebs uses this term. There is no necessity for Schlickum's later expression, 'conductor.'

the stem-bud during its passage through the soil, and later it is ruptured. The process of development of the sheath will be quite clear without further remark if we consider the younger embryos. In the resting seed shown in Fig. 273, I, the sheath, *S*, surrounding the stem-bud, is plainly visible on the cotyledon; in the young seedling shown in Fig. 273, II, the sheath, *S*, has grown out a little beyond the point of its attachment to the middle portion, *M*, which has elongated; in the older seedling shown in Fig. 273, III, the sheath, *S*, has elongated to a considerable extent, and is directed upwards in a negatively geotropic manner.

In some cases the form of the cotyledon which acts as a haustorium corresponds evidently with the space-relationships in the seed. This is seen in Alpinia nutans[1], where the cotyledon is two-lobed, the lobes extending as two processes into the sickle-like endosperm, as well as in Areca Catechu, where the cotyledon, as in Myristica, forms many lobe-like outgrowths which penetrate between the folds of the ruminate endosperm[2].

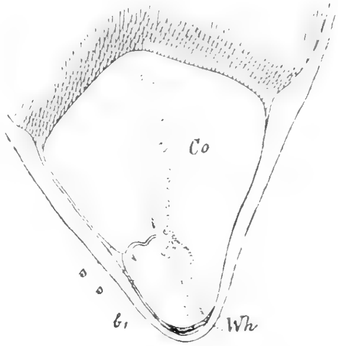

FIG. 274. Carex Grayana. Basal portion of the endosperm enclosing the embryo, in longitudinal section. *Co*, cotyledon; b_1, first leaf; *s*, cotylar sheath; *Wh*, cap of the oblique first root. The embryo is surrounded by the nitrogenous layer of the endosperm; a small portion of the starchy endosperm is indicated by shading.

COTYLEDON OF CYPERACEAE. The development of the sheath in the direction indicated above is especially well seen in Cyperaceae. There are two cases:—

(*a*) In some of them it takes place only *during the germination*, as is the case in Tradescantia.

(*b*) In others it occurs earlier and *within the seed* itself.

Carex. Carex may be taken as an example of the first case. The embryo lies at the base of the endosperm. It is surrounded (Fig. 274) by the many-layered nitrogenous-layer of this, and the flatly conical summit of its turbinate cotyledon touches the copious starch-bearing portion of the endosperm. The configuration of the cotyledon is from its lie and its function as a suctorial organ—the upper part swells up in germination—easily understood. The stem-bud on which the primordia of two leaves are visible (Fig. 275) in the figure, is enclosed by the cotylar sheath, *s s*, the narrow slit of which is almost closed. This sheath develops considerably in germination, and it serves evidently, as in the grasses, as a protective investment to the stem-bud during its boring through the soil; subsequently it is burst at the apex by the developing first leaves. The base of the cotyledon above the sheath

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[1] Tschirch, Physiologische Studien über die Samen, insbesondere die Saugorgane derselben, in Annales du Jardin botanique de Buitenzorg, ix (1891).

[2] See the chapter upon the development of seeds.

develops into a very short middle portion. It is noteworthy and of significance for the explanation of the formation of the organs in the embryo of grasses, that between the point of attachment of the sheath and that of the middle portion, a piece appears to be interpolated on the seedling so that the sheath and the rest of the cotyledon are separated from one another by an apparent internode (Fig. 275, *Me*). This piece is neither the hypocotyl nor an *internode*, but a greatly elongated *node* which may reach a length of from six to ten millimeters. Čelakovský[1] has named it the *mesocotyl*. It is certainly an unusual occurrence that two portions of one leaf-primordium should be separated one from another so that they appear to spring from different parts of the axis, but the process can be followed here in its development, and we may explain it so far biologically that it facilitates the boring through the earth of the sheath with the stem-bud which it encloses.

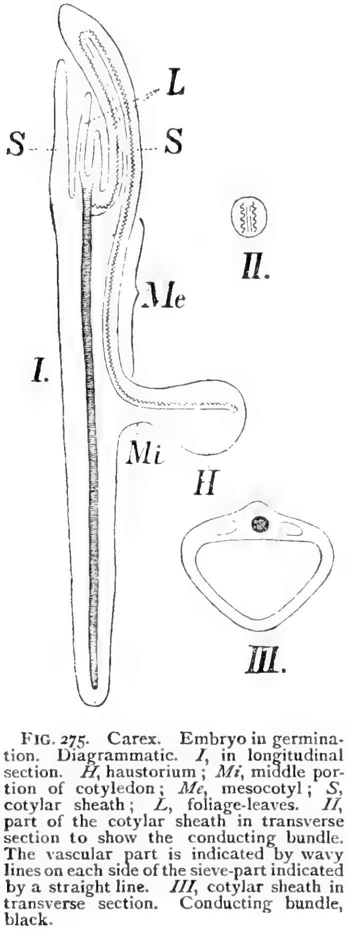

FIG. 275. Carex. Embryo in germination. Diagrammatic. *I*, in longitudinal section. *H*, haustorium; *Mi*, middle portion of cotyledon; *Me*, mesocotyl; *S*, cotylar sheath; *L*, foliage-leaves. *II*, part of the cotylar sheath in transverse section to show the conducting bundle. The vascular part is indicated by wavy lines on each side of the sieve-part indicated by a straight line. *III*, cotylar sheath in transverse section. Conducting bundle, black.

The anatomical relationships suit this explanation, and I shall very shortly refer to them here (see Fig. 275)[2]. The conducting bundle which passes out from the haustorium and upper part of the cotyledon does not attach itself directly to the vascular bundle-cylinder of the mesocotyl but runs upwards in the cortex of the mesocotyl. Consequently on tranverse section the vascular portion of this bundle, which is represented in the diagrammatic Fig. 275, *I*, by a wavy line, appears in an inverted position, that is to say it is turned outwards. At the point where the cotylar sheath joins on to the mesocotyl there is a conducting vascular bundle in which the vascular portion has the normal position; this bundle bends up through the sheath to its apex then descends again through the sheath, and is continued downwards, as the bundle with inverted xylem mentioned above, through the cortex of the mesocotyl into the upper part of the cotyledon ending in the haustorium. Upon the transverse section of the sheath (Fig. 275, *II*) there *appears to be but one* vascular bundle which has two sieve-portions almost touching one another and two vascular portions lying over against

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[1] Čelakovský, Über die Homologien des Grasembryos, in Botanische Zeitung, lv (1897), p. 141.

[2] See Van Tieghem, Morphologie de l'embryon et de la plantule chez les Graminées et les Cypéracées, in Annales des sciences naturelles, sér. 8, iii (1897), p. 259.

one another. This course of the conducting bundles shows that the bundle which enters the cotylar sheath belongs peculiarly to the cotyledon and that the cotylar base, in a certain measure, forms a cortical investment of the mesocotyl.

Cyperus alternifolius. In illustration of the second case the germination of Cyperus alternifolius may be quoted. Fig. 276, I, shows a longitudinal section through the *embryo in the seed.* The root, *W*, is only feebly indicated, and upon it there is observed the remains of the suspensor *Et.* The massive cotyledon shows at its suctorial end the cells already in a papilla-form, and its long axis does not fall, as in Carex, in nearly the same plane with the root, but makes a right angle with that organ. This is due to the strong development of the cotylar sheath, *S*, which completely invests the stem-bud, and only opens to the outside by a narrow slit above the point of the first foliage-leaf. As the young seedling shows (Fig. 276, II), the sheath develops in germination also very greatly in the first instance, and the elongation of its zone of insertion, which in Fig. 276, I, is indicated by the dotted line, forms the mesocotyl which brings the stem-bud

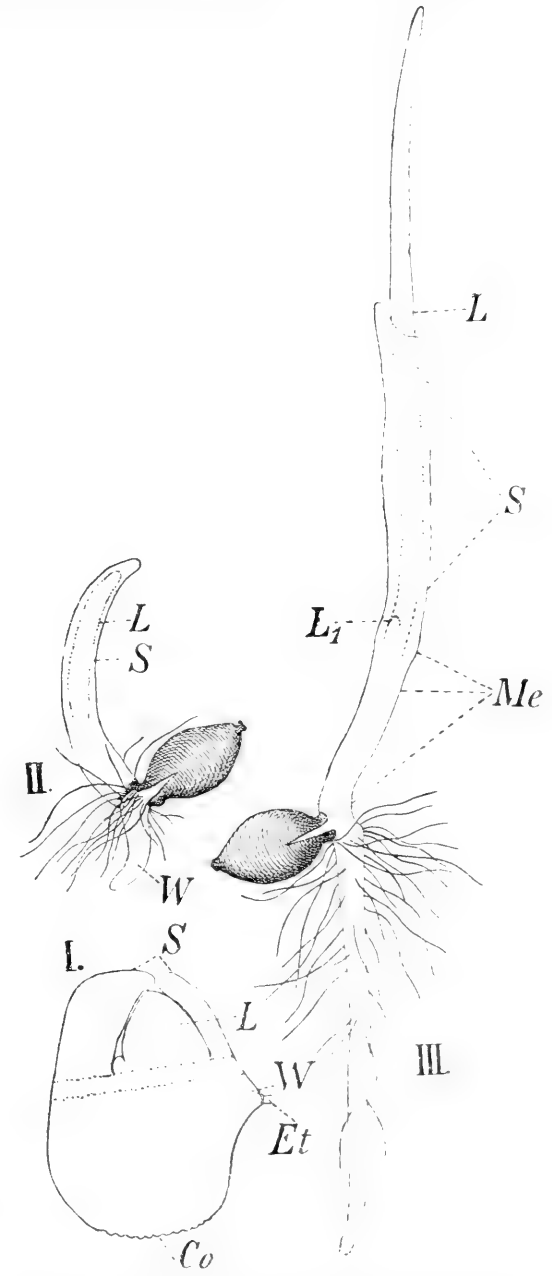

FIG. 276. Cyperus alternifolius. Embryo and germination. I. embryo in longitudinal section. *Co*, cotyledon; *S*, cotylar sheath; *L*, first foliage-leaf; *W*, primordium of a root upon which at *Et* is the remains of the suspensor. The zone between the dotted lines is that which forms the mesocotyl. II, and III, young and older seedling plants. Lettering as in I. The seed-coat is still attached to the seedling. In II the cotylar sheath is not yet ruptured. L_1, second leaf; *Me*, mesocotyl. All magnified.

above the soil, where finally the cotylar sheath is ruptured at its tip (Fig. 276, III).

Scirpus lacustris. A further example of this second case amongst the Cyperaceae is furnished by Scirpus lacustris (Fig. 277). In general, we may say that the *cotylar sheath is the more developed in the seed, the earlier and the more massively it has to be developed in the germination.* In Scirpus lacustris this is seen in marked degree. The sheath becomes green at the tip, and forms there, apparently, a second lamina—the first being the broad shield-like portion forming the hypogeous haustorium, and lying apparently over against the stem-bud. The great development of the sheath in the seed has given rise to misinterpretation. The portion marked *a*, in Fig. 277, is by most authors called the 'radicle.' The root, *r*, here, as in other similarly constituted Cyperaceae, occupies a lateral position[1], as is shown also clearly in the embryo of Carex (Fig. 274, *Wh*). That in the germination at first the stem-bud, as well as the cotylar sheath develops, is shown in Fig. 277, B, and there also we observe the strong development of the cotylar sheath *before* germination. This bears out what has been said above about the development of the foliage-leaves[2], that in general, the parts which are most developed in the matured condition, are the *first laid down* as primordia.

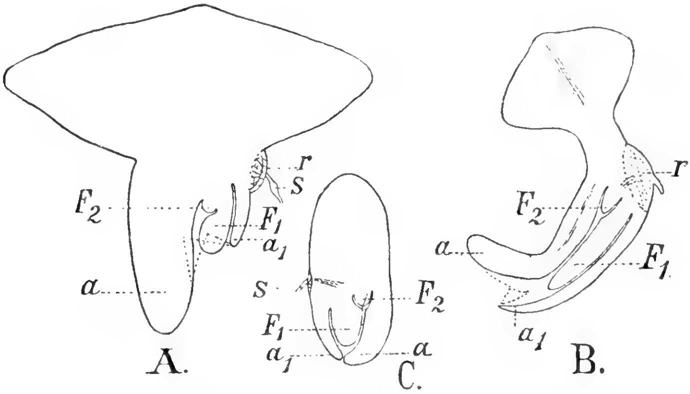

FIG. 277. Scirpus lacustris. A, embryo. B, seedling plant. C, Cyperus decompositus. Embryo in longitudinal section. In all figures: a, a_1, cotylar sheath; F_1, F_2, first leaves; r primary root; S, suspensor. A, magnified 75. After Didrichsen.

THE COTYLEDON OF GRASSES. These cases lead us on to an explanation of the much discussed formation of organs, in the embryo of grasses. As will be shown, we find nothing new when we compare the grass-embryo with that of the Cyperaceae just described.

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[1] Didrichsen, Om Cyperaceernes Kim, in Botanisk Tidsskrift, xix (1894), xxi (1897).

[2] See p. 331.

Let us see first of all what are the actual relationships[1]. In Fig. 278, we have a longitudinal section through the basal portion of a grain of wheat. The embryo lies at the base of the endosperm[2], and it turns towards the endosperm a broad shield-like portion, which since the time of Gärtner has been termed the *scutellum*, *sc*; this acts as a suctorial organ, and remains within the seed in germination. Opposite it is a small scale with no vascular bundles, which is termed the *epiblast*, *l*. Above it there follows a sheathing leaf, with a narrow slit, which appears above the ground in germination, but never becomes green; this is the *coleoptile* or *pileole*, *c*. The endogenetic primary root, *r*, which in germination breaks through the peripheral layer of tissue, *coleorrhiza*, *cl*, requires here no further description. I may only say that the *hypocotyl*, *hp*, is scarcely formed in the grasses, as the body of the embryo is almost entirely used for the laying down of root.

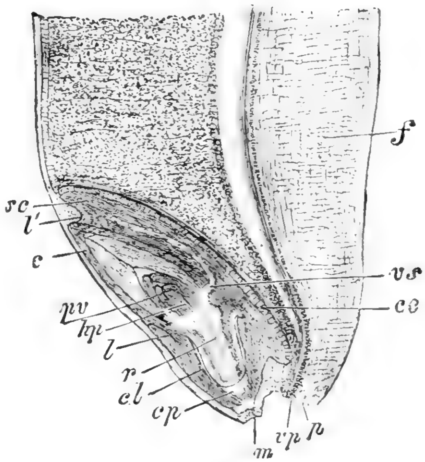

FIG. 278. Portion of grain of wheat in median longitudinal section. To the left the embryo. *Sc*, scutellum; *l'*, ligule; *vs*, vascular supply of scutellum; *ce*, cylindric epithelium of scutellum; *c*, cotylar sheath; *pv*, vegetative point of stem; *hp*, hypocotyl; *l*, epiblast; *r*, root; *cl*, root-sheath; *cp*, calyptra; *m*, point of exit of root; *p*, fruit-stalk; *vp*, vascular supply of fruit-stalk: *f*, lateral wall of the fork of the fruit. Magnified 14. Lehrb.

The morphological explanations that have been given of these organs may be grouped as follows:—

1. The cotyledon is not a leaf-organ. We may put on one side the quite untenable view of Nägeli, that the cotyledon is a thallus-lobe. Hofmeister and others consider the scutellum as an outgrowth of the axis of the embryo. But the history of development shows clearly that the scutellum arises as a terminal structure on the embryo, like the cotyledon in other Monocotyledones (Fig. 282).

2. The scutellum is the cotyledon, and the epiblast which lies over against it, but is not present in all grasses, is an arrested second leaf, and the coleoptile is the third leaf.

This view is supported by the following:—

(*a*) Between the coleoptile and the scutellum, there is in many grasses a strongly developed 'internode.'

(*b*) In the axil of the coleoptile an axillary bud is often found.

(*c*) The basal part of the scutellum in many grasses, for example Oryza (Fig. 281, V), Leersia, and others (Fig. 281, I) develops like the sheath of

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[1] These are most fully depicted by E. Bruns, Der Grasembryo, in Flora, lxxvi (Ergänzungsband zum Jahrgang 1892). The literature is cited there.

[2] Van Tieghem's statement that the embryo is completely surrounded by the nitrogenous layer of the endosperm is not true for Triticum vulgare. See Van Tieghem, Morphologie de l'embryon et de la plantule chez les Graminées et les Cypéracées, in Annales des sciences naturelles, sér. 8, iii (1897), p. 260.

the foliage-leaves of many Monocotyledones. It would therefore be extraordinary were there the formation of a second sheath in the coleoptile[1].

3. Scutellum and coleoptile form together the cotyledon, the epiblast is not a leaf.

This view would bring the formation of the organs in the embryo of the grasses into conformity with that of the Monocotyledones mentioned above, and it has therefore upon comparative grounds great probability.

Let us now pass in review the relationships between the embryo-plant and its functions.

Zea Mais. Fig. 279 is the representation of a seedling plant of Zea Mais, seen from in front. It has a chief root, *H*, and two upwardly directed lateral roots, *N*. The stem-bud is still invested by the coleoptile, *S*, which at its apex is split by the leaves unfolding within it. On the transverse section shown in Fig. 280, we observe that a large number of leaves already exist, which are thinner than is the coleoptile, and are also distinguished from it by having a large number of veins, whilst the coleoptile has only two vascular bundles. The coleoptile, which by its want of chlorophyll is very markedly distinguished from the foliage-leaves[2], has no sclerenchyma,

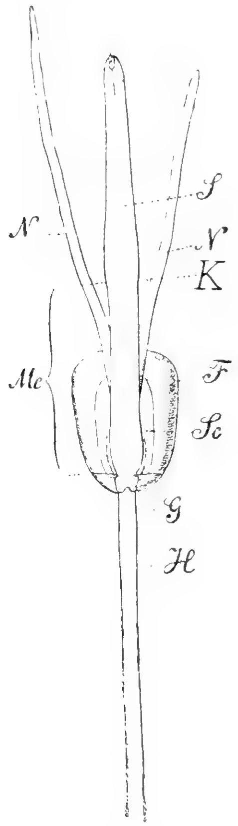

FIG. 279. Zea Mais. Seedling. *H*, primary root; *G*, coleorrhiza; *Sc*, scutellum; *F*, fruit; *Me*, mesocotyl; *K*, first node; *S*, cotylar sheath (coleoptile); *N*, secondary roots. Magnified 1½.

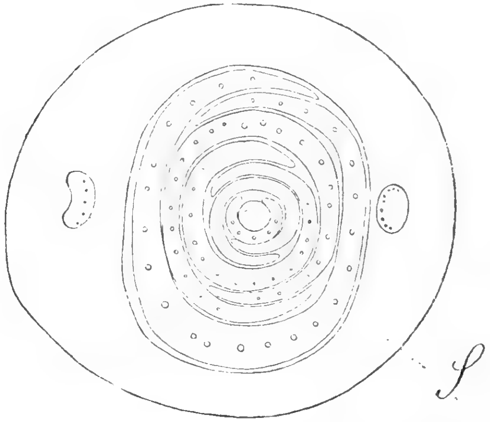

FIG. 280. Zea Mais. Seedling plant in transverse section. *S*, cotylar sheath.

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[1] These arguments were to me conclusive at the time of the appearance of Bruns' work. But the comparative standpoint appears to me to be now all the more strengthened by the proof that in Streptochaete we have a grass which has entirely the conformation of the flower that is 'typical' in Monocotyledones. See Goebel, Ein Beitrag zur Morphologie der Gräser, in Flora, lxxxi (Ergänzungsband zum Jahrgang 1895), p. 17, also Čelakovský, as cited there.

[2] It may become green in many grasses if light of no great intensity has access to it.

but its strong turgescent tissue enables it, in a very perfect manner, to protect the stem-bud it invests as this bores through the soil. To a certain extent it prepares the way, and gives to the leaves and the shoot-nodes, which have intercalary growth, the first necessary start. This coleoptile sits upon the node, marked *K*, which is indicated externally by a slight swelling, and below this is an 'internode,' *Me*, which is negatively geotropic. One sees further the scutellum, *Sc*, upon the surface of the fruit, *F*, and at *G* we have the coleorrhiza. The anatomical relationships here favour the view that the scutellum and coleoptile are independent leaves. The scutellum contains at its point of insertion on the internode, one vascular bundle which branches in the scutellum; the coleoptile contains two of these which are derived from the node *K*. The 'internode,' *Me*, has a quite different structure from the later internodes. It has, not like them scattered vascular bundles, but a vascular cylinder enclosed by an endodermis. In other grasses the anatomical relationships correspond, on the other hand, with those of Carex.

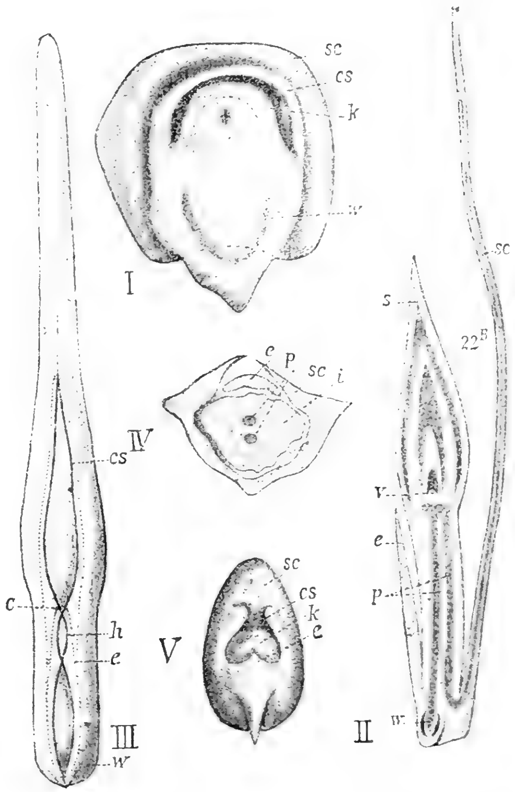

FIG. 281. I, Berchtoldia bromoides. Embryo from outside. II, III, IV, Zizania aquatica. II, embryo in longitudinal section. III, embryo from outside. IV, embryo in transverse section through scutellum and mesocotyl. V, Oryza sativa. Almost ripe embryo from outside. In all figures:—*sc*, scutellum; *cs*, sheathing-base or ligular formation of scutellum; *k*, coleoptile; *w*, root; *e*, epiblast; *i*, mesocotyl; *p*, vascular supply in mesocotyl; *v*, vegetative point of stem, *s*, sheathing-leaf; *h*, hypocotyl; *c*, marginal outgrowth of scutellum. I, magnified 44. V, magnified 22. I, II, IV, V, after Bruns. III, after Schlickum.

Zizania aquatica. In Fig. 281, II, we have the representation of a longitudinal section, through the embryo of Zizania aquatica. In the seed there is a structure which can be directly compared with the features observed in the germination of Carex. Between the coleoptile and the scutellum, a mesocotyl is developed. In this there run two vascular strands, *p*, of which the one forms the conducting cylinder of the mesocotyl, the other coming out of the scutellum runs upwards in the mesocotyl[1], and there giving off two

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[1] See p. 412.

branches which pass into the coleoptile it itself joins on to the bundle of the mesocotyl.

We find the same in Oryza sativa, Phalaris canariensis, and other cases.

Where no mesocotyl exists, the relationships of the vascular cylinder in its course are essentially the same, that is to say, the scutellum and sheath stand in direct connexion with one another. The bundles of the coleoptile may be considered as branches of that which enters the scutellum. If the coleoptile is greatly elongated the arrangements described in Zizania are developed. The mesocotyl is, as in Carex, no internode, but a node. Where, as in Zea, the anatomical relationships diverge, it may be asked if this is not only apparently the case. But even if in this species the anatomical relationships are really different, and they have been referred to particularly here because they are important, yet we cannot come to any other conclusion than that which is valid in the other grasses.

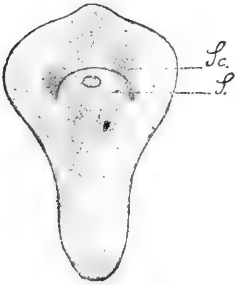

FIG. 282. Hordeum hexastichum. Half-ripe embryo. *Sc*, scutellum; *S*, cotylar sheath. Magnified.

Development. The history of development, owing to the peculiar relationships which are found in the embryos, cannot be here of so much general significance as elsewhere, yet it does not contradict the explanation that the coleoptile is an outgrowth of the scutellum, which is the upper part of the cotyledon, and that it corresponds to the cotylar sheath of other monocotylous plants. In Fig. 282, a half-ripe embryo of Hordeum hexastichum is shown. The coleoptile, *S*, arises at the base of the scutellum, *Sc*, grasps right round as an amplexicaul structure, and now forms a cup with a narrow mouth above, like the structure shown in Fig. 246, in the case of Caltha palustris. Like the axillary stipule of Caltha, it serves as a protection to the bud, and aids it also in germination, and is therefore strongly developed. That the basal portion of the cotyledon is also frequently constructed in the sheath-form (Fig. 281, I, V) may be connected with the fact that the coleoptile has here taken on a further function. Axillary stipules may, as we have seen above[1], stand also on the sheath-like leaf-base. Unlike the ligular formations which are found elsewhere in the grasses, the coleoptile is laid down early, and the place of its inception is associated with the fact that the end of the cotyledon remains as a haustorium in the seed.

The Epiblast. If the explanation I adopt is correct the epiblast cannot be a rudimentary leaf. It is undoubtedly a protecting arrangement for the embryo like the ligule of palm-leaves and of grasses, but whether we designate it as a growth from the sheathing-base of the cotyledon (and to this

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[1] See p. 372.

view the condition in Oryza represented in Fig. 281, V, gives support) or explain it as an independent formation, appears to me to be of little moment. At any rate it fills the gap left upon the outer side by the cotylar sheath.

C. RETROSPECT.

It follows from the preceding description that we fairly understand the relationship between form and function in the cotyledons. On the other hand we are entirely in the dark as to the conditions for their configuration.

6. LEAVES AS CLIMBING-ORGANS.

Leaves may be devoted to the purposes of climbing in many ways, sometimes with, sometimes without, a change in their original form. We find in Europe amongst plants which are leaf-climbers almost only those with *leaf-tendrils*; elsewhere the leaf-forms are more manifold. It is interesting to see how, in many plants, the leaf-organs become devoted to climbing which were originally formed for quite other 'purposes.' Drosera macrantha, which I found in West Australia, possesses a thin stem almost a meter in length. Systematic works describe it as 'twining,' but this is incorrect. The leaves have very long stalks and cling to shrubs by their outer tentacles, which are bent back specially as traps for insects, and the leaf-surfaces lie with their under side upon the upper surface of the twig, a sticky secretion of the recurved tentacles gluing them firmly to it. We shall leave out of consideration plants in which the leaves are useful in 'scrambling,' and direct our attention only to those whose leaves exhibit a more or less far-reaching transformation either into hooks or into tendrils.

Leaves as Hooks.

Here we have leaves or parts of leaves with a curved hook-like form, and these after they have grasped a support show no further change.

A. Pteridophyta.

Lycopodium volubile. Lycopodium volubile, a species which climbs high up in the trees in Java, gives us an example. The chief shoots have a radial arrangement of the leaves, and each of the leaves grows out at its base over the point of attachment. It is thus somewhat peltate. The blunt basal continuation standing out from the surface of the shoot serves as a hook for climbing, although not a very complete one. The formation of the leaves conforms in all essentials with what we have seen in Asparagus comorensis (Fig. 215). The branches of higher order do not form these hooks and climb; they are dorsiventral shoots like those of Lycopodium complanatum[1].

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[1] See Part I, p. 103.

B. Dicotyledones.

Stylidium scandens. Stylidium scandens climbs by means of leaves with hook-like ends.

Pereskia. Many species of Pereskia develop single thorn-leaves as hooks for climbing.

Quisqualis indica. The features of Quisqualis indica have already been referred to[1]. Upon the long shoots the stalks of well-developed foliage-leaves, whose lamina has functioned as a leaf, are transformed into hooks which remain after the lamina has fallen, and thus offer an instructive example of *seasonal change of function*.

Fig. 283. Bignonia albo-lutea. Portion of shoot. The two lower leaves are ternate, the two upper have a trifid tendril instead of the end leaflet. After A. Mann.

Other Dicotyledones show a transition from formation of hooks to formation of tendrils : the lamina, which forms a curved hook, serves as an anchoring-organ, whilst the stalk is a tendril.

Bignonia. Many Bignoniaceae have strong claw-hooks, for example Bignonia unguis. These are less developed in, for example Bignonia albo-lutea (Figs. 283, 284), where the history of development, as in Cobaea, shows that the hooks proceed from the lamina which is in a rudimentary condition visible on young tendrils (Fig. 284).

C. Monocotyledones.

Asparagus comorensis. The climbing-hooks of Asparagus comorensis, formed from the under portion of the peltate leaves, have been described[2].

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[1] See Part I, p. 9.

[2] See p. 334.

Palms. The climbing-hooks of the leaves of many Palms are larger. In Chamaedorea desmoncoides the pinnules of the leaf are so bent back that they form with the rhachis a very obtuse angle upwards, and these leaves act as hooks. They are, however, still assimilation-organs. But in the leaves of Desmoncus (Fig. 285) the upper leaf-pinnules are transformed into hooks which are climbing-organs *only*. We can recognize that they have taken origin from leaf-pinnules by the transition-forms that occur. We have again an illustration here of the oft-recurring series of transformations which ends with complete change of function and earlier transformation.

Calamus. The climbing-organs of species of Calamus, the well-known rotang palm, must not be confounded with the climbing-organs above mentioned. This palm, which has climbing-organs as much as ten meters long, is beset with claw-like, strongly silicified hooks, which are not formed by a transformation of leaf-pinnules but are highly developed prickles such as occur in species of Rubus and elsewhere. The long axis which bears these claws is either a transformed inflorescence or springs from the elongated rhachis of the leaf.

FIG. 284. Bignonia albo-lutea. Young tendril. At the end of each branch of the tendril a rudimentary leaf-lamina is laid down. Slightly magnified. After A. Mann.

Leaves as Tendrils.

A. Dicotyledones.

Only in relatively few cases do we find leaves combining the function of assimilation-organs and of tendrils without a change in their conformation, that is to say, there are parts of the leaf—the leaf-stalk of Solanum jasminoides, species of Tropaeolum, Maurandia, the leaf-spindle of species of Clematis—which are sensitive to contact, and in consequence of this are able to twine round a support. We usually find that a division of labour occurs here, and that one part of the leaf—in compound leaves the leaflets—only is constructed as a tendril, whilst its original function has entirely disappeared. There are not wanting examples where we can observe this process developing *in a single plant*.

Corydalis claviculata. Of special interest in this respect is Corydalis claviculata, which has been described by Darwin[1], and in which we observe a gradual transformation of the leaf into a tendril. In the juvenile condition the plant bears ordinary leaves, and all the leaflets of the bipinnate leaf are also formed as leaves. In the following leaves the upper part of the leaf, or leaf-spindle, becomes thinner and longer than the lower part, and the pinnules of the leaflets which sit on this portion which is elongated like a tendril become reduced in size, often so far as to be no longer

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[1] Darwin, The Movements and Habits of Climbing Plants, 5th thousand, London, 1891, p. 121.

visible, and we thus have all stages between them and normal leaves. Not infrequently on all the terminal leaflets of the leaf every trace of pinnule disappears, and leaflets appear then as complete tendrils.

Adlumia cirrhosa. We find the same thing in Adlumia cirrhosa. In it the leaf is constructed as a tendril only in its upper part; below it is not sensitive to contact. In the tendril-portion of the leaf the lamina of the leaflets is greatly reduced although it is still visible. It is the *stalk* of the leaflets which serves as the climbing-organ.

Cobaea scandens. What is visible in these plants to the naked eye may be seen in others if we follow the developmental history as it was first traced in Cobaea scandens[1]. The effective tendrils of this plant are formed out of the end-portion of the pinnate leaves. The tendril-branches are at their end provided with small curved claws, by means of which the shoot of Cobaea is able to climb for great distances over tree-stems, rocks, and like objects. The history of development (see Figs. 286, 287) shows that these claws, which are very small, are vestiges of reduced or transformed laminae of leaflets, and the tendrils are the leaf-stalks. The development of the arms of the tendrils entirely conforms to that of the leaflets in the earliest stages, only in the formation of the tendrils in the upper part of the leaf a richer branching sets in, and the laminar primordia of the leaflets is arrested very early. The same thing is seen in species of Bignonia (Figs. 283, 284) and of Eccremocarpus.

FIG. 285. Desmoncus sp. Leaf. Transition of leaf-pinnules into hooks. Much reduced.

The tendrils do not, however, in all cases proceed from leaf-stalks or the stalks of leaflets. They may be formed by the early elongation of

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[1] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 431; A. Mann, Was bedeutet 'Metamorphose' in der Botanik? Inaug. Dissertation, München, 1894.

the primordium of the whole leaf, or of a portion of a leaf, and then the inception of a blade may no longer be visible. This is what takes place, so far as my investigations extend, in the Leguminosae, Cucurbitaceae, and Tropaeolum tricolorum [1]. In the Leguminosae, as in other cases, it is the end of the leaf which is transformed into the tendril [2], and in Pisum the primordium of a tendril may be caused to develop partially as a foliage-leaf (Fig. 289) [3] by separation of all other leaves and leaflets of the plant, and this is in correspondence with what has been said above [4] in regard to the behaviour of kataphylls.

Cucurbitaceae. The formation of tendrils in the Cucurbitaceae demands special description, as it has been for long a matter of dispute. It would be of no interest to discuss the literature of the subject, especially as, according to my view, the questions at issue are now settled [5]. We find in the Cucurbitaceae both simple and branched tendrils. The simple tendrils are the transformed *prophylls* of axillary shoots. For a long time these were not recognized as such, because there usually appears beside each axillary shoot only *one* tendril, and the prophylls in Dicotyledones are normally paired right and left of the axillary shoot. But we find the pair of prophylls, not infrequently, in the seedling-plant of the Cucurbitaceae, especially in Benincasa cerifera, where they are also visible in older plants; in other Cucurbitaceae [6] they seem to be confined to the seedling-plant, for example in Coccinia indica, where, however, they are retained for a somewhat long period, and where there are, as also in Momordica balsamina, transitions between the prophylls and the tendrils. The seedling-plants in one and the same species may show some variation; sometimes they have prophylls, sometimes there are none.

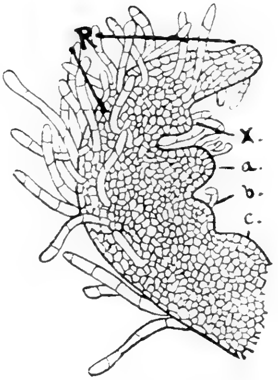

FIG. 286. Cobaea scandens. Young leaf. The upper part, *R*, is being formed as a tendril. *a*, *b*, *c*, leaf-pinnules; *x*, primordium of lowermost branch of tendril. Magnified. After A. Mann.

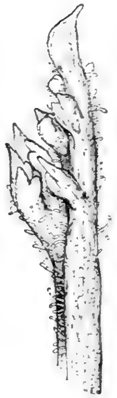

FIG. 287. Cobaea scandens. Young tendril formed from upper part of leaf. Branches of tendril are laid down like leaf-pinnules. The stalks of the leaf-pinnules, which are hardly visible in the figure, elongate into arms of the tendril. Magnified less than Fig. 286. After A. Mann.

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[1] See Part I, p. 163.

[2] See Part I, p. 162.

[3] As A. Mann has shown, Was bedeutet 'Metamorphose' in der Botanik? Inaug. Dissertation, München, 1894.

[4] See p. 388.

[5] Nevertheless, erroneous statements are still repeated, for example by Lubbock, On Buds and Stipules, London, 1899, p. 214.

[6] I have found, not infrequently, two prophylls on the seedling-plants of Cyclanthera.

Benincasa cerifera. If one follows the development of the embryo of Benincasa, one sees on the first axillary shoots one or two, on subsequent ones always two, prophylls of which one is transformed into a tendril which is at first rudimentary; occasionally this transformation does not take place. There may be observed sometimes[1] in the juvenile stages of these tendrils a trace of *the primordium of a leaf-lamina*, but, through the stretching in the formation of the tendril, this is no longer visible upon the mature tendril. The other prophyll is seldom developed into a form like the foliage-leaves (Fig. 288, 1), it mostly remains unsegmented (although traces of segmentation may be proved in the history of development), is scaphoid (Fig. 288, 4), deep green, and occasionally has an axillary shoot. Branched tendrils appear at a later period. They may arise in a similar way to those that will be presently described in Cucurbita[2].

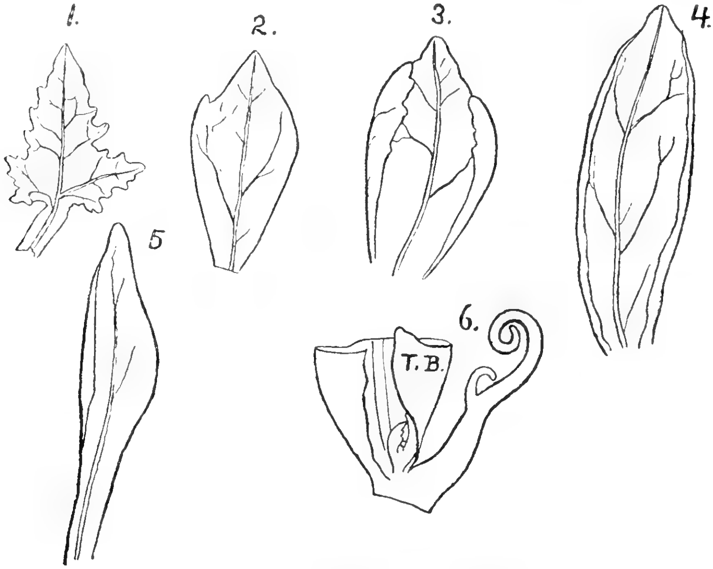

FIG. 288. Benincasa cerifera. 1–4, prophylls. 5, prophyll showing transition to a tendril. 6, portion of an axillant leaf, *T.B*, with two-armed tendril. All magnified. After A. Mann.

Cucumis sativa. I shall take next the case of Cucumis sativa. In the axil of a leaf we find a flower, beside it a vegetative shoot, and beside this a tendril. As the history of development shows, the flower is an axillary shoot of the foliage-leaf, and it bears only one prophyll which is transformed into the tendril. This position is determined by the fact that generally the *anodic side* of the leaf, that is to say, the side which is turned to the vegetative point, if one imagines the leaves disposed in a spiral[3], is furthered.

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[1] This, as I formerly showed, can be often seen in the Cucurbitaceae.

[2] Occasionally one tendril-arm takes the form of a foliage-leaf or a flower is formed upon the tendril. In that case the vegetative point of the axillary shoot usually is entirely used up in the formation of the second tendril-arm (see Fig. 201, III), which develops into flower.

[3] This assumes that the leaves are not inserted quite transversely but have the anodic margin inserted somewhat higher. The axillary shoot is not quite median.

Pilogyne suavis. In Pilogyne suavis we find that upon the *kathodic side* of the leaf-axil a tendril also arises which, however, is smaller than that upon the anodic side (see Fig. 290); evidently *one* axillary tendril is sufficient for climbing, and the plant raises itself up on its support like a gymnast who, freely suspended, climbs up a ladder using alternately the right and the left arm—just as in the shoot-tendrils of Ampelopsis the tendril-arms are placed alternately right and left.

We must assume that in other Cucurbitaceae the tendrils are transformed leaves—that the *simple tendrils* are the prophylls of axillary shoots of which only one prophyll is commonly developed, the other is wanting, but the *branched tendrils* are shoots which bear leaves transformed into tendrils. The reasons for this explanation are developmental and as follows:—

(*a*) We see that the tendrils belong to the axillary shoot beside which they stand.

(*b*) In the seedlings we can follow frequently the appearance of the prophylls, and in Benincasa a prophyll is often present beside the tendril in the mature plant.

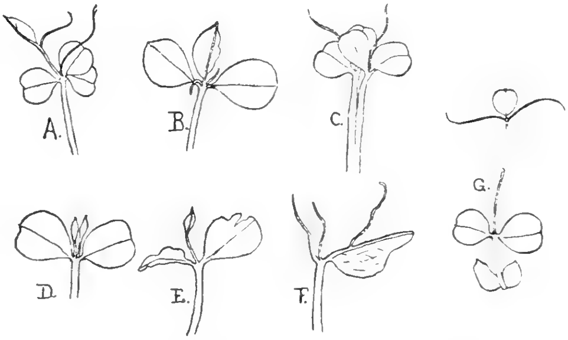

FIG. 289. Pisum sativum. A, B, C, D, E, F, G, artificial foliation of the tendrils. In G the stipules are shown. After A. Mann.

(*c*) The developmental history of the individual tendril shows in many cases clearly the direct transformation of the primordium of the foliage-leaf into a tendril: the leaf-lamina is still laid down but only in a rudimentary condition; it does not develop in breadth; the whole tendril grows markedly in length because there is often an embryonal apical growth which lasts much longer than it does in the foliage-leaves.

Müller's Investigations. This explanation of the tendril of the Cucurbitaceae does not quite agree with that which has been recently given by O. Müller[1] as the result of his anatomical investigations. According to him in some Cucurbitaceae which bear both simple and branched tendrils, for example Cyclanthera pedata, C. explodens, Thladiantha, as well as in some which have simple tendrils only, for example species of Bryonia, Coccinia, and Momordica, the non-sensitive base of the tendril is a shoot-axis, the upper portion is a 'leaf-spindle[2]'; whilst in Cucumis the lower part of the tendril also has the structure of a leaf-spindle. Upon this I may remark:—

1. Anatomical relationship *alone* can never solve a morphological problem.

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[1] O. Müller, Untersuchungen über die Ranken der Cucurbitaceen, in Cohn's Beiträge zur Biologie, v (1887), p. 97. The literature is faultily quoted in this work, for instance it is an error to say that Eichler considered the cucurbitaceous tendril to be a transformed stipule.

[2] The author does not say what he means by this term. The new anatomical school is not fond of giving clear morphological definitions.

There are shoots like, for example, the phylloclades of Asparagus medeoloides, which have entirely the structure of leaves, and there are leaves which have quite the structure of shoot-axes.

2. In many of the plants mentioned, for example Momordica balsamina, there are undoubtedly transitions between prophylls and tendrils.

3. It is indeed conceivable that in the formation of tendrils 'terminal leaves' may arise, that is to say the vegetative point of a shoot may be used for the formation of a tendril, and as a matter of fact such a condition appears to occur in the formation of the branched tendrils of Benincasa cerifera. But this process can only be determined for certain upon a basis of careful developmental and comparative investigation, which is indeed less easy than the popular riband-sectioning anatomy.

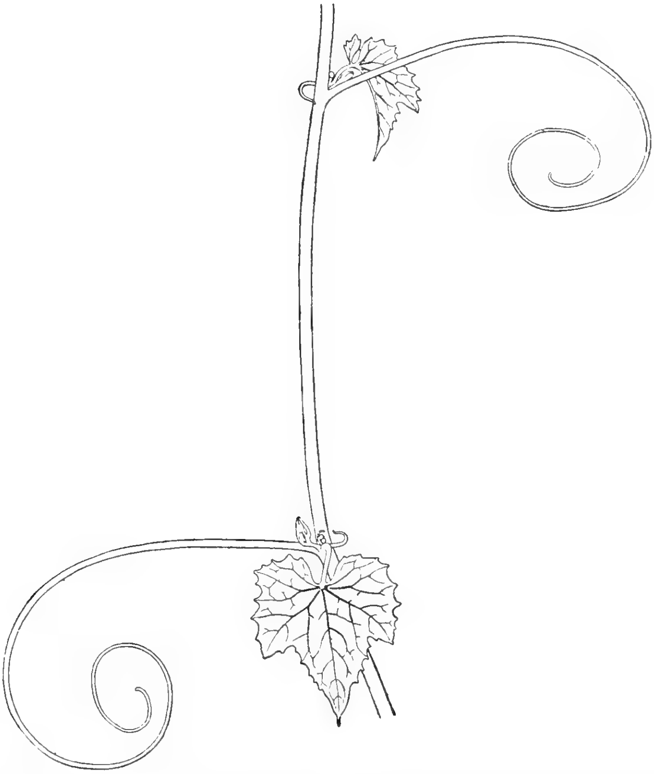

FIG. 290. Pilogyne suavis. Portion of shoot. Beside each leaf stand a developed and an arrested tendril.

An experimental 'foliation' of the tendrils of the Cucurbitaceae has not yet been achieved.

Cucurbita. We find spirally branched tendrils in Cucurbita. Here we have to do with an axillary shoot of the simple tendril, which itself is concrescent with its axillary shoot, and this axillary shoot brings forth a number of leaves which are developed as tendrils.

The tendrils of the garden cucumber consist of a stalk and a series of arms radiating from its apex. We may call them *compound tendrils*. The arms are really arranged in a spiral upon the stalk, and not infrequently this spiral position is exposed by the elongation of the internodes of the stalk, and one finds then single tendrils at the base of the stalk. In the seedling the elongation of the stalk from which the tendrils spring is suppressed at first, and it is clear that the stalk is of advantage in order to raise up the tendrils as far as possible and thus facilitate their getting hold of the support. Each tendril-arm is a transformed leaf, but the stalk which bears the tendrils is a shoot-axis. On the compound tendrils which I have studied, each tendril-arm has an axillary bud which not infrequently develops into flower, and in individual cases the stalk of the compound tendril became a shoot on which the tendrils in its upper part passed into leaves—often in such a way that only one-half of the leaf-lamina was developed, whilst the other part was wanting and the middle portion of the leaf was elongated beyond the leaf-surface in the form of a small tendril. Usually, however, the vegetative point of the shoot-axis, on which the tendrils are inserted, is arrested after their inception and they grow out apparently radiating from one point. That the stalk of the tendrils together with the tendrils is not to be considered as a single leaf is clear. We do not know of spirally arranged shoots upon a leaf, and besides the construction of the perfect tendril, as we know it in the cases described above, shows that it has nothing to do with such a configuration.

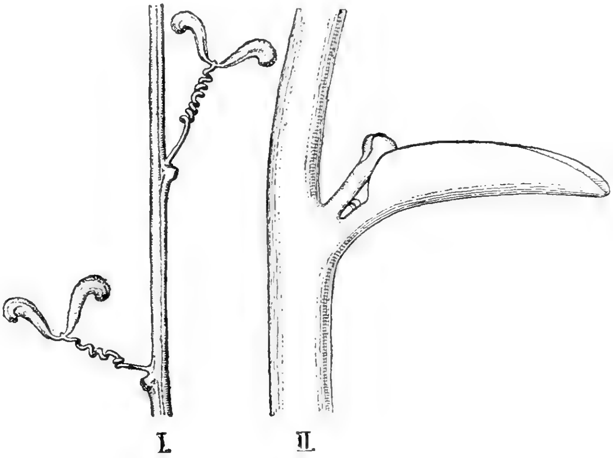

FIG. 291. Zanonia macrocarpa. I, portion of a shoot with axillary tendrils, The axillant leaves have fallen off. II, portion of shoot of a seedling plant, showing a tendril and a bud in the axil of the leaf. I, reduced.

Zanonieae. The relationships in the Zanonieae are not at all clear. In the year 1885 I concluded, from investigations previously made in Java, that dichotomously branched tendrils occur here and that the two arms become anchoring-disks (Fig. 291, I), whilst the lower part becomes coiled subsequently. On the seedling the primary leaves are reduced to small scales. In the axil of each of the two lowermost leaves there is found, at least at first, a resting-bud with two prophylls. Further up a two-armed tendril occurs in each leaf-axil, and its arms swell out without any stimulus of contact into anchoring-disks (Fig. 291). Beside the tendril is an axillary bud. Between the two arms of the tendril no vegetative point is visible.

Teratological phenomena. Teratological phenomena, which are not infrequent, especially in cultivated Cucurbitaceae, must be interpreted with care. Darwin mentions a case from Holland in which one of the short prickles of the fruit had apparently grown out into a tendril. In reality a tendril was here concrescent with the fruit.

B. MONOCOTYLEDONES.

In Monocotyledones tendrils are rare.

Smilax. The tendrils of Smilax have been already mentioned [1].

Gloriosa and **Littonia.** In Gloriosa and Littonia the narrow apex of the simple leaf acts as a tendril [2]. It is laid down at a very early period, and one might consider it as a transformed forerunner-tip. As for the conjecture which has been advanced that the leaf-lamina here is transformed into a tendril, and the leaf-base which gradually passes into the tendril is grown out in the same way as has that in Nepenthes, there is neither evidence in the history of the germination, nor, so far as I know, any other ground whatever for it.

THE FACTORS CAUSING TRANSFORMATION INTO TENDRILS. The manner in which the transformation into tendrils of leaves or parts of leaves takes place is evident from what I have said. What we want to know now is what factors come into consideration in the formation of tendrils and cause a strong transformation of the leaves. That the leaf-surface should be the more reduced the longer the tendril, is quite clear, as is also the advantage which accrues from the elongated form in the way of facilitating the tendril to find a support; for it gives a wider surface of grasping and a longer sensitive area. In tendrils which are formed out of the stalk of a leaf in process of arrest, one might refer back the abortion of the lamina to correlation, but that there is little probability in this we have seen, for the whole leaf-primordium can stretch into a tendril. Perhaps one of the influential factors to be considered in formation of tendrils is this, that in leaves, which were in the first instance sensitive to contact-stimuli but were not transformed even by their employment as climbing-organs, destruction of their other capacities, assimilation and the like, took place, and this resulted in a reduction in the formation of the lamina, and the consequent elongation of the leaf-parts into a tendril.

7. LEAVES AS THORNS.

The transformation of leaves into thorns may take place in different ways and in different degrees.

Astragalus. One instance in which it takes place relatively late has

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[1] See p. 223.

[2] The leaf thus resembles the primary leaf of Lathyrus Clymenum (Part I, Fig. 99, *II*).

been already mentioned in the case of some Leguminosae[1]. Species of Astragalus, for example A. horridus, A. Tragacantha, and others, and of Carragana, which live in dry localities, have pinnate leaves. The pinnules, which possess bilateral construction and have usually a profile position in nature, fall away, but the leaf-spindle remains behind and becomes a thorn.

Cicer subaphyllum. In Cicer subaphyllum, another leguminous plant, the leaf-spindle runs out into a hooked thorn, and the pinnules are also transformed into thorns[2].

Simple undivided leaves may also be transformed into branched thorns in another way:—

Berberis. Thus in Berberis the leaves of the long shoots are thorns. Transition-stages, which are known, show that the leaf-lamina becomes gradually more deeply cut at the edge as it diminishes in breadth, whilst several of the marginal teeth, which are fewer in number than appear in the foliage-leaves, develop considerably, and instead of the assimilation-parenchyma there is a dominance of sclerenchyma. The earlier in the developmental stages the formation of the thorn sets in, the more is the assimilating tissue reduced, and the more does the sclerenchyma predominate.

Cactaceae. The transformation of leaves into thorns is seen in greater degree in many cacti whose thorns[3] have a varying 'morphological value.' The thorns are here usually arranged in tufts on very short shoots. The view, which I have expressed elsewhere[4], that the thorns are transformed leaves, has been confirmed by the investigations of Ganong[5]. We must restrict our attention here to an exposition of the formation of the thorns in some of the Opuntieae. In Opuntia arborescens, for example, the arrangement of the thorns is peculiar, as they are all on the *outer* side of the vegetative point from which they shoot out, and therefore are disposed dorsiventrally. The foliar nature of the thorns is evident because one finds all transitions between thorns and leaves, and they can even be artificially produced. When a vegetative point of Opuntia ceases to produce thorns and begins to produce leaves, the transition is not a sudden one but gradual. After the last thorn there comes a structure which is leaf-like at the base, and then after that there is one which is more like a leaf. In the next there appears a trace of a vascular bundle and of an axillary shoot, and then comes a structure in which only the apex is thorn-like, and which possesses

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[1] See Part I, p. 9; also Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880).

[2] See the figure given by Reinke, Untersuchungen über die Assimilationsorgane der Leguminoseen, in Pringsheim's Jahrbücher, xxx (1897), p. 538.

[3] Stout spinose structures which are the result of the transformation of shoots or leaves are *thorns* not *prickles*, which are 'emergences.'

[4] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 36.

[5] W. F. Ganong, Beiträge zur Kenntniss der Morphologie und Biologie der Cakteen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 49, where the older literature is cited.

a well-developed axillary bud. Finally there follows a typical leaf. This development can be artificially induced if one causes the vegetative point of the short shoot, which produces thorns, to shoot out by cutting off the chief shoot. That the base of the incompletely transformed thorn retains its leaf-character is easily explained by the basipetal development of the leaf. The tissue in this region is embryonal, whilst at the apex it is already converted into a thorn. With regard to the function of the thorns there can be no doubt that they are protections against animals. I do not mean by that that the thorns have been produced by natural selection, they may have been induced by the dryness of the locality. Animals and men avoid most carefully an opuntia-bush because the small thorns especially are extremely irritating—they are beset with recurved hooks, and break off very easily because the tissue at the base is, with the exception of the fragile epidermis, disorganized.

Citrus. The thorns of Citrus and other genera of Aurantieae are also leaf-thorns. Owing to their position they were formerly considered as branch-thorns. They are found more or less accurately in the axil of the foliage-leaves, either singly or in pairs, and beside or between them lies a bud sometimes latent, sometimes active. In reality the bud is the axillary shoot, and its first leaf, or first pair of leaves, becomes thorny [1].

8. LEAVES AS NECTARIES.

The petals or stamens are transformed into nectaries in many flowers, for instance in the Ranunculaceae [2]. The transformation in the vegetative region of stipules into nectaries has been mentioned [3].

Cactaceae. The transformation of the whole primordium of a leaf into a nectary is as yet only known in the case of the Cactaceae. In a number of species of Opuntia [4], in which all transitions from thorns to nectaries occur, the nectaries are distinguished from the thorns, apart from their secretion, by their thickness and the possession of a vascular bundle. The same may be observed in some Mammillarieae. One would not consider the turbinate structure which secretes honey in the axil of the mammilla of Mammillaria macrothele and other species as a transformed leaf if the comparative history of development did not show that it was of this nature.

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[1] See Urban, Über die morphologische Bedeutung der Stacheln bei den Aurantieen, in Berichte der deutschen botanischen Gesellschaft, i (1883), p. 313.

[2] See p. 550.

[3] See p. 381.

[4] See Ganong, Beiträge zur Kenntniss der Morphologie und Biologie der Cakteen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 56.

B. BRANCHING OF THE SHOOT

The shoot develops out of the *bud* in which the internodes are still short and the leaves closely pressed together. Here, under the protection of the older parts, are the primordia of the new organs upon the vegetative point, in the first place those of the leaves, and next those of the lateral shoots. The formation of lateral shoots at the apex of the stem is suppressed entirely in only a few plants. We find this amongst the Pteridophyta in Ceratopteris, where an abundant formation of leaf-borne buds replaces them; in Ophioglossum, where there is a profuse formation of root-buds; in Isoetes, where leaf-borne buds appear exceptionally (Fig. 292)[1]; and in the Marattiaceae with tuberous stem. In many forms which are commonly unbranched the capacity for branching remains 'latent,' probably because the primordia of lateral shoots are present, but commonly are undeveloped. This is the case in tree-ferns. I saw Dicksonia antarctica frequently in Australia with many 'heads,' and the development of these was probably caused by damage done to the chief axis. Also in palms, which except in the inflorescences do not produce, as a rule, lateral shoots, vegetative branching sometimes, although perhaps rarely, appears. Such branching is entirely excluded in Welwitschia mirabilis.

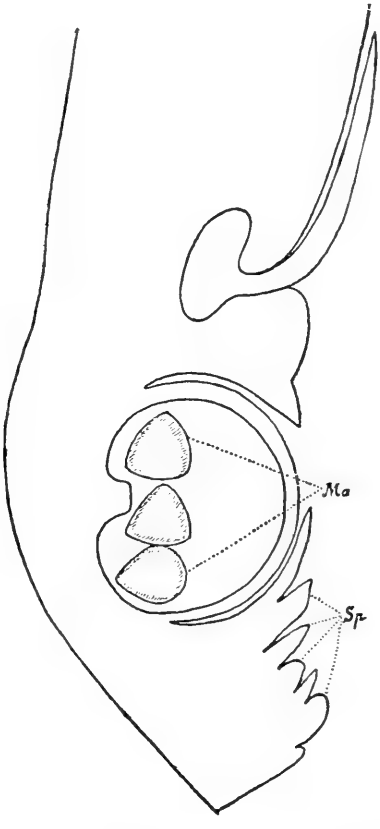

FIG. 292. Isoetes lacustris. Lower portion of a leaf in longitudinal section. Beneath the reduced megasporangium, *Ma*, a shoot, *Sp*, develops as a leaf-borne shoot. Magnified.

AXILLARY BRANCHING AND EXCEPTIONS. The method of the branching in the Pteridophyta and Spermophyta varies with the space-relationships of the leaves. In the Spermophyta *axillary branching* is the rule, that is to say, a lateral shoot arises out of the axil of a subtending leaf. This is, however, not without exception. In the Pteridophyta, as in the Musci, this

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[1] See Goebel, Ueber Sprossbildung auf Isoetes-Blättern, in Botanische Zeitung, xxxvii (1879).

relationship does not exist. In the Lycopodineae, for example, we have all transitions, from a dichotomous division of the shoot-apex to the formation of lateral shoots which are laid down indeed near the apex but are smaller than the shoot-apex of the chief axis. The primordia of the twigs do not, however, stand in the axil of the primordium of a leaf; as they far exceed these in size each twig-primordium stands over a great number of the leaf-primordia[1]. The lateral shoots in Equisetum too do not spring out of the axil of the leaves, but they alternate with the teeth of the leaf-sheath. With regard to the branching of the ferns nothing more can be said here. In the Spermophyta it is specially dorsiventral shoots which show a divergence in position of the lateral buds[2]. Formal morphology has made many efforts to refer back the branching of the Spermophyta to one definite scheme. Pringsheim[3], for example, as the result of insufficient observations, made out the branching to be a division of the vegetative point of the shoot. Hofmeister[4] believed that the lateral shoots always stood higher on the vegetative point than the youngest leaves. Nägeli[5] distinguished between 'acrogenous' and 'phyllogenous' (axillary) branching, and ascribed the latter to the Equisetaceae and the Spermophyta. There is really no such scheme as any one of these. The branching is indeed usually axillary but the relationship between leaf and axillary shoot is not the same everywhere.

TIME-RELATIONSHIP IN DEVELOPMENT OF AXILLARY SHOOT AND AXILLANT LEAF. Let us first of all consider the relationships in time. We may, so far as I can see, say generally, as was said in the case of the development of the leaf, that *the organs which are earliest unfolded are also earliest laid down.* Thus the leaf arises in the vegetative region usually much earlier than its axillary bud[6]. The winter-buds of Syringa, for example, consist of the leaves laid down in the preceding year, and the axillary buds of these leaves are only laid down in their axils *as the bud unfolds*; above the leaves in whose axil the first primordium of a bud is visible one finds three to four pairs of leaves without buds. The leaves then are laid down in one vegetative period, the axillary shoots are laid down in the next[7]. The axillary shoots proceed from groups of cells of the axis of the shoot immediately above the insertion of a leaf, and these groups derived from the embryonal tissue of the vegetative point have retained their embryonal character, but only at a late period, are stimulated to a new

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[1] As is shown by an examination of Lycopodium clavatum.

[2] See Part I, p. 90.

[3] Pringsheim, Über die Bildungsvorgänge am Vegetationskegel von Utricularia vulgaris, in Monatsberichte der Berliner Akademie, 1869.

[4] Hofmeister, Allgemeine Morphologie der Gewächse, Leipzig, 1868, p. 408.

[5] Nägeli, Theorie der Abstammungslehre, p. 478.

[6] See Warming, Forgreningsforhold hos Fanerogamerne, in Kongelige danske Videnskabernes Selskabs Skrifter, Række 5, x (1872); Koch, Die vegetative Verzweigung der höhern Gewächse, in Pringsheim's Jahrbücher, xxv (1893). The older literature will be found in these works.

[7] In other trees, for instance Fagus, axillary buds are already laid down in the winter-bud.

formation, into which also lower and already more differentiated cells can be brought. We see the same thing in other cases amongst trees and shrubs and in the seedlings of herbs where, if one may so say, the plant at first produces the necessary leaf-apparatus whose formation is later on lessened. Where, as in long shoots of Berberis, the lateral shoots, which are leafy short shoots, are unfolded rapidly, they also appear very near the apex. This also holds for many water-plants.

In the inflorescence also of many plants, for example Amorpha and Salix, the leaves nearest to the vegetative point have still no axillary bud, but it is more common to find in the flower-region the axillary buds developing so early that they are the lateral outgrowths of the axis nearest to the vegetative point and there are no primordia of leaves above them, and this independently of whether the axillary bud arises immediately after its subtending leaf as in Plantago, Orchis, and Epipactis, or at the same time with it as in the Gramineae, Cytisus Laburnum, Trifolium, Orchis mascula and Plantago, or before it as in Brassica oleracea var. botrytis and other Cruciferae, Umbelliferae. Lastly it may happen that lateral buds are developed without any trace whatever of a subtending leaf and this takes place in many Cruciferae, Compositae like Inula, Gramineae like Secale cereale in the upper part of its inflorescence. There is then in the flower-region a hastening in the formation of the lateral shoots which is often associated with a reduction in the development of the subtending leaves and which may go so far that these may disappear altogether. This reduction in some cases, as in the Gramineae, may be followed from below upwards upon one and the same inflorescence. The bracts of the twigs of the inflorescence are most developed in this family in the lower part of the inflorescence, where however they have but the form of short sheath-like primordial leaves or of cushions, whilst in the upper part they are only visible at the very first inception of the lateral twigs and do not reach any further development or as in the case of Secale cereale are wanting altogether. We find the same in Sisymbrium where the formation of the bract is still visible at the base of the inflorescence, but further up there is no trace of one. Similarly the outer flowers in the umbel of many Umbelliferae have bracts but the inner ones have none. In these, as in other cases, protection of the flower-bud is attained in other ways, in the Umbelliferae for instance by the concentrated position of the flowers and their envelopment by leaf-sheaths[1]. The lateral shoots, to which bracts fail, have the same origin as if these were present. They do not arise, as was at one time in a measure supposed, by division of the vegetative point of the chief axis. This only happens in flowering plants occasionally[2].

ACCESSORY SHOOTS. That the lateral shoots are products of the *shoot-*

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[1] See Part I, p. 59.

[2] See below, p. 435, for the case of Vitis.

axis and become displaced subsequently more upon the leaf-base can be clearly seen in the examples just mentioned, especially also in those cases in which out of one leaf-axil *many* shoots arise. This may either result from the early branching of an axillary bud or from the development of many independent shoots out of the embryonal tissue of the shoot-axis. In the leaf-axils of Aristolochia Clematitis we find a number of flowers arranged in two zigzag rows. The oldest is furthest from the leaf-axil. In Aristolochia Sipho and Menispermum canadense, above the cotyledons of Juglans regia, and in other cases, such lateral buds stand in a simple row above the axil. The history of development [1] of Aristolochia Sipho and A. Clematitis as well as of Menispermum canadense shows that the buds in these rows arise independently one from another out of the stem-tissue. 'The fact is simply this, that in a leaf-axil where otherwise one shoot occurs the tissue of the vegetative point of the stem remains long in the condition of a vegetative point and forms a number of buds in progressive serial succession.' These shoots then spring out of a tissue-cushion formed by the intercalary vegetative point of the stem above the leaf-base. Putting on one side the case of Aristolochia Clematitis—in which the upper of these serial buds form flowers whilst the under form leaf-shoots—it may be noted that most of these buds usually do not unfold; it is only the uppermost one which develops, whilst the others become resting-buds and only develop if the chief bud is injured. In Juglans regia, for example, there may be above the axil of the cotyledons as many as eight primordia of shoots and of these the uppermost is the strongest. Not one of all these primordia usually grows out but they gradually dry up and after some years, when the axis has become thicker and the outermost layer of the rind has died off and split, there is visible no trace whatever of them. But if in the course of the first or second year of the existence of the plant the end-shoot is destroyed then one or more of these primordia begin to grow. Gymnocladus canadensis behaves in a like manner. In Gleditschia sinensis the primordia of the shoots which occur in numbers in a row in the leaf-axils behave in such a way that the uppermost develops into a thorn, the next into a foliage-shoot, and those lower down either into foliage-leaf-buds or if they first shoot out on older portions of the stem they become thorns [2]. Many attempts have been made to refer these cases to a repeated branching of one axillary shoot [3], and sharp limits between the two interpretations can scarcely be drawn. If one supposes that the tissue of the first axillary shoot has with its inner (upper) side

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[1] Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arbeiten des botanischen Instituts in Würzburg, ii (1882), p. 391. Koch, Die vegetative Verzweigung der höhern Gewächse, in Pringsheim's Jahrbücher, xxv (1893), came to the same results.

[2] See A. Hansen, Vergleichende Untersuchungen über Adventivbildungen bei Pflanzen, in Abhandlungen der Senckenbergischen naturforschenden Gesellschaft, xii (1881), p. 169.

[3] See Russell, Recherches sur les bourgeons multiples, in Annales des sciences naturelles, sér. 7, xv (1892).

united with the tissue of the chief axis and produces upon its embryonal outer side a series of shoots, this construction would give in a certain measure the scheme of the axillary branching.

SHOOT-TENDRILS OF AMPELIDEAE. The shoot-tendrils of the Ampelideae have given rise to much discussion. They stand laterally on the primary axis without a subtending leaf in their developed condition. Phyletically these tendrils are derived from terminal inflorescences. They are pushed to the side by the formation of vegetative lateral shoots and the whole construction is then sympodial[1]. The history of development (see Fig. 293) has been examined by many observers and shows that the tendrils are not, as one would expect according to the theory just stated, formed as the evident continuation of the internode immediately below them and then only gradually pushed to the side by the stronger growth of their uppermost axillary shoot, but that they either from the first have the leaf-opposed position of the mature condition[2] or, that they proceed from the apex of the axis itself through its unequal division, and in this way the other portion of the vine is formed[3]. There occurs in the plant a rapid continuation of the vegetative skeleton which finds its expression in the behaviour of the vegetative point; whether we speak of a sympodium or a monopodium depends entirely upon what one chooses to express by these terms[4].

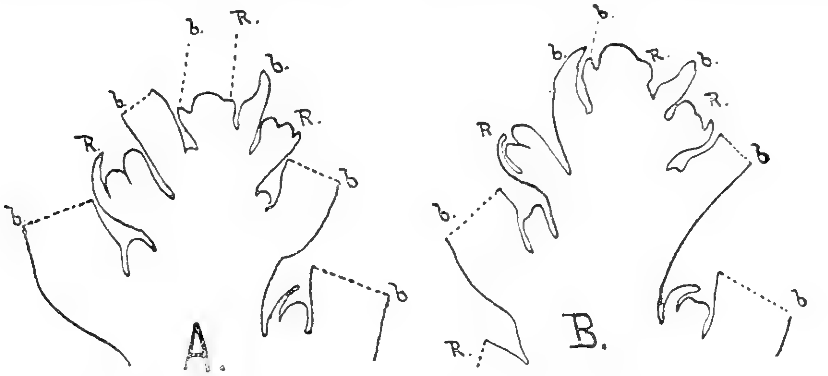

FIG. 293. *A*, Vitis vulpina ('odoratissima'). *B*, Vitis cinerea. *R*, tendrils; *b*, eaves. After A. Mann.

FOLIAR ORIGIN OF SHOOTS. The axillary shoot is, as has been said[5], the product of the shoot-axis in many cases and becomes displaced upon the base of the leaf. Koch is inclined to take this as the general rule but this

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[1] As this explanation is found in all textbooks I need not dwell upon it further.

[2] As Nägeli, Schwendener, and Warming have shown in Ampelopsis.

[3] As Prillieux and Warming have shown in Vitis vulpina.

[4] According as one gives preference to the phyletic (comparative) or the developmental standpoint. The assumption that a branch-system originally laid down as a sympodium may become monopodial is probable in more than one case—fern-leaf, inflorescence of Boragineae, Hyoscyamus. The biological significance of these phenomena has been discussed above, see p. 316.

[5] See p. 432.

appears to me to be a by no means well-founded generalization. There is no good reason why the primordia of shoots should not arise upon the *leaf-base.* We see them in this position in many ferns and in Isoetes (Fig. 292). In Bryophyllum calycinum also and other plants they occur even upon the leaf-surface and there they always develop out of *still embryonal* leaf-tissue. Formation of adventitious shoots upon cut mature leaves is an extremely common phenomenon. As has been already stated a sharp limit between leaf-base and shoot-axis does not really occur. There is at any rate in many cases an intimate connexion between subtending leaf and axillary shoot which finds expression especially in this, that the axillary shoot 'grows up upon' its subtending leaf—that is to say, the common base of the two is elongated. We find this in many Cactaceae[1] especially in Mammillarieae. Fleshy outgrowths appear in these plants upon the shoot-axis and bear at their apex a tuft of thorns and in their axils there are frequently flowers. These fleshy outgrowths were formerly regarded as leaves; but the mammilla consists of two parts[2]: first the lower strong-grown part of the leaf which may be called the 'leaf-cushion'; second the axillary shoot which is united throughout its length with the upper part of the leaf-cushion. The vegetative point of the axillary shoot frequently divides into two parts which are later separated by permanent tissue—an upper part which only brings forth leaf-thorns, and an under part which becomes a flower or a vegetative axillary shoot. In many Mammillarieae the flowers arise also upon the apex of the mammillae and then we have quite similar relationships to those in other plants where the *flowers or inflorescences are leaf-borne.* We must not confuse with these the cases where the flowers are falsely described as leaf-borne, as for example in species of Limnanthemum[3] or in the case of phylloclades[4].

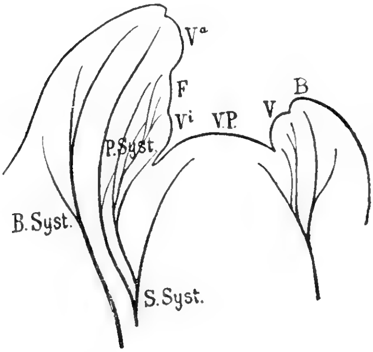

FIG. 294. Mammillaria. Diagrammatic representation of a vegetative point with forked mammillae in longitudinal section. *VP* vegetative point, the young mammilla to the right consists of leaf, *B*, and its axillary shoot, *V*, grown up upon it. The vegetative point of the axillary shoot will divide as the mammilla to the left shows into an upper, V^a, and a lower, V^i, separated by permanent tissue, *F*. *B. Syst*, leaf-bundles; *P. Syst*, axillary shoot-bundles; *S. Syst*, main shoot bundles. After Ganong.

EPIPHYLLOUS INFLORESCENCE. We find the inflorescence of some Dicotyledones on the leaves[5] for example in Helwingia japonica, Dulongia

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[1] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 79; Ganong, Beiträge zur Kenntniss der Morphologie und Biologie der Cakteen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 48.

[2] See Goebel, op. cit.

[3] See Goebel, Morphologische und biologische Studien: VI. Limnanthemum, in Annales du jardin botanique de Buitenzorg, ix (1891).

[4] See p. 449.

[5] See C. de Candolle, Recherches sur les inflorescences épiphylles, in Mémoires de la Société de

acuminata (Phyllonoma), species of Chailletia, Stephanodium peruvianum, Polycardia phyllanthoides, Begonia sinuata, B. prolifera, and others. In the most of these instances we might have to deal with a 'displacement' of the *bud from the leaf-axil* and a 'concrescence' of it with the leaf, taking place in exactly the same way as was described in the case of the Cactaceae and of Spathiphyllum platyspatha[1]. Such a concrescence occurs in Helwingia ruscifolia, where the inflorescence is laid down in the leaf-axil. But in other cases the axillary bud may from the first be produced rather upon the surface of the subtending leaf near its base. We find this in Dulongia which is shown in Fig. 295. The inflorescence arises here upon the upper side of the leaf below its 'forerunner tip' which differs from that of the other leaves. There is no reason for regarding the leaf as a leaf-like twig; it has stipules at its base; it had in the few cases I examined an axillary bud just like the mammilla of the Mammillarieae; and it has also the usual origin of a leaf. That the primordium of the inflorescence appears first of all near the base of the leaf corresponds to the intercalary growth of the leaf; the anatomical character of the 'sterile' leaves examined by C. de Candolle does not differ essentially from that of the 'fertile' leaves, and this may be so because the conducting system of the midrib of the leaf is sufficient for the care of the small-flowered inflorescence, from which only one or two fruits arise, so far as herbarium-specimens enable me to judge. Whether the peculiar phenomenon of epiphyllous inflorescences stands in relationship to the conditions of life or only illustrates what has been designated by the beautiful name of 'construction-variation' is unknown.

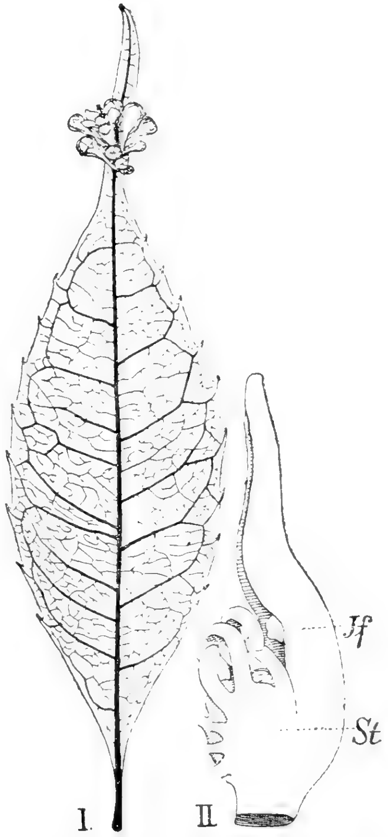

FIG. 295. Dulongia acuminata, H.B.K. I, leaf with inflorescence. II, young leaf seen from the side. *Jf*, primordium of inflorescence; *St*, one of the stipules with stalked marginal glands some of which have been broken off. I, magnified 2. II, more highly magnified.

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physique et d'histoire naturelles de Genève, Volume supplémentaire, 1891. De Candolle's investigations are inadequate for the solution of the question where the *first inception* takes place. He trusts chiefly to anatomy which is only of secondary importance in such problems. There are many transformations in configuration which find no expression in anatomy. De Candolle does not notice the instructive features in the Cactaceae.

[1] See Part I, p. 55, Figs. 23, 24.

ADHESION OF THE BRACT. In the cases just mentioned the *bract is predominant*; it is the most conspicuous part of the construction and we therefore commonly speak of the 'adhesion of the axillary shoot' to its bract. Quite the same process only with *predominance of the shoot* is seen in the very abundant cases of 'adhesion of the bract' to its axillary shoot. We cannot however here discuss this condition; its biological significance has not been investigated. That it has such a significance I do not doubt as the result of casual examination of the Solanaceae.

Atropa. In Atropa the sympodially constructed flower-bearing shoots are, as has been already pointed out[1], dorsiventral and the position and formation of the leaves stand in connexion therewith; but in the peculiar 'displacement' which the leaves obtain by the 'adhesion of the bract to its axillary shoot' we have, in my view, an arrangement for the protection of the flower-buds. If we examine a transverse section through a bud of the inflorescence of Atropa as we see it in Fig. 296, we shall find that each flower-bud is protected by two leaves turned towards the *outer side* of the whole inflorescence much more so than is shown in the figure which is taken through the lower portion of the older leaves where the lamina has only a narrow surface. One of these leaves is the bract, *T*, adherent to the flower-stalk, the other is one of the two prophylls, *V*, of the flower. Seeing that the bract stands at *about the same height* as the prophyll the

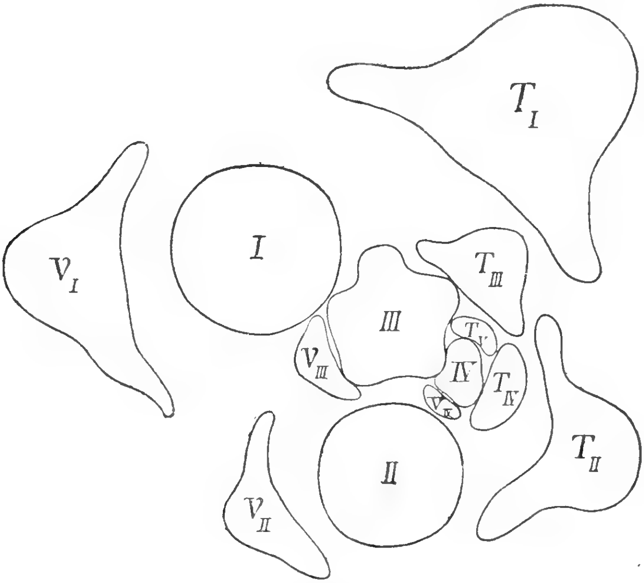

FIG. 296. Atropa Belladonna. Bud of inflorescence in transverse section. *I, II, III, IV*, flowers. T_{I}, T_{II}, T_{III}, T_{IV}, T_{V}, successive bracts concrescent with the flower-axes. To flower *I* belong as prophylls V_{I} and T_{II}, to flower *II* belong V_{II} and T_{III}, to flower *III* belong V_{III} and T_{IV}, to flower *IV* belong V_{IV} and T_{V}.

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[1] See Part I, p. 113.

closure round the flower *towards the outside* is made possible and this not only affects the individual flower but also all the parts which lie inside[1]. I believe that in this way it is possible to interpret, upon biological grounds, relationships which have hitherto only been treated from the side of formal morphology. At any rate, in the flower-bud, which is marked *III*, it appears that the first sepal arises in the position which is least protected by other parts, an incident which is self-explanatory. We shall speak of analogous cases when considering the development of the flower.

ARRESTED BUDS. Of the lateral buds which are laid down it is only seldom that all develop further. Some are arrested either at once if they are flower-buds or if they are vegetative buds they remain for some time capable of development and may under special conditions such as loss of other shoots enter into activity[2]. The branching renders easy also the division of labour amongst the several shoots, the more important different forms of which I must now refer to.

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[1] Other Solanaceae show the same features. In Datura the adhesion of the bracts closes the bud on the outside. The leaves have in Datura, as in Atropa, a large 'forerunner-tip.'

[2] See Part I, pp. 58 and 208.

C. DIFFERENT CONSTRUCTION OF THE SHOOT. DIVISION OF LABOUR

Just as we consider the foliage-leaf to be the typical leaf by the transformation of which the other leaf-forms arise so we take the foliage-shoot or assimilation-shoot to be the typical shoot, and we can show that there may be also a change of function in it, and that therewith is bound up a change in conformation. The transformation may take place here also early or late. A shoot of Prunus spinosa, for example, bears at first a number of foliage-leaves decreasing in size upwards and then it becomes a thorn. It is first of all foliage-shoot and then thorn, and it is easy to cause its further development as a foliage-shoot if one cuts off sufficiently early the apex of the shoot from which it arises—that is to say before the determination of the character of the twig as a thorn. The stolons of Circaea lutetiana and C. alpina arise in the ground, are stolons from the beginning, and produce only small scale-leaves, but by definite influences referred to below, we can induce a plant, which has already produced a number of leaf-pairs, to grow out at its apex—that normally would become an inflorescence—into a stolon below the soil. Even shoots, which are changed to the great extent observable in the flower-shoots, may in their earliest stages grow out further as foliage-shoots, for example the female flowers of Cycas. In other cases this takes place only exceptionally where pathological changes occur. The plant takes the organs which are necessary first of all for its existence, and these are the assimilation-organs, and adapts them to other functions.

We speak of the most important shoot-forms shortly in relation to their function, and this depends upon the manner of life of the plants, using this expression in its widest sense. Two factors have specially to be considered:—

(*a*) The relationship of the reproductive organs to the vegetative organs.

(*b*) The influencing of the vegetative organs by the external conditions of life.

Division of Labour and Duration of Shoots. In the Spermophyta the division of labour amongst the shoots is the less marked the more rapidly they proceed to the formation of seeds, and it is plants which last during many vegetative periods interrupted by periodic stages of rest before they produce flower that have shoot-forms adapted to very different functions.

In annual Spermophyta there is no division of labour between the vegetative shoots. All these shoots are attuned to a life in light and pass finally all of them to the formation of flower. The primordia of shoots in the under region of the plants remain however often undeveloped or only develop if the nutrition is particularly abundant or if there is injury to the chief shoot. The complex shoot-formations have sprung from that of the annual plants. The later in the developmental stages the formation of the reproductive organs is undertaken, the more opportunity is there, as has already been remarked [1], for the vegetative body to increase in mass and to experience that division of labour which is bound up with this.

Among the Pteridophyta there are relatively few annual forms, for instance Anogramme leptophylla and A. chaerophylla, Salvinia natans, and Selaginella Drummondi [2]. These are all adapted to localities in which there is a periodic interruption in vegetation, in the resting period the spores are the only things which are left over. Where more uniform conditions of life exist annual Pteridophyta are not present. The tropical species of Salvinia, for example, known to me have all an unlimited existence. The perennating Pteridophyta conform with the Spermophyta in the configuration of their shoots although they show in general a less varied adaptation than these do.

RELATIONSHIPS OF THE SHOOTS TO THEIR FUNCTION. The doctrine of the 'succession of shoots,' that is to say the construction of the plant-body out of shoots with different function and of different conformation, cannot be stated shortly here [3]. We can only speak in general of the relationships of the shoots to their function. This will be done in two sections, the first one dealing with the shoot as a vegetative organ and the second with the shoot in the service of reproduction.

THE SHOOT IN VEGETATION

The most striking differences observable in vegetative shoots are those between *epigeous* and *hypogeous* shoots; but there is really no sharp distinction to be made between them. Yet it appears to me better to treat of them separately because there are a number of biological characters which are different in each.

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[1] See Part I, p. 141.

[2] Ceratopteris thalictroides can hardly be included. It propagates freely by leaf-borne shoots, it is like many other marsh and water-plants adapted to rapid changes in environment expressed in the short limit of existence imposed upon single shoots. It is not adapted however to periodic changes in environment.

[3] Raunkiær, De Danske Blomsterplanters Naturhistorie, Bd. 1, Kjøbenhavn, 1895–9, gives an excellent account of these relationships so far as European monocotylous plants are concerned. The literature is fully cited.

I

EPIGEOUS (PHOTOPHILOUS) SHOOTS

(*a*) ORTHOTROPOUS RADIAL SHOOTS AND THEIR TRANSFORMATIONS.

1. ARRANGEMENT OF THE LEAVES AND LENGTH OF INTERNODES.

There are two important features in this configuration—

1. The arrangement of the leaves,
2. The length of the internodes.

In shoot-axes with *elongated* internodes the method of arrangement of the leaves within somewhat wide limits is of clearly little biological importance. Whether the leaves on an elongated shoot are in whorls or are distributed in the phyllotaxy of $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, and so on, is of little moment for the function of the leaves, because they cannot cover one another or shade one another for long.

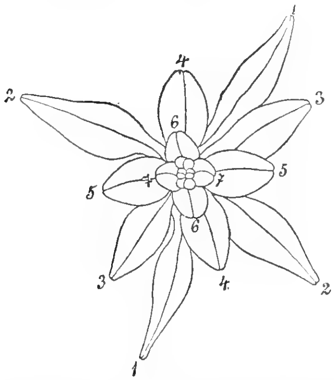

FIG. 297. Callitriche verna. Leaf-rosette from above. Magnified 3.

It is different in plants with short *contracted* internodes, and here there are frequently arrangements by which the overlapping of the leaves is prevented. Some examples of these may now be given:—

Callitriche. Callitriche (Fig. 297) has leaves in decussate pairs. The internodes are at first elongated. If the apex of the shoot of this water-plant reaches the surface of the water an arrest takes place in the elongation of the internodes. They remain short but one can cause them to elongate by submerging the plant[1]. If now the leaf-pairs were strictly decussate they would so cover one another that only the two uppermost pairs would be exposed to direct light. This is avoided by torsion of the internode (Fig. 297)[2] and the well-known 'water-star' is formed, the older leaves in which are brought beyond the younger ones by the stalk-like elongation of their bases.

Similar features are observed in some species of Cyperus which have a one-third spiral phyllotaxy. Figs. 298 and 299 show the torsion of the leaf-rows. It is well known that in Pandanus also and some species of distichous Aloe like features are observed.

It is clear that the same result would be obtained if the leaves were from the first spirally arranged with a higher divergence, and we find this in many species of Sempervivum and Sedum and in the floating leaf-rosettes of Trapa, Pistia, and others.

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[1] The plant at first endeavours by elongating the internodes to bring the leaf-rosette to the surface of the water, if this does not suffice then the internodes which normally would be short elongate.

[2] I leave on one side the question whether there is not a divergence from the decussate position in the inception of the primordia on the vegetative point.

Gentiana. Plants such as Gentiana acaulis, G. verna, Arnica montana which have decussate leaves in a basal leaf-rosette, are no exception. It can be readily observed in Gentiana acaulis, for example, that the number of leaf-pairs at the base is *very small*, I have usually found here only four assimilating leaves in the rosette[1], so that there can be no covering by the individual leaves. The species of Gentiana which form a greater number of leaf-pairs, like Gentiana lutea, G. asclepiadea, and others, have *elongated* internodes. Shoots with contracted internodes are found in plants of the most different cycles of affinity, and living under the most different conditions, so that no general explanation of this arrangement can be given.

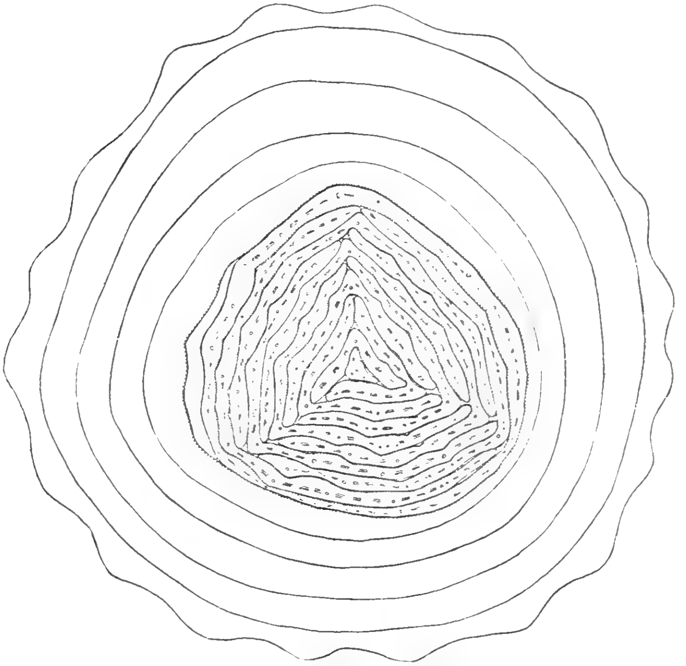

FIG. 298. Cyperus alternifolius. Bud invested by kataphylls shown in transverse section. The tristichous arrangement of the leaves is evident but is already somewhat distorted in the lower ones.

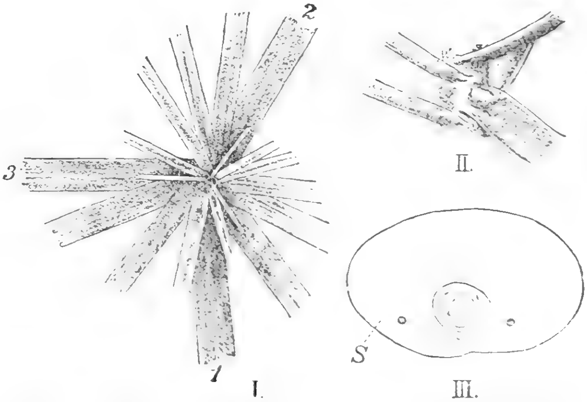

FIG. 290. Cyperus alternifolius. I, shoot from above, the leaves are clipped. The tristichous arrangement slightly distorted is indicated by the figures 1, 2, 3. II, leaf with axillary bud. III, axillary bud in transverse section. *S*, prophyll swollen up. I, half natural size. III, magnified.

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[1] If it were six the uppermost pair was very small and could only cover the lower part poor in chlorophyll of the leaf-pair below. I found the same in G. verna. The older etiolated leaves, which are still retained, are of course not considered.

2. SHORT SHOOTS AND LONG SHOOTS.

One of the most frequent divisions of labour observed upon the vegetative shoots, is that into *short shoots* and *long shoots*. This terminology is hardly fitting, because the diagnosis of the two shoot-forms lies less in their length than in their significance in the construction of the woody plants in which they are almost exclusively found. The short shoots take no share in the construction of the permanent skeleton of the plant. They die after a comparatively short time. Their shoot-axis does not branch vegetatively or form any mass of wood. Yet the short shoots are frequently those which produce the flowers, and this conforms entirely with the fact that restriction of vegetative growth favours the formation of flower[1]. It is impossible to draw a sharp limit between long shoots and short shoots. In many plants, for instance Larix europaea, short shoots may spontaneously grow out into long shoots, and under unfavourable conditions the formation of long shoots may be suppressed for years. In other cases the same result is brought about by the cutting off of the long shoots, even in cases where the short shoots are so sharply distinguished from the long ones as they are in species of Pinus. In Pinus, after the first few years of life[2], the long shoots produce the scale-leaves only, the assimilation-leaves are limited to the short shoots on which they appear in pairs, as in P. sylvestris, or in greater numbers, five for instance in P. Strobus. In Pinus also the short shoots may be caused to grow out into long shoots; they are only quantitatively, not qualitatively, different from them.

Double needles of Sciadopitys. In the remarkable short shoots of Sciadopitys there is occasionally observed a 'continuation of growth[3].' These short shoots are commonly called *double needles*. As a matter of fact one sees upon young just elongated shoots the combination of two 'concrescent' needles between which a longitudinal furrow is very conspicuous. These double needles stand in the axil of small scales upon the stem and have therefore the same position as the short shoots of Pinus. They are traversed by two completely separate vascular bundles which are enclosed by the peculiar *transfusion-tissue* of the coniferous leaf, and von Mohl[4] upon this basis suggested that they were the result of the concrescence of the two first leaves of an axillary shoot which was otherwise arrested. The history of development as published by Strasburger[5] is very peculiar and requires, I think, further proof. There arises in the axil of the scale the primordium of an axillary bud which shows very early an evident median indentation at the apex, and this is still recognizable on the mature double needle. According to Strasburger this whole structure is the

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[1] See Part I, p. 212.

[2] Regarding juvenile stages see Part I, p. 153.

[3] See Carrière's figure in Gardeners' Chronicle, March 1, 1884, p. 282.

[4] Von Mohl, Morphologische Betrachtungen der Blätter von Sciadopitys, in Botanische Zeitung, xxix (1871), p. 101.

[5] Strasburger, Die Coniferen und die Gnetaceen, Jena, 1872, p. 382.

primordium of the double needle. It grows at its base like other needles after apical growth has ceased at an early period. The apex then of the axillary shoot is here used up in the formation of the needles, but the individual needles of the combined body do not grow separately but by intercalary growth at their common base. There can be no doubt that the structure corresponds to the primordium of a short shoot of Pinus, in which only two leaf-primordia are laid down, but the interpretation of the double needle as being formed out of two concrescent 'leaves' appears to me [1] to be by no means devoid of doubt although Strasburger has found double needles both in Pinus sylvestris and in Pinus Pumilo. We do not know the mode of origin of these needles in Pinus. They might be the result of an actual concrescence of two needles whereby *the vegetative point of the short shoot remains behind at the base* and the needles are joined together by their contiguous sides; but in Sciadopitys the chief portion of the needle proceeds from the part of the axillary bud which lies below its vegetative point. Sciadopitys affords in the vegetative region an example which has no parallel elsewhere, and according to the ordinary terminology we must regard the double needle rather as leaf-like twig—a phylloclade—bearing on its primordium the tips of two needles as small points, notwithstanding the anatomical fact, which however is not after all of much importance, that we know elsewhere also phylloclades which in their structure resemble leaves. The actual name we use is of less importance; the fact remains that out of the axillary shoot there proceeds a structure which in its construction resembles two leaves united by their edges.

PRECEDENCE IN UNFOLDING OF SHORT SHOOTS. The short shoots precede in their unfolding the long shoots in most instances and this we can understand upon biological grounds, because less energy and less material is required for them than for the long shoots. The capacity for assimilation also of the short shoots partly comes into consideration. In Larix, for example, they have to furnish the material for the formation of the long shoots, and in plants like Pyrus and Prunus, which have entomophilous flowers, their development before the long shoots is of marked advantage for the exposure of the 'flag-apparatus' of the flowers. That the short shoots of Pinus and Berberis unfold at the same time as their subtending leaves, is a consequence of the transformation of these leaves into kataphylls and thorns.

ASSIMILATING SHOOT-AXES. Shoot-axes whose internodes are elongated may share in the work of assimilation if they contain chlorophyll, but the amount of this is small and much behind that in the leaves. In numerous plants we find, however, that there is a reduction of the leaves accompanied by an increased assimilation-capacity of the shoot-axes. That we have here

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[1] As I have shown, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 216, whence this passage is taken. Dickson, The phylloid shoots of Sciadopitys, in Journal of Botany, iv (1866), regarded the 'double needles' as phylloclades. See also Bower, in Gardeners' Chronicle, March 15, 1884, p. 346. Also Bertrand, Anatomie comparée des tiges et des feuilles chez les Gnétacées et Conifères, in Annales des sciences naturelles, sér. 5, xx (1874).

a correlation has been proved by the investigations of Boirivant[1] who found in a number of plants that the shoot-axis became richer in chlorophyll if the leaves were removed. In Sarothamnus vulgaris shoot-axes which are thus treated have a palisade-parenchyma much more developed than that of the untouched shoot-axes. The connexion between the removal of leaves and the increase of chlorophyll in the shoot-axes is not explained by this. We have yet to find out, for example, whether the shoot-axis would be constructed as a stronger assimilation-organ if the leaves were not removed but were merely prevented doing their assimilation work. We may, however, assume that there is a *direct* connexion between the reduction of the leaves and the formation of the shoot-axis as an assimilation-organ.

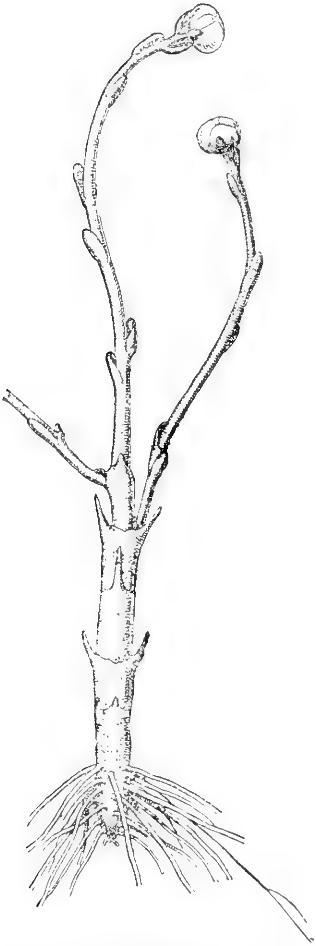

FIG. 300. Composite from West Australia. Nearly aphyllous.

REDUCTION OF LEAVES ON ASSIMILATING SHOOT-AXES. Arrest of the leaves on assimilating shoot-axes appears very markedly in xerophilous plants in which there is a general reduction of the transpiring surface. We find examples of this in the most different cycles of affinity, as in the Casuarineae, many Leguminosae, such as Spartium junceum and others, amongst the Ranunculaceae in Clematis afoliata, in most of the Cactaceae, and so on. But in marsh-plants also we have the same phenomenon, for example in the composite, shown in Fig. 300, which I found in a very moist marsh in West Australia. It is well known that many although not all marsh-plants have xerophilous features, but their relationships to life-conditions I cannot enter into here. Where there is copious branching of the shoot-axis with reduced leaves we get the same result in the matter of development of surface as we do when the leaves are present with less branching, and amongst our endemic species of Equisetum, E. hyemale may be designated xerophilous, but E. sylvaticum, E. pratense, and E. arvense are not so. We must here, as everywhere else, consider, besides the adaptation to external relationships, an 'internal'

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[1] Boirivant, Recherches sur les organes de remplacement chez les plantes, in Annales des sciences naturelles, sér. 8, vi (1897). The literature is cited here, but very imperfectly.

factor which conditions the formation of the organs but which does not allow us to regard them as purely adaptations. Thus amongst submerged plants also there are some which belong to this category—Scirpus submersus, C. Wright, for example, which I found in large masses in the Tapacooma lake. The shoot-axes of this plant are tuftedly branched, each produces some kataphylls and assumes, what is a character of the short shoots, the form of a cylindric leaf with a layer of assimilating cells under the small-celled epidermis (Fig. 301).

Assimilating shoot-axes with reduction of the leaves are very abundant in Monocotyledones, for example in Heleocharis, Scirpus lacustris, the Restiaceae, and elsewhere. The juvenile stages of these plants, so far as we know them, have foliage-leaves and it is only upon the elongated assimilating shoot-axes that the leaves are reduced to scale-leaves. Perhaps these assimilating shoot-axes are really *inflorescence-axes*—upon which, however, the flowers often abort. We shall have opportunity to return to this subject again when dealing with phylloclades. The striking similarity observable between the sterile shoot-axes of plants like Heleocharis[1] and Scirpus lacustris and the cylindric leaves of Juncus—these were formerly therefore designated 'sterile culms'—and the fact that all these plants live under essentially the same conditions have led to the supposition that the conformation of the assimilation-organs is utilitarian in both cases. The leaves of the species of Scirpus were perhaps not in a condition to take on the cylindric form and experienced, in consequence, a reduction in formation with a corresponding diminution in function[2]. In many of these Monocotyledones it can be shown that the leaf-formation may again set in under conditions which are unfavourable to the formation of assimilating shoots, and we have here then essentially a reversion to the juvenile stage[3]. Scirpus lacustris[4] for example forms long

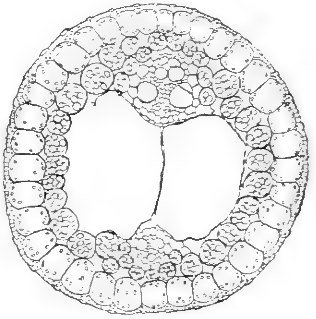

FIG. 301. Scirpus submersus. Axis of a long shoot in transverse section.

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[1] These consist of one long shoot-internode at the end of which a couple of scales is found if no flowers develop. On the rhizomes there are kataphylls only. In Cyperus alternifolius the elongated shoot-axis bears foliage-leaves. Here also perhaps originally there were inflorescences which in the first developmental stages of the plant suppressed their flower-formation and appeared as strengthening shoots. From the same standpoint we may regard the first still flowerless shoots that appear above ground in Polygonatum, Paris, and like plants, and it seems to me this gives us a more comprehensive view of the construction of these plants in which a process similar to that in the Cladonia amongst the lichens (Part I, p. 72) may have taken place—first of all the fructification was raised upon a stalk and then vegetative activity set in within it.

[2] See what is said about the formation of phyllodes, p. 353.

[3] See Part I, p. 171.

[4] In this plant the formation of foliage-leaves is not so completely limited to the seedling-stage as it is in Heleocharis, where, so far as I know, it is unknown in older plants, though perhaps

band-like leaves in deep or rapidly running water, and also if the plant is 'weakened' by repeated removal of the haulms. In Eriophorum alpinum also I saw leafy foliage-shoots develop as solitary vegetative organs like those of the young plants, upon plants 'enfeebled' by unfavourable conditions of cultivation.

INCREASE OF SURFACE OF ASSIMILATING SHOOT-AXES. The assimilating shoot-axis may experience an increase in surface in the most different cycles of affinity. This may be brought about in two ways which however are scarcely separable from one another:—

(*a*) By the flattening of the shoot-axis. Opuntia illustrates this.

(*b*) By the formation of wings. This is a consequence of 'decurrent leaf-bases.' These are found on the shoots of some plants, like species of Symphytum, Carduus, which have not reduced leaves. But in Genista sagittalis[1] the green membranous surface which is formed by the wing of the stem-internode far exceeds the total surface of the small unsegmented leaves. The stem in this species is still sharply segmented into internodes, and the nodes upon which the leaves arise are not 'winged.' Below each leaf the internode is widened by two 'wings' which are continuous with the leaf-surface. The leaves do not yet stand in two rows.

PHYLLOCLADES AND CLADODES. The more the segmentation of the nodes and internodes disappears, and the distichously arranged leaves become reduced, the more does the shoot-axis diverge from its ordinary habit, and if at the same time it assumes limited growth it acquires a striking resemblance to a leaf, and is designated a *phylloclade*. This name is best reserved for such leaf-like shoot-axes of limited growth, whilst other widened axes may be called *cladodes*. The following are some illustrations:—

Pteridophyta.

The Equisetaceae and some Lycopodineae especially the family of the Psilotaceae supply examples. The two epiphytic genera, Psilotum and Tmesipteris, have no roots but root-like shoot-axes and live in stations where temporary want of water can readily occur. In the two species of Psilotum the leaves are reduced to small scales for the protection of the vegetative point, whilst in Tmesipteris they are better developed, but by their vertical position approach xerophilous construction. It is noteworthy that in one species of Psilotum, Ps. complanatum, the shoot-axis is no longer nearly cylindric but is flattened in the way that we frequently find it in Spermophyta.

Gymnospermae[2].

The species of Phyllocladus are low trees or shrubs which are endemic in New Zealand and Tasmania. They have cylindric chief axes with spirally placed leaves, and these are small and scale-like soon dry and fall away. In their axils flat

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it might be artificially induced. The leaves at the base of the 'haulm' often have a very short lamina.

[1] See Part I, Fig. 124.

[2] Regarding Sciadopitys see p. 444.

leaf-like twigs, which in their outline resemble the leaves of ferns, are developed, and these are again branched but always in *one* plane. Individual branches of this form produce flowers. There is a difference in these leaf-like twigs between the structure of the upper side and of the under side as in most leaves. The under side has far more stomata than the upper, whilst the upper side has sub-epidermal palisade-tissue which is wanting on the under side[1]. The phylloclade-nature of these twigs is not yet fixed here, because the stronger ones may again grow out at the tip into radial cylindric shoots, whilst those in which this does not take place doubtless soon fall from the stem like the short shoots of Pinus, or those short shoots of Larix which are not developed into long shoots.

Monocotyledones.

Bowiea volubilis. The first example to be noted here is Bowiea volubilis. The shoot-axis produces long narrow foliage-leaves only in the seedling-stage, that is to say until the bulb is strongly developed. Subsequently there develops out of the bulb a very long—as much as two meters in cultivated examples — twining chief axis whose straggling lateral cylindric shoots may be recognized as scramblers. The elongated axis on which these cylindric shoots which are of limited growth arise forms only scale-like kataphylls; the cylindric shoot-axes themselves act as the assimilation-organs. In the upper part flowers appear whose stalks (Fig. 302) have exactly *the same form as the assimilating short shoots.* It appears to me that the whole shoot which springs from the bulb has arisen from *an inflorescence whose branchings have partially lost the capacity of forming flowers,*

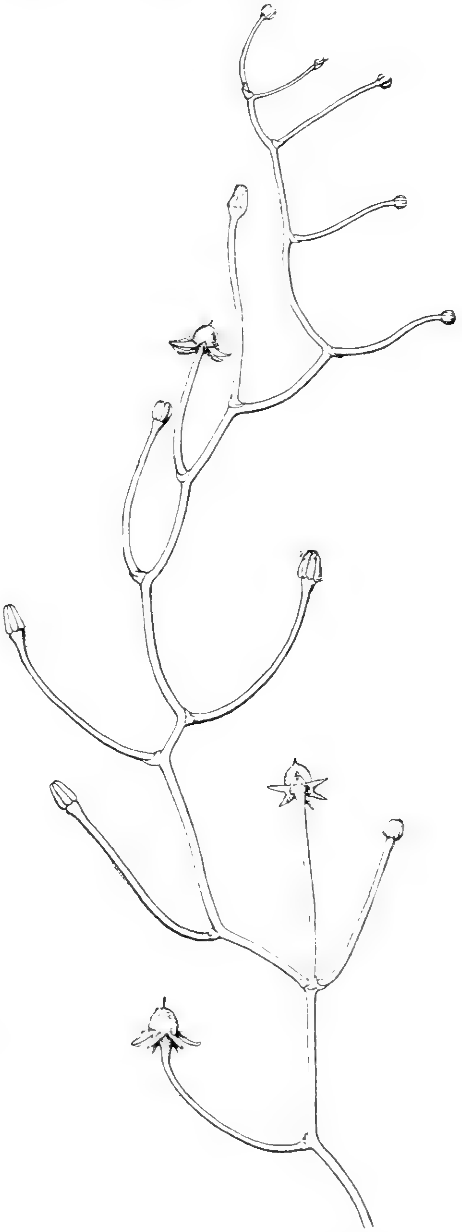

FIG. 302. Bowiea volubilis. The flower-stalks contain chlorophyll and act as assimilation-organs. In the lower region of the plant, and upon young plants, the flowers are arrested. Natural size.

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[1] Resembling both in habit and in structure these phylloclades is the twig-system of Thuja, in which, however, leaves are present but closely pressed to the twigs.

and that in conjunction with the formation of assimilation-shoots the formation of foliage-leaves dwindled. I have been led to speak of this liliaceous plant because it shows in a somewhat more primary form the same relationships as we meet with in the genus Asparagus.

Asparagus. The phylloclades here have somewhat varying forms. In Asparagus officinalis, for example, they are needle-like leafless shoot-axes standing in tufts in a double scorpioid cyme in the axils of the kataphylls. In Asparagus Sprengeri they are flattened[1], very leaf-like, but constructed alike upon both sides. In Asparagus (Myrsiphyllum) medeoloides the resemblance in appearance to a leaf is very marked, the anatomical structure is also dorsiventral, and the course of the vascular bundles conforms to that of the leaves. The conjecture, first put forward by Kunth[2], that the phylloclades of Asparagus proceed from the stalks of arrested flowers seems to me plausible, and it gives an explanation also of their deciduous character. Such a sterilization of the flower-stalks and inflorescence-axes takes place frequently in the formation of tendrils.

Ruscus. Ruscus from which the genera Semele and Danaë are separated[3] has, on account of its phylloclades, caused much discussion, and at all times, up to the most recent, there have not been wanting those who declared these to be leaves, and especially upon anatomical grounds: the vascular bundles form a cylinder only at the base of the phylloclade; they spread out in the leaf-like surface. That this fact is of no moment as against the morphological facts which stand as clear as day is evident. The species of Ruscus with leaf-like twigs, such as Ruscus aculeatus, R. Hypoglossum, R. Hypophyllum, possess a subterranean rhizome out of which annually in the spring turios appear above ground. These shoots bear in their lowermost part a number of sheath-like relatively considerable leaves which are usually green at the tip[4]. These leaves are reduced foliage-leaves as is shown by the fact that Semele androgyna possesses well-developed foliage-leaves upon the seedling-plant[5]. Askenasy[6] has also observed in Danaë racemosa the interesting anomaly that some leaves with a long stalk and oval green lamina, like the leaves of Convallaria, sometimes follow upon these sheathing-kataphylls—an appearance which may be considered a reversion to the leaf-form possessed originally by Ruscus before it had phylloclades. The stem, however, usually elongates above the sheathing-leaves and

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[1] See Reinke, Die Assimilationsorgane der Asparageen, in Pringsheim's Jahrbücher, xxxi (1898); where are figures, and the literature is cited. It may be noted here that the flower-stalk in Asparagus Sprengeri is not flattened but cylindric.

[2] See Kunth, Enumeratio plantarum, Stutgardiae et Tubingae, v (1850). Regarding Asparagus (Myrsiphyllum) medeoloides he says, p. 105, 'folia squamaeformia, pedunculos 1–3 fertiles, unifloros, basi bracteolatos, superne noduloso-articulatos et unum sterilem foliiformem, magis minusve inaequilaterum (cladodium) stipantia, saepissime nonnisi hunc.'

[3] In Semele the inflorescences arise on the margin of the phylloclade, in Ruscus on the upper side, in Danaë they are separate from the phylloclade.

[4] See Schacht, Beitrag zur Entwicklungsgeschichte flächenartiger Stammorgane, in Flora, xxxvi (1853), p. 457; Askenasy, Botanische morphologische Studien, Frankfurt, 1872, p. 3; Čelakovský, Über die Kladodien der Asparageen, in Denkschriften der Böhmischen Akademie, 1893; see also *résumé* by the author in Engler's Jahrbücher, xviii (1894), Litteraturbericht, p. 30; Reinke, op. cit.

[5] See Part I, p. 166.

[6] Askenasy, op. cit., p. 22.

produces then a number of small membranous scales which fall off early and in the axils of which the phylloclades stand[1]. The apex of the shoot itself commonly becomes leaf-like. The whole of the parts of a shoot of Ruscus are already laid down when its apex appears above ground in spring. The flowers, or rather the few-flowered inflorescences, arise out of the phylloclades, upon the upper side in Ruscus aculeatus (see Part I, Fig. 101) and Ruscus Hypoglossum, upon the under side in Ruscus Hypophyllum. They stand in the axil of a leaf, the only one which the phylloclade possesses; it shoots out early upon the phylloclade which is laid down like other twigs. The bract dries up in Ruscus aculeatus usually early, but in Ruscus Hypoglossum it is larger and leathery and takes the form and structure of the phylloclade itself, and this has given rise to erroneous interpretations. The phylloclades of Ruscus aculeatus place themselves in such a position that they do not have one surface directed upwards and another directed downwards but undergo a torsion through 90°, so that their edges are directed upwards and downwards as is the case in the phyllodes of Acacia. These relationships may, however, be changed by illumination.

Dicotyledones.

Phylloclades or cladodes occur in different families of this class, and the following are a few instances only of the manifold variations they exhibit.

Carmichaelia. In this, chiefly New Zealand, genus of Leguminosae[2] the reduction of the leaves and the consequent flattening of the shoot-axis are phenomena of adaptation. Some species have cylindric leafy shoots, for example C. Exsul, they are also found in C. flagelliformis, in which the leaves are arrested in sunny situations but are developed in shady positions[3]. Most species after the first juvenile stage have flattened shoot-axes whose leaf-development appears to be in great measure dependent upon external conditions. In cultivation the young shoots especially still bear foliage-leaves whilst the older ones only produce reduced leaves.

Bossiaea. Similar features to those in Carmichaelia are found in this leguminous genus.

Colletia. This genus of the Rhamnaceae has in one species, Colletia spinosa, cylindric shoots with reduced formation of leaves. Colletia cruciata, on the other hand, possesses short shoots flattened in the vertical plane, but seedling-plants have the form which appears during its whole life upon Colletia spinosa. Shoots showing a reversion to the juvenile state also appear on *adult* plants[4].

Phyllanthus. Features of some species of this genus of Euphorbiaceae have been already referred to[5]. There are dorsiventral lateral shoots bearing at their base a bud—just as a leaf has an axillary bud—out of which may proceed a long shoot.

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[1] In Ruscus aculeatus and Danaë they stand on the lateral axes; only in the seedling, for instance of R. aculeatus, are they on the chief axes.

[2] See Reinke, Untersuchungen über die Assimilationsorgane der Leguminoseen: I–VII. in Pringsheim's Jahrbücher, xxx (1897). The literature is cited here.

[3] See L. Cockayne, An Inquiry into the Seedling Forms of New Zealand Phanerogams and their Development, in Transactions of the New Zealand Institute, xxxi (1898).

[4] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 17, Fig. 8.

[5] See Part I, p. 97

It is probable that as Dingler[1] conjectures the construction of these leaf-like short shoots was the cause of the reduction of the foliage-leaves of the chief shoot to kataphylls. On the seedling-plant foliage-leaves still appear. Still further goes the transformation of the shoot in that section of the genus termed Xylophylla where the shoot-axes are transformed into leaf-like phylloclades[2] which bear kataphylls only in the mature plant but have still foliage-leaves in the seedling-plant. These phylloclades are laid down as normal cylindric axes, but they broaden later and become flat.

Other examples, like Muhlenbeckia platyclados one of the Polygonaceae, and Siebera compressa one of the Umbelliferae, do not require further explanation. We must, however, mention the—

Cactus-form. By this we understand assimilating shoot-axes with fleshy tissue acting as a water-reservoir. Storage of water appears also in other assimilating shoot-axes for example amongst the Leguminosae in Carmichaelia crassicaulis, Notospartium and others, in Kleinia and other Compositae, in Geraniaceae; but the cactus-form of the Cactaceae—a form which is repeated in the succulent species of Euphorbia and in the Stapelieae—has special characteristics. The formation of shoots of the Cactaceae has been already described[3], and further information may be obtained from the sources cited below[4].

3. TRANSFORMED RADIAL SHOOTS.

We must consider as transformed shoots all those in which the work of assimilation has been exchanged entirely or in great part for other functions.

THORNS. In the transformation of shoots into *thorns* as it takes place in species of Prunus, Rhamnus cathartica, Ononis spinosa, and others, we have features resembling those of the shoots mentioned above whose axis serves as an assimilation-organ, in so far as in the thorn-shoots the leaves are suppressed, and there are not wanting middle stages between shoots which have taken over the function of foliage-leaves and those which have been constructed as thorns. In many shoots both features appear together. Thus the phylloclade of Ruscus aculeatus ends in a thorn, and the same is the case in the flat shoots of Colletia cruciata. Transition-forms from normal foliage-shoots to thorns are also found, for instance, in the Pomaceae and Amygdaleae[5]. The thorn-twigs of Crataegus Oxyacantha, for example, before they close their growth at the apex by producing a thorn, form a

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[1] Dingler, Die Flachsprosse der Phanerogamen, Heft i: Phyllanthus, München, 1885.

[2] Dingler conjectures that the 'phanerogamous leaf' has arisen in the same way, that it is a flattened shoot. Against this it may be said (1) the development of the phylloclade in Phyllanthus itself evidently points to an origin from a *leafy* shoot, (2) in the Hepaticae the 'leaf' has developed in different series from different starting-points.

[3] See Part I, p. 168.

[4] Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 67; Ganong, Beiträge zur Kenntniss der Morphologie und Biologie der Cakteen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894).

[5] See Delbrouck, Die Pflanzen-Stacheln, in Hanstein's Botanische Abhandlungen, ii (1875), p. 17; Areschoug, Beiträge zur Biologie der Holzgewächse, in Acta Universitatis Lundensis, xii (1875–6).

number of rudimentary foliage-leaves which soon fall off, and have at their base a pair of buds which in the next year grow out into short twigs. Also other twigs become converted into thorns[1] after having produced some foliage-leaves whose axillary buds grow out in the next year. If in Crataegus one cuts off at the right moment a long foliage-shoot above the point where stands a normal lateral short shoot which would become a thorn, one may compel this short thorn-shoot to become a long foliage-shoot instead of a thorn-shoot. This same effect has, as is well known, been produced by cultivation in Pyrus Malus and other Pomaceae. As on the phylloclades so on the thorn-shoots the formation of foliage-leaf is rudimentary. In many thorn-shoots the leaf-formation is as entirely absent as in the needle-like twigs of Asparagus.

STORAGE-SHOOTS. I do not require to say anything further here about the shoots which are used as storage-organs. The configuration of bulbs and tubers is explained in every textbook, and we know nothing about the conditions which have brought about the appearance of these organs. Most of these storage-shoots proceed out of hypogeous (geophilous) shoots, yet the cactus-form—which must be reckoned amongst these—shows that epigeous (photophilous) shoots may be devoted to the same useful function, and many other plants form epigeous tubers or bulbs. Vitis pterophora shows this in remarkable degree, for at the end of its vegetative period the tips of the shoot are arrested and one or two internodes below it swell out, then they fall off with the buds, one or more, that are upon them, and after a period of rest—which probably enables the plant to live through a dry period—they again shoot out into active life[2].

4. TRANSFORMED RADIAL SHOOTS IN LIANES.

When speaking of the transformation of leaves into climbing-organs such as hooks and tendrils, as well as when discussing the formation of roots, reference was made to some species of liane. Here therefore we have only to note the formation of the shoot in some other lianes. The phenomena of growth of the shoots of lianes, such as circumnutation and the like, dealt with in physiological textbooks, will not be discussed here, and I shall refer only to a few cases illustrative of the formation of the shoot in relation to the conditions of life:—

SEARCHER-SHOOTS. In European lianes—plants which do not reach any great height, except in the case of Lonicera Periclymenum and Clematis Vitalba—the usual vegetative shoot-formation takes place. In tropical lianes, on the other hand, we find often shoots developed which may be termed

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[1] Areschoug's 'false short twigs.'

[2] See Lynch, On Branch Tubers and Tendrils in Vitis gongyloides, in Journal of the Linnean Society, xvii (1878), p. 306, plate 15.

searcher-shoots. They have the power of rapid growth and elongation in order to enable them to search for a support. They can grow for a long time in a vertical direction without a support, and thus their apex moves through a comparatively wide area. They will reach a greater length the less the weight of leaves they have to carry[1], and we find therefore a retardation in the formation of their leaves which is either (*a*) temporary, or (*b*) permanent. These searcher-shoots arise only if the plant is a strong grower and is living in favourable conditions.

(*a*) **Temporary retardation of foliage.** Here we have the cases of the plants whose leaves form 'forerunner-tips[2].' In other cases the stipules are formed whilst the leaf-primordium itself is still undeveloped, as, for example, in Buettneria pilosa and Leguminosae. Specially interesting is the fact that often a further development of the leaves only takes place if the searcher-shoots have reached a support, as, for example, in Banisteria aurea and Beaumontia grandiflora, and this condition may go so far that the searcher-shoots, which do not reach a support, throw off the young leaves, as in Combretum, many of the Apocynaceae, Derris elliptica, and finally even the whole shoot dies. There is here a special phenomenon of sensitiveness, the use of which to the plant is evident, and it spares the plastic material for the development of leaves and shoots for those shoots which can make use of it best. Its origin, however, is still obscure. It is not connected with 'contact-stimulus.' We may recall here that Sachs[3] pointed out that in European twiners 'vigorous shoots when they grow out beyond their support, or meet with none at all, become moribund; it is easy to observe that a shoot which has been growing for some time without a support, on being afforded opportunity to twine round a support obtains after a few days a new lease of life, so to speak, and grows out much more actively.' This sensitiveness—the dependence of vigorous life upon the exercise of a function, the reaching of a support in the case before us—is developed in special degree in these searcher-shoots. The searcher-shoots which throw off their leaves form in some measure a transition to the next group.

(*b*) **Permanent retardation of foliage.** Here the division of labour is of such a kind that the shoots which serve as searcher-shoots and subsequently anchor the plant have only kataphylls. The foliage-leaves are restricted to the short shoots which are not climbing-organs. We see this in, for instance, Gnetum funiculare, Melodorum bancanum, Myxopyrum nervosum. The same features are observed in tendrillous lianes in which the tendrils

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[1] Račiborski, Ueber die Vorläuferspitze, in Flora, lxxxvii (1900), p. 1; Treub, Sur une nouvelle catégorie de plantes grimpantes, in Annales du Jardin botanique de Buitenzorg, iii (1883), p. 44; id., Observations sur les plantes grimpantes du Jardin botanique de Buitenzorg, ibid., p. 160.

[2] See p. 308.

[3] Sachs, Lectures on the Physiology of Plants, English edition by Marshall Ward, Oxford, 1887, p. 674.

are placed upon the short shoots. The division of labour between short shoots and long shoots may, however, be of varying sharpness[1]. In Hiptage obtusifolia and other Malpighiaceae the long shoots, for example, have still foliage-leaves at their base and above that kataphylls, but the foliaged short shoots can grow out into long shoots which if they have not reached a support pass over at the apex again into the formation of foliage-leaves; they submit then to a retardation which is less strong than that of the searcher-shoots in the other plants mentioned above[2].

In other plants every bud by its position is, on the other hand, unalterably fixed as either a long shoot or a short shoot. There is then, even if the long shoots are removed, no transformation of the short shoots[3].

SHOOTS AS CLIMBING-ORGANS[4]. We can scarcely speak of a transformation in the case of 'scramblers' which simply hold on to other plants by their straggling branches. The formation of shoots in twining plants has been already described. Here we have to deal with—

Shoot-tendrils. When speaking of leaf-tendrils it was shown that in many plants, leaves, which are sensitive to contact-stimulus and are unchanged in their configuration, may function as tendrils; similarly we find that in many 'twig-climbers,' as Fr. Müller first of all pointed out, the ordinary twigs are capable of acting as climbing-organs. As an example of this we have Securidaca Sellowiana (Fig. 303), a Brasilian polygalaceous plant. It possesses long shoots with non-irritable elongated internodes, and on these

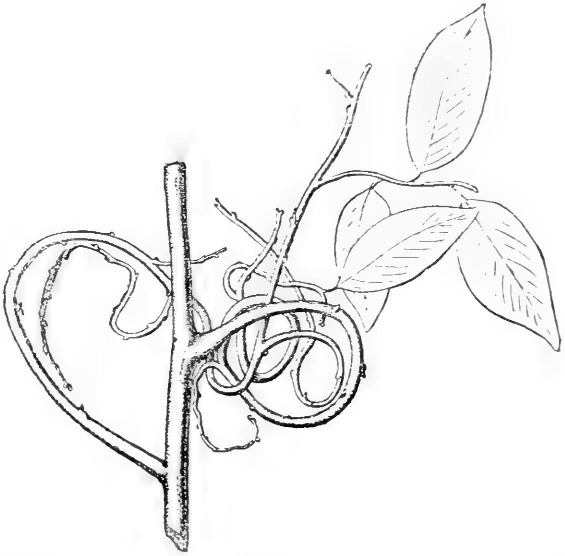

FIG. 303. Securidaca Sellowiana, Klotzsch. Shoot with tendrillous lateral twigs. Two-thirds of natural size. After H. Schenck.

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[1] See Massart, Sur la morphologie du Bourgeon, in Annales du Jardin botanique de Buitenzorg, xiii (1896).

[2] See also Račiborski, Ueber die Vorläuferspitze, in Flora, lxxxvii (1900), p. 36.

[3] See, for example, Massart, op. cit.

[4] See what is said about root-climbers and leaf-tendrils, pp. 286, 421. A comprehensive exposition of the features of lianes—not altogether above criticism from the morphological standpoint—is that of H. Schenck, Beiträge zur Biologie und Anatomie der Lianen, im Besonderen der in Brasilien einheimischen Arten, in Botanische Mittheilungen aus den Tropen, Jena, Heft iv (1892), Heft v (1893). The literature is cited.

there are foliaged lateral twigs which, like the twigs of higher order, are very sensitive to friction. In other plants we find upon the shoots which act as tendrils, a reduction of the leaves, as in species of Salacia. This reduction takes place in varying degree in different species of the genus, and its final result is a twig-tendril which has its leaves arrested at a very early period of development, and so appears at maturity to be leafless, as is also the case in Acacia lacerans, A. velutina, and others.

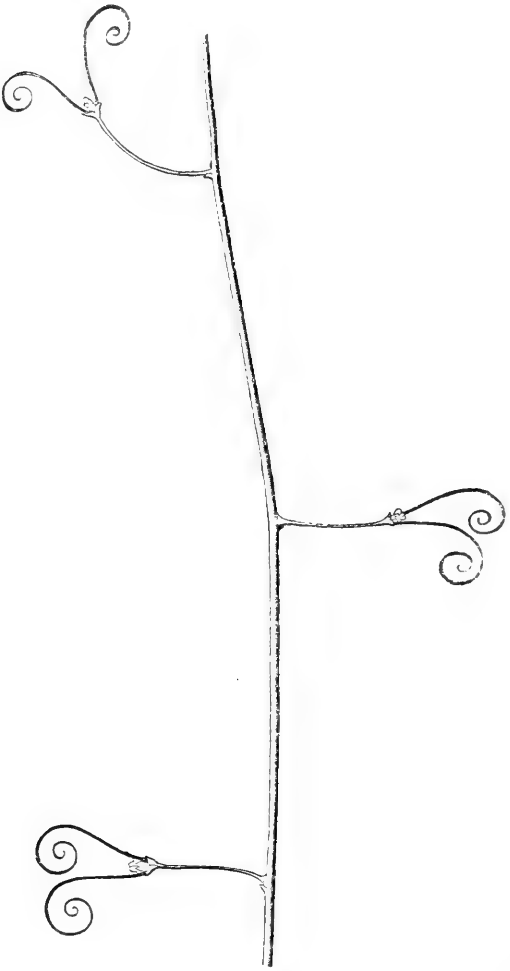
FIG. 304. Bauhinia sp. from Blumenau. Twig with watch-spring-climbers. Two-thirds natural size. After H. Schenck.

Shoot-hooks. The hook-climbers possess as climbing-organs hooks which after they grasp the support experience a thickening. They have in most cases taken origin from the stalks of inflorescences[1] in which the flowers have been suppressed. Inflorescences frequently become climbing-organs. The greatly elongated axis of the inflorescence twines in Utricularia reticulata, for example, whilst the vegetative shoot-axes remain in the ground. Were we to imagine that in other inflorescences an irritability of the axis or of a part of it were to set in, that then a division of labour between an irritable and a non-irritable part followed, and that then this appeared at a quite early stage in the development, we should obtain a picture of how change of function might have come about. Moreover transition-forms between tendrils and inflorescences are abundant enough, sometimes of the nature of *watch-spring-tendrils*, which are thin and spirally inrolled tendrils, and do not become firmly fixed to the support, but through contact-stimulus become thicker and harder (Fig. 304), sometimes of

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[1] The sensitiveness of the twig-thorns in Olaceae described by Schenck appears to me doubtful.

filiform tendrils, as in Passiflora, Vitis, and other plants—structures which do not require further notice in this place.

I may recall here those cases in which the shoot-axes which originally served for the formation of flowers have again turned back to a vegetative function[1], and that in such shoot-axes we may note—

1, the formation of flower is absolutely suppressed;

2, consequently the appearance of these shoot-axes may be relegated to an earlier stage of the development than that at which the inflorescences appear.

(*b*) PLAGIOTROPOUS SHOOTS.

The general relationships between orthotropous and plagiotropous shoots have already been described[2]. It has been shown that one and the same shoot at different stages of development may be orthotropous or plagiotropous, and that in many cases external factors, especially the intensity of light, exercise an influence upon the growth and determine it as orthotropous or plagiotropous.

In trees. To the relationships as they are found in trees, which have orthotropous chief axes and plagiotropous lateral axes, reference was made when speaking of the relationships of symmetry[3], of correlation[4], of anisophylly[5], and also when mention was made of the plagiotropous shoots in root-climbers[6]. I have therefore to mention here only the configuration of the plagiotropous shoot of herbaceous plants.

In herbs. In many herbaceous perennials the flower-bearing shoot is orthotropous, the vegetative shoot is plagiotropous. These plagiotropous shoots are chiefly distinguished from the flowering orthotropous shoots by the elongation of one or all of the internodes, by which process they provide for vegetative spreading. The plagiotropous shoot can behave in this way with some variation: the shoot at first orthotropous may subsequently bend, become plagiotropous, and as a creeping shoot root if it reach the soil; then it may raise itself again in the next year under favourable conditions and form an orthotropous shoot. We find this, for example, in Galeobdolon luteum. In other plants the shoot is from the beginning directed obliquely, as in Ajuga reptans and Glechoma hederacea, or it may be creeping, as in Potentilla anserina. In Potentilla anserina and P. reptans, as well as in Duchesnea (Fragaria) indica, the 'stolons' are properly the lateral flower-stems which end in one flower[7]; in the axil of the lowermost prophyll of the flower there arises a new rooting foliage-shoot which again produces lateral flowers and so on. In Fragaria there are also transitions between inflorescences and stolons, and

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[1] See pp. 447, 450.

[2] See Part I, p. 67.

[3] See Part I, p. 93.

[4] See Part I, p. 214.

[5] See Part I, p. 250.

[6] See Part I, p. 157.

[7] Irmisch, Einige Bemerkungen über die krautartigen Rosaceen, in Botanische Zeitung, viii (1850), p. 292. See also Maige, Recherches biologiques sur les plantes rampantes, in Annales des sciences naturelles, sér. 8, xi (1900), p. 249.

we may expect to find them elsewhere, especially in plants whose vegetative shoots are 'contracted,' that is to say, consist of internodes which remain short. In such plants the inflorescences are shoots which by the elongation of one or many internodes are raised above the leaf-rosettes. If in these inflorescences the formation of flower is suppressed, or is postponed to a later time, they may at once give rise to 'stolons.' Such a vegetative activity of the inflorescences has been several times mentioned in preceding pages [1], and it is found in some water and marsh-plants [2] which produce within the inflorescences vegetative buds which then spread out upon the surface of the water and become organs of vegetative multiplication for which they are most favourably constructed. We might imagine that the plant of Androsace sarmentosa, depicted in Fig. 305, was originally an annual plant which besides the terminal inflorescence produced also at a later period axillary ones; that in these axillary inflorescence-shoots the formation of flowers was postponed to the next vegetative period; then there would develop upon each of them, instead of the flower-umbel, a vegetative leaf-rosette upon

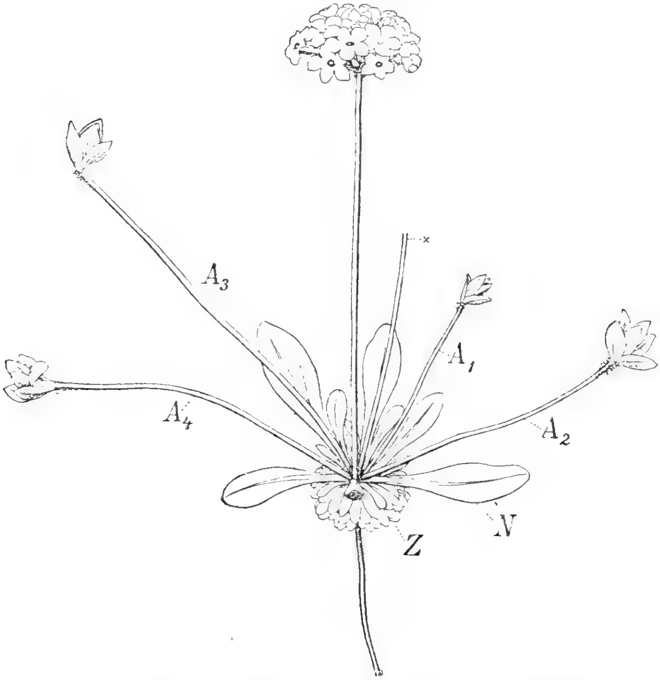

FIG. 305. Androsace sarmentosa. *Z*, storage-leaves; *N*, foliage-leaves; A_1–A_4, stolons. The flowering-plant is itself the product of a stolon, of which a small portion is seen below. One-half natural size.

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[1] See pp. 447, 449.

[2] See the cases of Alisma natans, Limnanthemum Humboldtii, in Goebel, Pflanzenbiologische Schilderungen, ii (1893), p. 329.

which in the following season the flowering-shoot would elongate and bear flowers. This of course is a purely arbitrary assumption. We have, however, every ground for the assumption that in the Labiatae mentioned below the plagiotropous shoots proceed out of orthotropous ones, which have experienced a retardation in the formation of their flower. The plagiotropous shoots in these cases serve also specially as vegetative propagating-organs—'wandering shoots' (Fig. 305)—which are of importance for the spread of the plant and the utilization of new stations.

Other plants show throughout the whole of their shoot-system a plagiotropous growth. They are glued to the ground and have frequently taken on the dorsiventral character. This is the case in Anthyllis tetraphylla, the leaf-formation of which has been previously described[1]. The direction is here certainly caused by light. In light of feeble intensity the shoots are erect, as cultivated plants have shown, and it may be that the plagiotropous growth is of importance for this kind of plant which grows in strong illumination, in that it hinders evaporation of water and that it facilitates the obtaining of water, as is the case in Hepaticae[2]. These relationships, however, as well as the factors which in alpine and polar regions, for example, cause plagiotropous growth, cannot be discussed further here.

RELATIONSHIPS TO CONDITIONS OF LIFE. I shall only now briefly refer to the relationship between the formation of *plagiotropous shoots with elongated internodes* and the conditions of life. This may be illustrated by examples from the Labiatae. So far as I can see such plagiotropous shoots *do not appear* in species which grow in *dry sunny* spots[3]. Plants in such stations form a woody framework of orthotropous shoots. Compare, for example, the small shrubby Thymus vulgaris of south Europe, growing on dry sunny localities, with the widely spread-out Thymus Serpyllum, which indeed grows upon relatively bright sunny dry areas but only between other plants which shade the shoots. The vegetative shoots are here plagiotropous. The shorter vegetative period of course must be taken into consideration also as it is less favourable to the construction of a woody framework of shoots, and there is also the question of exposure to cold. Lavender, rosemary, and other plants of sunny dry localities have no marked plagiotropous shoots, but we find in general these are the more developed the more shaded and moist are the localities, such as meadows

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[1] See Part I, p. 121.

[2] See p. 18.

[3] In other plants this is different as is well known, for instance, apart from those mentioned above, in many creeping plants of the sea-shore like Ipomaea Pes-Caprae. Research is required to show how the plagiotropous growth comes about here. It may have started more than once and in relation to *different* external stimuli. We have seen that the plagiotropous Hepaticae on tree-stems are never orthotropous, and that the plagiotropous growth has special relations to water. Temperature is influential in mountain and polar plants. I can only see in the above a *special* case of plants with radial flower-shoots and plagiotropous stolons, but this does not by any means give us a scheme for all.

and valleys, in which the plant grows. In such places the construction of vegetative orthotropous shoots which will rise up high into the light demands a considerable amount of material. The diminished light can be better used by plagiotropous shoots to which the moist soil offers at the same time an opportunity to root. We find therefore that as has been mentioned for other plants a transformation has taken place in the Labiatae of the orthotropous shoots—these alone are found in annual species — into plagiotropous ones, and of this the following plants offer illustrations :—

FIG. 306. Ajuga reptans. The flowering-shoot has developed from the stolon, *A*, and has given rise to plagiotropous lateral shoots. Reduced.

Ajuga reptans[1] (Fig. 306). The shoot of the seedling is orthotropous and it forms in the first year a rosette of decussate foliage-leaves, and in the second year bears the terminal inflorescence. The lateral buds become plagiotropous stolons with elongated internodes, they root later and form at their apex a new leaf-rosette with contracted internodes which can, in a plant growing in the sun, form flowers in its first year. Usually, however, this takes place only in the second year. Orthotropous shoots which produce only few flowers, and which occasionally

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[1] See Irmisch, Beiträge zur vergleichenden Morphologie der Pflanzen, Abth. ii, Labiatae, Halle, 1856, p. 29.

arise as lateral shoots, may after flowering time become plagiotropous stolons[1], and these stolons have taken origin from orthotropous flower-shoots by adaptation.

Glechoma hederacea. We have in this plant a case which we may compare with that of Hedera Helix[2]. In that plant we have seen that the juvenile form is adapted to plagiotropous growth, that the formation of orthotropous shoots only begins later, and that this behaviour is a derived one. In Glechoma hederacea the juvenile and adult forms are not markedly different in their configuration, but they show a different growth. The axis of the seedling-shoot is at once plagiotropous and it roots from its stem-segments which attain a length of thirty centimeters or thereabouts. In the next year under favourable conditions it forms[3] an orthotropous flowering-shoot, at whose base plagiotropous lateral twigs subsequently arise. But the orthotropous flower-shoot may pass over again at its apex into a plagiotropous shoot, as Irmisch and others[4] have observed, and this happens especially in plants which grow in deeply shaded habitats. These form but few flowers whilst the orthotropous shoots in stronger illumination produce many flowers, and do not as a rule grow out further as vegetative plagiotropous shoots. The tendency here to the formation of plagiotropous shoots is then much more deeply engrained, for not only is the seedling-axis plagiotropous, but also the orthotropous shoots pass over relatively easily into plagiotropous ones, and this may be connected with the relationships to the locality as Glechoma grows in more shaded places.

Stachys. The genus Stachys may be mentioned here because it shows a transition from plagiotropous light-shoots into hypogeous shoots. Stachys sylvatica has plagiotropous shoots which grow sometimes upon, sometimes beneath the surface of the soil. In the first case they have throughout foliage-leaves and come into flower often in October; in the second case they have kataphylls[5] and appear above the soil in the autumn usually with the apex covered with foliage-leaves[6]. According to Maige[7] these plagiotropous shoots may become orthotropous in direct sunlight, whilst, as might be expected, in feeble illumination the flower-bearing lateral shoots of the orthotropous inflorescence discontinue the formation of flower and become plagiotropous—a transformation which never happens in the chief axis. Stachys palustris, on the other hand, has stolons which force themselves into the soil and are therefore geophilous.

FACTORS WHICH CONDITION PLAGIOTROPOUS GROWTH. We do not learn from the above what factors condition the plagiotropous growth.

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[1] This has not yet been observed in the case of the terminal inflorescence. Moquin Tandon, who has been cited as the authority for such a change, only speaks of a foliation of the bracts which need not be connected with plagiotropous growth. See his Éléments de tératologie végétale, Paris, 1841, p. 205. Important results of experimental research are given by Klebs, Willkührliche Entwicklungsänderungen bei Pflanzen, Jena, 1903.

[2] See Part I, p. 160.

[3] The method of branching need not be described.

[4] As A. de St. Hilaire, Leçons de Botanique comprenant principalement la morphologie végétale, Paris, 1840, p. 104. He believes, however, that the shoots 'entraînés par leur poids' sink to earth.

[5] The stolons of other plants show also the formation of kataphylls in the light—Fragaria vesca, Saxifraga sarmentosa. The retardation of the development of the leaves here may have relation to the rapid elongation of the shoot-axis as in the shoots of many lianes. Experimental evidence is entirely wanting.

[6] See Irmisch, Beiträge zur vergleichenden Morphologie der Pflanzen, Abth. ii, Labiatae, Halle, 1856, p. 15.

[7] Maige, Recherches biologiques sur les plantes rampantes, in Annales des sciences naturelles, sér. 8, xi (1900).

A discussion of this question belongs to experimental physiology, and here I shall therefore only say this:—

Frank and others formerly thought that the plagiotropous shoots above mentioned were negatively geotropic and negatively heliotropic, because many of them although not all became erect in darkness. This erecting of the shoot I consider as an adaptation by which the plagiotropous shoot is protected from being smothered by other plants or by a covering of leaves and the like. Oltmanns[1] found, moreover, that the shoots of Glechoma became orthotropous in darkness only in the spring. Later in the summer the stolons grew out, even in darkness, to a considerable horizontal length. Negative heliotropism therefore does not play a part in directing the plagiotropism of these shoots but there is 're-attuning' of the geotropism by the influence of light[2]. The working of the light is here evidently somewhat complex and we must distinguish two things—

(*a*) the influence upon the *direction of the shoot*; and

(*b*) the influence upon the *processes of ripening*.

Let us consider the latter first. We find that the shoots grow out at different stages of development at which they react differently to the influence of directing forces. The external forces which are necessary for this development are in part those which affect the direction. The terminal stage is that of flower-formation, the shoot therewith reaches its 'ripeness.' Every shoot of Glechoma begins as a plagiotropous foliage-shoot and ripens then into an orthotropous one. This happens under the influence of light and its ripening process goes on in general more quickly the higher—within of course certain limits—the intensity of the light is. The coming of the orthotropy is then *indirectly* a consequence of the influence of light which causes a change in the inner peculiarities of the shoot. This has as a consequence that the shoot, so far as its *direction* is concerned, reacts differently to light in the different developmental stages. In the first unripe condition light causes a 're-attuning' of the positive to transversal geotropism—using this word in its most general sense—and the stronger the light, other things being equal, the more marked is the plagiotropous growth. The influence of light may gradually reach a climax in the summer, the shoot can, as we saw in Glechoma, be so 'induced' that it is no longer orthotropous in darkness. If we separate these points of view the behaviour of the plagiotropous shoots is as it appears to me much more easily understood. The ripening process does not of necessity lead to the cessation of the growth of the shoot. We have seen that in Campanula rotundifolia the growth can be interrupted, and that the juvenile-form can again be brought forth. The same is the case in many of the Labiatae mentioned above. If we designate a shoot with the properties of the plagiotropous shoot of Glechoma by x, it will be orthotropous if it has been formed under the influence of the light y. The shoot $x + y$ is orthotropous, but y is not always present in large amounts. If now there be only little of y present, and x is not exhausted, the shoot grows as x, that is to say, grows further as a plagiotropous shoot, but the plagiotropous growth also makes possible to it, as we have indicated, the better utilization of the light, and at the same time vegetative propagation in stations with less intense light.

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[1] Oltmanns, Über positiven und negativen Heliotropismus, in Flora, lxxxiii (1897), p. 24.

[2] See Czapek, Über die Richtungsursachen der Seitenwurzeln und einiger anderer plagiotroper Pflanzenteile, in Sitzungsberichte der Wiener Akademie, civ, i (1895).

II

GEOPHILOUS SHOOTS

With Areschoug[1] we may designate by the term *geophilous* such shoots as produce their renovation-buds under the surface of the earth. They occur especially in regions where vegetative activity is periodically interrupted, whether this is by cold or by drought, and they are united by many intermediate stages with 'photophilous[2]' shoots.

We have to distinguish two categories:—

PERENNIAL GEOPHILOUS SHOOTS. In this category we have shoots which are persistently hypogeous.

Paris quadrifolia. The rhizome of Paris supplies an example. It has unlimited monopodial growth in the soil, and sends up lateral shoots into the light.

PERIODIC GEOPHILOUS SHOOTS. By these we understand shoots which in the different vegetative periods of their existence are at first geophilous and then photophilous, or the reverse.

Polygonatum multiflorum. This is the case in sympodial rhizomes such as that of Polygonatum (Fig. 307). The shoots are here geophilous, and they remain in the soil and bear only kataphylls there. In the next year they are photophilous, and appear above the soil and produce assimilating foliage-leaves as well as flowers. The means which the plant adopts to bring its shoots into the soil or above it are evidently governed in the first place by changes in its geotropic sensitiveness, and this itself is most probably conditioned by processes of metabolism.

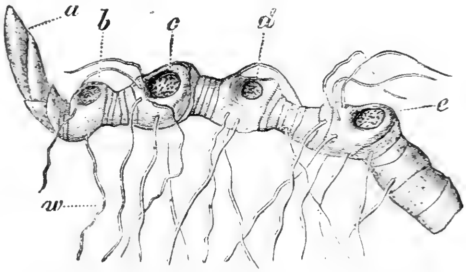

FIG. 307. Polygonatum multiflorum. Rhizome. *a*, bud for the epigeal shoot of the next year; *b*, scar of the epigeal shoot of the current year; *c*, *d*, *e* scars of epigeal shoots of preceding years; *w*, roots. One-quarter natural size. Lehrb.

Circaea intermedia. The case of Circaea intermedia offers an illustration to which I have called attention before now[3]. The photophilous shoots of this plant are negatively geotropic and end in an inflorescence. Beneath the soil the plant develops stolons which subsequently swell up at the end, and in the next year become photophilous orthotropous shoots. If now these overwintering shoots are stimulated to further development in the

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[1] Areschoug, Beiträge zur Biologie der geophilen Pflanzen, in Acta Univ. Lundensis, xxxi (1896).

[2] This name seems more suitable than Areschoug's term 'aerophilous,' which does not apply to the shoots of water-plants. The essential point is that a shoot sometimes or always is adapted to darkness or to light. 'Skotophilous' might be used for geophilous *shoots*, and more appropriately, because as has been shown (Part I, p. 232) darkness has a favourable influence upon the formation of the geophilous potato-tuber, and also upon many stolons.

[3] Goebel, Ueber den Einfluss des Lichtes auf die Gestaltung der Kakteen und anderer Pflanzen, in Flora, lxxxii (1896), p. 11. The plant there called Circaea alpina is C. intermedia.

winter, by cultivation in a higher temperature, certain peculiar phenomena are observed. The point of the shoot which ought to be an inflorescence becomes a stolon which again pierces the soil, and this may take place after the shoot has attained a height of many centimeters and formed a number of well-developed leaves (Fig. 308, II). The appearance of the shoots above the ground also may be quite suppressed, and the shoot, instead of forming a photophilous shoot with foliage and flower, may continue its growth as a stolon (Fig. 308, I). This depends in general upon the time at which the plant has been caused to 'shoot out.' The later this happens the longer time elapses before the formation of the stolon begins, and one might believe that one had completely normal plants under examination which were prepared to form flower, until one sees the tip of the shoot begin to bend downwards, and the formation of stolons is entered upon—this being recognized not only by the changes of direction, but also by the elongation of internodes and the like. So long as these stolons remain above ground they produce foliage-leaves only which are merely smaller than usual, but when they pierce the soil kataphylls are produced[1]; in the axil of the foliage-leaves stolons arise, which are commonly produced only in the seedling-plant.

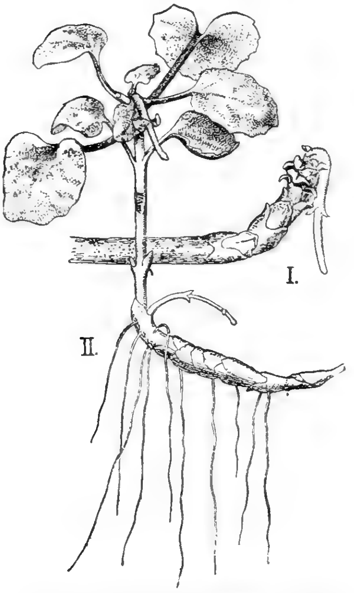

FIG. 308. Circaea intermedia. I and II, portions of stoloniferous plants whose shoot-apex becomes geophilous.

These facts will bear it seems to me but one interpretation: In the resting geophilous shoot, processes of metabolism take place which cause it to become negatively geotropic when it shoots out. These processes require a low temperature amongst other conditions. If one raises the temperature prematurely, that is to say before the metabolic changes about which we know nothing are completed, the stolons will at first be photophilous, but as they contain a certain amount of geophilous substance which has not been used up—if one may use this expression for brevity—after a certain time they bend down again to the soil. There appears thus an inversion of that order of shoots which is usual in plants with geophilous shoots—the geophilous shoots arise at the *base* of the photophilous ones, an arrangement the advantage of which does not require any explanation[2]. The transformation of primordia of photophilous shoots into geophilous ones may, moreover, as has been proved in some cases[3], be caused also by the early removal of the

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[1] See Part I, p. 256.

[2] See also Part I, pp. 215, 221.

[3] This is easily proved by water-cultures of Circaea.

primordia of the geophilous shoots, just as on the other hand a removal of the photophilous chief shoot causes [1] in many cases the geophilous primordia in the year of their formation to grow out into photophilous foliage-shoots.

DEPTH IN SOIL OF GEOPHILOUS SHOOTS. It is the alternation in the relationships between the geophilous and photophilous shoots or parts of shoots which evidently *regulates the depth* at which the geophilous shoots grow [2]. Many plants have indeed no definite depth in the soil at which they live best because their geophilous parts possess no power of movement, for example, the tubers of Corydalis cava. But most of them have the capacity to take up a higher or a deeper position in the soil, whether this is brought about by pull-roots or by a change in their geotropic sensitiveness.

Polygonatum multiflorum. Let us follow, for example, the development of Polygonatum multiflorum. The short fleshy shoot which is formed by the seedling-plant is at first erect (Fig. 309 to the left). It has the duty, which is performed usually only in the second year, of bringing into the light the foliage-leaf which follows upon the kataphylls. In this way is made possible the further development through the assimilative activity of the foliage-leaf. Subsequently the shoot, which is at first monopodial, penetrates the soil [3] and grows there in a horizontal direction (transversely geotropic),

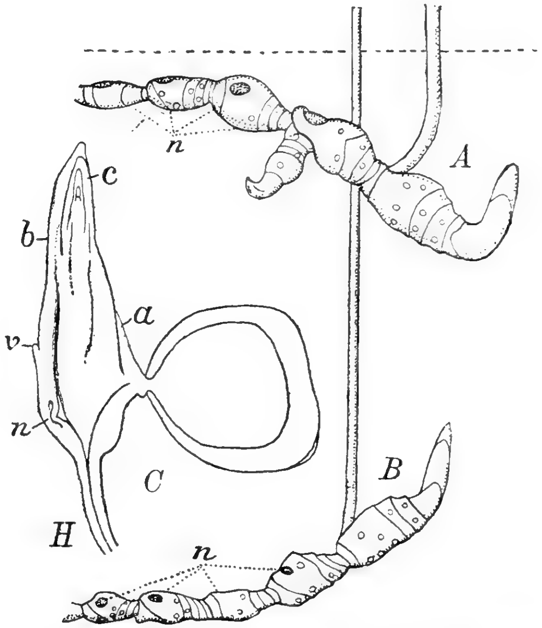

FIG. 309. Polygonatum multiflorum. *A*, rhizome placed artificially higher in the soil than the normal depth; its continuation-shoot has grown downwards. *B*, rhizome placed deeper than the normal depth; its continuation-shoot has grown upwards. The dotted lines indicated from *n* in *A* and *B* point to the annual growths in the rhizome. *C*, seedling plant. To the right the seed enclosing the haustorial end of the cotyledon; *H*, primary root; *n*, lateral rootlet arising within the axis of the shoot; *a*, posterior side of cotylar sheath; *v*, anterior side of same; *b*, *c*, kataphylls on the axis of the seedling. *A* and *B*, reduced. After Rimbach. *C*, magnified. After Irmisch.

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[1] Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880). The placing in darkness of the orthotropous chief shoot in Circaea sufficed to cause the shoot next the apex, which would otherwise have been plagiotropous, to become orthotropous.

[2] See Royer, Flore de la Côte d'or, p. xx; Rimbach, Das Tiefenwachstum der Rhizome, in Fünfstück's Beiträge zur wissenschaftlichen Botanik, iii (1898), p. 178. P. E. Müller's view of the importance of earth-worms in bringing about the sinking of rhizomes in the soil is, to my thinking, exaggerated. The worm will only sometimes bring the rhizome a little quicker into its definite depth.

[3] Investigation is required as to whether shortening of a pull-root does not take the germ-shoot into the soil.

and as it strengthens it turns upwards, forms foliage-leaves[1] and becomes photophilous, whilst a geophilous lateral shoot continues the rhizome. If one changes the depth by bringing the rhizome nearer the surface the continuation-shoot grows downwards (Fig. 309, *A*) and the converse is the case (Fig. 309, *B*).

Similar relationships are found as the investigations of A. Braun, Irmisch, Warming, and others, have shown in other tubers and rhizomes. For a detailed account of these relationships I cannot find space here. It must suffice if I merely mention this remarkable fact that the depth of geophilous shoots is regulated in this way:—during the strengthening period there is an endeavour through apical growth directed downwards to secure a definite 'normal depth,' the retention of which is striven for amongst higher or lower plants by changes in depth either upwards or downwards; the action of pull-roots, as they have been described in the case of Arum[2], is also important in relation to this. The regulation of the depth is effected through the influence of the processes of metabolism, as has been shown to be probable in the case of Circaea. All geophilous shoots must, so far as they are not saprophytes or parasites, send assimilating portions into the light, either single leaves or foliaged shoots. Between these and the geophilous shoots, or parts of shoots, there exists an exact regulating correlating relationship which, however, we cannot penetrate. We name the neutral line between the two that which is exhibited in the normal depth. If the lie is deepened there must be, as Rimbach has shown, more material used up for the formation of photophilous parts than otherwise, and this disturbance of the balance finds its expression in a change of geotropic sensitiveness. One might elaborate the picture further, in that one might consider that the bearers of the positive and geotropic sensitiveness are separate and distinct entities which by the capacity of their metabolism can increase or diminish and so sometimes hold the balance even, whilst at other times they might give a preference to one side or the other. But even then one would only arrive at an incomplete picture of phenomena requiring further investigation.

PHOTOPHILOUS SHOOTS IN THE SOIL. The photophilous shoots which are laid down under the soil show different adaptations which enable them to bore through the soil[3]. These are essentially the same as those which are found in many seedling-plants, for example:—convex bending upwards of the axis or of the leaf-stalk, which facilitates the boring through the soil and the drawing out of the leaves; protection by a kataphyll, like the coleoptile of the grasses, in erect shoots and so on. Where the leaves bore through the

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[1] It is characteristic that the foliage-leaves arising directly upon the rhizome are here stalked as in Paris. Those on the photophilous shoots are sessile. Another example of the phenomena referred to on pp. 300, 390.

[2] See p. 270.

[3] See Areschoug, Beiträge zur Biologie der geophilen Pflanzen, in Acta Universitatis Lundensis, xxxi (1896).

soil in the erect position we find the parts that are in front in the movement especially arranged to facilitate the passage through the earth. This is seen in the leaf-tips of many monocotylous plants, for instance in Gagea arvensis, where the apex of the leaf is conical and is somewhat horny at the tip, whilst the rest of the leaf is flat. But I have no room for a description of these phenomena.

THE SHOOT IN THE SERVICE OF REPRODUCTION

I

INTRODUCTION

A. Gemmae.

Space forbids the discussion of the different arrangements which we find in connexion with the formation of gemmae, but there are two illustrations which may be quoted to show the connexion between form and function. One of them is from the domain of the Pteridophyta, the other from the Spermophyta.

Lycopodium. Lycopodium Selago and some other species of the genus, for example, L. lucidulum and L. reflexum, form short deciduous shoots or *gemmae*, around which considerable literature has collected[1]. They fall off as small leafy shoots provided with the primordium of a root. They are not, as is usually the case, abscised at their point of origin from the chief shoot, but separate above their base, and the lowermost part of the shoot remains with some leaves. The point at which they fall off (Fig. 310, IV at *A*) is prepared—the axis of the shoot is here thinner, so that it easily breaks through. What then is the significance of the leaves that remain behind? Formal morphology has considered it sufficient to assume that the anterior of these (Fig. 310, II *A*) is the 'axillant leaf,' which is 'concrescent' with the bud-shoot developed in its axil. But this explanation is not very illuminating because the Lycopodineae do not generally possess axillary branches, and this leaf is inserted higher up upon the axis of the lateral shoot than the two lateral leaves. To me it appears that the lowermost leaves of the gemma can be nothing else than its *bud-scales*. We see that the leaf which stands on the outer side is the most strongly developed. It is concave inwards, and forms with the adjacent leaves of the mother-shoot of the bud a protective cover to this on the outside, and the other bud-scales fit in with it. By the elongation of the shoot-axis below the bud-scales the gemma is raised up beyond the foliage-leaves, and can thus be easily distributed; and indeed the bud-scales evidently help in this distribution, for it is probable that an *abjection* of the gemma takes place here, brought about by the pressure which its first two leaves

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[1] See Hegelmaier, Zur Kenntniss der Gattung Lycopodium, in Botanische Zeitung, xxxii (1874), p. 481. As regards history—Dillenius, Historia muscorum, p. 436, tab. 56, gave a good description of the gemmae, as also did Hedwig, Theoria generationis et fructificationis plantarum cryptogamicarum Linnaei, Lipsiae, 1797, p. 112, who took them to be male flowers.

exercise upon the adjacent leaves. These leaves experience a certain tension, and when this is released the gemma can be cast out for some distance[1].

The first leaves of the gemma possess a peculiar conformation. They are at first filled with reserve-material, and facilitate therefore rapid further development in the germination. Then the first two lateral leaves, whose surface is originally vertical, experience a torsion whereby their flat sides are turned upwards (Fig. 310, III)[2]. At the same time these leaves are *asymmetric*, as the course of their mid-nerve, which is but slightly developed, shows. The asymmetry evidently depends upon the almost horizontal position of the gemma, which diverges greatly from the erect growth which all other shoots of Lycopodium Selago have. The torsion of the leaves enables them to make use of the light better[3]. Evidently a part of the food-material accumulated in the bud is produced by its own activity.

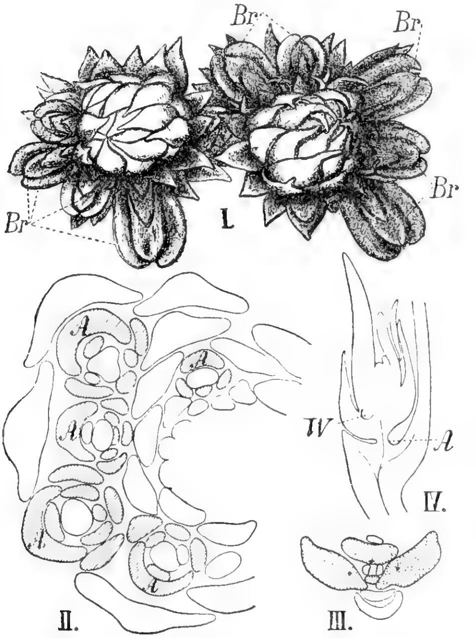

FIG. 310. Lycopodium Selago. I, view from above of the summit of a dichotomy. *Br*, gemmae standing all on the outer sides of the shoots only. II, portion of the apex of a shoot in transverse section. The leaves of the gemmae are shaded. *A*, anterior leaf in the gemmae. III, gemma in transverse section; the storage-leaves are shaded. IV, gemma in longitudinal section. *A*, line of separation; *W*, primordium of a root.

It is interesting to see here how under definite conditions a configuration appears which is found *generally* in the plagiotropous shoots in another species of the same genus. The large flat leaves of the gemma may further serve also as a kind of parachute, and thus aid the distribution. Altogether the gemmae exhibit marked, and in more than one relationship, excellently constructed organs for spreading; the special features are:

1. The construction of the shoot-axis—basal portion to raise up the gemma, point of rupture higher up.
2. The leaf-formation—bud-scales which persist and serve as agents in the abjection; storage-leaves; torsion of the first two leaves.

With regard to the origin of the gemmae, according to Hegelmaier they arise at the position where otherwise a leaf would have developed. The morphological explanation of this behaviour must be passed over here. I would only say that it appears easy to understand that the slender gemma from the outset would take up a smaller space on the apex of the shoot than the strong dichotomous shoot. The

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[1] In favour of this it may be noted that the two bud-scales right and left of the gemma curl inwards concavely after the gemma has been set free. Mr. F. Lloyd informs me orally that he has seen the abjection.

[2] See Part I, p. 105, where a like phenomenon is described in Lycopodium alpinum.

[3] See also what has been said above about the effect of pressure.

gemmae are not disposed all round the shoots, but are arranged unilaterally (see Fig. 310, I). The side upon which the gemmae stand appears to me to be always the *outer* side with regard to the whole stock (see Fig. 310, I). In two shoots of a fork which bear gemmae the gemmae will not, or will only exceptionally[1] stand upon the sides of the shoots which are turned towards one another. We have here, it seems to me, one of those frequent cases of furthering of the outer side to which I have several times referred.

Finally it may be mentioned that the formation of the gemmae takes place under conditions other than those under which the sporangia appear. We find them chiefly on the upper[2] part of the year's shoot. The leaves in this part have no sporangia, or only aborted ones, in their axils. Subsequently sporangiferous leaves are formed. The conditions under which the two kinds of organs develop have yet to be determined experimentally. Adaptations like those which have been so briefly depicted are found in many Spermophyta. The gemmae of Lycopodium are distinguished by no very great characters from the *bulbils* of many species of Allium and Lilium.

Remusatia Vivipara. This aroid bears, as has long been known, a misleading descriptive specific name. There is no 'vivipary,' that is to say, continuous development of the seed, without a resting period; there is only the formation of gemmae. The gemmae arise characteristically on kataphyllary shoots[3] which are *orthotropous* and stand up from the far-creeping stolons. The gemmae are small tuberous shoots which easily fall off. Their outer leaves are kataphylls and have hooked incurved leaf-tips, so that the gemmae can be easily distributed by animals, which their position on orthotropous shoots makes easier than it would be were they to spring from shoots on the surface of the soil. It appears that the propagation of this plant by gemmae far outstrips that by seed, at least under certain conditions[4].

The relationships of configuration of the gemmae to their function as organs of distribution is evident without further comment in the cases mentioned above, but we do not know the conditions for their formation.

Whilst I pass over with this brief mention these gemma-shoots, I must give a very full account of the formation of the *flower*.

B. The Flower.

I understand here by the term 'flower' a shoot beset with *sporophylls*[5], that is to say, leaves bearing sporangia. Such a shoot consists, as do all shoots, of two parts: an axis—here the *flower-axis*—and the leaves of which in the flower there are two kinds, the *essential* ones which are the sporophylls—

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[1] I found such an exception in a shoot whose twin, that is the other one belonging to the same dichotomy, was arrested at an early period. Upon it the gemmae were disposed radially.

[2] Using the ordinary expression; to me, however, this part seems rather the under.

[3] These are distinguished anatomically by an early development of cork.

[4] Wight, Icones Plantarum Indiae Orientalis, iii, Pl. 900, says that the seed-bearing form is 'exceedingly rare' at Courtallum, where the form-bearing gemmae is abundant. Probably seed-bearing takes place under other conditions than that of gemma-formation. In plants cultivated in plant-houses the formation of gemmae takes place regularly.

[5] This expression was originally used by Schleiden, but has only come into general use within recent years.

sometimes only one in number—and the *unessential* ones, which are frequently absent, and are the leaves which form the *envelope* of the flower.

The flower is a shoot of limited growth in a number of Pteridophyta, and in all Spermophyta with the exception of the female flower of Cycas[1]. Consequently in many the flower-axis is only slightly visible. It is sometimes entirely used up in the formation of the one or many sporophylls in the case of the Angiospermae, a fact the neglect of which has led to many false deductions. From this definition of the flower, which is based upon the results of Hofmeister's comparative investigations into the history of development, it follows that the old Linnean conception of the 'Cryptogamae' as flowerless plants is untenable, because we must speak of the flower of the Pteridophyta if the portion of the shoot which bears the sporophylls is different from the vegetative shoot, as is the case when the sporophylls are not mixed up with the foliage-leaves, but are confined to definite regions of the axis of the shoot. As in the case of all groupings and definitions, however, it is a matter of subjective opinion where one will draw the limit. It will be hardly necessary, for example, to designate as 'flower' the sporiferous portion of the shoot which is developed in regular alternation with the foliage-leaves in the fern Onoclea Struthiopteris. If we do this in the case of the genus Cycas, where quite similar relationships occur, it is only because in the other Cycadaceae the flower is sharply marked off from the vegetative shoot, and also upon comparative grounds. Moreover we find in the rudimentary[2] flower of the Pteridophyta all stages from the ordinary configuration of vegetative shoots[3] up to flowers which, like those of Equisetum, are large, and have for long been recognized as having a resemblance to the male flowers of many Gymnospermae[4].

If one wishes to construct a picture of the origin and development of the flower one must start from the flower of the Pteridophyta. Such a construction can only be a probable one for evident reasons. I shall here only indicate some general points which must be taken into consideration in regard to this.

1. The *arrangement* of the sporophylls on the shoot differs in many Pteridophyta from the arrangement of the foliage-leaves upon the shoot. Both evidently were alike to begin with. Two possibilities are offered to us:

(*a*) The arrangement of the sporophylls is the original one, that of the foliage-leaves has been derived;

(*b*) The converse is the case.

It is commonly held that the second alternative is the correct one. I shall recur to this subject when I speak of the flower of Selaginella.

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[1] Also Dacrydium Colensoi (?), see Fig. 348.

[2] Using this term in Sachs' sense.

[3] The sporophylls frequently resemble the foliage-leaves in this group.

[4] See Von Mohl, Vermischte Schriften botanischen Inhalts, Tübingen, 1845, p. 96.

2. In any comparison of the flower of Pteridophyta with that of Spermophyta the heterosporous Lycopodineae and Isoetaceae must be taken account of, especially because in them, more than in the heterosporous Filicineae, we can speak of flower. In them:

(*a*) The microsporophylls and megasporophylls of the flower appear in relatively large 'indefinite' number.

(*b*) The megasporophylls are less numerous, for instance, in Selaginella[1].

(*c*) A separation between male and female flowers has not been discovered in any living Pteridophyta. We meet with only an occasional indication of it in Selaginella. Hermaphrodite flowers, at least in the morphological sense, are therefore the primitive type. But if, for example, we tried to derive by arrest the unisexual flowers of the Gymnospermae from hermaphrodite flowers because Welwitschia shows in the male flowers the rudiment of a female organ, or if we tried the converse, we should be speculating upon very insecure foundation, because, in the first place, the Gymnospermae certainly are no single group, and secondly, the separation of the flowers into male and female may have taken place in their pteridophytous-like *ancestors*. One must not judge of all forms by one.

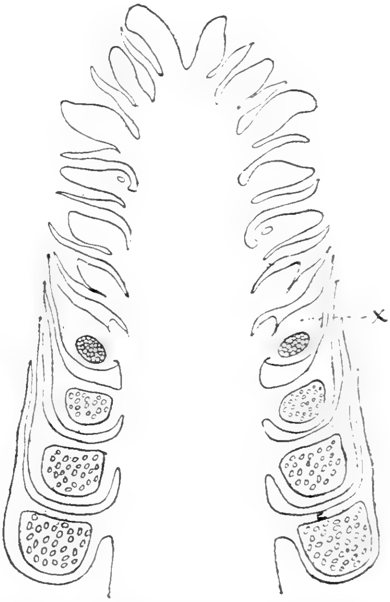

FIG. 311. Pinus maritima. Androgynous flower in longitudinal section; *x*, microsporophyll with rudimentary ovuliferous scale in its axil. Magnified.

Hermaphrodite flowers occur now occasionally as a 'variation' in the Gymnospermae. I found them in hundreds in an example of Pinus, probably P. maritima[2]. The male flowers standing near the apex of the twig in this example were transformed into female ones. At the point of transition I found not infrequently a stamen with a rudimentary ovuliferous scale in its axil (Fig. 311, *x*). Such a flower might serve in phyletic speculation as the type of a very simply constructed hermaphrodite spermophytous flower from which by reduction, concrescence, and transformation of single parts pretty well everything might come. But as regards this I will only point out briefly here that the separation of the flowers into male and female has in the case of some plants resulted in their different *arrangement* upon the plant. In Pinus the male flowers stand in the position of short shoots, the female in the position of long shoots. The biological reason for this is clear. The short shoots, as we have already seen, are retarded formations compared with the long shoots; they are worse nourished

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[1] The reason for this is obvious. [2] At Majori. Analogous cases are often described in the literature.

than are the long shoots, which occur at the most favourable position for nutrition at the end of the shoots. That the female shoots should occupy this position is of importance in view of their long-continued further development in connexion with formation of seed, whilst the male flowers soon fall away. Similar relationships are found in Juglans, Fagus, Quercus, Corylus, and elsewhere. The different position occupied by the male and female flowers in the system of shoots in these genera may, I think, be explained in this way: *the female flowers appear in the region of the shoot which is best nourished.* In herbaceous plants such differences do not appear, and there is absent amongst them also the polar differentiation of the annual shoots. We can understand therefore why the formation of the hermaphrodite flowers in Pinus described above appeared in the *upper* male flowers, and similarly that there is no reason why in the Pteridophyta the male and female flowers should have a different place of origin.

In the following pages we shall first of all deal with the formation of flowers and sporophylls in the Pteridophyta, and I may point out now that the conformity in habit of the male flowers of the Gymnospermae with the flowers of Selaginella and Equisetum is clearly connected with the fact that in all of them distribution of the spores takes place by the wind, whilst the configuration of the sporophylls is readily understood when it is regarded as having a special relation to the construction of the bud of the flower.

Regarding Terminology. The place upon the sporophyll at which the sporangia arise, especially if these are in numbers, differs frequently from the rest of the sporophyll. We designate this spot the *placenta,* and its function is to enable the sporangia to obtain a larger amount of nourishment[1]. We can understand therefore why solitary sporangia do not sit upon a placenta. They are found in Ceratopteris, the Schizaeaceae, Osmundaceae. The expression 'receptacle,' which is often used for the point of origin of the sporangia, is, I think, unnecessary. The designation placenta, which comes from the Spermophyta and took origin in a false comparison with the animal kingdom, is now so commonly used that it can scarcely be ousted. We use it according to the above definition in a biological, that is to say a functional, sense, and its use simplifies the nomenclature.

II

THE SPOROPHYLLS AND FLOWER OF THE PTERIDOPHYTA

A. *GENERAL FEATURES OF THE SPOROPHYLLS.*

We have assumed that the spore-bearing organs of the Pteridophyta and Spermophyta are produced by the leaf-organs which are designated sporophylls. In how far the microsporangia or megasporangia of the Spermophyta take their origin always from microsporophyll or megasporophyll will be explained when speaking of the formation of their flower.

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[1] Especially by storing up food-material, which afterwards can be used in the development of the sporangia.

In the Pteridophyta the origin of the sporangia from leaf-organs is almost everywhere conspicuous. They stand in the Filicineae mostly upon the under side or upon the margin of the leaf, in the Lycopodineae upon the upper side of the sporophyll, in Equisetum uniformly around it.

In Selaginella alone do the sporangia arise upon the vegetative point of the shoot immediately above the primordium of the sporophyll, and this is the case also in Selaginella spinulosa, although some authors have said that the sporangia are leaf-borne in this species [1]. Hypothetically the leaf-borne origin of the sporangia might be explained either by supposing a 'displacement,' or that in consequence of the relatively early appearance of the primordia of the sporangia the cell-layers out of which they arise (Fig. 312, 5, 6, 7, 8) would be drawn into the formation of the leaf if the formation of the sporangia did not begin, but this picture must remain purely conjectural until it is proved that the primordia of the sterile leaves of Selaginella do really extend gradually upwards. The whole question has lost interest since we have recognized that the place of origin of an organ is not critical for its 'morphological' significance.

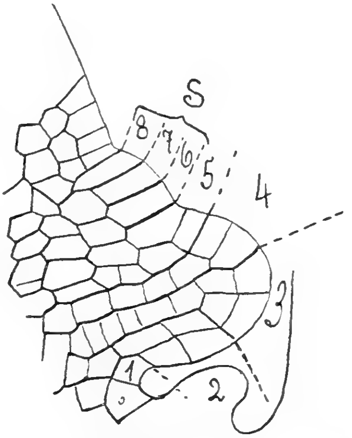

FIG. 312. Selaginella spinulosa. Young sporophyll with primordia of sporangia, *S*, in longitudinal section. Magnified 460. After Glück.

The function of the sporophyll is not only to produce the sporangia but also to protect them in their youth, to aid in the scattering of the ripe spores—in seed-plants to promote pollination and fertilization. It is easy to prove in many cases that the conformation of the sporophyll has a relationship to these functions, and this is evidently the reason why frequently its configuration differs so markedly from that of the foliage-leaves. In considering therefore the sporophylls from the organographical standpoint we have to seek for an answer to two distinct questions:

1. The biological one—in what relationship does configuration stand to function?

2. The purely morphological one—in what genetic relationship do the sporophylls stand to the foliage-leaves?

We might add a third question, namely—what are the efficient causes of the configuration, especially in cases where the sporophylls diverge far from the foliage-leaves?

To answer this third question we have not at present the necessary

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[1] Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien, in Botanische Zeitung, xxxviii (1880), p. 561; Glück, Die Sporophyllmetamorphose, in Flora, lxxx (1895), p. 355.

foundation. The answer to the other two is possible, although here also we have not yet the insight which is to be desired.

Biological relationships scarcely give us the cause of differences ; and indeed only the arrangements which serve for the protection of the sporangia are the biological ones which have been mainly considered, although, as we now know, there are relationships of configuration which are connected with the distribution of the spores.

BIOLOGICAL RELATIONSHIPS OF SPOROPHYLLS. Amongst the Pteridophyta the sporophylls present striking differences according as the distribution of the spores takes place by water or through the air. The distribution through water occurs in the case of the sporophylls of the Marsiliaceae, and these externally are very like the fruits of many Spermophyta. They owe their conformation to the circumstance that they are adapted to pass through a resting period [1]. They have the sporangia sunk within the *sporocarp*, and the tissue of the sporocarp is so arranged that it is only upon the entrance of a quantity of water that the opening of the sporocarp is effected by the swelling of the tissue whose function it is to do so. The advent of water is also necessary for the germination of the spores. Sporophylls which produce spores that are scattered by the wind facilitate the process of shedding by their *position* ; for example, in Aneimia, Onoclea Struthiopteris, Helminthostachys (Fig. 319), and others, the sporophylls are erect and projected beyond the vegetative parts, an arrangement which is repeated in the strobili of the Lycopodineae and other forms. The diminution in the amount of the assimilating tissue in many sporophylls relatively to the foliage-leaves—and in some cases this goes so far that the assimilation-tissue disappears altogether—will also make more easy the scattering of the spores. In the configuration of the sporophyll too less specialized arrangements for the distribution of spores are needed the more spores there are formed, or the easier these can acquire favourable conditions of germination [2].

Whilst there can be no fundamental difference of opinion regarding these relationships, it is otherwise with regard to the interpretation of morphological points involved in the relationship of the sporophylls to the foliage-leaves.

RELATIONSHIP OF SPOROPHYLLS AND FERTILE LEAF-PARTS TO FOLIAGE-LEAVES. The close relationship of the two is clear. In many cases they are entirely alike in their configuration, for example, in Aspidium Filix-mas, and many other Leptosporangiate Filicineae. In others there are gradual *transitions* from ordinary foliage-leaves, which are at the same time sporophylls, to leaves which are sporophylls alone—transitions which we know also to occur between foliage-leaves and hypsophylls, and tendrils,

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[1] In this period protection against drought is what is required.

[2] A like relationship *mutatis mutandis* has been already pointed out in the case of the archegonia. See p. 212.

and-bud scales, and storage-leaves. After the analogy of these it seems fair to conclude that the sporophylls also are merely more or less transformed foliage-leaves, and we have seen further that the *history of the development* of the sporophyll conforms often during a long period with that of the foliage-leaves; besides, we can *experimentally* cause the primordia of sporophylls to develop into foliage-leaves if we destroy or suppress the formation of sporangia. This happened in the cases of Onoclea Struthiopteris[1] and Selaginella mentioned above[2].

Experimental Proof in Onoclea Struthiopteris. The mature sporophylls of Onoclea are very different from the foliage-leaves; they are much smaller, quite erect, their differentiation of tissue and their external segmentation come to maturity much more rapidly than in the foliage-leaves. The plant is especially favourable for research because the sporophylls alternate regularly with foliage-leaves. Every year there arises at the beginning of the vegetative period a number of foliage-leaves, and at its end, so soon as the plant is strong enough, a number of sporophylls. If now all the foliage-leaves be removed from a plant whose sporophylls are not yet mature, foliation of the sporophylls may be caused, that is to say, the primordia of the foliage-leaves are checked in their development to sporophylls and develop further as foliage-leaves. The most various intermediate stages between sporophylls and foliage-leaves are thereby produced, and one of these is represented in Fig. 313. It might be said teleologically that the plant sacrifices its propagative organs in order to preserve its vegetative condition.

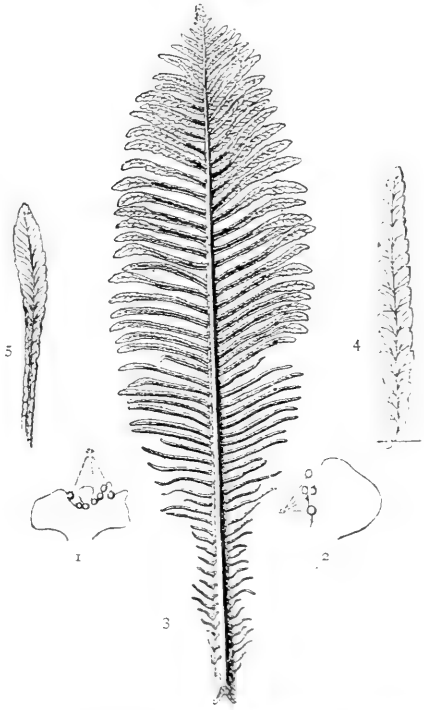

FIG. 313. 1 and 2. Botrychium Lunaria. Pinnae of the normal sterile portion of the leaf bearing sporangia, *sp*. 3-5. Onoclea Struthiopteris. 3, leaf between a foliage-leaf and a sporophyll produced experimentally. 4 and 5, pinnae which have become sterile in different degrees. Reduced.

Experimental proof in Selaginella. Selaginella offers a second case in which a correlation between the formation of sporangia and the configuration of the sporophyll diverging from that of the foliage-leaf has been

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[1] Goebel, Über künstliche Vergrünung der Sporophylle von Onoclea Struthiopteris, Hoffm., in Berichte der deutschen botanischen Gesellschaft, v (1887), p. lxix. Atkinson repeated this research with the same results in the case of Onoclea sensibilis.

[2] See Part I, p. 216.

experimentally proved[1]. The sporangia in this genus are arranged in spike-like strobili. If these are cut off and used as cuttings they grow out vegetatively, and the contrast between the two forms is very marked because the strobili in most species of Selaginella are isophyllous, whilst the vegetative shoots are anisophyllous[2]. The sporangia abort in the upper part of the strobilus which is used as a cutting, and the leaves upon the newly formed portion of the shoot take on the ordinary form of the foliage-leaf.

The features thus artificially produced appear spontaneously in nature. Sometimes sporophylls show a partial virescence, that is to say, may appear to have a vegetative formation, sometimes parts of foliage-leaves which normally bear no sporangia occasionally produce these and assume then quite the configuration of sporophylls. We may quote as an example:

Botrychium Lunaria. The sporophyll arises upon the upper side of the sterile leaf in this plant. It is richly branched, and the sporangia arise at the end of a vein on its margin somewhat approaching the upper side. If we compare a large number of examples we shall find that the difference between the sterile and fertile portion of the leaf is not constant, although in the majority of cases it is sharply marked. The variations, however, take different directions. The normally fertile portion of the leaf, the sporophyll, may become entirely or partially sterile, or the sterile portion of the leaf may become entirely or partially fertile. In both cases there are intermediate forms such as are shown in Fig. 313, 1 and 2. On these it may be clearly seen that the more the sporangia appear the more is there a division of the leaf into single segments, and the more do the leaf-lobes elongate and narrow. The sporangia are in these cases normal, and one cannot therefore speak of a malformation associated with a destruction of the function, as is the case in the phyllody of ovules.

These facts furnish irrefragable proof that there is a causal connexion, which we call correlation, between the formation of the sporangia and the divergent configuration of the sporophyll; and if we read into this further and say that the sporophyll arises from an earlier or later transformation of the primordium of a foliage-leaf, this is founded upon the fact that in all known Pteridophyta and Spermophyta the foliage-leaves appear first in the course of the development and are followed by the sporophylls. It by no means follows that we must interpret this process as also phyletic[3]. The reasons

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[1] See Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xxxviii (1880), p. 821; Behrens, Über Regeneration bei den Selaginellen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897), p. 163. The literature is cited here.

[2] See p. 506.

[3] Many authors who have dealt with these questions do not separate these two sides of the question. What I have been speaking of above is based upon the relationships as we see them *now*. It does not touch questions of phyletic speculation. So long as we know so little about the things that surround us, it will be more profitable to go more into *their* life-conditions before exorcising the shades of the past. There is nothing in the way of the assumption that originally all leaves were sporophylls, and that the formation of sporangia was introduced at a stage in the life which was

which have made it probable that the sporophylls are phyletically the older will be spoken of when the sporangia are discussed[1].

The interpretation of the sporophylls as transformed foliage-leaves supposes that they conform to foliage-leaves or parts of foliage-leaves in their position and their origin. This appears in many cases but not in all. That the sporophylls conform to the foliage-leaves in their position requires no illustration here. It is well known and seen everywhere. But the conformation of the sporophylls to the foliage-leaves or parts of foliage-leaves in respect of their origin is of special importance for the theoretical interpretation of the sporophyll.

In the Lycopodineae, Equisetineae, the Marattiaceae, Polypodiaceae, Gleicheniaceae, most Schizaeaceae, Osmundaceae, the sporophylls do not differ in position and origin from the foliage-leaves.

FIG. 314. Schizaea rupestris. Sporophyll. Natural size.

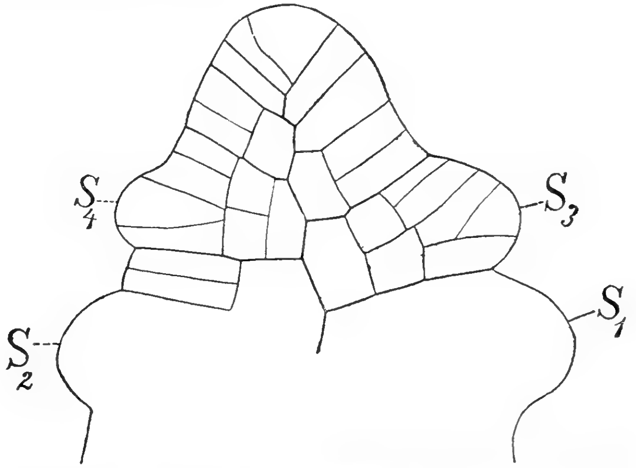

FIG. 315. Schizaea rupestris. Apex of sporophyll in profile; S_1–S_4, primordia of fertile pinnules. Magnified.

SPOROPHYLLS AND FERTILE LEAF-PARTS AS NEW FORMATIONS. In Schizaea, the Marsiliaceae and Ophioglossaceae we find that they do differ; the sporophylls or the fertile leaf-part cannot be traced back to a transformation of a sterile portion of a leaf, but they are really *new formations*, which have no representation on the sterile leaves. The following examples will illustrate this:—

(I) LEPTOSPORANGIATE FILICINEAE.

SCHIZAEACEAE. In this family the relationships are the simplest in so

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later the larger the dimensions attained by the sporophyte. We have indeed before now seen that even in the seedling-plant the configuration may be changed by adaptation. As in plagiotropous seedlings of ivy the orthotropous shoots proceed from the plagiotropous ones, although it is in the highest degree probable that the orthotropous are phyletically the older, so also at the present day the sporophylls proceed from the foliage-leaves.

[1] See p. 510.

far as the sporophylls although new formations appear in the same position as do sterile leaf-parts elsewhere. We may first of all discuss the case of Schizaea.

Schizaea Rupestris. I have examined Schizaea rupestris which I collected in Australia. The sterile leaf is here elongated, linear, and traversed by a single nerve. It grows by means of a two-sided apical cell. No branchings are laid down. The fertile leaf (Fig. 314) bears at its apex a number of pinnules which produce sporangia in two rows, and the terminal part of the leaf is likewise fertile [1]. The history of development shows (Fig. 315) that these fertile portions of the leaf develop as outgrowths of the margin beneath the continually growing apex (Fig. 315, S_1, S_2, S_3, S_4). There is formed in each of these outgrowths a two-sided apical cell, and thus the sporiferous pinnules grow like the whole leaf. One would have the sterile leaf if one removed the fertile upper portion as it is shown in Fig. 315. The appearance of the fertile parts here as *new formations* only supplies a specially instructive example of the fact that the development of sporangia occasions a richer segmentation than exists in the sterile leaf.

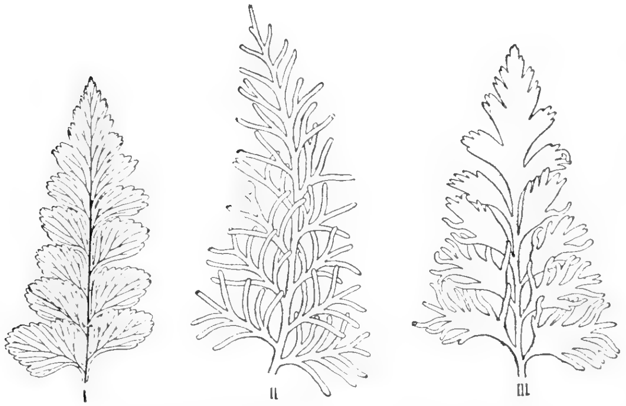

FIG. 316. Asplenium dimorphum. I, sterile pinna. II, fertile pinna. III, transition-form. All reduced.

Similar behaviour is found in other genera of the Schizaeaceae, for instance in Aneimia and Lygodium. In Mohria there is no essential difference between the sporophylls and foliage-leaves. That the striking conformation and disposition in Aneimia facilitates the distribution of the spores will be shown later [2].

POLYPODIACEAE. This family furnishes another example of like features:—

Asplenium Dimorphum. Fig. 316, I and II, show two pinnae of the first order of Asplenium dimorphum. The sterile pinna, I, is strikingly different from the fertile one ; its pinnules of the second order are broad, only

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[1] The sporangia are *marginal* on the pinnules of the sporophyll. The same is the case with the sporangia of the Marsiliaceae, although the relationships are evidently quite different. In both cases it is noteworthy that the fertile pinnules and sporangia conform to one another as regards their place of origin, and this is of value in relation to the hypothesis which derives the vegetative formation of the leaf from sporangia which have become sterile.

[2] See p. 592.

indented at the margin, whilst in the fertile leaf the pinnules of the second order are again pinnatifidly cut with narrow pinnules of the third order [1]. The case of Schizaea does not differ essentially from this.

MARSILIACEAE. In the Marsiliaceae we find relationships which conform essentially to those of the Schizaeaceae. It is evident that the peculiarly formed *sporocarps* in the species of Marsilia are outgrowths of the sterile leaves. To the solitary sporocarps in Pilularia another origin was formerly in part assigned, but they also arise from a foliage-leaf [2] as I have stated, and as the thorough investigations of Campbell, Glück, and D. S. Johnson have confirmed. The relationships in the species of Marsilia, whose leaves bear a large number of sporocarps, are specially peculiar, for instance in M. polycarpa:—

Marsilia Polycarpa [3]. The sporocarps arise in acropetal serial succession upon the part of the leaf-primordium which becomes stalk (Fig. 317). The first are laid down before the vegetative pinnules are present upon the leaf-primordium. As we have here a large number of sporocarps the plant is particularly suited for an accurate investigation of their position. The fertile segments spring from the *margin* of the sterile leaf. They arise, however, only on *one margin* in a series one above the other, although at the same time the serial arrangement is not always very strongly maintained, being probably affected by relationships of space. Fig. 317, III, shows clearly that the sporocarps assume upon the leaf-primordium the same position in space as do the sterile pinnules; the lowermost pair particularly [4] clearly appears as

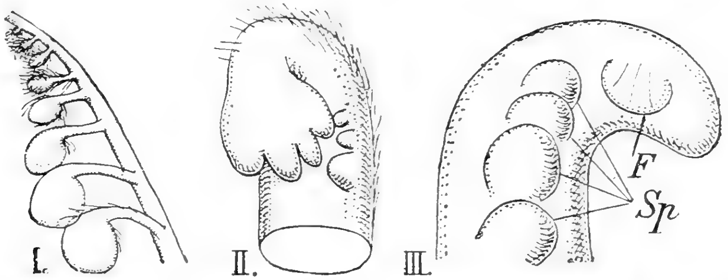

FIG. 317. Marsilia polycarpa. I, lower part of a sporophyll with eight sporocarps in profile. II, young sporophyll seen from above. III, younger sporophyll in profile. *F*, primordium of a pinnule; *Sp*, young sporocarp. Magnified.

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[1] This case differs somewhat from that of Schizaea because on the sterile leaf also the apex of each nerve corresponds to the vegetative point of a leaf (see p. 313), which in the fertile leaf develops further, but in the one-nerved sterile leaves of Schizaea pusilla the leaf is 'potentially' also quite simple. There is however only a graded difference. There are moreover species of Schizaea with dichotomously branched sterile leaves.

[2] See Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien: Über die 'Frucht' von Pilularia globulifera, in Botanische Zeitung, xl (1882), p. 771.

[3] I gathered the material for investigation some years ago in South America. As to the specific name:—Marsilia polycarpa I consider as an 'aggregate' species, especially as A. Braun himself was doubtful whether his Marsilia subangulata was actually different from Marsilia polycarpa.

[4] In the profile view only one pinnule is naturally visible.

a marginal outgrowth quite as the pinnules already described in Adiantum Edgeworthi[1]. The arrangement of the cells is different: the sporophylls grow for a long time by a two-sided apical cell, just like the apex of the sterile leaf; the sterile pinnules show from the beginning a marginal growth with diverging anticlines at the apex. I must not, however, attach much weight to this difference. We have already seen[2] that the arrangement of the cells at the apex of the leaf in ferns has a connexion with the configuration which will be reached; we need not therefore wonder that the sporocarps which develop into greatly elongated bodies show a cell-arrangement different from that of the flat leaflets. We have besides seen in Schizaea rupestris fertile leaf-pinnules growing with a two-sided apical cell, and these are marked out in like manner by an elongated conformation and absence of development in surface. The branching of the fertile leaves in Marsilia is, however, unilateral, and in this they show a difference from the sporophylls of Schizaea. The leaf of Marsilia stands obliquely upon the dorsiventral rhizome, the anterior leaf-margin being deeper than the posterior one. It is from the anterior one that the sporocarps spring, and this disposition is still visible even in the mature condition, as the leaf-stalk has a channel upon its upper side[3]. This unilateral position of the fertile leaf-portion is a striking one, and may be connected with the dorsiventral character of the whole shoot. Also the lateral buds stand upon the anterior margin of the leaves, and they find here at first just as do the sporocarps a specially protected position between the shoot-axis and the leaf-primordium. Unilateral formation of pinnules is found also elsewhere amongst the ferns, for example in the leaves of Pteris semipinnata. We may also compare the unilateral development of the fertile leaf-portions with the cases already described[4] of unilateral pinnations, for example of Anthyllis tetraphylla and other Leguminosae, only we saw there that we had to deal with a phenomenon of vegetative *adaptation* standing in relation to the dorsiventral construction of the whole plant. Putting aside phyletic speculation, such an adaptation can scarcely be admitted in the Marsiliaceae; but it is striking that a similar development is repeated in the Marsiliaceae, which are likewise *dorsiventral.* The important point is, however, the proof that the fertile leaf-portions, even where they appear in relation to the sterile leaves as *new formations*[5], yet *conform in position and origin to the leaf-pinnules.*

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[1] See p. 316, Fig. 204. The last two pinnules arise when the apex of the leaf-primordium has already expanded. It forks in more feeble primordia.

[2] See p. 316.

[3] See A. Braun, Neuere Untersuchungen über die Gattungen Marsilia und Pilularia, in Monatsberichte der Berliner Akademie, aus dem Jahre 1870, p. 653.

[4] See Part I, p. 121. Also the facts mentioned Part I, p. 88. In Fig. 228, IV, the pinnate leaves are partly unilaterally developed, so that the phenomenon is not at all rare.

[5] In many species of Marsilia many sporocarps are seated upon one stalk, for instance often in Marsilia quadrifolia. Usually we have a branching of the sporocarp, of which Johnson has

(II) EUSPORANGIATE FILICINEAE.

OPHIOGLOSSACEAE. In this family, at least in the large majority of species, the condition is somewhat different. The sporophyll does not arise upon the margin, but upon the *upper side* of the sterile leaf-portion. In Ophioglossum palmatum the marginal position is also found, but in most cases the sporophyll arises here also from the upper side of the sterile leaf, but more or less near its margin[1]. The history of development is unfortunately unknown. It is possible, although indeed not very probable, that the sporophyll originally marginal has become displaced upon the upper side. As it is we can give some 'reasons,' or rather hint at some relationships, which account for the divergent position of the sporophyll even in the Ophioglossaceae. It is laid down very early, and in correspondence with its later construction is relatively very thick. The young leaf is firmly ensheathed in envelopes, and the position of the sporophyll upon the upper side of such a primordium would take up less room than it would were it placed right and left; its median position secures that the sporophyll is enveloped and protected by the sterile leaf (Fig. 318, II), and this, in a case where there is such very slow development of the leaf as occurs here, must

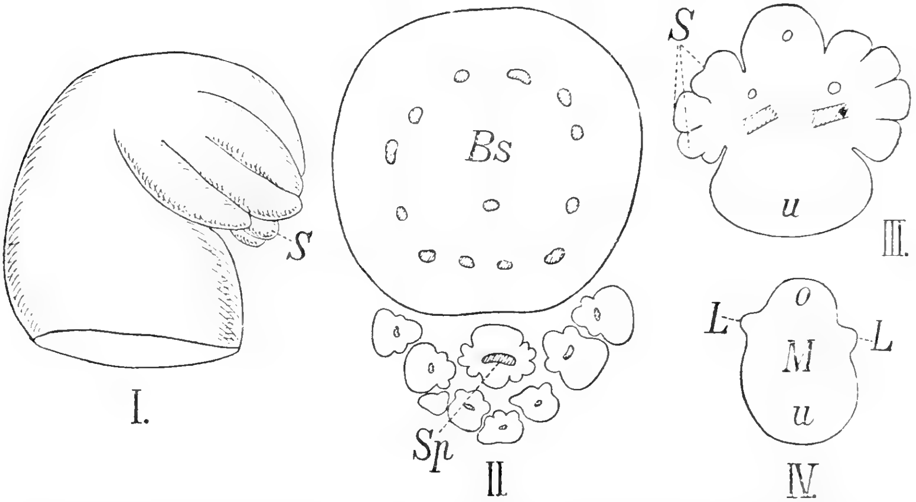

FIG. 318. Helminthostachys zeylanica. I, young leaf in profile. The sterile pinnules cover the sporophyll, the point of which, *S*, is seen projecting, but at a later period would be covered. II, leaf in transverse section; *Bs*, leaf-stalk; *Sp*, sporophyll invested by the pinnules of the sterile leaf-part. III, sporophyll in transverse section; *S*, sporangiophore. IV, young foliage-leaf in transverse section; *L*, primordium of lamina; *o*, upper side; *u*, under side; *M*, primordium of mid-vein. Magnified.

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traced the history of development in one species. It may be that in other cases an elevation of the common base takes place. See D. S. Johnson, On the Development of the Leaf and Sporocarp in Marsilia quadrifolia, L., in Annals of Botany, xii (1898), p. 119; id., On the Leaf and Sporocarp of Pilularia, in Botanical Gazette, xxvi (1898).

[1] Bower, Studies in the Morphology of Spore-producing Members: II. Ophioglossaceae, London, 1896.

be of great importance. We shall return below to the phyletic explanations which have been given of the divergent position of the sporophyll in the Ophioglossaceae. At present I wish only to indicate that the normal branching of the foliage-leaf in one plane is connected with the provision of an *assimilation-surface* exposed to the light, and that therefore in the biological connexion the divergent position of a non-assimilating leaf-segment is of no importance. As a matter of fact we find the same phenomenon in the leaf-structures of the flowers of higher plants[1], for example in the formation of the corona in Narcissus, Sileneae, and elsewhere, and in the multiplication of petals by splitting in double flowers. All these phenomena conform to that of the position of the sporophyll in Ophioglossum which has *nothing or only little to do as an assimilating portion of the leaf.* This resemblance of the sporophyll of the Ophioglossaceae to a leaf-segment expresses itself also in its remarkably dorsiventral character[2].

There is, therefore, no necessity, so far as living plants show us, for considering the sporophyll as anything else but a foliage-leaf which experiences soon or late, sometimes not at all, a transformation; otherwise the relationships of configuration of the sporophylls and of the flowers of the Pteridophyta are so manifold and so important for a consideration of the flowers in the higher plants that it will be useful to select here from the larger groups some illustrations. The arrangements for the protection of the sporangia will be spoken of separately[3].

B. *SPECIAL FEATURES OF THE SPOROPHYLLS.*

I. FILICINEAE.

1. EUSPORANGIATE FILICINEAE.

MARATTIACEAE. In the Marattiaceae the sporophylls are the ordinary foliage-leaves.

OPHIOGLOSSACEAE. In the Ophioglossaceae the fertile leaf-portion springs from the sterile, which is very different in appearance. It has no special assimilation-tissue, and is erect and stalked. The features are apparently strictly fixed in Ophioglossum[4]; in Botrychium we find frequently

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[1] The position of the ovules should be specially considered here. These, for example, in the Ranunculaceae are originally marginal on a megasporophyll. Where this forms a basal sac the ovule springs from a median position, and in Ranunculus and other genera frequently this is the only ovule that remains. Its position is originally like that of the sporophyll of the Ophioglossaceae to the sterile leaf-part.

[2] See especially the sporophylls in Helminthostachys, p. 483.

[3] See p. 496.

[4] The vegetative transformation of the sporophyll is very rare in Ophioglossum. Apart from the branching at the apex of many sporophylls, which for our purpose is of the same kind, I only know of one record of it, that of Presl, Supplementum tentaminis Pteridographiae, in Abhandlungen der Königl. Böhmischen Gesellschaft der Wissensch. in Prag, Folge 5, iv (1845–6), who says: 'vidi specimen Ophioglossi vulgati, cuius spica marginem foliaceum utrinque duas lineas latum evidentissime venosum habuit.'

intermediate forms[1]. The configuration of the sporophyll of Ophioglossum and Botrychium is described in every text-book, and need not be further spoken of here beyond the statement that the sporangia in both genera are marginal.

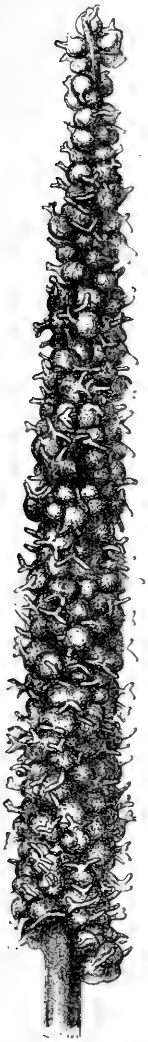

FIG. 319. Helminthostachys zeylanica. Sporophyll. Magnified.

Helminthostachys[2]. The relationships of configuration are peculiar and remarkable in this third genus of the Ophioglossaceae. The sporophyll differs most of all amongst the Pteridophyta from the configuration of the foliage-leaves, at the same time the construction offers interesting points of comparison with features that are observed frequently in the formation of the stamens of many dicotylous plants. The sporophyll arises as in other Ophioglossaceae in the form of an outgrowth upon the upper side of the foliage-leaf, which is here divided many times into a somewhat palmate form. The lobes of the sterile leaf-part are in their juvenile condition projected beyond the sporophyll (Fig. 318, I), so that the sporophyll is protected upon the one side by the downwardly curved sterile leaf-part, and upon the other by the massive leaf-stalk (Fig. 318, II). The whole leaf is originally covered in a cap-like manner by an outgrowth of tissue of the shoot-axis. The fertile sporophyll is evidently negatively geotropic (Fig. 319), is apparently radial, and its surface is densely occupied by supporters of the sporangia, which Bower has designated *sporangiophores*. These sporangiophores, simple or branched, only rarely bear one, more usually many, sporangia, and these are then most frequently disposed in two tiers one above another and in a radial manner (Fig. 320). The lower portion of the sporangiophore is usually narrowed to a stalk-like form. The upper part is broadened out and has grown out into lobes, so that the whole

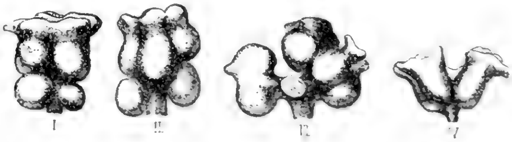

FIG. 320. Helminthostachys zeylanica. Sporangiophore. I, II, simple; III, IV, branched. Magnified.

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[1] See p. 476.

[2] See Prantl, Helminthostachys zeylanica und ihre Beziehungen zu Ophioglossum und Botrychium, in Berichte der deutschen botanischen Gesellschaft, i (1883), p. 155; Bower, Studies in the Morphology of Spore-producing Members: II. Ophioglossaceae, London, 1896. The account given in the text is based upon investigations carried out on material collected by me in Ceylon and Java in 1886, and which I have lately re-examined.

sporangiophore has some resemblance to a sporophyll of Equisetum. The upper broad portion forms a roof above the young sporangia and must be considered as a protective apparatus for them. Examination of the young sporophyll (Fig. 321) shows that its radial disposition is only apparent; it is really bilateral or dorsiventral, for there remains upon its upper side and upon its under side a strip free of sporangia, and these strips are still visible in many mature sporophylls. *These free strips correspond to the middle nerve of the sterile leaf-portion.* The sterile leaf-lamina is here, as in the case of some leptosporangiate ferns[1], laid down relatively late (Fig. 318, *L*). The development of the massive middle nerve (Fig. 318, *M*) precedes that of the lamina, which shoots out right and left from a zone of embryonal tissue remaining about the middle nerve (Fig. 318, IV, *L*)[2]. In the case of the sporophyll there is no laying down of one leaf-lamina. This is to a certain extent from the very first divided into a number of small papillae (Fig. 318, III, *Sp*) which indicate the sporangiophores[3]. The remarkable thing then is that the 'division' of the lamina takes place so very early, and that it does not as elsewhere proceed in the plane of the leaf-surface which is here undeveloped, but in directions which lie oblique to this. We speak figuratively of a division here because evidently a leaf-surface to the sporophyll is usually not developed, but in its place the sporangiophores appear. The leaf-surface may, however, develop in abnormal cases, such as I observed in Java in 1885[4]. The sporophyll had in these examples repeatedly divided at its end —thus approaching in its behaviour the sterile leaf-part —and the single portions of the leaf contained chlorophyll were flattened and were divided at the margin into lobes which bore the sporangia. In this case then *the sporangiophore appeared as a segment of a foliage-leaf.* Upon these general grounds then I regard the sporophyll of Helminthostachys as a portion of a foliage-leaf which has become modified at an early period and in a peculiar manner. The lamina is replaced by a sporangiophore which appears in its position. That the virescence should proceed most easily at the *end* of the sporophyll can be easily understood from the history of development. Fig. 321 shows

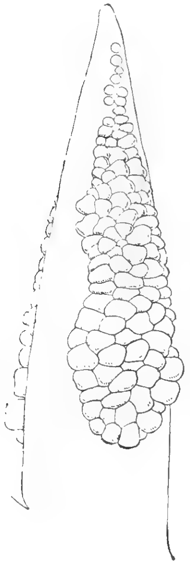

FIG. 321. Helminthostachys zeylanica. Young sporophyll in oblique profile. The primordia of the sporangiophores are densely clustered on the margin. Magnified.

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[1] See p. 320, and Fig. 207 of Pteris serrulata.

[2] The arrangement of the cells is different from that in Pteris serrulata.

[3] In many cases there is evidently a common base which one might recognize as the rudimentary primordium of the lamina. In rare cases in Java I found this developed as a wing.

[4] See also Bower, Studies in the Morphology of Spore-producing Members: II. Ophioglossaceae, London, 1896, Pl. ix, Figs. 138 and 139.

that the formation of the sporangiophores decreases towards the end of the sporophyll, and there they arise partly in a *single* row, which means that the lamina of the sporophyll approaches more the ordinary form [1].

We can, therefore, trace back the sporophyll to a specially far-reaching transformation of the vegetative leaf, and at the same time see that the sporophyll of Helminthostachys in its dorsiventral construction conforms with that of Ophioglossum and Botrychium. The hypothesis, which will be subsequently mentioned, that the sporophylls have proceeded from a further vegetative development of the sporangia, would assume that upon a sporophyll of Ophioglossum the sporangia were chambered by sterile plates of tissue nearly parallel with the leaf-surface, and that then these partial sporangia grew out vegetatively into sporangiophores. We content ourselves here with proving the fact that the sporophylls of Helminthostachys conform in their primordia to the foliage-leaves, although the two leaf-forms appear so very markedly different when we only regard their mature condition.

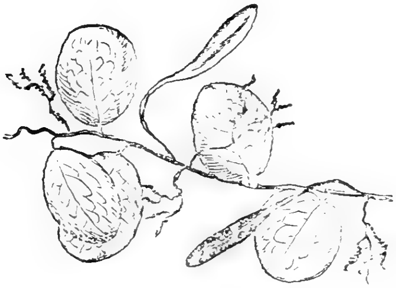

FIG. 322. Drymoglossum subcordatum, Fee. Habit. The sterile leaves are broad and shortly stalked. The sporophylls are erect, have long stalks, and a narrow lamina. After Christ.

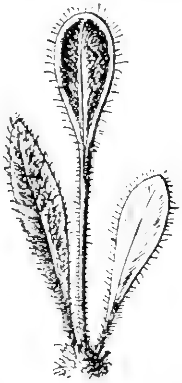

FIG. 323. Elaphoglossum spathulatum. Habit. After Christ. Natural size.

2. LEPTOSPORANGIATE FILICINEAE [2].

(*a*) ISOSPOROUS LEPTOSPORANGIATE FILICINEAE.

The manifold construction of the sporophyll in this group has been already mentioned [3], and it would take me too far were I to give a thorough account of it. Only a few points may be noted.

EXTERNAL FORM. The sporophylls often are distinguished from the foliage-leaves by having a different conformation of the stalk and the lamina. The stalk in many of the sporophylls is longer than that of the foliage-leaves, and thus facilitates the distribution of the spores (Figs. 322, 323).

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[1] Where the transformation has proceeded less far, there the vegetative formation can most easily enter in.

[2] See Glück, Die Sporophyllmetamorphose, in Flora, lxxx (1895).

[3] See p. 482.

In the segmentation of the lamina we have to recognize two cases:—

(*a*) The sporophylls have the segmentation of their lamina reduced as compared with that of the foliage-leaves[1]. This occurs in Onoclea Struthiopteris, Allosurus crispus (Fig. 324), Acrostichum peltatum, and it is the more common.

(*b*) The sporophylls have their lamina more richly segmented than is that of the foliage-leaves. This occurs in Asplenium dimorphum (Fig. 316), and also in Osmunda regalis, Aneimia, and elsewhere.

ANATOMY. The existence of anatomical differences, such as the reduction of the assimilating leaf-tissue and so on, in the sporophylls, can only be mentioned here.

It seems to me improbable—at any rate it is not yet proved—that the difference in the configuration of the sporophylls when compared with the foliage-leaves can be always explained teleologically[2]. More probably it is determined by the metabolic processes connected with the formation of sporangia, and these cannot always be brought into close relationship with the conditions of life. The endeavour to find such connexions is nevertheless a sound one. It must have as a starting-point a review of the relationships of life. I may here briefly refer to one illustration:—

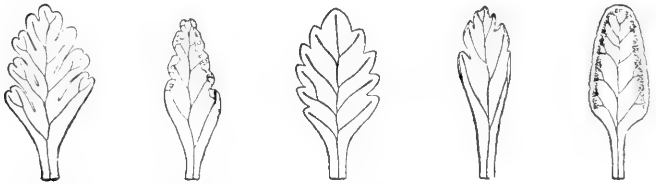

FIG. 324. Allosorus crispus. 1, sterile pinnule. 2, 3, 4, transition-stages between sterile and fertile pinnules. 5, fertile pinnule with the margin rolled back. After Glück.

Acrostichum (Rhipidopteris) peltatum. This fern owes its name to the configuration of the sporophylls, which indeed are not peltate, but which by their undivided lamina, in contrast with the richly segmented and frequently forked sterile leaf, are very striking[3]. The original resemblance of the two often shows itself, however, in the sporophyll by indenta-

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[1] That is to say the primordium of the leaf has remained stationary at a certain definite stage of segmentation. For the protection of the juvenile sporangia such sporophylls are much better suited than are those which are much divided.

[2] We must always remember that the configuration of the sporophyll has not only to do with the distribution of the spores, but also with the protection of the sporangium in its juvenile state.

[3] In systematic works, for example Christ's Die Farnkräuter, it is assumed that the sporangiferous side of the leaf is the under side, and this undoubtedly is in accordance with the usual behaviour and the lie. Moreover, the stomata are also limited, as in the sterile leaves, to the under side. The ptyxis, however, suggests that the sporangia stand upon the *upper side*. At least we find the marginal portion incurved towards this side—especially clearly is this seen in transition-forms between sterile and fertile leaves where the lamina is still more divided—but the incurving takes place in the sterile leaves as elsewhere towards the *upper side*. There is here then much that is still enigmatical.

tions at its margin which correspond to a division which has not proceeded very far. Probably the species has been derived from forms with slightly divided leaves[1], and the sporophylls approach more nearly the primitive leaf-configuration than do the foliage-leaves. The conformation of the sporophyll has moreover probably also a biological significance. The bright margin of the sporophyll is free of sporangia and is bent backwards. It is easy to observe that the sporophylls retain water-drops, which then will be carried to its sporangiferous side. Now the species grows in moist mountainous woods[2], but the leathery texture of the sterile leaves, their sharply differentiated epidermis bearing stomata only upon the under side, indicate that the plant is arranged to withstand temporary want of water. The sporophylls by their conformation hold water-drops for a time and pass it on directly to the young sporangia, which in other ferns are protected against wetting but here evidently are not injured by this.

(*b*) HETEROSPOROUS LEPTOSPORANGIATE FILICINEAE.

SALVINIACEAE. In the Salviniaceae[3] we may speak of microsporophylls and megasporophylls and of parts of these, because the microsporangia and megasporangia appear in separate sori, and these stand upon leaves[4]. There is a difference in the construction and conformation of the microsporophyll and megasporophyll respectively in the Salviniaceae[5], and a short explanation of this is necessary because the difference between microsporophylls and megasporophylls is much greater in the Spermophyta, and if we assume that the Spermophyta have sprung from pteridophytous ancestors a consideration of the sporophylls of the Pteridophyta offers us the best prospect of a basis for a satisfactory interpretation of the sporophyll of the Spermophyta.

Salvinia. In Salvinia the difference to which I have referred is essentially this: the number of the microsporangia is larger than that of the megasporangia[6]. The significance of this is of course that the number of the microspores is greater than that of the megaspores.

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[1] As a matter of fact the nearly allied Acrostichum flabellatum has such leaves. By some authors Acrostichum flabellatum is united with Acrostichum peltatum. In Acrostichum flabellatum there are sterile leaves also which are only indented at the margin and otherwise are undivided. This whole cycle of forms, whether we call it a species or a group of nearly allied species, is allied to the species of Elaphoglossum, whose leaves are almost throughout undivided. That the bearers of the organs of reproduction retain primitive relationships of configuration more than the vegetative organs which have been changed subsequently through adaptation is seen elsewhere, for example in Schistostega and others amongst the Musci, and also in the Cactaceae.

[2] I gathered it some years ago, for example, in the Cumbre de San Hilario in Venezuela.

[3] As in the heterosporous Lycopodineae.

[4] Both kinds may occur upon different lobes of the same leaf. That the two kinds of sporangia stand upon separate leaves in the Lycopodineae is easily understood because the sporangia arise singly.

[5] A difference in the structure and the conformation of the microsporophyll and megasporophyll in the Lycopodineae and Isoeteae is not known.

[6] We have no reason for supposing that Salvinia originally had sori composed of both micro-

Azolla. In Azolla the difference between the two kinds of sori is exaggerated by the appearance of only one megasporangium in the megasorus. The two kinds of sori can, however, be traced back to one type—to a sorus which consists of a placenta corresponding to a leaf-lobe round about which microsporangia are distributed, whilst the point is occupied by a megasporangium. In the microsori this megasporangium early aborts[1]. In the megasori, on the other hand, only the megasporangium develops, but there are found at later stages of development (Fig. 325) primordia of microsporangia which abort. The indusium appears as an annular wall, and thus the whole structure acquires a resemblance to the ovule of one of the Spermophyta. Azolla shows then a reduction of the number of megasporangia in relation to the number of microsporangia, and probably also a separation of the original hermaphrodite sori into male and female ones.

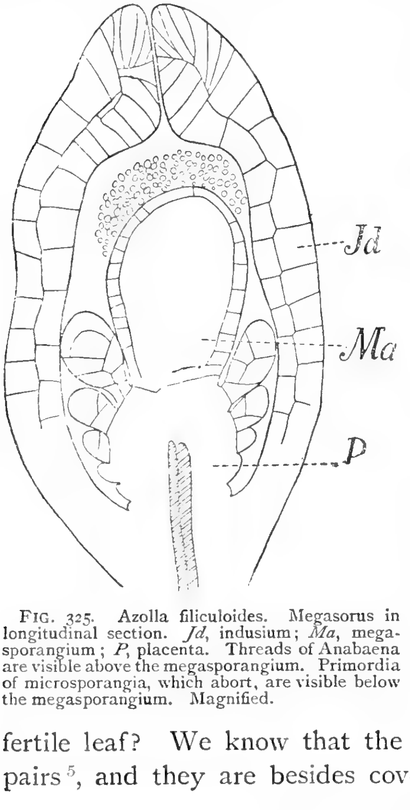

FIG. 325. Azolla filiculoides. Megasorus in longitudinal section. *Jd*, indusium; *Ma*, megasporangium; *P*, placenta. Threads of Anabaena are visible above the megasporangium. Primordia of microsporangia, which abort, are visible below the megasporangium. Magnified.

I was not able to form a definite picture of the sporophylls of Azolla from the statements of Strasburger[2] and of Campbell[3], and I have therefore examined the relationships in Azolla filiculoides, which some twelve years ago fruited freely in the Botanic Garden at Marburg. Each foliage-leaf very early divides, as we know[4], into an upper lobe and an under lobe, whose position is indicated in Fig. 227. How now do these two leaf-parts behave in the fertile leaf? We know that the sori enclosed by the indusium stand in pairs[5], and they are besides covered by a one-layered cap-like envelope.

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sporangia and megasporangia, yet the behaviour of Azolla suggests such a supposition. It is evident that the separation of the microsporangia and megasporangia favours cross-fertilization. Moreover Heinricher, Die näheren Vorgänge bei der Sporenbildung der Salvinia natans verglichen mit der der übrigen Rhizocarpeen, in Sitzungsberichte der Wiener Akademie, lxxxv (1882), found on one occasion in Salvinia natans a sporocarp which contained some megasporangia among a number of microsporangia.

[1] See Strasburger, Histologische Beiträge, Heft 2, Jena, 1889, p. 8. Campbell, On the Development of Azolla filiculoides, Lam., in Annals of Botany, vii (1893), found no primordium of a megasporangium in the microsori. Both exist in Azolla filiculoides according to my experience.

[2] See Strasburger, Über Azolla, Jena, 1873, p. 52.

[3] See Campbell, op. cit.

[4] See p. 348.

[5] Occasionally I found three upon the under side of the stem.

Strasburger maintains that the sori are transformed leaf-lobes and speaks of the envelope as the under lobe of the leaf, whilst Campbell came to the conclusion 'that the whole of the ventral lobe goes to form the sori, and that the involucre is derived from the whole of the dorsal lobe of the leaf[1].' Neither of these authors is altogether correct so far as my investigations show. I agree with Campbell that the sori proceed from one portion of the under lobe of the leaf which very early develops, but the upper lobe is by no means devoted to the formation of the involucre. This upper lobe is present as elsewhere, and contains also a branched vascular bundle and a pit inhabited by Anabaena. It produces at its base a wing-like one-layered *outgrowth* which partially covers the sori, and this is the origin of the 'involucre' (Figs. 326 and 327, *F*), which I need not say contains no conducting bundle. The under leaf-lobe, which is used for the formation of the sori, contains as elsewhere its conducting bundle. That Strasburger ascribed the involucre to the under lobe of the leaf is due to the fact that it is separated from the upper lobe by a somewhat deep depression. Com-

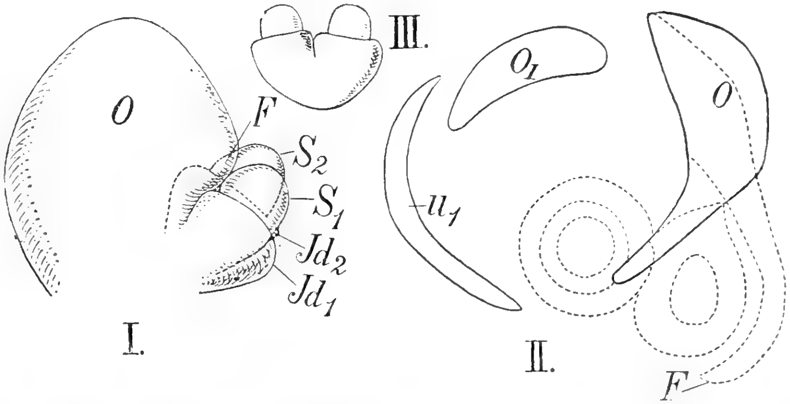

FIG. 326. Azolla filiculoides. I, sporophyll dissected out in surface view; *O*, upper lobe; *F*, primordium of wing of upper lobe; S_1, S_2, primordia of megasporangia; Jd_1, Jd_2, the indusium. II, two leaves in transverse section. To the left a sterile leaf; O_1, upper lobe; U_1, under lobe. To the right a fertile leaf shown in two sections, one lower down in the leaf by dotted lines, the other higher up; *O*, upper lobe; *F*, wing of the upper lobe covering two megasori. III, under lobe dissected out and seen from the surface; it is wholly used in the formation of two megasori, and the indusium appears as an annular wall. All magnified.

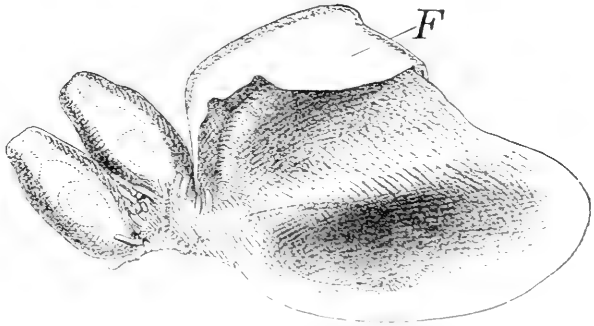

FIG. 327. Azolla filiculoides. Sporophyll spread out flat. To the left two megasori. To the right the upper lobe. *F*, wing-like outgrowth of the upper lobe, the mucilage-pit is visible below.

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[1] Campbell, On the Development of Azolla filiculoides, Lam., in Annals of Botany, vii (1893), p. 158.

paring then the fertile leaf with the sterile the following changes in configuration are found:—

(1) The under lobe, which is elsewhere undivided, divides into two lobes, more seldom three, and even into four in Azolla nilotica according to Strasburger, from the apex of these the single megasporangium proceeds in the megasorus[1]. Beneath this there rises up as an annular wall the indusium, which, being favoured upon the outer side, grows round the megasporangium like an integument[2].

(2) From the portion of the margin of the upper lobe which touches upon the under lobe a wing-like outgrowth at first proceeds, and one might designate it as an indusium if each of the two sori had not already its own indusium.

MARSILIACEAE. The microsporangia and megasporangia are found together in the same sorus in the Marsiliaceae. The sporocarps diverge in their configuration more than those of any other group from the sporophylls met with elsewhere. The sporangia apparently are enclosed within a body of tissue which is surrounded by a usually hard shell, and this, when it is ripe, is opened in a remarkable manner by the swelling up of mucilaginous tissue within it—an arrangement which makes possible the withstanding of a dry period, and as a matter of fact the sporocarp exhibits a resting period—and thus the germination of the spores can only begin if such a quantity of water is present as is necessary for the further development. It has been already shown[3] that the sporocarps are always leaf-borne, and like the pinnule of Marsilia they take rise upon the flanks of the foliage-leaf (Fig. 317). The history of development has also explained the rest of the structure of this remarkable body. The sporocarps are always dorsiventral, even where, as in Pilularia, this is not externally marked. The 'fruit' consists in Pilularia globulifera of four chambers, in which megasporangia and microsporangia lie. In Marsilia the chambers are more numerous and are arranged in two rows. I have pointed out[4] in opposition to the assumption, based upon the consideration of the mature condition only, that the sporangia arise actually within closed spaces, and also in opposition to Russow's statement, based upon beautiful but incomplete developmental investigations, that the 'sorus-canal' arises by a splitting of the tissue, and that the sori here are formed, as in other Leptosporangiate Filicineae, from *superficial cells* of the primordium of the sporophyll, and are only gradually *sunk subsequently* into the tissue. Büsgen, Meunier, Campbell, and Johnson have confirmed this, and supplemented it by showing that the placenta arises upon the

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[1] The division of the under lobe is specially plainly seen in Fig. 326, III.

[2] See the section upon the development of the sporangium, p. 595.

[3] See p. 479.

[4] See Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien: III. Ueber die 'Frucht' von Pilularia globulifera, in Botanische Zeitung, xl (1882), p. 771.

margin of the leaf. The processes which are thus brought about recall in more than one sense the features which will be depicted below in other ferns, for example in the cyatheaceous Balantium antarcticum, only that the sori do not appear in Azolla as they do there upon the under side of the leaf, but are displaced to the *upper side* whenever the formation of the pit sets in.

The diagrammatic representation of cross-sections shown in Fig. 328, I–III, will illustrate this. The youngest stage, Fig. 328, I, recalls the transverse section of a leaf of a young fern such as is shown in Fig. 207, II. We saw there a lamina, *L, L*, springing from marginal cells. In the sporocarp of the Marsiliaceae we find quite similar marginal cells, *R*, which, however, are displaced somewhat more towards the upper side. In some parts of the margin corresponding to the later-formed fruit-chambers an increased growth takes place, accompanied by characteristic divisions of the marginal cells. In Fig. 328, II, the marginal cells, from each of which a sorus springs, are marked with the letter *S*. They are already sunk in a shallow pit, and are pushed upwards by the growth of a portion of the *under side* of the leaf. At the same time the deepening of the pits begins. The portions which are marked *y, y* and *J, J* grow up and cause the sinking of the leaf-margin more and more in a deep pit which has a narrow mouth to the outside, and this subsequently forms by concrescence a closed canal. If now we compare the process with that of Dicksonia, which will be mentioned presently[1], we see quite analogous[2] processes if we only consider one-half of the Fig. 331, II. The portion of tissue marked *y, y* in Fig. 328, which, however, remains united with the rest of the sporocarp-tissue, corresponds to the outer indusium (Fig. 331, I, *Jo*), whilst the part marked *J, J* in Fig. 328 corresponds to the inner indusium (Fig. 331, I, *Ju*). As a matter of fact one may consider usually the tissue marked *J, J* as an indusium in the Marsiliaceae, especially because in the process of emptying of the sori in Marsilia each of these is surrounded by a sac-like envelope (Fig. 329, II). These indusia, however, are not laid down as separate tissue, but are raised as one tissue-mass common to all the sori, and in it the lines along which they will subsequently be separated one from the other can be recognized at an early age. If then these are to be regarded as individual indusia one must assume a 'congenital concrescence,' but even now I know of no ground for such an assumption.

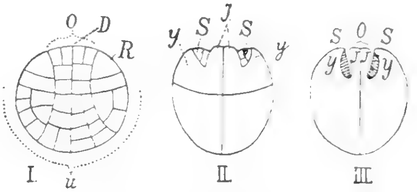

FIG. 328. Marsilia. Three sporocarps of different age in diagrammatic transverse section. I, youngest; *O*, upper side; *U*, under side; *R*, marginal cells; *D*, segment-wall. II, older; *J*, primordium of indusium; *S*, *S*, primordia of sorus; *y*, *y*, lateral outgrowths of the sporophyll. III, still older. Lettering as before. Sori are shaded.

The question may be asked now—how are we to interpret the sporocarp as a whole? I may state, in the first place, that I have nowhere said what Johnson ascribes to me, 'that it represents a simple leaflet or pinna with its edges folded in to meet at the ventral side of the capsule[3].' My view is that the sori are sunk in the *upper side* of the sporophylls. This upper side is, however, extremely narrow,

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[1] See p. 494.

[2] Not homologous.

[3] This is A. Braun's interpretation, not mine.

represented essentially only by the indusium. In Fig. 328, III, the limits are marked by the letter *O*. Everything else, apart from the margin, is strongly developed *under side*; an infolding does not take place. Johnson's statement that the sporocarp is homologous with the 'petiole only of the sterile branch of a leaf,' does not correspond with the facts. What is the 'petiole' of a fern-leaf? The portion of the leaf-primordium on which the formation of the lamina is suppressed entirely or in great part, and where the formation of mechanical tissue is conspicuous instead! The sporocarp is not homologous with this *differentiated* part of a leaf, but with a leaf-primordium on which the differentiation of the lamina is *not yet* begun, as is shown for Petris (Fig. 207, II). That is a difference! Büsgen's observations of monstrosities show also that in rare cases pinnules of Marsilia may develop to sporocarp-like structures, and A. Braun found a pinnule with narrow lamina instead of the sporocarp in Marsilia. Now, as heretofore, I regard the sporocarp as homologous with a leaf-segment, just as it is in Schizaea. The only point in doubt is whether one should consider the marginal portion which is devoted to the formation of the sorus as indication of a further pinnation which, however, remains fused with the leaf. In support of this I know of no weighty grounds at the present time.

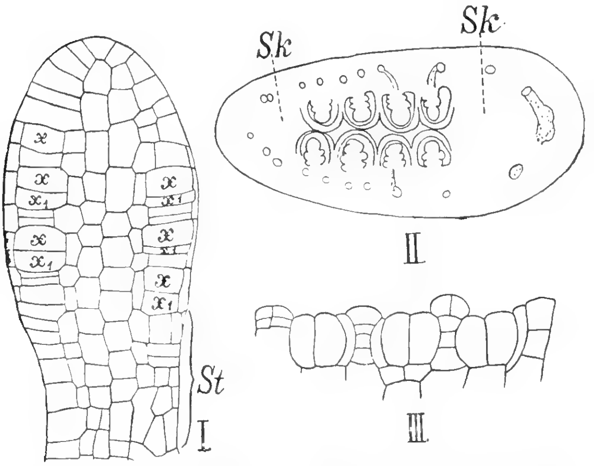

FIG. 329. I, Marsilia polycarpa. Very young sporocarps from the upper side: St, stalk; x, x_1, mother-cells of the sori which proceed from marginal cells, but appear to be displaced to the upper side. II, Marsilia Brownii. Older sporocarp in section parallel with the surface. Eight sori are seen. III, Marsilia polycarpa. Sporocarp like that of I in optical longitudinal section. The large cells are the mother-cells of the sori. I and III magnified.

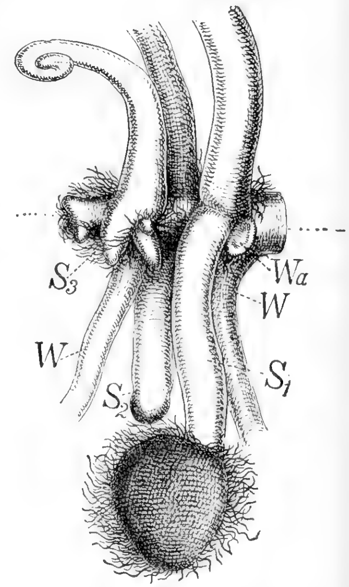

FIG. 330. Pilularia Novae-Hollandiae. Anterior portion of a plant in profile. Two rows of leaves are visible upon the dorsiventral shoot-axis. S_1, S_2, S_3, sporocarps; W, W, roots; Wa, broken-off root. Two roots arise beside each leaf. Magnified.

Marsilia polycarpa. In order to explain the relationships still further I would refer to a very instructive preparation of Marsilia polycarpa which is represented in Fig. 329:—In I we have a view of the upper surface of an *entire* sporocarp which has been dissected out. It is extremely small and still straight. It is a club-like body whose lower part, *St*, develops subsequently into stalk. The two-sided apical cell is still visible at the apex. The primordia of the sori, x, x_1, are evident, and are clearly superficial cells, and indeed, as a transverse section shows, are marginal cells which bulge up by their size. They are mostly divided by a cross-wall into two cells, and these cells it is which in the manner described above become subsequently sunk in pits. Fig. 329, III, gives a side-view of the margin, and already there are upon the upper side of the sporocarp three shallow longitudinal pits which are separated from one another by an intermediate elevation.

I need not go into details further here. It must suffice that we have determined that the remarkable relationships of configuration of the sporocarp of the Marsiliaceae can be referred back to the formation of the sporophylls in other leptosporangiate ferns, and that they only exhibit a special case in relation to the life-relationships.

HYPOGEOUS SPOROCARPS. A few words must be said about the Marsiliaceae which bury their sporocarps in the soil. In West Australia I gathered Pilularia Novae-Hollandiae, which is shown in Fig. 330. The stalk of the sporocarp in this plant bends very early downwards, and the sporocarp itself is directed with the mouth of the pit obliquely upwards. There is no doubt that we have here a phenomenon quite like that of the formation of tubers[1] in the Hepaticae, and that we have especially a protection against rapid and extreme drying. Quite similar relationships are apparently found in Marsilia subterranea, but I do not know this plant from my own observation. Amongst the Spermophyta there are a number of cases in which the ripening fruits are buried in the soil. The examples here mentioned show us anew how analogous adaptations are repeated in the most different cycles of affinity.

3. POSITION AND ARRANGEMENT OF THE SPORANGIA UPON THE SPOROPHYLLS AND THEIR PROTECTION IN FILICINEAE.

These relationships are amply explained in systematic works. Here only some general connexions will be set forth, in order that a comparison may be made with Spermophyta.

(*a*) POSITION OF THE SPORANGIA.

If we keep in view the relationships in *all* the Pteridophyta it would appear as if nearly all possibilities were realized. The sporangia are upon the upper side of the sporophyll in the Lycopodineae; upon the under side in most of the Leptosporangiate Filicineae and in the Marattiaceae; upon the leaf-edges in the Schizaeaceae where there is a slight displacement downwards, in the Marsiliaceae where there is a slight displacement upwards, and in the Ophioglossaceae where in the mature condition of the leaf they appear displaced upwards; uniformly distributed all round in Osmunda[2], in the Equisetaceae, and in Salvinia; on the placenta ('receptacle') in the

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[1] See p. 66.

[2] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 387. In the allied Todea they stand upon the under side.

Hymenophyllaceae. This variability we shall also meet with in the sporophylls of the Spermophyta.

General connexions in this variety will not be easy to find without the help of some more or less bold hypotheses. These will be of most service within narrow cycles of affinity, for example that of the Filicineae. We may here, as it appears to me, establish the fact that the *sporangia in general 'strive' for a position upon the under side of the leaf the more the portion of the sporophyll bearing the sporangia is constructed like a foliage-leaf.* The position of the sporangia upon the under side will be of advantage in many ways:—

(*a*) *The capacity of assimilation* of the side of the leaf turned towards the light will not be interfered with;

(*b*) The sporangia which in the land-forms only scatter their spores when they dry will be *protected from wetting*;

(*c*) The *distribution of spores* will be favoured because the spores will fall away from, and not upon, the surface of the leaf.

Only rarely do the sporangia occur upon the upper surface of sporophylls which are like foliage-leaves [1].

The following examples will illustrate what has just been said:—

The difference between Osmunda and Todea is very striking. In Osmunda the sporophylls are sharply distinguished from the foliage-leaves. In Todea they are not so. If in Osmunda only a few sporangia were to be found upon the leaf, they would stand as in Todea upon the under side. We have then here in one and the same plant the connexion mentioned above.

In the same way the marginal position is mostly found where the fertile leaf-part is not, or only seldom, assimilating, as in Ophioglossum, Botrychium, Aneimia (Section Euaneimia). The attempt has been made [2] to establish this position as the primary, and the position upon the under side as a displacement. Such a displacement has been observed in the history of development of many cases, for example amongst the Schizaeaceae, in Schizaea, Lygodium, Mohria, and in many species of Aneimia. In all these the sporangium is laid down as a marginal structure, and is displaced upon the under side by the development of the 'indusium.'

Dicksonia antarctica. A simple example of this is shown in Dicksonia antarctica (Fig. 331, III). The tufts of sporangia, which apparently spring from

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[1] For example, in Aspidium anomalum of Ceylon, which may be only a form of Aspidium aculeatum, and regarding which therefore it is questionable whether it is constantly reproduced by spores, and the more so, because in other ferns which normally bear sporangia upon the under side the position upon the upper side occasionally is found, as in Polypodium lepidotum, P. proliferum, and Asplenium Trichomanes. See Kunze, Über abnorme Fruchtbildung auf der Oberfläche der Wedel von Farrn aus den Polypodiaceen, in Botanische Zeitung, vi (1848), p. 687. It should be tried whether by sowing the spores of Asplenium anomalum the offspring may not in some cases produce also sporangia upon the under side. With regard to Acrostichum peltatum, see p. 486.

[2] Prantl, Untersuchungen zur Morphologie der Gefässkryptogamen: II. Die Schizaeaceen, Leipzig, 1881.

the under side of the leaf are enclosed by an envelope or indusium of two flaps. The upper overlapping flap, *Jo*, has the structure of the leaf-surface apart from its hairy margin; the under overlapped flap, *Ju*, is composed of cells without chlorophyll, and serves at first for water-storage, but later experiences a movement[1] which lays bare the sorus and so brings about the distribution of the spores. The history of development shows that the cushion of tissue—the placenta—upon which the sporangia sit, proceeds from the leaf-margin, which was, however, at an early period displaced upon the under side of the leaf. This process is begun in the stage shown in Fig. 331, I, where the wedge-shaped cell, *R*, which occupies the leaf-margin, is conspicuous; the under indusial flap, *Ju*, is also seen to be laid down as an outgrowth of the under side of the leaf, and the position at which the upper flap, *Jo*, takes origin is clearly visible. *Ju* is then an outgrowth of the under leaf-surface; *Jo* an outgrowth of the upper surface of the leaf. The first sporangia proceed from the marginal cells of the broadened leaf-margin itself, and there they follow one another in irregular serial succession.

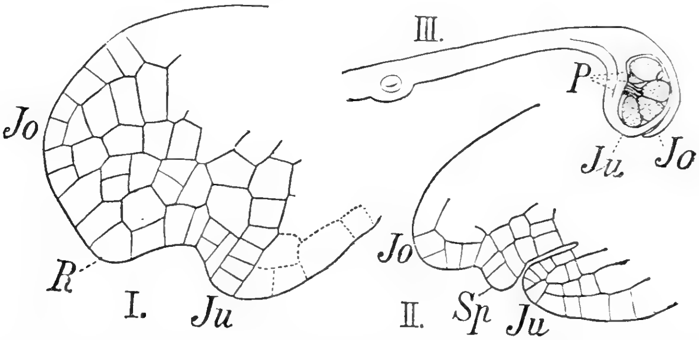

FIG. 331. Dicksonia antarctica. I, pinnule preparing for the inception of a sorus, in transverse section; *R*, marginal cell. II, the same in an older stage. *Sp*, primordium of sporangium. III, sorus almost ripe, in transverse section; *P*, placenta. In all figures: *Jo*, primordium of the upper indusial flap; *Ju*, primordium of the under indusial flap.

Essentially the same processes are observed in Davallia and in other cases.

If now we imagine this process to be shortened so that the upper indusial flap *from the very first* occupies the margin of the leaf instead of subsequently attaining this position in course of elongation, then in other words we have it that the sporangia appear upon the under side of the leaf[2]. They arise here often quite close to the leaf-margin, for example in Allosurus, Fig. 332, where the youngest sporangia—the outermost ones[3]—are only separated by one cell from the leaf-margin. Whether

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[1] How this takes place requires investigation, as does the movement of the indusium-lobes in many species of Hymenophyllum, but there can be little doubt that drying is the cause of the movement.

[2] We may constitute the following series:—

(1) Single marginal sporangia in the Schizaeaceae and Ophioglossaceae.

(2) In addition to these there are some which are further up on the upper side of the leaf, and upon the under side of the leaf.

(3) The formation of the marginal sporangia is suppressed, the margin grows vegetatively, and the sporangia on the upper side are usually suppressed in the Polypodiaceae and others.

[3] New ones also arise towards the inside.

this displacement corresponds with a phyletic process is at present beyond our knowledge.

(*b*) ARRANGEMENT OF THE SPORANGIA.

The sporangia stand upon the sporophylls either singly or in groups. If they arise upon a placenta into which a continuation of a vein enters, either directly or through a tracheid-group, we get the *sorus*. There is, however, no sharp limitation of the sorus in many cases, and Bower[1] has recently grouped succinctly the distribution of sporangia as follows:—

(1) *Simplices*: Sporangia solitary, or if in groups developed synchronously: in Marsiliaceae, Osmundaceae, Schizaeaceae, Gleicheniaceae, Matoniaceae.

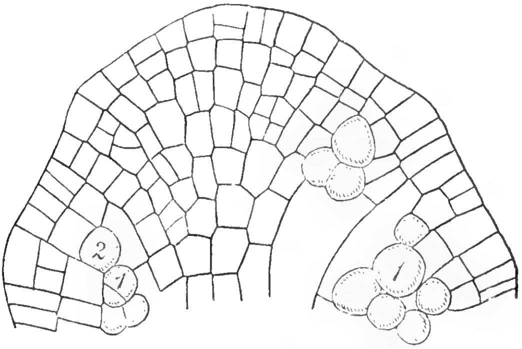

FIG. 332. Allosorus crispus. Apex of the pinnule of a sporophyll seen from the under side. Highly magnified.

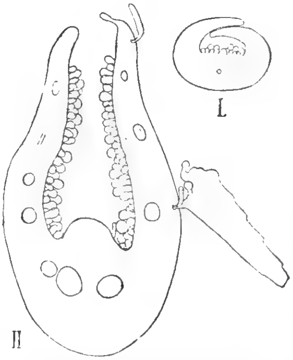

FIG. 333. I. Hymenolepis spicata. II. Elaphoglossum (Acrostichum) spathulatum. Still folded sporophyll in transverse section, underside upwards. When unfolded and mature the sporophyll is flat.

(2) *Gradatae*: Sporangia arising in basipetal succession upon a more or less elongated placenta: in Loxsomaceae, Hymenophyllaceae, Cyatheaceae, Dicksonieae, Dennstedtineae.

(3) *Mixtae*: Sporangia of different ages mixed together: in all the rest of the leptosporangiate ferns.

(*c*) THE PROTECTIVE ARRANGEMENTS FOR THE SPORANGIA.

BY THE WHOLE CONFIGURATION OF THE SPOROPHYLL. In many ferns the sporangia are protected by the ptyxis of the sporophyll, for example in Ophioglossaceae[2], or the margin of the sporophyll bends over the sporangium, just as the margin of the carpel of Angiospermae bends over the ovule. The resemblance is conspicuous in many Acrostichaceae. The sporophylls of Elaphoglossum (Fig. 333, II) have in their young condition a

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[1] Bower, Studies in the Morphology of Spore-producing Members: IV. The Leptosporangiate Ferns, in Phil. Trans., 1899, should be consulted regarding this point. I cannot go here into characters taken from the structure of the sporangia.

[2] See p. 481.

pod-like appearance. They have their margins bent downwards[1]. Hymenolepis spicata shows the same features only that a larger part of the leaf-surface is free from sporangia (Fig. 333, I). It is clear that such an arrangement will have relation to the age of the sporangia at the time when the sporophyll unfolds. If the sporangia at the time of unfolding of the sporophyll are already mature or provided with thick walls, they will require less protection than would young sporangia standing upon an unfolded leaf. Perhaps this is the reason why in the Gradatae and Mixtae protective arrangements are developed in profusion.

BY HAIRS UPON THE SPORANGIA. These occur in Gymnogramme villosa, G. Totta, Polypodium crenatum, and others[2]. These hairs may also occur between sporangia. Peltate hairs form a specially effective protection.

BY INDUSIA. These are outgrowths of the margin of the leaf, of the under side of the leaf, of the placenta[3]. The importance of the indusium was established long ago experimentally by Koelreuter[4] who found in different ferns that the sporangia *dried up* if the indusium was removed from young sori. In young sori of Scolopendrium vulgare he found an exudation of drops which according to his view proceeded from the indusium, a proof therefore that the indusia in the juvenile conditions are very rich in water. The indusia dry later and so allow of the distribution of the spores[5].

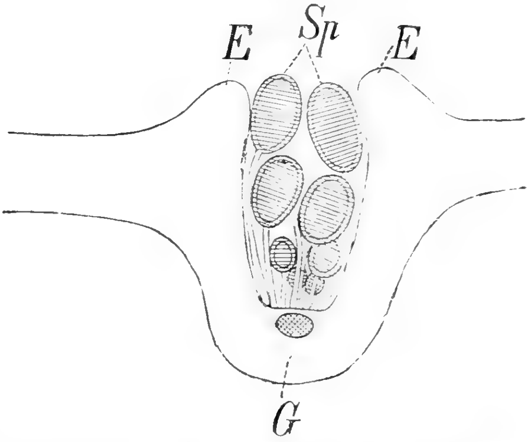

FIG. 334. Polypodium obliquatum. Sorus in somewhat diagrammatic longitudinal section: *Sp*, sporangia; *E*, elevation on the sporophyll; *G*, vascular supply. Magnified.

BY SINKING OF THE SORI IN PITS. This may be combined with the formation of an indusium, for instance in Scolopendrium. Polypodium obliquatum offers a simpler condition (Fig. 334). The sori are placed in depressions of the leaf-tissue which are surrounded by an annular growth (Fig. 334, *E*). The sporangia according to their age reach the mouth of

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[1] The sporangia here arise upon the whole surface excepting upon the margins and the midrib.

[2] See Glück, Die Sporophyllmetamorphose, in Flora, lxxx (1895).

[3] See Burck, Over de ontwikkelings geschiedenis en den aard van het Indusium der Varens, Academisch Proefschrift, Haarlem, 1874; Glück, op. cit.

[4] See Koelreuter, Das entdeckte Geheimniss der Kryptogamie, Karlsruhe, 1777.

[5] When speaking of the sporangia the specially peculiar formation of indusia in Lygodium will be described (see p. 592). Further investigation is required before we can say whether in many ferns the indusium when ripe experiences any other movements than those due to shrinking.

the pit by an elongation of their stalk, and then they discharge their spores. The young sporangia are protected by the old ones. In other ferns, for example Polypodium jubaeforme, P. saccatum, there are hairs between the sporangia which originally close the mouth of the pit. The sinking of the sporangia in the Marsiliaceae is not essentially different from this, only that there the mouth of the sorus-pit is closed subsequently.

4. CONDITIONS FOR THE APPEARANCE OF THE SPOROPHYLL.

The sporophyll does not appear in germination but only after a definite age has been reached by the plant—earlier naturally in annual ferns like Anogramme leptophylla, than in perennial forms which develop slower. There can be no doubt that the formation of the sporangium and the sporophyll are dependent upon definite external factors—intensity of light, relationships of nutrition—and upon inner relationships (correlation). That correlation exists here has been experimentally shown where we get a transformation of the primordia of sporophylls into foliage-leaves[1], and it is quite evident that the plants only proceed to the formation of sporangia when they have accumulated a sufficient amount of plastic material. Besides these conditions, which we may designate shortly as the reaching of a certain stage of 'ripeness,' some special stimuli appear to be concerned in isolated cases.

The dependence of the formation of sporophylls upon external factors has not been much examined. Račiborski[2] has proved a remarkable case in a fern allied to Acrostichum Blumeanum. This fern formed as it grew upon the ground very luxuriant leaves but no sporophylls, but the latter appeared when the plant was given the possibility of climbing upon a vertical support. What changes in the life-condition 'set free' the formation of sporophylls here is not known. I may, however, conjecture that a pre-eminent factor was the restriction in growth of the rhizome *after a preceding period of good nourishment*. The case would be analogous to that of Marsilia quadrifolia. If this plant grows in water it forms long, very luxuriant shoots but produces no sporophylls, whilst the sporophylls appear in quantity if it grows upon land[3]. If the plant be cultivated upon persistently dry soil then usually sporophylls do not appear[4]. The plant is then evidently enfeebled and under-nourished. In the fructifying shoots we may, however, observe that the internodes of the shoot-axis are shorter and more contracted than in the luxuriant water-shoots, and it might be possible

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[1] See p. 474.

[2] Račiborski, Morphogenetische Versuche: I. Beeinflussung der Sporophyllbildung bei dem Acrostichum Blumeano affine, in Flora, lxxxvii (1900), p. 25.

[3] The relationships of adaptation to moist and dry soils also are operative here.

[4] See A. Braun, Nachträgliche Mittheilungen über die Gattungen Marsilia und Pilularia, in Monatsberichte der Berliner Akademie aus dem Jahre 1872, p. 650.

experimentally to compel the formation of sporophylls here also by restricting the growth. We must therefore in every species consider with care the life-conditions to which it is adapted as these are of importance for the appearance of the sporophylls.

II. EQUISETACEAE.

The sporophylls of Equisetum are stalked disks which bear the sporangia distributed around the under side of their peltate surface. The divergence in form from the sterile leaf is great: the sterile leaves are concrescent in a sheath and form the single teeth of it; the sporophylls are free and peltate. The greatness of the differences between the two constructions shows that they appear early. The questions that we have to ask here are

(*a*) What is the biological significance of the conformation of the sporophyll?

(*b*) What connexion is there between the sporophylls and the sterile leaves?

(*a*) The sporophylls form a close-set spike-like flower. They lie with their disk-like margins at first close against one another and to a certain extent interlocked, and in this way the young sporangia upon the under side of the disks are completely protected, so that there is no need for an indusium or any other protective apparatus. The internodes between the whorls of sporophylls are primarily very short; they elongate later as do the stalks of the sporophylls, and then the sporangia when they are ripe open by drying and scatter the spores[1]. We find quite the same configuration of sporophyll in the male flowers of many Coniferae, for example Taxus. In Equisetum then the conformation of the sporophyll—the peltate form, and the possession of a stalk—is connected with the protection of the sporangia and with the dissemination of the spores.

(*b*) The vegetative leaves act as a protective apparatus to the stem and its still-growing internodes. It is probable that they are reduced, although it is difficult to speak with certainty in the absence of allied living forms. The primordia of the leaves arise as papillae projecting upon the vegetative point. The upper portion of the papilla is, however, in the vegetative leaves only applied to the formation of the leaf[2], whilst the lower portion of the primordium serves as an envelope to the internode of the shoot. But the cells of the primordium of the sporophyll are all drawn into the

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[1] This is facilitated in some species by the bending upwards of the stalk of the sporophyll which is evidently negatively geotropic. This is the case in Equisetum Telmateia; see Goebel, Outlines of Classification and Special Morphology of Plants, English Edition, Oxford, 1887, Fig. 221. The surface of the sporophyll is placed obliquely or almost horizontally, and this prevents the spore-masses from coming to lie in quantity between the sporophylls. There is certainly no chance of this happening in this species which possesses the largest sporophylls.

[2] Connected with the slight development of the leaf.

formation of the sporophyll, and we have a correspondingly more massive development of the sporophyll[1]. The difference of the development, apart from the relationship of volume, consists fundamentally in this, that at a very early period, even before the appearance of the stalk of the sporophyll, which arises by intercalary growth, that distribution of growth sets in which leads to a hypopeltate form of leaf[2], and by which a reduction of the leaf-surface constituting the *upper* part of the leaf takes place, at the same time the marginal growth which elsewhere results in the formation of a thin leaf-lamina is suppressed. The occasional occurrence of intermediate forms between sporophylls and vegetative leaves is quite in accordance with the development[3]. In these intermediate states a lamina is often more developed and it corresponds then always to the upper part of the sporophyll; the lower part of the sporophyll is, in relation to the sterile leaf, a new formation such as is found in the stamens of many Cupressineae, or in the kataphylls of Asparagus comorensis (Fig. 215). The fact that the first developed stages of vegetative leaf and sporophyll conform to one another, and that the primordium of the vegetative leaf only partially grows out, whilst that of the sporophyll grows out entirely, is to my thinking not an argument in favour of the view that the configuration of the sporophylls in the Equisetaceae is phyletically the original one[4]; it rather shows that here as always the development is in harmony with the condition arrived at in the adult. A thin organ demands less cell-material than a thick organ. At most one could find in the development of the primordia of the vegetative leaves a reason for saying that they were at one time more massively developed than they are now. But we see that even now we can derive without difficulty the sporophyll from the foliage-leaves. Assimilation-organs of the conformation of the sporophylls of Equisetum would be very wonderful constructions.

PROTECTION AT BASE AND APEX OF FLOWER. At the base of the flower of Equisetum there is one whorl[5] of leaves which differ both from the vegetative leaves and from the sporophylls. This whorl is called the *annulus*, and it is occasionally drawn into the formation of sporophylls. The question whether any functional significance attaches to this structure appears so far as I know to have been overlooked. Yet that it does possess such a significance in the bud-condition of the flower is indubitable. The sporangia are so crowded together that they are concealed under the peltate expansions of the sporophylls. The lower sporangia of the lowermost whorl of sporophylls would be exposed but that the annulus protects them, and is so

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[1] Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien, in Botanische Zeitung, xxxviii (1880), p. 549. Glück, Die Sporophyllmetamorphose, in Flora, lxxx (1895), confirmed this later.

[2] See p. 334.

[3] See Glück, op. cit.

[4] Whether there are *other* grounds for this may be left untouched here.

[5] In Equisetum arvense there are sometimes two.

constructed that it fits accurately into the projections of the sporophylls, like a bit of moulding wax, and closes the base of the flower. We may compare it in respect of this function with the calyx of the Spermophyta. In this function the arrest which this leaf-whorl has experienced may find a teleological, but not a causal explanation. At the top of the flower an analogous protective device is provided inasmuch as the sporophylls which stand at the tip are incompletely developed, and remain concrescent partially with the flower-axis[1]. Their configuration is, however, somewhat different from that of the annulus, and gives no support to the conjecture that the annulus is the result of the sterilization of sporophylls. The annulus is clearly an arrested formation of the vegetative leaves.

The flowers of the Equiseta are shoots of limited growth. This finds expression in the arrangement of the cells: the apical cell of the vegetative shoot is replaced by a cell-group. The formation of the flower is then not merely a consequence of a change in the configuration in the leaves but also involves a change in the axis of the shoot. In support of this we have also the fact that the leaf-sheaths enveloping the flower-buds are larger than those in the vegetative shoots, evidently in correspondence with the larger circumference of the flower-bud.

The production of the sporophylls in many species of Equisetum effects a change in the external configuration of *the whole shoot* whose end becomes the flower. In other species we do not find this. A. Braun has in consequence of this difference divided the species of Equisetum into two series:—

(*a*) EQUISETA HOMOPHYADICA, in which the sterile and fertile shoots are alike, as in Equisetum palustre, E. limosum, E. hyemale.

(*b*) EQUISETA HETEROPHYADICA, in which the sterile and fertile shoots are different, and the fertile shoots are distinguished by having no branches; they cannot assimilate because they have no chlorophyll, and their chromatophores contain a reddish colouring substance instead of chlorophyll. It may well be that in this way the fertile shoot obtains a greater amount of heat. The heterophyadic forms in turn fall into two series:—

(*a*) **Equiseta heterophyadica ametabola**, as in Equisetum arvense and E. Telemateia, where the fertile shoots remain in this stage of development, and after the shedding of the spores die away.

(*b*) **Equiseta heterophyadica metabola**, as in Equisetum pratense and E. sylvaticum, where the fertile shoot subsequently forms whorls of branches and becomes green—the process taking place in different ways[2]. In Equisetum sylvaticum the tissue of the internode of the fertile shoots

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[1] In Equisetum arvense the uppermost incompletely developed sporophylls are not infrequently concrescent into one, apparently terminal, peltate sporophyll.

[2] See Goebel, Über die Fruchtsprosse der Equiseten, in Berichte der deutschen botanischen Gesellschaft, iv (1886), p. 184.

remains at first embryonal, and is protected by the specially long leaf-sheaths. Subsequently this develops like that of the sterile shoot. In Equisetum pratense the persistence of embryonal tissue and the subsequent development only affects the *lower* portion of the internode; the upper portion has passed into permanent tissue, and does not change.

The fertile shoots appear then, when they are compared with the sterile shoots, as *formations arrested*[1] at a simpler stage of their configuration and of their anatomical structure. In the Equiseta heterophyadica ametabola this arrest is permanent; in the others it is temporary. Experiment shows us that the fertile shoots of the ametabolous species may be induced to proceed to at least a partial vegetative development[2]. If they are submerged some of them die away but a large number of them send out lateral shoots from the lowest up to the sixth internode, and the internodes themselves become green[3]. These shoots also appear to us as arrested formations, and it is probable that the arrest stands in connexion with both external and internal conditions.

With regard to the external conditions we may recall that the ametabolous Equiseta are those which develop their fertile shoots in the *early spring*. The soil, especially that of the moist stations in which the Equiseta are found, is at this time still cold, and their intake of water is correspondingly hindered. The degree of temperature suffices for the elongation of the fertile shoots which were already almost completely formed in the autumn. The vegetative development only begins later, and the vegetative shoots probably withdraw from the fertile shoots material—water and other substances—which these might use for vegetative development. The homophyadic Equiseta develop their fertile shoots later at a time when the conditions for the intake of water are more favourable. The metabolous Equiseta stand intermediate to the other groups—that is to say they grow, so far as my experience goes, upon soil that is less cold and wet.

Whilst the fertile shoots of the Equiseta as of the Filicineae appear to be the result of transformation of the sterile ones, experience also allows us to conclude that the differences in the behaviour of the fertile shoots can be brought into connexion with the relationships of life[4]. Further experi-

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[1] Compare the temporary and persistent arrest in the cotyledons. See p. 403.

[2] See Goebel, Über die Fruchtsprosse der Equiseten, in Berichte der deutschen botanischen Gesellschaft, iv (1886), p. 187.

[3] This phenomenon is seen also in nature in meadows which are under water in the early spring. See further descriptions of the different forms of construction of the fertile shoots of Equisetum given by Luerssen, Die Farnpflanzen oder Gefässbündelkryptogamen Deutschlands, Österreichs und der Schweiz, in Rabenhorst's Kryptogamen-Flora, Leipzig, iii (1889).

[4] We must not, however, forget that in the ametabolous Equiseta the influence of the conditions of life has evidently worked a change upon the whole organization. If the conditions for the uptake of water from the soil are favourable a vegetative development does not require to take place in them, because they are no longer adapted to the uptake of water and nourishment like the sterile shoots. In the upper portion of the fertile shoot a vegetative further development can no longer take place.

mental investigation must, however, prove still more definitely these connexions.

The remarkable fossil formations of the Equisetineae must be left undescribed here as in other groups. The result of phytopalaeontological investigation in recent years has been of the utmost importance. But it is evident that in the nature of the case the morphological interpretation of the flower-formation of the extinct forms is often very uncertain, and on the other hand the discovery of relationships between configuration and inner and outer conditions at the time when the plant lived is impossible[1].

III. LYCOPODINEAE.

Whilst in the Equiseta the sporophylls and foliage-leaves are always different, apart of course from teratological phenomena, we find in the Lycopodineae as in the Filicineae cases in which the foliage-leaves and the sporophylls are alike, for example in Lycopodium Selago[2], and cases in which they are different, as in Lycopodium annotinum. The case of Lycopodium annotinum may be described:—

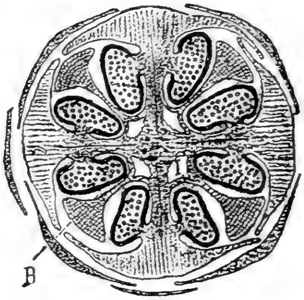

FIG. 335. Lycopodium annotinum. Flower in transverse section. The sporophylls stand in a tetramerous whorl. Two sporangia are apparently attached to each sporophyll, but there is in fact only one, which having a great curvature is twice cut in the section; *B*, the base of the sporophyll of the next succeeding whorl, shaped like a razor-blade. After Glück. Magnified about 14.

LYCOPODIUM ANNOTINUM. The sporophylls of this species are no longer assimilation-organs, and they have a yellowish, not a green, colour. The leaf-base is widened, and this fits the leaf better to embrace the large sporangium seated upon its base. The margin of the leaf is spread out in a wing-like manner. When the spores are ripe the membranous margins of the sporophyll, like its upper portion, bend backwards and thus facilitate the distribution of the spores[3]. A leaf-cushion[4] (Fig. 335, *B*) which has the form on transverse section of the blade of a razor also runs downwards from each sporophyll and fills up the spaces between the sporangia. The sporangia are carefully protected as is shown in Fig. 335, and it is easy to understand teleologically the deviation from the foliage-leaves in the configuration of the sporophyll[5].

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[1] The reader is referred for the description of fossil forms to the palaeophytological text-books, of which may be mentioned the following: H. Potonié, Lehrbuch der Pflanzenpaläontologie, Berlin, 1899; Zeiller, Éléments de paléo-botanique, Paris, 1900; Scott, Studies in Fossil Botany, London, 1900. Scott's book gives a particularly clear and concise account to the beginner.

[2] See also in the species of Isoetes, about which no further mention will be made here.

[3] There can be no doubt that this movement of the sporophyll is a consequence of its drying. On the edges of the forests the movement always begins upon the side of the flower directed outwards.

[4] In many Lycopodia, for example Lycopodium cernuum, the sporophyll is hypopeltate as it is in Selaginella Preissiana. See p. 506.

[5] With regard to the formation of mucilage in Lycopodium inundatum see the figures given by Glück, Die Sporophyllmetamorphose, in Flora, lxxx (1895).

The sporangia are laid down in the Lycopodineae as in the Equiseta when the sporophylls are still relatively small (see Fig. 312). I do not, however, see in this a point of phyletic importance, but only that the formation of the leaves in both of these cycles of affinity is reduced in comparison with that of the Filicineae. Very small-leaved ferns would show quite the same phenomena in their sporophylls as do the Equiseta and Lycopodineae.

PSILOTACEAE. The Psilotaceae, Psilotum and Tmesipteris, demand special mention because the sporophylls in them deviate further from the sterile leaves than do those of other Lycopodineae. The sporophyll is bifid, but the whole structure was formerly considered—and I shared the view—as a small branch bearing two leaves and a plurilocular sporangium. This interpretation has, however, been shown to be impossible by the investigations of Solms-Laubach[1] and Bower[2]. In support of the modern and accepted view that we have here a bifid sporophyll I may mention that I have often observed on simple undivided foliage-leaves in Tmesipteris one sporangium (Fig. 336, I), which in the cases I investigated was simple, although the sporangium is usually divided into two or more, rarely three, chambers, and there was no trace visible of a second somewhat reduced lobe of a sporophyll. Transverse sections show that a simple conducting bundle runs into the lower simple portion of the sporophyll, whence a branch proceeds towards the sporangium, and one finds tracheids proceeding even into the wall of the sporangium.

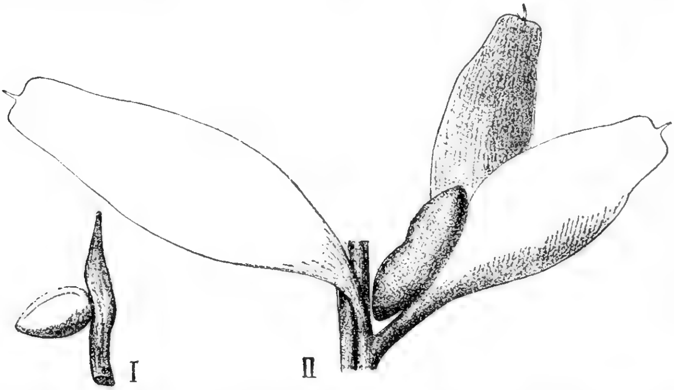

FIG. 336. Tmesipteris truncata. I, simple sporophyll with one sporangium. II, portion of a shoot bearing a sterile and a fertile leaf. In the sterile leaf the profile-position of the lamina is evident. Both magnified.

In Fig. 337 the end of a shoot of Psilotum complanatum (P. flaccidum) is shown. The shoot is flattened and provided with small distichous leaves. A conducting bundle does not enter the leaves, but a vascular bundle branches

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[1] H. Graf zu Solms-Laubach, Der Aufbau des Stockes von Psilotum triquetrum und dessen Entwicklung aus der Brutknospe, in Annales du Jardin botanique de Buitenzorg, iv (1884), p. 139.

[2] Bower, Studies in the Morphology of Spore-producing Members: Equisetineae and Lycopodineae, in Phil. Trans., 1894.

off towards the sporangium from the strand of the shoot-axis, and we have here a case which shows us that the distribution of the vascular bundles cannot always be trusted for a decision as to the morphological value of an organ:—the sporangium is leaf-borne, but is nevertheless supplied with a vascular strand from the shoot-axis; moreover the sporangia frequently are arrested, and then one finds apparently sterile bifid leaves, into which a strand of vascular bundles runs[1].

FIG. 337. Psilotum complanatum. End of a shoot. Sporangia in the axil of bifid sporophylls. Magnified.

That the forking of the sporophylls in the Psilotaceae is a 'morphological' character is supported by the fact that the plants in which it is found diverge so much in habit as do Tmesipteris and Psilotum. But we must not forget that the forking is at the same time 'useful.' It is evident that in Psilotum the young sporangium is invested and protected right and left by the two tips of the leaf (Fig. 337), whilst the undivided base of the leaf gives a protection to the outside. This feature is less marked in Tmesipteris[2]. The fork in the sporophyll in which the old sporangium sits in Psilotum serves besides as a mechanical support. Regarding the comparison which is frequently made of the sporangial group of the Psilotaceae with a sporophyll of the Ophioglossaceae, something will be said when the subject of sporangia is dealt with[3].

The flowers of Selaginella are of special importance for comparison with the flowers of the Spermophyta:—

ISOPHYLLOUS SELAGINELLEAE. We shall first of all deal with the isophyllous Selaginelleae and take as an illustration

Selaginella Preissiana. Selaginella Preissiana, which I collected in West Australia, is

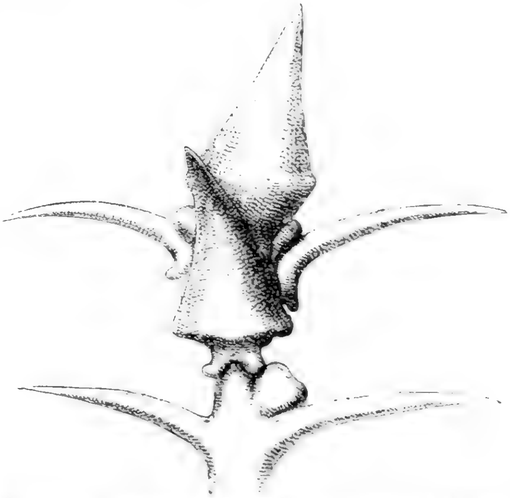

FIG. 338. Selaginella Preissiana. Lower portion of a flower. Magnified.

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[1] It is upon these cases that Solms has based the statement that the leaves have a well-developed conducting bundle. As a matter of fact the leaves I investigated showed no trace of a bundle.

[2] One may imagine that its leaves have arisen from those of Psilotum by the strong outgrowth of a basal part whilst the small apex keeps pace with it, this apex corresponding to the leaf of Psilotum.

[3] See p. 605.

very instructive. The leaves are in decussate pairs. Fig. 338 shows the base of the spike of sporangia. The lowermost leaf, which bears a microsporangium, is constructed like a sterile one. Those which follow it have grown out downwards beyond their point of insertion. These outgrowths are clearly protections not to the sporangium which is axillant to their sporophyll, but to the sporangium which lies immediately below each sporophyll. Analogous arrangements we have seen appearing in the vegetative region, as was stated when we considered the sporophylls of Equisetum, and exactly the same arrangements are met with in the stamens of many Coniferae and Angiospermae. At the same time the formative stimulus given by the appearance of the sporangia, and which leads to an external configuration of the sporophyll different from the vegetative leaf-form, evidently affects not the single sporophyll—for otherwise the lowermost sporophyll must also have the conformation of the others—but the vegetative point itself of the sporangial spike, and this then acts upon the primordia of the sporophylls [1].

ANISOPHYLLOUS SELAGINELLEAE. We must distinguish two groups of the anisophyllous Selaginelleae in respect of their formation of flowers—the *Tetragonostachyae* and the *Platystachyae*.

Tetragonostachyae. These are distinguished by the anisophylly of the vegetative shoot stopping short of the flower. The sporophylls are all of nearly equal size in contrast with the condition that is found in the vegetative leaves, and the leaf-pairs do not cross obliquely as in the vegetative shoot but nearly at a right angle [2]. When we remember that the vegetative shoots of the anisophyllous Selaginelleae owe the configuration of their leaves evidently to an adaptation to definite external factors [3], we may assume that the configuration and position of the sporophylls exhibit a retention of a phyletically primitive stage [4]. Why this should be is at any rate biologically or teleologically easily understandable, for in the flowers where all the leaves have the same function, which is essentially that of protecting the sporangium, it is natural that their configuration should be also the same. Moreover the flowers are frequently although not always orthotropous in contrast with the plagiotropous vegetative shoots.

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[1] In other words the transformation of the vegetative shoot into flower proceeds gradually, and expresses itself only plainly if the formative stimulus, of which we know nothing, has reached a definite intensity. That the lowermost sporangia in the flowers of many Selaginelleae and Lycopodia do not reach complete development, as will be more particularly shown hereafter (see p. 510), is probably connected with this.

[2] I examined the case of Selaginella erythropus.

[3] See Part I, p. 105.

[4] We must, however, point out that several isophyllous Selaginelleae, like Selaginella Preissiana, have also decussate leaf-pairs on the vegetative shoots, and that in the isophyllous Selaginella rupestris the flowers have likewise decussating sporophylls, although the foliage-leaves have a spiral position.

Platystachyae. There are also dorsiventral flowers in Selaginella[1] and these have a special interest in view of the presence of dorsiventral flowers amongst the higher plants. We find indeed two kinds of these:—

(*a*) The one continues the anisophylly of the vegetative shoots, that is to say the sporophylls upon the upper-surface of the flower are smaller than those upon the under-surface or flanks. This is, however, a rare condition, and it is only known in two species of very limited distribution, namely, Selaginella pallidissima and S. ciliaris, Spr.

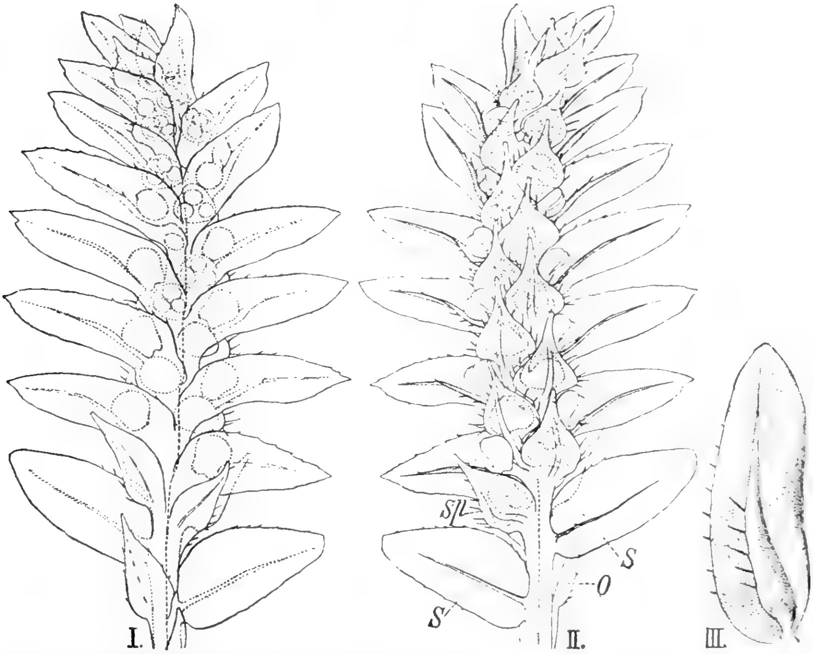

FIG. 339. Selaginella chrysocaulos. I, flower seen from above. II, flower seen from below: *S*, *S*, vegetative lateral leaves corresponding to the small sporophylls; *O*, upper leaf corresponding to the larger sporophylls; *sp*, sporangium. III, larger sporophyll. I and II slightly magnified. III highly magnified.

(*b*) The other which I have termed the *inverse-dorsiventral* flower is the more frequent[2]. In it the dorsiventrality is the reverse of that in the vegetative shoots. The sporophylls on the two surfaces of the flower are of unequal size, but the larger stand upon the upper-surface, and they form the continuation of the smaller leaves of the vegetative shoot. Selaginella chrysocaulos (Fig. 339) furnishes an example of this. The larger sporophylls which stand upon the upper-surface of the axis form a protecting cover to the whole flower, and this—as well as the increased capacity of assimilation established by these leaves—is, to speak teleologically, the reason why the

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[1] See Goebel, Archegoniatenstudien: IX. Sporangien, Sporenverbreitung und Blüthenbildung bei Selaginella, in Flora, lxxxviii (1901), p. 207. The older literature will be found here.

[2] The earlier expression for these flowers, *resupinate*, involves an erroneous statement, for here there is no torsion of the flower-axis.

sporophylls of the upper-surface are different from the foliage-leaves of the upper-surface. The sporophyll has also a wing-like appendage recalling the leaf of Fissidens (Fig. 339, III; Fig. 340, *F*); indeed the development of the leaf shows that it follows the same course as that of Fissidens, and the wing is an outgrowth of its back, and is the structure which specially forms with the under-surface a protecting cover for the sporangia [1]. The inverse-dorsiventral flowers appear so much more utilitarian than do those which are not inverted that we need not be surprised at the rarity of the latter, and they furnish at the same time a remarkable proof of the fact that in the formation of flower a complete change of the whole shoot takes place. If an inverse-dorsiventral flower should grow out vegetatively [2] the outgrowth assumes the dorsiventrality of the *original* vegetative shoot, so that the 'inversion' of the dorsiventrality was only caused by the formation of flower. No such inversion has yet been experimentally produced in the *sterile* shoots of Selaginella, yet it might be possible if we were in the position to 'disattune' the shoot in the same way as this is effected by inner processes in the formation of the inverse-dorsiventral flower.

FIG. 340. Selaginella suberosa. Flower in transverse section near the vegetative point: *F*, wing.

DISTRIBUTION OF SPORANGIA IN SELAGINELLEAE. In regard to the distribution of the two forms of sporangia in the flowers of Selaginella it is clear that everywhere originally there is hermaphroditism. The number of the megasporangia varies in the different species. In some only one or a few are found at the base of the flowers; in others they are mixed with the microsporangia, as in Selaginella rupestris and S. chrysocaulos. Only in a few species, so far as we know at present, are there occasionally—not exclusively—entirely male flowers, in for example Selaginella Martensii, or female flowers, as for example in Selaginella pectinata.

Fertilization of the megaspores by the microspores of the same flower, even in the hermaphrodite flowers of the Selaginelleae, only seldom occurs because:—

1. The megasporangia precede in their development the microsporangia,

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[1] With regard to the anatomical differences of the upper and under-surface of the flower see Goebel, Archegoniatenstudien: IX. Sporangien, Sporenverbreitung und Blüthenbildung bei Selaginella, in Flora, lxxxviii (1901).

[2] I have observed this in Selaginella Belangeri growing wild in Java, and in Selaginella suberosa in which it was artificially produced.

and the megaspores are mostly thrown out before the microsporangia have opened.

2. The megaspores are thrown out further than the microspores as I have noticed.

3. A *simultaneous sowing* of microspores and megaspores, in the few cases that have been investigated for this point, has resulted in the formation of no embryo, because the microspores discharged their spermatozoids before the archegonia of the megaprothalli were ripe.

In all these points the flowers of Selaginella remind us of those of much higher plants which have to be considered as only morphologically, not physiologically, hermaphrodite.

If we endeavour to arrange the flowers of Selaginella in series the radial ones appear to be the most primitive, and they also still appear in many species where the vegetative shoots have become by adaptation dorsiventral. In a number of species the dorsiventral construction has also extended to the flowers, but the attempt to continue here the usual vegetative dorsiventrality is of little utility and has soon been given up, being retained only in two species. In the large majority inverse-dorsiventral flowers have been developed.

RELATIONSHIPS OF FLOWER TO VEGETATIVE SHOOT IN LYCOPODINEAE. If, finally, we consider the flowers of the Lycopodineae in their relationship to the vegetative shoot-system we find frequently that when the flowers are shoots of limited growth the sporophylls diverge markedly from the foliage-leaves, but when there is no limited spike of sporangia then the sporophylls are like the foliage-leaves, for example in Lycopodium Selago and its allies. We cannot, however, establish this as a general rule. We have only now to mention some general biological relationships:—

1. Where the vegetative shoots are dorsiventral the flowers, apart from the Selaginelleae Platystachyae, are radial, as in Lycopodium complanatum and other similar species. It is probable that here the flowers have retained the original arrangement and configuration of the leaves whilst the configuration of the vegetative shoot has become changed by subsequent adaptations[1].

2. Orthotropous position is not necessarily associated with the radial construction of the flowers. Orthotropy appears rather only where the vegetative shoot grows more prostrate upon the soil, and it is therefore of advantage for the scattering of the spores that the flowers should be raised up above the substratum. In these cases, for example in Lycopodium inundatum, L. clavatum, L. carolinianum, Selaginella denticulata, S. helvetica, and others, a portion of the shoot-axis under the flower is elongated more or less, and at the same time is orthotropous and not infrequently beset with

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[1] See Part I, p. 102.

reduced leaves. This portion is named the *podium* and, in correspondence with what has been said, is everywhere wanting where

(*a*) The sporangia stand on a sufficiently long radial shoot-axis, as in Lycopodium Selago and L. annotinum, where it is orthotropous and erect, and as in Lycopodium Phlegmaria and L. linifolium, where it is orthotropous and pendent;

(*b*) The plagiotropous shoot-axes raise themselves well above the substratum[1].

Here as everywhere in regard to such rules we find examples which do not conform to what has been said because in them other relationships bring about a divergent construction, but on the whole, so far as I know, the relationships I have mentioned are valid.

It has then been shown that the sporophylls of Selaginella still exhibit frequently in their construction and arrangement relationships which appear to be primitive in comparison with the foliage-leaves which have been changed by adaptation. This does not controvert the assumption that the leaves of the Pteridophyta were originally all sporophylls which at the same time assimilated[2], and that then a division of labour set in by which some became sterile whilst others remained as sporophylls and now frequently in their construction differ more or less from the foliage-leaves. In support of this one may also adduce the fact that where foliage-leaves and sporophylls are formed alternately, as for example in Lycopodium Selago and other species, and in Isoetes, we frequently find sporophylls with aborted sporangia at the limits between the two kinds of leaf[3]. We know, however, that such an arrest of the sporangia may result from other causes if the formation of sporangia begins but does not proceed sufficiently vigorously, for example in Onoclea Struthiopteris whose sporophylls have been already mentioned[4]. Its germ-plant produces at first only foliage-leaves, then transitions between foliage-leaves and sporophylls the sporangia of which are generally in great part arrested at different stages of development. Later, when the plant becomes stronger, such an oscillation is normally no longer visible, yet it may be artificially called forth if the sporophylls are caused to become virescent. Vegetative organs and reproductive organs stand also otherwise in a certain opposition, that is to say their formation is dependent upon *different* outer and inner conditions. At any rate we will have to trace back the arrest of the sporangia at the upper end of the flowers of many Lyco-

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[1] Compare, for example, Selaginella Martensii, with apodial radial but not orthotropous flowers, with Selaginella denticulata (Fig. 174, *A*), S. helvetica, and others, in which the flowers have a podium and are orthotropous.

[2] With Potonié we may designate them *tropho-sporophylls*.

[3] See also Bower, Studies in the Morphology of Spore-producing Members: Equisetineae and Lycopodineae, in Phil. Trans., 1894. Also at the end of the flower in Selaginella and elsewhere aborted sporangia occur.

[4] See p. 475.

podineae[1] to other causes than those that are operative at the base. At the apex we have to deal chiefly with a general want of tone in the whole flower-development, not only are the sporangia arrested but also the development of the sporophyll; at the base we have to deal with a transformation of the vegetative shoot into a flower.

III

THE SPOROPHYLLS OF THE GYMNOSPERMAE

I. *CYCADACEAE.*

In this family not only are the relationships of configuration of the flower especially simple, but the configuration of the sporophyll enables us to recognize very clearly in what relationship it stands to the foliage-leaf and also how form and function hang together.

As regards the whole configuration of the flowers they have the form of cones, frequently of giant dimension, except in the case of the female flowers of Cycas where a sharply limited flower is not formed[2], but the carpels appear upon the shoot-axis which subsequently again forms foliage-leaves and kataphylls—the arrangement being comparable with that of Onoclea Struthiopteris amongst the ferns[3]. As will be shown presently, the configuration of the sporophyll has the closest connexion with this arrangement.

In the flowers which form cones it is noteworthy that the uppermost and lowermost sporophylls are frequently sterile. They are, however, not functionless, but close in the flower in the bud-condition both above and below after the method in the spike of Equisetum. It is a wide-spread phenomenon that the middle portion of an organ of limited growth is the best nourished; even in the leaves of many Cycadaceae the lowermost pinnules are aborted, the middle ones being the most developed, and there are all transitions from sterile to fertile sporophylls in the male flowers of Ceratozamia.

The configuration of the sporophylls will first of all be noticed, and then some general questions will be dealt with :—

MEGASPOROPHYLLS (CARPELS). We have before us in these an almost uninterrupted series. At its beginning there stand those which still resemble most closely in their form the pinnate foliage-leaves; at the other end stand those which are most widely separated from them. The megasporangia (ovules) are everywhere marginal.

Cycas. The carpels of Cycas revoluta are smaller than the foliage-leaves but they show still at their extremity somewhat long rudiments of pinnules, and resemble the pinnate leaves otherwise, especially in their flat and elongated form (Fig. 341). Only in Cycas circinalis are the pinnules indi-

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[1] And also in the case of Equisetum.

[2] See p. 470.

[3] See p. 475.

cated merely as teeth. Whether each of the ovules, which are here larger than those which appear elsewhere in pairs, stands in the place of a pinnule can only be determined by an examination of the history of development which is still unknown. The wall which surrounds on the outside the ovule at its base I consider for the reasons specified below to be no 'rudimentary pinnule,' but an outgrowth arising subsequently. In Cycas Normanbyana the number of the megasporangia has become reduced to two.

Interesting as is the leaf-like construction of the sporophyll of Cycas, and diverging as the sporophyll does from those of the other Cycadaceae, yet it offers little in its external form alone to detain us. Much more important is it to inquire whether we can discover any relationships by which to explain its deviation. It appears to me that there are such, and they are the following:—

FIG. 341. Cycas revoluta. Megasporophyll or carpel. After Sachs. Reduced. Lehrb.

1. The sporophylls do not stand as in the cone-flowers on an axis which, compared with the vegetative one, is relatively thin, but upon the thick vegetative axis itself. They form a much more massive tuft, and by their considerable development in length are in a position to protect the young ovules by covering them. It is quite clear then why in the upper part of the sporophyll there are no ovules—these upper parts form a protecting covering, and *close in the massive flower-bud above.*

2. The seeds attain the most significant size in the genus Cycas. To protect them in the same manner as the seeds are protected in other Cycadaceae, where a change in form of the scale-like sporophylls takes place, would be scarcely possible with the megasporophylls arranged as they are. In the other Cycadaceae the megasporophylls experience in the course of their development a special change in form corresponding to the enlargement of the ovule.

Dioon. The flower of Dioon comes nearest in outer configuration to that of Cycas. The carpels are still flat, and show the rudiment of a lamina (Fig. 342, *L*), and at their base also a rudimentary pinnule, sometimes two.

Ceratozamia. In the other genera of Cycadaceae the lamina of the megasporophyll is very much reduced, yet in Ceratozamia there are still rudiments of two pinnules[1] in the two 'horns' of the sporophyll. These are originally soft and lie upon the outer surface of the sporophyll in the young flower. Later they diverge and begin to harden into spiky structures, which may perhaps be considered as a mechanical protection of the flower.

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[1] Sometimes more than two.

The sporophylls themselves are originally flat (Fig. 343, I), and have scarcely any indication of a stalk. Subsequently when the megasporangia become larger changes ensue which bring it about that the sporophylls form a protecting roof. The first thing that takes place is a stalk appears (Fig. 343, II), and then there develops upon the upper side and upon the under side a thickening (*E*, Fig. 343, II) which gives the sporophyll a somewhat peltate conformation. Thus a process which occurs in Equisetum and elsewhere *before the formation* of the sporangium begins here at a much later moment in the development. Fig. 343, III, shows us how the peltate expansion of the sporophyll forms a mail-covering to the outside, and the 'horns' which have not hitherto been considered, so far as I know, as rudimentary pinnules appear displaced upon the outer surface of the shield.

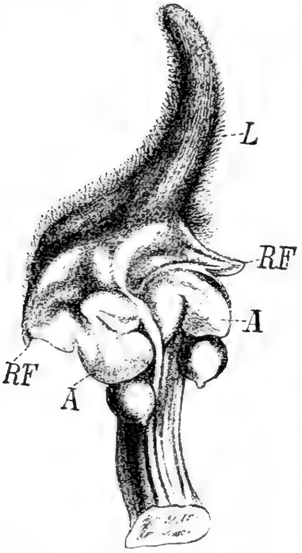

FIG. 342. Dioon edule. Megasporophyll: *L*, lamina; *RF*, *RF*, reduced pinnules; *A*, *A*, swelling of the sporophyll below the megasporangium whose micropyle is turned downwards in the figure. Reduced.

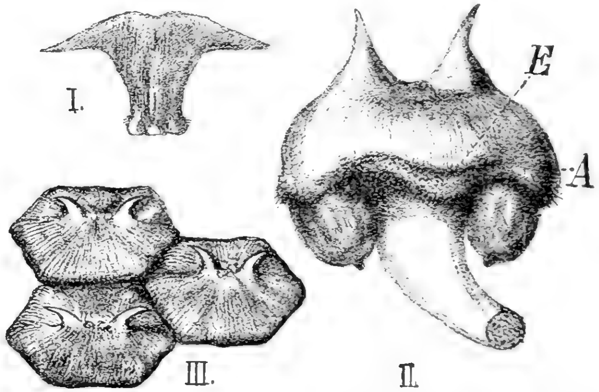

FIG. 343. Ceratozamia robusta. I, young megasporophyll, still flat; right and left of its still very short stalk is a megasporangium (ovule). II, older megasporophyll which is become shield-like through the outgrowth, *E*, which appears both above and below; *A*, swelling under the ovule. III, three sporophylls seen from outside the cone.

What the relationship of the configuration of the sporophyll is to pollination is not known. The question when the normal pollination takes place can only be certainly solved in the home of the plants, and up till now nothing definite is known about the pollination. The observations of Kraus seem to indicate that not all the Cycadaceae are wind-pollinated as is commonly supposed[1].

The other genera have megasporophylls which are distinguished essentially from those of Ceratozamia by the last traces of rudimentary pinnules having fallen away. Lang[2] found the megasporangia of Stangeria

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[1] G. Kraus, Physiologisches aus den Tropen, in Annales du Jardin botanique de Buitenzorg, xiii (1896), p. 273.

[2] W. H. Lang, Studies in the Development and Morphology of Cycadean Sporangia: II. The ovule of Stangeria paradoxa, in Annals of Botany, xiv (1900), p. 281.

paradoxa upon the under side of the sporophyll, which is of interest in so far as here a displacement has evidently taken place in the course of the development[1], a displacement which is no longer directly perceptible in the microsporangia.

MICROSPOROPHYLLS (STAMENS). These have a more uniform configuration in the Cycadaceae than have the megasporophylls. They are everywhere broad scales, in Zamia approaching the peltate form, and in Ceratozamia still showing rudimentary pinnules like the megasporophylls. The microsporangia stand upon the under side arranged in many evident sori (Fig. 344).

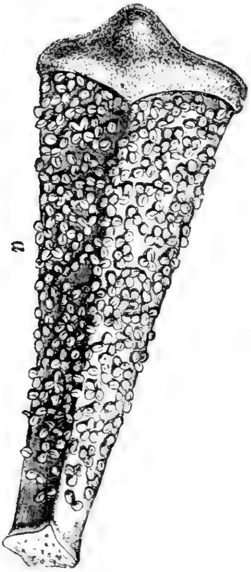

FIG. 344. Cycas circinalis. Stamen seen from below. After Richard. Lehrb.

The difference in the configuration of the microsporophylls and megasporophylls shows itself also in the number and position of the sporangia. It is clear that upon the under side of the microsporophyll many more sporangia will find room than upon the edges. One might then upon the ground of the assumption that the megasporophylls and microsporophylls must have been originally constructed alike take as a starting-point sporophylls constructed with marginal sporangia. In the case of megasporangia there has been reduction usually to two. In the case of the microsporangia there has been an increase in the number, and a displacement upon the under side. Whether—and regarding this I have no first-hand knowledge—the formation of the stamens of Zamia Skinneri, whose pollen-sacs are almost entirely pushed to the margins[2], may be considered as giving support to this conjecture is a matter for further examination. It may be pointed out, however, that these differences repeat themselves in other cycles of affinity.

II. GINKGOACEAE AND CONIFERAE.

MALE FLOWER. Relationships are here very simple and clear. It has been already pointed out[3] that the male flowers resemble very closely the spikes of sporangia of many Pteridophyta. Like them they consist of sporophylls and flower-axis. The scales which invest the male flowers in

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[1] Similar to that which takes place in Schizaea and other ferns.

[2] A. Braun, Die Frage nach der Gymnospermie der Cycadeen erläutert durch die Stellung dieser Familie im Stufengang des Gewächsreichs, in Monatsberichte der Berliner Akademie aus dem Jahre 1875, p. 357. On p. 351 he says that on the stamens frequently only two microsporangia are present, and they are placed so near the margin of the stamen that they may be said almost to have the same position, exactly as the megasporangia on the megasporophylls.

[3] See pp. 470, 472.

the bud-condition must be considered as bud-scales analogous with those of the vegetative buds, they are not sterile sporophylls.

The conformation of the stamens stands in the closest connexion with the protection of the microsporangia in the bud, and as in the case of the carpels of the Cycadaceae we meet with two chief relationships of configuration of the sporophylls, although they are united by many transitions :—

(*a*) Stamens which have more or less developed flat scale-like lamina.

(*b*) Stamens with a peltate lamina.

Where the stamens are scale-like the upper part of each is in the bud laid over the sporiferous lower part of the higher-placed sporophylls. The scale-like stamens of many Cupressineae and other groups show upon their under side an outgrowth which I regarded formerly as the analogue of an indusium, because it serves for the protection of the microsporangia. Through this outgrowth these stamens have become hypopeltate. Should this outgrowth arise in a still earlier stage the leaf would from the first be peltate, as it is in Taxus whose microsporophylls closely resemble the sporophylls of Equisetum in general form and likewise in having the sporangia distributed radially upon them. The significance of the configuration of the microsporophylls for the protection of the sporangium is conspicuous also where the sporophyll in the *mature* state appears very reduced, as in Ginkgo (Fig. 347, *a*, *b*) and Phyllocladus. Fig. 345 shows that the lamina, *L*, of the sporophyll of Ginkgo forms also in the bud-condition a closing structure towards the outside. It possesses many secretion-reservoirs, *H*, and there is abundance of calcium oxalate in the tissue of its upper part. Evidently it serves as a seat of deposit of the by-products of metabolism which arise in the formation of the sporangia. That the microsporangia of Ginkgo require at a later period, as they unfold, less protection may be connected with the fact that their wall is constructed out of relatively many cell-layers. We shall see that in the female flower of Ginkgo the sporophylls are likewise very reduced.

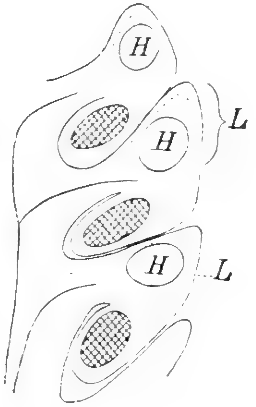

FIG. 345. Ginkgo biloba. Portion of a male flower in longitudinal section. Three stamens are involved. The sporogenous cell-tissue is shaded: *L*, lamina; *H*, resin-cavity. The oxalate-glands are indicated by dots.

POSITION OF THE MICROSPORANGIA. The position of the microsporangia upon the microsporophylls is not everywhere the same. In Ginkgo, Phyllocladus, the Abietineae, two sporangia are normally present and we may call them 'marginal.' The number is sometimes greater in Ginkgo, and the additional ones stand then upon the under side which is the normal position in the Araucarieae, Cupressineae, and other groups. The radial distribution in Taxus has been referred to above.

VARIATION OF MICROSPOROPHYLLS IN ONE FLOWER. The construction of the microsporophylls of many Coniferae varies somewhat in one and the same flower. In illustration we may consider the case of

Juniperus communis. Its stamens are of the very greatest interest on account of their variations, although hitherto this matter appears to have been overlooked[1]. The 'typical' form of the stamen is well known: it has a scale-like lamina, and bears upon its under side three or four pollen-sacs; the lamina has the function as it is described above. In the upper portion of the flower we see two phenomena:—

(*a*) The lamina of the sporophyll is reduced.

(*b*) The number of pollen-sacs is reduced.

The reduction of the lamina can be easily understood biologically. In the upper part of the flower-bud the area which has to be protected is much smaller than is that of the wider part below, and the protection is shared with the lamina by the staminal primordia standing lower down. The cause of the phenomenon is that the processes which finally lead to the stoppage of the growth of the whole flower do not set in all at once but gradually—we have a developmental arrest. Fig. 346, I, gives a view from above of a flower very near the time of its unfolding and provided with perfect pollen-sacs. The sporophylls stand in a trimerous whorl, the stamens of the second whorl from the top, st_2, have each only two pollen-sacs which are evidently *lateral* upon the stamen, as we find them in Abies, Pinus, and others. The lamina, *l*, is

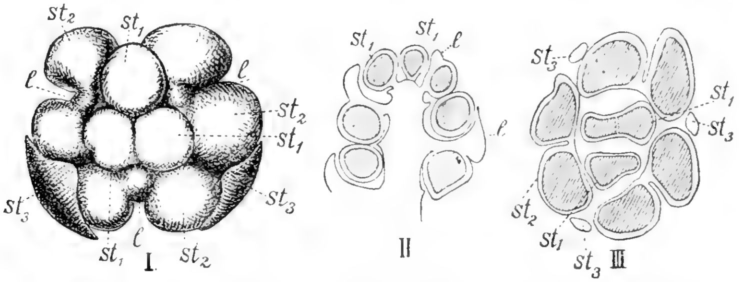

FIG. 346. Juniperus communis. I, summit of a male flower seen from above; st_1, the uppermost staminal whorl of three stamens; st_2, the second staminal whorl, shows on each stamen two pollen-sacs and the indication of a lamina, *l*; st_3, the third staminal whorl, of which only the tips of the laminae of two stamens are seen; each of the stamens of this whorl had three pollen-sacs not shown in the figure. II, the same in longitudinal section. III, the same in transverse section.

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[1] Čelakovský, Nachtrag zu meiner Schrift über die Gymnospermen, in Engler's Jahrbücher, xxiv (1898), for example, expressly states that all the stamens of the Coniferae still possess above the pollen-chambers a vegetative end-portion which disappears in the stamens of the Gnetaceae. The same author, Die Gymnospermen, eine morphologisch-phylogenetische Studie, in Abhandlungen der königlich-böhmischen Gesellschaft der Wissenschaften, Folge 7, iv (1890), further declares that the anthers of the Coniferae 'do not have their pollen-sacs terminal but sub-lateral, and there is always a vegetative terminal portion developed above the pollen-sacs, the *crista* or *shield*, which indeed may be much reduced, as it is in Ginkgo, and still more in Torreya, without, however, the pollen-sacs thereby being made terminal.' I believe that I show in the text that the pollen-sacs are often terminal in Juniperus.

greatly reduced. As the stamens become broader a third and then a fourth sporangium appear. Thus the hypothetical procedure premised above for the stamens of the Cycadaceae here actually takes place within one and the same flower. Further, it is clear that between the configuration of the stamens of the Cupressineae and those of the Abietineae there is much less difference than one would be disposed to admit at first. The two sporangia of such a stamen are sometimes found united with one another, a condition evidently connected with the reduction of the lamina. *Higher up upon the flower-axis are found instead of the sporophylls single sporangia* at the end of the flower (st_1, Fig. 346, I, II). There can be no doubt that this is a consequence of a reduction of the sporophyll, as indeed the transition-forms show. But this reduction is often so fundamental that nothing but the sporangium remains. The history of development would doubtless show that the sporophyll has not entirely disappeared. To it evidently belongs the lower stalk-like part of the sporangium which, did we not know of the transition-forms, might well be regarded as the stalk of the sporangium. Such a stalk is not found upon microsporangia arising upon the under side of the stamens. The proof which we have here, without any application of hypotheses, that a sporophyll may be reduced to one sporangium appears to me of momentous interest, and it supplies us with a sound ground for the assumption of far-reaching reduction in the case of the megasporophyll which will be presently mentioned, for in the case before us it is based upon observation, and not merely upon comparison. Those who would have it that the sporophylls have arisen from a partial sterilization of sporangia will be able to use Juniperus as an example of the occurrence of the process they assume—if they do not read the writing from below upwards but inversely. When speaking of the formation of sporangia I shall deal briefly with this question[1]. Here I may only point out that in all such comparisons one is treading upon uncertain ground. This is shown, for example, by the fact that in Juniperus two of the last sporangia occasionally unite with one another. Fig. 346, III, shows a transverse section through the apex of a male flower which has only two sporangia of unequal size at its end. At the base of the larger of the sporangia I found, however, as the following section in the series showed, a rudimentary, very short partition-wall indicating that the structure was the result of the concrescence of two sporangia. One might then in fancy derive the three sporangia from the splitting of one single one, and finally the whole flower from *one sporangium* by 'progressive sterilization,' 'amplification,' and so forth! Here, as in other cases, the first thing that has to be sought is not the phyletic value of the phenomenon depicted, but the determination of the conditions under which they occur.

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[1] See p. 606.

FEMALE FLOWER[1]. The female flowers are much more variously constructed than are the male flowers, so much so that the questions what is carpel? what is flower? what is inflorescence? have been much discussed. We proceed from the cone-like flower as it is found in many Coniferae, and name as *sporophylls* or *carpels* the leaves which are sessile on the axis of the cone which has some resemblance in habit with the female flower of the Cycadaceae. The ovules stand in the axil of these leaves, sometimes as in the Abietineae upon a special scale—the *seminiferous scale*.

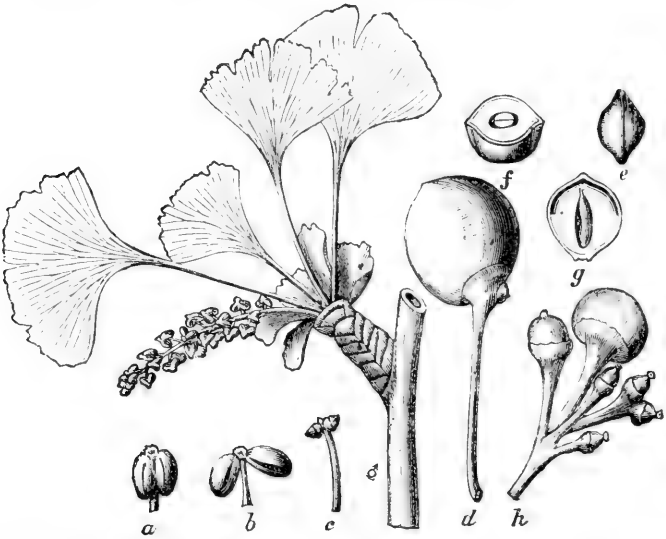

FIG. 347. Ginkgo biloba. ♂, portion of a branch with a short shoot bearing a male flower; *a*, *b*, stamens; *c*, female flower; *d*, the same with seed; *e*, stone of the seed; *f*, seed in transverse section; *g*, seed in longitudinal section; *h*, flower with many ovules. After Richard. Lehrb.

We may first of all point out that the carpels at the period of flowering are in general the less developed the less they are required for the protection of the ripening seed. We see this particularly in Ginkgo.

GINKGO. The female flowers of Ginkgo (Fig. 347, *c*) are small axillary shoots on which normally two ovules are found (Fig. 347, *h*)[2]. The sporophylls are usually not visible here as separate formations, and it is highly probable that an entire reduction has taken place, as we have seen it in the male flowers of Juniperus, that is to say the sporophylls are reduced to single megasporangia. Only if these appear stalked, as in Fig. 347, *h*, the

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[1] A detailed description of the relationships of the female flower is more within the province of systematic botany. There are, however, a few facts which must be stated on account of their organographical bearing. Of the literature see specially Strasburger, Die Coniferen und die Gnetaceen, Jena, 1872; id., Die Angiospermen und die Gymnospermen, Jena, 1879; Čelakovský, Die Gymnospermen, eine morphologisch-phylogenetische Studie, in Abhandlungen der königlich-böhmischen Gesellschaft der Wissenschaften, Folge 7, iv (1890); id., Nachtrag zu meiner Schrift über die Gymnospermen, in Engler's Jahrbücher, xxiv (1898). The further literature is cited in these works.

[2] This figure shows a great number, and thus the ovules appear stalked.

stalk, as in the megasporangia of Juniperus, is the lower portion of a carpel upon which the megasporangium is terminal. The sporophyll is indeed also very reduced in the male flower of Ginkgo, but in abnormal cases, as Fuji has observed, megasporangia can also appear upon the foliage-leaves. The seeds are specially large (Fig. 347, *d*) and have as in Cycadaceae a fleshy outer coat and hard inner one. The hook-like swelling at one side of the base of the megasporangium may be compared with the outgrowth of the sporophyll arising in a similar position in the Cycadaceae.

TAXINEAE. In this family likewise the ovules ripen without the protection of carpels, and the seeds like those of Ginkgo have a hard inner coat and a succulent outer coat, and are thus adapted for distribution by animals, especially birds.

Cephalotaxus and Torreya. In Cephalotaxus and Torreya the ovules stand in pairs in the axils of one leaf, the sporophyll (Fig. 348, V). In Cephalotaxus these sporophylls are united into small cones, and of the ovules usually only one develops further. Between the ovules there is a flat enlargement which has been interpreted as the vegetative point of the axillary shoot which bears the ovule [1], or as a third sterile carpel.

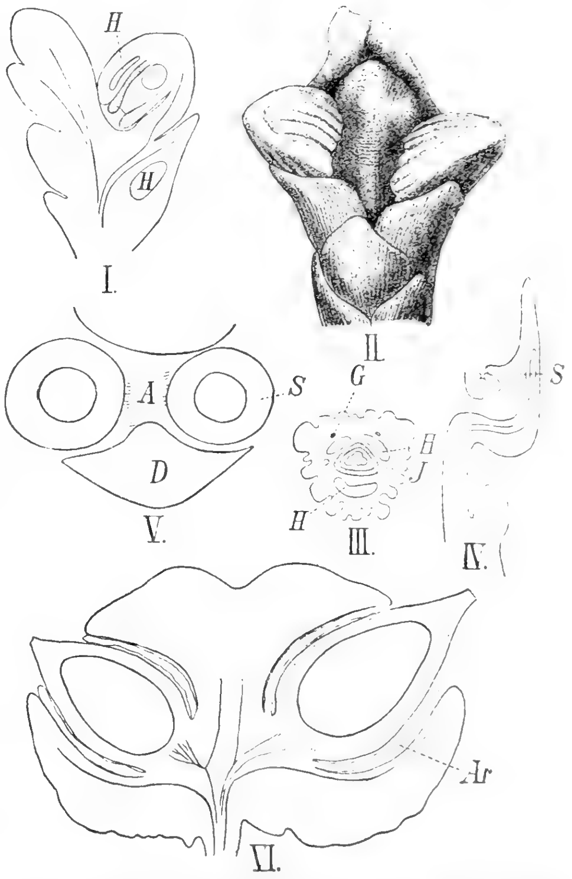

FIG. 348. I–III, Dacrydium Colensoi. I, flower with an ovule in longitudinal section; *H*, resin-canal. II, flower with two ovules. III, ovule in transverse section; *G*, vascular bundles; *H*, resin-canals; *J*, woody envelope. IV, Sequoia sempervirens. Cone-scale in longitudinal section; *S*, ovule. A resin-canal and a vascular bundle are seen in the scale. V, Cephalotaxus Fortunei. Portion of a female flower in transverse section; *A*, axis; *D*, sporophyll; *S*, ovule. VI, Phyllocladus alpinus. Young fruit in longitudinal section; *Ar*, aril.

Phyllocladus. In Phyllocladus (Fig. 348, VI) the ovules are solitary in the axil of a carpel. They are provided with an aril and are protected, at least in the cases which have been examined, by the sterile carpel standing above them. Formal morphology takes the ovule in this genus to be the single carpel of an axillary carpellary shoot that is no longer perceptible.

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[1] By this explanation we should have here as in Ginkgo a carpel reduced to an ovule.

In the illustrations that have been given the 'flowers[1]' consist of a large number of carpels which bear one or many ovules in their axils.

Podocarpeae. A reduction in the number of the ovules takes place also in the Podocarpeae, where we have sometimes flowers in which there are many sporophylls each bearing one anatropous bitegminous ovule (Fig. 349, IV), sometimes flowers in which only one sporophyll is fertile, or, it may be, only one sporophyll exists. In Podocarpus ensifolius[2] (Fig. 349, I–III) the flowers begin with two sterile prophylls which are frequently like foliage-leaves, whilst the sporophylls thicken fleshily at their base (Fig. 349, I). In Fig. 349, II, two sporophylls are fertile, that is to say, bear ovules. In Fig. 349, III, only one sporophyll is fertile notwithstanding the number of leaves which are combined together in the cone.

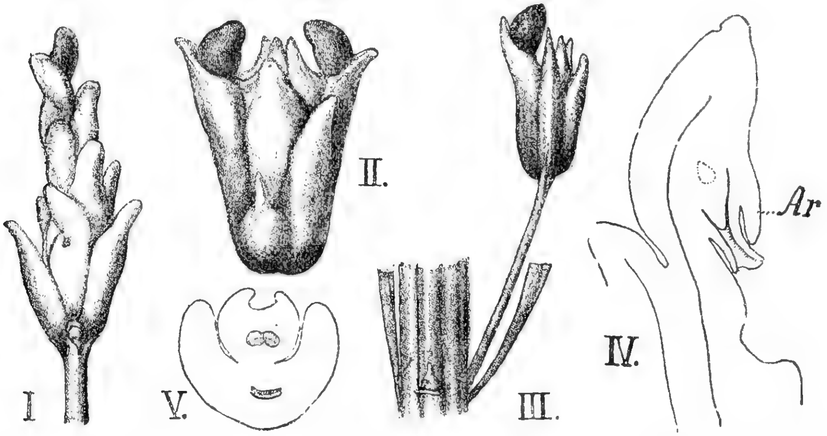

FIG. 349. Podocarpus ensifolius. I–III, female flower-cone in different stages of construction. IV, apex of a cone-scale with ovule in longitudinal section; *Ar*, aril. V, point of insertion of ovule in transverse section; vascular portion of the conducting bundle shaded, sieve-portion dotted.

Dacrydium Colensoi[3] (Fig. 348, I–III) has flowers which are no longer sharply limited. On a branch which may subsequently elongate vegetatively[4] some leaves develop bearing one or two sporangia (Fig. 348, I, II). This is the flower. We can imagine that such a flower has arisen out of one like that of Podocarpus ensifolius by the flower-axis forming vegetative leaves above the carpels, and in connexion therewith showing no limited growth but growing forth further as a vegetative shoot.

Taxus. In the genus Taxus (Fig. 350) the female flower is composed of a single ovule which forms the end of a small shoot, and below the ovule there are a number of small scales. It is a form of flower which differs much more from the sporangial grouping in the Pteridophyta than do the forms which have been mentioned above.

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[1] According to other interpretations really inflorescences.

[2] I gathered this in West Australia.

[3] I collected this in New Zealand thinking it was Podocarpus, but Dr. Pilger of Berlin has been good enough to identify it for me.

[4] One sees then on the twig a scar indicating the place where the seed sat.

With regard to the female flowers of the other Coniferae:—

ARAUCARIEAE. We have a simple construction in the Araucarieae. The ovules are solitary or many upon the upper side of the sporophylls which stand on an axis and compose with it the female cone. We should obtain the relationships of position of the female flower of Dammara rightly enough if we replaced by ovules the sporangia of a spike of Lycopodium.

TAXODIEAE. CUPRESSINEAE. A complication appears in other forms where an outgrowth arises upon the sporophyll above the primordium of the ovule and becomes only a membranous wing, as in Cunninghamia; or a scale-like formation, as in Cryptomeria japonica, where it ends above in several leaf-point-like teeth which are also indicated in Sequoia sempervirens (Fig. 348, IV)[1]; or a massive outgrowth not segmented off from the sporophyll or seminiferous scale, as in the Cupressineae, where in most cases it is unmembered but in Cupressus Lawsoniana such teeth are also seen. The ovule stands here upon a small growth in the axil of the scale of the cone. The scale itself develops after fertilization in the same way as does the megasporophyll of Ceratozamia[2].

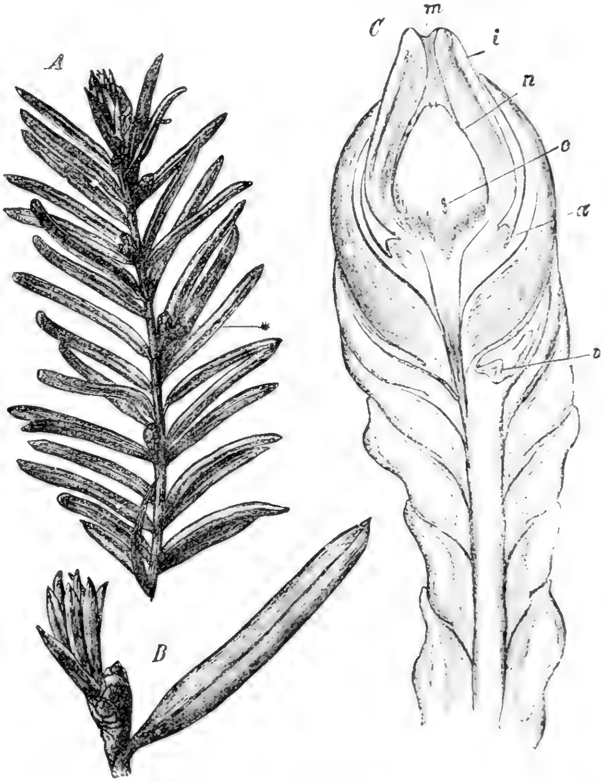

FIG. 350. Taxus baccata. *A*, twig with female flowers; * two ovules on the same shoot. *B*, leaf with fertile axillary shoot. *C*, shoot in longitudinal section whose apex, *v*, is displaced to the side. At the top a female flower; *a*, incipient aril; *n*, nucellus; *e*, megaspore; *i*, integument; *m*, micropyle. After Strasburger. Lehrb. *A*, natural size. *B*, magnified 2. *C*, magnified 48.

ABIETINEAE. The Abietineae show the most peculiar formations. The ovules are placed upon a body called the seminiferous scale which covers and reaches beyond the scale of the cone. The cone is composed of a spindle on which scales, the sporophylls[3], are inserted, and in their axils the seminiferous scales arise. Each seminiferous scale bears two ovules upon

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[1] Where, however, the teeth do not fall over the ovules.

[2] See p. 512.

[3] The 'bract-scales' of authors.

its upper-surface. The history of development makes clear the relationships, and I may describe them briefly as they are known in the silver fir[1]:—

Development of the female flower in silver fir. The bud out of which the female flower proceeds is distinguished at first only slightly from a foliage-bud. It stands in the axil of a foliage-leaf or needle upon the upper side of a twig, and is, like the buds which will unfold as new shoots in the following spring, covered with bud-scales. Its thick vegetative cone which is enclosed by the bud-scales produces a number of primordia of leaves as does the foliage-bud. These primordia which in their young condition quite conform to those of the foliage-leaves do not, however, develop into foliage-leaves but into the sporophylls mentioned above, and they remain somewhat small. After some time, at the beginning of October, there is found at the base of each sporophyll a hemispheric swelling. This is the primordium of the seminiferous scale upon which later the ovules arise. Were the seminiferous scale in this stage to be arrested it would appear as an ordinary placenta, like the placental cushions of many ferns, or those upon which the microsporangia of the Cycadaceae arise. But instead of doing this when the further development begins in May of the succeeding year this cushion begins to grow into the form of a scale, becomes much larger than the sporophyll, and quite covers it. At the base of this seminiferous scale the ovules arise; they are at first erect, and later become inverted so that their micropyle is directed downwards towards the spindle of the cone. This peculiar construction has a connexion with pollination[2], which is somewhat different in the different species because the seminiferous scale at the time of pollination does not show everywhere the same relationship to the sporophyll. Everywhere in the cone-flower the scales open out at the time of pollination and subsequently lie close together upon one another. The separation of the scales is occasioned by a stretching of the internode of the axis of the flower. The closing is the result of the strong growth upwards of the seminiferous scale.

Pollination in Pinus Pumilio. As regards pollination, we may describe it in Pinus Pumilio. The seminiferous scales, as in the other species of Pinus, are much larger at this time than the sporophylls. They have a bright red colour, and possess upon their middle a keel-like elevation (Fig. 351, *K*), and the pollen-grains slide along the erect seminiferous scale on both sides of this median keel (Fig. 351, *a*, *b*) and so reach the micropyle of the ovule (Fig. 351, *M*) which is drawn out into two long lobes. This, however, is not the only path for the pollen-grains. The margins of the sporophyll are bent back so as to produce four channels (Fig. 351, *c*, *d*, *e*, *f*), and these all lead finally to the micropyle.

In Abies excelsa, Larix, and elsewhere, where the seminiferous scales at the time of flowering are still smaller than the sporophylls, it is the sporophylls which form the passage for the pollen-grains, and the seminiferous scales take only a secondary share in it, inasmuch as they cause the pollen-grain in the last portion of

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[1] See Schacht, Grundriss der Anatomie und Physiologie der Gewächse, Berlin, 1859, pp. 182 ff.; also Strasburger, Die Coniferen und die Gnetaceen, Jena, 1872.

[2] See Vaucher, Histoire physiologique des plantes d'Europe, Paris, 1841, tome iv; Strasburger, op. cit., p. 268.

its way to slide downwards to the ovule. After fertilization the seminiferous scale enlarges considerably and encloses the seed closely. It fulfils now the same function as does the outgrowth which appears only after fertilization upon the sporophyll of Cupressus. In the two functions—the protection of the ovule and the conduction of the pollen-grain to the ovule—the seminiferous scale conforms to the ovary of the Angiospermae. The important part played by the exudation of a drop at the micropyle of the megasporangium has long been known in the fertilization of all the Coniferae [1].

POSITION OF THE FEMALE FLOWER IN CONIFERAE. As regards the position of the flowers: the female flower in the majority of the Coniferae is so placed that the pollination takes place from *above*. Where they are not erect they curve negatively geotropically upwards, as is especially seen in the case of Larix. It appears to me to be significant that this takes place specially in the coniferous flowers which possess ovules whose micropyle by a subsequent growth is turned downwards, as in the Abietineae and Podocarpus.

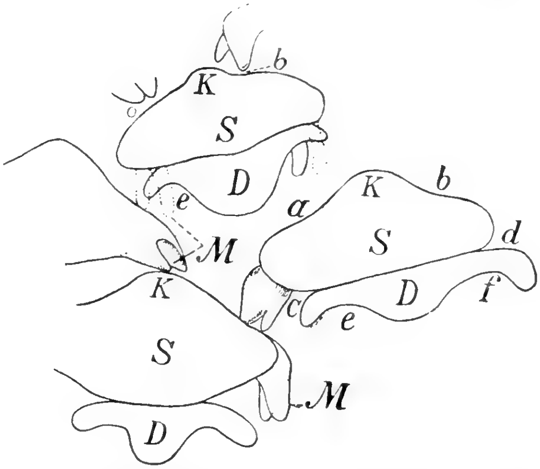

FIG. 351. Pinus Pumilio. Portion of a tangential section through a female cone at the time of pollination; *D*, sporophyll; *S*, seminiferous scale; *K*, median ridge on seminiferous scale; *M*, micropyle; *a*, *b*, *c*, *d*, *e*, *f*, channels along which the pollen-grains slide to the micropyle.

BIOLOGICAL RELATIONSHIPS. Regarding the biological relationships of the female flower there is little of a general character to relate. There is, however, the question of the pollination of the ovules and the protection of the ripening seed.

This problem can be solved in different ways. In many cases the aid of carpels is entirely got rid of, as in Ginkgo and Taxus, and the flowers then appear to be extremely reduced. The outgrowth of the carpels appears the earlier, the earlier its function is performed; where its work is only that of protecting the seed, as in the Cupressineae, it arises late; where it aids in the conduction of the pollen-grain, as in the Abietineae, it appears earlier.

The lie of the megasporangium within the flower may be connected with its size or with that which the seed will reach. So far as I see, the ovules of flowers where there are numerous ovules retain the upright position only if they are relatively small and belong to cones of small dimensions. Where

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[1] Vaucher, Histoire physiologique des plantes d'Europe, Paris, 1841, tome iv.

the seeds are larger and are arranged in larger cones they can be better looked after if their longer axis falls in with that of the cone-scales[1]. Nevertheless in the Abietineae the ovules are inverted. What significance the anatropous configuration in the ovules of the Podocarpeae has we do not know.

THE QUESTION OF FLOWER OR INFLORESCENCE. The relationships of configuration of the female flowers of the Ginkgoaceae and of the Coniferae have received very different morphological explanations. Worsdell has given recently an historical account of these to which I may refer[2]. I would only refer to one point. What has been spoken of above as a female flower in the Abietineae, Podocarpeae, and Cupressineae, is by others regarded as an inflorescence. This interpretation is with great ingenuity defended by Čelakovský, who bases it chiefly upon two grounds:—

(*a*) the structure of the female flower of Ginkgo;

(*b*) the 'anamorphose' which has been frequently observed especially in the Abietineae.

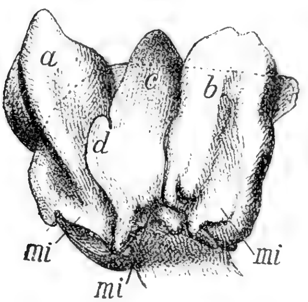

FIG. 352. Pinus maritima. Malformde seminiferous scale. Explanation in the text. The 'bract-scale' lying behind the seminiferous scale is partly indicated by the dotted line. The indices from *mi* are too long in the figure.

The argument from anamorphose. In this we have to deal with malformations—when compared with the normal—in which a shoot appears in the position of the seminiferous scale, and various intermediate states between normal seminiferous scales and vegetative shoots arise—a consequence of the vegetative transformation setting in at an earlier or later stage. We may meet with, for example, a shoot which begins with two leaves bearing upon their under-surface rudimentary ovules. From this it has been concluded that the seminiferous scale is an axillary shoot producing two leaves which twist through about 90°, become concrescent by their edges, and bear each of them one ovule upon the under-surface which is turned to the axis of the cone. In Pinus a third rudimentary leaf is added, which is constructed as a 'keel.' Fig. 352 will help to explain this. It shows a malformed seminiferous scale from an androgynous cone[3]. Instead of the normal seminiferous scale there are three leaf-like structures, *a*, *b*, *c*, united at their base and each bearing upon its under-surface one malformed ovule recognizable by the abnormal micropyle, *mi*. *a* and *b* correspond to the first two leaves of the axillary shoot of the bract-scale. They have not, however, undergone complete torsion and they bear the ovular primordia evidently still upon their outer side. Whether *c* is a new formation or corresponds to the keel, which might also be

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[1] We have seen the same features in the Cycadaceae; one may compare the lie of the megasporangia of Ceratozamia (Fig. 343) with that of Cycas.

[2] Worsdell, The Structure of the Female 'Flower' in Coniferae. An Historical Study, in Annals of Botany, xiv (1900).

[3] See the account of this cone on page 471 where it is figured (Fig. 311). Malformed scales frequently appear here as well as normal seminiferous scales.

represented by *d*, is not of importance. That we have to do here with a check of the development is shown by the arrest of the ovules. If we regard the occurrence from the 'purely morphological' side the whole structure corresponds to an axillary shoot of the bract-scale which usually is reduced to two leaves; in Araucaria and Podocarpus there would be only one present, in Cryptomeria and others there would be many laterally confluent with one another. If these leaves be the sporophylls, the covering scales are the bracts of the flower.

Argument from virescence. Similar phenomena appear when virescence takes place. There can be no doubt that in virescence we have a vegetative transformation of the seminiferous scale, but it does not follow that we must endeavour to make out that the observed phenomena are those of the 'normal' course of development. The plant devotes to the construction of the ovules and to the protection of these an axillary outgrowth of the bract-scale which can appear in vegetative development as a shoot. This transformation is brought about by external influences, at least in many cases[1]. We find virescent cones on pruned spruce-hedges, and on trees growing at the upper limit of tree-growth where they easily lose their top. Naturally other factors can act also.

Summary. Putting on one side, however, the causes which bring about the virescence and other checks, we may sum up as follows:—

If the development of the primordium of the seminiferous scale of the Abietineae is stopped at an early enough period it can grow out into an axillary shoot whose first leaves bear the arrested ovules on their under-surface. It is possible to construct a series which, starting from the seminiferous scale of the Abietineae, passes to the dorsal outgrowth of the cone-scale of the Cupressineae. This does not require the primordium of the seminiferous scale to have been a shoot with developed leaves. It may have experienced its transformation into seminiferous scale before such a segmentation set in, and in phyletic relationship I see no necessity for the assumption that the seminiferous scale corresponds to a small greatly reduced flower. There are wanting transition-forms which would demonstrate any such history. The analogy with Ginkgo is of less value as an argument because a common origin of the Coniferae and Ginkgoaceae is extremely improbable.

Hypothesis. We may, however, if we wish to construct hypotheses suggest others. Starting from a carpel like that of Ceratozamia which bears two lateral ovules, if these are displaced upon the upper-surface of the carpel they may assume an axillary position to it. If their number increases then we at once have the relationship in many Cupressineae; if it diminishes we have that of Podocarpus. For the protection of the seeds the carpel develops into the peltate form of the Cupressineae, and soon there arises a more or less independent axillary outgrowth of this, which in its extreme form exhibits the construction as it occurs in the Abietineae. Virescence and other malformations seem to me only to show that the primordium of the seminiferous scale has the capacity, although this usually remains latent, to develop into an axillary shoot, but not that it ever was a functionally active one. The mycelium of a fungus induces the leaf of Pteris quadriaurita to produce shoots—a capacity

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[1] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 123.

which usually remains latent—which are then provided with leaves. The galls caused in Aspidium aristatum[1] by Taphrina cornu cervi may be termed a rudimentary attempt at the formation of shoots. The unfolding of a latent primordium does not of necessity require us to conclude that it is a 'reduction.'

The foregoing hypothesis, which of course is only *one* of the many that might be suggested to bring the facts into union one with another, appears to me, however, to lead to greater simplification. Whilst there is something to be said for the hypothesis which traces the construction from Ginkgo, yet I must state that it seems to me to be a 'purely formal' one, and that it has not as yet explained to us in its teleological connexion why the female coniferous flower should have experienced such far-reaching transformations whilst the relationships to pollination at least are nearly alike in all.

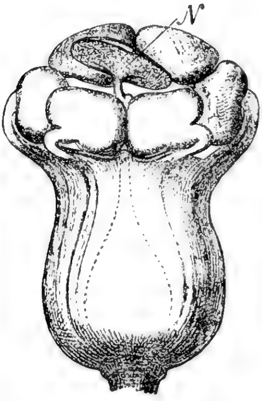

FIG. 353. Welwitschia mirabilis. Male flower after removal of the flower-envelope; *N*, stigma-like apex of the integument of the ovule which does not attain to full development.

III. GNETACEAE.

The third group of the Gymnospermae—or, if one makes the Ginkgoaceae a separate group, the fourth—is the Gnetaceae, and it does not require here any elaborate description. The flower is surrounded by a perianth, indications of which are also found in the flowers of other Gymnospermae, and in Welwitschia we meet with for the first time a hermaphrodite flower, which, however, becomes unisexual by the arrest of the stamens or of the female apparatus. It is possible that Welwitschia (Fig. 353) originally possessed hermaphrodite flowers. That consequently all gymnospermous flowers must be considered as primarily hermaphrodite does not appear to me to be a consequence[2]. The stamens of Welwitschia are concrescent below into a cup-like structure, and each bears at its apex three microsporangia arranged radially, and opening by splits. In Ephedra there stands in the middle of the flower which is invested by two envelope-leaves a stalk-like column on which two or more bilocular sporangia are seated, and these may well be regarded as reduced stamens. The function of the filaments which are absent is performed here by the elongation of the flower-axis which thus raises up the sporangia for the proper distribution of the spores[3].

The essential thing here is that the conformation of the stamens stands in relation to the presence of a flower-envelope *which encloses the stamens until a short time before their unfolding*. In the other Gymnospermae it has

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[1] See Giesenhagen, Die Entwicklungsreihen der parasitischen Exoasceen, in Flora, lxxxi (Ergänzungsband zum Jahrgang 1895), p. 330.

[2] See in this relation what has already been said, p. 471, and Part I, p. 60.

[3] It is therefore of little moment whether one derives the column from the flower-axis or from a congenital union of leaf-structures in whose formation the flower-axis is quite used up.

been shown that the conformation of the stamens has the closest connexion with the protection of the microsporangia in the bud, and that the special 'aim' of the configuration of the lamina of the stamens is the protection of the microsporangia during their ripening and there is no question of an envelope of the male flower for this purpose. But in the Gnetaceae where the envelope itself encloses the microsporangia the configuration of the stamens is correspondingly simplified. The majority of Angiospermae behave in exactly the same way.

The construction of the female flower will be briefly referred to when megasporangia are described[1].

The flower-envelope of the Gnetaceae may be considered as being constructed out of hypsophylls. When speaking of the envelopes in the Angiospermae reference will be made to this again[2].

An approach to the Angiospermae is also found in this—the ovule is invested by an outer envelope. This may be regarded as composed of two concrescent leaves, and it is present, for example, in Ephedra, even when the seed is ripe, forming a thick outer shell like a pericarp in an angiospermous fruit. This structure may be regarded as a rudimentary ovary which has not reached the stage of forming a stigma; the stigma-like organ of the Gnetaceae belongs rather to the integument of the ovule.

IV

THE SPOROPHYLLS OF THE ANGIOSPERMAE

A. THE FLOWER IN GENERAL.

The flowers of the Angiospermae are much more varied than are those of the Gymnospermae[3]. They differ from those of the Gymnospermae particularly in this, that the *ovules* (megasporangia) are enclosed before pollination in an ovary which has developed a special organ—the *stigma*—for the reception of the *pollen-grains* (microspores). The *carpels* (megasporophylls) are therefore differently constructed from those of the Gymnospermae. The *stamens* (microsporophylls) have in almost all Angiospermae an essentially similar construction about which more will be said later on. The flower-envelopes which in the Gymnospermae only give protection in the bud, are much more conspicuously developed in the Angiospermae. In many forms, especially those in which pollination is effected by the agency

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[1] See p. 629.

[2] See p. 549.

[3] I can only briefly refer in this book to some general relationships and to some of the chief peculiar organographical features. Valuable material from the morphological side will be found in Payer, Traité d'organogénie comparée de la fleur, Paris, 1857; Eichler, Blüthendiagramme, Leipzig, 1875; Engler und Prantl, Die natürlichen Pflanzenfamilien; Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1894). As regards the configuration of the flower in relation to pollination see Knuth, Handbuch der Blütenbiologie, Leipzig, 1898–1904.

of animals, this envelope is entirely or partially developed as a *flag-apparatus*. And we may mention as a further peculiarity of the angiospermous flower that it is predominantly hermaphrodite, and unisexual flowers can be proved to be frequently the result of arrest of either the microsporophylls or the megasporophylls.

The great importance of the construction of the flower in systematic botany has led to extended investigation of it, and its innumerable variations have received very full treatment in systematic works. I can therefore pass over these here, as well as the consideration of the relationships of the flower to pollination[1], and confine myself only to an account of some of the chief peculiarities by which flowers are distinguished from vegetative shoots. Apart from the construction of its several leaf-organs, which is bound up with their function, and the special features of its axis which have been shortly mentioned above[2], we may say that the flower of the Angiospermae chiefly differs from the vegetative shoot by features which can be traced back to

(1) changes in the arrangement of the parts,
(2) concrescences,
(3) arrests.

I propose now to give some illustrations showing only the general relationships[3].

(1) ARRANGEMENT OF THE PARTS OF THE FLOWER.

It has been already shown[4] that the flower in Selaginella possesses an arrangement of the leaves which is in part different from that in the foliage-shoots. This is repeated in the flower of the Gymnospermae and the Angiospermae, and not only in the flower but also in the inflorescence, very strikingly, for example, in many Orchideae. This evidently is a consequence of the *changed relationships of space at the vegetative point of the inflorescence and of the flower*. This change can be brought about in different ways. Some of the processes are as follow:—

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[1] It is incorrect to speak of this subject as 'flower-biology,' a term which has a much wider significance.

[2] See p. 470.

[3] The account I give is based essentially upon what I have already published in Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884). I here once and for all make reference to Hofmeister's Allgemeine Morphologie der Gewächse, Leipzig, 1868. With regard to the mechanical theory of leaf-position I may refer to Schwendener, Mechanische Theorie der Blattstellungen, Leipzig, 1868, and to Schumann, Blüthenmorphologische Studien, in Pringsheim's Jahrbücher, xx (1889); id., Neue Untersuchungen über den Blüthenanschluss, Leipzig, 1890; id., Morphologische Studien, Heft 1, Leipzig, 1892. A criticism of the researches which have been made to establish a mechanical explanation of the relationships of configuration in flowers is here impossible, but I must state that my view of the results to which the mechanical theory of leaf-position leads in the domain of flower-morphology differs altogether from that given by Weisse, Die Zahl der Randblüthen am Compositenköpfchen in ihrer Beziehung zur Blattstellung und Ernährung, in Pringsheim's Jahrbücher, xxx (1897); see also Part I, p. 84.

[4] See p. 509.

(*a*) RELATIONSHIP OF RELATIVE SIZE OF PARTS IN THE FLOWER.

If the vegetative point of the flower or inflorescence retains the dimensions of that of the vegetative shoot, whilst the size of the primordia of the leaves—whether these be leaves within the flower or bracts upon the inflorescence—decreases, then we shall find numerous primordia of leaves with a different arrangement from that in the vegetative shoot. Again, if the vegetative point of the flower or inflorescence broadens relatively to the foliage-shoot this likewise occasions a change in the arrangement of the primordia of the leaves. Changes in arrangement are all the more prominent if the two processes mentioned are combined together as they are in the capitulum of Compositae. This connexion between relationship of size and arrangement becomes specially conspicuous if there are changes in the numerical relationships of the parts within the flower itself. The microsporophylls in particular furnish us with examples. They are almost never leaf-like in the Angiospermae, but commonly possess a narrow thread-like *filament*, consequently each of the stamens occupies at its origin a smaller area of the torus than does, for example, the sepal. Whilst then in the case of foliage-leaves if their arrangement is cyclic the number of members in the several succeeding whorls normally remains the same, this is not generally the case in flowers. The disposition of the stamens in many Rosaeflorae supplies us with a striking illustration of this [1].

Geum. Rosa. The young flower-bud of a species of Geum or of Rosa shows the usual form of this organ:—there is a broad convex vegetative point, upon which the sepals arise in the usual successive series. Then before the inception of the five alternisepalous petals there develops upon the peripheral zone of the torus an annular ring or cup which surrounds the central portion of the torus upon which the carpels arise. The primordia of the stamens shoot out upon the inner margin of this cup, appearing in basipetal serial succession as the toral cup grows by means of its intercalary vegetative point. The number of the staminal primordia is very variable, not only in the different genera and species but also in one and the same individual—and this in accord with the size of the staminal primordia and also with the relationships of growth of the torus shortly before their origin. The number increases if either the size of the primordia diminishes or that of the zone of the torus upon which they arise increases immediately before their inception. According to the earlier or later entrance into the development of either of the two factors just mentioned we find at first five alternipetalous staminal primordia, or ten stamens appear after the pentamerous corolla.

Agrimonia. Agrimonia gives us an illustration of the five alternipetalous staminal primordia. Here, after the inception of the five petals, there appear five strikingly large alternipetalous staminal primordia which fill up the space between the primordia of the five petals. In Agrimonia pilosa a second pentamerous staminal

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[1] See Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xl (1882), p. 353.

whorl follows and alternates with the first[1], but in other species of the same genus the size of the staminal primordia decreases after the inception of the first whorl, and a second staminal whorl which is decamerous follows the first pentamerous one. The members of this decamerous second whorl link themselves in pairs to those of the first. This construction is not the result of chorisis[2]. In consequence there is a variation in the number of the stamens: Agrimonia Eupatoria, for example, has some flowers which have twenty stamens and some flowers which have only five stamens, and in numerous cases the number of stamens oscillates between these extremes. The whole condition depends upon relationships of nutrition. We have no reason for assuming that the most completely furnished flowers are the typical ones, that is to say, are to be considered as phyletically the older; and this is shown by a comparison with other species. We can only conclude from what has been said that there is here no constancy in the number of the stamens from the beginning.

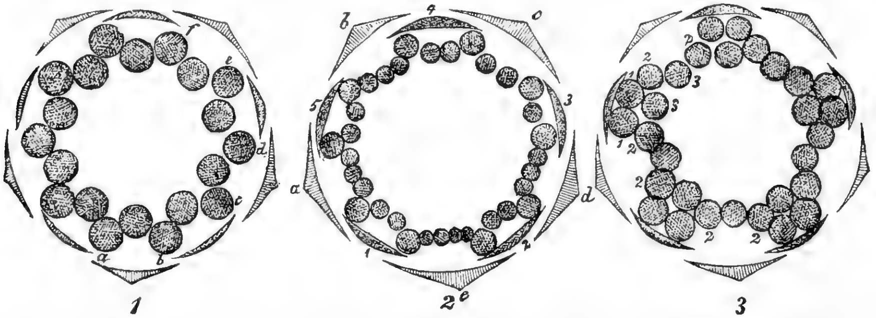

FIG. 354. Scheme of staminal arrangements in Rosaceae. 1, species of Potentilla; *a b*, *c d*, *e f*, pairs of stamens of the outermost whorl. 2, Rubus Idaeus, only the outer stamens indicated; *a*, *b*, *c*, *d*, *e*, sepals; 1, 2, 3, 4, 5, petals. 3, Potentilla fruticosa; 1, 2, 3, successive staminal whorls.

Similar relationships occur in other Rosaceae, but the diminution of growth in the organs, and the consequent multiplication of the number of stamens, appears in the first staminal whorl. Following upon the five petals there are therefore ten stamens which in general are so distributed that the pairs are separated from one another by an equal distance (Fig. 354).

Potentilla. These relationships of space are retained in a number of flowers, for example in many species of Potentilla, and then a second decamerous staminal whorl (Fig. 354, 1)—in many cases even a third (Fig. 354, 2)—alternates with the first.

Rubus. It is otherwise in Rubus of which Rubus Idaeus may be taken as an example. Here the first ten stamens arise at almost equal distances from one another, but very early this arrangement is changed, inasmuch as the zone of the torus opposite the sepals (Fig. 354, 2, *a*, *b*, *c*, *d*, *e*) experiences a considerable growth, so that the separation of the antisepalous stamens is greater than is that of the antipetalous ones. On account of the extent of this growth there are usually two—seldom one—staminal primordia opposite each sepal. These again by further growth of the torus may be pushed aside from one another, and between them one stamen or, should the size of the space and of the staminal primordia permit of it, two stamens may be interposed. Thus there is no uniformity even within one and the same flower, as the diagram shows. Likewise in front of each of the petals (Fig. 354, 2, 1,

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[1] It is frequently, however, incompletely formed.

[2] See p. 532.

2, 3, 4, 5) there may appear two—seldom only one—stamens, usually synchronously but often one before the other, and in that case the earlier is placed somewhat higher than the other, so that we can suppose that there has been chorisis. The further staminal primordia place themselves in the gaps between those that precede them.

In other Rosaceae[1] there are found like variations in the number of the staminal primordia according to the relationships of space and the relationships of position which in one form occasionally vary in another appear to be nearly constant; thus Potentilla nepalensis has usually two antipetalous staminal primordia instead of one, a relationship which is almost constant in Rubus.

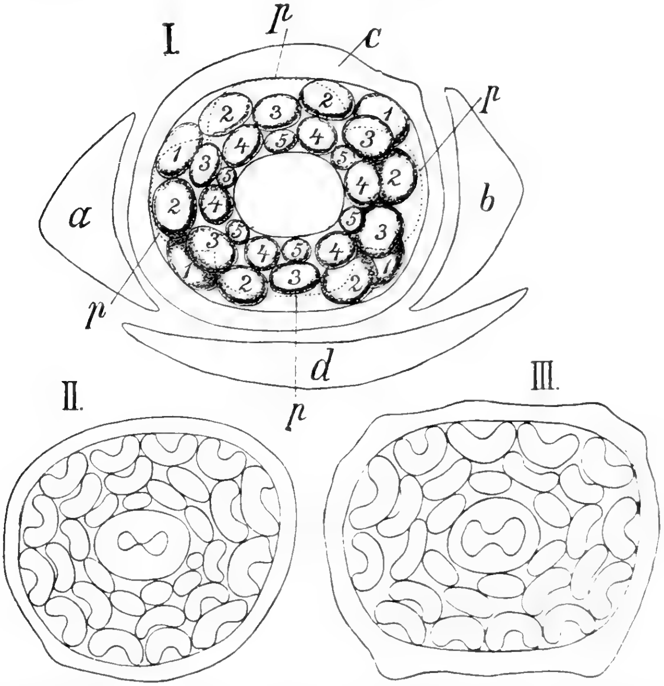

FIG. 355. Eschscholtzia californica. Flower-bud in transverse section. I, the two carpels removed; *d*, bract; *a*, *b*, prophylls; *c*, calyx; *p*, petals; then follows one tetramerous staminal whorl, 1, and four hexamerous staminal whorls, 2–5. II, shows thirty-one stamens. III, shows twenty-eight stamens. The anthers in II and III almost all extrorse through the medianly convex curvature of the connectives.

Relationships of position like those of the stamens of the flowers of the Rosaceae are found also in the primordia of other organs, for example in the bristles which stand upon the outer side of the receptacle of Agrimonia, the body of pappus of many Compositae, and I have found the same in the androecium of a number of flowers in other families, for example Mimoseae, some Anonaceae, Clematis, Papaveraceae. I shall give one more example taken from the Papaveraceae.

Eschscholtzia californica. In Fig. 355, II and III, we have representations of two transverse sections of the flower of Eschscholtzia californica. The stamens are

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[1] See the treatises that have been cited.

numerous; their connective shows later a strong convex curvature upon the inner side so that the *extrorse* position is assumed. The number of the stamens is here, as in Rosaceae, by no means constant. There are, for example, twenty-eight in Fig. 355, I, thirty-one in Fig. 355, II, and twenty-eight in Fig. 355, III. How these are arranged is shown in the young flower-bud (Fig. 355, I). Following upon the dimerous calyx comes the corolla of two dimerous whorls *p*, *p*, and the petals are set on the torus with a broad base. With these four petals there alternates a tetramerous staminal whorl[1] whose members are marked with 1. Now the conformation of the flower-bud is not circular but transversely oval in cross-section, and the narrower sides are turned to the prophylls *a* and *b*. Upon the broad sides[2] of the flower there is more room for the insertion of the stamens with narrow base on the flower-axis, and as a matter of fact we find here two, whilst upon the narrower side there is only one. A hexamerous whorl follows the tetramerous one and its members are marked with 2, and in turn it is succeeded by two other hexamerous whorls until finally what is left unoccupied of the torus is used up by two carpels. In the flower represented in Fig. 355, II, the last leaf-whorl is not complete.

In other Papaveraceae the relationships are the same[3]. In Bocconia the cyclic arrangement of the stamens is somewhat confused.

CHORISIS. The examples which have been quoted show that there is a connexion between the number of the stamens and the relationships of space in the primordium of the flower, and this explains why we have changes in the numerical relationships in the several whorls. The old morphology gave a much simpler explanation in these cases, namely, the word 'chorisis.' Even in the latest text-books[4] this notion is still brought forward as an 'explanation.' I must repeat what I said about it twenty years ago.

Moquin-Tandon was the founder of the theory of 'dédoublement[5].' Later the same notion was designated 'chorisis,' a name introduced indeed by Dunal, who

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[1] It is a not uncommon occurrence that the change of the numerical relationships in cyclic flowers does not take place abruptly but only *gradually*. Thus we see in the first staminal whorl still a tetramery.

[2] The transverse position of the carpels is no doubt connected with this also. Elsewhere, if two carpels are present, they are usually median.

[3] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 300. It is there shown that in the Cruciferae, where usually the two pairs of longer stamens are interpreted as a chorisis of two primordia, the analogy with the Papaveraceae speaks strongly in favour of the independence of each staminal leaf. The relationships of space are quite the same. Before the broad side of the carpel there is more room than before the narrow side.

[4] In Strasburger's Text-book of Botany, 2nd English Edition, London, 1903, it is said (p. 526) that in the Rhoeadinae to which the Papaveraceae belong the androecium consists often of more than two whorls on account of the splitting of its members, and again (p. 561) that in the Rosaceae a 'splitting of the whorls and of the individual members of the androecium' has taken place phyletically. Neither statement corresponds with facts; they are hypotheses which long ago have been shown to be untenable.

[5] Or perhaps we should say Dunal. See Moquin-Tandon, Essai sur les dédoublements ou multiplications des végétaux, Paris and Montpellier, 1826.

also is the author of the term 'carpel[1].' German authors distinguish between 'splitting,' in the narrower sense, and 'dédoublement' or 'chorisis' proper. If the portions proceeding out of a common primordium appear as halves of one whole then one speaks of 'splitting,' but if each of these parts has the nature of a whole leaf-organ then one speaks of 'dédoublement' or 'chorisis[2].' Moquin-Tandon's original definition ran[3] 'when in the place of one stamen, which ordinarily exists in an organic symmetry[4], one finds many stamens, these have become many by dédoublement or by multiplication.' Have we now a right to make any such assumption? It is clearly based upon a comparison. We might just as well say that if a woman bears twins there is a dédoublement because in place of one child one finds two. It may be asked, if the expression has a palpable meaning—do the twins arise through the splitting of an embryonal primordium or through fertilization and further development of two independent separate eggs? It is clear that only the history of development and the comparison with allied forms can give information as to which is the actual process. In dédoublement Moquin-Tandon included also cases in which later botanists spoke of 'branched stamens,' for example in Hypericum; moreover he enumerated amongst the cases in which dédoublement occurred those of the Ranunculaceae, Anonaceae, and indeed all plants with many stamens. That dédoublement which corresponds with the present-day meaning of this word is his 'dédoublement complete but simple'—in which the organs arising by dédoublement stand either in one line beside one another, or in many phalanges around the gynaeceum, as in Hypericum. The first is the case, for example, in Alisma Plantago: 'six stamens opposite in pairs to each of the three petals, and produced by the dédoublement of three stamens each into two.' More particular examination of this case tells us that the history of development[5] by no means bears out that two staminal primordia have proceeded from the splitting of an originally simple one, but on the contrary the two supposed split portions are wholly independent and arise upon the torus completely separated from one another by an angle of it. Yes! But this is 'congenital dédoublement.' In other words we quiet our minds regarding the fact that in the position of the primordium of an organ two completely independent ones arise in this way: we write down the fact in two words, which indeed say no more than that nothing of a splitting or branching is to be seen here from the very first. Yet many see in this an 'explanation'! More consequently it might be maintained that the 'congenital dédoublement' may be an actual one, as our methods of investigation—and this is doubtless true—are imperfect, and the splitting takes place very early. But in many cases as is shown by the whole configuration of the flowers concerned, those, for example, of Alisma, as well as those of Rosaeflorae and

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[1] See regarding this terminology Moquin-Tandon, Éléments de tératologie végétale, Paris, 1841, p. 335.

[2] See Eichler, Blüthendiagramme, i, p. 5.

[3] See Moquin-Tandon, op. cit., p. 8.

[4] By this he understands with de Candolle what one now expresses by the word 'type' or 'plan of structure.'

[5] See Buchenau, Über die Blüthenentwickelung von Alisma und Butomus, in Flora, xl (1857), p. 241; Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xl (1882).

Papaveraceae above described, this contention is quite untenable, and the general conception out of which it has sprung is certainly not one that need be maintained at all hazards. It is possible to show in a number of cases that the replacement of one stamen by two or more is not the result of a splitting, but depends upon the relationships of growth in the torus, and variations in the size of the primordia of the organs. An 'explanation' is indeed not given by this, but only one of the conditions or accompanying circumstances in which the phenomena in question appear is made clear[1]. An explanation of the causes of these relationships of growth we do not possess. That usually alternation takes place is moreover only a fact of experience for which we cannot adduce a causal but at the most a teleological connexion. That a splitting and branching of staminal primordia takes place should not surprise us. We have indeed seen in the sporophylls of the Filicineae that these are often richly branched like the foliage-leaves. But there is no doubt that comparative morphology has landed itself frequently in a misuse of this notion. In recent times, however, even amongst morphologists a reaction has begun to make itself felt in the direction of the view early pleaded for by me, but naturally then ignored by the 'morphologists'—a reaction which has led to the notion, to be mentioned below, of 'negative chorisis.' I must, however, next deal with the question of the occurrence of branching or splitting of stamens and carpels in general.

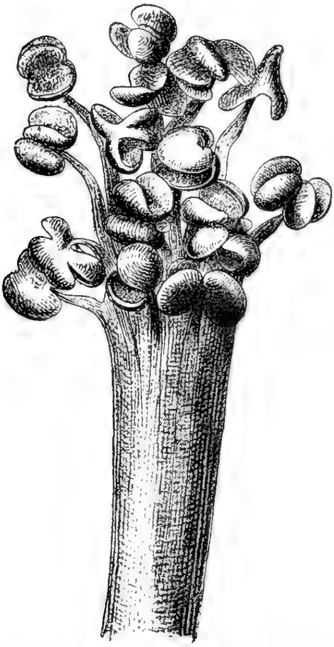

FIG. 356. Hypericum aegyptiacum, Linn. (H. heterostylum, Parl.). Staminal phalange. Magnified 20.

BRANCHING OF THE STAMENS. We start from a special case:—

Hypericaceae. The stamens in the flower of Hypericum aegyptiacum are arranged in bundles, one of which is shown in Fig. 356: a number of perfect stamens spring both from the edge and from the outer side of a common flat column. This structure has been recognized as *one branching leaf* for the following reasons:—

1. The history of development shows that each bundle of stamens arises out of a specially limited part of the torus upon which the staminal primordia are laid down.

2. The staminal primordia are laid down in descending serial succession, an

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[1] If we see in a flower that the primordia of the organs appear in greater number where there is more room at the vegetative point of the flower, this does not necessarily mean that we can say that the relationships of space are those conditioning the numerical relationships; just as well can we assume that there is more space provided where the vegetative point of the flower is disposed most to the building of primordia of organs. All 'mechanical' explanations are excluded in these relationships.

arrangement which in 'comparative' morphology is not permitted for the parts of a leaf or for the inception of leaves upon a shoot.

Against this I have already shown [1] that the comparison of the different forms of flower and their development makes possible another suggestion, namely, derivation from a flower which forms numerous stamens in descending serial succession uniformly distributed on the torus [2]. Such forms are found in the Hypericaceae. In Brathys prolifica [3] the torus forms five antipetalous primordia separated from one another by depressions, and the stamens arise preferably—that is to say appear first of all—upon these elevations of the flower-axis, but not exclusively there for staminal formation also takes place in the depressions of the torus. Loasaceae show like features. It is not necessary to regard these antipetalous primordia as basipetally branching staminal primordia the branchings of which become partial stamens, but we may recognize in them merely areas of the torus on which the staminal formation in many Hypericaceae is localized, especially in forms which we may designate as impoverished when compared with Brathys where the whole torus is still covered with stamens. In the species of Hypericum in which five such antipetalous primordia are present this method of origin shows itself in the perfect flower mainly in the assemblage of the stamens in five groups; in Hypericum aegyptiacum the antipetalous primordia grow out into long columns. It will be evident that the two explanations differ in their starting-point; the old one proceeds from a pentamerous androecium; the other from a polymerous androecium [4] which breaks up into single groups—a segregation which is also expressed at an early time in the parcelling of the torus, and is correlated with an arrest of the staminal primordia lying between the antipetalous primordia. It appears to me that this last explanation gives us a better picture of the facts [5], and I see no reason why we should not extend it to the Loasaceae, Myrtaceae, and other families. Of course only careful comparison within a cycle of affinity can show in any case what explanation is the best.

CHORISIS OF STAMENS. It is indeed possible that in many cases a complete splitting of the staminal primordia takes place, and there are certainly constant examples of an incomplete splitting.

Adoxa. In the lateral pentamerous flowers of Adoxa, for example, there are apparently ten stamens which alternate in pairs with the petals and possess in the ripe

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[1] Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xl (1882), p. 378; id., Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 302.

[2] See Part I, p. 41.

[3] See Payer, Traité d'organogénie comparée de la fleur, Paris, 1857, p. 8, pl. 1, Figs. 19-25.

[4] I have searched recently many authors without finding any mention of this which was published in 1882 and 1883.

[5] Schumann, Beiträge zur vergleichenden Blüthenmorphologie, in Pringsheim's Jahrbücher, xviii (1887), p. 151, says that my explanation is not *necessary*. I agree. Every explanation or theory is only of value in so far as it gives the *most satisfactory* picture of the phenomena according to the present state of our knowledge. As to the causes of the parcelling of the torus, it appears to me probable that the trimery of the primordia of many species of Hypericum is connected with the trimery of the carpels, and this relationship may be not merely one of space but differences of physiological nutrition may come into consideration.

condition only unilocular anthers. The history of development shows that as a matter of fact we have here a splitting of an originally simple staminal primordium[1]; each half develops certainly into a half stamen possessing one loculus.

Malvaceae. We know also of other cases, for example in the Malvaceae, where each single stamen splits likewise into halves, each bearing a unilocular anther.

DOUBLING OF STAMENS. With this we may link on cases in which an actual doubling, and not a splitting, takes place, in so far as the halves become complete, each usually having a bilocular anther. According to Payer we find this in Phytolacca and Rumex.

Phytolacca. In Phytolacca there appear at first simple papillae alternating with the leaves of the perianth, and they then divide into two parts each of which develops into a complete stamen, and this process is repeated in Phytolacca icosandra once more in a second staminal whorl.

Rumex. In Rumex where the androecium is composed of six outer and three inner stamens the outer ones are derived in pairs from the division of an originally simple primordium. We leave untouched the question whether one could explain this process otherwise in the phyletic sense.

DOUBLE FLOWERS. Specially evident examples of the multiplication of flower-organs by splitting or branching are supplied by double flowers[2]. Splitting or branching may occur here in the petaline primordia, as in some Onagrarieae like Fuchsia, Clarkia pulchella, and in the staminal primordia, as in Petunia, Primula sinensis, all the Caryophylleae which have been examined, the Cruciferae. The large number of petals in 'perfectly' doubled carnations is well known; in one not very strongly doubled flower I counted forty-eight. These are all, with the exception of the five normal petals, the result of a splitting of the ten staminal primordia. This splitting takes place in different directions, and to a greater or less degree. In slightly doubled flowers of Dianthus barbatus for example, there is no chorisis—the outer stamens are transformed into petals, and the others show middle stages between stamens and petals; but in more fully doubled flowers the splitting takes place (Fig. 357).

It is difficult to see why such a process should not also occur in the 'normal' development of the flower, and therefore the number of the stamens be increased. We usually assume a diminution of these. We are always too much inclined to reduce the processes of configuration which occur in nature to 'single' schemes, because these make easy for us their orientation in the midst of their manifoldness, and we forget that to nature, if we may be allowed the expression, there are offered many ways of reaching one 'goal' from which she selects the most practicable in the several cases.

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[1] Payer, Traité d'organogénie comparée de la fleur, Paris, 1857, p. 414, pl. lxxxvi.

[2] See Goebel, Beiträge zur Kenntniss gefüllter Blüthen, in Pringsheim's Jahrbücher, xvii (1886), p. 207.

Of this the double flowers furnish an instructive example. The excess of the petals in such flowers can be reached in very different ways: by transformation into petals of the organs which in the normal flower are devoted to other purposes, usually the stamens or more rarely the carpels; through splitting or branching of the primordia of organs and the petaloid construction of the new primordia which so arise; by formation of primordia of organs which did not exist in the normal flower, as, for example, by the origin of new whorls in cyclic flowers [1]. We learn from these facts that the inner nature of the vegetative point of the flower is proportioned to the formation of organs. If the vegetative point is 'induced' to bring forth more petals than usual it offers for these the necessary conditions of development. It is in it likewise that the changes first of all take place. Such considerations make us from the outset very sceptical regarding great mechanical influences such as have been used frequently in morphology as 'explanations.'

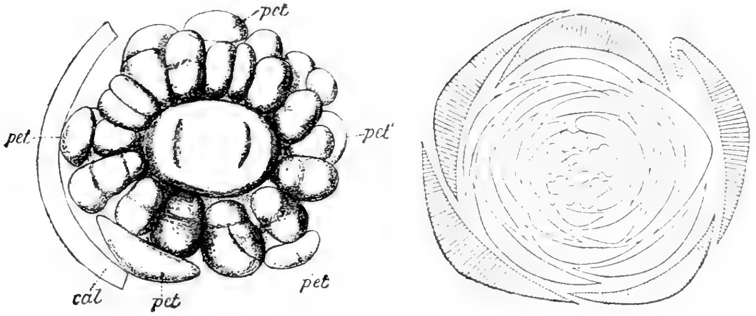

FIG. 357. Figure to the left: Dianthus Caryophyllus. Bud of a double flower dissected out; *cal*, calyx; *pet*, petals. The ten staminal primordia fork and so produce a great number of organs which develop as petals. Figure to the right: Nerium Oleander. Bud of a double flower in transverse section. Between calyx and androecium there are four pentamerous corolline whorls instead of one.

BRANCHING OF THE CARPELS. The number of the carpels may also increase by branching, for example in many Malvaceae. Payer found in Kitaibelia vitifolia five carpellary primordia [2] out of which by branching and the formation of false septa numerous monospermous ovaries are developed. In Malva and others the numerous carpels appear to be separated from the first. The process is in any case a rare one, and it is undoubtedly connected here with the development of the monospermous mericarps in place of the capsule. More common is it to find a diminution in the number of the carpels, as will be pointed out below.

FACTORS DETERMINING NUMERICAL RELATIONSHIPS IN THE FLOWER. The numerical relationships in the flower are in most cases

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[1] For examples see Goebel, Beiträge zur Kenntniss gefüllter Blüthen, in Pringsheim's Jahrbücher, xvii (1886), p. 207. Compare also Fig. 357, figure to the right. I may specially note the fact that the primordia of petals, which in the 'normal' flower are arrested, are developed in double flowers. This happens, for example, in Delphinium which gives us an illustration of the development of 'latent' primordia under definite stimuli. The latent primordia are not, however, always to be traced to those which formerly were developed, as is shown by the behaviour of other double flowers.

[2] See Payer, Traité d'organogénie comparée de la fleur, Paris, 1857, p. 35, pl. viii. I have convinced myself by examination of the correctness of his figures of Kitaibelia vitifolia.

determined by 'inner' causes, and in their variations we cannot usually trace the operation of outer factors. Yet as has been shown above in the Rosaceae the number of the stamens is often dependent upon relationships of nutrition, and the like occurs elsewhere. Thus the first flowers of some Caryophylleae are hexamerous, the following ones are pentamerous; the terminal flower of the cyme of Ruta graveolens is pentamerous, the others tetramerous; and we find the same thing in Lythrum Salicaria. The carpels of Nigella damascena furnish another example. Normally, that is to say in well-nourished flowers, they are five; in later flowers they are partly four and partly three, and it may be noted that this last number is the normal one in the allied genus Aconitum. Such cases are interesting because they lead us to the conjecture that what in one plant is directly caused by external conditions is determined by the internal economy of the plant from the beginning in another allied plant constructed after the same 'type.' Such cases will perhaps furnish a clue for our determining by further experimental research what are the factors which condition the numerical relationships in the flower.

(*b*) CHANGE IN THE NUMERICAL RELATIONSHIPS OF THE FLOWER THROUGH CONFLUENCE.

We have dealt above with the appearance of higher numbers in the leaf-whorl. We have now to look at cases where *diminution* in number of parts takes place.

We refer here not to the absence of single leaf-organs of the flower, but to the changes in the numerical relationships dependent upon confluence of parts which may take place at different stages, and there are all transitions from the separate inception of two leaf-structures to the appearance of one instead of the two—a phenomenon of which we have seen also examples amongst the vegetative organs[1]. The phenomenon is observed in the calyx, corolla, and androecium. It is best known and most easily proved in the corolla.

Confluence of petals. The corolla of the Labiatae is composed of five leaf-organs which are quite separate from one another as primordia. Of these two form the upper lip, three the lower lip. Those of the upper lip become confluent at a very early period, so that they appear as if they were a single leaf[2], and in the perfect condition the upper lip shows in consequence only a slight indentation, as in Lamium, or this is scarcely visible as in Betonica officinalis. It is possible that the upper lip appears from the beginning as *one* leaf in these cases; this happens at any

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[1] See page 370.

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), where I have shown that this union stands in connexion with the fact that the fifth stamen (which falls opposite the upper lip) has entirely disappeared, and that the four other stamens arrange themselves into a tetramerous whorl with nearly equal intervals. This would affect the construction of the corolla, that is to say the confluence of the two upper leaves.

rate in Veronica where in the mature condition, apart from the presence of the fifth sepal which is found in many species, the larger size of one petal alone suggests that it is to be considered as replacing two. The upper lip of the calyx of Utricularia is similarly never laid down in three parts[1]; the lower lip consists of two separate primordia. In the nearly allied genus Polypompholyx the calyx is laid down as five primordia[2]: it is evidently quite immaterial for the function of the organs in question whether the original segmentation is abolished or not.

Confluence of stamens. We find similar features in the androecium. In the Cucurbitaceae, for example, there are visible in the male flower frequently three stamens, two perfect, that is to say each with four pollen-sacs, and one a half-stamen.

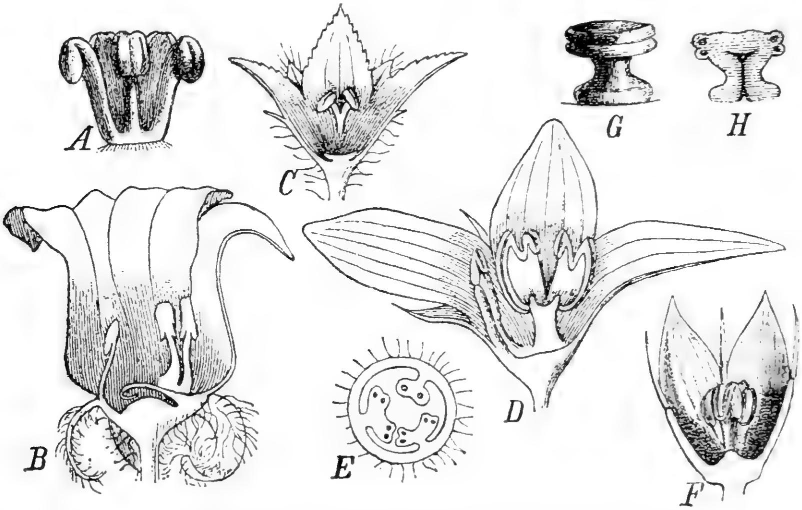

FIG. 358. Cucurbitaceae. Androecium. *A*, Fevillea trilobata; male flower in vertical section, showing five free stamens, each with a bilocular anther opening independently. *B*, Thladiantha dubia; male flower in vertical section; one stamen free, two others of the five close together as a pair. *C*, Sicydium gracile; male flower in vertical section; one staminal pair visible, filaments coherent below only. *D*, Bryonia dioica; male flower in vertical section; the filaments of this one staminal pair visible are completely coherent. *E*, the same in transverse section showing corolla and androecium. *F*, Sechium edule; male flower in vertical section; five stamens concrescent. *G*, Cyclanthera pedata; synandrium in profile. *H*, the same in vertical section. After E. G. O. Müller and Pax from Flora Brasiliensis.

Comparative consideration shows that in this family, starting from an androecium composed of five half-stamens such as is found in Fevillea (Fig. 358, *A*); there are in Thladiantha (Fig. 358, *B*) four stamens approached in pairs; in Sicydium (358, *C*) the filaments of these pairs are confluent with one another to a greater or less extent, in Bryonia the anthers only are still free (Fig. 358, *D*); in the majority of the Cucurbitaceae the anthers also are confluent; in forms like Sechium (Fig. 358, *F*) the confluence involves the whole five stamens, but the anthers are separated from one another; in Cyclanthera (Fig. 358, *G*, *H*) there is in the middle of the flower a structure provided with two pollen-sacs which runs right round it and which shows ontogenetically no longer any trace whatever to indicate that it takes the place of five stamens which are

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[1] See Buchenau, Morphologische Studien an deutschen Lentibularieen, in Botanische Zeitung, xxiii (1865), p. 94.

[2] See F. X. Lang, Untersuchungen über Morphologie, Anatomie und Samenentwicklung von Polypompholyx und Byblis gigantea, in Flora, lxxxviii (1901), p. 167.

confluent with one another. This example is of interest on different grounds, for the problem takes its first start in the establishment of such a series. Those who maintain that all 'morphological' characters are adaptations find in the flower of the Cucurbitaceae 'hic Rhodus, hic salta'! To those who like myself do not share this view the question arises whether there is any other causal factor for the special confluence. Researches in the comparative history of its development from this standpoint are unknown to me, but it appears to be probable that the trimery of the stamens produced here by confluence has a relationship to the trimery of the carpels, whose rudiments are visible in the male flower and reach a considerable size in the mature flower of Cucurbita. A process analogous with that which has been described in the Cucurbitaceae is found likewise in Hypecoum[1]. I need hardly recall that this process of concrescence may come about in different ways[2]. We may find staminal primordia, for example, so closely pressed together that they appear as a single primordium (Part I, Fig. 22, III) and then in later stages grow out separate. Čelakovský has lately designated this process 'negative chorisis'—a somewhat unhappy term.

(*c*) SUPPRESSION OF THE ELONGATION OF THE TORUS.

It is in consequence of this that we so often find a cyclic arrangement in the flowers of plants which have alternate phyllotaxy on the vegetative shoots. As the single leaves which compose, for example, the corolla discharge their function together, their *synchronous origin* is easily understandable; on the other hand, it will be a distinct advantage to the vegetative shoot that the foliage-leaves unfold in a gradual serial succession, and with this their *spiral arrangement* is consonant. The alternation of the foliage-leaves secures their efficient disposition without overlapping[3], but this consideration does not count in the leaves of the flower which do not assimilate, and we find that the alternation of whorls is not always retained. It is a matter therefore of no moment whether superposition, for instance of the stamens and petals of the Primulaceae, is phyletic and brought about by the arrest of a previously existing leaf-whorl, or is primitive. We can only assert that the relationships are of a kind other than those of the vegetative shoot.

If comparative morphology makes the assumption in the case of the Primulaceae —and indeed correctly—that the position of the stamens opposite the petals is 'explained' by the abortion of an alternipetalous staminal whorl, only the historical side of the question is kept in view. From the standpoint of what has been said above such a superposition requires no explanation if the space-relationships in the vegetative point of the flower are favourable to it. It is from the point of view of

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[1] See Payer, Traité d'organogénie comparée de la fleur, Paris, 1857, p. 229; Eichler, Über den Blüthenbau der Fumariaceae, Crucifereen und einiger Capparideen, in Flora, xlviii (1865), p. 433.

[2] See the scheme, Part I, p. 53, Fig. 22.

[3] The unfolding of a whole leaf-whorl when the leaves are of equal size makes a greater demand upon the root-system than does a single leaf, and we have already seen that the shoot-axis must stretch out in order to avoid the shading of one leaf by the other. See p. 442.

efficiency quite as correct as is the alternation of the whorls. Schumann[1] has pointed out that such a superposition of stamens and petals is found in particular if the petals are very small[2] and their development remains behind at first that of the stamens, a phenomenon which is partially responsible for the earlier view that the petals of Primula arise as dorsal outgrowths of the stamens—a view which nowadays hardly finds a supporter.

(*d*) LIMITED GROWTH OF THE TORUS.

Two special features of the flower are connected with this[3]:—

1. The fact that in the flower terminal leaves are not uncommon.

2. The serial succession of the parts of the flower not infrequently deviates from the acropetal succession of the vegetative shoot.

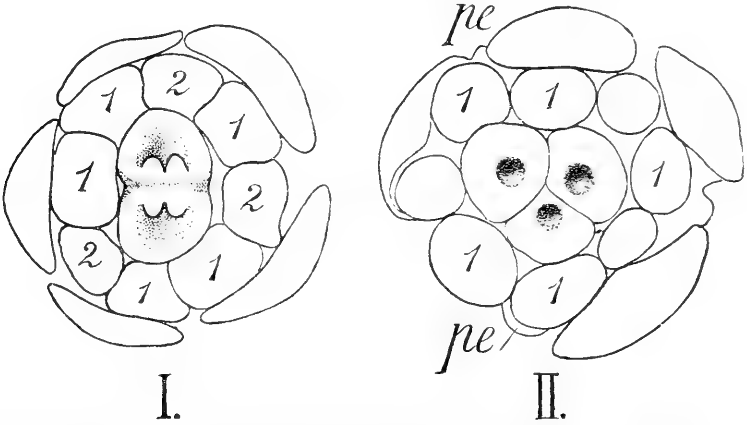

FIG. 359. Acer Pseudoplatanus. Flower-buds dissected and seen from above. I, bicarpellary. II, tricarpellary; *pe*, petals. 1, earliest formed stamens; 2, interposed stamens. Magnified.

(*a*) **Terminal flower-leaves.** These arise if the vegetative point which is the embryonal region of the shoot is entirely used up in the formation of leaves. It is easy to understand that this may readily occur in a shoot of limited growth. Many leaves may share in a certain proportion in the vegetative point, or only one may be produced. The process in each case is essentially the same. The former is frequent in the formation of the gynaeceum, and this is a matter of importance for the 'explanation' of the ovary[4]. Acer furnishes an example (Fig. 359). The carpels in Acer form the termination of the flower-bud. Whether there be two or three carpels *the whole area of the vegetative point of the flower is used up by these*, and what holds for two or three leaves is likewise true in other cases for one. In this narrower sense single stamens or carpels are terminal on the flower-axis, and we have such stamens in Callitriche, Casuarina, Najas, and such carpels in Typha and elsewhere.

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[1] Schumann, Neue Untersuchungen über den Blüthenanschluss, Leipzig, 1890, p. 479.

[2] In Urticaceae and elsewhere other relationships have to be considered.

[3] See Part I, p. 41.

[4] See Goebel, Zur Entwicklungsgeschichte des unterständigen Fruchtknotens, in Botanische Zeitung, xliv (1886).

(*b*) **Basipetal succession of flower-leaves.** The general rule for the succession or origin of lateral organs is that they appear in progressive serial succession[1], that is to say the youngest stand next the embryonal region whether this lies next to the apex or elsewhere. It has been already shown[2] that in *organs of limited growth* the apex often takes precedence in the development whilst zones lower down continue to bring forth new formations. This is frequently seen in the flower[3]. The stamens in particular arise frequently in descending progressive series, for example in the Cistineae (Fig. 369), Malvaceae, and others. This is also the case with the hook-like structures upon the outer side of the calyx of Agrimonia. It is also frequent in the case of the ovules. Nowhere do we know what the biological relationship of this order is.

(*e*) DORSIVENTRALITY.

A deviation in the succession of origin of the parts of the flower is found in many dorsiventral flowers[4]—repeated also in many inflorescences—and in particular in those in which the dorsiventrality expresses itself in a conformation of the vegetative point different from the ordinary radial one, which is uniform on all sides before the primordia of the leaf-structures appear, and upon which the primordia of the organs arise upon all sides in progressive series towards the apex. One side of the vegetative point of the flower is furthered—either the side next the chief axis, as in Reseda, or the side farther away from this—there is a symmetric configuration[5].

Reseda. In Reseda the side of the vegetative point that is turned towards the inflorescence-axis is higher than that which is turned away from it, and the development of the sepals and petals corresponds to this construction[6]. The first sepal appears upon the side next the inflorescence-axis, and then in progression anteriorly the subsequent sepaline primordia. The petals and stamens follow suit, and the first stamen is showing before all the petals are formed.

Lentibularieae. This method of development is known also in the Lentibularieae[7]. Before the appearance of the leaf-organs a furthering occurs of one side of the vegetative point, and upon this side in Pinguicula vulgaris the sepals, petals, and stamens first appear before the sepaline primordia are visible on the other side. In Utricularia also the upper part of the corolla arises only *after* the inception of the

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[1] This expression is more comprehensive than that of the 'acropetal' and 'basipetal' origin. See Goebel, Über die Verzweigung dorsiventraler Sprosse, in Arbeiten des botanischen Instituts in Würzburg, ii (1882). De Bary has also used it in connexion with the Fungi.

[2] See p. 330, also Part I, p. 41.

[3] Without, however, our being able to discover teleological connexions as can be done in the case of the foliage-leaves.

[4] The phenomenon is also repeated in many inflorescences. See Goebel, op. cit.

[5] In the case of dorsiventral inflorescences also the dorsiventrality appears in the *conformation of the vegetative point*, and this is a fact of great importance in all attempts to give an explanation.

[6] See Payer, Traité d'organogénie comparée de la fleur, p. 193, pl. xxxix; Goebel, Beiträge zur Morphologie und Physiologie des Blattes, in Botanische Zeitung, xl (1882), p. 388.

[7] See Buchenau, Morphologische Studien an deutschen Lentibularieen, in Botanische Zeitung, xxiii (1865).

stamens which are two in number and are formed upon the favoured side of the axis.

Papilionaceae. A similar symmetrical succession of development is found in the flower of the Papilionaceae[1], only the progression is towards the posterior side, that is to say towards the inflorescence-axis.

There is in these cases only an unequally-sided development by which the lower standing flower-whorls always arise earlier than those which stand higher, yet there may well be exceptions to this behaviour.

That the succession of development of the leaf-organs in these dorsiventral flowers has been derived from that in radial flowers is probable for more than one reason[2]; on the other hand, the method in which the deviation has come about is not at all clear. Payer's investigations show that there are attempts at unequal-sided development even in radial flowers[3].

Cruciferae. The Cruciferae, for example, have two dimerous calyx-whorls, one median and one transverse. In many, for example Cochlearia, the median appears first—its sepals synchronously—in consequence of the radial construction of the flower, and then the transverse. In Cheiranthus, on the other hand, the anterior (outer) leaf of the first whorl arises first, and then two transverse ones, and last the posterior leaf of the first whorl. Such deviations may be connected with, to speak teleologically, the great need for protection of the flower-bud upon the outer side, but more accurate investigation will perhaps show why Cochlearia differs in this relation from Cheiranthus. The difference is not one of habitat but the whole behaviour of the inflorescence to the rest of the plant must be considered.

It is possible that these relationships have given the occasion for the construction of the dorsiventral flower as we find it in Resedaceae and the Papilionaceae. Another possibility is that, as we have already said, these flowers which are dorsiventral from the first have been derived from those which are only dorsiventral after unfolding[4]. Whether now the two kinds of dorsiventral flowers have arisen in different ways or not we may at any rate see that the dorsiventral construction of the flower has set in in *different developmental stages.* In Hyoscyamus, for example, the calyx, corolla, and androecium are laid down as in a radial flower[5], only after this does the extension of the torus begin which brings about the oblique insertion of the

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[1] See Payer, Traité d'organogénie comparée de la fleur, p. 517; Hofmeister, Allgemeine Morphologie der Gewächse, p. 464; Frank, Über die Entwicklung einiger Blüthen, mit besonderer Berücksichtigung der Theorie der Interponiring, in Pringsheim's Jahrbücher, x (1876), p. 205.

[2] See Part I, p. 128.

[3] For example in the development of the calyx of Symphoricarpus. Payer, op. cit., p. 617. According to Payer's figures, Plate cxxviii, Figs. 3, 4, 5, which are opposed to what he says in the text, the serial succession starts from the sepal over against the bract, and then proceeds laterally. Buchenau gives a like account of the involucre of Lagascea. Further, in species of Begonia, for example Begonia xanthina, Hooker (see in Hofmeister, Allgemeine Morphologie der Gewächse, Fig. 87), the staminal primordia appear earlier upon one side of the flower-axis than upon the other, but here the vegetative point of the flower is not uniform all round.

[4] See Part I, p. 128.

[5] Schumann, Neue Untersuchungen über den Blüthenanschluss, Leipzig, 1890, p. 317.

carpels to the median plane of the flower, and the other changes in the flower-construction set in.

Schwendener[1] has conjectured that the oblique position of the flowers in the Solanaceae depends upon relationships of pressure. The flower-shoot, *III*, in Fig. 296, for example, is exposed at the time of the inception of the carpels to the pressure of the leaves marked *Viii* and *Tiii*, because these are inserted at the same height. These behave like *one leaf*, and the plane of symmetry undergoes on account of the pressure a torsion which brings it nearer to the median of this one leaf[2]. The history of development of Atropa showed me nothing in support of Schwendener's hypothesis. The position of the carpels stands indeed in the nearest relationship to the *whole symmetry of the inflorescence*, but is certainly not affected by pressure. Such pressure would at first make itself felt upon the calyx; but it is laid down as in radial flowers[3]. The first sepal (in Fig. 296, *III*, that turned upwards) falls upon the outside and appears then in the widest gap, where therefore the protective need of the flower-bud is the greatest. The factors which condition its appearance in this place we do not know[4]. We can only see that it is of advantage that the protection of the bud begins on the most exposed side. A plane through the middle of this first sepal and the centre of the flower-bud marks the median plane of the carpels. The whole of the median planes of the flowers of an inflorescence fall in this direction if one considers them as vertical. The flowers are intrinsically all dorsiventral, but in the whole of them the dorsiventrality is not clearly seen apart from the oblique position of the carpels. In the construction of the flower in this sympodial inflorescence the *outer side* is differently organized from the inner side[5].

We may say in general that in flowers which are laid down dorsiventrally the succession of origin which deviates from the radial, and the arrangement of the leaf-organs, depends upon an earlier or later setting in of the change of configuration of the vegetative point, but we do not know why a furthering of the outer side or of the inner side begins. One might indeed be inclined to assume[6] that those leaf-structures in the flower which attain the most conspicuous size are most furthered in the time of their appearance. This may well be the case in for example the calyx of the Papilionaceae, as well as in the corolla and the 'disk' in the

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[1] See Schwendener, Mechanische Theorie der Blattstellung, Leipzig, 1878, p. 124.

[2] Otherwise the plane of symmetry of the carpels falls in with that of the bract.

[3] See also Schumann, Neue Untersuchungen über den Blüthenanschluss, Leipzig, 1890, p. 315.

[4] The numerous other cases in which a mechanical influence has been assumed are quite analogous. Fig. 296 shows also that the first sepal does not fall over the median between *Viii* and *Tiii* but is nearer *Tiii* and over the median between this leaf and the flower *I*.

[5] In this the dorsiventral flowers of the Solanaceae conform with those of other plants, but in other plants the outer side is mostly marked by the bract.

[6] As has been stated in the case of the vegetative organs. See pp. 305 and 364.

Resedaceae—the calyx of the Resedaceae is more strongly developed in the mature condition upon the *outer side* than upon the inner side.

We arrive therefore at two conclusions:—

(*a*) the furthered organs are laid down earliest;

(*b*) *after* the inception an unequally strong construction may ensue even within the leaves of one whorl[1].

The anatomical method in flower-morphology. It hardly needs to be pointed out that where there is limited growth of the flower-axis, the distinction between what is axis and what is flower-leaf is much more difficult than in vegetative shoots. We shall recur to this point later, but here I would only comment upon an aid which has been used frequently in the solution of this and all other questions of flower-morphology. The so-called 'anatomical method' is based upon the claim[2] that it can say better than anything else what is an axis and what is a leaf. The axis is quite generally radial, the leaf has a dorsiventrally arranged vascular bundle-system. That this behaviour is as little constant as other marks has long been proved. Dorsiventral shoot-axes have the dorsiventrality abundantly expressed in the arrangement of their vascular bundles, for example the inflorescences of Urtica dioica[3]. The phylloclades of some Asparagineae show this also very strikingly and the anatomical method has consequently declared them to be leaves in opposition to the facts which are as clear as day! It is nothing less than the old idealistic morphology in anatomical dress which asserts that the distribution of the vascular bundles as it occurs in radial vegetative shoots and assimilating leaves must also be found in the flowers. Where the axis stops its growth and its further development this fact will be expressed in its completed anatomical structure, and the formation of the conducting bundles will gradually recede in the leaves which are remaining rudimentary and will finally entirely cease. In such cases the anatomical method is useless. It has the advantage of easy handling and of course its results must be considered. But these can never be regarded alone as critical and as determining interpretations within the flower. They are in their nature essentially of less importance than are those which are obtained by the comparative history of development. If Payer and other phyletic researchers have come to untenable results regarding the formation of the placenta through their investigations by the comparative historical method, these were not due to faults in the method but rather to the omission of one weighty consideration from their survey, namely, that of 'what area of the torus—that is to say of the vegetative point —the carpels occupy at the time of their appearance[4].' Payer's investigations gave

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[1] It is to be noted that the *unilateral* inception of leaf-organs at the vegetative point is not limited to the flower-region. It takes place also in the vegetative shoots, in which, however, it has been much less considered. See, for example, Ganong, Beiträge zur Kenntniss der Morphologie und Biologie der Cacteen, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 52. The comparison of this vegetative shoot, which is laid down dorsiventrally, with the dorsiventral flowers is all the more apt, inasmuch as there can be no doubt that they are both derived from originally radial shoots.

[2] See Van Tieghem, Recherches sur la structure du pistil, in Annales des sciences naturelles, série 5, ix (1868).

[3] See Goebel, Über die Verzweigung dorsiventraler Sprossen, in Arbeiten des botanischen Instituts in Würzburg, ii (1882), p. 430.

[4] Goebel, Zur Entwicklungsgeschichte des unterständigen Fruchtknotens, in Botanische Zeitung, xliv

frequently no ground for a conclusion upon this point, and consequently the distinction between the share of leaf and axis in the construction was not correctly expressed. The history of development when more accurately used leads to results which conform with those which have been obtained in other ways, as will be pointed out more fully when the development of the ovary is considered.

(2) CONCRESCENCE IN PARTS OF THE FLOWER.

Concrescences are frequent in flowers, both of flower-leaf with flower-leaf and with flower-axis. The cases of confluence which were discussed above[1] may be reckoned here, but we shall only speak of the cases in cyclic flowers where all the members are concrescent with one another or with the other members. It only rarely happens that there is an actual concrescence or growing together—the latter, for example, in the anthers of the Compositae. More commonly the concrescence is 'congenital.' What takes place has been already explained[2], and one need only repeat that the concrescence occurs in different degrees. We may regard as the original condition that in which there is no concrescence and the several neighbouring primordia of leaves develop free from one another. A concrescence begins if they are raised upon a common usually annular base. The last stage is that where, for example in the corolla of Cucurbita, the single primordia are no longer separate. It has been a matter of dispute with regard to the concrescence of the leaf-whorls in many cyclic flowers how far the flower-axis shares in the construction. I may therefore here recall that the differentiation of leaf and axis is usually not prominent in the flower; it would therefore be incorrect to apply a scheme derived from the vegetative organs to the interpretation of the flowers and to imagine that axis and leaf must be separated sharply in the flower, and that one must accurately recognize what belongs to the one and what belongs to the other. This will be illustrated below, especially when speaking of the formation of the ovary. Here I may only remark that one can the more speak of the axis sharing in the concrescence of different leaf-whorls with one another the earlier this takes place.

(3) ARRESTS.

A flower may be reduced to a simple sporophyll terminal on the flower-axis[3], and in every large cycle of affinity we find the numerical relationships changed by arrests, especially in the staminal whorl in which there is no lack of transitions from complete construction to abortion. The series which have been constructed regarding flower-formation in the Angiosperms are exclusively reduction-series[4]. Here a few examples will be given of

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(1886). See also the detailed work of my pupil Schaefer, Beiträge zur Entwicklungsgeschichte des Fruchtknotens und der Placenta, in Flora, lxxiii (1890), p. 62.

[1] See p. 538.

[2] See Part I, p. 52.

[3] See Part I, p. 52.

[4] See Part I, p. 60. See in particular Čelakovský, Das Reductionsgesetz der Blüthen, das Dédou-

the more or less probable reductions which can only be regarded as correct *if we can give biological reasons for the reduction*[1]. Hitherto botanists have limited themselves almost exclusively to the purely formal side. If we put on one side the causal standpoint into which it is quite impossible to enter, there remains the *biological*, that is to say, the question of the connexion of the arrests with the function of the flower, and without doubt this is a very complex one. We are concerned with not only the number of the stamens, but also with that of the microspores and the relation of the number of these to that of the ovules in which fertilization is to be effected as well as to the method in which pollination is carried out. We have tried to show when speaking of the Pteridophyta that the number of the archegonia is the smaller the more the fertilization appears to be secured. A similar relationship can certainly be often proved in the flowers of the Spermophyta.

In the anemophilous flowers of Monocotyledones the number of the stamens is specially reduced in those which have by reduction only one ovule in the ovary, for example most Gramineae and Cyperaceae. The case of the Irideae where there are numerous ovules in the ovary, and one staminal whorl is arrested, cannot be brought forward against this connexion for there quite other relationships have to be considered—the whole flower is specialized and adapted preferably to definite insect-visitations, the pollination is also made certain, and the formation of the inner staminal whorl would be superfluous in *view of the whole scheme of the flower*. The same holds for the Orchideae and others. Flowers which are less sharply adapted to special insect-visitors have more stamens than the specialized ones.

Amongst the Dicotyledones a comparison of the flower of Eschscholtzia with that of the Cruciferae may be made in order to illustrate the numerical relationships of the stamens just spoken of. In Eschscholtzia there are numerous stamens; in the Cruciferae there are only six; similar relationships of position obtain in both cases. The Papaveraceae, to which Eschscholtzia belongs, have pollen-flowers. The number of the stamens is therefore *caeteris paribus* easily understandable because the pollen-production will be all the greater the more stamens there are. The flowers of the Cruciferae on the other hand have honey-glands, and as they do not require to furnish pollen to the insect they produce less pollen than Eschscholtzia. This relationship is clear; whether it is phyletic or not we cannot say[2]. We should have ground for such an assumption in regard

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blement und die Obdiplostemonie, in Sitzungsberichte der königlich böhmischen Gesellschaft der Wissenschaften, 1894.

[1] This is a subject which the text-books of flower-morphology say nothing about.

[2] Cruciferae with more than six stamens are known, for example Megacarpaea, and there are some which have less than six. The biological behaviour, especially in the first case, is unknown. Perhaps they are in part pollen-flowers. In the Fumariaceae we can directly prove the reduction of the ovules, and following upon this is the probability of a reduction in the androecium. See Goebel.

to it if we could establish the probability that the forefathers of the Cruciferae had pollen-flowers, and then along with reduction of the staminal whorl passed over to the formation of honey-flowers. Such an assumption will offer no difficulty to those who can see that nectaries simply arise through the prodding of the insects into the flower. These, however, are mere fancies which we leave out of consideration[1].

In the simple formal construction of arrests we must not rely upon reductions, we have rather to seek to prove on the basis of biological relationships the reductions which are assumed in consequence of the morphological evidence. For this at present there are only small data. In general too we have a somewhat safe basis for the assumption of arrest only within families; the more we go beyond these the more insecure becomes the ground for this.

Phenomena of reduction are abundant in the gynaeceum, and this has been already pointed out, and it has been shown[2] that the object, namely the diminution in the number of the ovules, is partly brought about by the diminution in the number of carpels, partly by that of the ovules themselves; in many cases both phenomena appear together.

B. INDIVIDUAL ORGANS OF THE FLOWER.

In what follows the several organs of the flower will be shortly considered, all details which can be read of in systematic works being omitted.

(1) THE FLOWER-ENVELOPES.

The conformation and biological significance of the flower-envelope are supposed to be familiar. So far as we know the biological significance of the envelope is of a double character:—

(*a*) it protects the flower in the bud-stage[3];

(*b*) it secures pollination.

The strengthening which the flower-envelope frequently receives through an epicalyx, envelope of hypsophylls, and so forth, will be left untouched upon. A few points only require notice:—

(*a*) MORPHOLOGICAL SIGNIFICANCE OF THE FLOWER-ENVELOPES.

The question of the origin of the parts of the flower-envelope has exercised botanists from early times. When we proceed from the flowers

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Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 318.

[1] The case would be different if it could be shown that such glands in any one case developed more in consequence of mechanical stimulus than without the stimulus, but such a case is at present unknown.

[2] Part I, p. 58.

[3] See Račiborski, Die Schutzvorrichtungen der Blüthenknospen, in Flora, lxxxi (Ergänzungsband zum Jahrgang 1895).

of the Pteridophyta and many Gymnospermae which have no special flower-envelope, there are evidently two possibilities for the origin of the flower-envelope of the Angiospermae:—

(1) Either it has arisen from the hypsophylls in the vicinity of the flower;

(2) It has been formed either entirely or partially by the transformation of the sporophylls.

The latter view is supported by A. P. de Candolle, especially for the corolla [1], and many later authors have followed [2] him mostly without quoting him. This explanation appears to me to be well founded in a number of cases, as is also the view that the outer portion of the flower-envelope, the calyx, has proceeded from hypsophylls. The conclusion is arrived at, as de Candolle showed, from the *position* of both structures, not from the colour; the calyx can, as is known, be petaloid. One must never forget, however, that here as elsewhere in the plant kingdom the same result may come about in different ways.

It must suffice to put forward as examples some cases from one family—that of the Ranunculaceae [3]—which on account of their instructive relationships have been frequently used for illustration of the question under discussion:—

Anemoneae. As a starting-point we may consider a flower which has a simple petaloid flower-envelope and numerous stamens and carpels. Such a flower occurs, for example, in the Anemoneae. In them the number of the leaves which form the *flag-apparatus* is not constant, because frequently the outermost stamens are transformed into petaloid leaves [4]. The simple petaloid envelope of the Anemoneae we consider to be the result of the transformation of stamens, but within the same group other organs may be formed out of the stamens. The outer stamens are transformed into nectaries in Anemone Pulsatilla where there are all transitions between the normally constructed stamens and the nectaries at the base of the androecium, which nectaries still have the conformation of the stamens: normal stamens with four pollen-sacs [5] whose filament is shortened; stamens with only three or two pollen-sacs;

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[1] A. P. de Candolle, Théorie élémentaire de la botanique, Paris, Ed. 1, 1823, Ed. 3, 1844. See also Considérations générales sur les fleurs doubles et en particulier sur celles de la famille des Renonculacées, in Mémoires de Physique et de Chimie de la Société d'Arcueil, iii (1817), p. 394. 'As I have shown in my "Théorie élémentaire" the petals are merely the outer stamens which in the natural state of things are transformed into plates or into horns.'

[2] In recent times Čelakovský, Über den phylogenetischen Entwicklungsgang der Blüte und über den Ursprung der Blumenkrone, I und II, in Sitzungsberichte der königlich böhmischen Gesellschaft der Wissenschaften, 1896, 1900, has in an extreme manner supported this. He derives all perianth-leaves as well as the foliage-leaves from transformed sporophylls. How plants with non-assimilating sporophylls can exist is difficult to understand.

[3] The following account conforms in all essential points with that which I gave in 1886. See Goebel, Beiträge zur Kenntniss gefüllter Blüthen, in Pringsheim's Jahrbücher, xvii (1886). Subsequently other authors have also expressed the same view.

[4] See what is said about Anemone Hepatica, Part I, p. 177.

[5] See also Familler, Biogenetische Untersuchungen über verkümmerte oder umgebildete Sexualorgane, in Flora, lxxxii (1896), p. 149.

and as a final stage stamens in which the pollen-sacs are entirely suppressed. If we imagine that these nectariferous staminodes have a pit upon their upper surface we are on the road to forms such as are found in Trollius, Helleborus, and elsewhere, and finally to the nectariferous petals of Ranunculus. But in some forms of the Anemoneae another series of transitions runs alongside of this one. In the Pulsatilleae, Anemone nemorosa, and others, the flower-bud is surrounded by three foliage-leaves which elsewhere pass over into hypsophylls, experiencing at the same time a reduction of their segmentation [1]. In Anemone Hepatica the internode between these entirely calyx-like leaves and the flower is not elongated as it is in the other species of Anemone mentioned, and the *involucre* has become actually a calyx. This calyx may now itself become petaloid, but it shows through many interesting transitions its relationship with hypsophylls.

Trollius europaeus. The same is the case in Trollius europaeus. Its flower is surrounded by a number of yellow-coloured leaves which are mostly unsegmented, and are distinguished in that way from preceding hypsophylls. An examination of a large number of flowers brings to light transition-forms which show that the outer flower-envelope consists of only specially constructed hypsophylls, the whole having come to pass in the same way as in Astrantia [2]. These transition-forms [3] have still at their apex indications of the segmentation of the foliage-leaves (Fig. 360), as well as a tinge of green colour whilst the greater part of the leaf has become yellow. We shall consider them as hypsophylls which have become an element of the flower and serve thus both as a flag-apparatus and as a protection to the bud. Following them we have the nectaries consisting of transformed stamens which correspond to the corolla of Ranunculus, then we have the stamens, and then the carpels.

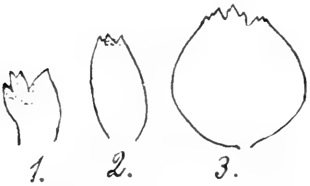

FIG. 360. Trollius europaeus. Three leaves showing transition from hypsophyll to outer flower-envelope. They are yellow, with the exception of the dotted area which contains chlorophyll.

A flower-axis then which possessed originally sporophylls can attain to richer endowment by:—

(1) The hypsophylls in the vicinity of the flower entering into its service, forming themselves into a *calyx*, as in Anemone Hepatica, and at the same time becoming a flag-apparatus.

(2) The outermost stamens either forming only a flag-apparatus, as in many Clematideae, for example Atragene alpina, or becoming nectaries, as in Anemone Pulsatilla, or becoming structures which serve both as a flag-apparatus and as

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[1] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 288, Fig. 61, of Anemone stellata.

[2] See p. 395.

[3] These are also found in the terminal flower of Gentiana asclepiadea. We can there follow how the two uppermost foliage-leaves are, as it were, drawn into the formation of the calyx. Not infrequently one of them is only partially united with the calyx-tube, and shows then a widened sheath-like basal portion, whilst the apex of the calyx-tube corresponds to the lamina of a foliage-leaf. There are to be found, if one examines a large number of plants, all transition-stages from flowers which are sharply shut off from the vegetative shoot to those which gradually pass into it.

nectaries, as in Ranunculus and also in Trollius, where, however, the relatively small nectaries in spite of their orange colour can scarcely be considered as a flag-apparatus.

That in many other families, especially the Nymphaeaceae, Mesembryanthemum, the Zingiberaceae, the Candollean view fits well; and without forcing of the morphological facts appears to me incontestable. In many flowers indeed the stamens clearly act as a flag-apparatus with or without loss of function, and our knowledge of double flowers tells us that the stamens are transformed specially easily into petals. That this transformation can take place in foliage-leaves also follows, not only from what has been said about Trollius but also from what was said before about Nidularium[1].

FACTORS INFLUENCING COLOUR AND SIZE. The colour of the flag-apparatus of the flower, by which it differs so markedly from the vegetative part, is purely an arrangement in relation to pollination. We find male and female flowers which have a lively red colour in many Coniferae, for example the spruce, although here the pollination takes place by the wind, and in Musci frequently the same phenomenon is observed in the sexual organs. It is therefore very probable that the feature of colour which so often appears when the propagative organs are being brought forth has some connexion with definite metabolic processes, although up till now we cannot recognize what these are. It has been shown[2] that the capacity for respiration of the flower is greater than that of the green leaf-organs, whilst its transpiration is less, but we do not know yet how this functional behaviour affects the whole economy of the flower, nor what is the reason from the purely physiological standpoint why in many flowers, for example those of the Urticaceae, corolline organs are entirely wanting.

That the size of the corolla, and in many cases also the intensity of its colouring[3], is dependent upon external factors, especially upon the intensity of light[4], has been already pointed out, and it was shown that this is only an individual illustration of the fact that the different developmental stages of the plant are bound up with different external conditions, and that other factors besides light have an influence upon the formation of flower[5]. Here we shall only further say that the 'unessentially zygomorphous' flowers

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[1] See Part I, p. 10.

[2] Curtel, Recherches physiologiques sur la fleur, in Annales des sciences naturelles, sér. 8, vi (1897).

[3] The dependence of the intensity of the colouration upon light is not equally expressed in all plants. Askenasy, Über den Einfluss des Lichtes auf die Farbe der Blüthen, in Botanische Zeitung, xxxiv (1876), has moreover shown that flowers of Antirrhinum majus and Digitalis purpurea, which had developed on the shoots of plants deprived of their leaves remained white, and that therefore the disturbance of nutrition affects the formation of colour.

[4] See Part I, p. 243.

[5] G. Klebs, Einige Ergebnisse der Fortpflanzungsphysiologie, in Berichte der deutschen botanischen Gesellschaft, xvii (Generalversammlungs-Heft 1900), p. 201, has confirmed this. He found, amongst other things, that the size of the corolla of Myosotis palustris was changed not only by feeble light but also by too moist air or by too strong nutrition.

which we formerly described[1] as they are found on the margin of many inflorescences, that is to say those with unilaterally—outwardly—furthered corollas, owe their conformation perhaps to the fact that the outer part of the corolla has been the more intensely illuminated side in a long series of generations, and therefore we have to deal most probably with an inherited influence. It is at any rate of interest to note that we can produce quite similar phenomena experimentally[2]. In Fig. 361 is shown an inflorescence of Helianthus annuus. On it the ray-florets are developed unequally in consequence of unequally strong illumination. If now we substitute for the capitulum figured in Fig. 361, II, a single marginal flower of Scabiosa we obtain fundamentally quite similar configuration. Whether the analogy here assumed is actual or only apparent can only be shown by experimental investigation of the plants which from this standpoint possess 'plastic' flowers.

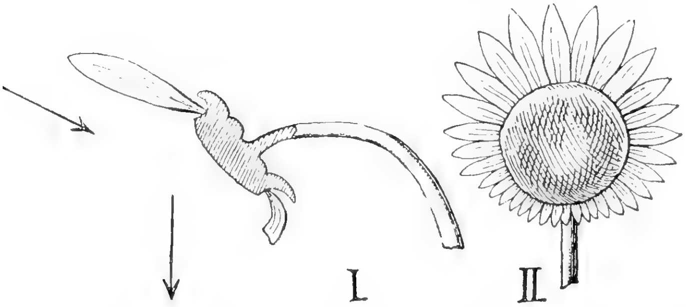

FIG. 361. Helianthus annuus. Capitulum grown in feeble unilateral illumination. The ray-florets on the feebly illuminated side are smaller than on the side under stronger illumination. I, capitulum in vertical section. II, the same seen from above. After N. J. C. Müller.

(*b*) DIFFERENCES IN CONFIGURATION DUE TO DIFFERENCES IN DISTRIBUTION OF GROWTH.

An account of the numberless differences in configuration of the flower-envelope could only be given along with a discussion of their function and will not be attempted, but there is one point of general importance which may be briefly referred to, namely, that marked changes in form may appear in the mature condition through relatively small differences in the distribution of growth. This is a generally effective cause. I have endeavoured to explain it in an example of the grass-inflorescence[3], and

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[1] Part I, p. 130.

[2] See also N. J. C. Müller, Handbuch der Botanik, i, p. 269. Curtel, Recherches physiologiques sur la fleur, in Annales des sciences naturelles, gives us nothing essentially new. I may here recall what was said about the unilateral construction of Hepaticae and Musci; see p. 77, note 4. In the prophylls of some Dicotyledones I have recently found relationships of construction.

[3] Goebel, Beiträge zur Entwicklungsgeschichte einiger Inflorescenzen, in Pringsheim's Jahrbücher, xiv (1884).

Sachs[1] has subsequently in his instructive manner illustrated it in the development of the foliage-leaves.

With regard to the corolla, we may start from the primordium of a radial pentamerous corolla of concrescent primordia as it occurs in many dicotylous flowers. The concrescence depends, as we have seen, upon a displacement of the growth. If each of the five leaf-primordia were to grow into a free part, then we should have a choripetalous corolla. But the free parts grow only insignificantly, the zone of insertion of the five primordia grows strongly, and there arises the tube with the five teeth with which we started. This develops further into a radial corolla such as we find in Campanula, or into the tubular flower of some of the Compositae, if the subsequent growth is chiefly upon the cup-like or tube-like basal portion, whether this grows uniformly throughout or only retains a zone of embryonal tissue, which is then usually at the base. If, however, the zone below the teeth grows strongly, then according to the course of this zone of growth other relationships of configuration appear. Let us suppose that the growing zone is below 1 and 2 in Fig. 362 in the position of the dotted line there. This runs left from 1 and right from 2 up to the indentations which separate the two corolla-lobes, but it runs between 1 and 2 under the separating depression. If now such a zone of growth occurred also below the lobes 3, 4, 5, a two-lipped corolla must arise if the lobes 1 and 2 were early checked in their growth—the conformation which the marginal flowers of the tubulifloral Compositae show; if the zone of growth touch only at one position upon the separating depression, then we obtain the 'unilaterally split[2]' corolla, which is subsequently spread out flat, of the liguliforal Compositae.

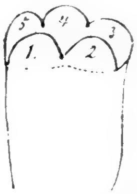

FIG. 362. Scheme of change in configuration in a sympetalous corolla in consequence of different distribution of growth.

(2) THE ANDROECIUM.

The conformation of the microsporophyll is much more uniform amongst the Angiospermae than amongst the Gymnospermae. In the Gymnospermae the number of microsporangia is somewhat variable, even within one and the same flower, for example in Juniperus, but in the Angiospermae the number four predominates.

The pollen-sacs in the majority of cases run parallel with the length of the staminal leaf, so that they correspond to the four angles of the anther. By the growth of the *connective* the pollen-sacs may be pushed towards the inner side (*introrse*) or to the outer side (*extrorse*) of the flower—

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[1] See Sachs, Lectures on the Physiology of Plants, English edition by Marshall Ward, Oxford, 1887, p. 506.

[2] That this expression is not literally correct is clear from the description that is given.

changes which have an intimate relationship to the manner in which pollination is effected. There are, however, cases in which the anthers have two pollen-sacs above and two below, as in the Laurineae, but I do not know whether this is the result of a displacement taking place in the course of the development. Where there are deviations from the number four in the microsporangia we can refer them back to this type by the following assumptions:—

(*a*) Division of the anther.
(*b*) Arrest or suppression of pollen-sacs.
(*c*) Confluence of pollen-sacs.
(*d*) Division of pollen-sacs by sterile plates of tissue.

The following are illustrations of these:—

(*a*) **Division of the anther.** This scarcely requires an explanation. It is found in Betula, Althaea and other Malvaceae, and in Salvia along with sterilization and transformation of one anther-lobe.

(*b*) **Arrest or suppression of the pollen-sacs.** In the case of the Asclepiadeae[1] only the pair of anterior sporangia are developed. The arrest of the posterior pollen-sacs is evidently connected with the peculiar construction of the stamens. Arrest also occurs in the Marantaceae, where one-half of the stamen has become petaloid.

(*c*) **Confluence of pollen-sacs.** We have seen confluence in Juniperus amongst the Gymnospermae, and its occurrence in the Angiospermae is less striking because the microsporangia are less independent than they are in the Gymnospermae. This confluence may take place by the subsequent breaking down of sterile tissue, or by the development of fertile tissue in places where otherwise sterile tissue should be.

Which process takes place in the Orchideae where confluence occurs, for instance in Stanhopea, Gongora, Trichopilia, I do not know, but it seems to me probable that it is the second one. This can only be determined by an examination of the development. It is probable that the body possessing two annular pollen-chambers in the middle of the flower of Cyclanthera has arisen by simplification of an androecium which consisted of five stamens, each having two horizontal chambers between which sterile tissue was no longer formed[1].

(*d*) **Division of pollen-sacs by plates of sterile tissue.** This process is a more frequent one and will be referred to again when the formation of sporangia is discussed

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[1] See Engler, Beiträge zur Kenntniss der Antherenbildung der Metaspermen, in Pringsheim's Jahrbücher, x (1876). With regard to the Cucurbitaceae see the description in the text on p. 539. The convolution of the pollen-sacs makes possible an abundant formation of pollen, notwithstanding the halving of the anther. The convolution is greatest where the need of pollen is greatest, that is to say, where there are many ovules.

[2] Whether one should consider these anthers as *appendicular* and arising out of concrescent leaves, or as *axial*, seems to me little more than a matter of words. The question only is how they have been derived. It is clear that in their inception there can be no separation into axis and leaf.

It is found along with the 'normal' formation of anthers in different families, for example, amongst the Onagrarieae, in Clarkia where there are four to five chambers, in Gaura biennis where there are six chambers, whilst in Epilobium and Oenothera and others there is only a single chamber. The occurrence of chambering in different cycles of affinity appears to me important, because here a derived, not an original, character lies before us, and its biological significance corresponds evidently to that of the 'trabeculae' in the sporangia of Isoetes[1]—by the formation of these sterile plates of tissue the nourishment of the sporogenous cell-complex is facilitated. We find this construction therefore, as might be expected, especially in massive broad and long anthers, for example in Rhizophora (Fig. 363).

TRANSFORMED STAMENS. That the stamens of many flowers experience a transformation along with a change in function will be evident from what has been said regarding the Ranunculaceae[2], with which many others might be associated. In many cases the function of the transformed or deformed stamen is not known, as for example in Boronia and Cassia. At any rate there is between transformed stamens and stamens which are deformed[3] in the course of their normal development no sharp limit.

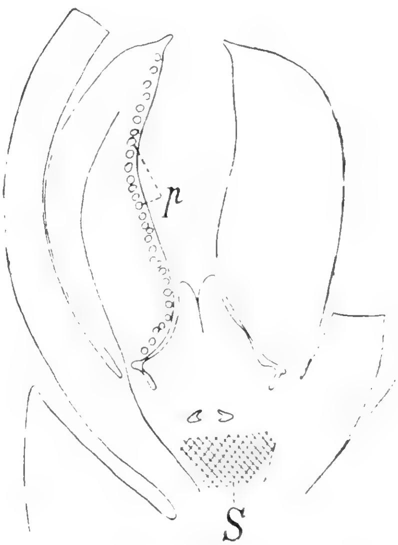

FIG. 363. Rhizophora mucronata. Flower in longitudinal section. Numerous spherical microsporangia, *p*, in the anther; *s*, spongy tissue under the ovary into which the growing seed penetrates.

(3) THE GYNAECEUM.

The enclosure of the megasporangium within a chamber—the ovary—is a characteristic feature of Angiospermae. The manner in which this comes about has given rise to much discussion. The differences of interpretation are a consequence partly of the peculiarities in the development of this organ, which have not been always clearly appreciated, and to which reference will be made presently, but they are also in great part purely differences in the use of words. The essential points in dispute are to what extent the carpel (megasporophyll) and the flower-axis (torus) share respectively in the construction of the gynaeceum, and in particular what is the correct interpretation of the placenta. Comparative morphology, starting from the behaviour of the Cycadaceae, where the foliar origin of

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[1] See p. 604.

[2] See p. 549.

[3] See Familler, Biogenetische Untersuchungen über verkümmerte oder umgebildete Sexualorgane, in Flora, lxxxii (1896).

the ovules is evident, as well as from other cases, and particularly from conditions of phyllody, endeavoured to prove that the placenta and therefore the ovules were everywhere the products of the carpels[1], and to maintain this it was necessary to assume concrescence and unions which were altogether hypothetical. The history of development appeared to lead to quite other results. Payer, for example, believed that the placenta should be interpreted always as an axial organ[2]. There were no less differences in the views upon the nature of the inferior ovary and other questions.

An attempt has been made above to show that the flowers are indeed derived from vegetative shoots, but that in consequence of their whole construction a number of deviations from the behaviour of purely vegetative shoots show themselves. It would be, therefore, incorrect to endeavour to find the scheme of segmentation of the vegetative shoots without modification in all the relationships of configuration of the flower, and to consider the flower—at least in idea—as being based upon this scheme. Every explanation must, in the first instance, closely fit the individual facts. We have here, as in other cases, to construct a picture after comparison of all the observed phenomena *as they actually occur*, or, to speak more accurately, to arrange the manifold phenomena in series, but we shall gain little if we still read into the terminal member of a series its beginning stages. We shall do better if we admit that nature steers straight forward to its end, and in consequence takes short cuts, the evolution of which we can to a certain extent follow by comparison. We may recall the instructive case of the microsporangia of Juniperus amongst the Gymnospermae, which, originally clearly leaf-borne, finally become axis-borne by reduction of the sporophylls at the end of the flower. There is, indeed, still a remnant of the sporophylls existing, but things would be little changed were it too to disappear and the sporangium were to spring directly from the flower-axis. The interesting point in this is not the fact that the sporangium, which arises in the ordinary case on a sporophyll, has here at last taken up a position on the flower-axis, but the tracing of the path by which this axial position has been acquired. Hitherto morphologists have considered leaf-borne and axis-borne organs as having a different 'morphological value,' and have therefore endeavoured to avoid tracing to the same place of origin organs which in their other peculiarities appear as evidently similar. To me the place of origin is more or less a subordinate point, as I have several times said—everything else can change, so also can this. What we should endeavour to find out is the method and manner of *how* the change has taken place, and—what is a much more difficult but also

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[1] See especially Čelakovský, Vergleichende Darstellung der Placenten in den Fruchtknoten der Phanerogamen, in Abhandlungen der königlich böhmischen Gesellschaft der Wissenschaften, Folge 6, viii (1876).

[2] Payer, Traité d'organogénie comparée de la fleur, Paris, 1857, p. 728.

a much more stimulating question—the *conditions* under which it has been completed. In Juniperus, as we have seen, we had to deal with a shortening in the development. Such shortenings are found in predominant degree in the construction of the gynaeceum of the Angiospermae. Whilst we may in regard to it start from cases where the phenomena as we know them of the vegetative shoot and the flower of the Gymnospermae are still perceptible, the carpels are sharply marked off from the axis and produce the ovules either on their concrescent margins or on their surface; at the end of the series we shall find cases in which the differentiation not only of the carpels from the flower-axis, but also of the ovules from the carpels, is entirely suppressed. Such a case will be mentioned when speaking of the ovules in Balanophora. Should we endeavour to read into them our scheme? Are we to expect nature to adjust itself to our abstractions, or is it not rather the right way to adapt our opinions to its innumerable changes?

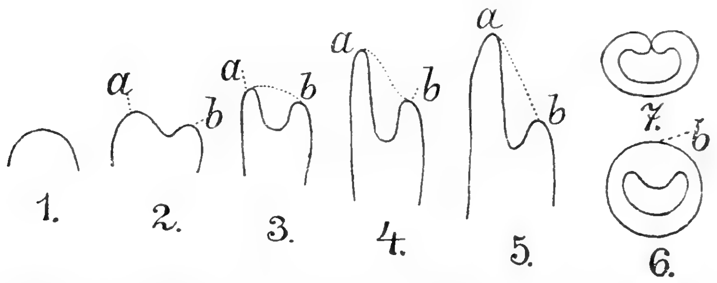

FIG. 364. Scheme of the development of the ovary in many Angiospermae with formation of the sole. 1-5 in longitudinal section. 6-7 in transverse section. *a*, apex of the carpel; *b*, the sole.

The shortenings which we can recognize in the formation of the ovary are specially the following:—

(*a*) The differentiation of axis and leaf is at different stages only slightly marked, because the area of the vegetative point of the flower is often entirely used up by the carpels.

(*b*) Concrescent parts appear from the beginning in combination with one another, instead of subsequently uniting.

(*c*) This is not only true of the combination of many carpels with one another, but also for each single carpel itself. The chamber which a single carpel has to build is relatively seldom formed by the union of originally free margins; much more frequent is it that the carpel develops like a peltate leaf, only without a stalk; that is to say, there appears upon the upper side of the carpel a depression very like what is found in the formation of a tubular leaf of a Sarracenia, and then this deepens. One part corresponding to the apex of the carpel (Fig. 364 *a*) grows most strongly; it forms the style where that exists, and the stigma. The other may be called the *sole* of the carpel. It is continued upwards on the margin of the carpels, and is so placed that the margins have not separated here from one another. At this point, especially where their number is reduced, the ovules are by preference formed—a phenomenon which may be connected with the fact that the most protected place to be found is in this basal pit. If only one ovule is found here, it takes up a median position, whilst higher up the margins of the carpel are the positions of origin[1].

The gynaeceum forms originally the terminal structure of the flower. Its position is more or less early changed in perigynous and particularly in epigynous flowers. The history of development and comparison show us how this process comes about, and that there is no essential difference between the structure of the gynaeceum in hypogynous and epigynous flowers. Transition-forms between these are also known. It will, however, be more instructive to deal with these two kinds of flower separately.

Terminology. The expressions *monomerous*, *dimerous*, *polymerous*, referring to the number of the carpels, explain themselves. By *apocarpous* we designate a gynaeceum in which the several carpels are not concrescent with one another, and by *syncarpous* one in which two or more carpels are united to form one ovary. I think it is useful to add the expression *paracarpous* to indicate ovaries whose carpels are joined together by the margins only — their position corresponding to that of the leaves in valvate aestivation — as in Dionaea and Primula; the term syncarpous would then be retained for gynaecea in which the carpels are united by their outer surfaces.

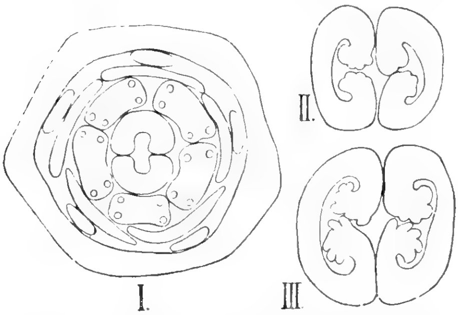

FIG. 365. Erythraea pulchella. I, flower-bud in transverse section. The two carpels of the gynaeceum in the middle touch by their edges, but ovules are not yet formed. II and III, older gynaecea in transverse section. The carpels have curved inwards more conspicuously and have produced ovules on their *under* surface. Magnified.

OVULES ON THE UNDER-SURFACE OF CARPELS. The ovules may arise at different positions upon the carpels, chiefly on their margins, which are often greatly swollen, but they also occur upon the upper-surface, as in Butomus and Cabomba, and also upon the under-surface. Their occurrence upon the under-surface is really not a rare phenomenon, and yet Čelakovský has recently expressly denied it, and therefore I must say something about it. There are syncarpous ovaries in which the margins of the carpel are strongly bent inwards, but are only united over a relatively small surface[2], for example in Erythraea, where the ovary is composed of two carpels

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[1] See Ophioglossum, p. 481.

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 432. Chauveaud, Sur l'insertion dorsale des ovules chez les Angiospermes, in Comptes Rendus de l'Académie des Sciences de Paris, cxiv (1892), p. 142, subsequently came to the same result for the Asclepiadeae and Apocynaceae. See also A. Braun, Die Frage nach der Gymnospermie der Cycadeen erläutert durch die Stellung dieser Familie im Stufengang des Gewächsreichs, in Monatsberichte der Berliner Akademie aus dem Jahre 1875, p. 352.

which become concrescent at a relatively late period. Their inturned margins bear the ovules upon the under-surface, and upon the margin (Fig. 365, II and III). It is evident in the figure that the incurving of the margins of the carpel increases in course of the development, and analogous cases are found elsewhere. With regard to the question which position of the ovules—whether marginal or surface—is to be considered the primitive one, I can only refer to what has been said in the case of the sporophylls of the Filicineae and Gymnospermae. These are questions which at the present time we cannot expect to solve with certainty.

(*a*) THE SUPERIOR OVARY.

1. The Apocarpous Gynaeceum.

The simplest case is that of an ovary formed from a single carpel which, originally open, grows together later at the margins, and bears the ovule on the concrescent margin.

Papilionaceae. We have this in the Papilionaceae. In them the single carpel arises in the form of a horse-shoe shaped primordium investing one side of the flower-axis before the whole of the stamens are laid down, and gradually the primordium encloses the whole apex of the axis in the same way as does the primordium of the leaf of a grass. The growth is always furthered upon the side where originally there was the most prominent part of the primordium. At a later stage[1] the carpel appears in a form which Payer aptly compares with a sack slit upon one side: the slit is formed by the margins which have approached one another, but are not yet concrescent. The ovules sprout from these leaf-margins and form then two rows opposite the middle line of the carpel; and as the edges later become completely united, the pod of the Papilionaceae is produced, which primarily is unilocular, and only in a few species is divided by growths from the inside of the carpel throughout its length in Astragalus, or at right angles to its axis in Cassia Fistula—a phenomenon which is not uncommon in other ovaries.

Numerous monomerous ovaries are found in many Rosaceae and Ranunculaceae.

Rosaceae. Amongst the Rosaceae, of which the tribe Dryadeae will be specially kept in view, the flowers are perigynous, that is to say, sepals, petals, and stamens stand upon a cup-like zone of the flower-axis, which invests the terminal conical portion of the same axis which bears the carpels. The carpels arise from this conical portion of the flower-axis in numbers, and the first of them appears, for example in species of Rubus, always before the stamens are all laid down upon the cup-like zone.

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[1] Vicia Faba was used as a subject of investigation.

A single carpel of Geum[1] or of Rosa has at first the form of a hemispherical papilla, which becomes flattened in its further growth, and takes on the form of an ordinary leaf-primordium. The surface then becomes concave, the margins approach one another, a considerable elongation takes place, and the margins close together as in the cases already described[2]. But at the same time the basal part of the leaf—the sole—is raised upwards[3]. With this we observe here, as in other cases, a reduction in the number of the ovules: the Spiraeeae have still numerous margin-borne ovules; in Rosa there are two ovules, which spring immediately above the lower sack-like portion of the carpel; in Geum one of the two ovules regularly aborts very early, or its formation may be entirely suppressed, and then the one that is left assumes a nearly median position, and stands then immediately above the lower sack-like portion of the ovary, which develops *pari passu* with its further development.

Ranunculaceae. A similar process—reduction of the ovules to one and its adoption of a median position—may be observed in the Ranunculaceae. The carpels of Ranunculus and Myosurus are spirally placed upon the conical vegetative point of the flower. Each produces one ovule. The carpel is concave upon its upper surface as it is in Rosa (Fig. 364, 2), then it becomes cap-like, and the originally free margins approach one another and subsequently coalesce. Immediately below the position where the concrescence begins the ovule arises, in Ranunculus apparently in the axil of the carpel[4], but really, as the case of Anemone specially shows, it arises upon the surface of the carpel, from indeed its sole, immediately below the middle of the split limited by the two concrescent carpel-margins. If the ovule is not clearly limited from the sole of the carpel it appears in longitudinal section as the direct prolongation of this, and therefore gives the impression of being axillary, and was formerly partly so described. Other Ranunculaceae, like Clematis calycina[5], possess besides this median ovule two others upon each carpel-margin—a transition to the behaviour of Helleborus, where, as in the Papilionaceae and Spiraeeae, there are numerous marginal ovules in each carpel. The cap-like hollowing out or formation of the sole of the carpel follows exactly the same course as that in the construction of the horned petals of Delphinium[6], where a concave excavation of the upper side takes place along with the appearance of a transverse cushion at the base of the petal, quite as in the formation of the tubes of Utricularia or of the petals transformed to nectaries of Helleborus.

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[1] See Payer, Traité d'organogénie comparée de la fleur, Paris, 1857, p. 502, pl. c; also Warming, De l'ovule, in Annales des sciences naturelles, sér. 6, v (1878), p. 181.

[2] See also Payer, op. cit., pl. c, Fig. 15.

[3] See the definition upon p. 557.

[4] As seen in longitudinal section.

[5] See Payer, op. cit., p. 253, pl. lviii, Figs. 18 and 19.

[6] See Payer, op. cit., pl. lv, Figs. 20–27.

More correctly than in the Ranunculaceae we can speak in some other apocarpous gynaecea of ovules which apparently spring from the flower-axis and are axillary to the carpel[1]. Fig. 366 furnishes us with an instructive example. Both in Ailanthus and in Coriaria five carpels are laid down beneath the broad flattened vegetative point.

Ailanthus. The carpels of Ailanthus show the formation of a cap as do those of Ranunculus (Fig. 366, 2). At *s* we have the carpellary sole, above this a broad quadrangular split which is closed subsequently by the concrescence of its edges (Fig. 366, 3). That the split, as in the Papilionaceae, is not prolonged to the point of the carpels does not depend upon the fact that a process analogous with the formation of a sole takes place, but upon the strong development of the surface underneath the carpellary apex. The carpel sits here upon the flower-axis with a broad base, as in Ranunculus, and consequently in longitudinal section it has the appearance as if the carpellary sole (*s* in Fig. 366, 3) is itself a sprout from the flower-axis, but the process is, as accurate tracing of the history of development shows[2], quite like that in Ranunculus, only the separation between carpel and vegetative point of the flower-axis is less sharp.

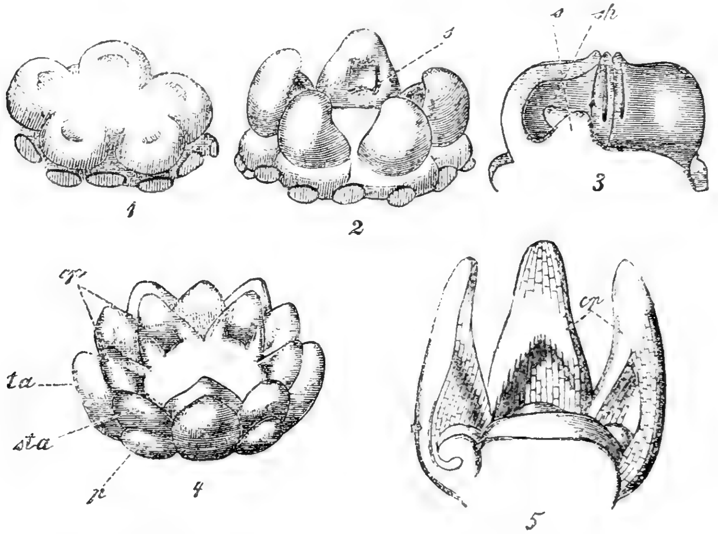

FIG. 366. 1–3, Ailanthus glandulosa: development of ovary; *s*, sole of the carpel; *sk*, ovule. 4–5, Coriaria myrtifolia; *ta*, sepal; *p*, petal; *sta*, stamen; *cp*, carpel; the ovules arise as in Ailanthus in front of the middle of the carpel, but no sole is perceptible.

Coriaria. In Coriaria, on the other hand, this process proceeds still further. The carpellary sole is not differentiated in longitudinal section

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[1] That Payer's view is also here untenable I have already shown. See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 432.

[2] See Schaefer, Beitrag zur Entwicklungsgeschichte des Fruchtknotens und der Placenten, in Flora, lxxiii (1890), p. 69.

from the vegetative point of the flower, yet the investigation of the history of development would doubtless show here also that it arises as a portion of the carpel in the same way as in Ailanthus, but it grows up together with the vegetative point of the flower so that a separation of the two does not appear. We can of course imagine a purely ideal limit running up between them, as is shown in Fig. 366, 5, by shading of the carpel to the left[1]. The origin of the ovule is here the same as in the cases mentioned above. The same origination is valid in cases where only one carpel exists and in its origin uses up the substance at the vegetative point at the apex. This is the case in Gramineae where, however, the ovule has been considered, though incorrectly, as springing out of the vegetative point of the flower; the formation of the carpel and the fact that the ovule is displaced later upon the lateral wall of the ovary both point to its belonging to the carpel in this family.

2. The Syncarpous Gynaeceum.

In different families we find not only forms with apocarpous ovaries, but also those in which the ovaries are syncarpous, and there are transitions between them. We must first of all distinguish two categories of the development of the syncarpous ovary:—

(*a*) That where the apex of the flower-axis does not share in the development;

(*b*) that in which the apex of the flower-axis does share.

The two categories are not sharply separable, as we see in those ovaries where the lower part belongs to the first category, the upper to the second category. In the following a few examples only will be given to illustrate some of the great variations in the processes concerned here.

According to the area of the torus which is occupied by the carpels the placentation is different:—

1. If the carpels in their origin from the torus use it all up amongst them we obtain a bilocular or plurilocular ovary which bears the placentas upon the septa.

2. If a middle zone of torus is left over which remains behind in growth there arises a unilocular ovary with parietal placentation.

We shall speak of the first case to begin with because the latter one connects better with cases where the axis shares in the formation of the ovary.

(1) THE SYNCARPOUS SUPERIOR OVARY WITH SEPTAL PLACENTATION.

(*a*) *The Flower-axis does not share in the Formation.*

Acer. We may start from a case like that of Acer which has been already mentioned and figured[2]. The carpels use up entirely the vegetative

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[1] Payer's figures tell us nothing on this point.

[2] See p. 541.

point of the flower, and upon the upper side of each arises the depression already spoken of. Thus from the first there is a bilocular ovary whose septum is produced by the non-separation of the two carpels at their base, or rather by their common growth together upwards. This behaviour can be seen, *mutatis mutandis*, in other plants such as the Boragineae and Labiatae. In each chamber two ovules only arise.

Solanaceae. Scrophularineae. The process is exactly the same where we have in each loculus a many-ovuled placenta developed, as in Solanaceae and Scrophularineae[1]. The ovary in its upper part is unilocular with two *parietal* placentas, and the process of development is quite the same as that in Acer[2]; the carpels use up entirely the torus, and form to a certain extent a double sole, the septal wall. The margin of the cup of the ovary shows an increased growth at the points corresponding to the apices of the carpels, and the lateral parts raise themselves somewhat at the position of concrescence, and there form the parietal part of the placenta.

Beyond this the question of how far the flower-axis is drawn into the formation of the ovary is of quite subordinate importance[3], yet there are some examples of septal placentation in which the axis shares which deserve notice.

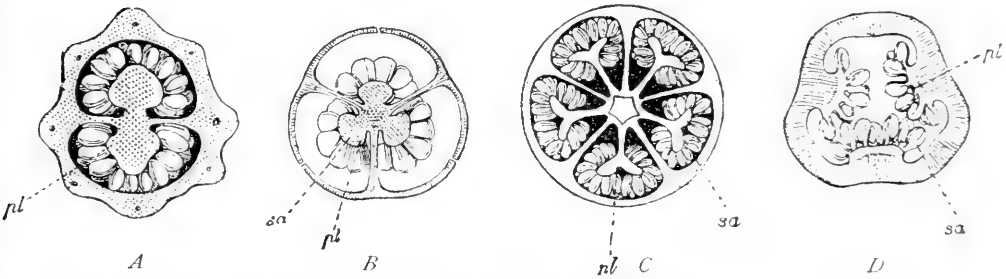

FIG. 367. Ovaries in transverse section. *A*, Lobelia. *B*, Diapensia. *C*, Rhododendron. *D*, Passiflora. *pl*, placenta; *sa*, ovule. After Le Maout et Decaisne. Lehrb.

(*b*) *The Flower-axis shares in the Formation.*

We shall specially refer to the cases of Oxalideae and Caryophylleae.

Oxalis. In Oxalis stricta (Fig. 368) the five carpels arise in a whorl around the broad flattened apex of the flower-axis, but they do not use this up entirely. Each carpel shows also here the formation of the sole, but the flower-axis from which the sole is not separated grows up with it. In this way there is produced a quinquelocular ovary to which the upper free

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[1] See Fig. 367, *A*, which, although it represents the transverse section of an inferior ovary, shows the same placentation. I formerly supposed that there was a sharing of the axis in these families, misled by the incomplete and therefore incorrect statements of Payer.

[2] Schaefer has proved by the history of development that this, which I had conjectured, is the case.

[3] Even allied forms may, as it appears, behave differently, as we see, for example, in the Caryophylleae.

portion of the carpels forms the style. A transverse section through the lower part—the ovary itself—shows then a central axis on which the margins of the carpel are set, and they remain united with this central axis, and at the position of the union there run in each loculus two longitudinal cushions, the placentas. Doubtless these latter correspond each to a marginal part of a carpel which has, however, not separated itself from the tissue of the vegetative point of the flower[1]. The process in Impatiens and elsewhere is similar.

Caryophylleae. In Caryophylleae, like Lychnis, Malachium, Silene, and others, we have the same. The so-called 'free central placenta' of these forms arises because the septa are early broken down. As Van Tieghem says[2], 'one sees then how great is the mistake of the organographer who recognizes in this complex column only a simple axis which will produce the ovules on its surface.' Much more correct is the view, which is supported by the history of development[3], that the placentas correspond to the margins of the carpels united with the axis. In this large family, however, there are transitions from the condition in which the vegetative point of the flower is entirely used up for the formation of the carpels to those where the flower-axis remains as a relatively large portion, and is distinguished anatomically by special vascular bundles. It is easy to understand that a long massive column in the middle of the ovary which stores up material for the development of the seeds must be specially constructed anatomically. At the same time the question whether the flower-axis shares in the formation of the ovary or not is by no means of first-class importance.

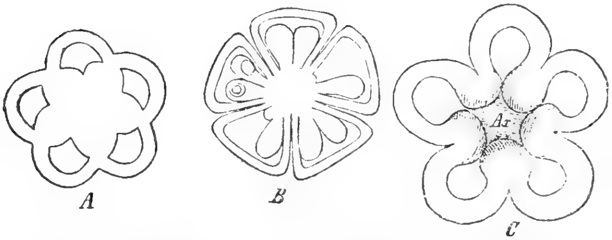

FIG. 368. Oxalis stricta. Ovary in transverse section. *A*, before inception of ovules. *B*, older, with two rows of ovules in each loculus. *C*, older than that in *A* and cut in the upper part; the margins of the carpels implanted on the flower-axis, *ax*, to which they are subsequently united.

(2) THE SYNCARPOUS SUPERIOR OVARY WITH PARIETAL PLACENTATION.

Here the vegetative point of the flower remains at the base of the cup of the ovary; the placentas do not reach it (Fig. 367, *D*), and they appear

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[1] Anatomically speaking, the axial tissue in Oxalis stricta does not appear. The bundles which run in the central column of the ovary belong to the margins of the carpel in the sense given above.

[2] Van Tieghem, Recherches sur la structure du pistil, in Annales des sciences naturelles, sér. 5, ix (1868), p. 181.

[3] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 372; G. Lister, On the Origin of the Placentas in the Tribe Alsineae of the Order Caryophylleae, in Journal of the Linnean Society, xx (1883), p. 442; Schaefer, Beitrag zur Entwicklungsgeschichte des Fruchtknotens und der Placenten, in Flora, lxxiii (1890).

therefore as projections from the wall of the ovary. One example will suffice:—

Cistus populifolius. The carpels of this species (Fig. 369) are laid down in the form of transverse cushions which approach one another somewhat, but at first are not connected together. In Fig. 369, 1, the ovary is shown already in the form of a cup with five angles, whose points indicate the middle of the carpellary primordia, which have become raised up early upon a common annular base. At those places which correspond to the lines of separation between the several carpellary primordia upon the open cup of the ovary, a thick longitudinal cushion appears upon the inner wall of the cup; these are the placentas. The free margins of the several carpels ending above at the angles of the cup of the ovary grow in many cases, for example in Reseda and species of Hypericum, into as many styles, in that the margins lay themselves together and so form the tubes of the styles, and we thus have an ovarian cavity which is continued into many distinct styles. In Cistus this is not the case. The style-tube is formed by the elongation of the upper part of the ovarian cup, and that it took origin at the time of the formation of the five distinct carpellary leaves is shown by the appearance upon its outside of the five stigmas (Fig. 369). The placentas project inwards as cushions into the middle of the ovary, and bear upon each side two rows of ovules. The ovary thereby becomes incompletely quinquelocular.

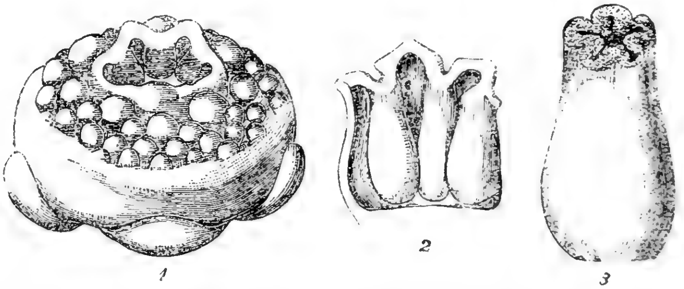

FIG. 369. Cistus populifolius. 1, young flower seen obliquely from above: the ovarian cup is laid down with five placentas; numerous stamens around it. 2, ovarian cup in vertical section: five placental cushions before the inception of ovules. 3, older ovary in oblique profile: the upper part will become subsequently the style. After Payer.

An ovary which is laid down in this way as a unilocular one may become plurilocular by different processes: in most Cruciferae by the formation of a false septum through the union of two outgrowths from the placentas; in the Geraniaceae the placentas bear ovules only in the lower part of the ovary, in the upper part they grow together into a column occupying the canal of the style from which the wall of the ovary is subsequently thrown off in five valves, a process which is closely connected with the distribution of the seeds.

3. The Paracarpous Gynaeceum.

Dionaea. Fig. 370 shows a transverse section of the lower part of the ovary of this droseraceous genus from which we may start. There are five carpels which are concrescent, and in such a way that their margins only are in contact. Within this ovary we find an annular swelling which produces ovules in serial succession from within outwards. As the longitudinal section in Fig. 370, II, shows, this swelling belongs evidently to the carpels. It represents the basal portions of the carpels which are *not separated from one another*. It is no longer possible to assign the ovules to the several carpels to which they belong. The excavation in the middle (Fig. 370, *A*) represents the remains of the vegetative point of the flower-mass which is not devoted to the formation of the ovary. We can easily derive this case from the common one: no infolding of the carpellary leaves takes place here, but a paracarpous carpellary ring is produced in which the united carpels raise up their base and bear the ovules.

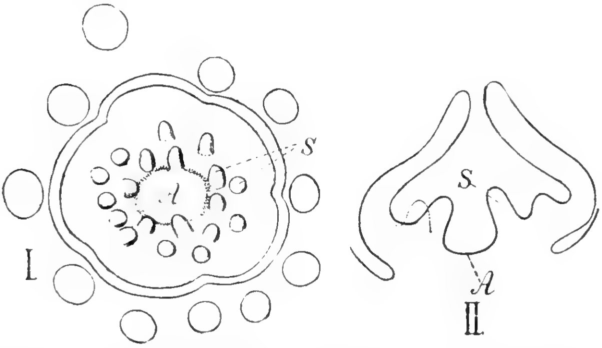

FIG. 370. Dionaea muscipula. I, young flower in transverse section. II, the ovary of a similar flower in longitudinal section. *A*, vegetative point of the flower; *S*, ovules.

Primulaceae. Lentibularieae. From this it is easy to derive the free central placenta which we find in the Primulaceae, Lentibularieae, and others. In them the differentiation of the placental portion of the carpels is suppressed. The whole of the portion of the vegetative point of the flower which is not used for the formation of the wall of the ovary is prolonged in the middle of the ovary. What now is this central placenta? ‘Orthodox morphology’ considers the central placenta as formed out of the axis on which run up the basal portions—the soles—of the carpels, and defends this interpretation very well against those who have declared the placenta to be the continuation of the flower-axis alone. The anatomical school, on the other hand, regards the placenta as formed from the carpellary soles alone, because it is pierced by a system of conducting bundles, which have their vascular portion turned outwards, and are connected with the conducting bundle-system of the carpels. This condition, however, is by no means general; where the placenta is weak, the supply of vascular bundles is simplified. In Primula farinosa, for example, there is a simple concentric strand in the middle of the placenta, and the same is the case in

Androsace villosa and others[1]. From this we learn that the anatomical structure gets its direction after the formation of the placenta, and is not inverted; in other words, the relationships of the vascular bundles are determined by the claims of physiology, not by those of morphological behaviour, and they require an explanation based upon the whole configuration; they themselves cannot give an explanation.

The view which has been put forward here may be stated in the following way: in the free central placenta we should distinguish neither *appendicular* nor *axial* parts. We have to do with a placenta which has probably come about by a process like that which has been shown above in the case of Dionaea, but which now exhibits a peculiar *new formation* of the flower. Can orthodox morphology say where the axis begins and where the carpellary sole ends? Must it still sing the old song that in every development nothing really new occurs, but that there is only a congenital union of the old? This gives us no insight into the processes themselves. That in abnormal cases the placenta itself can elongate into a shoot depends in our view upon the fact that the transformation of the primordium of a foliage-shoot into a flower is a *gradually* completed process, and if it be disturbed then the apex of the flower-axis can grow further as a shoot. It is peculiar that in many Primulaceae, especially in Soldanella, a process of the placenta stretches up into the style. Possibly it shares in the conduction or nourishment of the pollen-tube. Biological relationships which might make understandable the appearance of the free central placenta are as yet unknown. That the free central placenta contains as elsewhere substances which are used for the development of the seed scarcely requires to be mentioned, as these are found in other placentas.

(*b*) THE INFERIOR OVARY.

There are repeated here all the relationships of configuration which we have learnt in connexion with the superior ovary, and in particular the different kinds of placentation, as well as the condition that the vegetative point of the flower is either entirely used up by the carpels, or that a portion of it remains behind. On account of deficient historical investigation, the view was formerly advanced that the ovary in the epigynous flower is formed from the cup-like flower-axis, and the carpellary leaves only produce the styles and stigmas. Comparative morphology has rightly contradicted this interpretation, which, however, is still found in many books. As the history of development shows[2], the carpels share in the construction

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[1] Vidal, Recherches sur le sommet de l'axe dans la fleur des Gamopétales, Thèse de Paris, Grenoble, 1900.

[2] Goebel, Zur Entwicklungsgeschichte des unterständigen Fruchtknotens, in Botanische Zeitung, xliv (1816), p. 729; Schaefer, Beitrag zur Entwicklungsgeschichte des Fruchtknotens und der Placenten, in Flora, lxxiii (1890).

of the ovarian cavity, and the ovules have no other origin than that which is found in the superior ovary. It is common in all inferior ovaries that the vegetative point becomes at an early period more or less concavely hollowed out, and that the leaf-structures of the flower sprout out partly from the margins, partly from the inner surface of this depression. Whether one describe the marginal part of the flower-axis as a 'congenital concrescence' of the different leaf-whorls of the flower is an arbitrary matter, because the flower-axis ends its active existence with the bringing forth of the leaf-structures of the flower [1]. The earlier the flower-axis assumes the cup-like form, the more will we in general ascribe its character to the flower-axis; the later this form is assumed, the more will its features approach the more primitive condition as we find it in hypogynous flowers. Where, as for example in many Cactaceae, the outer surface of the inferior ovary is able to produce leaves and lateral shoots, we can have no doubt about its axial nature; the flower-axis has here become drawn into the formation of the ovary at a late period. In other cases, however, this takes place very early, and then the axis appears, as has been said, to pass right back into the leaf-structures of the flower.

(*a*) *The Vegetative Point of the Flower-axis is not used up.*

In the flowers of many Rosaeflorae we find transitions from perigynous to hypogynous flowers, and amongst these we have the flowers of some Pomeae.

Pyrus Malus. Fig. 371, 1–6, exhibits the development of the ovary of Pyrus Malus. The flower-axis has already become cup-like in Fig. 371, 1, and the five carpels appear as papillae upon the hollowed-out inner surface. They take up the whole *inner margin of the cavity*, but at the base there is visible—and even at later stages it is so—the flattened vegetative point of the flower, *v*. From now onwards we should have an ordinary perigynous flower in which the carpels *alone* produce the ovary, if the shaded zone, Fig. 371, 4, in one carpel to the right exhibited a strong intercalary growth corresponding with the distribution of growth in the leaves of most angiospermous plants. But this is not the case. What happens is that the ovarian cavity is formed by the growth of the zone, Fig. 371, 4, which is shaded to the left [2]. This, however, involves both the flower-axis and the base of the carpels which quite cover its inside. The ovarian cavity, which is produced by the growth of the zone, is then clothed on the inside by the carpellary leaves, and we need not be surprised therefore that the placentation is quite the same as in the superior ovary. We have to deal here with a common growth of the torus and the carpels [3], and this is a widely-spread

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[1] And this is naturally expressed also in the anatomical structure.

[2] This is a further illustration of the fact that relatively small displacements of a zone of growth may lead to great results.

[3] See p. 556.

phenomenon in the vegetative shoots also, for example in the encrusting of the shoot-axis in Chara, and in the formation of the leaf-cushions of many Coniferae. We find the same in other investigated cases, and it is clear therefore that the view that the carpels only form the styles is quite untenable.

(*b*) *The Vegetative Point of the Flower-axis is used up.*

Umbelliferae. We may cite as an illustration of this the case of the Umbelliferae (Fig. 371, 7–9). The features that we have seen in Acer are repeated here, but they are complicated by the fact that the carpels are not free, but are united on their outer surface with the vegetative point of the flower. The two soles of the carpels upon which the ovules arise are united with one another, and they form a septum. In each chamber are two ovules, of which one—that turned upwards—is regularly aborted, whilst the other develops further. The ovules were originally laid down at the base of the ovary, but thereafter, by the further growth in the young ovarian cavity, were pushed upwards.

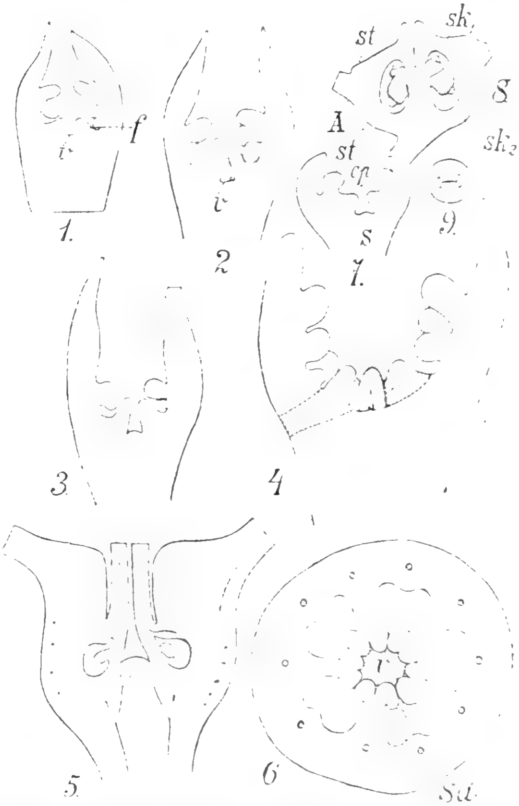

FIG. 371. 1–6, Pyrus Malus. 1, young flower in longitudinal section; *v*, vegetative point of the flower; *f*, carpel. 2–5, older stages of the same. 6, ovary in transverse section: *v*, vegetative point of the flower; *sa*, ovule. 7, Eryngium maritimum. Young flower in longitudinal section; *S*, vegetative point of the flower; *st*, stamen; *cp*, carpel. 8, 9, Angelica sylvestris. 8, Young flower in longitudinal section; *sk*₁, *sk*₂, two ovules in an ovarian loculus of which one directed upwards (*sk*₁ in right loculus) aborts; *st*, incipient stamen; *A*, axis. 9, young ovary in transverse section; the ovules are parietal and arise in the position which corresponds with the concrescent margins of the carpels. They are subsequently carried upwards.

Valerianaceae. This process takes place also elsewhere, for example in the Valerianaceae. In them we find three carpels, and a trilocular ovary is laid down, but there is an ovule in only one chamber, and this chamber is always much larger than the others. The two other carpels share only in the formation of the style and the stigma. In Fig. 372, *I*, a young flower of Valeriana Phu is shown in longitudinal section. A comparison of *I* and *III* shows at once how the stamens are concrescent with the tube of the corolla by the further development of the zone which is marked *x*. The ovule, *s*, is visible as a papilla at the base of the ovary. The flower-axis is entirely used up by the carpels. In *II* the ovule appears to be pushed somewhat upon the right side by a unilateral broadening of the base of the ovarian cavity. Now the portion of the ovarian cavity lying below the ovule grows. It is the portion between the dotted lines in Fig. 372, *II*, and is marked *y*. The ovule must therefore be pushed up within the ovary, and it hangs later downwards from the upper part of the ovarian cavity. Here also we do not recognize the biological significance of this displacement, but it is a step forward to have attained to this, that the different forms of ovarian formation can be referred back to the different distribution of growth in the primordium of the flower, as this must be the point whence further investigation must take its start.

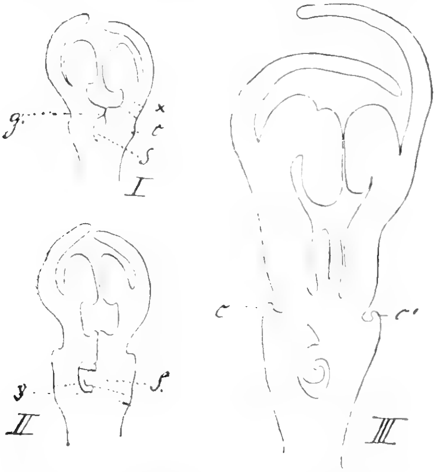

FIG. 372. Valeriana Phu. Flower in different developmental stages in longitudinal section. *I*, *s*, ovule still very young; *g*, primordium of style; *c*, calyx, rudimentary; *x*, zone in which corolla and stamens arise together. *II*, older flower; *s*, ovule; *y*, zone of growth which carries up the ovule into the ovary. *III*, still older flower; *c*, *c'*, calyx.

In what has been said only a brief indication of the construction of the gynaeceum in the Angiospermae has been attempted. It does not seem to be necessary to enter here into the details of the formation of the style and stigma, especially as these are expressly connected with the relationships of pollination. A description also of the changes which take place in consequence of the fertilization in the flower and the formation of the fruit must be passed over here, and a description of forms of fruit is beyond the scope of this book. The relationships of the configuration of the ripe fruits and seeds to their distribution have in the last ten years so often been described comprehensively that there is no need for a further description.

BIOLOGY OF RIPENING FRUIT. Another problem, the biology of the ripening fruit, that is to say the relationship between the formation of the fruit and the life-conditions in their widest sense, has hitherto scarcely received attention. I may say of it here only that in dry fruits frequently arrangements arise which make possible a rapid transpiration, and consequently a more rapid ripening. The great surface-development which appears in these fruits is in marked contrast with the relatively small more or less spherical form which is found in most fleshy fruits. Many arrangements which have hitherto been considered merely as a parachute-apparatus on the ripe fruit are in my view to be considered as a transpiration-apparatus for the ripening fruit, and these subsequently can be used for distribution, but are not necessarily for this. Thus we have winged fruits which open and do not fall, for example in Sophora tetraptera; the lively red and brown colour in many ripening pods of Leguminosae may facilitate also the outgo of the water-vapour; and the same may be said of the exposed lie of these fruits through which many become easily dried as they hang down. Investigation of the anatomical relationships, and experiment, can alone give us information upon these points.

C. *TRANSFORMED FLOWERS.*

It is a remarkable fact that a structure which is so peculiarly constructed and which is so markedly different from the vegetative shoot as is the flower, should yet submit itself to certain transformations again. As transformed flowers we consider all those which show a departure from the function of producing at least a single sporophyll. Amongst them we can reckon flowers which are only flags, and which no longer take any share in sexual reproduction, such as we find in Compositae, Viburnum Opulus, species of Hydrangea, Muscari botryoides, some Orchideae; also the double flowers mentioned above may be reckoned at least partly here. It has been said[1] that probably phenomena of correlation have to be considered here. The transformation mostly affects the corolla, but the flower-stalk is involved in Muscari botryoides and Rhus Cotinus[2]. More peculiar are the following cases:—

Sesamum indicum. In the flower-region below the normal flowers of Sesamum indicum some flowers are transformed into glands. The primordia of sepals, petals, and stamens are to be found usually still in them. The sepals are small and inconspicuous; the petals have become secretion-organs, and appear as thick, yellow, cylindric bodies[3]; the stamens have also become thick, club-like secretion-organs. The primordium of the gynaeceum is usually entirely suppressed or is only seen in the earliest developmental stages.

Trifolium subterraneum. In Trifolium subterraneum[4] the inflorescence bores into the soil. It is protected against detachment by the primordia of the upper flowers of the inflorescence being transformed into organs which anchor the inflorescence. On the uppermost of the transformed flowers all the calyx-lobes are present, whilst the other flower-parts are aborted. The further up the flowers stand

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[1] See Part I, p. 211.

[2] For an account of the stages of development at which the transformation takes place, see Familler, Biogenetische Untersuchungen über verkümmerte oder umgebildete Sexualorgane, in Flora, lxxxii (1896).

[3] See Familler, op. cit.

[4] See Warming, in Botanisches Centralblatt, xiv (1883), p. 157.

the less are the calyx-lobes developed, and the uppermost flowers are only short, thick, spherical, somewhat crumpled bodies, without a trace of leaves. But whilst normal flowers possess almost no stalk these transformed ones have stalks as much as two to four millimetres long. It is clear that we have here an instructive example of a gradual transformation. An arrest of the flower-primordia at different stages of development has taken place, and then a transformation in other directions. The conditions of the new formation require experimental investigation.

THE ORGANS OF PROPAGATION

Our account of the sporophyte of the Pteridophyta and Spermophyta has hitherto been concerned with the vegetative organs only, which as bearers of organs of propagation may experience peculiar transformations—a phenomenon which we have also observed in the gametophyte of the Bryophyta. The *sporangia* are the organs of propagation of the sporophyte.

Whilst in the Bryophyta the whole sporophyte is made use of in the formation of spores, and with reference to its function therefore can be designated as *one sporangium*, the other Archegoniatae and the Spermophyta devote only a relatively small portion of the whole plant to the formation of spores, which arise in the special structures—the sporangia. The possession of more or less large vegetative organs which may repeat the spore-formation, often one year after another for a considerable time, permits of the formation of a large number of spores. In the tree-ferns there may be millions. That the *pollen-sac* and *ovule* (*nucellus*) in the Spermophyta are merely sporangia is now generally recognized.

I propose to give here a short comparative account of the construction of the sporangium, with special reference to the connexion between its structure and its function.

I

THE SPORANGIUM

The function of the sporangium is twofold.

(*a*) to produce the spores;

(*b*) to scatter the spores[1].

Other organs of the plant besides the sporangia are involved in these functions inasmuch as they furnish the necessary building-material to the sporangia, and they bring them into a position which facilitates the sowing of the spores. When speaking of the sporophyll this was pointed out. Now in considering these functions we have to look at

(*a*) the construction of the sporangium in the mature condition;

(*b*) the course of the development of the sporangia.

EMBEDDED AND FREE SPORANGIA. Sporangia may be embedded or may be free[2]. Embedded sporangia are enclosed in the tissue of the

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[1] The sowing of the spores is not a function of the megasporangia in the Marsiliaceae, Salviniaceae, and Spermophyta, nor of the microsporangia in the Salviniaceae and Marsiliaceae.

[2] As is the case with antheridia and archegonia, see p. 173.

sporophyll. Free sporangia project beyond this, and are therefore provided usually with a shorter or longer stalk, which during their youth conducts the nutritive material and in the adult gives the sporangium a favourable lie for the sowing of the spores. As transitions between embedded and free sporangia, we have the unstalked sporangia of the Equiseta which, with a broad base, sit on the sporophyll. Sporangia in Ophioglossum are embedded; so also are the microsporangia of most Spermophyta. In the Coniferae both types appear, as well as forms which may be considered as transitions[1]. The embedding of the sporangia favours their nutrition. The free position and the existence of a stalk favours the scattering of spores. The tissue of a young sporophyll of Ophioglossum pedunculosum within which the sporangia are sunk will be found to be gorged with starch, and probably also other reserve-materials which are used up by the ripening sporangia. Sporangia which throw out their spores are, so far as I know, never embedded. The transition-forms between embedded and stalked sporangia, as we shall presently see them in Botrychium, offer a subject for our special attention, as they enable us to obtain some insight into the origin of the stalk. We may ascribe it either to the sporangium itself or to the sporophyll; the question—to which of them—appears of itself to be somewhat unimportant, but is of significance for a critical judgement on the connexion between the several forms of sporangia, especially also for the interpretation of the megasporangium of the Spermophyta. An attempt will be made below to show that the history of the stalk is not the same in all sporangia, but that the leptosporangiate Filicineae are specially distinguished from the eusporangiate Filicineae and the other Pteridophyta by the formation of the stalk of their sporangium.

THE RELATIONSHIPS OF SYMMETRY OF SPORANGIA. The sporogonia of the Bryophyta are constructed radially in by far the greater number of instances. Where a dorsiventral form appears, as, for example, in Diphyscium and some other Musci, we are able to trace it to a change from the radial construction which begins earlier or later, and which stands in relationship to the distribution of the spores, and is caused by external factors, especially unilateral illumination. The sporangia of the Pteridophyta are never radial, apart from those of the Salviniaceae and Marsiliaceae, where, however, we must consider them as reduced structures. Most sporangia are dorsiventral, as for example in Equiseta, Polypodiaceae, Schizaeaceae, Osmundaceae, Lycopodium inundatum; others are bilateral or at least nearly so, as in most of the Ophioglossaceae and Lycopodineae. We must inquire how far the relationships of symmetry of the sporangia are related to the distribution of spores, and we shall show that such relationships are very clearly visible in a number of cases where the

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[1] Embedded in Abietineae; free in Cupressineae; Equisetum-like in Araucaria and others.

conformation of the sporangium is asymmetric, as in the Hymenophyllaceae. The direction in which the sporangium opens is specially dependent upon its conformation and lie, a relationship about which more must be said as it has hitherto received far too little attention.

We can clearly recognize in some cases that the outer conformation of the sporangium stands in relation to the place of its appearance. If a sporangium of Botrychium standing free upon a sporophyll approaches the spherical form, if the sporangium of a Lycopodium lying parallel to the surface of the leaf in whose axil it stands possesses the greatest extension, we scarcely require to point out the relationship between the conformation and the lie. The sac-like sporangia of Equisetum are also so formed that they fit under the space which is made by the peltate sporophyll. Analogous cases are found in the Hymenophyllaceae. In other cases, however, such simple relationships are not probable.

ARRANGEMENT FOR DISTRIBUTION OF SPORES. The arrangement for the distribution of spores consists, in the first instance, in a characteristic structure of the wall of the sporangium, just as the structure of the wall of the antheridium of the Bryophyta and Pteridophyta is arranged for the distribution of the spermatocytes, only that by far the greater number of the spores are adapted to distribution by air-currents, not by water, as is the case with the spermatocytes. In the relatively small number of cases in which the spores are spread by the water, as in the Marsiliaceae, Salviniaceae, and Isoetaceae, the sporangial wall, so far as we know, does not take an active share in the opening; it has a very simple construction probably as the result of reduction, and it finally withers. We thus have in them phenomena which recall the aquatic Bryophyta, such as Riella, which ripen their sporogonia under water. In the sporangia which discharge their spores into the air we find arrangements in the wall-structure for its opening, and frequently also for the scattering of the spores. A point of opening which we may designate the *stomium* occurs *in all sporangia* which discharge their spores into the air[1]. The cells of the sporangial wall condition by their characteristic structure the emptying of the sporangium of the spores, whether these be only exposed, be slowly pressed out, or be ejected. Other arrangements for distribution, that is to say arrangements not conditioned by the construction of the wall of the sporangium, are found only in Equisetum and Polypodium imbricatum in the conformation of the organs which have been erroneously named 'elaters,' although neither in structure nor in function are they like the elaters of the sporangia of Hepaticae.

'Elaters' in Equisetum. It is well known that the spores of Equisetum are provided with two membranous bands which are formed by splitting of the episporium.

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[1] Notwithstanding what is said in the latest literature.

and which when dried spread out but when moistened coil up round the spore. They have been considered as means for spreading the spores as these, when they are shed, if they come in contact with alternating moist and dry air, undergo movements in space. As the spores could in this way approach one another as well as move apart no scattering of them is associated with this movement. The question therefore is, How do the 'elaters' behave in the opening of the sporangium? De Bary has made an incidental communication upon this subject which I here quote[1]: 'If one leaves a dehiscing spike of sporangia quiet in dry air the spores are pressed slowly out of their receptacles in consequence of the progressive crumpling through drying of the wall of the sporangium. The "elaters" of each spore at the same time stretch themselves. As, however, they never can become *quite straight*, and as also on account of the roughness of their outer surface they hook and interlock one with another, after a time there come in this way large, loose, woolly flocks together which are easily broken up into small flocks.' These flocks consist always of many spores which are therefore sown together—an arrangement which receives its explanation in the fact that the prothalli of Equisetum are normally dioecious[2]. The 'elaters' then hinder a segregation of the spores. I would, however, add to what De Bary says that I think this is not the only function of the 'elaters,' but that they also serve as a parachute, for the spores embedded in the loose flocks offer a larger surface to the wind. If the spore-flocks reach moist ground they become smaller by the coiling up of the 'elaters,' and heavier by the taking up of water. The 'elaters' also act to a certain extent in temporarily fastening the spores to the substratum by their roughness, whilst from a dry place the flocks are again easily blown away. The spores, however, are not arranged for long flight in the air as they quickly lose their capacity for germination.

'Elaters' in Polypodium imbricatum. Within the sporangium of this epiphytic fern are found besides the spores fine hygroscopic fibres which are slightly cuticularized and which arise out of the plasm of the degenerated tapetal cells[3]. The function of these 'elaters' is here unknown. Karsten thinks that they contribute to the loosening of the spore-mass after the rupture of the sporangia, but this could scarcely be the case, seeing that in the sporangia of the Polypodiaceae, which are provided with an annulus, the spores are not gradually pressed out as in Equisetum but are thrown out all at once[4]. I think Karsten's further suggestion is better founded, 'that by their not inconsiderable length they favour the fixation in moist weather of the relatively large spores to the tree-stems,' in the same way as Beccari has shown that tufts of hairs on the seeds of Asclepiadeae act. At any rate these structures have no more right to be called 'elaters' than have the structures so-called in the Equiseta. Further investigation must show whether or not they are found elsewhere amongst the ferns.

DIFFERENCES IN STRUCTURE OF THE SPORANGIAL WALL. The wall of the sporangium is specially adapted to the distribution of the spores

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[1] De Bary, Notiz über Elateren von Equisetum, in Botanische Zeitung, xxxii (1881), p. 782.

[2] See p. 195.

[3] See p. 596.

[4] Karsten, Die Elateren von Polypodium imbricatum, in Flora, lxxix (Ergänzungsband zum Jahrgang 1894), p. 87.

by a special structure of the cells, in particular by peculiar thickenings of the cell-membrane. There is a great multiplicity of details, but there is one feature that must be specially mentioned as I do not find that it has hitherto been carefully considered. Wherever in the Pteridophyta and Gymnospermae there are specially thickened cells—*active cells*—of the wall of the sporangium serving as an opening or scattering mechanism, these always *belong to the outermost cell-layer of the sporangial wall*[1], which in many cases is the only one present in the ripe sporangium. In Angiospermae this is never the case[2]. Even where apparently the active cells, as they may be called, belong to the outermost layer this is not really so. This is a difference which we cannot well say is of great functional significance, yet it is of great interest from the comparative morphological standpoint, because we have regarded for long, and rightly so, the structure of the wall of the sporangium as an important systematic mark. We shall presently speak about the genetic relationships of the sporangium, and endeavour to answer by individual instances the question of the relationship between conformation and function in the sporangia of the several groups.

DIVISION OF LABOUR IN SPORANGIA. The division of labour between microsporangia and megasporangia that is found in the three classes of the Pteridophyta which now possess living representatives furnishes us with one of the most remarkable illustrations of 'parallel formations' in the plant kingdom. We start in the group from isosporous forms, but we have not yet succeeded in tracing back the division of labour to an 'adaptation.' We have already seen, when speaking of the germination of spores[3], that in the heterosporous forms the spores as they leave the mother-plant are 'induced' to a definite limited development which is little dependent upon external conditions. In Equisetum there is so far biologically an approach to this behaviour inasmuch as the 'induction' is practically a consequence of the manner of the distribution of the spores. The spores are indeed all potentially alike, but through the scattering of many together it follows that the conditions of nutrition are not equally alike for all, and the worst nourished will give male prothalli. When the development of the sporangia is considered, it will be shown that the separation of microsporangia and megasporangia appears at different stages in the development of the Filicineae and Lycopodineae; the most extreme case is again offered by the Spermophyta. Our short account of the mature sporangium will follow the same sequence of groups as that adopted when the construction of the gametophyte was described, because in the Lycopodineae, with the exception of Selaginella, and in Equisetineae less specialized arrangements are to be found than in the Filicineae, especially the Leptosporangiate Filicineae.

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[1] With the exception of Ginkgo. See Goebel, Morphologische und biologische Bemerkungen; 13. Über die Pollenentleerung bei einigen Gymnospermen, in Flora, xci (1902), p. 253.

[2] Some Ericaceae are an exception. See Artopoeus, Über den Bau und die Öffnungsweise der Antheren und die Entwicklung der Samen der Ericaceen, in Flora, xcii (1903), p. 309.

[3] See p. 189.

II

THE MATURE SPORANGIUM OF THE PTERIDOPHYTA

A. *LYCOPODINEAE*[1].

We have in this group two kinds of sporangia to consider.

1. Lycopodium, and Phylloglossum which is perhaps not generically separated from it, as well as Selaginella, possess solitary sporangia sessile upon the sporophylls.

2. In the Psilotaceae there are two sporangia on the sporophylls, as in Tmesipteris (Fig. 336), or three to four.

We shall leave unanswered the question whether the sporangia of the second group are the result of the 'concrescence' of separate sporangia, or of the division of a single sporangium[2] by the development of plates of sterile tissue. At any rate they are so far independent that each opens by a special longitudinal split. It may be also stated that in Tmesipteris the formation of one of the two sporangia may be entirely suppressed. The single sporangia of Lycopodium and Selaginella also open by a longitudinal split, but this does not reach the stalk. The line of opening is always prepared for. The opening is brought about by the structure of the cells of the outermost cell-layer of the wall of the sporangium. The side-walls of these cells are thickened equally in Psilotaceae and Selaginella, unequally in Lycopodium and Phylloglossum, and show the lignin-reaction with phloroglucin[3], whilst the outer wall, if it is thickened apart from the cuticle, shows a cellulose-reaction. This is the common character of the structure of the sporangial wall in Lycopodineae. As regards individual cases we may remark[4]:—

PSILOTACEAE.

The Psilotaceae have, besides the outer layer of the sporangial wall, many inner ones which furnish material for the formation of the relatively numerous and large spores, and of course also act as an effective protection to the ripening spores.

Tmesipteris. Tmesipteris is a remarkable exception, according to Leclerc du Sablon[5], because its outer layer also consists of cells with lignified outer walls, and in consequence the usual causes of dehiscence

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[1] We exclude Isoetes from this class for the reasons already stated. See p. 172, footnote 5.

[2] I observed in Lycopodium clavatum the occasional division of the sporangium, which reached either only up to the stalk or also into this.

[3] In Psilotum the lignified layer also still shows a cellulose-reaction.

[4] In the following I do not deal with the mechanism of the opening of the sporangium, but only with the question how far the different forms of sporangia in a group can be referred to a common fundamental 'type.'

[5] Leclerc du Sablon, Recherches sur la dissémination des spores dans les Cryptogames vasculaires, in Annales des sciences naturelles, sér. 7, ii (1885), p. 24.

have disappeared; on the other hand the sub-epidermal cells are lignified. But I find the following: the middle lamella of the lateral cell-walls is lignified, and the lignin-reaction is also stronger at the point where the cells stand in contact. The inner layer of the cell-wall is present in exceptional amount only under the position of opening, which is quite the same as what we find in Lycopodium clavatum which will be mentioned below. In the outer cell-wall a subcuticular layer more often colours red, but a complete lignification of the outer cell-wall I never found, nor can I discover that in Tmesipteris there is an essentially different construction from that in the other Lycopodineae.

LYCOPODIEAE.

Lycopodium. Here, as in Selaginella, the wall of the sporangium apart from the tapetal cells consists usually of two cell-layers when ripe[1]. The majority of cells of the outer layer of the wall, for example in Lycopodium clavatum, have an undulated outline, and possess thickened ridges at the points of bending of the cell-wall (Fig. 373, I). They recall the nature of the same cell-layer in the wall of the microsporangia of many Coniferae, for example some Cupressineae. In the lower portion of the sporangium the cells are elongated, the thickened ridges frequently extend and join into half-hoops, and thus lead on to the character of the wall-cells in Lycopodium inundatum, for example, where the half-hoop-thickening is specially evident. The cells which limit the line of separation approach more nearly rectangular form. The statement of a recent author that there is in the Lycopodiales 'positively no contrivance for dehiscence, and no vestige of an annulus or stomium[2]' is incorrect. The stomium is quite evident, not only through the cells in the line of opening being differently constructed—usually lower than are the others—but also by their behaviour

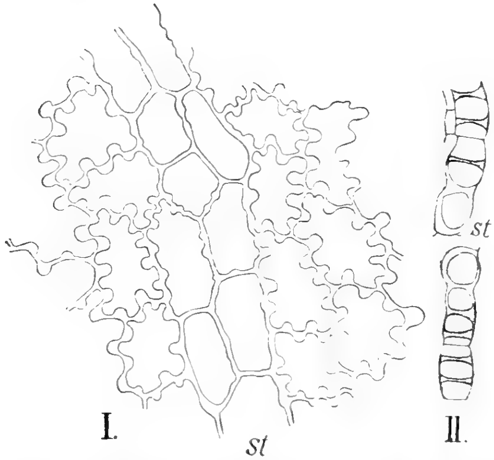

FIG. 373. Lycopodium clavatum. I, portion of the wall of sporangium in surface view; *st*, stomium. II, portion of wall of sporangium in longitudinal section; *st*, stomium-cells separated from one another by the cut, the thickenings of the wall-cells are shaded.

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[1] In many the lower portion of the sporangium has an increased number, for example in Lycopodium inundatum.

[2] See R. Wilson Smith, The Structure and Development of the Sporophylls and Sporangia of Isoetes, in Botanical Gazette, xxix (1900), p. 331. The error is probably the result of the examination of longitudinal sections only.

otherwise. I may shortly describe this in Lycopodium clavatum. If one adds phloroglucin to a surface-section such as that shown in Fig. 373, I[1], the opening cells will appear as a red band which is easily visible to the naked eye. In the ordinary wall-cells here[2] it is the side-walls only which are lignified, especially at the thickened portions. At the stomium[3] the inner wall, to which the thickening may have spread, is also lignified. Doubtless this is of importance for the opening mechanism. An annulus is at any rate not specially formed. Almost all the cells of the wall of the sporangium by their structure bring it about that as they dry they cause movements which lead to the opening.

The ejection of the spores has not been observed in isosporous Lycopodineae. I could only see in Lycopodium annotinum that in the wide-open sporangium when the sporangial wall dried the spores lay in a loose mass which projected somewhat, and the spores could then be carried away by the wind. This would be facilitated by the rolling back of the margins and the apices of the sporophylls.

Selaginella. There are remarkable phenomena in this genus[4]. In the first place there is a difference in structure between microsporangia and megasporangia which is of importance for the physiology of propagation. Both kinds of sporangia open (Fig. 374). The megaspores as well as the microspores are ejected in the process of opening of the sporangium, the megaspores much further than the microspores. In Fig. 374 a megasporangium and a microsporangium are shown from the narrow side, both with the same slight magnification. They have split in two valves which do not reach to the base, and they also show two lateral lines of splitting (Fig. 374, *r*, *r*). In the alveolar lower portion of the megasporangium there appears very evidently a stripe of cells passing out on each side from the stalk. This is the hinge, and it is composed of low thin-walled cells (Figs. 375, 376) very different from the other cells of the wall. When the sporangium opens the two valves bend out from one another with such force that the sporophyll is bent downwards, and then the four spores are

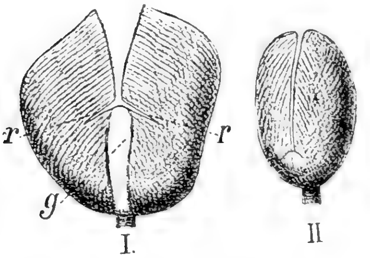

FIG. 374. Selaginella erythropus. I, megasporangium. II, microsporangium in profile. *g*, position of the hinge; *r*, *r*, position of the lateral splits.

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[1] This was taken from a sporangium which was not quite ripe but possessed well-developed spores.

[2] It is different, for example, in Lycopodium Selago.

[3] That is to say the nearly rectangular cells, frequently also those at their sides.

[4] See Goebel, Archegoniatenstudien: IX. Sporangien, Sporenverbreitung und Blüthenbildung bei Selaginella, in Flora, lxxxviii (1901), p. 207. I treat here in some detail of the relatively far-reaching adaptations in the structure of the spores of the Selaginella, especially in relation to the spore-distribution, because these have been expressly denied by R. Wilson Smith, The Structure and Development of the Sporophylls and Sporangia of Isoetes, in Botanical Gazette, xxix (1900).

suddenly thrown out. A surface-view of the sporangium shows that when this has taken place the whole sporangium has experienced a change in form. In this the lower portion of the sporangium plays an important rôle. As the process of drying proceeds it becomes narrower and longer, the convex outer walls endeavour to straighten themselves and approach one another (Fig. 377, to the right), and this movement is rendered possible through the thin hinge-cells which are in consequence pushed outwards. During this movement the megaspores are thrown out suddenly by it. In the microsporangium the formation of the hinge is only slight. A comparison of the two forms of sporangia shows very clearly how structure and function are connected, and that this mechanism is much more developed in the megasporangium of Selaginella as compared with Lycopodium. In the outlines of their structure the microsporangium of Selaginella and the sporangium of Lycopodium conform with one another, but the megasporangia of Selaginella show a much greater specialization which is evidently of advantage and requires no further demonstration.

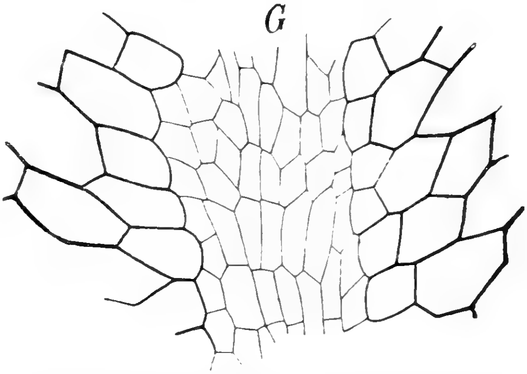

FIG. 375. Selaginella erythropus. Surface-view of a portion of the wall of the sporangium; *G*, position of the hinge, the more thickened cells of the wall are the 'atresia.' Magnified.

FIG. 376. Selaginella chrysocaulos. Hinge, *G*, in transverse section. The inner wall-layer is not shown.

Having in view the multiplicity of forms in the sporangia of the Filicineae and their not always clear relationships, it may be asked whether there is any relation between the manner of opening of the sporangium of the Lycopodineae and the conformation which it presents. This may be answered in the affirmative. The sporangia of the Lycopodineae are either dorsiventral or bilateral, and the opening takes place in such a way that the spore-masses can be most easily and most completely cleared out. We may compare the form of a sporangium in Lycopodium, if we leave out of account the stalk, with a gold-purse: the opening runs along the length of the broad side, not across it. In the Psilotaceae, *mutatis mutandis*, we have the same. It is clear that if the sporangia stand nearly upright the opening will be best along the apical line of the sporangium, for there it will best serve for the distribution of the spores. Where we find exceptions to this they demand an explanation. Two cases seem to be possible: either the deviation is a consequence of inner causes, that is to say without connexions perceptible to us with the other relationships of configuration and life, or these connexions do exist. We find such exceptions, for example, in Lycopodium inundatum and L. cernuum[1].

Lycopodium inundatum. I think this plant shows that the deviation in the lie of the position of rupture is connected with the lie and conformation of the sporangium—a result which is of special interest on account of the relationships which will be described in connexion with the sporangia of the Filicineae. The sporangia in Lycopodium inundatum are markedly dorsiventral. Their upper side, which is turned to the flower-axis, is larger than the under side turned to the sporophyll. The upper side is not flat but has in the middle a projection, and is flattened from there towards the sides. This conformation, as well as the lie, depends upon the pressure to which the sporangium is subjected by the sides of the two sporophylls which stand immediately above it. In consequence of this the sporangium comes to occupy a nearly horizontal position, and its upper side is closely covered by two indusium-like curtains, as each sporophyll has upon its under side an elongation which shows right and left a pit-like depression into which one half of a sporangium fits, and which is modelled in corre-

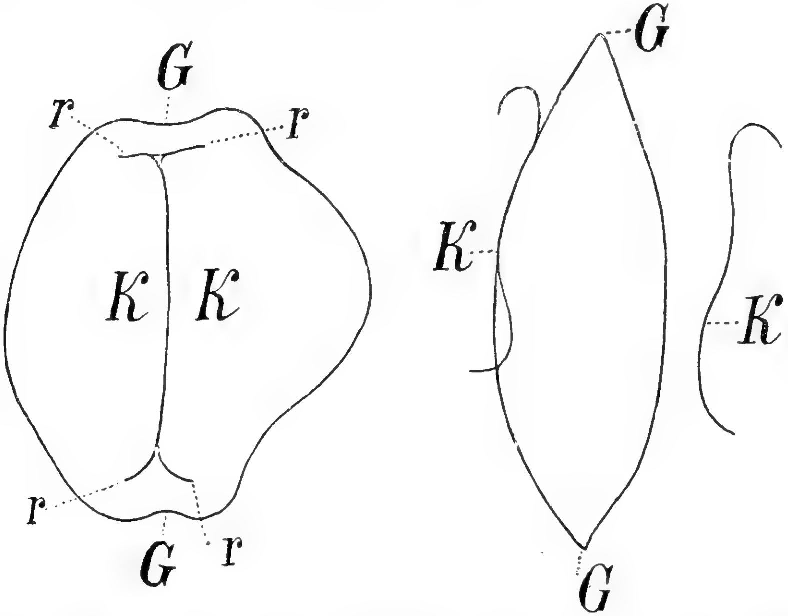

FIG. 377. Selaginella erythropus. Empty megasporangium; moist in figure to the left, dry in figure to the right; *K*, *K*, the two valves; *G*, *G*, hinge; *r*, *r*, lines of split.

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[1] Kaulfuss, Das Wesen der Farrenkräuter, Leipzig, 1827, p. 19, has remarked this. I do not find, however, that the sporangium is spherical as Kaulfuss has it, or transversely oval as Luerssen (Die Farnpflanzen oder Gefässbündelkryptogamen Deutschlands, Österreichs und der Schweiz, in Rabenhorst's Kryptogamen-Flora, Leipzig, 1890, iii, p. 800) has it, but as it is represented in the text.

spondence with the upper surface of the sporangium. The line of rupture lies now not along the apical edge of the sporangium[1] but upon its *under side* (Fig. 378), and this corresponds with the conformation and lie of the sporangium, which, as has been shown, departs from the nearly erect position of those in the other Lycopodineae and has a nearly horizontal lie. If the sporophyll curves back towards the outside the *under side* of the sporangium will be left free, and the sporangium opens here nearly in the middle of the *free side*, so that out of the longitudinal opening of the other Lycopodineae a cross-opening has been reached here. The *upper side of the sporangium is at the period of opening still covered by the curtains of the two sporophylls standing over it*, for the emptying of the sporangia proceeds gradually from below upwards. We see then why it is that the sporangium is not opened by a longitudinal slit but by a cross one. Really this cross-slit is only a long slit pushed downwards. The displacement is an actual one, not merely a fancy, if we consider as the original the behaviour of the great majority of the Lycopodineae, including Selaginella[2]. We shall have to discuss the same problem in the case of the Filicineae, but whilst in the Lycopodineae, so far as we know, there is only a divergence in regard to the opening of the sporangia in two species, there is amongst the Filicineae a much greater variation.

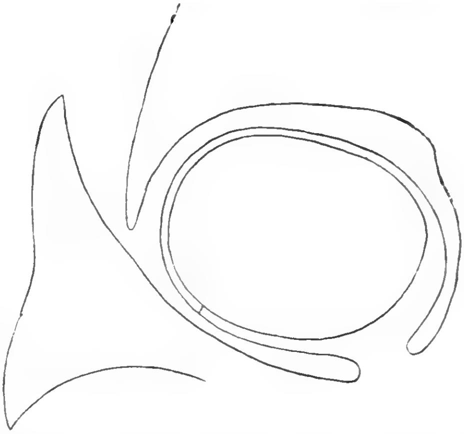

FIG. 378. Lycopodium inundatum. Sporangium in longitudinal section. The point of opening, which is indicated by a line across the sporangium-wall, lies upon the under side, not upon the summit. Magnified.

B. *EQUISETINEAE.*

The distribution of the spores has been already described[3]. The wall of the ripe sporangium is commonly but incorrectly represented as one-layered. I find it is—at least in Equisetum Telmateia, and less strikingly in Equisetum arvense—many-layered at the angles, but over large stretches the cell-layers have disappeared with the exception of the outermost. This outermost layer shows very characteristic thickenings in the formation of

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[1] That is the one over against the stalk. We do not discuss here the question whether the apical edge does not here coincide originally with the position of rupture which is subsequently displaced upon the under side, because this is of no significance for the point under discussion.

[2] The reason for this I will not give here. The gametophyte of Lycopodium inundatum and L. cernuum is rather a primitive than a derived one. See p. 192.

[3] See p. 576.

'lignified' spirals or rings, which are occasionally double. The sporangium always opens upon the inner side by a longitudinal slit, and subsequently gapes widely. The opening is effected by an arrangement of cells[1] which are shorter than others of the wall, and have their long axis placed nearly at right angles to the line of opening. As these cells dry, they shorten in the direction of their long axis[2], so that a slit must occur. The formation of the slit upon the inner side makes possible the free movement of the sporangial wall outwards[3], and it experiences besides a curvature making it concave upwards, so that the widely gaping opening is turned more downwards[4].

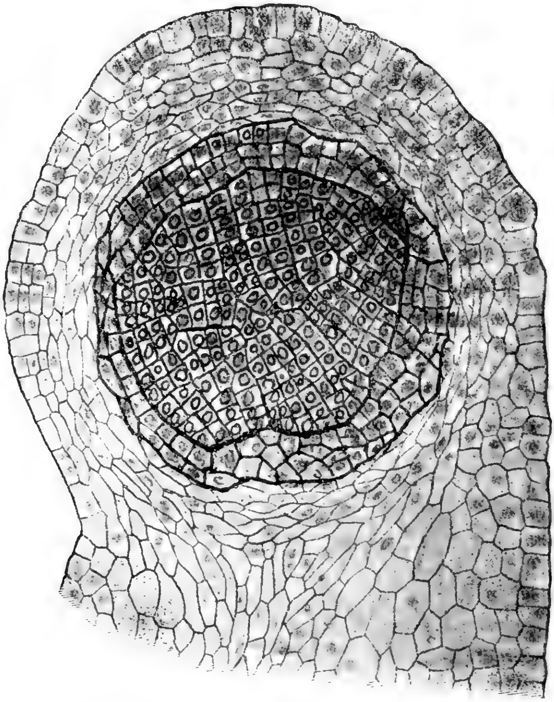

FIG. 379. Botrychium Lunaria. Sporangium in longitudinal section, showing the sporogenous mass of cells surrounded by the tapetal cells and the many-layered wall. From a photograph.

C. *FILICINEAE.*

I. EUSPORANGIATE FILICINEAE.

OPHIOGLOSSACEAE.

Although the sporangia of Ophioglossum and Botrychium are outwardly somewhat different, those of Ophioglossum being embedded in the tissue of the sporophyll, whilst those of Botrychium project freely beyond it, they are in structure and development essentially alike. In Botrychium the outermost cell-layer of the wall of the sporangia runs directly into the epidermis of the sporophyll. The sporangia project at their origin only

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[1] See Leclerc du Sablon, Recherches sur la dissémination des spores dans les Cryptogames vasculaires, in Annales des sciences naturelles, sér. 7, ii (1885). The description of the sporangia of Selaginella in this paper is incorrect.

[2] We cannot discuss the peculiar mechanism of the opening of this and other sporangia, especially as views regarding it are not very definite. That the arrangement of the thickenings of the cell-wall, whether these be spiral or ring-like, the elongated form of the wall-cells, and in particular the shortening of the wall-cells in their long axis are connected with the opening is clear. It appears to be a common feature in the 'active' cells of the sporangia of all Pteridophyta that the thickenings are so arranged that in drying a stronger deformation takes place in the tangential direction than in the radial.

[3] Analogous cases will be mentioned in the Filicineae.

[4] Particularly well seen in Equisetum arvense.

slightly above the surface of the sporophyll. The cells which lie underneath the sporogenous tissue and which belong peculiarly to the sporophyll push the sporangium, whose wall-layer also experiences a considerable increase of growth, beyond the sporophyll[1] (Fig. 379). A branch of a conducting bundle runs to each sporangium, and we may say that each of the sporangia of Botrychium is embedded in a branch of the sporophyll. The similarity with Ophioglossum is seen also in the method of opening, which takes place by a longitudinal slit in the wall of the sporangium in a definitely determined position. As in Ophioglossum there are two series of small cells, between which the separation occurs[2]. An ejection of the spores is impossible in Ophioglossum on account of the lie of the sporangium. Whether it happens in Botrychium and Helminthostachys is not known, and is, I think, improbable. In Helminthostachys the sporangia open outwards, and their conformation approaches the dorsiventral, inasmuch as the slit extends deeper downwards on the side of the sporangium which is turned away from the apex of the sporangiophore. The lie of the sporangium resembles—but in a slight degree only—the hanging lie of the sporangium in Equisetum. That this lie is not more expressed depends upon the looser position of the sporangiophores compared with the close-set sporophylls of Equisetum.

MARATTIACEAE.

In this group the sporangia always project above the surface of the sporophyll. In Angiopteris and Archangiopteris they are free single sporangia which are united together in a sorus. In the other genera we find *synangia*—structures with several sporiferous chambers. We can regard the synangium either as the result of the concrescence of single sporangia, if we consider forms like Angiopteris as primitive, or as a single sporangium which has become chambered by the formation of sterile isolated portions between many sporogenous cell-masses. In speaking of the development of the sporangia we shall revert to this question, and now will only shortly refer to the relationships of the configuration of the synangium or sporangium to the function of distribution of spores.

Danaea. Kaulfussia. The synangia of Danaea and Kaulfussia are built upon the principle of the pore-capsule, that is to say, each of the single chambers opens by a single pore, through which the spores are

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[1] With this corresponds the fact that stomata are found at the base of the sporangium even in that part of the 'wall' which lies above the spore-bearing inner space. It is a matter of moment for the interpretation of the funicle of the ovule whether the lower part of the sporangium in Botrychium belongs to the sporangium or to the sporophyll.

[2] The slit lies at right angles to the long axis of the sporophyll. In Helminthostachys it is in the long axis of the sporangiophore, which stands at nearly a right angle to the long axis of the sporophyll.

gradually shaken out. Considering the whole structure of the synangium, any other arrangement is scarcely possible[1].

Marattia. The chambers of the synangium in Marattia are not nearly circular, as in Kaulfussia, or connected together all round, as in Danaea, but are in two rows separated from one another by a groove (Fig. 380). This gives the possibility that the whole synangium when ripe can break up into halves[2], whilst each single chamber opens inwards. The position of opening is laid down beforehand.

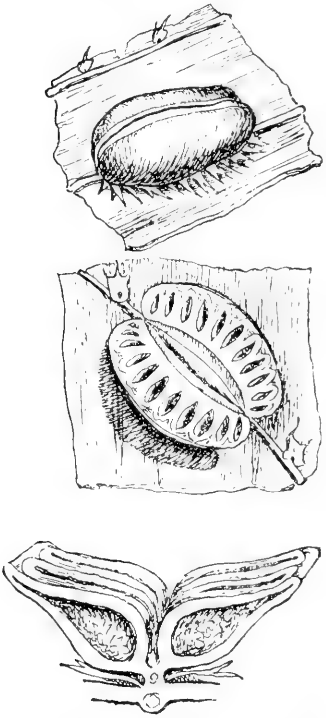

FIG. 380. Marattia fraxinea. Synangium. Uppermost figure, closed and viewed obliquely from above. Middle figure, open and viewed from above. Lowermost figure, in transverse section. Magnified. After Hooker.

Angiopteris. In Angiopteris we find separate single sporangia, which are arranged in two rows as they are in the synangium (Fig. 381). Not infrequently a sporangium stands at the end of the sorus before the two rows, and this gives us a transition to the arrangement in Kaulfussia. Each sporangium opens for itself, and the spores—according to observations upon Angiopteris evecta—are ejected, although not very energetically. The emptied sporangia gape widely. The mechanism of the valvular opening requires further explanation[3]. Doubtless the antagonism between the cells whose inner and outer walls are thickened and 'lignified' and those whose walls remain unthickened plays a part. The thick-walled cells are found particularly at the apex and on the flanks of the sporangium, which is constructed as a markedly dorsiventral structure, as in all Marattiaceae. Whether now the opening is effected by the disappearance of the unthickened cells has to be determined. At any rate *one sporangium* of Angiopteris corresponds to *one chamber* of the synangium of Marattia and Kaulfussia. Whether we are to reckon Angiopteris at the end or at the beginning of the series is at the present time a mere matter of opinion. Still, Angiopteris shows us the most specialized structure of the sporangial wall, and approaches in that feature the behaviour of the Leptosporangiate Filicineae, the Osmundaceae in particular, which otherwise stand nearest to the Eusporangiate Filicineae.

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[1] See the systematic works. Also Bower, Studies in the Morphology of Spore-producing Members: III. Marattiaceae, in Phil. Trans., 1897.

[2] The chambers extend deeper than the groove.

[3] See Bower, op. cit.

As regards the relationship of the direction of the opening of the sporangia to their lie, we observe that in all the Marattiaceae the point of opening lies upon *the side of the sporangium turned away from the sporophyll.* The sporangia stand upon the under side of the sporophyll, and the strong dorsiventral conformation of the sporangium, which deviates very greatly from that of the sporangium in Botrychium, is evidently closely connected with the 'endeavour' of the sporangium to bring the point of opening into such a position.

II. LEPTOSPORANGIATE FILICINEAE[1].

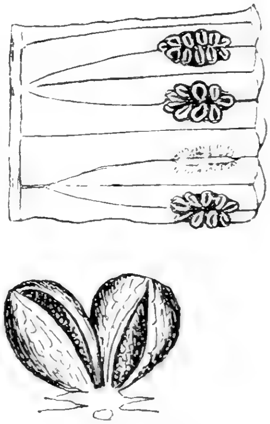

FIG. 381. Angiopteris evecta. Upper figure, portion of a leaf-pinnule with sori, one has fallen off. After Kunze. Lower figure, sporangia. Magnified. After Hooker.

The structure of the sporangia in this group is characteristic by the fact that the thickened cells which effect the opening of the sporangium and the scattering of the spores are localized upon one part of the sporangial wall. They constitute an *annulus*, even where it has not the form of a ring, and they bring about, as the sporangium dries, movements which have as a result an energetic ejection of the spores. The arrangement of the cells of the annulus determines not only the manner and method of the rupture of the sporangia, but is, as is well known, of systematic importance. For the details the systematic text-books may be consulted, and the elaborate exposition of the subject by Bower. Here I shall only bring forward a few examples bearing upon the question of whether the construction and lie of the annulus is one which is purely the result of 'internal' factors, or whether we can discover relationships between its form and function. There are such relationships. It can be shown, at least in the cases which have been investigated, that the arrangement of the annulus is 'purposeful,' that is, stands in connexion with the form and lie of the sporangium. *The annulus is so arranged that the slit by which the sporangium opens is always towards the side whence the distribution of the spores can proceed unhindered*, to speak generally, *to the outside*—the 'outside' being differently placed according to the lie of the sporangium. There are three chief methods of opening to be distinguished:—

1. By a slit transverse to the long axis of the sporangium. The annulus is vertical. In the great majority of Leptosporangiate Filicineae.

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[1] Excluding the Salviniaceae and Marsiliaceae. See Bower, Studies in the Morphology of Spore-producing Members: IV. The Leptosporangiate Ferns, in Phil. Trans., 1899.

2. By a slit oblique to the long axis of the sporangium. The annulus is oblique. Hymenophylleae, Cyatheaceae, and allies.

3. By a slit parallel with the long axis of the sporangium. The annulus is transverse or oblique. Gleicheniaceae, Schizaeaceae, Osmundaceae, Loxsoma.

(1) SLIT TRANSVERSE TO THE LONG AXIS OF THE SPORANGIUM. ANNULUS VERTICAL.

The sporangia are always *independent* of one another even if they stand in dense groups. They have usually long stalks[1] (Fig. 382, I), and they do not ripen together[2]. The vertical annulus has therefore free room for play. It stretches itself at first straight, bends then so that it is concave outwards—even so far that the two ends of the ring touch—springs back, and throws out the spores. Frequently on account of this the sporangium splits off at its base, as in Platycerium grande and others. A definite position of rupture, the *stomium*, is present. Frequently at this point there are flat cells with thickened walls, which may be designated as the *seam-cells* (Fig. 382, I, *J*, II and III, *S*). Their function is to secure that the split takes place in a *definite position*, and in a *definite direction*. Once the split has begun then the thin-walled cells behind the seam split through also. Through alternations of moisture and dryness this spring-like mechanism can be brought into operation more than once.

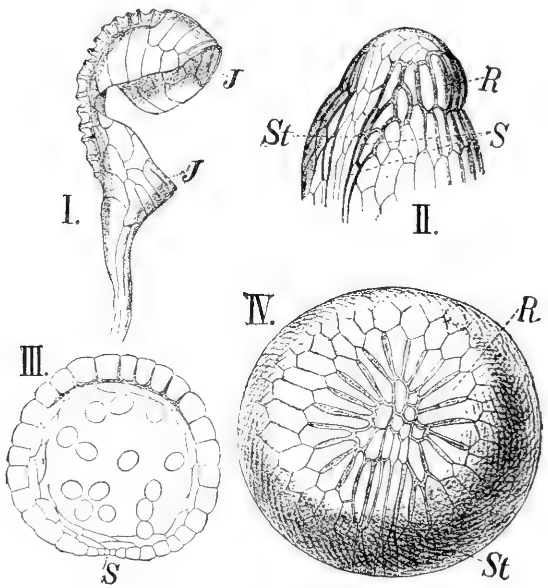

FIG. 382[3]. I, Platycerium grande. Ruptured sporangium; *J*, *J*, seam-cells. II, Aneimia fraxinifolia. Upper portion of a sporangium; *R*, annulus; *S*, seam-cells; *St*, stomium. III, Osmunda regalis. Sporangium, not quite ripe, in transverse section; *S*, stomium. IV, Mohria caffrorum. Sporangium seen from above; *R*, annulus; *St*, stomium. All magnified.

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[1] This is not the case in Ceratopteris.

[2] See the striking example in Polypodium obliquatum in Fig. 334.

[3] Professor Giesenhagen has been so good as to supply the figures 382, 386, and 388, which are drawn from his own investigations.

(2) SLIT OBLIQUE TO THE LONG AXIS OF THE SPORANGIUM. ANNULUS OBLIQUE.

Trichomanes. We may take as an example of this Trichomanes. Its sporangia are distributed radially on an elongated placenta, upon which they arise in basipetal serial succession (Fig. 383). The sporangia have only a *very short stalk* (Fig. 384), their long axis is *oblique to the placenta*, and they *cover one another* imbricately. A glance at Fig. 383 shows that the annulus lies in such a position that it has *free room for play*, because it runs obliquely to the long axis of the sporangium. The position of the slit is found near the base of the sporangium, and the annulus becomes detached at this point and takes with it the greater part of the sporangial wall, and the spores also. The annulus bends first of all to the side of the sporangium which lies over against the position of rupture, and this tears off the sporangial wall right and left of the annulus, then it springs back, the whole sporangium is torn off, and the spores are thrown out. This is what occurs in Trichomanes tenerum. Atkinson's statement 'that the spores in the Hymenophyllaceae are not very effectively dispersed' is incorrect [1]. We have here one of the most

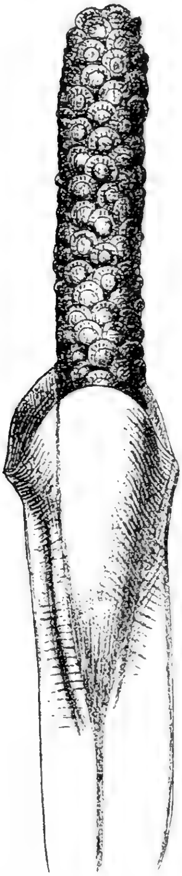

FIG. 383. Trichomanes tenerum. Sorus in surface-view; the placenta bearing radially distributed sporangia issues from the two-lobed beaker-like indusium. The annulus is visible on the several sporangia. Slightly magnified.

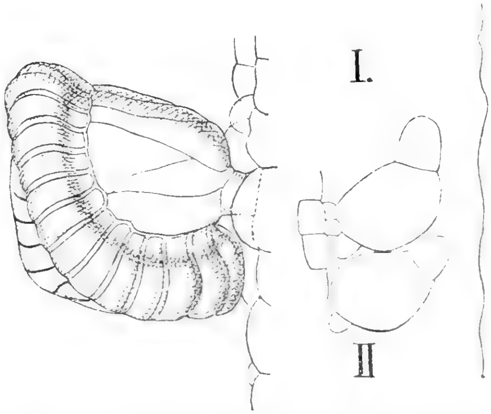

FIG. 384. Trichomanes tenerum. I, sporangium seen from the side. II, portion of the placenta in longitudinal section with two sporangia; the annulus is visible above and below each. I, magnified.

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[1] Atkinson, The Biology of Ferns, p. 72. The lie of the annulus of the Hymenophyllaceae is incorrectly given there. It is not horizontal but oblique. Bower shows it correctly. The ring

perfect mechanisms amongst the Filicineae, for the sporangia seated on the long placenta, where moisture can be retained between them, are shot free one after another at short intervals until finally the placenta is quite freed from them or only solitary sporangia remain occasionally upon it. The spores of the Hymenophyllaceae often germinate within the sporangia, but this is by no means the normal behaviour, and only occurs apparently if during long periods of rain there has been no opportunity for their drying[1]. So soon, however, as a short dry period begins the numerous ripe sporangia shoot out their spores in all the greater number.

Alsophila. The cyatheaceous Alsophila shows the same connexion of the lie of the annulus with that of the sporangium in the sorus. The species examined was Alsophila Leichardtiana.

Plagiogyria. The genus Plagiogyria, which up till now has been placed amongst the Polypodiaceae, but which at the same time has an oblique annulus, does not show the same imbrication of the sporangia as the Hymenophyllaceae and Alsophila. The sporangium is from the first unilateral and shortly stalked, and the sporangia stand close together.

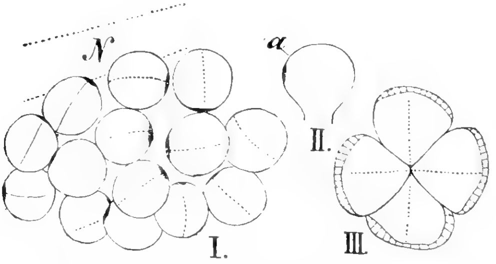

FIG. 385. Osmunda regalis. I, sporangia *in situ* seen from above; *N*, leaf-nerve. The annulus is indicated by a black spot. II, one of the dorsiventral sporangia in profile; *a*, annulus. III, Gleichenia circinata. Sorus seen from above. The dotted lines indicate the lines of rupture.

(3) SLIT LONGITUDINAL. ANNULUS TRANSVERSE OR OBLIQUE.

OSMUNDACEAE. (Figs. 382, III; 385, I, II; 386, II, III.) The sporangia stand all round the sporophyll in a somewhat loose manner in Osmunda. A surface view of a group of sporangia shows (Fig. 385, I) that the place of rupture is here everywhere upon the side of the sporangium turned away from the sporophyll[2], so that in those which are found upon the under side it is directed downwards, in those which stand upon the edge it is directed outwards[3]. The annulus, on the other hand, shows no different orientation. It is formed by a plate of cells which lie

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extends upon the one side (Fig. 384, I, to the right below) over the point of the insertion of the sporangium, but not upon the other which is the side of the opening. In consequence of this we have the movement described.

[1] That the sporangia are able, owing to their density, to retain between them water on the exposed placenta is of importance for the spores which do not bear a long drought; besides this brings it about that the sporangia dry from above downwards, and their spores are gradually thrown out, not all at once. In the moist stations which are inhabited by the Hymenophyllaceae it is important that every dry period should be used for copious spore-distribution. Evidently the arrangement of the sporangia is connected with this.

[2] This is true also for the microsporangia of the Cycadaceae.

[3] None of these marginal sporangia is represented in the figure.

upon one side of the dorsiventral sporangium. In my view this annulus lies immediately under the apex of the sporangium, but is displaced on account of the unilateral development of the sporangium (Fig. 385, II, *a*), and lies then not over against the stalk but laterally. There is a similar displacement in Lygodium. The place of opening is marked by lower cells, as is shown by a section taken at right angles to the stalk (Figs. 382, III, *s*; 386, II). The plate of the annulus in drying 'endeavours' to become concave outwardly, and this is facilitated by the conformation of the cells, by the oblique position of their cross-walls, or by their cross-walls being somewhat thin in the middle—an arrangement which brings about an approach of the thickened longitudinal walls[1]. By the throwing back of the sporangial valves the spores are thrown out.

GLEICHENIACEAE. In the Gleicheniaceae also the lie of the sporangium is connected with that of the annulus (Fig. 385, III), and the line of rupture is upon the side of the sporangium turned away from the sporophyll, as it is in Osmundaceae. The annulus has really the form of an incomplete ring which has a somewhat oblique, nearly transverse, direction to the long axis of the sporangium below its apex. It is very evident here that the lie of the annulus is only a 'means to an end,' that is to say, it hinges upon the lie of the line of rupture. The annulus would have freer play if the position of rupture were to lie turned towards the sporophyll, but such a lie would prejudice the distribution of the spores.

SCHIZAEACEAE. (Figs. 382, II, IV; 386, I; 387; 388; 389; 390.) The Schizaeaceae show analogous cases. The annulus is generally transverse beneath the apex of the sporangium, and the sporangium opens by a longitudinal slit which is turned outwards. 'Outwards' has here, as elsewhere, a different significance in different cases, as will be pointed out in the several genera.

Mohria. In this genus the sporangia have a short stalk and sit upon the under side of the sporophyll at nearly a right angle. They are consequently less markedly dorsiventral than in other genera, and the point of rupture I found to be directed always towards the margin of the leaf.

Schizaea. Aneimia. The sporangia in these genera are oblique to the sporophyll, and the point of rupture looks outwards (Fig. 387), consequently the sporangia are on this outer side somewhat swollen, and in their

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[1] Luerssen, Die Farnpflanzen oder Gefässbündelkryptogamen Deutschlands, Österreichs und der Schweiz, in Rabenhorst's Kryptogamen-Flora, Leipzig, 1890, iii, Figs. 35, 36, represents almost all the cross-walls as actually transverse. I have not seen such cases. Only occasionally were the walls transverse in the sporangia investigated. In Osmunda there is formed in the vicinity of the annulus, right and left of it, and before the slit of dehiscence, a short transverse slit, somewhat like that in Selaginella, and this facilitates the outward movement of the valves. This fact is not shown in any of the published figures. These transverse slits are prepared for in the structure of the sporangial wall, but have been entirely overlooked.

whole external conformation markedly dorsiventral. The point of rupture is very clearly constructed (Fig. 386, I).

Lygodium. The most interesting relationships in the Schizaeaceae are, however, found in Lygodium, where the sporangia stand singly enclosed in pockets (Fig. 388), and directed so that the annulus is oblique towards the under side[1]. Does this change in conformation of the sporangium, when compared with the other genera, have any connexion with the scattering of the spores? It is most remarkable that this question has nowhere been discussed in descriptions of Lygodium. Even the method of rupturing is often incorrectly given[2]. In reality this conformation secures under the given conditions the best distribution of the spores. Given the position of the annulus, longitudinal dehiscence, and the indusial pocket in which the sporangium lies. This pocket consists of two parts[3], one, the indusium proper springing from the under side of the leaf, and one the leaf-

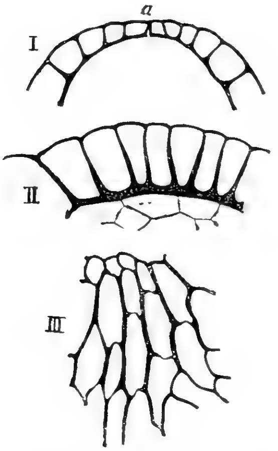

Fig. 386. I, Aneimia rotundifolia. Line of rupture of the sporangium in transverse section. II, Osmunda regalis. Cells of the annulus in transverse section. III, Todea barbara. Cells of the annulus in surface-view. All magnified.

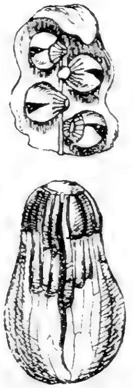

Fig. 387. Aneimia tomentosa. Upper figure: tip of a sporangiferous pinnule. Lower figure: sporangium seen from the side of rupture. Magnified. After Prantl.

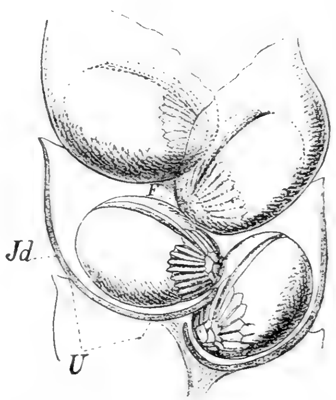

Fig. 388. Lygodium microphyllum. Portion of a fertile leaf-lobe seen from below. Four sporangia. The indusium removed from the two lower ones. The two upper ones seen through the indusium, *Jd*; *F*, position of annulus; *U*, under-surface of indusial pocket.

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[1] The long axis of the sporangium, however, does not lie as it is figured by Prantl, and in many other figures, in the *plane of the sporophyll*, but it forms with the short stalk an angle of 90°.

[2] Thus Luerssen, Handbuch der systematischen Botanik, Leipzig, 1879, p. 570, Fig. 146, *A*, says that the sporangium opens by a longitudinal slit turned towards the *under half of the indusium*.

[3] Prantl has represented the whole indusial pocket as a single indusium, because it arises as a crescentic wall beneath the sporangium which is laid down on the margin. I do not think that we have here anything but what is found in Schizaea and a number of species of Aneimia where the sporangia laid down upon the margin are displaced to the under side by a growth of the upper surface of the leaf. Coincident with this outgrowth the indusium is formed upon the under side. Prantl's explanation, influenced evidently by a desire to find an analogy with the formation of the integument of the ovule, must assume a complex concrescence of the indusium, whilst the explanation given above seems to me to find the relationship without any strain.

surface into which the indusium passes over. The free margin of the indusial pocket lies directed obliquely downwards, and so does the point of rupture of the sporangium (Fig. 388). The annulus opens wide when ripe, and in that way presses outwards the under half of the indusial pocket, and this is made possible by the annulus occupying the position where the indusium projects freely beyond the leaf-surface and where a movement can proceed unrestrained (Fig. 388, *F*). The configuration of the sporangium has therefore the most intimate connexion with its lie. Were the annulus to lie above instead of below in the indusial pocket the exit of the spores would be essentially hindered, as a twisting or movement of the indusium at this point where it joins the leaf-surface is scarcely possible. The great elongation of the outer side of the sporangium (Fig. 389), which leads to a bending of the sporangium through 90°, brings the annulus, according to our explanation, into the most suitable place for its function; at the same time we must point out that the peculiar growth of the sporangium is only an exaggeration of the behaviour which is found in Aneimia, and that here also the outer side of the sporangium is more strongly developed than is the inner side. The 'disposition' to dorsiventral development of the sporangia which exists in the whole group reaches an extreme in Lygodium. The great protection afforded to the sporangium in this genus by its inclusion within an indusial pocket evidently is connected with the climbing habit of the plant. The leaves climb far up into the shrubs[1]. The fertile leaf-pinnae (Fig. 390) are only formed in the *uppermost* part. Climbing-leaves are relatively very much exposed, and with this the marked protection of the sporangia corresponds.

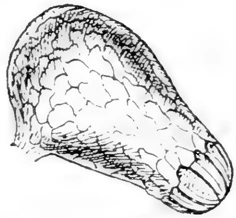

FIG. 389. Lygodium japonicum. Sporangium. Magnified. After Prantl.

The different lie of the annulus of the sporangia of the Filicineae which has just been depicted may give rise to phyletic speculations. Has a 'displacement' of the annulus taken place or not in the several groups? I do not think that at the present time we have a sufficient number of facts to warrant an answer to the question. We should have this if we could prove that starting from a definite *well-differentiated* form others have arisen by its transformation. Such a transformation is found in many cases where there has been a *change of function*, but more frequently it would seem that the 'capacity for development' belonging to the construction of the protoplasm has under the influence of external or internal formative stimuli unfolded *from the outset in different directions*. If we assume a 'primitive sporangium' we do not require

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[1] This is effected in two ways:—(1) by twining leaf-spindles, (2) by scrambling-pinnae. In Lygodium japonicum, for example (Fig. 390), the apex of the leaf-pinnae of the first order is usually undeveloped, whilst the two lower pinnae of the second order are well developed, stand out far, and act as scrambling-organs. The circinate persistent vegetative point of the pinnae of the first order may, however, resume its growth. The case resembles that of the Gleicheniaceae (see p. 318).

to ascribe to it a definite lie of the annulus, but only the capacity of thickening the wall-cells in greater or less number in relation to the lie of the sporangium and so to construct an opening apparatus. Whether one therefore will start from sporangia which still want a thickening of their wall, as, for example, those sometimes occurring in Ceratopteris, or from a form of sporangium like that of Lycopodium in which the majority of the wall-cells are 'active,' appears to be of no great moment. What should be here laid stress upon is that a sporangium of Hymenophyllum, for example, never required to have possessed another lie of its annulus than that which we now find. To assume a displacement of it would only be justified if we had ground for the further assumption that the lie and configuration of the sporangium were different at an early period. A displacement of the point of rupture of the sporangia is probable as we have seen in Lycopodium inundatum, but in Lygodium we have a case which shows how within one cycle of affinity after the lie of the annulus is once fixed the *whole configuration* of the sporangium is adapted to the work of distribution of the spores. We could prove that the divergences in the conformation of its sporangium from the allied forms is conditioned on the one hand by its pocket-like envelope, and on the other hand by the once given lie of the annulus. Lygodium appears to be not a primitive but a greatly changed form of the Schizaeaceae.

There is still another side of the question as to the significance of the lie of the annulus in the Filicineae which must be touched upon here. I have elsewhere briefly shown[1] that the lie of the annulus in the fern-sporangium should not be regarded as a character of adaptation. This view I still hold although it appears to stand in opposition to what has been brought forward above. It is evident that the arrangement of the annulus has the closest connexion with the whole configuration of the sporangium on the one hand and with its lie upon the other, and that under the

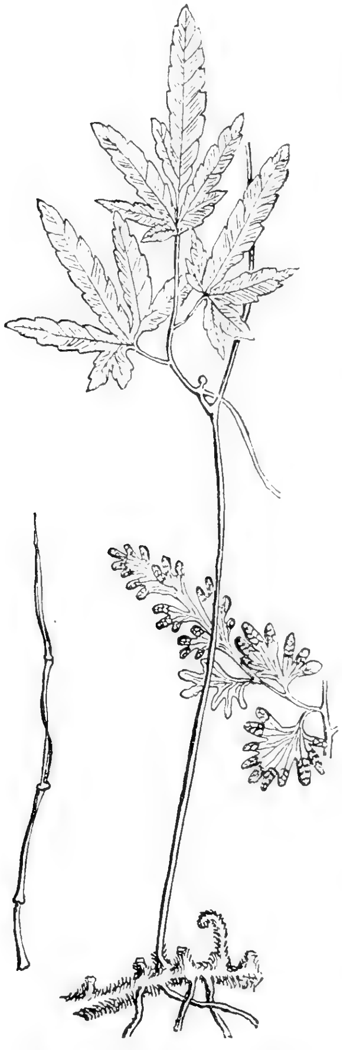

FIG. 390. Lygodium japonicum. Central figure shows habit. The leaves arise from a horizontal creeping rhizome. Only a portion of one leaf is shown. On the rhachis is a branched pinna of the first order. It has two pinnae of the second order between which is the undeveloped persistent apex. The pinna to the left is represented complete, that to the right has only its rhachis. Figure to the right below shows a fertile leaflet. It is much more branched than the sterile leaflet of the same order and shows the indusial pockets. Reduced. After Christ.

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[1] Goebel, Über Studium und Auffassung der Anpassungserscheinungen bei Pflanzen, München, 1898, p. 23.

given relationships it is a purposeful one. But the purpose cannot of itself explain why the work of opening of the sporangium and the distribution of the spores is performed in such *different ways*. The sporangium of Osmunda would function well with an annulus of the Gleicheniaceae or of the Schizaeaceae. We have here as everywhere to consider the 'inner constitution' of the plant on the one hand and its aim on the other. What we can prove sometimes in a number of sporangia is the connexion of the lie and the conformation of the sporangium with its manner of opening. In all other questions we have only to do with hypotheses.

The structure of the sporangial wall is extremely constant in the different forms of Pteridophyta, yet there are species where there are variations.

Ceratopteris. The most striking example is Ceratopteris, in which all stages occur, from that of a complete vertical annulus to that of entire absence of annulus[1]. In an example which I gathered in British Guiana[2] the annulus consisted of usually five or six cells, but in the rest of the sporangial wall it was not developed. Such a rudimentary annulus can scarcely be of importance in the distribution of the spores. The cause of this variation is unknown, but biologically we can understand that the annulus might disappear in a fern which floats upon the water, and which would not need to scatter its spores as these would be readily carried by currents in the water. Besides Ceratopteris, on account of its rich asexual propagation, is less dependent upon the distribution of spores than most other ferns. This phenomenon requires, however, a more close investigation, because the connexion of the lie of the annulus with the configuration of the spores is somewhat obscure in the sporangia of Ceratopteris. In its structure also the annulus diverges from that of the Polypodiaceae—it consists of very many low and broad cells. When the sporangium opens only few spores are thrown out, most of the spores remain behind in the sporangium[3], and this fact again leads us to the view that the spore-distribution proceeds here in a manner somewhat different from that which is observed in ordinary land-ferns.

III

DEVELOPMENT OF THE SPORANGIUM

The history of development has shown us that sporangia run through a course of development which in its main features is much alike in all.

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[1] See Hooker, Species Filicum, London, 1858, ii, p. 236.

[2] This form, which was described by Hooker and Greville, Icones Filicum, Taf. 97, as Parkeria pteridioides, is very different from the plant cultivated in our plant-houses, at least I have never been able to obtain from the latter the floating form with massive swollen leaf-stalks which I gathered in British Guiana. Whether or no there is a connexion has still to be proved experimentally. I do not know that similar forms have been described from other tropical countries, and perhaps in South America a special 'physiological race' of this fern has developed.

[3] Readily seen on examining a sporophyll in the inverted position.

In the first place it is characteristic that all the spores, as in the Bryophyta, proceed from sporocytes which, with reduction of the number of chromosomes, divide into four daughter-cells. This is also the case in the microsporangia of the Spermophyta, whose development therefore can be treated of in this place also. In the megasporangia of the Spermophyta peculiar relationships arise which demand a special treatment.

The sporangium at a middle stage of development consists of a *wall* composed of a number of cell-layers, the number varying in different cases[1]; of an inner tissue whose cells are densely filled with protoplasm and later form the sporocytes—the *sporogenous cell-mass*; and of one or more cell-layers of characteristic aspect which envelop the sporogenous cell-mass and lie below the wall—the *tapetal cells* which together constitute the *tapetum*.

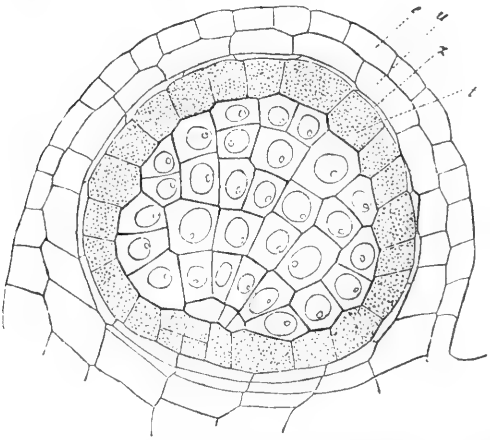

FIG. 391. Symphytum officinale. Portion of anther with microsporangium in transverse section. Sporogenous cell-mass in the middle, its cells having large nuclei: *t*, tapetum; *e*, epidermis; *u*, outer parietal layer which forms endothecium; *z*, compressed inner parietal layer.

The significance of the tapetum is nutritive. It furnishes the sporocytes with plastic material, especially what is required at a later period for the construction of the outer spore-membranes. It appears that we may distinguish two kinds of tapetum between which, however, there are a number of transitions:—

1. *Plasmodial tapetum*, in which the wall of the tapetal cells is broken down; its plasm along with the nuclei, which are often fragmented, wanders between the isolated sporocytes, or their daughter-cells, and is by them used up. The Filicineae (Fig. 379), Equisetum, and the microsporangia of the Spermophyta (Figs. 391, 392) have typically a plasmodial tapetum.

2. *Secretion-tapetum*, in which the tapetal cells remain until the ripening of the spores, but they excrete evidently soluble substances which are used by the sporocytes, and they have, as elsewhere, the function of supplying the sporangium-wall with plastic material in an available form. The sporangia of the Lycopodineae, and especially that of Selaginella (Fig. 394) and Isoetes[2], have a secretion-tapetum.

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[1] If the sporangial wall is many-layered, we designate in what follows the cells which lie under the outermost layer and *outside the tapetum* as the parietal *layer*.

[2] See Fitting, Bau- und Entwicklungsgeschichte der Makrosporen von Isoetes und Selaginella, in Botanische Zeitung, lviii (1900), p. 107.

Apart from the case of Isoetes this grouping conforms with the arrangement in the Pteridophyta[1].

The idea of the tapetal cells is not morphological[2], but is only functional[3]. In correspondence with this the origin of the tapetum is not uniform. Where the sporogenous cell-mass reaches a larger size there are frequently arrangements which make possible a more profuse supply of food-material. These are—

(*a*) an increase in surface of the sporogenous cell-mass. This is the case in the sporangia of Lycopodium clavatum and L. annotinum, for example, as well as in the microsporangia of many Angiospermae, where the sporogenous cell-mass becomes curved, and thus comes in contact with many sterile cells, especially at its base (Fig. 393, *pl*);

(*b*) individual cells, or in extreme cases many cells, or a cell-complex of the cell-mass, become sterile and serve to supply food-material to the fertile ones[4]. Isoetes supplies the most striking case of this. Its large broad sporangia are traversed by *trabeculae* of sterile tissue. Their appearance is easily understandable on account of the size of the sporangium. They serve to bring nourishment to the sporogenous cells, and they also facilitate by their intercellular spaces the exchange of gases. Bower has shown that similar arrangements exist in Lepidodendron. He also found irregularly arranged sterile cells in the sporogenous tissue of Equisetum, Tmesipteris, and Psilotum, as well as in Ophioglossum, where Rostowzew had also found it[5]. These cases recall that of the Hepaticae. The microsporangia of many Spermophyta show similar arrangements[6]. In some of the Onagrarieae the microsporangia are penetrated by plates of tissue; in Viscum, Rhizophora (Fig. 363), and others, the fertile cells in the anthers are limited to isolated groups.

THE ARCHESPORIUM. The origin of the sporogenous cell-mass has given rise in recent years to a series of investigations especially directed to the solution of the question whether this could be traced back to a single cell, cell-row, or cell-layer, which in the very young stages of the sporangial development is marked out by a rich protoplasmic content, and which produces by divisions the sporogenous cells. These primitive sporocytes have been called the *archesporium*[7].

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[1] See p. 172, footnote 5.

[2] As recent authors like Körnicke have maintained in the ovule of the Angiospermae.

[3] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 384.

[4] With regard to the connexion between configuration of this sporogenous cell-mass and its nutrition, see Goebel, On the Simplest Form of Moss, in Annals of Botany, vi (1892), p. 356.

[5] In Ophioglossum pedunculosum and Equisetum arvense I could only find a plasmodial tapetum, no sterilized sporogenous cells.

[6] See p. 554.

[7] Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien, in Botanische Zeitung,

Strasburger[1] has recently pointed out that the centre of gravity of the process of development which takes place in the sporangium does not lie in the archesporium, but that the new generation starts from the sporocytes, as in their division a reduction of chromosomes takes place which is accompanied by the separation of these cells from their condition of a tissue. Certain is it, however, that the centre of gravity of the development does not lie in any one stage, and on this ground one cannot speak of a 'centre of gravity' in the process of development. We have before us a series of definite processes following one upon the other which in the case under consideration lead up to the formation of spores. That in these the changes in the nuclear division appear to us to be the most striking is in part certainly a consequence only of the imperfection of our methods of investigation. We may with truth say that in the protoplasm itself there are changes occurring, and indeed not suddenly but gradually, and these express themselves in my view in the development of the sporogenous tissue out of the archesporium. That the archesporium has a different quality from the rest of the tissue will be shown when we speak of apospory. Moreover the aim of comparative investigation of the sporangia is the 'proof' of the homology of the development in the whole series of sporangia[2]'—a proof which remains established even if the differentiation of the archesporium is not everywhere so early as it is in some cases.

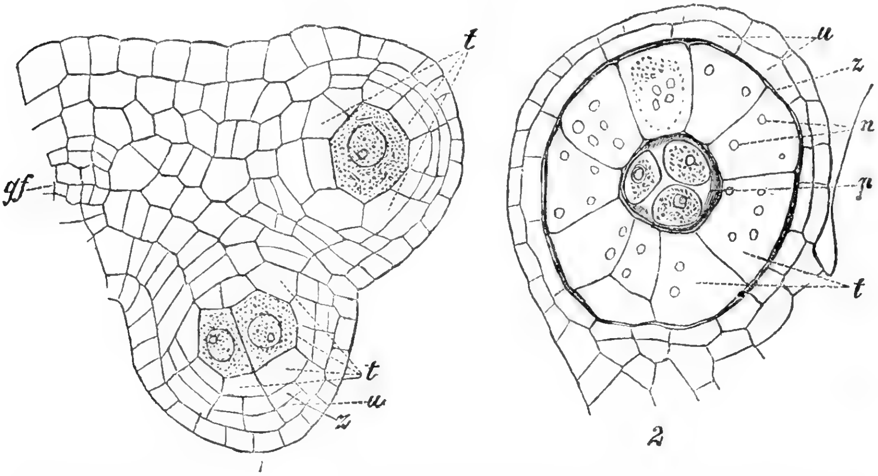

FIG. 392. Knautia arvensis. Anther in transverse section. 1, younger stage. 2, older stage at which one of the microsporocytes, *p*, has already divided into four daughter-cells. *t*, tapetal cells which in 2 have many nuclei, *n*; *u*, *z*, parietal layers, of which *u* becomes compressed, and *z* forms the fibrous parietal layer or endothecium; *gf*, vascular cylinder.

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xxxviii (1880); xxxix (1881); id., Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 384.

[1] Strasburger, The Periodic Reduction of the Number of Chromosomes in the Life-history of Living Organisms, in Annals of Botany, viii (1894).

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 384, footnote 2.

(*a*) MICROSPORANGIA OF THE ANGIOSPERMAE.

Warming[1] has shown that the archesporium, as well as the wall-layers which subsequently surround the sporogenous tissue, proceed from a hypodermal cell-row or cell-layer. At each of the four angles of the anther a hypodermal cell-row or cell-layer divides by periclinal walls (Fig. 393, 2). Of the cells thus produced the inner give rise to the *archesporium*, the outer form the *primary tapetal layer*, the cells of which now divide further by periclinal walls, and the innermost layer of cells so formed becomes later *tapetum* (Figs. 391, *t*, 392, *t*), its cells are *tapetal cells*, and this layer is completed on the inner side of the archesporium by other tapetum-cells which are furnished by the cells limiting it there. The process which in all details corresponds to that in the sporangia in the Pteridophyta is made clear by a comparison of the figures.

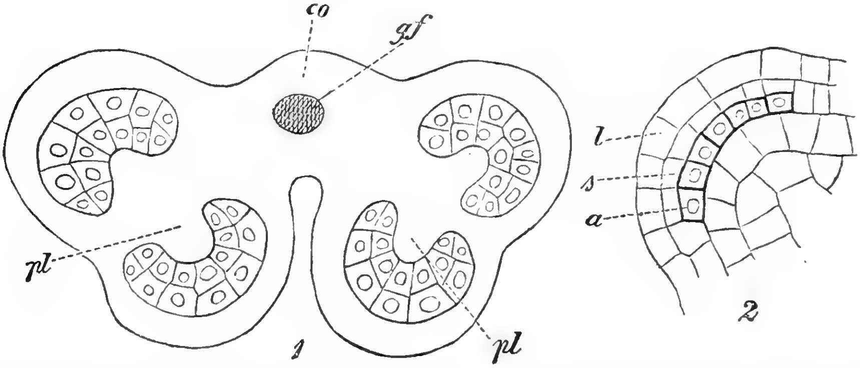

FIG. 393. Hyoscyamus albus. 1, anther in transverse section; *gf*, vascular bundle of the connective, *co*. The sporogenous tissue is shown in the four microsporangia; *pl*, sterile tissue within the sporogenous cell-masses—the placentoids of Chatin. 2, scheme of young anther in transverse section; *a*, archesporium; *s*, primary tapetal layer; *l*, epidermis.

Hyoscyamus. In Hyoscyamus (Fig. 393, 2) the archesporium shows on transverse section a cell-row. The sporogenous tissue which proceeds from this is not very large. It is composed only of two cell-layers, and is curved in a horse-shoe shape, so that the tissue of the stamen is pushed into the pollen-sac. These portions of staminal tissue have been called by Chatin *placentoids*, but they have really nothing in common with the placenta.

Symphytum officinale. In Symphytum (Fig. 391) the sporogenous tissue is much greater in amount. It proceeds here from a cell-layer which in transverse section consists of only a few cells[2].

Knautia arvensis. There are also cases in which the archesporial cells become directly sporocytes. We find this in Knautia arvensis (Fig. 392). The archesporium is here a cell-row. The cells double themselves in some

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[1] Warming, Über pollenbildende Phyllome und Kaulome, in Hanstein's Botanische Abhandlung, ii (1873).

[2] See Warming, op. cit., Taf. iii, Figs. 1-8, representing Symphytum orientale.

pollen-sacs by one—seldom two—longitudinal walls (Fig. 392, 1, below), and the cells of the two rows which thus arise become now sporocytes. In other cases (Fig. 392, 2) this division does not take place, and the archesporial cells directly become the sporocytes.

The outer envelope of the pollen-sac is formed of four cell-rows in Fig. 392, 1—the tapetal cells, *t*, two parietal layers, *u*, *z*, and the epidermis. The outer tapetal cells and parietal cells have proceeded from the division of one layer of cells—the *primary tapetal layer*—and this origin is still evident. The inner of the two parietal layers, *z*, after sharing at first in the conduction of plastic material to the sporogenous cell-mass, is subsequently compressed by the tapetal cells, which, as Fig. 392, 2, shows, enlarge greatly. The outer parietal layer forms here as in many other pollen-sacs the fibrous cell-layer of the anther—the *endothecium*. The walls of the cells of the endothecium have fibrous thickening upon their inner side. They are the 'active' cells, and in the process of drying a tension arises which ruptures the anther-wall at its weakest position, which is opposite the septum separating the two pollen-sacs of one anther-half. The separation-wall consisting of many cell-layers has been destroyed earlier either entirely or only in its lower part. The tapetal cells are also here dissolved about the same time that the young pollen-grains become isolated. First of all there is usually a multiplication of the cell-nuclei within them (Fig. 392, 2) which is the result of fragmentation, according to Strasburger. The protoplasm of the tapetal cells is used up by the growing pollen-grains.

A doubt remains as to the first differentiation of the archesporium in some of the plants investigated by Warming, for example Zannichellia, Gladiolus, Ornithogalum, Funkia ovata, Eschscholtzia californica, Tropaeolum. It is possible that sometimes more than one cell-layer is employed in forming the archesporium, at least Warming gives this behaviour in the case of Tropaeolum. Yet it seems to me that according to his figures this case also can be traced back to the ordinary scheme, especially if one assumes that in the archesporium very irregularly directed division-walls appear.

(*b*) SPORANGIA OF THE PTERIDOPHYTA.

Like differences with regard to the sharp differentiation of the archesporium are found amongst the Pteridophyta. A sporangium of a medium development in Selaginella, such as is represented in Fig. 394, shows clearly that it corresponds throughout with the like stage of development of a microsporangium in Angiospermae. Above and to the left is a longitudinal section through a young sporangium; *a* is an archesporial cell[1]; *t* is the first tapetal cell which is given off from the archesporium. The wall of the sporangium becomes later two-layered by division.

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[1] As a matter of fact there are many archesporial cells side by side owing to the flat conformation of the sporangium, and this can be seen in a tangential section.

According to Bower[1] the separation of the wall from the archesporium does not take place so early as I had assumed[2], but the cell, *t*, proceeds from the division of the outer cell, and it itself shares in the formation of the sporogenous cell-mass. He also says the limitation of the archesporium is frequently less sharp than I supposed. He thinks that in Equisetum arvense and Isoetes, for example, sporogenous cells can be furnished by those which I had considered as the primordium of the wall of the sporangium. That the wall can be differentiated at a relatively late period from the sporogenous cells I had already shown in the case of Ophioglossum, and according to Bower's investigations this occurs elsewhere. A variation in the formation of the sporogenous cells is found also in the Musci; cells of the columella may occasionally be fertile even in the Musci which have a sharply differentiated archesporium, and it seems to me that the question whether the archesporium may be differentiated earlier or later has no fundamental importance, evidently both cases may occur. Absolute rules are never found in relation to organisms.

So far as I can see the simplest expression of the facts regarding the first inception of the sporangia is this: the essential content of the sporangium—the sporogenous cell-mass + sporangial wall—can be traced back to a superficial cell, cell-row, or cell-mass. This divides by periclinal walls. In this way the primordia of the wall and sporogenous cell-mass are separated, but the outer cells or cell-layer may also share in the increase of the sporogenous mass, and the wall then is only later differentiated. One might then designate as archesporium that superficial cell-row or cell-layer which earlier or later gives off sterile cells, whilst in the sporangia of the Angiospermae the archesporium is a layer lying under the already differentiated epidermis, and upon this would depend the above-mentioned differences in the structure of the wall within the Pteridophyta and the Gymnospermae on the one hand and the Angiospermae on the other[3].

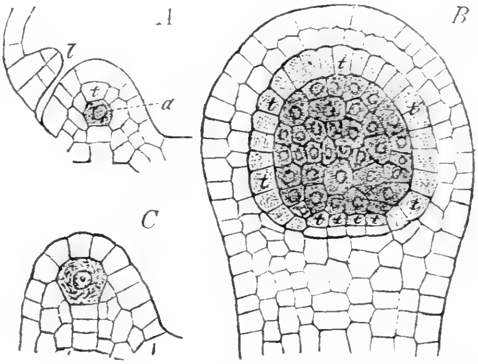

FIG. 394. *A* and *B*, Selaginella spinulosa. Young and old sporangium in longitudinal section. *a*, archesporium, shaded in all figures; *t*, tapetum; *l*, ligule. *C*, Cuphea Zimpani. Nucellus of ovule in longitudinal section. *C*, after Johnsson.

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[1] Bower, Studies in the Morphology of Spore-producing Members: I. Equisetineae and Lycopodineae, in Phil. Trans., 1894; II. Ophioglossaceae, London, 1896; III. Marattiaceae, in Phil. Trans., 1897; IV. Leptosporangiate Ferns, in Phil. Trans., 1899.

[2] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884). I have not myself examined into this question anew, and therefore refer only to the very thorough investigations of Bower, which have frequently completed and partly corrected my investigations made before the time of microtome-work.

[3] I do not regard as well founded the statement of R. Wilson Smith, The Structure and Development of the Sporophylls and Sporangia of Isoetes, in Botanical Gazette, xxix (1900), p. 255. 'The origin of the sporogenous tissue from a hypodermal layer, separated from the beginning from the epidermis, is a spermatophyte character.' The microsporangia of the Gymnospermae behave quite like those of the Pteridophyta.

All sporangia *in the outline* of their process of development are the same. The differences in details are more a question for systematists, and may be omitted here[1]. I must, however, refer to the difference between *eusporangiate* and *leptosporangiate* forms:—

EUSPORANGIA AND LEPTOSPORANGIA. Eusporangia are sporangia which proceed from many cells and have, at least in the primordium, a many-layered wall. Leptosporangia are sporangia which proceed from one cell and have a one-layered wall. There are transitions in the Osmundaceae.

It probably may be also added as a distinction that the stalk in the eusporangium consists of a portion of the tissue of the sporophyll[2]; the stalk in the leptosporangium proceeds from the archesporium, so that if the mother-cell of the sporangium of the Leptosporangiatae is designated as the 'archesporium[3],' the archesporium would appear to be here in most cases a derived structure in that only after formation of a number of sterile cells it proceeds to the formation of the fertile ones. Leptosporangia occur only in Leptosporangiate Filicineae; all other Pteridophyta, as well as Spermophyta, have eusporangia. This distinction is, however, not absolute, as may be expected from what has been already said[4], and the sporangia of the Osmundaceae are probably a connecting link between the two forms of sporangia.

One other question must be dealt with here, namely, that of the origin of the distinction between microsporangia and megasporangia:—

MICROSPORANGIA AND MEGASPORANGIA. When we compare the development of the megasporangia in the heterosporous Pteridophyta with that of their microsporangia, two facts of general interest appear:—

1. The development of the two kinds of sporangia proceeds for a long time in the same way, and the whole development of the microsporangia corresponds with that of sporangia which have only one kind of spore; but in the megasporangia an abortion of a number of the sporocytes takes place. The megasporangia show in their development also that they are derived from sporangia which have possessed a larger number of spores than is now the case, and, as a matter of fact, in fossil forms a larger number of megaspores are present[5].

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[1] For these details see the thorough investigation of Bower, Studies in the Morphology of Spore-producing Members: I. Equisetineae and Lycopodineae, in Phil. Trans., 1894; II. Ophioglossaceae, London, 1896; III. Marattiaceae, in Phil. Trans., 1897; IV. Leptosporangiate Ferns, in Phil. Trans., 1899.

[2] See p. 476, Botrychium.

[3] Not, as has been customary up to now, the tetrahedral inner cell from which the sporocytes proceed.

[4] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884).

[5] In Calamostachys Casheana—a fossil equisetineous plant—numerous spores are present in the megasporangium, although they are fewer in number than in the microsporangia. See Scott, Studies

2. Amongst the heterosporous forms which have now living representatives, a reduction takes place which we can follow. Tetrad-formation goes on in all the sporogenous cells together of the megasporangia of Salvinia and the Marsiliaceae, but it is only in one of the tetrads that one of the four daughter-cells forms a megaspore. Whilst then only one megaspore is found in each megasporangium, the heterospory has proceeded less far than it has in Selaginella, where four megaspores arise from one tetrad.

The Megasporangium of Selaginella. In Selaginella the development of the megasporangium is characterized throughout by the fact that usually only *one cell* of the sporogenous mass[1] arrives at the formation of tetrads. Fig. 395 shows a megasporangium in which the cells of the sporogenous cell-mass have degenerated. One is larger and richer in content than the others, and this is the megasporocyte which will divide into four daughter-cells. There can be no doubt that the sterile and undivided[2] sporocytes are used up as nutrition, although their remains may long be retained. We may well assume that each one of the sporogenous cells was in the condition to become fertile, and that the relationships here are somewhat like those in the case of bees, whose female larvae have all the potentiality of developing into queens, whilst in reality this usually only happens in one special one that is well fed. Anyhow it appears in Selaginella, so far as my observations reach, that the most favoured cell is one which lies about the middle of the sporangium. Even if it should take up no material from the sporocytes which remain sterile[3], it would be still favoured in its nutrition, as to it alone all material would stream from the tapetal cells. It is recognizable even before the breaking up of the sporogenous cell-mass[4].

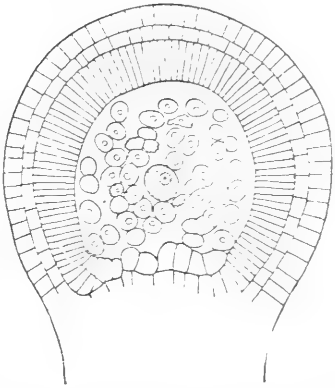

FIG. 395. Selaginella erythropus. Megasporangium in longitudinal section. The megasporocytes are isolated; a central one is larger than the others, and is the one that will divide.

The Megasporangium of Isoetes. The differentiation of the mega-

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in Fossil Botany, London, 1900, p. 53. Also in Lepidostrobus Veltheimianus more than four spores (8 to 16?) are found in each megasporangium, ibid., p. 173.

[1] In Selaginella erythropus I found, not infrequently, two.

[2] As Sachs rightly showed. The statement of Campbell, The Structure and Development of the Mosses and Ferns, London, 1895, p. 504, that the differentiation of the megasporocyte takes place only after the tetrad-division in all the sporocytes, is erroneous—at least for the species examined by me.

[3] In Selaginella helvetica and S. denticulata the sporocytes degenerate in the microsporangia. See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 389. This shows also that the difference between microsporangia and megasporangia is only one of degree.

[4] See also Fitting, Bau- und Entwicklungsgeschichte der Makrosporen von Isoetes und Selaginella, in Botanische Zeitung, lviii (1900).

sporocytes in Selaginella takes place always at an earlier stage in the development than it does in Isoetes, where both in the microsporangia and megasporangia there is a further approach to the behaviour of the Spermophyta. This view, which I published long ago, I still maintain after renewed investigation of both Isoetes lacustris and I. Hystrix[1].

The contradiction which my statement has met with at the hands of Fitting[2] and of Smith[3] relates to subsidiary points, such as the arrangement of the cells, the question when the separation of wall and content takes place, and the like. I have said[4] that from the archesporium a cell-mass proceeds, composed at first of similar cells arranged *nearly* at right angles to the surface of the sporangium; isolated cell-rows of the mass lose their rich protoplasmic content, remain also in their growth behind the others, and become the trabeculae. I do not find that Smith's account deviates from this in any essential point. He finds the arrangement of the cells less regular; doubtless it varies. In Isoetes Hystrix, for example, they run nearly in rows which are directed obliquely towards the base of the sporangium. I have never designated the sporangia as 'chambered' or as 'compound,' although Smith thinks this to be a consequence of my work, and the trabeculae are expressly designated as 'sporogenous tissue which has become sterile.' The tapetal cells are, as in Selaginella, not broken down. With regard to the megasporangia I stated[5] that at a medium stage of development there is one large sporocyte lying in the middle of the sporangium. This is the case; but I was wrong, as the investigations of Fitting and Smith have shown, in the statement that the megasporocyte exercises a destructive influence upon the surrounding cells. I still find stages in which the megasporocytes are separated from the surface by two or three cells which I had considered as proceeding from the division of an archesporial cell out of which the megasporocyte also came, and I see nothing to lead me to regard this interpretation as wrong. This point is, however, quite subordinate. What is more important is the fact that in the megasporangia of Isoetes the cells which do not become megasporocytes *divide further*, although no further than do megasporocytes, and take on a much more vegetative character than do those of Selaginella. In the megasporangium of Isoetes Hystrix there appears moreover, as I find in conformity with Smith, at the beginning a number of cells marked out by their size, all of which, however, do not become megasporocytes. Those which remain sterile evidently divide later. In this and not in the relationships of the arrangement of the cells lies as it appears to me the interest of the development of the sporangium in Isoetes, for we have in it a further approach to the behaviour of the megasporangium of the Spermophyta—an approach which is also expressed in the differentiation of the microsporangia and megasporangia at an earlier period in Selaginella than in Isoetes.

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[1] From material kindly supplied by Graf zu Solms-Laubach.

[2] Fitting, Bau- und Entwicklungsgeschichte der Makrosporen von Isoetes und Selaginella, in Botanische Zeitung, lviii (1900).

[3] R. Wilson Smith, The Structure and Development of the Sporophylls and Sporangia of Isoetes, in Botanical Gazette, xxix (1900), pp. 225, 323.

[4] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), a work which Smith has not referred to.

[5] Goebel, op. cit.

IV

PHYLETIC HYPOTHESES RELATING TO THE FORMATION OF SPORANGIA

I propose to deal briefly here with the hypotheses to which origin has been given by the necessity for the endeavour to connect the different forms of sporangial formation one with another, and at the same time to connect the relationships of propagation of the Pteridophyta and Spermophyta with those of the Bryophyta. I cannot pretend to give an account of the different views, more or less well founded, of different authors; I must content myself in this respect with specially calling attention to Bower's views, because they are founded upon a number of exact historical developmental investigations. All I can do here is to put forward some general thoughts lying at the base of this research.

The principle from which we start is that first formulated by Nägeli[1]. In the year 1853 Nägeli wrote 'One of the first laws is that a higher species or group repeats the phenomena of the lower, but proceeds therefrom to a new phenomenon. This first law finds its explanation and its origin in a second which to me appears to be of the highest significance for the succession of the groups in the Plant Kingdom :—*the reproductive phenomenon of one stage is at a higher stage vegetative.*' In 1884 Nägeli more fully set forth this view[2] and assumed that the sporophyte-generation of the Pteridophyta has arisen by the branching of a sporophyte like that of the moss; it formed a spike-like strobilus in which the terminal sporangium disappeared, and the lateral ones 'by adaptation' became constructed in a leaf-like form. That Nägeli's 'law'—apart altogether from the hypothesis just mentioned—is one of great importance admits of no doubt. In Part I of this book it was shown in examples of the construction of colonies, for example in the Myxomycetes, how a 'higher' construction of the vegetative body comes about by the postponement of the propagation to a later stage of development, and this is really the essence of Nägeli's law. We see further that the sporogonia of the Bryophyta arrange themselves in a series which begins with forms in which all the cells are devoted to spore-formation, as in Riccia—with the exception of a peripheral layer—and ends with forms in which the majority of the cells of the sporogonium have become sterile. Also in the sporangia of the Pteridophyta such a sterilization appears as we see in the trabeculae in Isoetes[3], and in the chambering of the sporangia of Psilotum, the synangia of Marattia, and elsewhere as interpreted by Bower. Further in the shoots a sterilization of those which originally were flower-shoots or inflorescences is a wide-spread phenomenon. The question then is how far do the *facts that are before us* warrant our extending the principle? Let us look at a special case.

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[1] Nägeli, Systematische Übersicht der Erscheinungen im Pflanzenreich, Freiburg i. B., 1853, p. 35.

[2] Nägeli, Mechanisch-physiologische Theorie der Abstammungslehre, see specially p. 472.

[3] Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien, in Botanische Zeitung, xxxviii (1880), p. 565.

When speaking of the sporophyll the peculiar position of the sporophyll of the Ophioglossaceae was pointed out: how it arises upon the upper side of a foliage-leaf. The whole sporophyll is now regarded by many authors as a sporangium of equal value to that of Lycopodium [1]. Now the sporangia of Lycopodium arise in the leaf-axils (Fig. 396, I). If we suppose such a sporangium is gradually increased in size, a large number of sterile cells will be necessary for the nourishment of the spores. We might then suppose that as in Anthoceros or Sphagnum the archesporium surrounds like a dome the inner sterile mass (Fig. 396, II), and that further as in the Musci also the upper part of the archesporium was sterilized (Fig. 396, III). Upon the transverse section of such a construction we might find the archesporium no longer annular but at two places only—right and left (Fig. 396, IV). If now further sterilization throughout its length breaks it up into single sections (Fig. 396, V), we could thus obtain the sporangia of Ophioglossum, and if these were to project slightly those of Botrychium (Fig. 396, VII) [2]. Were these sporangia now partly sterilized we should obtain a lateral sporangiophore sterile at the tip as it is found in Helminthostachys (Fig. 396, VIII), and eventually by complete sterilization a sterile leaf.

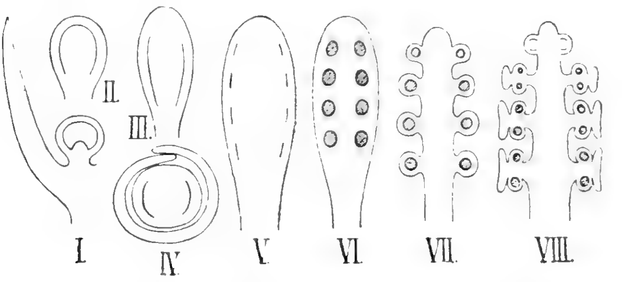

FIG. 396. Scheme of the transformation of a sporangium, say of Lycopodium, into a sporophyll like that of Helminthostachys. The stages follow the numbers I to VIII. VIII represents the sporophyll of Helminthostachys. IV represents a transverse section of the sporophyll of Ophioglossum with enveloping sterile leaf-portion.

It has been shown [3] that if we read backwards the history of development of the microsporangia of Juniperus we find there the transition from a sporangium into a sporangiferous leaf. The sporangia were then primary, the foliation of these secondary. That such a process is possible cannot be denied, but the facts which have been used as a starting-point do not form a sure foundation for it. According to the present state of our knowledge, far-carrying phyletic constructions which deal with processes which were in progress in the very earliest periods of the earth's history, of which the vegetation is known to us now only by some straggling remains, for instance that of the Carboniferous Period, are certainly stimulating, especially if they are founded with sagacity, but there are numerous problems which offer more prospect of a certain solution than these. In this connexion I may refer to what I have said regarding the sporophyll.

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[1] We must not forget that the selection of a single organ without reference to others must often lead to untenable conclusions. The Ophioglossaceae are undoubtedly Filicineae by their structure, the development of their leaves, shoot-axes, roots, and sporangia. One must therefore compare them with Filicineae not with Lycopodineae.

[2] This figure corresponds more with the sporangial spike of Botrychium simplex. In most species of Botrychium we find that the portion bearing the sporangia is branched. One must therefore suppose that a division by branching of a marginal sporangium has taken place.

[3] See p. 516.

V

APOSPORY

By apospory is meant the remarkable phenomena which are expressed in the suppression of the formation of the spores. To a certain extent it is the converse of the apogamy[1] of the prothallus, and it appears in two different forms:—

(*a*) The sporangia are replaced by a vegetative propagation of the sporophyte, the gametophyte is, as it were, entirely kept out.

This case is as yet only known in Isoetes, and here only from the single station, Lake Longemer in the Vosges[2]. It is, however, probable that it will be found elsewhere. The phenomenon comes about probably under the direct influence of external factors. The facts are shortly these:

There are plants of Isoetes which bear neither megasporangia nor microsporangia, but, in place of these, young plants are developed upon the leaves. In some cases sporangia are found as well. In Fig. 292 a case is represented in which a leaf bears a reduced sporangium, and below it a shoot[3]. There are also intermediate stages between the normal construction and complete suppression of the sporangia, coupled with their replacement by the formation of shoots. That the suppression of the sporangia takes place under conditions which are unfavourable for the development of sporangia—be these failure of illumination or the nature of the soil—is very probable, but exact information upon this can only be obtained by experimental cultures—observations in the natural habitat alone are insufficient. I have already compared this case with that of the formation of the gemmae in Lycopodium Selago, in which species it is characteristic to find the gemmae appearing in the region of the shoot where the formation of the sporangia is suppressed[4]. The conditions for this in Lycopodium Selago are in the first place given by periodicity, probably induced primarily by external factors; in Isoetes it is a consequence probably directly of the environmental conditions of the station. The general interest of the case lies in this, that, apart from the remarkable morphological fact, a rich shoot-development takes place in a plant which otherwise usually remains unbranched.

(*b*) The gametophyte is formed directly from the sporophyte, without the intervention of spores.

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[1] See p. 220.

[2] Goebel, Über Sprossbildung auf Isoëtesblättern, in Botanische Zeitung, xxxvii (1879), p. 1; xxxviii (1878), p. 413; also Mer, De l'influence exercée par le milieu sur la forme, la structure et le mode de reproduction de l'Isoetes lacustris, in Comptes-rendus de l'Académie des sciences, xcii (1881).

[3] It may be remarked that also amongst the normal plants the sporangium often keeps only to the upper part of the leaf-base on leaves which have restricted formation of sporangia.

[4] See p. 467.

Druery was the first who found in Athyrium Filix foemina clarissima (Fig. 397) an arrest of the spore-formation and development of the prothalli out of the sporangium without the intervention of spores. Bower made a thorough investigation of the phenomenon, and named it *apospory*[1]. He found that the arrest of the development of the sporangia may take place at different stages, and an aposporous further development of the sporangia, from which prothalli grow out, ensues all the more completely the earlier this arrest takes place. In the sporangia which have proceeded furthest in their 'normal' development, no further development takes place, or this goes on only in the stalk, and it is of special interest that the *archesporium*[2] *takes no share in the further vegetative development.* We may in this see an indication that the archesporium is distinguished from the other cells of the sporangial primordium, just as we saw that a further development can proceed in the wall-layers of the antheridium or the archegonium, but not in the spermatocytes[3]. The prothalli which grow out from this sporangium produce normal sexual organs.

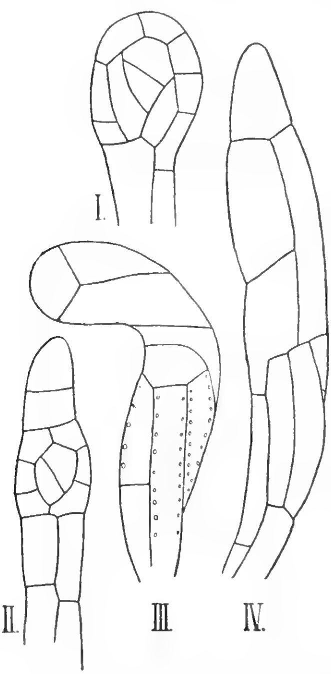

FIG. 397. Athyrium Filix foemina clarissima. I and II, abnormal sporangia in optical section. III and IV, similar sporangia from the outside.

In Polystichum angulare, var. pulcherrimum, the apospory goes further. Prothalli here arise from the arrested sporangia, from the base of the sorus, from the surface of the pinnules, or from the leaf-tip. The development of the sporangium is thus entirely cut out.

The same thing is observed in Scolopendrium vulgare, var. crispum Drummondiae.

In Lastraea pseudomas, var. cristata, Druery found[4] the leaf-tip of a germ-plant growing out into prothalli, and he described germ-plants in which the primary leaves consisted of erect prothalli standing upon stalks which corresponded well with leaf-stalks.

The causes of these remarkable phenomena are unknown to us. We only know that they have nothing to do with the influence of cultivation.

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[1] Bower, On Apospory and Allied Phenomena, Transactions of the Linnean Society, London, 1889.

[2] Using this term in its ordinary sense, that is, for the tetrahedral cell out of which the tapetal cell and the sporogenous cell-mass proceed.

[3] See p. 187.

[4] Druery, Notes upon Apospory in a Form of Scolopendrium vulgare, var. crispum, and a new Aposporous Athyrium; also An Additional Phase of Aposporous Development in Lastraea pseudomas, var. cristata, in Journal of the Linnean Society, xxx (1894).

Speculations innumerable may, however, be based upon them, but they do not give us much insight. We may, for example, derive the Pteridophyta from a plant which had no alternation of generations, but somewhat the conformation of a prothallus of Lycopodium inundatum; whose lobes bore partly sexual organs and partly spores, and only later its development divided into a gamophytic and sporophytic section, which originally were constructed alike; then the gametophyte experienced a regression and the sporophyte a progression. This may be spun out further, but it is mere fancy, which does not help us forward. We do, however, see here that the cells of the sporophyte can furnish the gametophyte without the reduction of the chromosomes to one half, as it takes place in the division of the sporocytes. Moreover, apospory also can be combined with apogamy[1].

The transitions which lead from the normal behaviour to apospory appear to me to show that apospory is not an original but a derived condition in which two factors are concerned:—

1. The arrest of the development of the sporangia;
2. The introduction of a new vegetative development leading to formation of prothalli.

Favourable objects for experimental investigation would be furnished by the Hymenophyllaceae with their basipetal development of the sorus. That apospory is found frequently in forms of fern in which the configuration of the leaf deviates from the normal type, shows us that the formation of the organs has connexions about which at present we know nothing. A slight change in the whole constellation can effect a destruction in another place. We have to do with a system of connexions where 'one thread holds thousands.' An insight into these connexions can only be obtained experimentally, and a work of Atkinson[2] is of interest, who, repeating my research into the virescence of Onoclea[3], found apospory in virescent sporophylls of Onoclea sensibilis which were produced experimentally. Here the influence is certainly one from the outside, but up till now we only know the external jog which brings it about, not the chain which conditions

1. the destruction of the sporangial development, which also takes place in Onoclea Struthiopteris under like conditions;
2. the development of the prothalli.

The examination into these connexions, and not the creation of phyletic pictures, will be the work of the future.

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[1] See Bower, On some Normal and Abnormal Developments of the Oophyte in Trichomanes, in Annals of Botany, i (1888).

[2] Only known to me by a reference in Just's Botanischer Jahresbericht, Jahrgang xxiv (1896), p. 433.

[3] See p. 475.

VI

THE SPORANGIUM OF THE SPERMOPHYTA

A. *MICROSPORANGIA.*

(*a*) MICROSPORANGIA OF THE GYMNOSPERMAE.

The structure of the microsporangia of the Gymnospermae links on closely to that of the sporangia of the Pteridophyta, in that the outermost layer of their sporangial wall shows the same characteristic thickenings of the active cells of the opening mechanism—at least this is the case in all the Cycadaceae, Coniferae, and Gnetaceae which I have examined[1]. The development of the microsporangia also[2] is so like that of the sporangia of the Pteridophyta that it does not appear necessary to enter into this question here, and the relationships of arrangement and of number have already been spoken of when the sporophyll was described[3]. I will only state that in the arrangement of the microsporangia, especially if these are few in a sorus, we can readily see that they are uniformly distributed in the space available—for instance, if there be three they stand at about 120° from one another—and that they also have a marked dorsiventral structure, and in correspondence therewith they open by a longitudinal slit which is directed *downwards*—reckoned from the stamen. In the Coniferae there occur both longitudinal and transverse slits, the latter, for example, in Abies, and doubtless the difference in the method of opening is connected with the conformation and lie of the sporangia[4]: elongated nearly cylindric sporangia, like those of Pinus, best open along their long axis; those of Abies are more spherical. In a more spherical sporangium the direction of opening is a matter of little moment, yet in such a case it is influenced by the position, for instance in Juniperus and other Cupressineae the opening takes place on the side which is *turned away from the sporophyll*—an arrangement regarding the advantage of which it is unnecessary to speak, especially as it has been shown how in the Pteridophyta there is a connexion between the lie and the manner of opening of the sporangia.

(*b*) MICROSPORANGIA OF THE ANGIOSPERMAE.

The microsporangia of the Angiospermae differ from those of the Gymnospermae in this that their *active cells* where such exist are always

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[1] Regarding Ginkgo see p. 515.

[2] See concerning the Cycadaceae: Warming, Bidrag til Cycadernes Naturhistorie, Afdryk af Overs. over d. K. D. Vidensk Selsk. Forhandl., 1879; Treub, Recherches sur les Cycadées, in Annales du Jardin botanique de Buitenzorg, ii (1881); W. H. Lang, Studies in the Development and Morphology of Cycadean Sporangia: The Microsporangia of Stangeria paradoxa, in Annals of Botany, xi (1897). Concerning the Coniferae: Strasburger, Die Coniferen und Gnetaceen, Jena, 1872; Goebel, Beiträge zur vergleichenden Entwicklungsgeschichte der Sporangien, in Botanische Zeitung, xl (1882), p. 771.

[3] See p. 511.

[4] Compare Goebel, Über die Pollenentleerung bei einigen Gymnospermen, in Flora, xcii (Ergänzungsband zum Jahrgang 1902).

hypodermal. Even where in the mature condition the active cells apparently form the outermost layer, for example in Casuarina, the history of development nevertheless shows that there is an epidermis over them, but its cells soon become inconspicuous, and in the examination of the mature anthers can be readily overlooked. In many cases the formation of active cells is suppressed entirely, for example in the parasitic Pilostyles Ulei and in the Ericaceae, or partly as in many plants like Berberis, which have valvular dehiscence of the microsporangia and in which the active cells only occur at the valves[1]. The epidermis of the microsporangia in the Angiospermae may also have a characteristic construction, but we never see in its cells, so far as I know, the peculiar construction of the cell-wall, especially the characteristic thickening which is found in the cells that lie immediately under the epidermis[2] and constitute the hypodermal *endothecium.*

Ericaceae[3]. Fig. 398 shows certain relationships which are found in the Ericaceae and which require further investigation. The epidermal cells of the microsporangia are large, and possess as it appears a slimy content. At the position where dehiscence will occur they are much smaller, and probably the opening which takes place usually in the flower-bud is brought about by the drying up of these cells. At any rate, there are no thickenings in the cell-walls of the endothecium.

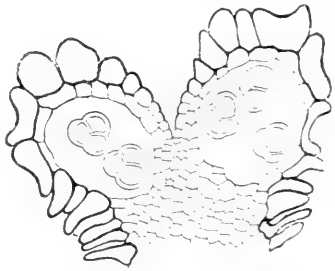

FIG. 398. Erica carnea. Half of an anther in transverse section beyond the point of opening. No endothecium is present, although the pollen-tetrads are already formed. Magnified.

It is then evidently a weighty systematic character of the Angiospermae that the active cells of the microsporangium, if they are present, are in the endothecium, *whilst in the Pteridophyta and Gymnospermae they are in the exothecium*[4].

As to the lie of the point of opening of the sporangium in the Angiospermae there are many variations. The significance of this depends specially upon the relationships to pollination by insects and must remain here unexplained. It lies within the province of the biology of pollination.

MICROSPORES.

Space forbids us a discussion of the construction of the microspores. I will only briefly recall the differences in the pollen in wind-pollinated and insect-pollinated flowers, the remarkable thread-like pollen of Zostera and Halophila, the pollen-tetrads and pollinia as they occur in different cycles of affinity.

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[1] See Chatin, De l'anthère, Paris, 1870.

[2] These extend often over the connective.

[3] See Artopoeus, Über Bau und Öffnungsweise der Antheren und die Entwicklung der Samen der Ericaceaen, in Flora, xcii (1903).

[4] Whether this is without exception further investigation alone can tell. See p. 577.

The gametophyte in the Spermophyta is so dependent that it appears best to deal with it along with the sporophyte. We must therefore speak here of the germination of the microspores.

GERMINATION OF THE MICROSPORES.

The development of the microspores in germination has been made known to us specially by the investigations of Strasburger, Belajeff, Ikeno, Hirase, and Webber. It shows us so far a parallel formation with that in the megaspore, as we find in both a vegetative development which is always very much shortened.

The form of the microspores varies; sometimes it is tetrahedral, sometimes bean-like (dorsiventral), sometimes more spherical. The rounded basal surface of the tetrahedral microspore may be designated the *base*; the portion over against it the *apex*; and, similarly, in the dorsiventral microspore the convex outer surface is the base.

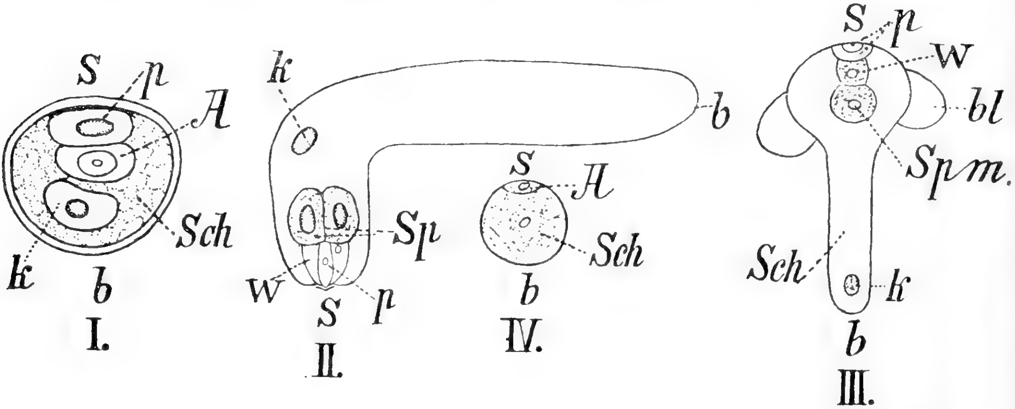

FIG. 399. Scheme of germination of the microspore. I and II, Cycadaceae. Webber's figures have been used in the construction. III, Abietineae. IV, Angiospermae. *S*, the apex of the microspore; *b*, the base; *p*, prothallus-cell; *A*, mother-cell of the antheridium; *Sch*, tube-cell; *k*, nucleus of the tube-cell; *W*, wall-cell of the antheridium; *Spm*, mother-cell of the male sexual cells; *Sp*, spermatocytes; *bl*, vesicular parachute of pollen-grain.

Amongst the Cycadaceae[1] the germination of the microspore of Zamia has been made known to us through the researches of Webber. In the ripe microspore we find three cells[2] (*p*, *A*, *Sch*, in Fig. 399, I). Cell *p* lies at the apex of the microspore and is a cell of the prothallus; cell *A* is the mother-cell of the antheridium; cell *Sch* is the tube-cell which, developing in the pollen-chamber, at first acts as a haustorium to bring nourishing material out of the nucellar tissue to the germinating microspore; only

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[1] See Ikeno, Untersuchungen über die Entwicklung der Geschlechtsorgane und den Vorgang der Befruchtung bei Cycas revoluta, in Pringsheim's Jahrbücher, xxxii (1898); H. J. Webber, Spermatogenesis and Fecundation of Zamia, in U. S. Department of Agriculture, Bureau of Plant-Industry, Bulletin No. 2, Washington, 1901. Webber gives the literature.

[2] Whether occasionally a fourth appears is of no significance here.

later does the tube-cell bring the apex of the microspore into contact with the archegonia by the formation through intercalary growth of a sac-like outgrowth (Fig. 399, II). Such pollen-tubes I call *acrogamous*. Acrogamous pollen-tubes are only found in the Cycadaceae and Ginkgo, and this fact has no doubt the closest connexion with the existence of a pollen-chamber.

At the apical end of the pollen-tube the following changes take place:—The mother-cell of the antheridium is divided by a wall oblique to the long axis of the pollen-tube into two cells, an upper and an under. The upper cell is the central cell of the antheridium out of which by division two spermatocytes proceed, and these give origin to two giant spermatozoids. The under cell has received the unfortunate name of 'stalk-cell' which is inapplicable upon the two grounds that the antheridium is sunk and can therefore have no true stalk-cell, and that we never see that a stalk-cell is separated from a spermatocyte, but there is a separation of the *wall-cell*[1].

The first cell of the prothallus at the apex of the microspore (Fig. 399, I, *p*) swells up and surrounds the stalk-cell like a ring. Both are limited to the outside only by a membrane, not by a wall. Nevertheless these cells may reach a considerable size, and it is remarkable that no function has yet been ascribed to them. One might suppose, as they contain starch, that they aid in the nourishment of the strongly growing spermatocyte, but I think that they constitute an apparatus for the opening of the pollen-tube at its point. The pollen-tube is cuticularized. Both in the pollen-tube and in the cells which are found under the spermatozoids the osmotic pressure gradually increases. The prothallus-cell, *p*, presses upon the stalk-cell it encircles, and this again is under the pressure of the content of the pollen-tube. The pressure so acts that the membrane of the pollen-tube bursts at its least stretchable place—that is, at the point of attachment to the cells of the prothallus—the spermatozoids are pressed out and are able then to force themselves into the egg.

The tube-cell has been also considered as the wall of the antheridium. I see no ground for this. We know of no case in which the antheridial wall functions as a haustorium, but we have many cases, on the other hand, in the megaspores of the Angiosperms where the cells of the prothallus are converted into haustoria [2].

We have then in the microspore of the Cycadaceae the following structure:—

1. Two cells of the prothallus, of which one becomes a pollen-tube

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[1] See p. 180. Wettstein, Handbuch der systematischen Botanik, ii (1904), has recently called the stalk-cell a 'wall-cell.'

[2] The whole orientation of the antheridium is against the view also.

which originally is a haustorium, and later conducts the spermatozoids to the archegonium, whilst the second one effects the opening of the pollen-tube.

2. The antheridium, consisting of wall and spermatocytes.

In the other Gymnospermae and in the Angiospermae the pollen-tubes are *basigamous*. They serve indeed at first as haustoria, and later as canals, which here conduct the massive male gametes to the egg. As the opening of the pollen-tube takes place at the basal end the cells of the prothallus have become, with the exception of the tube-cell, functionless. They are indeed in many still formed—two, for example, in Larix, Picea vulgaris, Pinus silvestris, P. Pumilio—although in such cases they usually collapse soon, but in the Cupressineae and Taxodium their formation is entirely suppressed, as it is in all Angiospermae. We have, therefore, in these cases only the tube-cell and the mother-cell of the antheridium. This mother-cell in the Gymnospermae divides into two cells—one corresponding to the spermatocyte, which furnishes the two spermatozoids; the other is the wall-cell which we prefer to designate the *dislocator-cell*. Its function is to set loose the spermatocyte from its point of attachment, as is particularly evident in Juniperus, where the dislocator-cell is very large. Perhaps it bursts and in that way promotes the passage of the spermatocytes into the pollen-tube, but in other cases the simple swelling of the dislocator-cell may effect this. Only in some Gymnospermae is it suppressed, but in Angiospermae its formation is always suppressed, because there it would be unnecessary, seeing that the spermatocytes from the first are not firmly fixed and have no attachment to the wall of the microspore.

The views that have been here expressed require to be proved by investigation, but it seems to me hardly to admit of doubt that we shall obtain a proper understanding of the germination of the microspore only when we obtain more information about the *function* of the cells which are found in the pollen-tube. If what has been said above be correct there is in the microspore of the Spermophyta clear connexion between structure and function, and functionless parts are evidently reductions.

B. *MEGASPORANGIA.*

(*a*) GENERAL FEATURES.

Hofmeister's epoch-making investigations determined once and for all that the ovule in the Spermophyta is the homologue of the megasporangium in the Pteridophyta. A thorough comparison of these sporangia only is possible, however, if the historical development of their relationships are discussed. Here we shall deal first of all with the grosser configuration of the ovule.

We distinguish usually in it a *stalk* or *funicle*, one or more *integuments*, and the *nucellus* enveloped by the integuments. The nucellus is the megasporangium[1]. This is undoubted. On the other hand the views upon the morphological significance of the integuments are various. So far as functional importance is concerned we have to consider the following:—The integuments act as a protective envelope to the ovule, and then later they form the seed-coat. Where, as in Sympetalae, the ovule consists of a thin nucellus and one thick integument, the integument has to provide nutrition to the embryo-sac which grows out into it[2]. The micropyle in all *porogamous* plants evidently conducts the pollen-tube. In the germination of the seed the most rapid uptake of water also takes place at this point.

Porogamy and aporogamy. In a number of Dicotyledones the micropyle does not function as a conductor of the pollen-tube, and the plants are therefore designated *aporogamous*. In Cynomorium[3] coccineum the micropyle withers very rapidly and forms no longer an open canal. The same thing happens in the genus Gunnera[4], which stands so isolated in the plant kingdom; also in the Cannabineae[5] and in Alchemilla arvensis[6]. This aporogamous condition has evidently appeared independently in different dicotylous plants. In Cynomorium the pollen-tube forces its way through the apex of the ovule. This method is *acrogamous*. Gunnera ripens its seeds most probably parthogenetically. Pollen-tubes have never been proved here. In Alchemilla the pollen-tubes force themselves in between the cells, and grow up from the chalazal region to the egg-apparatus. This method is *basigamous*. It also happens in Casuarina[7] as well as in the Corylaceae and Juglandeae, notwithstanding that they possess a micropyle. These variations have evidently no importance for the systematic grouping within the plant kingdom, but an explanation is still required of why they should appear so frequently in plants which have specially simply constructed flowers[8]. An intermediate position is taken by the ovules in which a pollen-tube partly grows through the tissue of the ovule. We see this in the Ulmaceae[9] and in the Cannabineae. It may well be assumed that in all these plants special reasons exist, either in the structure of the cells or in the conditions of nutrition of the pollen-tube, which cause it to take the path it does.

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[1] I may mention here that the nucellus may sometimes be abnormally developed as a microsporangium. I observed such a case in Begonia; see Goebel, Beiträge zur Kenntnis gefüllter Blüthen, in Pringsheim's Jahrbücher, xvii (1886), p. 246, Figs. 48 and 49. The literature is cited.

[2] See p. 638.

[3] Pirotta e Longo, Osservazioni e ricerche sulle Cynomoriaceae, in Annuario del R. Istituto Botanico di Roma, ix (1900), Fasc. 2.

[4] Schnegg, Beiträge zur Kenntnis der Gattung Gunnera, in Flora, xl (1902).

[5] Zinger, Beiträge zur Kenntnis der weiblichen Blüthen und Inflorescenzen bei Cannabineen, in Flora, lxxxv (1898), p. 189.

[6] Murbeck, Über das Verhalten des Pollenschlauches bei Alchemilla arvensis, (L.) Scop., und das Wesen der Chalazogamie, Acta Universitatis Lundensis, xxxvi (1900).

[7] Treub first discovered the process in this plant and called it *chalazogamy*.

[8] Yet the Fagaceae have porogamous fertilization. How do Sagina and like forms behave?

[9] Nawaschin, Über das Verhalten des Pollenschlauches bei der Ulme, Nachrichten der Kaiserl. Akad. der Wissenschaften in St. Petersburg, 1897. The pollen-tube here pushes out of the tissue of the funiculus through the integuments to the apex of the nucellus.

THE INTEGUMENTS.

THE NATURE OF THE INTEGUMENT. From the morphological standpoint there are two possible explanations of the formation of the integument:—

(*a*) We may consider it as a new formation which finds no analogy in the Pteridophyta.

(*b*) We may link it on to the indusial formation of the Pteridophyta, finding an analogue in the megasporangia of Azolla (Figs. 325–327), which are invested by an indusium laid down like an annular wall.

The second interpretation was mainly founded by Warming. Under it it is most natural to consider the nucellus only as the megasporangium, to regard the funiculus as a portion of the sporophyll on which the megasporangium arises as a terminal new formation, just as a megasporangium of Azolla arises on a placenta which is formed from a transformed leaf-lobe. This view may find confirmation in the remarkable construction of Lepidocarpon, a fossil lycopodiaceous plant recently described by Scott[1]. The sporophyll of Lepidocarpon bears at its base a megasporangium, in which one only of four spores that are laid down develops, and the megasporangium is surrounded by a thick integument which proceeds from the sporophyll. The microsporangia too have a similar integument. The assumption then that the integument of the ovule in Spermophyta took origin from the sporophyll is not altogether unsupported by analogy, and the known cases of virescent malformation[2] are conformable also with this. We may also recall in this connexion that the outgrowth beneath the ovule in the Cycadaceae (Fig. 400, *IV*) certainly belongs to the carpel,

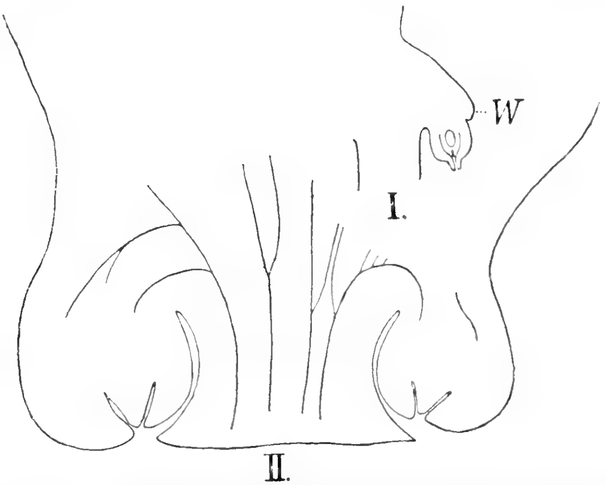

FIG. 400. Ceratozamia robusta. I, surface-section through the basal portion of a carpel. One ovule is cut through longitudinally; *W*, swelling below the integument. II, the same in a younger stage. The swelling below the integument is not yet visible.

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[1] Scott, Note on the Occurrence of a Seed-like Fructification in Certain Palaeozoic Lycopods, Proceedings of the Royal Society, lxvii (1900).

[2] Part I, p. 182.

and may be considered as an approach in some measure to a second integument, and that in the Eusporangiate Pteridophyta the stalk of the sporangium has been explained as arising through an outgrowth of the tissue of the sporophyll[1].

DEVELOPMENT OF THE INTEGUMENTS. To enter into a description of the development of the integuments here is unnecessary as no new point of departure or facts has been brought forward during the last twenty years. I will mention therefore only shortly the following:—

1. The integuments arise always as lateral outgrowths on the ovule below the nucellus, which is laid down everywhere as a terminal structure, even in cases where in its *later stages*, on account of the massive development of the integuments, its terminal position is not apparent, as in many Sympetalae, whose ovules have a thin nucellus and *one* massive integument.

2. In *atropous*[2] ovules the integuments arise as a circular wall.

3. In *anatropous* and *campylotropous* ovules the development of the integument, if only one is present, is arrested on the side turned towards the funicle, or forms there only the portion of the integument devoted to the micropyle.

4. Where two integuments arise, in the majority of cases, the inner is the one first formed, then the outer—Euphorbia is an exception. In anatropous ovules the outer integument then shows the arrest above mentioned, that is to say, is not developed upon the side next the funicle.

5. In small ovules the integuments proceed from the outermost cell-layer. Where there is more massive construction of the integument deeper cell-layers also share.

6. The number of the integuments is generally within one large cycle of affinity constant: two in most Monocotyledones and choripetalous Dicotyledones[3] also in the Primulaceae; one in most sympetalous Dicotyledones, the Cupressineae, Abietineae, and elsewhere. Yet there are within one family variations which more accurate investigation may show perhaps to be derived. For example, Aconitum has two integuments to its ovule, whilst the nearly allied Delphinium has only one. But ovules of Delphinium[4] at a middle stage of development show clearly at the micropylar end—especially if they be looked at whole and not in section—that the integument is double, and we may regard the integument of Delphinium as the result of a concrescence of two. The phenomenon is quite like that of the origin of a sympetalous corolla. In the cycle of affinity of the Ranunculaceae one might, upon the basis of the facts above mentioned, conjecture that the ovules provided with two integuments were a more primitive type

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[1] See p. 602.

[2] The expression *orthotropous* for straight ovules should be avoided, as it is used now of shoots in a definite sense, which does not fit most atropous ovules.

[3] One integument is possessed by the Umbelliflorae and many Ranunculaceae.

[4] Delphinium cashmirianum was examined. See also Strasburger, Die Coniferen und die Gnetaceen, Jena, 1872, p. 415. The indentation of the outer integuments often appears slight, or not at all, upon sections, even where a study of the inception of an outer integument shows that, as usual in anatropous ovules, it is only developed upon the side turned away from the funiculus.

from which that with one integument has been derived. We might see the like also in other cycles of affinity, especially in the Rosaceae. Spiraea Lindleyana[1] has two separate integuments; in Spiraea Fortunei and others they hang together, except at the micropylar region; in Spiraea Aruncus, S. Ulmaria, and S. Filipendula there is only one. Also in Hippuris Van Tieghem considered that the integument is the result of the fusion of two which are quite separate from one another in Myriophyllum.

ATEGMINOUS OVULES. Naked ovules—that is to say ovules with no integument—occur both in Monocotyledones and Dicotyledones, but the question arises whether this behaviour is a reduction or a primitive one, and with what biological relationships it stands in connexion. Some examples therefore of it will be given:—

MONOCOTYLEDONES.

AMARYLLIDEAE. In this family we find ategminy of the ovules in

Crinum. The ovules of this amaryllidaceous plant, which is neither a parasite nor a saprophyte, have no integument[2]. The ovules appear on the placenta as slightly differentiated swellings provided with a funiculus, and they contain, not infrequently, more than one embryo-sac. This rudimentary construction may be connected with the fact that no seed-coat is formed[3]. The seeds are arranged for immediate germination, and are protected only by some layers of cork-cells which are formed from the *endosperm*. As a matter of fact the endosperm develops here, in the main, independently of the nucellus. It contains chlorophyll also and forms, in a certain measure, a passage to a development independent of the megasporangium.

The other Amaryllideae have mostly two integuments. Amaryllis Belladonna has only one. Although we have no comparative history of the development of the seeds of this family, such as is necessary in order to form a secure basis for phyletic conclusions, it appears to me that the facts, so far as we know them, are in favour of a *reduction*.

DICOTYLEDONES.

Amongst these we find ategminous ovules chiefly in some parasites and saprophytes, but also in other plants.

GENTIANEAE. Whilst other gentianaceous plants possess ovules with one integument the saprophytic Voyria has an ovule which is described as naked[4].

Voyria. The ovules in this genus occur in large numbers within the ovary. They are elongated but have a normally constructed and normally arising embryo-

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[1] Van Tieghem, Structure de quelques ovules, Journal de Botanique, xii (1898), p. 213.

[2] See Goebel, Pflanzenbiologische Schilderungen, i (1889), p. 129, confirming the statements of Prillieux and of A. Braun. See also the literature cited by A. Braun, Über Polyembryonie und Keimung von Coelebogyne, in Abhandlungen der Berliner Akademie (1859).

[3] That is to say, the laying down of an integument may be suppressed because the whole economy of the seed is of such a kind that the seed-coat, which would protect it otherwise during the resting period, is not required.

[4] Johow, Die chlorophyllfreien Humusbewohner West-Indiens, in Pringsheim's Jahrbücher, xvi (1885), p. 442.

sac[1]. Some years ago I had the opportunity of gathering in Venezuela, on the slopes of the Cumbre de San Hilario, plants of Voyria azurea, which decked with its blue flowers the soil of the shady woods and grew along with a number of monocotylous saprophytes. After examination of, I must admit, only a small amount of material, there seemed to me to be an indication of an integument, and of a micropyle as a shallow, easily overlooked indentation (Fig. 401, *Mi*). Johow has remarked that the ovule, after the formation of the embryo-sac, corresponds essentially with an anatropous one. I would consider the terminal outgrowth of the ovule as belonging to the integument, which here in other respects remains stationary at an early stage of development. The extremely rudimentary nucellus experiences no curvature, as in anatropous ovules elsewhere, but it develops from the first in an inverted position, so that, to speak in comparative morphological terms, we have a 'congenital curvature.' I have shortly referred to this case because it appears to me to support clearly the assumption of a reduction. Why this condition should be brought about we do not know. It is probable that it is teleologically[2] connected with the great number of ovules, perhaps causally with the saprophytic, in others the parasitic, mode of life, But then against this we have the fact that ategminous ovules occur also in a number of autotrophic plants. It is then very possible that the want of the integuments of the ovule has really nothing whatever to do with parasitism and saprophytism, but that amongst plants with this kind of ovule a certain number have retained a parasitic type.

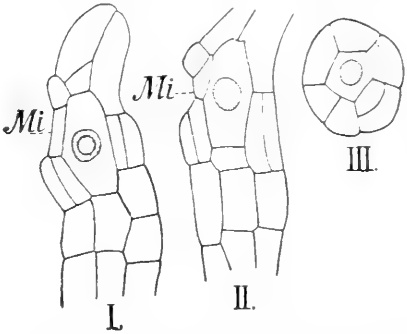

FIG. 401. Voyria azurea. I and II, ovule of middle development in longitudinal section. III, the same in transverse section. Megasporocyte shown; *Mi*, rudimentary micropyle.

OLACINEAE. Valeton and Van Tieghem[3] have shown that ategminous ovules occur in some plants which are commonly reckoned in the family of the Olacineae—in Olax, Liriosma, Schoepfia—whilst other plants belonging to this family, in the old sense, have ovules with one or two integuments. A parasitic or saprophytic mode of life of those Olacineae which are provided with ategminous ovules, has not yet been shown.

Regarding Van Tieghem's peculiar systematic views I do not require to say anything after what has been said above about the Amaryllideae and Gentianeae; I may add only that the rubiaceous plant Houstonia, which is autotrophic, has ategminous ovules[4].

SANTALACEAE. In this family we find, for example in Thesium[5], three naked ovules upon a free central placenta. Each of them stands opposite one of the three

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[1] By tetrad-division.

[2] See p. 254.

[3] Van Tieghem, Sur les phanérogames à ovules sans nucelle, formant le groupe des Innucellées ou Santalinées, in Bulletin de la Société Botanique de France, xliii (1896), p. 543. See also Engler, in Engler und Prantl, Die natürlichen Pflanzenfamilien, Nachträge zu III, i, p. 144.

[4] According to a communication in a letter from F. E. Lloyd.

[5] See Guignard, Observations sur les Santalacées, in Annales des sciences naturelles, sér. 7, ii (1885), p. 181. The literature is cited here.

carpels. A small depression can be seen at the apex of this ovule, as in Voyria, and may be considered as the remains of a micropyle, so that the Santalaceae possess the indication of *one* thick integument. The formation by the embryo-sac at its basal end of a haustorium, which bores deeply into the placenta, is a feature which is widely spread in the Sympetalae. The growing out from the ovule of the embryo-sac at its apex, where the formation of endosperm takes place, is seen also in Crinum, and is probably connected with the rudimentary construction of the whole ovule. That no relationship exists between this rudimentary construction and the number of the ovules is clear. Of the three ovules only one becomes perfect, and the envelope of this is supplied by the ovarian wall, as there is no seed-coat present.

Such rudimentary ovules are found in particular in parasites which form rich endosperm and a complete embryo—at least this is true for

LORANTHACEAE[1]. We owe our knowledge of the ovules in this family to the investigations of Treub[2].

Loranthus sphaerocarpus. In Loranthus sphaerocarpus a free central placenta rises up at the base of the ovarian cavity, which bears some very rudimentary ategminous ovules, and later becomes concrescent completely with the inner surface of the ovary, so that the embryo-sacs then are embedded apparently in a tissue filling the ovary. The reduction goes further in Viscum articulatum and Loranthus pentandrus, where there is a central placenta, and ovules are no longer formed upon it.

Viscum articulatum. Viscum articulatum[3] possesses an ovary formed of two carpels which so closely unite with one another that only a narrow slit remains between them. Where this slit ceases at the base of the ovary many embryo-sacs proceed out of some cells rich in protoplasm, which lie near one another or are separated by parenchymatous cells; of these embryo-sacs, however, only one experiences a further development.

Loranthus pentandrus. A similar development appears in Loranthus pentandrus. If we compare it with that found in Loranthus sphaerocarpus we can have no doubt whatever that we have to deal with a reduction. The placenta and the ovule are then not 'congenitally concrescent' with the tissue of the ovary, but have not come into existence—like the pollen-mother-cells of Cyclanthera[4], which do not differentiate in a specially constructed pollen-sac, but in a ring-like swelling of the flower-axis; the mother-cells of the embryo-sacs of the Loranthaceae do not develop in the ovule, but in the flower-tissue beneath the ovary. The megasporangium then is suppressed in its differentiation, only the megaspores develop, and, as in the Santalaceae, they show often peculiar phenomena of growth which have a most

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[1] Van Tieghem's more recent work is set forth by Engler, in Engler und Prantl, Die natürlichen Pflanzenfamilien, Nachträge zu III, i, p. 124.

[2] Treub, Observations sur les Loranthacées, in Annales du Jardin botanique de Buitenzorg, ii (1881), p. 54; iii (1883), p. 1. Treub's results completed and corrected the older work of Hofmeister, Neue Beiträge zur Kenntniss der Embryobildung der Phanerogamen: I. Dikotyledonen, in Abhandlungen der Königlich sächsischen Gesellschaft der Wissenschaften, vi (1859).

[3] The same is the case in Viscum album, see Jost, Zur Kenntniss der Blüthenentwicklung der Mistel, n Botanische Zeitung, xl (1888), p. 357. The mother-cell of the embryo-sac divides here into two daughter-cells, the lower of which soon forms upwards an outgrowth, this I consider as an early haustorial formation.

[4] See p. 554.

intimate connexion with the nutrition of the megaspores—a connexion which of course is different from what it would be were the megaspore in a well-formed megasporangium. Other cases, which will be presently mentioned, show us that the embryo-sac lives as a parasite, and that it derives its nourishment from wherever it best can.

BALANOPHOREAE. The reduction goes furthest in the Balanophoreae, whose behaviour Treub[1] has made clear. There is neither a flower-envelope nor carpels visible in the female flower here. The whole flower consists of a cell-body, of which a hypodermal cell (Fig. 402) becomes an archesporium[2], whilst the outer cell-layer grows out into a long pointed process; the whole structure has a certain resemblance to an archegonium, but there is no neck-canal. As other Balanophoreae[3] possess usually two carpels with a central placenta, and two very slightly differentiated ategminous ovules, it appears most natural to derive Balanophora from them by assuming that

1. The formation of the carpels is suppressed.
2. The number of the ovules is reduced to one.
3. The formation of the ovules takes place out of the primordium of the flower itself[4], in which one can no longer speak of an 'axis,' as this expression has a meaning only when we understand a structure that possesses at least the possibility of bringing forth organs as appendages.

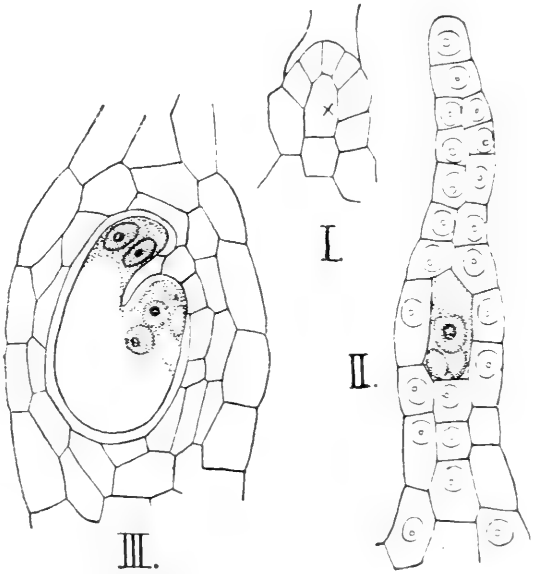

FIG. 402. Balanophora elongata. I, young female organ in longitudinal section. II, older female organ in similar section showing the archesporium, which is shaded. III, female organ nearly mature in like section; embryo-sac developed. I magnified 230. II and III magnified 300. After Treub.

The case is quite like what occurs in the vegetative organs of many parasites. We know from the researches of Solms-Laubach that, for example in species of Pilostyles[5], the vegetative body of the parasite which bores into the host may be

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[1] Treub, L'organe femelle et l'apogamie du Balanophora elongata, Bl., in Annales du Jardin botanique de Buitenzorg, xv (1898), p. 1.

[2] Sometimes this divides once, sometimes it does not divide at all, and then at once becomes a megaspore.

[3] See Lotsy, Rhopalocnemis phalloides, in Annales du Jardin botanique de Buitenzorg, sér. 2, ii (1901), p. 73. Lotsy thinks that the Helosideae, to which Rhopalocnemis phalloides belongs, are better separated from the Balanophoreae; even if one does so their near relationship would not be doubtful.

[4] An analogous case would arise if the male flower of Juniperus were reduced to one of its microsporangia. See p. 516.

[5] See p. 225.

reduced to a single hypha-like strand of tissue. In this there is no possibility of applying the ordinary morphological schemes. The same is the case in the flowers of Balanophora. We do not know here, as elsewhere, in what connexion the reduction stands to the parasitic mode of life. If such a connexion exists it may be of two kinds,—

(*a*) *direct*—that is to say, conditioned by the parasitic mode of life itself;

(*b*) *indirect*—that is to say, the parasitic mode of life permits of the retention of variations in structure which may also appear in non-parasitic plants, but are there incapable of persistence. An indirect connexion of this kind—of reduction with mode of life—has been already shown to be probable in Utricularia and the Podostomaceae[1].

From what has been said we gather that in the ovule, and partly also in the whole gynaeceum of the Angiospermae, considerable reductions may take place. We can hardly designate as a reduction the limitation of the integument to one, but we may certainly call it a reduction if the formation of the integuments is entirely suppressed, although we may not be able to give the reason for this. At the same time it is easy to understand that where the integument plays no longer any part in the formation of the seed-coat—and this is the case in many plants in which the envelope of the seed is formed by the pericarp, the seed-coat being at the same time destroyed, for instance in Gunnera, the grasses—the formation of the integument may from the first be suppressed. We must assume that the 'tendency to disappear' may show itself in all organs in individual forms, and that this then leads to an abortion if this can take place without injury to the whole economy of the plant. It would be of course quite absurd to endeavour to group plant-forms which have naked ovules into *one* systematic group. It is quite clear that this condition is developed in different cycles of affinity.

A further stage of reduction is that in which the ovules and placenta no longer appear as definite organs within the gynaeceum, as in Viscum, but the megasporangia are sunk in the tissue of the megasporophyll. Finally, in Balanophora the differentiation of the megasporophylls themselves is suppressed, the whole flower is evidently reduced to one megasporangium. It has been shown[2] how this example specially illustrates the fact that we cannot deny the occurrence of *far-reaching changes* in the formation of organs, and that our work at first must be to make a picture of how they have come about, but not to endeavour to read into a terminal member of a series its first beginnings.

THE NUCELLUS.

DEVELOPMENTS WITHIN THE NUCELLUS IN RELATION TO STIMULI. The megasporangium of Spermophyta is distinguished from that of the

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[1] See p. 241.

[2] See p. 557.

Pteridophyta by the fact that the megaspores germinate within the sporangium, and that the megasporangium with its envelope or envelopes develops, after fertilization, into a seed. Approaches to this behaviour are found in some Pteridophyta. In Salvinia the megaspores germinate within the megasporangium[1]. The megaspores in many species of Selaginella[2] undergo the first stages of germination within the megasporangium, are then emptied out of the megasporangium, and only later resume their germination. An actual transition to seed-formation does not appear in any living forms; such a transition would not even exist if, for example in Selaginella, there were found forms in which the megaspores were not shed from the sporangia, but remained enclosed in the megasporangium until germination of the embryo of the sporophyte[3]. From the teleological side one might consider it a step forward were the megaspores, which represent a considerable expenditure of plastic material, no longer shed from the mother-plant, away from which it is uncertain whether they find favourable conditions for germination and fertilization, but from which when they separate they carry usually reserve-material sufficient for the first development of the embryo which proceeds from the fertilized egg. As a matter of fact we observe that the plant is, so to speak, always more sparing with material the higher we rise in the series of the Spermophyta: the Cycadaceae form in their megaspores large prothalli even without pollination[4]; the Coniferae allow of the germination of the megaspore within the megasporangium only after the stimulus of a pollen-tube; upon this stimulus is dependent in some Angiospermae the laying down of the ovules, in others their further development at least. Some examples may be quoted.

The female flowers of Quercus and Fagus, also Corylus, show no trace of ovule at the time of pollination. So far as I know it has not been experimentally proved, but it appears probable that the stimulus exercised by the pollen-tube starts a further development[5]. It is certain that this is the case in the Orchideae whose ovules are quite rudimentary at the time of pollination, and also in some Dicotyledones, for example in Fraxinus, Forsythia, and Syringa dubia; whilst in other Oleaceae[6], such as Syringa vulgaris, Fontanesia Fortunei, and species of Ligustrum, there are well-developed ovules at the time of pollination.

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[1] This may be connected with the aquatic life.

[2] Bruchmann says that Selaginella spinulosa is an exception.

[3] Compare F. M. Lyon, A study of the Sporangia and Gametophytes of Selaginella apus and Selaginella rupestris, in Botanical Gazette, xxxii (1901), p. 124.

[4] How far the several genera differ in this character requires investigation. In Cycas, as it grows in our plant-houses, the formation of archegonia takes place in the prothallium of some, usually not all, of the unpollinated ovules.

[5] The further development of the ovary is suppressed in Corylus if the male catkins discharge their pollen before the development of the stigmas, and this happens in many springs and may be considered an experimental proof of the connexion mentioned above.

[6] See Billings, Beiträge zur Kenntniss der Samenentwicklung, in Flora, lxxxviii (1901).

In the Coniferae the development of the megaprothallium depends upon the pollination but not upon the fertilization[1]; the Angiospermae go one step further. Out of the germ-tube of the microspore two nuclei pass into the megaspore in fertilization, as has been shown by the investigations of Nawaschin, Guignard, and others[2]. One of these stirs up the egg to a further development. It effects the fertilization. The second one stimulates the formation of endosperm. Whether we speak of this as a 'double fertilization' or not is to my mind non-essential. I have always seen in the process, since it became known, only an arrangement which secures the further development of the endosperm in those cases where formation of an embryo takes place.

PARTHENOGENETIC STATE. This feature too is not without exception. We have come to know of, in recent times, many examples of parthenogenetic formation of embryo, and these are being multiplied. In these cases the formation of the endosperm proceeds at the same time without the stimulus which is given in other plants in the way described, whether the embryo proceed from an unfertilized egg, as in Antennaria alpina and most of the species of Alchemilla that have been examined, or from a cell of the endosperm, as in Balanophora. We have learnt to distinguish in sexual reproduction two processes:—

1. the taking over of paternal and maternal qualities into the germ;
2. the stirring up of this germ to further development.

The stirring of the germ to further development may result through factors other than the union of the male and female cells. What is the development-stimulus in the seeds produced parthenogenetically we do not know, but it appears to me very probable that in many cases it is the pollen-tube which without causing fertilization stimulates the further development and the formation of embryo. Where as in Balanophora and Alchemilla, with the exception of Alchemilla arvensis, usually no pollen-tube is formed, we naturally cannot speak of this, but in the formation of the adventitious embryos out of the nucellus, as they occur in Funkia, Citrus, and elsewhere, and also in Casuarina, as will be mentioned below, we have analogous cases. I do not see why the pollen-tube should not in many cases stir up the egg also to further development without effecting fertilization.

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[1] Hofmeister, Allgemeine Morphologie der Gewächse, p. 637, showed that, for example, in orchids the further development of the ovules can also be brought about by foreign pollen, which can cause no fertilization.

[2] I pointed out, in 1883, that the effect of fertilization also reached the secondary embryo-sac-nucleus :—'In all the cases examined by me this (nucleus) is connected with the egg by means of a plasma-strand, so that a material influence upon this from the egg or pollen-tube can take place.' This material influence consists in a union of nuclei as the beautiful investigations of the various authors mentioned have shown. Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 429. See also Strasburger, in Botanische Zeitung, lii (1900), p. 293.

DEVELOPMENT OF THE MEGASPORE. The most important part of the nucellus is the megaspore or embryo-sac, and we may ask now how far the megaspore in its origination conforms with that of the Pteridophyta [1]. In the Pteridophyta it arises everywhere by a division into four of the sporocyte. The megaspore of the Spermophyta proceeds also from a sporocyte, but the daughter-cells of this do not all become megaspores, although all have the potentiality of so doing [2]. The number of cells into which the megasporocyte divides is in many Spermophyta likewise four, and in recent times it has been many a time shown that this behaviour is far more general than was earlier supposed, when the number of the daughter-cells was considered as variable [3]. That the division into tetrads is a generally spread phenomenon seems very probable, since Overton's investigation of the relationship of nuclear division, directed to establish the homology of the megasporocyte and microsporocyte, showed that in both cases the number of the chromosomes in each is one-half that of the other cells [4]. Four daughter-cells have been found in Gymnospermae [5], as well as in a number of Monocotyledones and Dicotyledones. That a reduction of the divisions can take place is shown by the fact that in many plants the megasporocyte passes directly into the embryo-sac without division, for instance in Tulipa and other Liliaceae. I do not see why if in these cases the division is generally suppressed there should not also occur a reduction in the two or three divisions.

In the arrangement of the walls of the division the tetrad-formation varies from that which is usual in sporocytes, because the daughter-cells are usually arranged in one longitudinal series. Seldom do they lie through longitudinal division two beside one another. This variation often occurs also in pollen-tetrads. The lie of the division-walls in the pollen-tetrads is determined by the conformation of the pollen-mother-cells [6]. I may illustrate this shortly in one example. Fig. 403 shows pollen-tetrads of Typha Shuttleworthii. The most usual arrangement is that of Fig. 403, 1,

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[1] I do not require to quote any literature, for it is found in all text-books.

[2] See Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884).

[3] See Juel, Beiträge zur Kenntniss der Tetradenteilung, in Pringsheim's Jahrbücher, xxxv (1900), p. 626; Körnicke, Studien an Embryosackmutterzellen, in Sitzungsberichte der Niederrhein. Gesellschaft für Natur- und Heilkunde, 1901. The literature is cited here.

[4] See Strasburger, Histologische Beiträge, Heft vi; id., Über periodische Reduktion der Chromosomenzahl im Entwicklungsgang der Organismen, in Biologisches Centralblatt, xiv (1894).

[5] In Larix, by Juel, op. cit. In Pinus Laricio, Coulter and Chamberlain, Morphology of Spermatophytes, New York and London, i, p. 161.

[6] Goebel, Zur Embryologie der Archegoniatae, in Arbeiten des botanischen Instituts in Würzburg, ii (1880), p. 441. The assumption there made regarding the succession of the division-walls was incorrect. There evidently takes place, as Wille later pointed out, a repeated bipartition of the mother-cell. This is, however, of subordinate importance as against the general connexion, that is now also accepted by later authors, between the conformation of the mother-cell and the direction of division.

where the pollen-mother-cell has divided into four in one plane of division. In Fig. 403, 2, the two planes of division have crossed. In Fig. 403, 3, they have an oblique position to one another, and the arrangement approaches that of the tetrad. More rare are the forms which are shown in Fig. 403, 4 and 5, which, however, are of especial interest for a comparison with the megasporocyte. We may well assume that the elongated conformation of the pollen-mother-cells, which determines the arrangement of the daughter-cells, is connected with the relationships of space within the microsporangium. Further, in the megasporangium it is of the first importance to remember that the megaspores do not lose touch one with another, and therefore cannot acquire the spherical form, which for the ordinary tetrad-arrangement is the most suitable. The division by transverse walls suits much better their position in the long axis of the megasporangium [1].

The phenomenon that only one of the four daughter-cells normally develops further into a megaspore may be connected with the reduction in the number of spores in the megasporangium, a reduction which finds its extreme expression in the suppression of the tetrad-formation altogether in cases like Tulipa. Moreover, there are analogies with this in the megasporangia of Salviniaceae and Marsiliaceae, and in the formation of the microspores of some Monocotyledones [2]. The megaspores of the Cycadaceae and of many Coniferae have still an evident cuticularized exosporium which, as a reminiscence of the behaviour of free-living megaspores, is of interest.

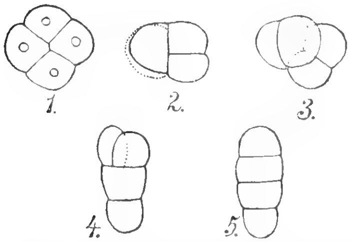

FIG. 403. Typha Shuttleworthii. Pollen-tetrads. Magnified.

We must now speak shortly of the structure and the development of the megasporangia in Gymnospermae and in Angiospermae.

(*b*) SPECIAL FEATURES OF THE MEGASPORANGIUM OF GYMNOSPERMAE.

CYCADACEAE. Owing to the difficulty of obtaining material, the development of the megasporangia in none of the Cycadaceae is completely known, yet we do know that the ovule has a primitive character, that is to say, it is allied to that of the sporangia of the Pteridophyta. This conclusion is based upon the following:—

(1) The existence of a somewhat copious sporogenous tissue (Fig. 404,

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[1] That in an arrangement of tetrads, as is shown in Fig. 403, only three cells may easily be visible upon the section is evident, and Johow has figured a case like this for Voyria.

[2] See regarding Carex, Juel, Beiträge zur Kenntniss der Tetradenteilung, in Pringsheim's Jahrbücher, xxxv (1900), and Wille's work cited there.

Sp), from which, however, so far as we know, only one cell develops further as the megasporocyte.

(2) The funicle arises by a *subsequent* elongation of the tissue of the sporophyll.

(3) The nucellus arises evidently by a further development of the *wall of the sporangium.*

To these may be added that the development of a pollen-chamber in the nucellus may be considered, as in Ginkgo, a primitive character.

Our knowledge rests upon the investigations of Warming[1], of Treub[2], and of W. H. Lang[3]. We shall take Treub's investigations of Ceratozamia longifolia as our starting-point, as they deal with the earliest stages, and confirm and complete Warming's work.

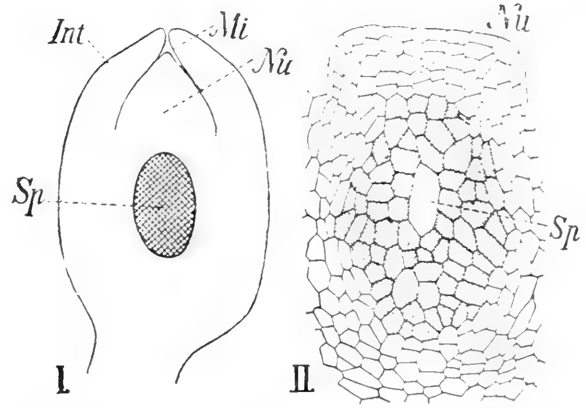

FIG. 404. I, Ceratozamia longifolia. Ovule in longitudinal section; *Int*, integument; *Mi*, micropyle; *Nu*, nucellus; *Sp*, sporogenous tissue. II, Stangeria paradoxa; *Nu*, nucellus in longitudinal section; *Sp*, sporocyte surrounded by sterile sporogenous tissue. I slightly magnified; after Treub. II after W. H. Lang.

Ceratozamia longifolia. An ovule springs from the edge of the sporophyll where it passes over into its zone of insertion. The tissue at this point has a meristic character, and produces two outgrowths, which may be recognized as the primordia of two ovules. If a longitudinal section be made through this we obtain a picture which is quite like that observed in the transverse section of a young sporangium of Ophioglossum: under the epidermis is a group of sporogenous cells which have clearly arisen by the division of one or some few archesporial cells. Their appearance is then the first differentiation within the primordium of the ovule, which at this period is essentially like the primordium of the sporangium of Ophioglossum. Between the epidermis and the sporogenous cell-mass there lies one or it may be more cell-layers which have a different destiny; they do not share in the formation of the sporogenous cell-mass, but they become cells which are designated *layer-cells.* Two changes proceed in the older stages: by the growth and splitting of the layer-cells an outgrowth is formed covering the sporogenous cell-mass (Fig. 404, *Nu*), and simultaneously there rises up around the

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[1] Warming, Undersøgelser og Betragtninger over Cycaderne, in Oversigt over de kongelige Danske Videnskabernes Selskabs Forhandlinger, 1877; id., Bidrag til Cycadeernes Naturhistorie, ibid., 1879.

[2] Treub, Recherches sur les Cycadées, in Annales du Jardin botanique de Buitenzorg, iv (1884).

[3] W. H. Lang, Studies in the Development and Morphology of Cycadean Sporangia: II. The Ovules of Stangeria paradoxa, in Annals of Botany, xiv (1900).

sporogenous mass an annular wall which is the primordium of the integument. The outgrowth referred to is the primordium of the nucellus which now like the integument continues to grow. The number of the cells of the sporogenous cell-mass increases, and the whole cell-mass becomes more sharply delimited, and is surrounded by narrow cells stretched in the longitudinal direction, regarding which it is questionable whether they may be considered as tapetal cells. Somewhere in the middle of the sporogenous mass there is found a large cell—the mother-cell of the embryo-sac (Fig. 404, II, *Sp*). It divides into usually three cells, but it is possible that the formation of tetrads also occurs here. At any rate one of the daughter-cells grows into the megaspore, and overwhelms the others. It becomes filled subsequently with the prothallus which produces the archegonia. In Stangeria the formation of the prothallus appears to be dependent upon pollination. The differentiation of the megaspore is completed here in quite the same way as is that in Isoetes[1], and we may assume that the tapetal cells also proceed from the sporogenous cell-mass. At the apex of the nucellus the pollen-chamber arises by resorption in the nucellar tissue (Fig. 400, I).

CONIFERAE. The ovules have sometimes two integuments, sometimes only one. The integument develops into a wing in some forms when they are ripe, for example in Dammara; in the Abietineae the wing appears to unite with the seminiferous scale, but evidently is derived originally from the integument. The relationships otherwise conform essentially with those of the Cycadaceae, yet, so far as investigation enables us to judge, the sterilization of the sporogenous cell-mass appears to have proceeded a stage further in many cases; nevertheless it is fairly developed in the Cupressineae, where its origin, as shown in the young stages which have been observed in Cupressus, can be traced back to a few-celled hypodermal archesporium[2]. The material is laid down in the nucellus, for use later by the megaspore.

Strasburger found in Larix one megasporocyte as is the case in other Abietineae. In Thuya and Taxus he found many. The earlier the sterilization of the sporogenous cells begins the less do they differ from the other cells of the nucellus, so that it is often merely a matter of opinion what one will designate as 'sporogenous cell-mass.' This is a consequence of the nature of the course of development which has been briefly sketched.

GNETACEAE. Space forbids our entering into an account of the interpretations of the much-discussed relationships of the ovule, especially

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[1] See p. 212.

[2] This gives off, however, numerous cells also for the construction of the nucellus. At the moment of pollination I find in the Cupressineae that have been examined a more or less developed sporogenous cell-mass, which is overlain by a copious nucellar tissue which serves later for the nutrition of the megaspores, just as nutritive material which is laid down in the many-celled wall in the young sporangium of Botrychium serves chiefly for the construction of the spores. The sporogenous cell-mass in Juniperus, where it consists of only few cells, lies about the place where the integument is inserted. In Callitris it is somewhat deeper. The megasporocyte appears in Juniperus at this time often clearly marked out by its size and richness of content.

of the formation of the integument in this family[1], and a short exposition would not serve to make clear the relationships of the several forms[2].

FEMALE SEXUAL ORGAN OF GYMNOSPERMAE.

The formation of the female sexual organ, however, may be noticed here:—

Cycadaceae, Ginkgoaceae, Coniferae. These families possess archegonia which are embedded deeply in the prothallus, and there is an egg which reaches giant dimensions in the Cycadaceae. In consequence of the size of the egg there is always a special cell-layer around it which plays an important part in its nutrition[3]. The neck of the archegonium, except perhaps in Cycas, does not project beyond the surface of the prothallus, and as it does not open no neck-canal-cell is formed. The formation of the neck-portion is strikingly variable. In the Cycadaceae, Ginkgo, Cephalotaxus Fortunei, Sequoia sempervirens, Tsuga canadensis, there are only two neck-cells, but in the most of the Coniferae there are four—the so-called *rosette*—which may divide by periclinal walls into one or more tiers, each composed of four or eight cells, as in Abies. We do not know whether this varying behaviour of the neck-portion has any biological significance.

Gnetaceae. The Gnetaceae exhibit peculiar and remarkable relationships. According to Strasburger[4] Ephedra possesses a typical coniferous archegonium with a long neck which appears to be but little different from the surrounding cells of the prothallus. In Welwitschia[5] Strasburger found a considerable simplification in the formation of archegonia. The twenty to sixty initials lying at the apex of the prothallus do not divide further, but form only outgrowths which grow into the nucellar tissue and against the pollen-tubes. Each archegonium is then reduced to a single cell surrounded by a membrane.

The behaviour of the megaspore in Gnetum, which has recently been studied by Karsten[6] and Lotsy[7], has special interest. In Gnetum Gnemon (Fig. 405) free nuclear division at first takes place in the embryo-sac and leads to the formation of the prothallus, as in the Coniferae, but the formation of cell-tissue only follows at the lower end of the embryo-sac. At the upper end the nuclei remain free, embedded in

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[1] I may only mention that Ephedra possesses one integument, the outer integument-like envelope is evidently formed by the concrescence of two leaves, as it is in Welwitschia, whose integument often forms a stigma-like structure above (Fig. 353). Gnetum has evidently three integuments. I may refer to Lotsy's interpretation according to which there is here only one integument, and the outer envelopes constitute a peculiar perianth. With regard to Ephedra, see Jaccard, Recherches embryologiques sur l'Ephedra helvetica, Diss. inaug., Lausanne, 1894.

[2] See Coulter and Chamberlain, Morphology of Spermatophytes, New York and London, p. 119, where more recent literature is cited although not fully.

[3] Arnoldi, Beiträge zur Morphologie der Gymnospermen: IV. Was sind die 'Keimbläschen' oder 'Hofmeisters-Körperchen' in der Eizelle der Abietineen? in Flora, lxxxvii (1900), p. 194. The literature is cited here.

[4] See also Jaccard, op. cit.

[5] The relationships here require renewed investigation. It is questionable whether the archegonia are really functional.

[6] Karsten, Untersuchungen über die Gattung Gnetum, in Annales du Jardin botanique de Buitenzorg, xi (1893); id., in Cohn's Beiträge zur Biologie der Pflanzen, vi.

[7] Lotsy, Contributions to the Life-history of the Genus Gnetum, in Annales du Jardin botanique de Buitenzorg, xiv (1899).

the protoplasm, and they may be regarded as free cells, although a definitely limited portion of the protoplasm around each single nucleus cannot be proved. These cells or nuclei are egg-cells. They can all be fertilized, although only one embryo develops further. The germinated megaspore then has two regions, which, at least in the beginning, are marked out by a slight constriction: the *upper generative region* and *lower vegetative region*. The vegetative region has the duty of bringing up the plastic material for the further growth of the megaspore at the cost of the nucellar tissue, in the same way as happens in the Angiospermae. The formation of the cell-tissue in the antipodal region of the megaspore did not occur in the species of Gnetum (Fig. 406) examined by Karsten, but the *whole embryo-sac* behaved like the upper end of that of Gnetum Gnemon.

FIG. 405. Gnetum Gnemon. Megaspore. To the right, above, another megaspore compressed and pushed to one side. Magnified 37. After Lotsy.

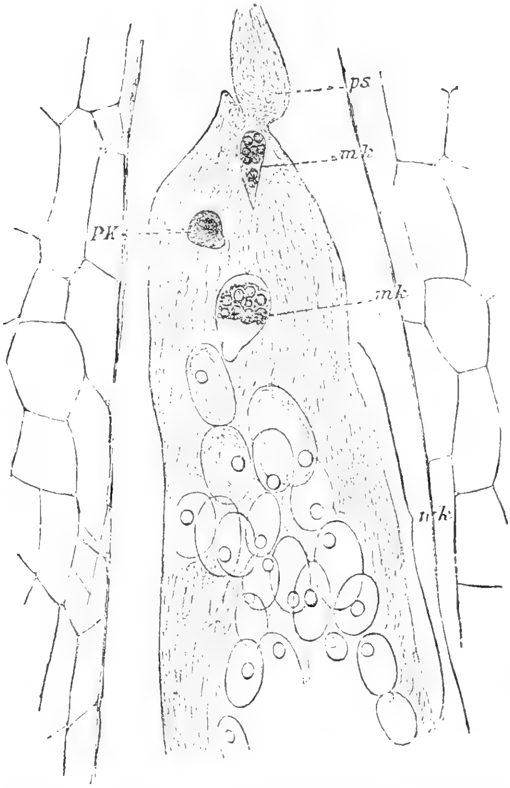

FIG. 406. Gnetum. Upper part of a megaspore in longitudinal section; *ps*, apex of pollen-tube; *mk*, *mk*, male nuclei; *PK*, tube-nucleus; *wk*, female nuclei. After Karsten. Lehrb.

Although our knowledge of the development of Welwitschia presents many gaps, and that of Ephedra requires careful reinvestigation, yet we can arrange the behaviour of the megaspores of the Gymnospermae evidently in one series, of which the following are the members [1] :—

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[1] Apart altogether from the rôle which the pollen-tube exercises as a developmental stimulus.

(*a*) The megaspore becomes filled completely with prothallus which bears normal archegonia: Cycadaceae, Coniferae, Ephedra.

(*b*) The megaspore forms a prothallus whose uppermost cells no longer unite together, but become unicellular fertilization-cells: Welwitschia.

(*c*) This process takes place still earlier, whilst the growth of the reduced archegonia is suppressed, there are still evidently distinguishable two regions in the megaspore, but in the generative region the cells are not sharply limited from one another: Gnetum Gnemon.

(*d*) The formation of a cell-tissue before fertilization is entirely suppressed: other species of Gnetum.

In other words, we observe here that the course of development which was visible in the heterosporous Pteridophyta has proceeded a step further, and the vegetative development of the prothallus has become always more shortened, and consequently the fertilization takes place at an always earlier stage.

It must, however, be remembered that it is doubtful whether the series above constructed is a phyletic one, for a polyphyletic origin of the Gymnospermae is more probable than a monophyletic one. At the same time we may conclude that the development is not a fortuitous one, but has proceeded progressively in a definite and regular manner.

(*c*) SPECIAL FEATURES OF THE MEGASPORANGIUM OF ANGIOSPERMAE.

The development of the megasporangium in the Angiospermae diverges in no essential point from that in the Gymnospermae, different though the external appearance of the ovule in the different families of Angiospermae is[1]. In general we may say that the structure of the ovule stands in relation to that of the perfect seed. Small seeds without endosperm, like those of the Orchideae, or seeds which have only small endosperm and small embryo, like those of the Begoniaceae, Rafflesiaceae, and others, proceed from ovules which have both the integuments and the nucellus very slightly developed. Seeds whose construction makes larger demands are provided from the first with a greater development of the integument or nucellus; as special adaptations are to be noted the formation of an *epithelium* in not a few cases, and the development of the *haustorium*

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[1] We know, unfortunately, very little about the biological significance of this difference. Why is it that the ovules are atropous, anatropous, epitropous, apotropous, and so on? Is the course of the pollen-tube a specially important factor—the path along which it must pass, the rapidity with which the fertilization must take place, the material of which it stands in need, the arrangement of the conducting tissue—or is it only the 'internal' factors which determine the configuration? Regarding these we know nothing, but I have no doubt that definite relationships will be discovered, as in so many other cases, between the conformation and functions of the ovule. That the frequency of the anatropous and campylotropous states, as compared with the atropous, is connected with the fact that in the former the micropyle, *ceteris paribus*, always comes nearer to the conducting tissue appears to me to be beyond doubt.

in the embryo-sacs, about which more will be said immediately. We have first of all to consider the origin and construction of the megaspore[1].

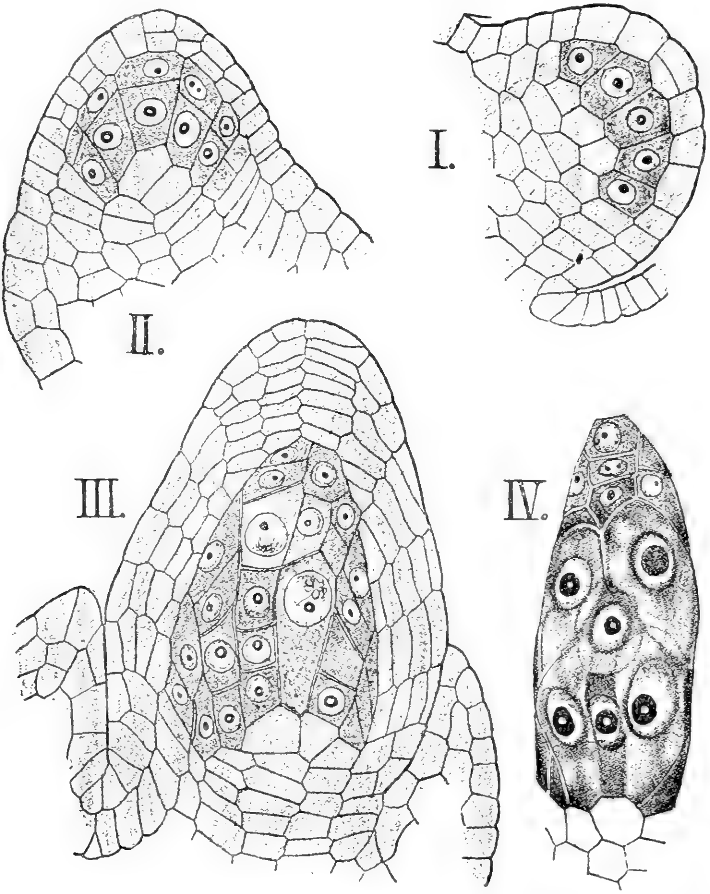

FIG. 407. I–III, Alchemilla alpina. IV, Alchemilla pubescens. Nucellus in longitudinal section, showing development of megasporangium. In I, five archesporial cells are shown. In IV, sporogenous tissue, with six ripe megaspores and some tapetal cells. After Murbeck.

ORIGIN OF THE MEGASPORE.

The archesporium is frequently unicellular, even in megasporangia with massively constructed nucellus, and this is evidently the case because other cells have been early sterilized. There are, however, not wanting cases of

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[1] Strasburger, Die Angiospermen und die Gymnospermen, Jena, 1879; Fischer, Zur Embryosackentwicklung einiger Angiospermen, in Jenaische Zeitschrift für Naturwissenschaft, xiv (1880); Jönsson, Om embryosäckens utveckling hos Angiospermerna, in Acta Universitatis Lundensis, xvi (1879–80); Guignard, Recherches sur le sac embryonnaire des phanérogames angiospermes, in Annales des sciences naturelles, sér. 6, xiii (1888); Nawaschin, Über die gemeine Birke (Betula alba, L.), in Mémoires de l'Académie Impériale de St-Pétersbourg, sér. vii, xlii (1894); id., Zur Entwicklungsgeschichte der Chalazogamen, Corylus Avellana, in Bulletin de l'Académie Impériale de St-Pétersbourg, x (1899); Benson, Contributions to the Embryology of Amentiferae, in Transactions of the Linnean Society, series 2, iii (1894).

pluricellular archesporia. We find them especially in Rosaceae, Aesculus Hippocastanum, Paeonia arborescens. Sometimes also many embryo-sacs are developed, as in Alchemilla (Fig. 407).

Alchemilla. Fig. 407 shows the development of the primordium of the ovule in Alchemilla[1]. The behaviour of the nucellus recalls the development of the microsporangia[2]. The archesporium is a cell-plate, from which layer-cells are given off to the outside, and the epidermis itself experiences periclinal divisions (Fig. 407, II). It is peculiar that a central cell is not devoted here, as elsewhere, to the formation of a megasporocyte, but it lies somewhat to one side, and then it divides into three or four—most commonly four—daughter-cells, of which more than one may become an embryo-sac. The superfluous embryo-sacs, which are later pushed to one side, evidently help in the draining of the nucellar tissue. The longitudinal section (Fig. 407, III) will enable a comparison to be made readily with a sporangium such as is shown in Figs. 379 and 391, whilst in other ovules of Angiospermae, in which the sporogenous tissue remains less developed, the outer differences in relation to the sporangia are much greater.

Casuarina. The structure of the megasporangia in Casuarina is very peculiar. We owe our knowledge of it to Treub[3]. Copious sporogenous tissue is developed, and the sterile tissue of the nucellus conspicuously corresponds in general features to the wall of the sporangia of the Pteridophyta (Fig. 408, I). The cells of the sporogenous tissue divide all in the same manner as the sporocytes of other Angiospermae, yet the number of the daughter-cells cannot be certainly determined from Treub's account. The daughter-cells which do not function as megaspores evidently serve for a long time as nutritive cells. Many megaspores are laid down, but the most of them remain sterile, and only bring the nutritive material to the favoured megaspore. They elongate into a tube-like form and become haustoria, which force themselves into the funiculus (Fig. 408, III). Biologically this repeats the case of the embryos of the Abietineae, where, of the many embryos which arise from one egg, only one develops, and the others function as haustoria for it[4]. The favoured megaspore in Casuarina lays down no antipodal cells, for these would be functionless, the megasporial haustoria having taken their place. At the apex of the favoured megaspore there will be found two to three—seldom only one—cells, which appear to proceed from one mother-cell, and are usually provided with cell-walls. They are formed before fertilization. The egg has the thickest membrane. Besides there is one nucleus present which later divides, and initiates the formation of the endosperm. Whether this takes place before or after fertilization—if a fertilization takes place—is doubtful. Many circumstances appear to me to point to the conclusion that the

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[1] See Murbeck, Parthenogenetische Embryobildung in der Gattung Alchemilla, in Acta Universitatis Lundensis, xxxvi (1900).

[2] See p. 599.

[3] Treub, Sur les Casuarinées et leur place dans le système naturel, in Annales du Jardin botanique de Buitenzorg, x (1891), p. 145. Fujii, The embryo-sac of Casuarina stricta, in Botanical Gazette, xxxvi (1903), has pointed out that the embryo-sac of Casuarina stricta shows the normal behaviour of the embryo-sac of Angiospermae; there is no parthenogenesis: results confirming my view that Casuarina is not a 'primitive' form.

[4] See Part I, p. 208.

pollen-tube, which forces its way through the chalaza[1], stirs up the megaspore to further development, but does not effect a fertilization, and that Casuarina really exhibits parthenogenesis. The reasons for this conjecture are as follows:—

1. The egg forms before fertilization a somewhat thick cellulose-membrane. This might, of course, be somewhat softened or absorbed.

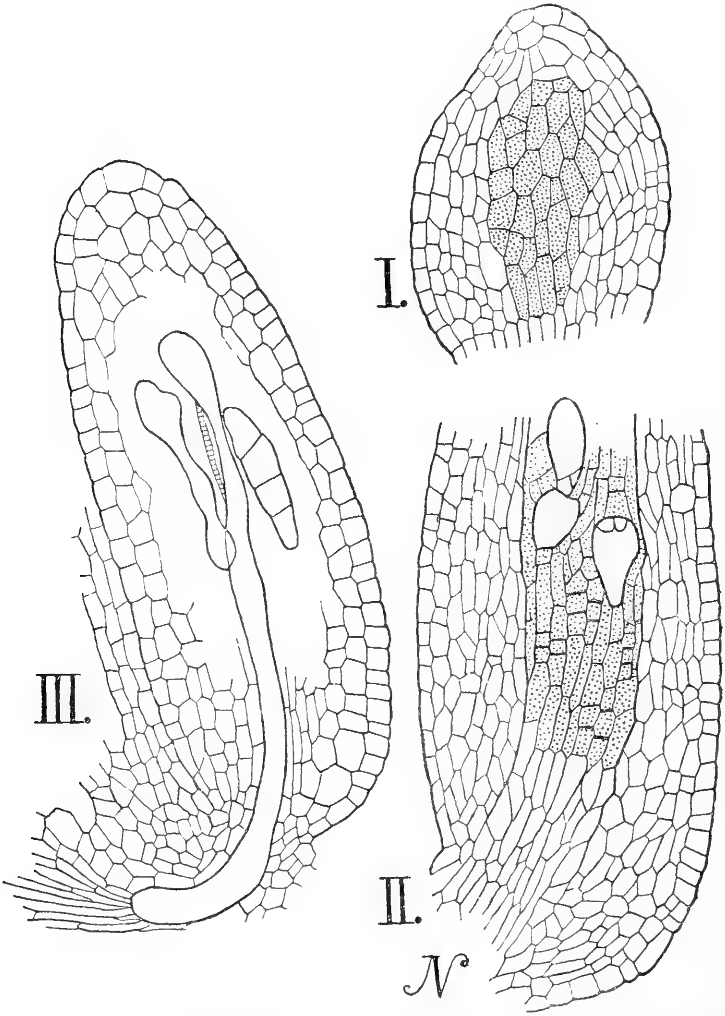

FIG. 408. I, Casuarina Rumphii. Megasporangium in longitudinal section. Sporogenous tissue dotted. II, Casuarina tuberosa. Portion of an older nucellus in longitudinal section. Three megaspores visible in the sporogenous tissue which is dotted. III, Casuarina glauca. Older stage of a megaspore grown out into a haustorium. A tracheid is visible in the sporogenous tissue. After Treub. I magnified 100.

2. The pollen-tube does not here reach the sexual apparatus, but implants itself on the embryo-sac at a point separated from this.

3. There is no fusion of two polar nuclei.

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[1] Casuarina was the first example known of chalazogamy. See p. 615.

This is, of course, only a conjecture, but it seems to me to be not unwarranted. The investigation of the fertilization in this genus is attended with great technical difficulties, and only when they are overcome shall we obtain a settlement of the question.

In speaking of Casuarina, I have considered it from the biological and not from the phyletic standpoint. I see in it a plant which shows interesting arrangements for the nourishment of the megaspores, which are not known in other Angiospermae in the same degree of completeness, but I can see little that is 'primitive' in its behaviour apart from the existence of a copious sporogenous cell-tissue, which, however, is found also in a similar condition in other different cycles of affinity of the Angiospermae. The processes within the megaspore seem to me to point rather to a reduction. Apparently the nucleus divides in two—the endosperm-nucleus and that which forms the egg-apparatus and the two cells which accompany it. Everything else is uncertain[1], and we must restrain ourselves from indulging the natural desire to find here a 'missing link' with the Gymnospermae, for this is an interpretation which the facts, as we know them at present, do not support. The whole economy of the plant, too, must be kept in mind, for it will perhaps give us the explanation of why the reserve-material is here laid down at first partly in the sporogenous cell-mass, partly in the funiculus, and then subsequently is apparently quickly used up by the megasporial haustoria. The case of Alchemilla, moreover, shows us in the nucellus remarkable links with that of Casuarina.

Most of the Angiospermae have a sporogenous tissue which is much less developed than in the plants mentioned above, and often consists of only one cell. The terminal result—usually only one megaspore—is the same.

GERMINATION OF THE MEGASPORE.

The processes of germination in the megaspore are not always the same, but they group themselves about one centre which we may consider the most usual and the most typical. It was first made clear by Strasburger, and is as follows:—

The young embryo-sac possesses *one nucleus*—the primary nucleus of the embryo-sac. This divides in further growth. The two daughter-nuclei pass one to each end of the embryo-sac, and there each divides, so that four nuclei are found at each pole of the embryo-sac. Two of these nuclei—one from each pole, the *polar nuclei*—move back again to the middle of the embryo-sac, and they are united sooner or later to form the secondary nucleus of the embryo-sac. Thus at each end of the embryo-sac are found three naked cells; those at the micropylar end

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[1] Engler, in Engler und Prantl, Die natürlichen Pflanzenfamilien, Nachträge, III, i, p. 113, is quite unjustified when, in referring to Treub's investigations, he says, 'There arises *before fertilization* a rudimentary prothallus consisting of twenty or more cell-nuclei.' Treub has mentioned this only as possible and eventually probable. As we know nothing, however, of where and when fertilization takes place we can naturally say nothing whatever about it.

forming the *egg-apparatus*, those at the lower end the *antipodal cells*. This behaviour stands nearest to that of Gnetaceae, where we have seen that the fertilization takes place at a stage in which the germination of the megaspore has not yet proceeded to the formation of a cell-tissue, and the cells are all potentially alike, although there is a more or less expressed polar differentiation, which is determined by the lie of the micropyle, into an upper generative and a lower vegetative portion of the megaspore. We have the same polar differentiation in the Angiospermae[1]. The antipodal cells, at least in many cases, have certainly an important function in the nutrition of the megaspore[2], and this we can quite well conceive of as being like that of the epithelium, which will be described below—it secretes an enzyme which brings about the solution of the nucellar tissue, and thus shares in the carrying over of the plastic material into the embryo-sac. This function will naturally be specially assigned to the antipodal cells where they remain for a relatively long time and reach a significant size, as, for example, in Asarum, many Helleboreae (Fig. 409); in other cases they lose their function very early and disappear. The egg-apparatus

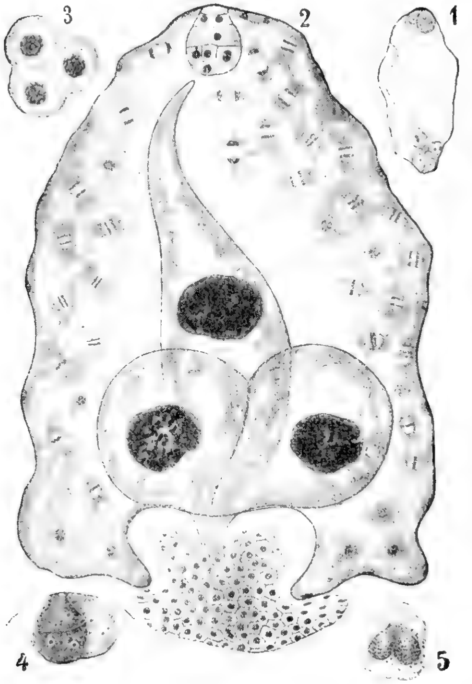

FIG. 409. Aconitum Napellus. 1, embryo-sac shortly before fertilization. 2, embryo-sac with giant antipodal cells at the time of free formation of endosperm-nuclei. 3, antipodal cells from above. 4, 5, one of the synergidae and one embryo. After Dodel.

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[1] I consider then the whole content of the megaspore as a slightly differentiated prothallus with a vegetative and a generative part. The union of the two polar nuclei is a purely vegetative process, and stands in relation to the fact that the formation of endosperm proceeds from *one nucleus*, strengthened here by union with another, and is only started by the act of fertilization. Whether we consider the endosperm of the Angiospermae, in contrast with that of the Gymnospermae, as a *new formation* or as a consequence of a *further development* following upon fertilization of the prothallus existing before fertilization, appears to me to have no essential significance. From what I have said upon the course of development of the Spermophyta I hold the latter connexion to be the more correct. In other words the endosperm of the Angiospermae is the same as that of the Gymnospermae, only it develops first of all in consequence of the stimulus given by fertilization, whilst this stage of development of the megaspore in the Coniferae is set going by the pollination.

[2] As was first shown by Westermaier, Zur Embryologie der Phanerogamen, insbesondere über die sogenannten Antipoden, in Nova Acta der kgl. Leop.-Carol. Deutschen Akademie der Naturforscher, lvii (1890); id., Historische Bemerkungen zur Lehre von der Bedeutung der Antipodenzellen, in Berichte der deutschen botanischen Gesellschaft, xvi (1898), p. 215.

consists of the *egg* and the two *synergidae*. The function of the synergidae is unknown. The most probable conjecture regarding them is that, probably by the extrusion of soluble substances, they determine the pollen-tube to grow to an egg. Occasionally the synergidae as well as the antipodal-cells may form embryos[1], which will surprise us the less as Treub's investigations have shown that the embryo of Balanophora arises from an endosperm-cell, and in plants which have marked polyembryony, like Citrus, Mangifera indica, Clusia alba, Opuntia Ficus indica, Funkia coerulea, the adventitious embryos, as Strasburger has shown, proceed from the nucellar tissue—a condition which may be compared with the phenomena of apospory in some of the Pteridophyta.

There would be little interest in enumerating here the cases in which relationships in the megaspore different from the 'normal' have been observed. So far as we know at present they have no significance, either in the way of leading to phyletic conclusions or in giving us a deeper insight into the processes of germination of the megaspore. The number of the nuclei arising by division of the nucleus of the megaspore is sixteen in Peperomia[2], but in the ripe embryo-sac a behaviour quite like the normal results, for a larger number of these nuclei, usually eight, unite to form the secondary nucleus of the embryo-sac. Similar variations occur also elsewhere. The number of the antipodal cells is more than three in many Monocotyledones, for example Zea Mais, and in many Dicotyledones, for example Stackhousia[3]. In Sparganium and Lysichiton[4] they are stirred up in fertilization to further development and multiplication; they may increase up to one hundred and fifty, and they remain for a long time. Biologically this process might be scarcely different from the enlargement of the antipodals after fertilization in other plants. In both cases they have that function which is elsewhere performed by the epithelium.

THE FEEDING OF THE MEGASPORE, ENDOSPERM, AND EMBRYO.

The arrangements which make possible the nutrition of the megaspore and the endosperm and embryo arising within it in the ripening seeds are very different, and only in recent times have they begun to receive attention. The most simple case is that where the megaspore increases, and, without the help of any structural relationships apart from the antipodal cells, gradually absorbs and displaces the surrounding cells. We find this particularly in many Monocotyledones, but also in not a few Dicotyledones.

Epithelium. In a number of cases the ovule possesses a layer of cells

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[1] See Ernst, Beiträge zur Kenntnis der Entwicklung des Embryosackes und des Embryo (Polyembryonie) von Tulipa Gesneriana, L., in Flora, lxxxviii (1901). The literature is given here.

[2] See Johnson, On the Endosperm and Embryo of Peperomia pellucida, in Botanical Gazette, xxx (1900); Campbell, The Embryo-sac of Peperomia, in Annals of Botany, xv (1901).

[3] See Billings, Beiträge zur Kenntniss der Samenentwicklung, in Flora, lxxxviii (1901).

[4] Campbell, Notes on the Structure of the Embryo-sac in Sparganium and Lysichiton, in Botanical Gazette, xxvii (1899), p. 153.

marked out by a rich protoplasmic content, and evidently also by the nature of the substances within its cells, as well as by its behaviour; this layer we designate the *epithelium*[1]. Its signification can only at present be concluded from external considerations, which point to the fact that it has the duty in a certain degree of dissolving the tissue which serves for the nutrition of the growing megaspore, and of transferring this plastic material to the macrospore. The indications for this, besides the nature of the contents, which have been already pointed out, are in particular the long duration of this layer—in Linum it is still present in the ripe seed, in other cases it remains at least longer than the other layers—and the fact that where the embryo-sac forms haustoria the epithelium is wanting in the parts that form the haustoria. Where it exists it belongs usually to the inner integument. In Drosera, however, it belongs to the nucellus. It forms the innermost layer of the single integument in many Sympetalae. An epithelium has been shown in the Choripetalae, for example in the Geraniaceae, as well as in many Sympetalae; yet it is even within one family, according to the usual limitations, not present everywhere. It is wanting in the species of Gentiana, but it is present in Menyanthes, which is usually considered as belonging to the Gentianaceae (Fig. 410).

Haustoria. An epithelium may be combined with the presence of *haustoria* (Fig. 411). These occur in manifold forms. They grow out in most cases through the tissue of the nucellus or the integuments, in extreme cases appearing even outside the micropyle, and they are distinguished from the other part of the embryo-sac usually by this, that they

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[1] Frequently this is also designated the *tapetum*, which can certainly, in a purely functional sense, be correctly applied. I have elsewhere (Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884), p. 407) referred to this, and shown that the designation tapetum is a functional, not a formal, historical-developmental term (see also p. 597 of this book), and that it is therefore incorrect to give the name tapetal cells to the sterile cells that are separated from the archesporium, because they contribute to the wall of the megasporangium; further, that a tapetum does exist and has an epithelium-like construction in the ovule and has a definite nutritive importance. This explanation found at first no attention, but it has been confirmed by later research, and has been better substantiated. M. Goldfuss has also accepted my expression and designated the tapetum-like absorbing layer as 'assise épithéliale.' The expression tapetum might here lead to a misunderstanding, as it must be used in a different sense from the ordinary. The epithelium of the ovule is *morphologically* different from the tapetum of the sporangia. The activity of the tapetum of the sporangium falls in the time *before* the complete construction of the spore; the activity of the epithelium falls *during* the period of germination of the spore, but as we could speak in many ovules also of tapetal cells around the megaspore during the development, in the same way as in the case of the megasporangium of Isoetes, so it has come about that if the epithelium be called tapetum, as is done by my pupils who have investigated the development of the seed—see Merz, Untersuchungen über die Samenentwicklung der Utricularieen, in Flora, lxxxiv (Ergänzungsband zum Jahrgang 1897); Balicka Iwanowna, Contribution à l'étude du sac embryonnaire chez certains Gamopétales, in Flora, lxxxvi (1899); F. X. Lang, Untersuchungen über Morphologie, Anatomie und Samenentwicklung von Polypompholyx und Byblis gigantea, in Flora, lxxxviii (1901); Billings, Beiträge zur Kenntniss der Samenentwicklung, in Flora, lxxxviii (1901)—a double terminology is introduced which is better avoided.

do not share in the permanent construction of the seed, at least in those which are not—or only slightly—filled with endosperm. The following are some illustrations :—

Linum. The megaspore enlarges in this genus considerably after fertilization. Only one part of it is, however, filled with endosperm; the other serves as haustorium, and is later separated from it[1].

Torenia. In Torenia the apical portion of the embryo-sac grows as a haustorium out of the micropyle before fertilization. Torenia belongs to the Sympetalae, and the formation of haustoria is widely spread[2] in this group.

Byblis gigantea. Fig. 412 shows a longitudinal section of Byblis gigantea. Only the middle part of the embryo-sac is filled with endosperm, within which the young embryo lies. The embryo-sac at the upper micropylar end, as well as at the chalazal end, has become a haustorium. These haustoria are filled with cell-tissue, and are apparently structures which have only a temporary function. The haustorium experiences a large increase in surface by outgrowths which spread like a fungus-mycelium into the thick integument[3]. Subsequently the upper and lower portions of the embryo-sac

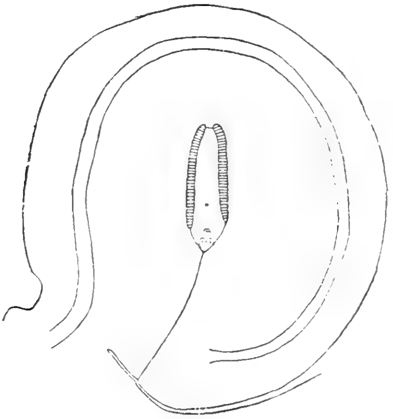

FIG. 410. Menyanthes trifoliata. Ovule in longitudinal section. There is a thick integument in which a conducting bundle runs to near the downwardly directed micropyle. The embryo-sac fills the nucellus. It is surrounded by an epithelium. After Billings.

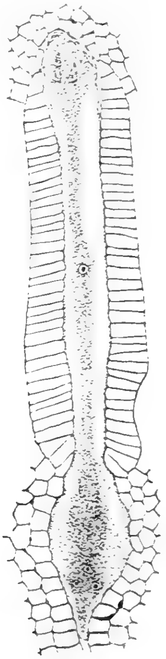

FIG. 411. Myoporum serratum. Embryo-sac in longitudinal section. It is surrounded by an epithelium excepting in the upper (antipodal) and the lower (egg-apparatus) regions, where haustoria are subsequently formed. After Billings.

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[1] See Billings, Beiträge zur Kenntniss der Samenentwicklung, in Flora, lxxxviii (1901), and the works of Hegelmaier and others cited there.

[2] See Balicka Iwanowna, Contribution à l'étude du sac embryonnaire chez certains Gamopétales, in Flora, lxxxvi (1899); Billings, op. cit.

[3] In plants we find frequently the phenomenon of autoparasitism, that is to say, that an organ lives at the cost of another belonging to the same plant. The phenomenon is very strikingly seen, especially in the development of the seed and fruit. That this parasitism is essentially different from alloparasitism, where a foreign organism is used as a host, as some people say, I do not believe.

are cut off from the remaining portion of the endosperm by tabular endosperm-cells with cuticularized walls.

Globularia. The haustoria are even more developed in Globularia (Fig. 413), where they also grow out of the micropyle.

Utricularia and Polypompholyx. The behaviour in these genera is also remarkable. The nutritive materials for the haustoria are laid down before their appearance, and are only later sought out by the haustoria and absorbed by them. The phenomenon probably occurs elsewhere, although it is usually less visible. The points of deposition of nutritive material may be designated as *nutritive tissue.* They are found in these plants in two places:—

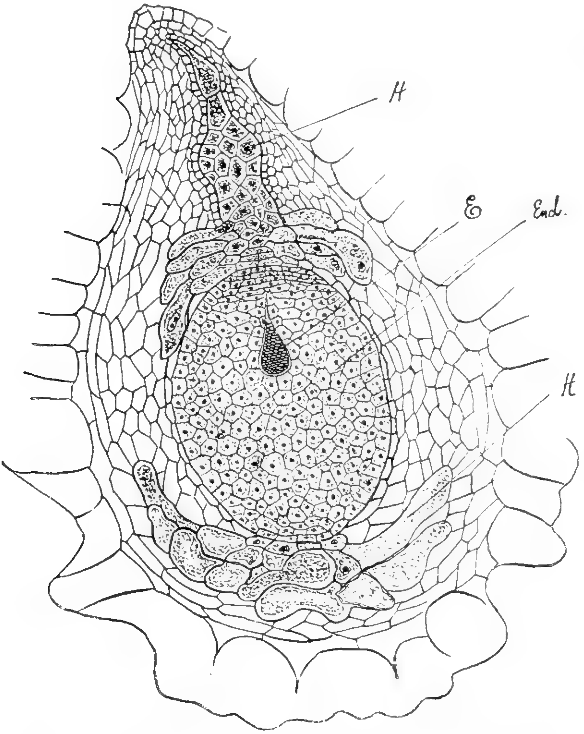

FIG. 412. Byblis gigantea. Young seed in longitudinal section; *E*, embryo embedded in the endosperm, *End*; *H*, *H*, haustoria at the end of the seed, and showing hypha-like outgrowths. After F. X. Lang.

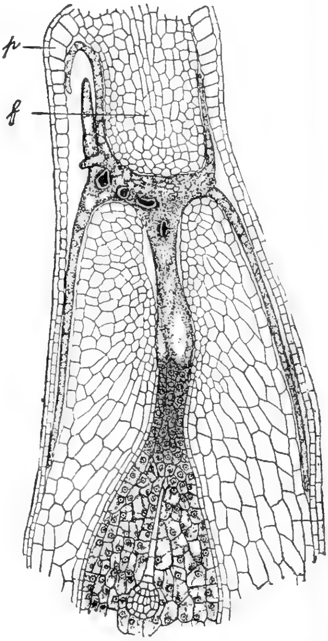

FIG. 413. Globularia cordifolia. Portion of a young seed in longitudinal section. The haustorium has grown out of the micropyle and has branched, the branches lying against the ovarian wall, *p*, and against the funicle, *f*. After Billings.

1. Internal in the chalazal region (Figs. 414 *Dr* above; 415, *oDr*; 417 *tN*).

2. External within the funiculus. In Polypompholyx the external position is clearly in the funiculus (Fig. 417, *bN*), in Utricularia it is at the place where the funiculus passes into the placenta (Figs. 414 *Dr* below, 415 *uDr*); but even here, as the behaviour in Polypompholyx shows, the nutritive tissue should be reckoned as funicular. The megaspore sends out at both ends a haustorium; the micropylar haustorium grows out of the micropyle and into the external funicular nutritive tissue; the chalazal one pierces the internal chalazal nutritive tissue. Both haustoria

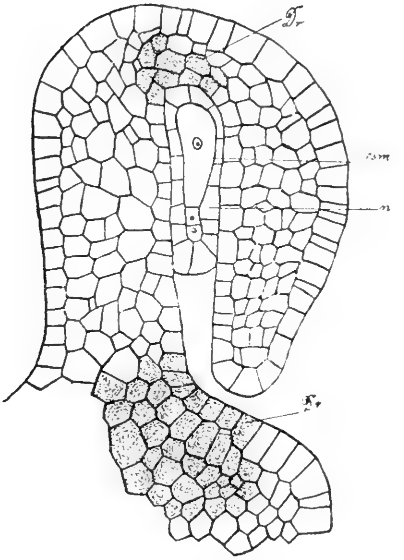

FIG. 414. Utricularia inflata. Ovule in longitudinal section; *Dr*, nutritive tissue; *n*, nucellus; *esm*, megasporocyte. Magnified 500. After Merz.

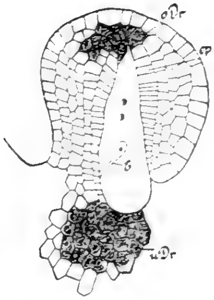

FIG. 415. Utricularia stellaris. Ovule in longitudinal section; *oDr*, chalazal nutritive tissue for the embryo sac; *uDr*, funicular nutritive tissue for the embryo-sac, which has quite used up the nucellus and is protruded from the micropyle; *ep*, epithelium; *b*, young embryo. After Merz.

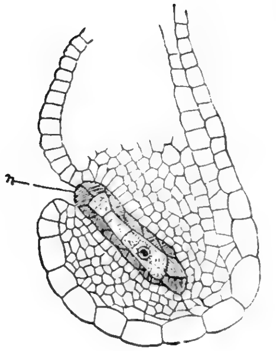

FIG. 416. Polypompholyx multifida. Young ovule in longitudinal section: *n*, nucellus composed of an axile row of cells. The lowermost cell is the megasporocyte. The outer cell-layer is shaded.

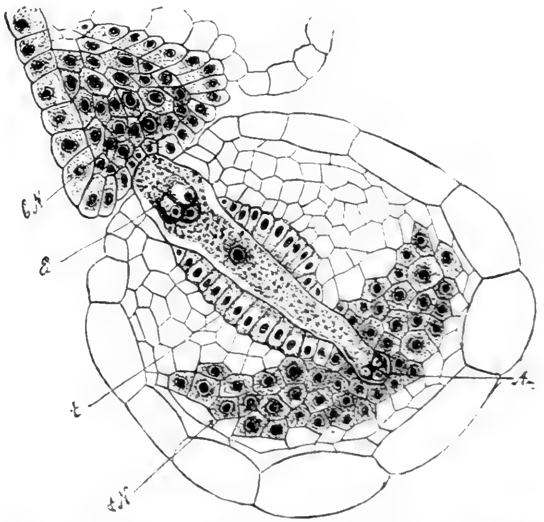

FIG. 417. Polypompholyx multifida. Older ovule in longitudinal section. The micropyle, from which the megaspore has grown out, is turned obliquely upwards: *Ei*, egg-apparatus; *An*, antipodal cells; *tN*, chalazal nutritive tissue; *bN*, funicular nutritive tissue; *t*, epithelium. After F. X. Lang.

are, as in Byblis, cut off later from the middle portion of the embryo-sac carrying the endosperm.

Fundamentally we have here only special cases of the general behaviour that in the ovule or outside of it material is stored up which can be absorbed by the megaspore in its further growth.

Similar relationships repeat themselves in the development of the embryo.

DEVELOPMENT OF THE FERTILIZED EGG.

With regard to the development of the fertilized egg I must refer to what I have said elsewhere[1], and also to Areschoug[2], for nothing fundamentally new has been added to the subject. I will only here indicate the following points:—

1. The fertilized egg does not usually become *in toto* the embryo, but the embryo develops only out of the distal portion of the embryonal primordia—the so-called *pro-embryo.* The proximal portion becomes the suspensor.

2. The function of the suspensor[3] is a double one:—

(*a*) The uptake of nutritive material, and in connexion therewith we often observe a considerable increase in its surface. In many plants haustorial outgrowths appear, as in Stellatae, Ribesiaceae, and Orchideae.

(*b*) To bring the embryo into the most favourable position for its nutrition, especially during germination, and we have seen this function very markedly in the species of Lycopodium and Selaginella as well as in most Gymnospermae.

The functioning of the suspensor as a haustorium finds analogy in the megasporial haustoria which have been mentioned above. Treub's investigations of the Orchideae have in this respect a special interest, and have supplied a number of remarkable examples. Also the case of Tropaeolum, which has been so frequently described, may be placed in the same category. If in this and like cases we are satisfied with giving as an 'explanation' that the 'need acts as a stimulus,' we do not seem to get any further than a paraphrase of the fact that this phenomenon is one which is evidently advantageous.

The processes which lead to the formation of the seed-coat and its appendages, as well as the appearance of the aril and caruncule, must be left untouched. They belong to the question of the distribution of the seed which does not require a new exposition at this time.

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[1] Goebel, Vergleichende Entwicklungsgeschichte der Pflanzenorgane, in Schenk's Handbuch der Botanik, iii (1884).

[2] Areschoug, Om de Phanerogames Embryo Nutrition, in Lunds Universitets Årsskrift, xxx (1894).

[3] See Goebel, op. cit., p. 172.

LIST OF THE ILLUSTRATIONS

(I and II respectively refer to Parts I and II.)

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