The Structure and Morphology of the 'Ovule.'

An Historical Sketch.

BY

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With twenty-seven Figures in the Text.

INTRODUCTION.

THE great aspect of botanical science known to us as Morphology comprises that department of study which is concerned with the form and the differential characters of the various structures or organs composing the individual plant. As this study advanced in the past it became clear that all the various parts or organs of the higher plants are capable of being grouped or classified into a few main categories, the *raison d'être* for the existence of these latter being that the organs constituting each, although exhibiting an extensive range of variation in accordance with the equally varied environmental conditions to which they inevitably become subjected, yet possess certain well-defined, exclusive characters of form, structure, and position which have rendered them during the course of ages of progressive differentiation so stereotyped and fixed as to preclude the possibility of the existence of any intermediate or transitional forms between any two of these categories. It is true that in some cases it is excessively difficult, perhaps even impossible, to determine the morphological category to which a given organ or structure pertains, and this owing to the extreme modification of the latter, resulting from certain special adaptive requirements, e.g. the submerged bladder-bearing portion of the *Utricularia*-plant and the seminiferous scale of the *Abietineae*. But this, it seems to the writer, is due solely to our ignorance and incapability of tracing all the stages of adaptive modification which, during its long phylogenetic history, the organ in question has undergone, the original and all the intermediate forms having long since become extinct; the ontogeny, or individual development, may yield us no clue; for in the majority of these cases the highly modified organ arises congenitally as such. If we are unable to discover, say, in the submerged organ of *Utricularia* a prevalence either of the distinctive characters of the phyllome

or of those of the caulome, we surely dare not conclude that this organ exhibits within itself a fusion of those two categories! for if, in this particular case, such a fusion actually exists, we ought occasionally to find here and there in other plants, normally or abnormally, true transitional forms between, say, stem and leaf, or leaf and root, &c. If the existence of these could be demonstrated it would, in the writer's opinion, prove our morphological categories to be mere figments of the imagination; but he has no hesitation in saying that he believes such transitions never will be demonstrated.

Until within comparatively recent years it was usual to regard the categories as four in number, and as consisting of the caulome or stem, the phyllome or leaf, the trichome or hair, and the root. A few writers, however, have advocated the introduction of a fifth category, viz., that of the sporangium; a discussion of the validity of this view will be afforded at the proper time and place in this thesis.

The *ovule*, which forms the subject of the present paper, does so on the ground of its being one of those highly complex (as may be assumed from the evolutionary point of view), much modified structures whose morphological nature has on that account remained for so long a doubtful quantity and the cause of deep debate and argument on the part of many able investigators. It will be the writer's present object to endeavour to afford a presentation of the various views on the subject held by many of the leading botanists of the century, leaving his readers to judge for themselves which of those views contains the fullest measure of the truth. The facts thus collected and presented in a concise and accessible form will also, he hopes, prove useful to the student and the teacher of morphology.

At the outset let us consider the few, simple *facts* connected with the structure and position of the ovule as they are familiar to us to-day. The ovule is well known to appear in very various positions on the plant; in the majority of cases it appears as an outgrowth from the *margin* of the carpel; in other cases as a development from the *inner surface* of that organ, as in *Butomus* and *Nelumbium*; in older types of plant, the writer would submit, as *terminal* to a carpel of radial symmetry of structure, as in the fossil *Bennettites*; in some instances, as in Caryophyllaceae and Primulaceae, it is apparently a product of an upgrowing axile placenta; in yet others there are indications of its actually terminating the floral axis, as in Compositae¹, Piperaceae, *Najas*, Polygonaceae, *Taxus*. The facts connected with the *position* of the ovule have had no small share in influencing the decision of botanists as to its morphological nature. There have, indeed, been not a few who have placed their whole reliance on this set of data, constituting it the central pivot of their deductions. The ovule, whatever its position on the plant, consists, as a general rule, of

¹ But the ovule here is really lateral.

three distinct parts: a central structure, the *nucellus*, which assumes a terminal position on the ovular rudiment, and *two integuments*, which ontogenetically arise as annular outgrowths from the basal portion of that structure; the order of development of these integuments is basipetal, the inner, as regards the great majority of cases, preceding the outer (Fig. 1). To these facts of the normal structure a few exceptions occur: the integument may be entirely absent, as in *Crinum*; there may be only a single integument present, as in Ranunculaceae, Piperaceae, and apparently also in the group of the Gamopetalae¹; on the other hand, the number of integuments may be increased, for C. Schimper is said to have found three in *Reseda lutea*, the third integument arising in the acropetal direction, i. e. within the two normal ones; such a case as this latter, however, requires confirmation.

In the present thesis the writer is purposely omitting any reference to the nature of the ovule in parasitic plants, as he hopes to treat this subject separately on some future occasion.

The facts of the normally constructed ovule being given, viz., a central papilla, the nucellus, enveloped by two basipetally-developed integuments, the problem which both past and present botanists have set themselves to solve is this: to which of the morphological categories does this important structure belong?

The views which have been held on this subject may be classified

FIG. 1.

FIG. 2.

FIG. 3.

FIG. 1. Diagrammatic representation of the ovule to illustrate the *actual* structure apart from its morphological interpretation. FIG. 2. Diagrammatic representation of the ovule to illustrate its interpretation according to the axial-theory (after Čelakovský). FIG. 3. Diagrammatic representation of the ovule to illustrate its interpretation according to the foliolar theory (after Čelakovský). *n*, nucellus; *i. int.*, inner integument; *o. int.*, outer integument.

under three main headings, according as the ovule has been held to possess the morphological value of:—

1. a shoot;
2. a leaflet;
3. a new structure or sporangium.

¹ In this group of plants, at any rate, the 'single' integument is probably due to congenital fusion of the two integuments.

These views may be termed (1) the *axial*, (2) the *foliolar*, and (3) the *sui generis* theory respectively.

The most striking of the arguments which, during a period of some seventy years, have been advanced in support of each of the above theories will now be presented.

HISTORICAL SKETCH.

As regards the first of these views, the shoot-, bud-, or axial-theory—whichever term most appeals to the reader—appears to have been the one prevalently held about the middle of the last century (Fig. 2). Its most weighty supporter is undoubtedly the great German botanist Alexander Braun (15), who, nearly twenty years after Schleiden, in a paper dealing more particularly with certain phenomena in the life-history of *Coelebogyne*, embodies ideas which, at first appearing to support the foliolar-theory of the ovule, are eventually seen to practically dispose of this in favour of the axial view. 'Leaves,' he says, 'suppose an axis; and as the idea that placentae are axile in nature as regards the majority of plants has been decisively refuted, the notion that ovules are *entire* leaves also falls to the ground.' So that 'the first explanation of ovules must be accepted, viz., that they are parts of a leaf, marginal structures, either peculiarly modified *teeth*, *lobes*, or *pinnae* of the carpel,' as Roeper and Brongniart stated, but with the recognition that the ovule must be regarded as something beyond a mere *continuation* of the carpel. But this idea of the ovule as a marginal lobe, &c., of the carpel cannot be of universal application, as seen in the case of free central placentation and in cases where the ovules are distributed, multi-seriately or irregularly scattered on very thick or extended placentae. These cases show that ovules are not mere marginal structures, but outgrowths from the surface, comparable to the normal or abnormal emergences of many leaves. He says that numerous observations show that the flowers, leaves, or leaf-segments arising on expanded structures in cases of antholysis do not represent an entire ovule, but only part of such. There is to be distinguished a stalk (*Träger*), which must be regarded as a portion of the carpel, or in rare cases as an independent leaf, and sprouting from this a new structure—a *bud*. In metamorphosed ovules of *Adonis autumnalis* and *Nigella Damascena* he observed the outer integument expanded into a leaf-like structure. He remarks that in these cases there is no reason to regard it as part of the carpel, nor for aught else but an independent leaf belonging to the ovule (Eiknospe¹). 'If this is correct, the bud-nature of the entire ovule is assured.' He is not decided as to which, the carpel or the ovule, the funicle belongs. The bud-nature of the ovule, the latter being

¹ The terms 'Eiknospe,' 'Samenknospe' ('Egg-bud,' 'Seed-bud'), clearly indicate the prevailing view as to the nature of the ovule held in Germany about the middle of the last century. The term 'Eichen' ('ovule'), as now generally adopted, is preferable.

a structure capable of further development, is proved by the following phenomena :—

(1) *Multiplication of integuments*, the latter arising in acropetal succession (he thinks that it is not strange that the abnormal integuments should arise in the opposite direction to that of the normal ones, seeing that the regions from which the annular protuberances arise are already formed).

(2) Unilateral expansion of one or both integuments.

(3) Proliferation of the ovule into an elongated shoot.

(4) Production of a leafy bud in place of the nucellus within the normal integuments. On one leaf of this bud he found an ovule, which he regards as a case of 'one ovule arising out of another.'

Having introduced Al. Braun first, as the most important of the supporters of this theory, let us now take up the views of the remaining authors in the historical order of their publication. We find that in 1840 Aug. de St. Hilaire (6), in his noteworthy '*Leçons de Botanique*' (p. 543), in support of the axial-theory of the ovule remarks: 'We can only regard the ovule as a miniature branch composed of an axis and appendicular organs. The placenta, as we already know, is a continuation of, and represents the stem, whose branches are the ovules.' 'The primine and secundine are the appendicular organs of the young branch, and are comparable to the sheathing leaf-bases found in great numbers of Monocotyledons . . . ; it is therefore not surprising that the ovular axis, the least vigorous of all axial structures, should produce nothing but such sheaths.' On p. 490 he further says: 'We know that every part of a plant bearing ovules—or, rather, every placenta—springs from the axial system, and is nothing more than a prolongation of this latter; so that in cases of axile or parietal placenta it is clear that the axis of the flower, after producing the carpellary leaves, has, in order to produce ovules, to divide by means of a partition, for supplying branches, double or equal in number to that of the carpels, but which, in the latter case, are susceptible of forming double placentas.'

This same view, as to the universally axial nature of the placenta, is put forward by the author in his earlier memoir on the Resedaceae. As affording a slight variant on the axial-theory, the coupled names of Endlicher and Unger (8) may be introduced, who held the ovule to be of the nature of a *disc* ('*Nebenaxe*') produced on the axial placenta.

Schleiden (14), who, in 1839, as also in his subsequent work the '*Grundzüge der wissenschaftlichen Botanik*,' published in 1843, promulgated, like St. Hilaire, the view that the placenta is always an *axial* structure, and that the ovules borne on it are of the nature of buds. Doubtless, this view of the matter, owing to the great weight of the epoch-making work containing it, would have had much influence both among the author's contemporaries and among many of those who came after him.

Payer (23), in his great work on the organogeny of the flower, evidently—at least, in certain cases—regards the ovule, although he nowhere explicitly states it, as the morphological equivalent of a portion of the axis, this being the view definitely entertained by him with regard to all placental structures. In describing the development of the ovary in the Polygonaceae he says: 'At the bottom of this cup [the depression arising between the developing carpels] the apex of the axis is observed, which becomes successively clothed with two envelopes, thus constituting an erect and orthotropous ovule.' He applies the same interpretation to the nature of the ovule in Urticaceae, Chenopodiaceae, Paronychiaceae, and Amaranaceae.

FIG. 4. Portion of flower of *Polygonum*, showing both ovary and ovule terminal to the axis (after Payer).

Magnus (44) offers a precisely similar explanation of the ovule, terminal to the axis, in *Najas*.

These two latter authors may be regarded as typical examples of those who, in their endeavours to determine the morphological value of any given organ are primarily influenced by the *position* in which it arises on the plant. Hence we may speak of such as *topical* morphologists.

The well-known observations made by Peyritsch on abnormal structures in the ovaries of Cruciferae and other plants will be referred to more fully hereafter.

Penzig (57) examined proliferated ovules of *Scrophularia vernalis* L., which he found, in the extreme metamorphosed condition, were toothed leaflets bearing a nucellus at different levels on their upper surfaces or apex. He also found nucelli borne at the apex of elongated structures growing on the placenta which were often fused with the leaflet on the dorsal side; the appearance of the bundle in the nucellus showed the latter to be of ovular nature. He came to the conclusion that such phenomena are in greatest harmony with the bud-theory of the ovule.

Many other authors have put forward this theory of the ovule, reference to whose works will be found in the subjoined bibliography. A discussion of the validity of the axial-theory will be deferred until Čelakovský's views on the whole subject are brought forward.

We have next to notice that which we have termed the *sui generis* theory of the ovule; in this connexion there are the writings of four or five botanists to be taken into account.

Schmitz (43), in his study of floral development in the Piperaceae, and especially of *Peperomia repens*, makes this general remark: that 'as the ovule arises sometimes as an emergence on a leaf, and sometimes by metamorphosis of the vegetative apex, its relation to the shoot as a whole

cannot have the same morphological meaning. The ovule does not always possess the same morphological value.' The idea of an ovule, he thinks, only includes a tissue which encloses the embryo-sac and nothing more ; and there need necessarily be no differentiation into integument and nucellus. 'The origin of the embryo-sac is not confined to the members of a definite morphological category.' He considers that the ovule in Piperaceae represents a continuation of the axis of the flower¹, the integuments being its leaves, and equivalent to the carpels and stamens. In order to form the ovule the apical portion of the axis undergoes a metamorphosis through the disappearance of all internal differentiation ; the integuments arise *basipetally* ; and on these grounds he regards the ovule as a *new structure*, for it cannot be made to fit into the morphological categories of caulome, phyllome, or trichome. From this author's views on the nature of the ovule generally, it appears justifiable to include his name under our present heading.

Sachs (51), in the second edition of his Textbook, enunciates a very similar view ; on p. 573 (Eng. ed.) he says : 'I am induced to ascribe different morphological significations to the ovules, according to their mode of origin and their position.' On p. 575, after citing the various theories held up to that time on the ovule, he says : 'Of these views, the one which appears to be most true to nature is the one which allows the greatest latitude ; but it is not always possible to refer an ovule to one of the categories, caulome and phyllome, for its position does not *necessarily* indicate its morphological significance. Thus a lateral ovule, as in Compositae and Primulaceae, might be either a leaf or a bud ; its probable leaf-nature in these cases depends entirely on teratological evidence, which is of very doubtful value, for an organ in a monstrous condition does not necessarily assume its primitive archetypal form.' The following sentence affords us the key to his whole position and characteristic view of the matter : 'The difficulties met with in endeavouring to regard the ovule as a caulome or phyllome may be transcended by regarding it as an "emergence" borne sometimes on an axial, sometimes on a foliar member.' (This is practically equivalent to regarding it as an organ *sui generis*.)

Strasburger (47), in his time, has held two distinct theories on the subject ; the earliest of these, embodied in his classical work, 'Die Coniferen und Gnetaceen,' supported the position of Braun and Payer. This view arose naturally from his researches on the Gymnosperms, the ovule of which he regarded as a metamorphosed bud whose stem was the nucellus and the integuments the leaves. But in course of time his views changed, until in 'Die Angiospermen und die Gymnospermen' we find him fully qualified for being classed among those who support the *sui generis* theory of the ovule, in regarding the latter as homologous with an independent

¹ In this order the single ovule terminates the floral axis.

structure like the sporangium of the Vascular Cryptogams, and with an *emergence*, which may arise promiscuously on either a foliar or an axial organ. It is to be noted that he founds his morphological views entirely on the phenomena of the *individual development* or ontogeny of the ovule. After stating that the funicle and sporangial-stalk, the nucellus and spore-capsule, are respectively parallel structures, he goes on to say that 'the integuments of Angiosperms cannot be directly identified with the indusia of Ferns, for they arise not from the structure which bears the ovule, but from the ovule, thus the sporangium itself, and from the upper margin of the funicle.' 'The nucellus is terminal to the funicle; the integuments, on the contrary, are of lateral origin.' After a careful investigation of certain ovular 'monstrosities' in *Rumex scutatus* and *Helenium Hoopesii*, A. Gray, he arrived at the following conclusions with regard to metamorphosed ovules generally: that metamorphoses (sports) are not retrogressive phenomena¹, 'but rather the expression of a competitive supplanting of one structure by another. In place of generative, vegetative rudiments arise, in accordance with the place of origin; so that, e. g., pinnae are formed as divisions of the carpels and buds as prolongations of the floral axis.' During the process of struggle between these two opposing tendencies, transitional forms occur, which will vary according as the one or the other tendency gains the upper hand. If the phenomena of oolysis were really retrogressive in character one would expect to see a cryptogamic sporangium appearing now and again, which, however, is never the case. In cases where an emergence appears on the surface of the leaflet, he regards the former as representing an entire ovule and not merely the nucellus; nor is the leaflet to be considered as the extreme form of the integuments, for he does not believe in the existence, as put forward by Čelakovský and others, of a series of transitional forms consisting at one extreme of almost normal integuments, and at the other of a vegetative leaflet. 'Each case must be considered in and for itself alone, and represents a compromise which has been arrived at between the struggle to form an ovule on the one hand and that to produce a leaflet on the other.' And again he says: 'If only a mere emergence is present on the leaflet, I regard this as the consequence of the tendency to leaflet-formation having early gained the upper hand, and not as the result of a reversion of already formed integuments into the leaflet. The hybrid-cases observed cannot be regarded as constituting a series of developmental stages which must be traversed in order to arrive at the extreme forms.'

He agrees with Čelakovský that where buds occur on fully formed parts of the carpel these are usually to be regarded as adventitious. But from his own standpoint, he must adhere to the view that the ovule may be directly supplanted by a vegetative bud.

¹ This has reference to Čelakovský's earlier view on the subject, which will be introduced in its proper place.

Finally, with reference to 'sports' generally, I may quote a sentence from his 'Lehrbuch der Botanik,' p. 132, where he says: 'Sports (Missbildungen) can only in rare cases be made use of in drawing morphological conclusions.'

Goebel (56) is a staunch upholder of the *sui generis* theory of the ovule and a severe critic of the method of settling morphological problems by the aid of 'sports.' In his 'Organographie' he recapitulates his views on the subject, put forward much earlier in Schenk's 'Handbuch der Botanik' and elsewhere. Speaking of the replacement of sporangia by vegetative organs, as in cases where stamens become foliaceous or petaloid, he says that 'a metamorphosis of the former into the latter does not occur, and the transitional stages between the normal and abnormal condition do not establish such a metamorphosis, but only show that there may be a varying degree of disturbance of the normal state of affairs.' The morphological character of stamens is determined by means of the development and a comparison with vascular Cryptogams. In treating of proliferated ovules, he considers it unjustifiable to regard these as reversions, and absurd to represent the simple leaf into which the ovule has become metamorphosed as the most primitive phylogenetic stage of development. 'The only conclusion it would be possible to draw from the proliferations would be that the integuments are formed from carpellary substance or represent outgrowths of the carpel which are the better adapted to vegetative development in proportion as the reproductive organs (the nucellus) are hindered in their growth.' We are to regard these proliferated ovules as crippled structures which have suffered a pathological modification of form; they may not be used for the determination of homologies. 'We are surprised to hear the assertion made that a leaflet bearing the abortive nucellus is homologous with the sorus- or sporangium-bearing leaflet of a fern. As if an abortive rudiment, showing no sign even of an embryo-sac, could in the remotest degree have anything to do with a sporangium.' He urges that 'it is a more profitable task to consider how such abnormalities have arisen and to discover the causes which condition the deviation from the normal development,' and this is the burden of his article on 'The Teratology of Plants' which appeared a few years ago in 'Science Progress.'

Here too we may place Eichler (49), who during his career held in turn all three views on the subject, but at length appears to have found repose for his ideas among those who support the theory we are now considering. In 1875, in the first volume of his 'Blüthendiagramme,' he upholds the axial-theory of the ovule, influenced largely by the facts resulting from Schmitz's recent work on the Piperaceae, and by those cases where the ovule is apparently replaced by a shoot; further, from the teachings of the theory of descent he felt bound to regard the ovule

as everywhere of similar morphological dignity; the placenta, on the other hand, as possessing a varying morphological value. But in 1878, in the second volume of the same work, he becomes an adherent of the foliolar theory, and says: 'I must side with Čelakovský and accept both his placental and ovular theory from beginning to end.' It is in the *Botanisches Centralblatt* for 1882, in his well-known thesis on the female flower of the Coniferae, that we find him finally throwing in his lot with the professors of the *sui generis* hypothesis; his observations on the coniferous ovule have evidently altogether influenced him in taking this step, for, after referring to the varying positions of this organ in the different genera of Coniferae, he says: 'We must, therefore, give up the idea that the ovule everywhere corresponds either to a leaf-segment or everywhere to a bud arising as a rule from the metamorphosis of those structures; it is rather the more or less modified macrosporangium of the higher plants [Vascular Cryptogams] which has been inherited by the Phanerogams, representing, like that organ, a structure *sui generis*. It may be compared to an emergence which it cannot be the exclusive privilege of leaves to produce, nor may it be regarded as invariably occurring on shoots; on the contrary, we must recognize that the ovule, like other emergences, may arise as well on the one as on the other organ, or on the margin of both, i. e. in the axil: this is not only clearly the case in the Coniferae, but undoubtedly also in the Angiosperms.'

Bayley Balfour's view (72) resembles that of Strasburger, as clearly shown by the following statement: 'I do not share a view which sees in integuments or other parts of the ovule anything of an axile or of a foliar nature. To me the funicle is a sporangiophore or a sporangial stalk, and the integumentary system is an outgrowth of the sporangial primordium of somewhat variable origin and development,' &c. As regards the schools of botanists who interpret the ovule from the standpoint of teratology and vascular anatomy respectively, he says: 'I do not accept the starting-point of either the one or the other.' Speaking of the sporangium his view is as follows: 'All recent investigations . . . tend to confirm the view that it is, and always has been, an organ *sui generis*. To that category the nucellus of the ovule is now pretty generally admitted. It is the body of a sporangium.' His general views on the nature of the ovule appear (as in the case of Strasburger) to be chiefly influenced by the facts of the individual development, or ontogeny of that organ; and he seems to hold the idea that the integuments, for instance, are structures arising *de novo* in the life-history of the nucellus or sporangium to subserve the special physiological function of water-carriers and food-reservoirs.

We have now to take up the consideration of the third, the '*foliolar*' theory of the nature of the ovule, that theory which explains this mysterious

organ as in fact representing the homologue of a *segment or leaflet of the carpel* which bears it (Fig. 3).

The notable founder of this view of the matter is Brongniart (9), who in 1844 made in the first place observations on abnormal carpels of *Delphinium elatum*, and noted the occurrence of transitions between the tridentate lobes of the foliaceous carpel and the ovules themselves. In his conclusions formulated from these facts he says that the veins of the placenta are really the lateral veins of the carpellary leaf; each ovule corresponds to a lobe or a large tooth of this leaf, while the funicle, as also the raphe, is formed by the median vein of this lateral lobe; the outer integument is the terminal portion of this leafy lobe folded on itself and forming a hood, the nucellus being a new production—a cellular protuberance arising on the upper surface of this lobe. It is thus impossible to regard the ovules together with the placenta as a production distinct from the carpellary leaf, and as part of the main or lateral axis. In *Brassica Napus* again, he observed transitions between the ovary and two foliage-leaves, and between the ovules and lobes of the leafy carpel. In abnormal ovaries of *Anagallis arvensis* the ovules are represented on the *axial* placenta by tiny leaves. In this case he evidently regards the ovules as the homologues of *entire* leaves, and also states his belief in a double origin for placentas: from the margins of carpels and from a prolongation of the floral axis. Finally, his estimation of the value of abnormalities, in the opening words of the paper, are worth quoting: ‘There is hardly a botanist at present who does not recognize how much light the study of these aberrations from the normal structure, to which the name of monstrosities is given, sheds on the essential and fundamental structure of certain parts of the plants, or on that which is peculiar to certain groups of plants.’

Robert Brown (35), in his paper on *Rafflesia* (p. 211), says: ‘The principal point in which the antherae and ovaries agree, consists in their essential parts, viz. the pollen and ovula, being produced on the margins of the modified leaf.’ On p. 211 he says further: ‘The marginal production of ovula not infrequently becomes apparent where its formation is in some degree imperfect, and is most evident in those deviations from the regular structure where stamina are changed more or less completely into pistilla,’ as in *Sempervivum tectorum*, &c. On pages 379 and 556 of the first volume of his Miscellaneous Botanical Works he speaks of the margin of the carpels as the proper place for ovules, and he gives instances of exceptions to this rule, as in Nymphaeaceae, *Mesembryanthemum*. On p. 563 we find the remark that ‘ovules belong to the transformed leaf or carpel, and are not derived from processes of the axis united with it, as several eminent botanists have lately supposed. That the placenta and ovula really belonged to the carpel alone is at least manifest in all cases where stamina are changed into pistilla.’

Caspary (25), in a paper, accompanied by beautiful illustrations, on abnormal ovules of *Trifolium repens*, states that the funicle in this plant is morphologically equivalent to the lower part of the leafy lobe or pinna of the carpel; at no stage is any limit between the funicle and the outer integument to be found. The inner integument, being so similar, must possess the same meaning and origin. It may disappear in the tissue of the leaflet, just as the outer integument has done in the funicle. 'The funicle, along with the integuments, is in *Trifolium repens* the morphological equivalent of a leaflet (pinna), whose stalk or midrib is in the lower part of the funicle and whose campanulate or conical outgrowths of the upper part are the integuments. The nucellus is the new shoot seated on this leaflet.' He thinks the nucellus also probably forms an integral part of the carpel.

Through that classical work of his, the 'Bildungsabweichungen,' Cramer (30) established his reputation as one of the most distinguished exponents of the morphological nature of the ovule. He observed metamorphosed ovules of Primulaceae; these were in the form of small foliar organs, developed on the free central placenta, which he regarded as entire leaves. He regards the nucellus as the product of a leaf. As for the integuments, if, he says, they were two distinct leaves and not part of one leaf they should both proliferate. That they are not such is shown by their becoming concave towards the upper side. The metamorphosed ovules are to be regarded as 'the outcome of the working of ideal successive combinations of formative forces fighting against each other, and not as developmental stages which have succeeded each other from time to time.' He is strongly in favour of the use of abnormalities for the solution of morphological problems. To him, the ovule of Compositae is, like that of Primulaceae, an entire leaf. He also observed proliferous flowers of *Delphinium elatum* in which the green carpels bore either sterile or vegetatively developed ovules in the form of lobes; the latter he held to be integumental in nature and the protuberances borne by them nucelli. In his paper 'On the Morphological Significance of the Ovule,' occurring in the same volume, he sets forth that the nucellus is a new structure and not of the nature of a shoot, as he does not believe that the latter, as asserted, could ever arise from an ovule. The nucellus is merely an *emergence*, like pollen-sacs and fern-sporangia. His researches in the development of the ovule in *Centaurea jacea*, *Lysimachia punctata*, and *Anthericum liliago* show that the primary papilla is *not* the nucellus but later gives rise to both this and the integuments. It is the funicle which first appears, and on this the nucellus is developed *laterally*. From his observations on *Trifolium repens* he concludes, with Caspary, that it is the *outer*, and not the inner integument which proliferates and which bears the nucellus in the middle of its upper surface.

Prantl (53) stands conspicuous as one of the bold, yet not necessarily

rash, thinkers who feel themselves at full liberty to compare certain organs of the Phanerogams with what they regard as related organs in the Vascular Cryptogams. It will suffice to quote a remark from page 11 of his work of 1875, where he says: 'Perhaps the integument (of *Cycas*) may be regarded as the equivalent of the indusium' (of Ferns). This view will be further elaborated when the tenets of the last author on our list are considered. Again, on page 13 he says: 'From my point of view I am unable to believe in actually axile ovules or anthers; these organs are derivatives of sori,' which are parts of the leaf. Further, he remarks: 'Ovules I must regard as under all circumstances originally parts of the carpel.'

At first (as seen from his paper of 1872, in which he says: 'Ovules are certainly most frequently metamorphosed axes') a defender of the axile nature of the ovule, Warming (46), in his most valuable thesis: 'De l'ovule,' published in 1878, and containing a series of researches into the development of the ovule-rudiment of the nucellus, unequivocally upholds the Brongniartian theory of the ovule. 'In every ovule we have considered two parts essentially different: the funicle and the integuments, which are of foliolar nature, and the nucellus, which is a new creation, a sporangium, a "sorus" composed of a single sporangium, as Prantl would say.' The origin and mode of development of the ovule-rudiment is similar to that of leaves, leaf-lobes, metablastema, emergences, and buds. Histogeny tells us nothing as to the morphological nature of the rudiment; it only informs us as to how the latter arises on the placenta as a new formation. 'There is but one method which can lead us to the goal: the gradual comparative study of allied forms, relying on all the means at the disposal of the morphologist.' On page 195 he writes: 'The comparative study of the carpels and placentation in the entire vegetable kingdom, the scrupulous examination of antholyses and the course of the vascular bundles, lead us, as Čelakovský and Van Tieghem have recently proved, to the conclusion that carpels and placentas are everywhere phyllomes, and that the ovule-rudiment is a leaf-lobe; I do not know if, in certain cases, they should not be regarded as metablastema, but the difference between the latter and a leaf-lobe is not essential and cannot be everywhere sustained.' On page 200 he proceeds: 'The so frequent foliar transformation of the ovule-rudiment which will later become the funicle, and its fusion with the carpel, is indomitable proof that this organ is really a leaf-lobe, a conclusion which had already been rendered very probable by the position and order of appearance of the ovules. Ovules are not buds; I know of no complete and well-studied teratological transformation which absolutely confirms the contrary, and I dare add that it will not be discovered. The ovular rudiment is therefore a leaf-lobe.' The developmental history and teratology show us:—

1. That the nucellus is a new formation on the ovule-rudiment, which is itself merely a lobe of the carpel.

2. That the pollen-sac and nucellus are identical as to their mode of development, which is here a proof of true homology, confirmed besides by a comparative study of these organs in the whole vegetable kingdom and by a series of teratological cases.

3. That the pollen-sac, like the sporangium (the common fundamental form of pollen-sac and nucellus), is everywhere attached to a leaf; conformably with this truth we are assured, in a totally different manner, that the ovule-rudiment is, in fact, of foliar nature.

This last view is supported by the study of Cycads. And he further says that we have seen that these metablastemata are everywhere attached to phyllomes and not to caulomes. As regards the true position of the nucellus, he says that in a general way it is to be regarded as *terminal* to the ovular rudiment. On the other hand, the teratological cases show it to be *lateral*, and appear to indicate the true, or at least the primitive, relations existing between the two organs.

At the end of Chapter III he says: 'It seems proved that the integument of Angiosperms is a special structure pertaining to the ovular leaflet and of foliar nature.' This author's treatise must be regarded, from its thoroughness of detailed investigation and breadth of treatment, as one of the most weighty contributions to this great and difficult subject, and of great interest in demonstrating how far developmental data serve in fixing the morphological dignity of the ovule.

Čelakovský (38) stands out as a very brilliant exponent of the foliolar theory of the ovule, his contributions to the subject being, in the writer's opinion, remarkable for their deep insight into, and ingenious handling of, one of the most difficult problems in botanical science. As the writer is also inclined to believe that in the sum of the numerous treatises of this author on the subject is contained a probable solution of the great problem as to the real morphological nature of the ovule, more space will be allotted to the consideration of his views than has been the case with the other authors cited above.

Firstly, with regard to the various methods employed in determining the morphological nature of any doubtful structure, these may be said to be four in number, and may be termed: (a) the developmental, (b) the comparative, (c) the anatomical, (d) the teratological. Applying these methods in turn to the solution of the nature of the ovule, it will be seen, in the first place, that the study of the *development* or ontogeny of this organ tells us simply that it is a protuberance borne sometimes on an axis, sometimes on a foliar organ, producing in basipetal order two lateral, cup-shaped appendages. Relying entirely on the ontogenetic facts and assuming that the ovule is a bud would surely be dangerous; for we cannot be sure that it is not an organ of a totally different nature, arising from the earliest stage of development, as a *congenitally-modified* structure. Of this latter

the ovary of the Primulaceae is another example, affording us excellent proof of the unreliability of developmental evidence in such cases. The *comparative* method is a useful one, but taken alone is not finally reliable, for the standard of comparison is likely to be ever a shifting quantity varying with each botanist who employs it; indeed, it seems impossible to apply this method by itself to the *solution* of the nature of an obscure structure like the ovule. The Bohemian Professor further regards *anatomical* data as powerless when directed to the same purpose; Van Tieghem's method of research along these lines must be regarded as stilted and artificial; for vascular tissue is developed where it is needed and is quite independent of the morphological character of the organ which it supplies, and no *absolute* reliance is to be placed on the character of the course or structure of the bundles. Yet all three of these methods may be usefully employed as collateral aids and adjuncts in solving the morphology of a doubtful structure. For this latter purpose, however, the direct and principal method is that of the study of *teratological* phenomena; it is on the 'metamorphogenesis' that Čelakovský rests the whole weight of his argument; for he maintains that these abnormalities, or deviations from the normal structure, are not of the nature of 'sports' or 'monstrosities,' as is usually supposed, but, on the contrary, are phenomena *controlled by definite laws* of development, producing thereby structures which are *not new or monstrous* (except, indeed, as regards the limited life-cycle of the particular organisms or group of organisms concerned), but whose homologues will inevitably be found occurring as *normal* structures in organisms belonging to other sections of the vegetable kingdom. For all vegetable life is one, and the four types of organs: caulome, root, phyllome, and trichome, are the common heritage of all members of the vegetable world. But the question arises: how is the morphological value of any given doubtful organ to be determined by means of the abnormal structure which it assumes under the influence of these laws of 'metamorphogenesis'? It would not be justifiable, on the ground of a mere *supplanting* or *replacement* of the abnormal structure, to regard the two as homologous in nature. But if (and this the writer regards as Čelakovský's unassailable position) there can be traced in the metamorphogenesis *a series of gradual transitions* (whether occurring in a single individual or scattered over a number of individuals, matters not) between the normal form and the extreme stage of the metamorphosed structure replacing it, then this must prove the absolute homology of the two, i.e. that they possess an identical morphological value. It seems to the writer that a certain shallowness of thought and the influence of preconceived ideas on the subject are the cause of the rigid adherence by so many eminent botanists to the oft-reiterated statement that 'abnormalities can be made to prove anything'! It betrays an utter neglect of the possibility

that, as stated above, these same 'abnormalities' may be the outcome of the working of rigid laws of development whose activity is reproduced in other departments of the vegetable kingdom. It is a view which can be easily refuted along the lines laid down above.

Čelakovský regards the ovule as the homologue of a trilobed leaflet or segment of the carpel, of which the terminal lobe, involuted towards the upper surface to form a cup-shaped structure enclosing the nucellus (this latter being an organ of the nature of an emergence or sporangium borne on the *upper* surface of the lobe) is the *equivalent* of the inner integument; while the two lateral lobes, fused by their *inner* margins across the *upper* surface of the leaflet, *represent* the outer integument (Figs. 5, 6). It is to be noted that, in accordance with what the author terms the 'law of laminar inversion,' which ordains that two foliar laminae

FIGS. 5 and 6. Diagrams of a trilobed leaflet showing how, by fusion of the two lateral lobes across the upper surface of the terminal lobe through union of the lines *fa*, *ac* and *gb*, *bc*, a structure homologous with the virescent ovule is obtained. The nucellus is seen seated as an emergence on the terminal lobe of the leaflet (after Čelakovský). *fun*, funicle.

are invariably in contact with each other by means of the *similar* surfaces of each, the lower surface of the outer integument contacts the lower surface of the inner integument. The above-outlined general position of the author derives its entire support from the facts revealed by the so-called 'monstrosities' of ovules where gradual transitional forms between the normal ovule and the three-lobed or simple leaflet have been observed.

In the case of abnormal ovules of the Crucifer, *Alliaria*, it was the inner integument which exhibited the greatest amount of proliferation or virescence; and another remarkable feature consisted in the preponderating tendency to proliferation of the *funicle* rather than of the outer integument. So that the ovular leaflet (the virescent ovule) sometimes assumes the form

of a leafy structure (the funicle) bearing the inner integument, subtended by the rudimentary sheath of the outer integument, on its lower surface (Fig. 8); or, in some cases, the outer integument may be completely absorbed in the funicular lamina. (For all details, both in this and other cases of abnormal ovules described by our author, the reader is referred to the original papers, which amply illustrate the various stages of the metamorphogenesis.) In the case of *Trifolium repens* it was also the funicle which chiefly proliferated, assuming the form of a bilobed structure at the

FIG. 7.

FIG. 8.

FIG. 9.

FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.

FIG. 7. *Alliaria officinalis*: normal ovule. FIG. 8. *Alliaria officinalis*: ovule in which funicle has proliferated, bearing at its base the outer integument ensheathing the inner integument. FIG. 9. *Alliaria officinalis*: ovule showing funicle subtending the much proliferated bifid inner integument, bearing the nucellus on its upper surface and an adventitious shoot (*ad*) at its base. FIG. 10. *Trifolium repens*: ovule in which funicle has proliferated, bearing inner integument in sinus between its two lobes (cf. Fig. 16). FIG. 11. *Trifolium repens*: virescent ovule proliferated as three-lobed leaflet. FIG. 12. *Hesperis matronalis*: virescent ovule with proliferated outer integument bearing inner integument on its lower surface. FIG. 13. *Hesperis matronalis*: proliferated outer integument bearing several inner integuments on its lower surface (Figs. 7-13 after Čelakovský). FIG. 14. *Cupressus*: seminiferous scale (= proliferated outer integument) bearing several ovules (= inner integuments and nucelli) on its lower surface (diagrammatic).

base of whose sinus sometimes occurred the small sheath of the outer integument (from the *upper* surface of which the funicular lamina is an outgrowth), enclosing the weakly-developed inner integument either in the form of a cup-shaped organ or as a simple leaflet bearing the nucellus on its upper surface (Figs. 10, 11). This is a very important stage, and will be referred to hereafter.

Hesperis matronalis differed from both of the last two plants, inasmuch as the leafy structure bearing the inner integument consisted solely of the *outer integument*, as is shown by its *sheathing base* and by the fact that the margins of the lamina passed gradually over into this sheath (Figs. 12 and 20). Hence our author terms it the 'basal lamina' (Grundspalte). The funicle takes therefore no part in its formation. In this plant the ovule frequently appeared as a simple leaflet bearing the nucellus on its *upper surface*; this leaflet cannot be the outer integument, because formation of the inner integument being always the primary process this latter organ could not arise as an emergence from the surface of the outer integument; it must also be situated invariably on the *lower* surface of the latter. The leaflet in question must therefore contain within itself *both* the inner and the outer integuments. This case resulted from the proliferating tendency setting in at the period when the ovule was nothing but a mere undifferentiated rudiment, this latter containing within itself the two integuments *in potentia*. The integuments, whether the outer or the inner, *once laid down as completely sheathing structures*, never proliferate as laminae. *Hesperis* is particularly interesting as having exhibited a case of a proliferated outer integument *bearing two or more inner integuments*, the extra ones occurring on the lateral lobes of the leaflet (Fig. 13); this case, as our author has elsewhere pointed out, is of considerable value for the interpretation of the female parts in *Cupressus* (Fig. 14).

With *Aquilegia* and its various stages of metamorphosed ovules our author winds up his investigations. The virescent ovules of this plant are probably the most difficult to understand and to unravel. The first stage, in which proliferation sets in rather late, shows the inner integument seated on the *upper* surface of the 'basal lamina'; the two lobes of the latter are bent back and fused together *behind* instead of, as in all other cases, in front of the inner integument. As this lamina is to constitute the outer integument, there here occurs an apparent contradiction to the usual law of 'laminar inversion'; but our author finds it to be *only apparent*, for differentiation into an upper and a lower surface has not yet taken place in the inner integument. In the second stage there is an anatropous cup-shaped structure which, from the mode of development and the various modifications occurring during the metamorphoses, is shown to be the *inner integument*, with which the outer integument is intimately fused along its whole length; the whole constituting a single undivided structure. This plant differs from *Trifolium* and *Alliaria* in the fact that the lower portion of the leaflet never grows out to form a separate individualized lamina. In the second stage just mentioned, where 'proliferation' sets in early, the outer integument remains stationary, while the inner integument alone proliferates as the apical portion of the entire leaflet. The usual relation-

ship between the outer integument and the ovular leaflet is described as follows: the former is an upgrowth out of the *lower* surface of the lower portion of the leaflet, after this latter has become *inverted and folded in towards the upper surface*. There exists, therefore, no essential difference between the case of *Aquilegia* and that of the other plants mentioned above.

As demonstration of the fact that these variable structures, known as the 'ovular leaflet' or virescent ovule, are all governed in their development by definite laws of growth and sequential differentiation, and are not the fortuitous and haphazard result of 'sportive' tendencies on the part of the plant producing them, it may be mentioned that *precisely identical phenomena* have been observed as curious modifications of the *entire* foliage-leaves of the common Lilac (*Syringa vulgaris*).

Again, exact homologues both of the metamorphosed ovule and of the unaltered ovule or 'ovular leaflet' may be found as *normal* structures in other departments of the vegetable kingdom. Čelakovský finds such in the apparatus of the female 'flower' of the Coniferae. The Taxaceae present the case of the normal ovule along with its two integuments; the remaining groups that of the semi-proliferated ovule, of which the seminiferous scale (or rather one-half thereof, seeing that each scale possesses two ovules) is the vegetatively developed outer integument bearing the involuted nucellus-producing inner integument on its lower (dorsal) surface. The case of *Cupressus*, in which a single seminiferous scale bears *several* such inner integuments on its lower surface (Fig. 14), finds its counterpart, as we have seen, in *Hesperis*; such a structure as this might conceivably arise out of a *compound ovular leaflet*, the terminal segment of each lobe becoming, as in the simple three-lobed leaflet, the inner integument borne on that lobe's lower surface. Descending lower in the scale, precisely the same set of structures (although naturally modified in accordance with the idiosyncrasies of the special group of plants in which they occur) are exhibited as *normal* stages of development in the sporophylls of the Ferns. In *Thyrsopteris* and Hymenophyllaceae (Figs. 15, 16) we see the case of the normal ovule of Angiosperms and of Taxaceae, in which the receptacle bearing its numerous sporangia (homologue of the nucellus), terminal in position, is ensheathed by the integuments, of which the indusium is the morphological equivalent of the inner, while the outer integument is represented by the laminar extension (when present) of the pinnule-segment *on either side* of the indusium. If now this structure be compared with the virescent ovule in *Trifolium repens*, its similarity to the bilobed funicular lamina enclosing the inner integument is obvious: the two structures are to be regarded as homologous although naturally presenting differing degrees of development of the respective parts. In *Dicksonia* the sorus is also terminal to the leaf-segment, but the indusium is here two-

lipped instead of cup-shaped. In *Davallia* and *Microlepia* the first stage in the projection of the sorus on to the lower surface is seen, this being caused by the elongation of the *upper* side of the indusium, which becomes green and is (in part) an extension of the pinnule-segment (the outer integument (Fig. 17).

The final stage is seen in *Cystopteris*, where the sorus, with the lower lip of the indusium, is projected completely on to the lower surface of the pinnule-segment (Fig. 18). In *Cibotium* and *Cyathea* there is a distinct cup-shaped indusium situated on the lower surface of the segment (Fig. 19); in the former this is at first terminal and marginal, becoming sub-

FIG. 15. *Thyrsopteris*: sorus with indusium (*ind*) and terminal receptacle bearing sporangia (*spg*). FIG. 16. *Trichomanes*: receptacle and cup-shaped indusium (= inner integument) seated in sinus between two lobes of leaflet (= outer integument) (cf. Fig. 10). FIG. 17. *Davallia*: early phylogenetic stage in projection of indusium on to lower surface of leaflet; indusium one-sidedly developed. FIG. 18. *Cystopteris*: later stage in same process. FIG. 19. *Cyathea*: same stage, but indusium here completely formed; *spg*, receptacle bearing sporangia. FIG. 20. *Hesperis*: proliferated outer integument bearing inner integument on its lower surface; this is precisely the same structure as that in *Cyathea*. (All after Čelakovský.)

sequently displaced into an inferior position; in the latter it is inferior from the first. In these two latter cases we have the exact counterpart of an inner integument situated on the lower surface of a 'basal lamina' or proliferated outer integument or funicle, such as occurs in *Alliaria* or *Reseda* (Fig. 20).

As regards the Rhizocarps: in the Salviniaceae the fruit is equivalent to an ovule with one integument; the indusium represents the inner integument and the leaf-lobe bearing the sorus is probably homologous with the outer integument. There is a striking resemblance, admitted by most botanists, between the monangic sorus of *Azolla* and an ovule (Fig. 21). Prantl regarded the two as homologous structures, and Campbell suggests the same thing. In the Marsiliaceae the fruit has the value of a compound fruit of Salviniaceae. In *Pilularia* it is homologous with a pinnately quadri-foliate leaflet of the entire leaf of *Marsilia*; in *Marsilia* with a pinnately multifoliate leaflet; in these cases the leaflet of the sporangiferous leaf possesses the compound structure of the vegetative leaf,

while the leaflet of the latter is simple. The outer wall of the sporocarp is homologous with the *upper* surface of the outer integument of the ovule; here, as in *Hesperis* and *Cupressus*, it is polysorous, bearing a number of indusia or inner integuments (each with its enclosed sporangia) on the lower surface (Figs. 22-25).

FIG. 21.

FIG. 22.

FIG. 23.

FIG. 24.

FIG. 25.

FIG. 21. *Azolla*: megasporangium enclosed by indusium (after Campbell). FIG. 22. *Pilularia*: diagram of morphological structure of sporocarp from two pairs of leaflets, each bearing a sorus on its lower surface. FIG. 23. *Pilularia*: transverse section (taken through dotted line in preceding figure) of leaflet, showing sorus and indusium; *ma* = mega-, *mi* = microsporangia. FIG. 24. *Marsilia*: diagram of morphological structure of sporocarp, from several pairs of leaflets, each bearing sorus on its lower surface. FIG. 25. *Marsilia*: transverse section (taken through dotted line in preceding figure) of leaflets here supposed to be folded together from opposite sides of midrib to form the sporocarp; sorus shown.

For a further elaboration of this subject of the homologies in the different groups the reader is referred to our author's exhaustive paper in 'Pringsheim's Jahrbücher.'

In the Lycopodiaceae are again found equivalents for our ovule and its various parts. The *ligule* of the Selaginelleae our author, in the above-mentioned paper, regards as the same leaf-lobe which later in the Schizaeaceae grows out over the sporangia, but here, owing to the ventral position of the sporangium, the ligule is also ventral, and as such is so weakly developed that it is partly fused with the carpel, so that it *de facto* springs from the carpel; the sporangium, as in the Schizaeaceae, springing

from the lower surface of this modified leaf-lobe. He regards the *velum* as 'unquestionably equivalent to the indusium of the Ferns.' 'The ligule along with the velum and sporangium is homologous with a leaf-segment

FIG. 26. *Lepidocarpon*: diagrammatic lateral view of sporophyll, showing 'integument' and its mode of attachment to sporophyll; position of ligule and sporangium are seen through the supposedly transparent 'integument.'

Lepidocarpon he regards the ligule as really (i.e. morphologically or ideally) situated *outside* the 'integument,' which is here open at its distal end (Figs. 26, 27). In other genera either the velum or both this and the ligule have quite aborted or never developed: the result, probably, of an efficient protection of the sporangia being afforded by the peltate ends of the sporophylls, as in *Lepidodendron* and *Spencerites*. The same may be said with regard to the Equisetaceae.

FIG. 27. *Lepidocarpon*: diagrammatic transverse section taken through dotted line in preceding figure. *int* = integument; *sph* = sporophyll.

Before proceeding further it is necessary to direct attention to one very important consideration. Čelakovský, until comparatively recently, regarded the virescent conditions of the Angiospermous ovule as *retrogressive* phenomena, as *reversions* to the primitive ancestral structures of the organ. After a deeper study, however, of the phylogenetic relationships of the various organs of plants, from which he gathered that the primitive position of the sporangium on the sporophyll was a *terminal* one, he was eventually led to regard the *normal* structure of the ovule as representing a more ancestral state of affairs, inasmuch as the nucellus or sporangium occupies a position *terminal* to the ovular leaflet. The more *vegetatively* developed is any structure, the more modified will it be in the direction of an *advance* away from the primitive reproductive condition. The *virescent* condition of the ovule merely reveals to us the *homologies* of the latter; it tells us nothing as to its phylogenetic origin; this can alone be determined by the *comparative* method of research.

We have thus been able to trace the homologue of the ovule in three great phyla of the vegetable kingdom; and this is only what one would *a priori* expect, for if there is a unity underlying vegetable life, and if all forms of plant-life own a common origin in the far past, the same organs, under a more or less modified or disguised form, will be produced by plants belonging to most of the great phyla of evolution.

Finally, some of the objections urged by Čelakovský against the other two theories of the ovule may be brought forward.

Against the bud-theory may be placed the fact that in almost all cases the integuments arise *basipetally* and not *acropetally*, a strange and exceptional state of affairs if they really represent foliar appendages of the nucellus. Eichler, Schmitz, and at one time Warming, held that the terminal organs belong to the caulome-category on account of their position; but this reliance on topical morphology is useless, as terminal organs other than axes are known. Hanstein showed that where the apex of the stem ceases to grow the apical periblem continues to do so and forms a terminal organ, which is a leaf, as the latter is always formed from periblem, whereas it is by growth of the plerome in length that an axis is continued in growth. The terminal cotyledon of Monocotyledons is another case in point. Thus, terminal ovules are not necessarily axial in nature. As regards the occurrence of adventitious buds in connexion with the ovules, our author determines, as far as his own investigations on *Alliaria* are concerned (Fig. 9), that the bud always represents a pathological new formation, and not a transformation of the ovule; he found never a trace of an axis on which integuments are borne as lateral leaves.

He enters into a lengthy criticism of Peyritsch's views and observations, which is in itself of considerable value towards the further elucidation of the nature of the ovule. The conclusions of this author, that the adventitious shoots are derived from and homologous with ovules, is shown to be groundless.

Čelakovský says: 'It may be stated with certainty that shoots replacing ovules are never met with in virescent structures, and much less is this the case with transitions between ovules and such shoots.'

Peyritsch's study of ovular metamorphosis is throughout influenced by the idea that the nature of the ovule can be determined from *developmental* data. He regards the ovular rudiment and the nucellus as identical (shown by Warming to be incorrect); that, therefore, the nucellus arises directly on the placenta and bears the integuments: but this never happens. He thinks, further, that the terminal ovule of *Rumex scutatus* is a shoot owing to its position; but it is no more so than is a terminal nucellus.

Other criticisms of Peyritsch's observations and theories could be

given, all going to show that that writer entirely misconstrued the nature of the various structures which came under his notice.

Referring to the case described by Penzig of adventitious shoots on ovular leaflets of *Scrophularia vernalis* which bore nucelli at their apex, our author holds that this phenomenon arises from a coincidence of the two constructive forces of the two structures respectively. The shoot arises below the nucellus after the latter has been formed and carries it upon its apex; but here no intermediate forms can exist between the two; 'in all truly intermediate forms an homology exists between all the parts, so that a transformation of the same basic structure obtains.' An analogy for such an enclosed apex is found in a case of *Helianthus annuus*, mentioned by Sachs, in which the normal apex was damaged.

From all this we gather that inasmuch as no true transitional structures between an ovule and a shoot have ever been seen, but that, on the contrary, all so-called ovular shoots are either axillary productions of the carpels or else of the nature of adventitious buds on the ovular integuments or the placenta, therefore the ovule can no longer be held to possess the morphological nature of a shoot.

Finally, as regards the *sui generis* theory of the ovule, Čelakovský's criticism of the views of Strasburger, the chief champion of this view, are very instructive and illuminating. This author's main theory, as also in the case of the abnormal female parts of Coniferae, with regard to the various virescent conditions of the ovule, is this, viz., that they represent the varying results of a simultaneous strife between two forces: the *generative*, tending to produce the ovule which is of the nature of a sporangium or emergence, and the *vegetative*, tending to form a leafy structure. Now, Čelakovský maintains that, according to this view of Strasburger's, the transitional forms which occur must be those between two quite heterogeneous plant-organs: a leaflet or segment of a carpel on the one hand, and a sporangial emergence on the other; this is, on the face of it, an absurdity, and represents the same fallacy as that underlying his position with regard to the female flower in Coniferae. For the transitional forms clearly betray their derivation from the self-same organ, their origin from the same morphological substratum.

Moreover, the virescent phenomena clearly show that the generative and vegetative forces assume possession of the ovular leaflet successively rather than simultaneously.

Further, 'if the ovule is not a metamorphosis of the carpellary segment, but a macrosporangium, an emergence, and this purely in place of the leaf-segment, the ovule with its integuments should contract more and more and gradually vanish, the leaflet or segment, on the other hand, become more fully developed.' There can be no other compromise. And yet, as has been repeatedly shown, this is precisely what does not happen, for the

integuments increase in size and become fused with and an integral part of the carpel.

Čelakovský does not suppose, as was thought by Strasburger, that the various transitional forms represent the different stages of development which are to be run through in order to reach the extreme form; nor does he regard it as ever possible that the integuments could, once they are laid low, revert back into a carpellary segment. A series composed of metamorphosed structures is of greater morphological importance than a developmental series.

Strasburger asserts that each of these forms ought to be treated and studied separately, in and for itself alone. Our author, on the contrary, affirms that 'each single case taken by itself is of little value; it is only the comparatively arranged complete series which can guarantee us real insight into the essential being, metamorphosis, and origin of the ovule.'

Our author further urges that a comparison of an orthotropous ovule with the macrosporangium and sporocarp of *Azolla* tends to destroy Strasburger's views founded on the ontogeny; for the integument of *Azolla* arises not from the sporangium, but from the leaf-segment beneath it. And, moreover, as the present writer would add, Warming has clearly shown that both nucellus and integuments develop *independently* from the ovular rudiment. The terminal position of the nucellus does not prevent it from being altogether distinct from the ovular rudiment producing it.

As regards the view held, for instance, by Balfour, that the nucellus is an organ *sui generis*, Čelakovský points out that inasmuch as, in the virescent ovule, the nucellus, as an emergence from the surface of the ovular leaflet, may become completely absorbed into, and form an integral part of, the latter, it cannot possibly constitute one of the distinct morphological categories; for the respective organs belonging to these latter have never been known to merge or be absorbed into each other in such a manner. The same will be true of the eusporangium of Vascular Cryptogams, which is the homologue of the nucellus.

GENERAL SUMMARY.

In conclusion is appended a brief *résumé* of the various theories on the morphology of the ovule.

Axial Theory.

St. Hilaire (1830, 1840), Schleiden (1839, 1843), Payer (1859), Braun (1860), Peyritsch¹ (1872-76): the nucellus is of the nature of a bud bearing the two integuments as lateral foliar appendages.

¹ It must be borne in mind that this author nowhere makes any definite statement as to the morphology of the ovule, but his writings betray the trend of his ideas on the subject.

Sui Generis Theory.

Schmitz (1870); Sachs (1874); Goebel (1882-1901); Strasburger (1879); Balfour (1901): the ovule does not (necessarily) belong to any of the morphological categories, but is an independent structure, borne either on stem or foliar organs.

Foliolar Theory.

Brongniart (1844); R. Brown (1845-66); Caspary (1861); Cramer (1864); Prantl (1875); Warming (1878); Čelakovský (1874-1900): the ovule belongs morphologically to the category of the phyllome; it is the homologue of a (usually) three-lobed leaflet or segment of the carpel (or female sporophyll), the outer integument and funicles representing the lower portion of the leaflet whose lateral lobes, fused across its upper or ventral surface, constitute a lamina having the *lower* surface directed towards that of the involute cup-shaped terminal lobe; the representative of the inner integument. The nucellus is, like the eusporangium of Ferns, of the nature of an *emergence*, borne on the *upper* surface of the leaflet's terminal lobe. The morphological value of the various parts of the ovule here set forth is ascertained and demonstrated by the occurrence, in teratological conditions of the ovule, of gradual transitions between the structure of the normal ovule and that of the extreme virescent organ in the form of a carpellary leaflet. This latter must not be regarded as a reversion to the primitive condition; on the contrary, the normal ovule possesses a structure essentially primitive and archetypal.

BIBLIOGRAPHY.

1. MIRBEL: Observations sur la famille des végétaux conifères, Ann. du Mus. d'Hist. Nat., vol. xv, p. 473, 1810.
 ——— Recherches sur la structure et le développement de l'ovule végétale, 1828.
 ——— and SPACH: Notes sur l'embryogénie des *Pinus Laricio*, &c., Ann. d. Sci. Nat., sér. 2, vols. xix and xx, 1843.
2. JAEGER: Missbildungen der Gewächse (*Aquilegia*), 1814.
3. ROEPER: Enumeratio Euphorb. (*Delphinium*), 1824.
4. RICHARD, L. C.: Commentatio botanica de Coniferis et Cycadeis, 1826.
5. SCHIMPER, K. FR.: On Umbelliferae, Cruciferae, Resedaceae: *Salix babylonica*, *Papaver somniferum*, *Symphytum Zeyheri*, Flora, vol. ii, 1829.
 ——— Beschreibung des *Symphytum Zeyheri*, &c., Geiger's Magazin für Pharmacie, vol. xxviii, 1835.
6. ST. HILAIRE, A. DE: Premier mémoire sur la structure et les anomalies de la fleur des Résédacées, Ann. de la Soc. d'Orléans, 1830.
 ——— Deuxième mémoire sur les Résédacées, Montpellier, 1837.
 ——— Leçons de Botanique comp., princip. la morphologie végétale, 1840.

7. ENGELMANN: De Antholysi (*Sisymbrium, Torilis, Gilia*), 1832.
8. ENDLICHER: *Linnaea*, vol. vii, p. 21 (axial placenta), 1832.
— and UNGER: *Grundzüge der Botanik* (disk-theory), 1843.
9. BRONGNIART: *Beobachtungen an Primula chinensis*, *Annales des Sciences Naturelles*, sér. 2, vol. i, p. 308 (leaf-theory), 1834.
— Examen de quelques cas de monstruosités végétales propres à éclairer la structure du pistil et l'origine des ovules, *Archives du Muséum d'Hist. Nat.*, Paris, vol. iv, p. 43, 1844.
10. FRITSCHKE: Ueber die Entwicklung des Pflanzeneies in seinen frühesten Zuständen, *Wieg. Archiv*, ii, p. 229, 1835.
11. MOHL, VON: Sur la métamorphose des anthères en carpelles, *Ann. d. Sci. Nat.*, sér. 2, vol. viii, 1837.
12. TREVIRANUS: *Physiologie der Gewächse*, vol. ii, p. 333, 1838.
13. VALENTIN: Antholysen von *Lysimachia ephemerum*, *Act. nat. cur.*, vol. xix, i, p. 225, 1839.
14. SCHLEIDEN: Sur la signification morphologique du placentaire, *Ann. des. Sciences Nat.*, sér. 2, vols. ix and xii, 1839.
— *Grundzüge der wissenschaftlichen Botanik*, p. 389, 1843.
15. BRAUN, AL.: Vortrag auf dem Congrès scientifique de France, 10. Sitzung, Strassburg, pp. 172-2 (seminif. scale of Coniferae), 1842.
— Ueber Polyembryonie und Keimung von *Coelebogyne* (axial theory), 1860.
— Die Frage nach der Gymnospermie der Cycadeen, &c., *Monatsber. d. Königl. Akad. Wiss. Berlin*, 1875.
16. REISECK: Ueber das Wesen der Keimknospe, *Linnaea*, vols. xvii and xx (*Alliaria*, leaf-theory), 1843.
17. SCHLECHTENDAHL: *Pflanzen-Monstrositäten*, *Bot. Zeit.*, 1847.
18. UNGER: Antholysen von *Primula chinensis*, *Act. nat. cur.*, vol. xxii, ii, p. 543, 1850.
19. WIGAND: *Grundlegung der Pflanzenteratologie*, p. 39 (*Reseda*, axial theory), 1850.
— *Beiträge zur Pflanzenteratologie, Botanische Untersuchungen*, p. 23 (*Rosa, Turritis, Crepis*), 1853.
20. GERMAIN DE ST. PIERRE: *L'Institut*, no. 1021, p. 255, 1853.
21. ROSSMANN: Die Entwicklung der Eiknospen aus dem Fruchtblatte und Deutung des Samenträgers, *Flora*, pp. 657, 705 (*Aquilegia*, axial theory), 1855.
22. NORMAN, J. M.: *Observations sur les Chloranthies*, *Ann. d. Sci. Nat., Bot.*, sér. 4, vol. ix, 1858.
23. SCHACHT: *Grundriss der Anatomie und Physiologie der Gewächse* (disk-theory), 1859.
24. PAYER: *Organogénie de la fleur*, 1859.
25. WYDLER: Beschreibung einiger Antholysen von *Alliaria*, *Denkschrift der Regensburger Bot. Gesellsch.*, vol. iv, Abth. i, p. 77, 1859.
26. CASPARY: De Abietinearum floris feminei structura morphologica, *Ann. d. Sci. Nat.*, sér. 4, vol. xiv, 1860.
— *Vergrünungen der Blüthe des weissen Klees*, *Königsberger Schriften der physik.-ökon. Gesellschaft*, p. 50, 1861.
27. BAILLON: *Recherches organogéniques sur la fleur femelle des Conifères*, *Adansonia*, vol. i, 1860-1.
— *Nouvelles recherches sur la fleur femelle des Conifères*, *Adansonia*, vols. v-vi, 1864-5.
— *Description d'une Primulacée à fleurs monstreuces*, *Adansonia*, vol. iii (*Lysimachia*), 1862-3.
28. HOFMEISTER: *The Higher Cryptogamia*, Ray Society, 1862.
29. PRINGSHEIM: *Zur Morphologie der Salvinia natans*, *Pringsh. Jahrb. f. wiss. Bot.*, vol. iii, 1863.
30. MARCHAND: *Monstruosités végétales*, 1^{er} fasc., *Adansonia*, vol. iv, 1863-4.
31. CRAMER: *Bildungsabweichungen bei einigen wichtigeren Pflanzenfamilien und die morphologische Bedeutung des Pflanzeneies*, Zürich, 1864.
32. PARLATORE: *Studi organografici sui fiori e sui frutti delle Conifere*, *Opuscula botanica*, 1864.
33. ØRSTED: *Bidrag til Naaetræernes Morphologi*, *Videnskab. Meddelelser Nat. Foren.*, Kjöbenhavn, 1864.

34. HALLIER: Phytopathologie (*Verbascum*), 1864.
35. SALTER: On a Sexual Monstrosity, consisting in the Development of Polliniferous Ovules in two species of *Passiflora*, Trans. Linn. Soc., vol. xxiv, p. 143, 1864.
36. BROWN, R.: Miscellaneous Botanical Works, vol. i, 1866.
37. MEYEN: Beiträge zur Kenntniss der Azollen, Act. Acad. Leop. Carol., vol. xxxii, 1867.
38. MASTERS: On Polliniferous Ovules in a Rose (*Rosa arvensis*), Seemann's Journal of Botany, vol. v, p. 318, 1867.
 ————— Pflanzeneratologie, trans. by U. Dammer, Leipzig, 1886.
39. ČELAKOVSKÝ: Ueber die allgemeine Entwicklungsgeschichte des Pflanzenreiches, Königl. böhmische Gesellschaft der Wissenschaften, Naturwiss.-mathem. Section, 1868.
 ————— Ueber den Zusammenhang der verschiedenen Methoden morphologischer Forschung, Lotos, Oct., 1874.
 ————— Ueber die morphologische Bedeutung der Samenknospen (*Anagallis*, *Dictamnus*), Flora, 1874.
 ————— Die Vergrünungsgeschichte der Eichen von *Alliaria officinalis*, Botanische Zeitung, 1875.
 ————— Zur Discussion über das Eichen, Bot. Zeitung, 1875.
 ————— Vergleichende Darstellung der Placenten in den Fruchtknoten der Phanerogamen (*Scrophularia*, *Anagallis*), Abhandl. der böhm. Ges. d. Wissensch., 1876.
 ————— Die Vergrünungsgeschichte der Eichen von *Trifolium repens*, Botan. Zeitung, 1877.
 ————— Ueber Chloranthie der *Reseda lutea*, Bot. Zeit., 1878.
 ————— Ueber vergrünte Eichen der *Hesperis matronalis*, Flora, 1879.
 ————— Die Vergrünungsgeschichte der Eichen von *Aquilegia* als neuer Beleg zur Foliolartheorie, Bot. Centralblatt, vol. x, 1882.
 ————— Untersuchungen über die Homologien der generativen Producte der Fruchtblätter bei den Phanerogamen und Gefässkryptogamen, Pringsh. Jahrb. f. wiss. Botanik, vol. xiv, 1883.
 ————— Neue Beiträge zur Foliolartheorie des Ovulums, Abhandl. d. böhm. Ges. d. Wissensch. (*Raphanus*), 1884.
 ————— Die Gymnospermen: eine morphologisch-phylogenetische Studie, Abhandl. d. königl. böhm. Ges. d. Wiss., 7. Folge, vol. iv, 1890.
 ————— Nachtrag zu meiner Schrift über die Gymnospermen, Engler's Botanische Jahrbücher für Systematik, &c., vol. xxiv, 1897.
 ————— Epilog zu meiner Schrift über die Placenten, Sitzungsab. d. Königl. böhm. Ges. d. Wiss., 1899.
 ————— Ueber den phylogenetischen Entwicklungsgang der Blüthe, &c., part ii, p. 192. Sitzungsab. d. Königl. böhm. Ges. d. Wiss., 1900.
 ————— Neue Beiträge zum Verständniss der Fruchtschuppe der Coniferen, Pringsh. Jahrb. f. wiss. Bot., vol. xxxv, part iii, 1900.
40. VAN TIEGHEM: Anatomie comparée de la fleur femelle et du fruit des Cycadées, des Conifères et des Gnétacées, Ann. d. Sci. Nat., sér. 5, vol. x, 1869.
 ————— Traité de botanique, vol. i, p. 405, 1884.
 ————— Éléments de botanique, vol. i, p. 398, vol. ii, p. 266, 1898.
41. KOEHNE: Ueber Blütenentwicklung bei den Compositen, p. 65, Inaugural-Dissertation, Berlin, 1869.
42. SPERK: Die Lehre von der Gymnospermie, Mém. de l'Acad. Impér. des Sciences Nat., sér. 5, Bot., 1868-9.
- 42A. ROHRBACH: Die Samenknospe der Typhaceen; Bot. Zeit., 1869.
43. HANSTEIN and SCHMITZ: Ueber die Entwicklungsgeschichte der Blüten einiger Piperaceen, Botanische Zeitung, 1870.
44. SCHMITZ: Die Blütenentwicklung der Piperaceen, Hanstein's Botanische Abhandlungen, vol. ii, 1875.
45. MAGNUS: Beiträge zur Kenntniss der Gattung *Najas*, 1870.
 ————— Ovula der vergrünten Blüten von *Reseda lutea*, Sitzungsab. d. Ges. naturf. Freunde zu Berlin, Bot. Centralbl., vol. ii, p. 430, 1882.
46. PEYRITSCH: Ueber Bildungsabweichungen bei Cruciferen, Pringsh. Jahrb. f. wiss. Bot., vol. viii, 1872.

46. PEYRITSCH: Teratologie der Ovula, Festschrift d. Wien. Zoolog.-bot. Ges., pp. 115-144, 1876.
 — Zur Aetiologie der Chloranthien einiger *Arabis*-Arten, Pringsh. Jahrb. f. wiss. Bot., vol. xiii, 1882.
47. WARMING: Recherches sur la ramification des Phanérogames, Schriften d. dänischen Gesell. d. Wiss., Ser. 5, vol. x, 1872.
 — Bemerkungen über das Eichen, Bot. Zeit., 1875.
 — De l'ovule, Ann. d. Sci. Nat., Bot., 1878.
 — Bidrag til Cycadeernes Naturhistorie, K. Dansk. Vidensk. Selsk. Forhandl., 1879.
48. STRASBURGER: Die Coniferen und die Gnetaceen, 1872.
 — Einige Bemerkungen über Lycopodiaceen, Bot. Zeit., 1873.
 — Ueber *Azolla*, Jena, 1873.
 — Die Angiospermen und die Gymnospermen, 1879.
49. JURANYI: Ueber die Entwicklung der Sporangien und Sporen der *Salvinia natans*, 1873.
 — Ueber die Gestaltung der Frucht bei *Pilularia globulifera*, Botanisches Centralblatt, p. 201, 1880.
50. EICHLER: Sind die Coniferen gymnosperm oder nicht? Flora, 1873.
 — Blüthendiagramme, vol. i (axial theory), 1875.
 — Blüthendiagramme, vol. ii (foliolar theory), 1878.
 — Ueber die weiblichen Blüten der Coniferen, Monatsber. d. Königl. Akad. d. Wiss., Berlin, 1881.
 — Ueber Bildungsabweichungen bei Fichtenzapfen, Sitzungsber. d. Königl. Akad. d. Wiss., Berlin, 1882.
 — Ueber die weiblichen Blüten der Coniferen, Bot. Centralbl., vol. ix, p. 49 (*sui generis* theory), 1882.
51. CHATIN: Études sur le développement de l'ovule et de la graine dans les Scrofularinées, &c., Ann. d. Sci. Nat., sér. 5, vol. xix, 1874.
52. SACHS: Lehrbuch der Botanik, 4th edition, 1874.
53. BURCK: Indusium der Varen, Haarlem, 1874.
54. PRANTL: Bemerkungen über die Verwandtschaften der Gefässkryptogamen, Verhandl. d. Phys. Med. Ges. in Würzburg, 1875.
 — Morphologische Studien, Flora, 1875.
 — Untersuchungen zur Morphologie der Gefässkryptogamen, vol. i, Hymenophyllaceen, 1875; vol. ii, Schizaeaceen, 1881.
55. BEKETOFF: On Proliferated Flowers of *Cichorium Intybus*, Mém. de la Soc. Nat. d. Sc. Nat. de Cherbourg, vol. xxi, 1877.
56. DYER: The Morphology of *Selaginella*, Nature, 1877.
57. GOEBEL: Ueber Sprossbildung auf *Isoëtes*blättern, Bot. Zeit., 1879.
 — Beiträge zur Entwicklungsgeschichte der Sporangien, Bot. Zeit., 1880-2.
 — Die vergleichende Entwicklungsgeschichte der Pflanzenorgane, Schenk's Handbuch der Botanik, vol. iii, part. i, pp. 114, 120.
 — Archegoniatenstudien, Flora, 1892-3.
 — Organographie der Pflanzen, 1901.
58. MAGNUS, P.: On virescent Ovules of *Aquilegia atrata*, Verh. bot. Ver. Brandenburg, vol. xxi, 1880.
59. PAX, F.: Metamorphogenese des Ovulums von *Aquilegia*, Flora, vol. lxxv, 1882.
60. PENZIG: Ueber vergrünte Eichen von *Scrophularia vernalis*, L., Flora, vol. lxxv, 1882.
 — Pflanzenteratologie, vol. i, 1890.
61. NÄGELI: Mechanisch-physiologische Theorie der Abstammungslehre, p. 496, 1884.
62. MEUNIER: La Pilulaire: Étude anat.-génétique du sporocarpe chez la *Pilularia globulifera*, La Cellule, vol. iv, p. 325, 1887.
63. CAMPBELL: The Structure and Development of the Ostrich Fern, Mem. Boston Soc. Nat. Hist., 1887.
 — The Development of *Pilularia globulifera*, L., Annals of Botany, vol. ii, p. 233, 1888.
 — The Systematic Position of the Rhizocarpeae, Bull. Torrey Bot. Club, Oct., 1888.
 — On the Affinities of the Filicineae, Bot. Gaz., Jan., 1890.
 — Contributions to the Life-history of *Isoëtes*, Ann. Bot., vol. v, August, 1891.

86 Worsdell.—*The Structure and Morphology of the 'Ovule.'*

63. CAMPBELL: On the Relationships of the Archegoniatae, Bot. Gaz., Dec., 1861.
——— The Development of the Sporocarp of *Pilularia americana*, Bull. Torrey Bot. Club, April, 1893.
——— On the Development of *Azolla filiculoides*, Ann. Bot., 1893.
——— The Structure and Development of Mosses and Ferns, 1895.
64. VINES: On the Systematic Position of *Isoetes*, L., Ann. Bot., 1888.
65. ENGLER and PRANTL: Die natürlichen Pflanzenfamilien, 1889.
66. BÜSGEN: Untersuchungen über normale und abnormale Marsilienfrüchte, Flora, vol. xlviii, p. 169, 1890.
67. FARMER: On *Isoetes lacustris*, Ann. Bot., vol. v, Dec., 1890.
68. WOJENOWIĆ: Beiträge zur Morphologie, Anatomie und Biologie der *Selaginella lepidophylla*, Inaug. Dissert., Breslau, 1890.
69. GIESENHAGEN: Die Hymenophyllaceen, Flora, 1890.
70. BOWER: On the Structure of *Lepidostrobis Brownii*, Ann. Bot., vol. vii, 1893.
——— Studies in the Morphology of Spore-producing Members, I, Philosophical Transactions of the Royal Society, vol. 185 (Equisetaceae, Lycopodiaceae), 1894.
——— Studies, &c., iv; The Leptosporangiate Ferns, Phil. Trans. Roy. Soc. B., vol. 192, 1899.
71. SCOTT: On *Spencerites*, a new Genus of Lycopodiaceous Cones from the Coal-Measures, &c., Phil. Trans. Roy. Soc., vol. 189, 1898.
——— The Seed-like Fructification of *Lepidocarpon*, a genus of Lycopodiaceous Cones from the Carboniferous Formation, Phil. Trans. Roy. Soc., vol. 194, 1901.
72. JOHNSON, D. S.: On the Development of the Leaf and Sporocarp in *Marsilia quadrifolia*, L., Ann. Bot., vol. xii, 1898.
73. MASLEN: The Structure of *Lepidostrobis*, Trans. Linn. Soc., vol. v, 1899.
74. SMITH, R. WILSON: The Structure and Development of the Sporophylls and Sporangia of *Isoetes*, Bot. Gazette, 1900.
- 74A. DUNN, L. B.: Morphology of the Development of the Ovule in *Delphinium exaltatum*. Proc. Amer. Assoc. Adv. Sci., vol. 49, 1900.
75. WORSDELL: The Structure of the Female Flower in Coniferae: an Historical Study, Ann. Bot., vol. xiv, March, 1900.
——— The Morphology of the 'Flowers' of *Cephalotaxus*, Ann. Bot., Dec., 1901.
——— On abnormal Flowers of *Helenium autumnale*, L.; Journal Roy. Hort. Soc., vol. xxvii, part 4, April, 1903.
76. BALFOUR, I. BAYLEY: Address to the Botanical Section, British Association for the Advancement of Science, Glasgow, 1901.
- 76A. ——— Angiosperms. Reprinted from the new volumes of the Encyclopaedia Britannica, 1902.
77. HALLIER, H. G.: Beiträge zur Morphogenie der Sporophylle und des Trophophylls in Beziehung zur Phylogenie der Kormophyten, Beiheft zum Jahrbuch der Hamburgischen Wissenschaftlichen Anstalten, vol. xix, 1901.
78. SCHUMANN, K.: Ueber die weibliche Blüthe der Coniferen, Abhandl. des botan. Vereins der Prov. Brandenburg, vol. xlv, 1902.
79. OLIVER, F. W.: The Ovules of the older Gymnosperms, Annals of Botany, vol. xvii, June, 1903.
80. COULTER and CHAMBERLAIN: The Morphology of Angiosperms, p. 52 (*sui generis* theory), 1903.

Worsdell, Wilson Crosfield. 1904. "The structure and morphology of the ovule." *Annals of botany* 18, 57–86.

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