Contribution to the knowledge of the morphological value and the phylogeny of the ovule and its integuments

by

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CHAPTER I.

Introduction.

The question about the morphological value of the ovule, has long been the subject of investigation and discussion, but a decisive answer is stil waited for. The first step to be done in order to throw light on this problem, is to determine to which category of organs, shoot, root or leaf, it can be classified as a whole. Especially during the nineteenth century there has been a good deal of disputing about this subject and nearly all morphologists have occupied themselves more or less with this question.

Finely their conceptions and opinions settled on three theories, which are to be mentioned later on, but nobody could give such convincing arguments, that one theory was accepted every where.

Gradually, however, the botanists have adopted the principal idea of one of those theories, and now-a-days it is generally granted, that the ovule is borne by a leaf, at least belongs to it, but a correct interpretation of the nature and the origin of both integuments and the nucellus is very little certain.

The investigations concerning the ovule started from the conditions of the Angiosperms and in order to state the nature of nucellus and integuments, five different methods were used, viz. the ontogeny, the anatomy, the topographical-morphology, the phylogeny and the teratology.

As to the ontogeny, this is often of very little importance for plants in general, as the organs after passing through a long phylogenetical development unfold immediately or grow into the now existing form, without repeating more or less their phylogeny, as is often the case in the animal kingdom. In most cases we see the origin of the ovule as a small papillate protrusion, around which both integuments originate and develop as annular walls in basipetal succession.

Though the ontogeny itself gives little occasion of research, so much the more several botanists made use of teratologicals. There is much difference of opinion about the value we may attach to such deviations and it occurs rather often that investigators are willing to take teratologicals into consideration, when they are useful in the authors argumentation, whereas they are rejected, when in contradiction to their statement. Therefore it is necessary to make a very cautious use of them, and we may only speak with certainty of retrogressive metamorphoses when deviations are found, clearly indicating a lower state of development as is already known in related plants, less far advanced in evolution. In this case they are of great importance and we owe many links of relation and origin to the observation of these teratologicals.

A great value was always attached to what we may call the topographical morphology, according to which an organ can be determined by the place where it occurs on the plant. To give an example, the ovules of the *Primulaceae*, which are borne on an axial placenta, are sometimes said to belong to the shoot, whereas the parietal or marginal ovules, such as are found in the greater part of the other Angiosperms, are considered as parts of a leaf.

It is especially van Tieghem and his followers, who have treated the anatomical method, and recently also many English botanists attach a great value to the vascular-supply, and form their morphological conclusions accordingly. However constant the vascular-supply may be in many cases, we may not, as to my opinion, lose sight of the fact that these organs are always secondary, that a leaf does not originate for the sake of a vascular bundle, but that a vascular bundle has the function to supply the leaf. And though it may be possible that in many cases the remaining vascular bundles indicate the place of reduced organs they supplied, and thus can be used to sustain the other arguments, it is not allowed to make far-reaching conclusions from the vascular-supply alone.

Finely the phylogeny though acknowledged as being of great importance, has hardly been used by any of the former botanists. No one has treated the subject in comparing the same organs of the different divisions of the vegetable kingdom to its utmost consequence, which indeed was not possible in that time through lack of sufficient material. At most the results obtained by a comparison of the higher- with the lower-developed plants, were accepted as a proof of a once founded theory.

And yet this manner of research, sustained by the study of obvious retrogressive deviations, is the most certain mean to determine morphological values.

It is true that Čelakovský takes the phylogeny into consideration but his views are wholly based on teratologicals and „Vergrünungsgeschichten" without accounting for wether these deviations are really retrogressive. Though he acknowledges (33) p. 169 the difficulty of knowing for certain to which cause the deviations are to be attributed and which consequences may be concluded from, he starts entirely from the supposition that his „ovulum-antholysen" are „Rückschlagserscheinungen".

According to these methods of investigation, but chiefly by means of the three first ones, the three groups of opinions mentioned in the beginning were formed. Worsdell in his paper „On the structure and morphology of the ovule" (180) has given a review on these different theories, in which the ovule is said to have the value of a bud or of a leaf, or cannot be classified at all in one of those catagories, and which theories can be indicated for shortness' sake respectively as the axial, foliolar and sui-generis theory.

For a more detailed treatment I can refer to this excellent article of Worsdell, and I will confine myself to mention only the contents and the names of the followers of those views:

Axial theory.

The nucellus is of the nature of a bud and both integuments are its lateral foliar appendages St. Hilaire, Schleiden (129), Payer, Braun, Peyritsch, Pearson (113).

Foliolar theory.

The ovule belongs morphologically to the category of the phyllome; the nucellus is of the nature of an emergence, borne on the upper surface of a leaflet of the carpel, whereas the integuments are the fused lateral lobes of the same segment of the female sporophyll.

Brogniart (26), R. Brown (28), Caspary, Cramer (53), Prantl, Warming, Čelakovský.

Sui Generis theory.

The ovule is an independent structure, borne either on cauline or foliar organs. The integuments are new formations around the nucelles.

Schmitz (130), Sachs (124), Strasburger (150), Goebel (68), Balfour.

As is proved by his treatment of this subject, Worsdell too is an upholder of the second theory, which is based for the greater part on the investigations of Čelakovský. The latter has adopted his opinions as to the foliar origin of the integuments, in consequence of a great number of the above mentioned Antholysen of ovules.

And really it is no wonder that, where he has found several cases (*Anagallis, Dictamnus, Alliaria, Hesperis, Trifolium* a.o.) in which both integuments are proliferated more or less and appear to be the fused lobes of a leaflet of the carpel, the nucellus originating on this lobe, like an emergence or like a sporange, it has become his conviction that both integuments are nothing but slips of the carpel: „Das verlaubte blattbürtige Eichen ist also ganz gewiss ein wirklicher Blatttheil, ein Fiederblättchen des Carpells, und da der morphologische Werth eines jeden der drei morphologischen Grundgebilde eines differenzirten Sprosses, nämlich des Kauloms, Phylloms und Epiblastems durch keine Metamorphose, also auch nicht durch die rückschreitende abgeändert werden kann, so ist auch das normale behüllte Eichen einem Carpellar-Fiederblättchen aequivalent" (33) p. 201.

The axial ovules of the *Primulaceae* too were proliferated and at the end of his article he says: „die behüllten Eichen sind immer und überall metamorphosirte Blattsprossungen oder Blattfiedern der Carpelle, entweder des Blattkörpers selbst (sogenannte blattbürtige Eichen) oder der Blattsohle (sogenannte axenbürtige Eichen): Selbständige Ovularblätter giebt es nicht."

„Aus diesem Satze folgt schon, dass die Hülle des Eikerns der Coniferen kein Integument sein kann, denn wäre sie es, so müsste man nach dem zugehörigen Carpelle fragen, welches aber nicht vorhanden ist" p. 230[1]).

And somewhat further: „Wir dürfen nunmehr ganz allgemein sagen, dass alle Eichen, behüllte und unbehüllte auf einem Fruchtblatte entspringen oder von ihm abhängig sind. Kein Eichen ohne Carpell" (p. 232). After having stated this axioma Čelakovský (40) tries to homologize the integument of the Angiosperms with the sporange-envelopments of the lower plants. In the first place he makes a comparison between the indusium of the ferns and the integument, and though it seems rather unjustifiable to connect in a direct way, a leaflet of a fern with a carpel from an ordinary flower, he yet says according to a comparison with a proliferated ovule of *Hesperis* „Somit ist auch der Blattzipfel eines Farnblattes, der das Indusium (den Schleier) auf seiner Unterseite trägt, das Aequivalent des äusseren Ovularinteguments von *Hesperis*" (p. 304).

His further papers, published on this subject, amount to this, that he wants to defend the theory he once put forth, and though he gives many sagacious proofs, the suppositions from which he starts are not quite certain, so that his method of investigation is the exact counterpart of what would be desirable in this case. For in stead of controling a same organ in its phylogenetical development from low to high, he first states the morphological value of nucellus and integument in their highest degree of development and then he puts the organs of lower plants aequivalent to them.

As I said already in the beginning it seems to me the weak point in Čelakovský's theory, that he has immediately assumed, that the proliferations of the Angiosperms would be retrogressive phenomena. Though lateron he begins to doubt this view and agrees with the possibility,

[1]) Lateron he is obliged to accept an integument in the Conifers.

that the proliferations could be progressive deviations, he doesnot change his opinions accordingly.

In this supposition his theory is not sufficiently established, for if this be true, a virescent condition can never throw light on the phylogenetical origin; a comparative investigation only can do this.

Now it is just in the latter half of the last century that new ways are opened for this comparative method by the discovery and accurate descriptions of fossil seeds. And almost independent of the discussed theories, which were founded for the greater part by German botanists, the question concerning the origin of the integument has been treated in England from a quite different point of view on account of discoveries such as *Lagenostoma Lomaxi, Trigonocarpus* a.o.

It is especially Miss Benson (15) who has given a quite new theory, being led to this in comparing the seed *Lagenostoma Lomaxi* with the microsporange *Telangium Scotti*, which is probably borne as well as *Lagenostoma* by *Lyginodendron Oldhamium*.

For the description of *Lagenostoma* I may refer to a following chapter of my paper, where the several seeds are described separately. Of *Telangium Scotti* I will cite here the diagnose given by Miss Benson herself (p. 162).

„Fertile and barren pinnae dissimilar; fertile pinnae represented by synangia only; synangia borne at the entremity of the ultimate ramifications of rachis, composed of 6—12 sporangia which taper to the apex and are united primarily for almost their whole length to form a body which is continued into a sterile base of decreasing diameter through which runs longitudinally a single vascular strand. Each sporange, ultimately becomes almost free from the others by septicidal dehiscence and liberates large spores from a ventral suture."

Everyone, who compares both organs with one another, will be struck by the resemblance in organisation of the synangium *Telangium* on the one hand and the seed on the other.

„The chambers surrounding the nucellus seem to represent its sister sporangia, which have become sterile, the large-celled, thin-walled tissue and delicate vascular strand being all that represents the ancestral sporogenous tissue; while the micropyle corresponds with the original space between the tips of the sporangia. The seed in fact is assumed to be a synangium in which all but one of the sporangia are sterile, and form an integument to the one fertile sporange which has become a megasporange with one large megaspore. In *Lagenostoma physoides* the integumental ridges are continued into tapering tentacles around the micropyle, and this still further accentuates the resemblance to a sorus" (p. 169). „Hence we have only to imagine that one of the sporangia of a sorus of eight or ten sporangia gradually evolved megaspory, and that the remaining seven or nine sporangia became a sterile envelope" (p. 169).

Here we have the whole so-called synangial-theory, which is based entirely on the undeniable resemblance between a synange and a seed, but which has this great disadvantage, that nothing of it is duely established and that the evidence of the facts is too meagre, to allow the drawing of such far reaching conclusions.

It occurs in several fern-sori, that some synangia remain sterile and are scattered amongst the others as paraphyses, but that the middle-one should always be fertile and the surrounding sporangia sterile, to form a closed outer envelopment, is quite unknown as a rule in any plant.

Oliver (104) therefore opposes this opinion of Miss Benson and regards the integument as being a new structure. He compares the fructifications of the Pteridosperms rather with those of *Lepidocarpon* and

Azolla, where an envelope occurs around the macrosporange as a new entirely independent annular covering.

„Though it may be premature to attempt to define in terms of stimulus and response the precise sequence of events that leads up to encasement, it will be readily admitted that a new departure such as the inception of the seed habit (where provision has to be made for the increased nutrive drain involved by the retention of the gametophyte) would be accompanied by nutrive disturbances that might easily favour the appearance of new formations" (p. 104).

Now that I have endeavoured to give some of the most important theories, concerning the origin and value of the integument, and to show how much these conceptions differ from one another, some questions are obvious viz.

1. The integuments of the Pteridosperms, Gymnosperms and Angiosperms are they comparable with one another, or is their origin polyphyletic.
2. If the integuments are homologous organs, are they also homologous with the indusium of the Ferns.
3. Is the integument composed of several units, which may be evident as ribs or sutures or as slips at the micropyle.
4. If the integument is composed of units, what is their value.

It is the intention of the present paper to try to solve these questions or at least to throw a new light on these problems. I shall therefore describe in the second chapter some of the most characteristic fructifications provided with an integument, attempting to mention the results of each investigation as objectively as possible, without falling into any subjective supposition.

Though in the descriptions of the palaeobotanical seeds no new observations are recalled, I have collected the data from the literature in the same order as the others, because they were not complete in any textbook.

In the third and last chapter, I will try to give a conclusion, based on a mutual comparison of these different seeds and ovules.

The material I used. I received partially from the Botanical Gardens of Lisbon, Rome and Buitenzorg, for which I desire to express my gratitude to the directors of those institutes. A thankful use I was enabled to make from a collection of dried seeds, present in the Botanical Laboratorium in Groningen.

Finely several specimens I could collect in the Hortus Botanicus of the fast mentioned University.

CHAPTER II.

Isoetales.

§ 1. *Isoetes.*

Literature: Smith (139).

The lowermost and outer leaves of the plant bear the microsporangia, those coming next are the megasporophylls, whereas the innermost ones are sterile.

The megasporange is borne on the broad base of the leaf below the ligule, and is attached to the base of a cavity in the leaf with a short stalklet. From this cavity at the side of the ligule an indusium or velum is stretched out above the sporange. Between the apex of this indusium and the border of the cavity in general a fissure is left, which sometimes is very narrow and then gives the impression of the micropyle of an ovule, which indeed induced Braun to use this name.

Lycopodiales.

§ 2. *Selaginella.*

Literature: Lyon (93).

The description of the normal spore-producing members of *Selaginella* falls outside the scope of this paper, but I will call the attention to a remarkable condition, found in *Selaginella apus* by Miss Lyon (93). Here the fertilization takes place when the megaspore is still attached to the strobilus. This is the first step taken in the direction of a closer relation between the new generation and the mother-plant, which is still more accentuated in *Sel. rupestris:* „quite late in the development after the embryo has formed, the megasporangium becomes sunken in a shallow pit formed by the cushion-like upgrowth of the sporophyll around the pedicel (p. 125).

We have here the first indication in still living Lycopods of the formation of a seed-like organ, as is known already for the fossil *Lepidocarpon*.

§ 3. *Lepidocarpon*.

Literature; Oliver (99).

The axis of the megastrobilus bears in spiral order the sporophylls, which are bent up at their distal apex.

On the upper surface of the sporophyll the megasporange originates, in the mature condition enclosed by an indusium, growing up from the body of the sporophyll on both sides of the sporange. Both parts meet at the top, leaving a long fissure in the apical surface. At the proximal side of the sporange the indusium forms a closed wall, whereas in the distal portion it becomes entirely fused with the apex of the sporophyll. Inside the sporange, only one functional megaspore develops, filled in the ripe state with a prothallium. It then becomes detached from the plant with the sporophyll and the indusium like a seed.

The microsporanges too are partially enclosed in an integumental organ.

§ 4. *Miadesmia membranacea*, Bertrand.

Literature: Benson (13).

The megasporangiate strobilus is composed of an axis with several sporophylls.
At its base the fertile sporophyll has a groove in which the megasporange and a large and prominent ligule ly. Both are entirely covered by an indusium, arising in the proximal part of the leaf. Only at the apex of the sporange an aperture is left in the velum, which is surrounded by numerous hairs.
Within this thin membranaceous wall a single megaspore is found; in some cases the walls of the sporange and the containing megaspore were not to be distinguished, a feature comparable with a seed structure.
The microporanges were not provided with a velum or integument as it is called by Benson (13).

Pteridospermae.

§ 5. *Lagenostoma Lomaxi* Will.

Literature: Benson (14), Oliver and Scott (106, 107).
Figure: 107. pl. 4—10.
135. p. 57.

Lagenostoma Lomaxi is the seed of *Lyginodendron Oldhamium*, the greatest specimens reach a length of about 5,5 mM. with a diameter of 4,5 mM. They are attached to a pedicel and surrounded by an envelopment or cupule, which originates from the pedicel just below the base of the seed. In its lowest part the cupule envelopes the seed completely as a closed ribbed cup, but about half way up its height, it separates into a number of lobes or segments.

As regards the morphological value of the cupule, whether it has to be considered a sporophyll or a modified pinnule of a compound leaf, or an integument, I will discuss that later on. We may now consider the place where the seed was attached to the plant bearing it. Scott says about this (133). „We have seen that the structure of the pedicel shows that the seed-bearing organ formed part of a leaf. Evidence from closely allied species leaves no doubt that the seeds were borne on compound fronds or pinnae, only differing from the sterile foliage in the suppression of the laminae of the leaflets, or rather, perhaps, their modification to form cupules" (p. 393).

Characteristic are the great prominent multicelled glandular capitate hairs, which are found on the pedicel and cupule.

Within the cupule stands the seed properly, composed of a nucellus, enveloped by an integument. This integument or testa is concrescent with the nucellus to about four-fifths of its height. Round the apex of the nucellus it is free and forms the so-called canopy. In this region the integument is segmented by septa in about nine loculi or chambers, whilst lower, these septa disappear and make place for deep furrows in the inner surface. Gradnally these furrows dy out to the place of insertion of the canopy. The loculi of the canopy are filled with a delicate tissue, which is generally not preserved, and a single tracheal strand in each chamber.

Surrounding the micropyle small ridges can be seen, but as they overlie the well-marked septa between the chambers of the canopy, it is quite possible, as Oliver (104) remarks, that „they owe their prominence to post-mortem contraction or collapse of the filling-tissues of the chambers" (p. 105) and thus should not be mistaken for the unitlobes of the integument.

The outer side of the testa is formed by a closed layer of palisade cells, which cloth the septa of the canopy at the upperside. On the outersurface of this layer, there are little black spots, which are sometimes covered by a thin membrane; perhaps they may be considered as the remainder of small cells on the outside of the palisade layer, which have segregated mucilage.

The rest of the integument is composed of layers of soft, often collapsed tissue, which has disappeared entirely in the centre of the nine canopy-loculi.

The pedicel contains a single vascular strand, which before entering the chalaza, lets off a number of branches into the cupule, running up its whole length into the segments. The bundle in the pedicel is concentric, whereas the branches in the cupule are becoming collateral, with a normal orientation of xylem and phloem.

After letting off the ring of vascular bundles into the cupule, the main bundle enters the chalaza and splits into nine separate branches, which run through the delicate tissue of the testa close to its surface and end in the loculi of the canopy. The chalaza itself is built up of a comparatively great mass of sclerotic tissue, its form being compared by Oliver (106) to a champagne glass. „The hollow in the sclerotic cushion has the form of a champagne glass, and as the bowl expands the entering bundle separates into the peripheral vascular strands, which run in the plane of the glass" (p. 207). In this cushion stands the nucellus, forming the central part of the seed, but of which the cells are collapsed and shrivelled. This mass of cells contains perhaps the softer layers of the integument.

The top of the nucellus, which is free from the integument forms the „lagenostome". This has the shape of a bottle, which stands sharply marked off on the vaulting of the nucellus, its neck reaching the micropyle. The centre of the lagenostome is occupied bij a cone of soft tissue, which, however, is not coherent with its epidermis. Between this and the tissue, there is a cavity, which has undoubtedly been formed by the separation of the epidermis and the underlying tissue. This bell-shaped cavity is the pollen-chamber, in its lower part the pollen grains are found.

In the nucellus lies a megaspore containing a prothallium. As in all pteridospermous seeds an embryo has never been found.

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§ 6. *Sphaerostoma ovale* Benson.

Literature: Benson (16).
Figure: 16 p. 3.

Sphaerostoma ovale formerly described by Williamson as *Conostoma ovale* and *intermedium*, is likely the seed of *Heterangium Grievii*.

The seed strongly resembles that of *Lyginodendron Oldhamium*, like the latter it is composed of an outer envelopment, the cupule (called by Miss Benson 'the outer integument') and a central portion, formed by the nucellus and an integument, which are concrescent for the greater part.

Without cupule the seed has a length of about 3,5 mM and a diameter of 2,2 mM. In transverse sections it seems to be round, except in the lower and upper part, where the form is more or less octagonal.

Mostly the cupule is no longer preserved so that for the present a minute description cannot be given. The tissue is much more regular than that of the integument and contains several vascular bundles, structure and number of which were difficult to observe. It is possible that at the top, just as in *Lagenostoma* it consisted of lobes, but in most transverse sections it was seen as a closed ring.

The integument is for three thirds of its height concrescent with the nucellus and a definite line of demarcation between them is not to be traced. At the top, where the integument is free from the nucellus, it forms the canopy, formed by eight segments.

At the outer side the integument is covered by a clearly marked epidermis, composed of oblong bricklike cells, that mostly bear papils at their outerside, which segregate mucilage. At the top near the micropyle, on the lobes of the canopy these cells change their forms and become very long, forming then the so-called „frill".

Under the epidermis is a layer of sclerotic cells, this hypoderma perhaps may be compared with the palisade-layer of *Lagenostoma*.

The nucellus is for its greater part filled up by the embryosac, and at its apical side it is dome-shaped, bearing the lagenostome, a hemi-sphaerical mass of tissue surrounded by the annular pollenchamber. In *Sphaerostoma* the pollenchamber has always been found closed, caused by a solid closure, made by the dome of the lagenostome, at the place where it stands on the nucellus. As is the case in *Lagenostoma* the pollenchamber is formed as a lysigen cavity.

In the pedicel under the plate of sclerotic fibres running beneath the chalaza as a continuation of the sclerenchyma of the integument there is a thin layer of tissue, in which the separation takes place, when the seed is ripe and is shed off. The cupule remains on the plant.

§ 7. *Physostoma elegans* Will.

Literature: Oliver (104).
Figure: 104. p. 76.

Physostoma elegans is an oblong seed and has a length of about 6 mM. In transverse section it is almost round, but on account of the ten prominent ribs, running over the whole length, it obtains the form of a decagon. In the middle it has its greatest diameter.

The seed is built up of a testa and a central part the nucellus.

The testa forms a ribbed envelopment, at its lower part tightly closed, and concrescent with the nucellus, but in its apical region it becomes free and there it is divided into ten arms or tentacles, forming a ring around the nucellar apex. The ribs are less visible at the base, but higher they become more and more prominent, till at last they are continued in the entirely free tentacles. In these tentacles, which take up one-third of the whole length of the seed, *Physostoma* has a distinctive character, and is clearly distinguished from the other seeds, where at best, as in *Lagenostoma* and *Sphaerostoma*, the micropylar tube is formed by a ring of loculi, the canopy, which probably indicates an original ring of arms or lobes, but which are now concrescent and form a closed tube.

Very characteristic too is the dense covering of the ribs and the abaxial portion of the tentacles with long club-shaped hairs. They attain a length of about 0,5 mM. near the median line of the rib. Undoubtedly they formed a thick clothing of the seed in its life-time.

The testa or integument is formed of a thinwalled tissue, which gives no indication of fibres or sclerotic cells; on the whole the tissue is very delicate, probably in connection with the dense hair-covering.

The vascular system is like that of *Lagenostoma Lomaxi*. At the base of the seed a vascular strand enters the chalaza and is divided into ten bundles, running through the body of the ribs, on a level with the intermediate grooves, and which are continued in the tentacles.

The nucellus is concrescent for two-thirds of its length with the integument, as far as the level at which the arms separate.

At its apical side a large pollenchamber is formed, into which the nucellus rises like a conical hollow papilla „like the bottom of a wine bottle" (p. 78).

The nucellus is filled up for the greater part with a large megaspore or embryosac and it contains numerous secretory cavities.

§ 8. *Trigonocarpus Parkinsoni* Brogn.

Literature: Arber (3), Hooker and Binney (73), Oliver (102, 103), Scott and Maslen (134).

The seed is oval-shaped, with a length, without the micropyle of 2,5 cM. and a diameter of 1,5 cM. The micropylar region is very long and has a length equal to that of the body of the seed, but it never is found preserved very well. Occasionally a seed is found with a micropyle twice as long as the seedbody, but it is possible that this belonged to an other species. The total length therefore is about 4—5 cM.

In transverse section the seed is nearly triangular, caused by the three prominent ribs on the testa, which characteristic has induced the name *Trigonocarpus*.

The testa is composed of three to four layers. The middle one is most characteristic, is hard and formed by thick-walled sclerotic cells, and therefore is called the sclerotesta. Outside is a layer of delicate thin walled cells, the sarcotesta, whereas the innermost layer the endotesta too is composed of a delicate tissue.

The sarcotesta has often disappeared, but when preserved, it seems to be largest at the base and the upperpart of the seed. In these regions it is less differentiated from the sclerotesta and it is obvious that the structure and form of the innermost layers of the sarcotesta are essentially the same as in the outer-layers of the sclerotesta. At the out-side is a well-differentiated epidermis and a hypodermal layer and there are many intercellular cavities and mucilage-canals within the sarcotesta. The coherence of sclerotèsta and sarcotesta clearly indicates the existance of one integument and it must not be regarded as a fusion of two morphological surfaces.

At the top, near the micropylar region the outer fleshy layer has a winglike form, but it is rather difficult to examine this part of the sarcotesta well, on account of the bad condition of preservation.

The sclerotesta in general form is ovoid, the pointed end corresponding with the chalazal region, whilst the blunt end is surmounted by the triangular micropylar tube, the angles being the continuation, of the sibs lower down. The ribs are borne by the sclerotesta, at the innerside of which are three corresponding grooves, marking the place of three sutures. Between these principal ribs there are two or mostly three less prominant ones, the secondary ribs, but with no corresponding ridges beneath them at the innerside of the sclerotesta. The total number of ribs is thus mostly twelve, but, this number is liable to many changes and also the grade of prominence is very different, so that often the three principal ribs only are visible. These principal ribs, when traced from the centre of the body of the seed to and along the micropylar beak, gradually become less prominent and ultimately disappear, whereas the grooves at the inner side become more and more deep.

On thin transverse sections the sclerotesta seems to consist of two parts, the plane at which the different structure is assumed being variable. The inner zone contains longitudinally directed fibres, whereas the outer zone is formed by cells which have a horizontal orientation. It is perhaps possible that this outer zone represents the terminations of the longitudinal fibres. At any rate there is little doubt about these two zones being homogen in origin.

Though not preserved in a very good condition there seems to have been a thin layer of delicate tissue at the innerside of the sclerotesta, the endotesta, but when present, it is only to be seen in the micropylar region.

The stalk of the seed consists of sclerotic tissue in the centre, surrounded by parenchyma, probably these layers are continued into the sclerotesta and sarcotesta of the body of the seed.

The nucellus has always been found standing free within the integument, a large space being left between nucellus and sclerotesta (perhaps endotesta) from the chalazal region.

Within the nucellus is a large megaspore. The pollen-chamber has a bell-form with a narrow beak at its top pointing into the micropylar tube.

The vascular organisation consists of a sarcotestal system without, and a nucellar one within. The main vascular strand enters the chalaza and lets off several branches into the sarcotesta, running opposite the secondary ridges of the sclerotesta. However, they do not run opposite all the secondary ridges, only opposite the outer ones of each complex of three, never opposite the middle one. Their total number therefore seems to be six.

The nucellar system is formed by the continuation of the chalazal strand, which entering the nucellus, spreads out in its lower part, splitting up there into a number of bundles, which can be traced through the whole length of the nucellus to the base of the pollenchamber.

§ 9. *Trigonocarpus Shorensis* Salisb.

Literature: Salisbury (126).
Figure: 126 p. 42 and 43.

As regards the organisation of this seed, it is nearly the same as *Trigonocarpus Parkinsoni.*

§ 10. *Mitrospermum compressum* Will.

Literature: Arber (2).
Figure: 2 p, 494 and 495.

The palaeozoic seeds may be divided into two groups the *Radiospermae*, which are in transverse section radial-symmetrical, and the *Platyspermae* which are bilateral-symmetrical. To the first group the seeds belong described in the foregoing pages: *Lagenostoma, Sphaerostoma, Physostoma* and *Trigonocarpus*, to the latter belongs *Mitrospermum.*

Mitrospermum (Cardiocarpon) compressum has a length of about 5 mM and is flattened in the plane of symmetry.

The testa is composed of three layers: sarcotesta, sclerotesta and endotesta. The first forms a thin layer of delicate tissue on the sclerotesta, but in the principal plane (the plane in which the seed has its greatest diameter) it becomes flat in order to form a broad wing. The most conspicuous feature of the sarcotesta is an outer layer of large mucilage cells, the hypoderma, which is covered, in the best preserved specimens, by a thin small-celled epidermis.

In the principal plane the sclerotesta is divided into two valves, and it is possible that these valves ultimately separate, though there is not such a clearly defined dehiscence plane, as in the seed *Diplotesta* (135). On both valves in the secondary plane two less prominent ribs are to be found, running from the base of the seed as far as the micropylar region. At the top near the micropyle, the sclerotesta has a rhomboidal-shape in transverse section. Near the chalaza it rises inside to form a small cushion of tissue.

The nucellus stands free on its base within the testa, but it may be, that the cavity between integument and nucellus is formed after contraction of the latter.

The vascular bundle enters the base of the seed through an opening of the sclerotesta. On the cushion beneath the nucellus it is divided into two branches, lying in the principal plane, which after passing the sclerotesta in a horizontal direction, bend upwards running through the sarcotesta up to the micropylar region, following the grooves formed by the valves of the sclerotesta.

It is still uncertain to which plant *Mitrospermum* belongs, because it is always found without any connection, but it is possibly the seed of one of te *Cordaitales*.

Bennettitales.

§ 11. *Bennettites*.

Literature: Lignier (85), Wieland (170, 171).
Figures: 171, p. 110 and 122.

The most characteristic feature of this group of fossil plants is the occurrence of bisporangiate strobili, which are borne on short axillary branches, expanded at their top into a receptacle, having a hemisphaerical or more or less conical shape. On this receptacle the members composing the strobilus occur placed in spiral order. Lowermost are the sterile bracts, enclosing entirely the central portion, a series of leaflike sporophylls are coming next, whereas on the top a large number of the characteristic ovulate sporophylls are borne, intermixed with sterile bracts, the interseminal scales.

When the seeds have become mature the microsporophylls have disappeared, and when they are present the female sporophylls are still in a very young condition. Thus we may call the whole fructification protandrous.

The microsporophylls resemble strongly the long fernlike leaves, and are composed of an axis with about twenty slender pinnae, bearing two lateral rows of synangia at their undersurface.

The macrosporophylls, however, are much more advanced from the fern type, and have already reached a high degree of specialisation. Each ovuliferous organ is formed by a long slender stalk, having at its tip a single erect ovule and is surrounded at its base by the interseminal scales.

In connection with the Pteridosperms, where the seeds are borne terminally on thin stalklets, being the reduced remnants of a modified frond, it is generally accepted, we have to do here with the same feature. Thus the seed bearing stalk of the Bennettitean seeds may be regarded as the ultimately reduced megasporophyll.

The internal structure of the seed is not known very completely. The integument is composed of an outer and an inner fleshy layer and a middle stony one. At the apex it forms the long micropylar tube, which protrudes from the surface of the enveloping scale-leaves.

The nucellus is provided with a beak and a pollen-chamber, and innerside a megaspore with a heavy membrane is developed.

At the base the ovule is invested by a small dish-like cupule.

Cycadales.

§ 12. *Cycas revoluta*, Thunb.

Literature: Stopes (145, 146).
Material: Bot. Gard. Lisbon.
Figure: 145 p. 438.

In the genus *Cycas* the sporophyll is a distinct foliar organ, more or less divided into lobes, bearing the ovules on its margins. In contrast with the other genera of the Cycads, where are always only two ovules on each sporophyll, here their number may be greater.

The ovule (which name I will use in this and following descriptions, for the whole female organ borne on a megasporophyll) is bilateral symmetrical, with a length of about 3 cM. and a greatest diameter of 2,7 cM. Ripe ovules are orange coloured and covered near the micropyle with hairs, whereas young ovules are wholly clothed by a dense hair covering.

The testa is very thick and composed of the three layers already mentioned in the former descriptions of the pteridospermous seeds.

The sarcotesta is formed by large, thinwalled undifferentiated cells, filled up with starch, and there are many mucilage canals and tannine cells within it. Outside is an epidermis composed of radial-elongated cells with thick outer and radial walls, which is very characteristic for the whole genus.

The sclerotesta is thickest at the top and near the chalaza. In the chalazal region it slightly protrudes, accompaning the vascular bundle entering the seed. The cells are thickwalled and two layers are to be distinguished, an inner one with cells elongated in a longitudinal direction and an outer one with cells directed in a more horizontal plane.

The endotesta is well developed, nearly 4 mM. thick, and composed of great-cellular, thinwalled, delicate tissue, soon collapsing in the ripe seeds. As in the sarcotesta it contains many tannin cells.

At the top in the micropylar region the sarcotesta forms two thick cushions, with a groove between them, in which the micropyle stands as a little prominent tube. Eichler (63) says, speaking about the micropyle of *Cycas* „an der Micropyle finden sich zuweilen noch einige unregelmässige Läppchen, aus denen man auf eine Zusammensetzung aus mehreren Blättern hat schliessen wollen, während sie in Wahrheit nur secondaire Effigurationen einer ursprünglich einfachen Hülle darstellen" (p. 15). The seeds I have seen had a micropyle that was always round without any indication of slips. But it is quite possible that other specimens will show those lobes more distinctly.

The testa in young ovules is still quite undifferentiated and nowhere, even in older ones, I could observe anything that was to indicate that it was built up of more organs, sutures or ribs always being absent.

The nucellus is concrescent with the endotesta to three-fourths of its height. At the top it bears a prominent beak in which the pollenchamber is to be found. The beak points into the micropylar tube.

The vascular system consists of three bundles entering the base of the ovule. The median one runs straight on, till the endotesta is reached and there it divides into several branches. The two lateral bundles enter the sarcotesta, at the base of which they let off one bundle each, breaking through the sclerotesta and running in the endotesta to the micropyle. The main-bundels continue their way through the sarcotesta to the top. According to Stopes (145) these two sarcotestal bundles are the remnants of the original radio-symmetry and many-bundled condition of the outer flesh.

In the nucellus no vascular system is present.

§ 13. *Dioon edule* Lindl.

Literature: Chamberlain (46).
Figure: 46 p. 356.

The female strobilus of *Dioon* is formed by an axis bearing sporophylls, placed in spiral order. These are composed of a stalk with a peltate lamina at its top, which bears two ovules at its under surface. The lower sporophylls of a strobilus do not bear ovules or at least slightly-developed ones. In ripe condition the ovules have an orange colour.

The sarcotesta is not sharply marked off from the stony-layer, and it is not possible to separate them. As in *Cycas* the epidermis has thickwalled cells, whilst in the underlying tissue many tannine-cells and large mucilage-canals are present.

In the sclerotesta four layers are to be destinguished according to Chamberlain, principally characterized by an other orientation and form of the cells.

The endotesta is well differentiated from the stony layer, and in a young condition it reaches a considerable thickness, but in a ripe seed the inner flesh is reduced to a thin dry membrane which peels off easily.

The nucellus is for a small portion only free from the endotesta and protrudes into the micropyle with a rather sharp beak, in which lays the pollenchamber. „The beak closes and hardens immediately after pollination" (p. 335).

Two vascular bundles enter the base of the seed each of which divides into a branch running in the sarcotesta and one in the endotesta. Those in the outer fleshy layer often divide into the lower part, but then continue their way in a straight direction to the micropyle. Their total number is about fourteen. The bundles of the innermost system divide at a greater height, and on a transverse section at the level of the archegonia some fifty bundles are to be seen. They run on in the free part of the endotesta, but are never observed in the nucellus.

§ 14. *Bowenia spectabilis* Hook.

Literature: Kershaw (80).
Figure: 80 p. 634.

The strobilus is formed by a compact mass of megasporophylls, each consisting of a stalk ending in a peltate head, bearing an ovule on the underside of each of the horizontal extensions. The ovule is attached without a stalk to the sporophyll and when ripe has a size of about 2 cM to 1,8 cM.

The sarcotesta has a thickness of more than half the whole of the testa. It is composed of large parenchymatous cells filled with starch; scattered tannin sacs are lying in the hypoderma. A well differentiated epidermis is present.

At the base of the seed the sclerotesta is closed, interrupted only by the vascular bundle breaking through. As in the other Cycads it is composed of two layers of cells.

Contrary to *Cycas* and *Dioon* there is a sharp line of demarcation between the innermost cells of the sarcotesta and the adjoining ones of the stony layer.

The endotesta, however, is difficult to separate from the sclerotesta, especially in those places where the latter is sclerised.

Nucellus and endotesta are concrescent for three-fourths of their height, the beak of the former is put forwards in the micropylar tube, which protrudes out of the testa. The pollenchamber has been distinguished into a lower and an upper one. The latter developing first, serves as a storage place for the pollengrains, the former is a large cavity into which the pollen passes and where the spermatozoids are developed. Later on the upper pollenchamber becomes hard and shrivelled.

The vascular system consists of a sarcotestal complex, seven to nine bundles, which branch seldom, running from the base to the micropyle and an inner complex consisting of twelve to fourteen bundles at the base of the seed and branching within the endotesta, till at the level of separation of testa and nucellus the number is about forty. According to Kershaw (80) these bundles would continue their way within the nucellus in contrast with the other cycadean-seeds.

§ 15. *Stangeria paradoxa* T. Moore.

Literature: Chamberlain (46), Lang (84).

The strobilus and ovules resemble in general form those of the genera of the Cycads already described, except *Cycas*, so that I shall not repeat the diagnose for *Stangeria*.

Lang (84) has examined the development of the young ovule and he compares it with the microsporangium of *Stangeria*.

In the youngest ovules the nucellus is to be seen as a free projecting point within the annular wall, the testa or integument. The nucellus is marked off from the testa by a layer of flattened cells „which can be traced down from the place of separation of the free portions of the integument and nucellus" (p. 283). Later on the testa grows in its apical region and closes over the nucellus, forming the micropylar tube. In a more advanced stage, when the testa has considerably thickened, the micropyle forms a long passage, with a narrow external opening, widening at its base.

The testa becomes differentiated into the three layers, the middle one becoming sclerosed in a later age. In the ripe ovule the testa projects as a thick margin round the narrow external opening of the micropyle.

„As regards position the ovule of *Stangeria* clearly corresponds to a microsporangium or to a sorus of microsporangia" (p. 301). The testa of the ovule would be homologous with the sporangial wall of the microsporangium and the free portion of the testa above the nucellus, unrepresented in the microsporangium: „an annular upgrowth, around the apex of the nucellus, of the bulky sporangial wall, or which comes to the same thing, of the edge of the receptacle, which had kept pace with the single sporangium" (p. 302).

„We compare the ovule to a sorus consisting of a single sporangium, which develops in the whole similarly to a microsporangium, save that it is bulkier, and the wall from the first thicker" (p. 302).

In the discussion I will say more about this meaning. Now I shall mention a case in which Stopes (146) has found lobes in *Stangeria schizodon*, at the base of the ovule outside the testa which in some cases became so large „that they unite to completely enclose and cover over the growing ovule, even after it has attained a considerable size." „The outgrowth I observed in *Stangeria* is entirely free from the outer integument of the ovule, it is undifferentiated in character, and its tissues are those of the sporophyll. It is obviously not split off from the outer integument, but is the free upgrowth round the already doubly integumented ovule" (146 p. 565).

As I lateron will discuss Stopes regards the sarcotesta of the Cycadean seeds to be homologous with the cupule of *Lagenostoma* and therefore she calls them double-integumented ones.

§ 16. *Encephalartos Altensteinii* Lehm.

Literature: Stopes (145).
Material: Bot. Gard. Sydney * [1]).

The female strobilus is built up of sporophylls with broad pointed laminae, each bearing two ovules. Sometimes the lamina envelopes the ovule more or less by „Wucherungen" (Stopes 145).

The sarcotesta is very thick in the micropylar region and there it has a square form. In connextion with this great extension of the outer flesh, the micropyle is very long and the vascular bundles have a remarkable branching in that region (see 145 fig. 36 p. 467).

The sclerotesta is formed by two layers, the cells of the outer one have very thick walls, but have the same form as those of the inner one. On the outersurface a great number of ribs are to be seen running from the base of the seed towards the micropyle.

In the ripe seed the endotesta is represented only by a brown dry papery membrane.

The nucellus is concrescent for its greater part with the inner fleshy layer, provided in its apical region with a sharp beak in which the pollenchamber is formed.

The sarcotestal vascular system is composed of about fourteen bundles, their course corresponding with the ribs on the sclerotesta.

In the stony coat, surrounding the micropyle little ridges of about 2 mM. length can be seen, corresponding with the ribs lower-down, the latter being less prominent, and lacking any trace of sutures. Their number is different and amounts from eleven to sixteen.

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1) The material indicated with * is from the dried-seed collection.

§ 17. *Macrozamia corallipes* Hook.

Material: Bot. Gard. Sydney *.

The organization of the strobilus and the seed is generally the same as that of the above described *Encephalartos*.

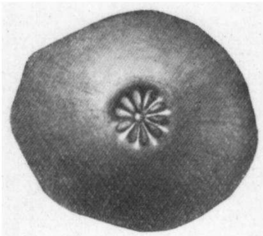


Fig. 1. *Macrozamia corallipes;* seed seen from above, ten lobes surrounding the micropyle. The sarcotesta is peeled off.

When the thick sarcotesta is peeled from the seed, no ribs can be seen on the sclerotesta, but the apical region is very remarkable. A ring of eight to eleven lobes, separated by short but deep grooves surrounds the micropyle (fig. 1) and thus gives the impression of free apical slips of units, entirely fused together, forming the integument.

§ 18. *Ceratozamia mexicana* Brongn.

Material: Garden Maastricht *.

In general shape and organization the seed resembles that of *Encephalartos* and *Macrozamia*.

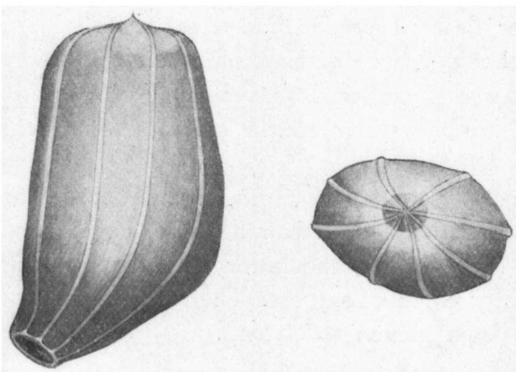


Fig. 2. *Ceratozamia mexicana;* seeds without sarcotesta, showing ribs and ridges around the micropyle.

On the sclerotesta about eight prominent ribs are found running from the base towards the micropyle, which suddenly die out when they reach the flat apical region of the seed. Surrounding the micropyle ridges, corresponding with the ribs, indicate the place of the probable fusion of the integumental units (fig. 2).

Ginkgoales.

§ 19. *Ginkgo biloba* L.

Literature: Affourtit and La Rivière (1), Caruthers (31), Celakovský (45), Cook (50), Fujii (66), Heer (70), Jeffrey and Torrey (74), Salisbury (127), Seward and Gowan (136), Spiess (141), Sprecher (142), Tupper (161), Wettstein (168).
Marerial: Huize ten Donck, Slikkerveer (Holland). Botanical Garden, Rome.

The female fructifications of *Ginkgo* are borne on short shoots or brachyblasts. In the axils of the ordinary leaves and in those of the bracts, thin stalklets arise with generally two or three ovules at their top. The morphological value of this organ has been uncertain for a long time. At first Eichler (61) speaks of inflorescences having „ein transversales und häufig noch ein zweites medianes Blüthenpaar oder nur eine Blüthe desselben" (p. 65) afterwards, however, he changes his opinion (64) and calls them „einfach behüllten Samen auf rudimentären kurz manchettenförmigen Fruchtblättern" (p. 109). Other authors amongst whom Engler, Čelakovský (45), von Wettstein (168), Velenovský (165), Fujii (66), Seward and Gowan (136) have adopted this last view, and acknowledge that we have to do with a strobilus bearing two or more macrosporophylls, generally being reduced to the collarlike arillus at the base of the ovule. There are, however, amongst them, several differences left as to some of the details.

That the arillus surrounding the ovule is nothing else but the reduced lamina of the leaf, appears clearly from teratologicals found bij Fujii (66): „The ovule is partially enclosed at the base in a cup-shaped swelling just as in the normal ones, and this swelling gradually passes into the lamina of the leaf." But as to the position of the sporophylls on the axis of the strobilus, the opinions are not settled. Strasburger (147) and also Eichler (61) describe the strobilus as being formed by an axis bearing a pair of transverse leaves and in some cases a second pair of median leaves besides. The latter has given in his „Blüthendiagrammen" (61 p. 65) a diagram of such a „vier blüthiges Zweiglein". In this the „Blüthen" are decussate, each consisting of a nucellus, a „Blüthenhülle" composed of two segments and the fused „Vorblätter" (the arillus). It will become evident from my futher discussion that this diagram does not agree with the true interpretation of the composing organs.

Von Wettstein (168) agrees also with the decussate position as being the most normal one, and has come to this, owing to his investigations upon the vascular supply in the axis of the strobilus.

Afterwards the vascular supply has been further examined by Seward and Gowan (136), which I have repeated.

Every ordinary leaf contains two collateral vascular bundles' lying close together in its petiole. Below the place of insertion they form a ring in the main branch with the bundles of the other leaves. A transverse section through the axis of the strobilus shows entirely the same behaviour as that of a leaf bearing stalk, each ovule receives a double vascular strand. In the normal cases in which the strobilus bears two, three or four sessile ovules, the stalk of the strobilus shows also two, three or four pairs of vascular bundles lying in one ring. But when the strobilus is split more or less, we see on transverse sections that the two vascular bundles coming from each ovule converge and fuse in the stalklet. Beneath the place of fusion of the stalklets, they again form a ring with the bundles from the other ovules, in the main axis.

According to this data von Wettstein (168) says: „Die normale Blüte von *Ginkgo* besteht aus einem Gebilde, das einem blos zwei transversale Fruchtblätter tragenden Sprosse gleichwertig ist. Die Fruchtblätter tragen normalerweise je ein Ovulum. Durch Auseinanderweichen der beiden Blätter und stielartige Ausbildung ihrer Basis entstehen die gestielten Samenanlagen, durch Theilung der Fruchtblätter 3—4 samige Blüten, durch Ausfall eines der Fruchtblätter 1 samige Blüten". Now he further makes a comparison between the phyllotaxis of the sporophylls on the strobilus and that of the ordinary leaves on the long shoots, and he says that the decussate order of the sporophylls is most probable too, by this fact, that the first leaves, the bracts, on a long shoot are entirely transversal, and only the third pair of leaves shows an indication of the transition to the spiral order.

Spiess (141, who has continued the research of von Wettstein does not agree with his opinion that the stalked ovules should originate by a leaflike splitting of the ordinary ones „Das nun aber ein so reduciertes Gebilde, wie das Ovulum von *Ginkgo*, das ja nichts mehr von einem Blatte an sich hat, sich nachträglich wieder theilen sollte, entsprechend den Blattähnlichen Verhältnissen bei den Cycadeen und in Homologie mit dem abnorm fertilen Laubblatt von *Ginkgo* ist allerdings möglich, aber sehr unwahrscheinlich."

He will explain these forms by a division of the original pair of unstalked decussate ovules themselves. But it has not become clear to me in which manner he supposed that this has taken place.

After von Wettstein. Čelakovský (45) too has asked himself, to which cause the multiplication of the ovule was to be attributed and he begins to distinguish two kinds of multiplication: „1. Vermehrung durch Hinzubildung weiterer Ovularcarpelle zu den zwei normal bestehenden, und 2. Vermehrung durch dichotome Spaltung der zwei normalen, eventuell auch der überzähligen Carpelle" (p.6). He comes to the same results as von Wettstein, except in one point viz.: It occurs that strobili bear three sporophylls, which von Wettstein denies, who thinks that when three sporophylls occur, the third one has always been formed by a division of one of both decussate sporophylls.

It is a pity Čelakovský seems not to have had enough material for his investigation for he says. „Zwei alternirende Paare von *sitzenden* Samenanlagen sind mir nie vorgekommen, und ich finde auch bei keinem anderen Autor weder eine Angabe, noch eine Abbildung derartiger Blüten, daher ich glaube, dass solche überhaupt nie gebildet werden. Wohl aber findet man hin und wieder vier Ovularblätter, die aus gestielten Eichen bestehen. Es scheint somit, dass eine Blüte, die im Stande ist, vier Ovularblätter zu erzeugen, auch die nöthige kräftige Ernährung erhält, um die Stiele der Samenanlagen auszubilden. Ebenso waren auch die zahlreichen und spiralig zerstreuten Ovula in den abnormen Blüten Fujii's, welche ebenfalls ganzen Blättern gleich waren, gestielt. Man kann es also als eine allgemeine regel aufstellen, dass sitzende Ovularblätter nur in der Zwei- und Drei-zahl vorkommen, und dass solche, die zu vier in zwei alternirenden Paaren oder gar in grösserer Anzahl abnormaler Weise auftreten, immer gestielt sind; die zwei- und dreizähligen blattwerthigen Ovula können aber sowohl sitzend als gestielt sich ausbilden" (p. 7).

As the result of his research he says: „Demnach ist es jetzt auch meine feste Ansicht, dass die normale weibliche Blüte von *Ginkgo nur aus zwei Ovularblättern*, nämlich den zwei transversalen Samenanlagen besteht" (p. 14). The conclusions, to which von Wettstein and Čelakovský have come, however, are not wholly complete, which may be attributed partially to the material being unsufficient in number. The occurrence of four unstalked ovules on one strobilus I have found amongst my own material in 21 of these specimens.

It seems to me that von Wettstein attaches too much importance to the morphological value of the vascular supply. When the vascular bundles are divided in the axis of the strobilus to enter the stalklet of the ovule, this may have a clearly physiological tendency, because if new ovules have originated in some way as a retrogression or as a progression, they miss a nutritive strain, which can only be required by a splitting of the existing ones. The ovules are not divided for the sake of the vascular bundles, which have split, but these are splitting because new ovules are formed. And as concerns the view, that the normal order of the ovules should be the decussate one, I can not agree with this. The position of the sporophylls on the strobilus in the probably most original form, has just been the same as the leaves on the ordinary shoot, the one or two lowermost pairs standing decussate, the others in a spiral order. Therefore it is clear, that in the now existing reduced strobili, on which only the lower sporophylls are developed, these are decussate, but it may not be called the *normal order*, this being the spiral one.

My own research may confirm this. I have examined a great many short shoots, in which strobili were present, and I have found the following. Of the 114 examined brachyblasts were 76, in which the first strobilus, which stands in the axil of the budscale, had an abnormal shape, that is to say was split, or had only one terminal

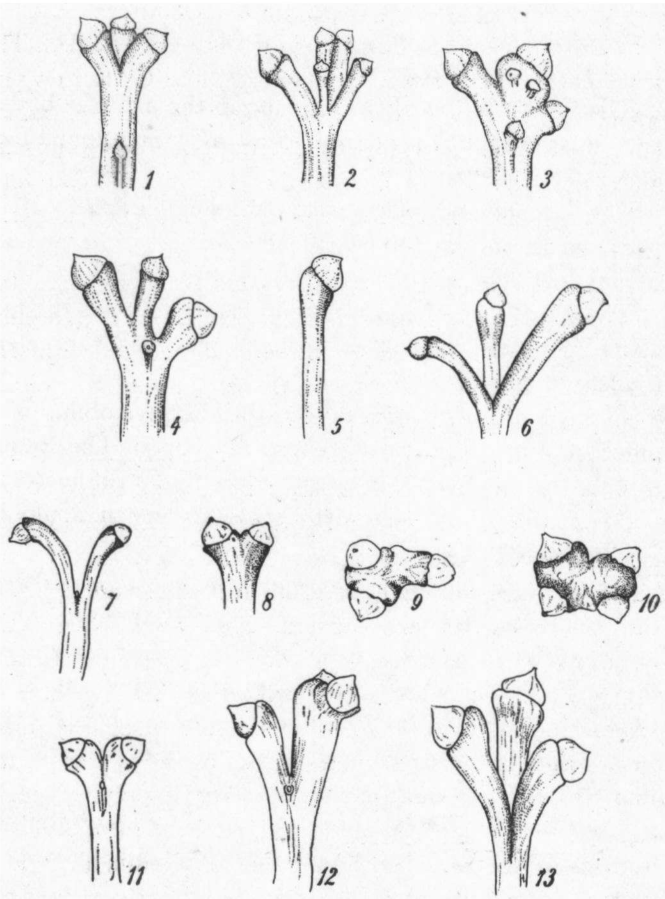


Fig. 3. *Ginkgo biloba*; young strobili with ovules; 1, 2, 3 and 4 strobili with stalked ovules; 5 strobilus with one terminal ovule; 6, 12 and 13 strobili with three stalked ovules: 7 and 11 strobili with two stalked ovules; 8 strobilus with two sessile ovules; 9 strobilus with three sessile ovules, seen from above; 10 strobilus with four sessile ovules, seen from above.

ovule, or was in some other way curiously formed.

Their dominating feature was the division in slender stalklets with one terminal ovule, contrary to the normal strobilus with sessile ovules.

Generally each brachyblast contains five strobili, which are ranged as follows:

The first strobilus always arising in the axil of a budscale, has mosttimes an abnormal form, as I mentioned before. fig. 3 — 1, 2, 3, 4.)

The second strobilus, also standing in the axil of a budscale is normal, in nearly all cases bearing two sessile ovules. (fig. 3—8.)

The third one sometimes, and nearly always the fourth, standing in the axil of an ordinary leaf, bears three sessile ovules.

The number of ovules on the fifth strobilus is very different and often they are less developed. The frequenty of four sessile ovules is greatest on this strobilus.

Sometimes there is a sixth strobilus which again bears two normal ovules.

As the lowest budscales were the most primitive, and the following formed a gradual transition to the normal leaf, and as in general from a series of successive organs, the lowermost, which originate first, represent a more primitive stage than the higher ones, coming later, the conclusion may be ventured that the first strobilus represents the most original case, and we may accept that the strobilus, with two or three unstalked ovules, now being the normal form is derived from the divided one. This view agrees with Worsdell's (182) „In the maidenhair tree (*Ginkgo biloba*) we find abnormally an increase of the number of carpels (here reduced to ovules), which also become long-stalked; doubtless a case of reversion, the normal female flower of *Ginkgo* being palpably a reduced structure." (II. p. 96).

The ovule of *Ginkgo* is composed of a nucellus and an integument being fused together to half way the height of the former.

The greater part of the integument is formed by a large sarcotesta, composed of great parenchymatous cells, among which a lot of mucilage canals are scattered. Outside it is lined by a well defined epidermis.

The stony layer, though very hard is thin and in it three layers may be distinguished. Of the middle one the sclerenchymatous cells are stretched in a horizontal plane, whereas the inner and outer one have cells with a more vertical orientation.

At the innermost side the sclerotesta is lined by the endotesta, composed of a few layers of cells, which are collapsed in a ripe seed and then form a brown papery membrane, adhering to the stony coat.

The nucellar tissue is quite distinct from that forming the integument and is covered in its free part by a rather solid membrane, forming in its upper part a large cone in which the pollenchamber is developed, the beak of which points into the cavity below the micropylar tube.

Within the sarcotesta no vascular bundles are to be observed, which is a point of difference to the Cycads. According to Caruthers (31) two vascular bundles are present in the endotesta, coming up through a little gap in the stony coat, running along the inner surface and ending at the level of separation of nucellus and integument.

Different authors among whom Eichler (64) Seward and Gowan (136) describe the micropyle to end into two or three slips. As this reminds us strongly of what we have seen already in the pteridospermous and cycadean seeds, the investigation of these slips might perhaps throw light on the origin of the integument. In superficial examination sometimes we see lobes around the micropyle but mostly it proves to be round or oval.

Its border is often curved, but very irregularly, therefore giving the impression of having slips (fig. 4).

Now we may ask, what is primary? Are those slips buildings of a plain border, or is the plain border a peculiar fusion of the slips. If the latter should be the case and the slips should really have a more profound significance, they probably yet stand in connection with the underlying anatomical structure.

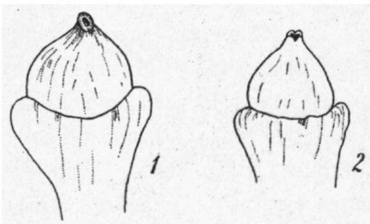
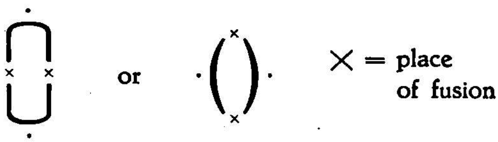


Fig. 4. *Ginkgo biloba;* young ovules. 1. micropyle oval, 2. slight indication of lobes round the micropyle.

On transverse sections through the micropylar region, the cavity formed by the integument, in which the nucellar beak protrudes, seems to be or oval or triangular. In the former case we may suppose that there are two units, which may be still fused in two ways:



If the slips were the external proofs of such a unit, they should occur at the micropyle on places corresponding to: .

Let us see if this is the case. In the very few cases, 1 to 10, in which we may speek with some certainty of two slips, I marked the places of the slips, by making two lengthwise scratches on the outer surface of the ovule. In transverse sections I saw then, that the places of the scratches had no relation whatever to the possible places of fusion. In cases with three slips, the situation was the same. Therefore wether slips occur on the ovules of *Ginkgo* or not is to my opinion of no morphological importance.

A second criterion as to the presence of units in the integument is the ribbing. In the ripe seed ribs are to be seen, very faint on the outer flesh, but clearly

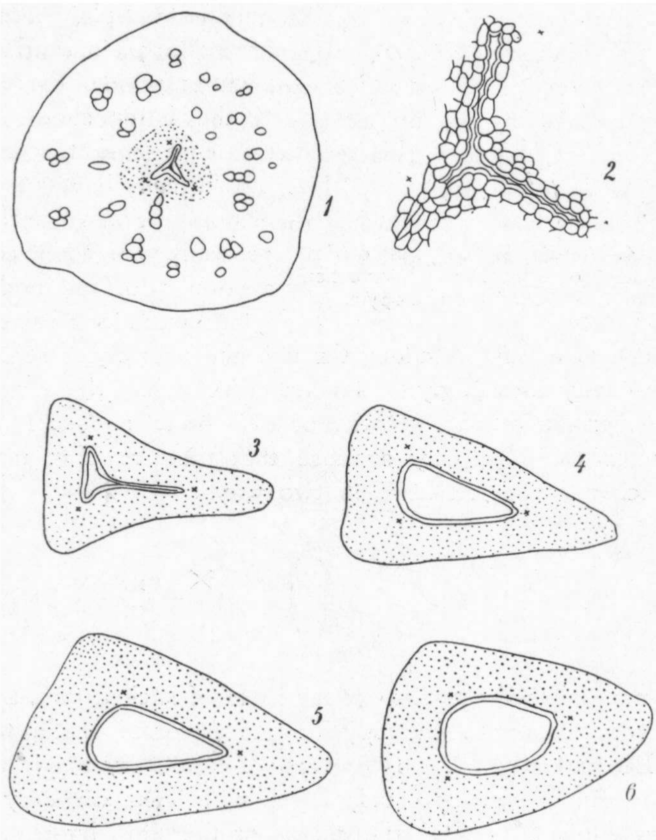


Fig. 5. *Ginkgo biloba*; transverse sections through a young ovule. 1. Micropylar region, sarcotesta with mucilage cavities, place where the sclerotesta begins to differentiate is dotted, the micropyle is seen as a triangular fissure. 2. Portion of 1, around the micropyle magnified. 3, 4, 5 and 6 transverse sections through lower parts, the angles gradually dy ont.

marked on the sclerotesta, their number being two, three or four. In very young ovules no trace of them is to be seen, only when they have reached a rather considerable size, the stony coat begins to differentiate, and herewith the ribbing occurs. The first indication of it is to be seen on transverse sections at the micropyle. In a young stage this is entirely round, but when the ovule has attained a diameter of about half a centimeter, it looks like a long stretched fissure or like a triangle with collapsed sides (fig. 5). Sections made lowerdown, show clearly the places of the ribs.

In sections close below the micropyle, at the places of the ribs, an elongation of the cells is to be seen as a

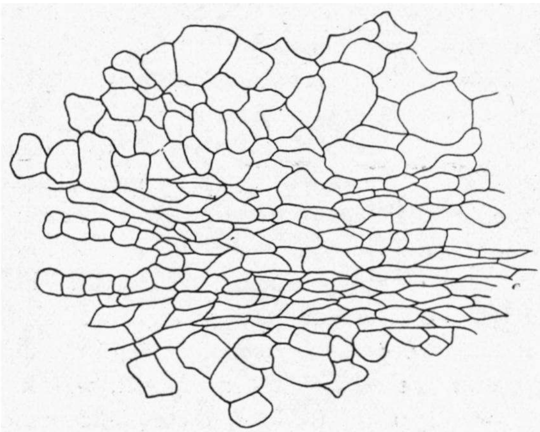


Fig. 6. *Ginkgo biloba*, transverse section below the micropyle, on the place of the rib; an elongation of the cells is to be seen.

lengthening of the fissure, giving the impression of a suture (fig. 6).

A resarch has been made by Affourtit and La Rivière concerning the ribbing of the seeds (1). The irregularity of those ribs has struck them and they made a statistic of their occurrence with the help of a great number of seeds, originating from the same tree from which my material was collected. Trom the 117 examined seeds, there were 47 with two, 65 with three and 5 with four ribs.

At the end of their note they compare the seeds of *Ginkgo* with those of *Trigonocarpus Shorensis*, and say: „Since in *Ginkgo*, however, no valves occur — the stony coat lacking fissures at the place of the ribs — and as vascular bundles are absent from the sarcotesta, those seeds cannot, as it seems to us, be compared with the seeds here [1]) described" (p. 594).

On account of the above mentioned cases, in which there are sutures to be seen, though they may be limited to a small region and only to be observed in a defined stage, I can not quite agree with their conclusion, and a comparison with *Trigonocarpus* may certainly be made, but to this I will return in the last chapter.

Caruthers (31) has observed cases where three ribs were present on the sclerotesta and in connection with them three lips at the micropyle, and three vascular bundles in the endotesta: „In some cases there is a three-lipped integument and a three-angled nucellus, there being also three bundles, one ending in each angled side" (p. 126). As I have examined the correspondence of the slips at the micropyle and the ribs on the seed coat, with the result I already mentioned, I question the significance of those slips, but it is quite possible that in other materials they are better developed, as is the case in *Macrozamia* formerly described. If they are present, they may strengthen the view, obtained in connection with the ribs and sutures, of the multiple origin of the integument.

[1]) Salisbury: „On the structure and relationship of *Trigonocarpus shorensis*". (126).

Coniferales.

§ 20. *Cupressus.*

Literature: Bayer (9).

Material:	*Cupressus Goveniana*	Bot. Gard.	Groningen.
	„ *torulosa*	„ „	Valentia.
	„ *Benthamii*	„ „	Rome.
	„ *funebris*	„ „	Lisbon.
	„ *sempervirens*	„ „	Rome. *)
	„ *australis*	„ „	Rome.

The female strobilus of *Cupressus* stands terminal on short shoots. In the lower part on the axis of these shoots, six pairs of decussate ordinary leaves are borne, whereas the four pairs of uppermost leaves form the strobilus and have the function of sporophylls. Sometimes the vegetative leaves are continued above the fertile ones.

The sporophylls are peltate and in ripe condition their rhombic outer surfaces close together and form a berry-like structure, which however is not fleshy as is the case in *Juniperus*. Each fertile bract bears in its axil or on its uppersurface a different number of flat ovules.

The outer layer of the integument, a thin sarcotesta forms on both sides a small wing lying in the plane of greatest dimension of the seed.

The sclerotesta too is very thin and protrudes in the base of the wings, as two sharp ridges.

A soft endotesta forms the innermost layer. Within the integument the nucellus stands entirely free and points with the beak of the pollen-chamber into the micropylar tube.

A curious fact has been observed and described by Sperk (140), the integument in *Cupressus Knightiana* originating as two different papillate protrusions, between which a third papilla, the nucellus is to be seen. According to him the integument would be an ovarium built up of two carpels. This view, that the integument is built up of carpels has been rejected, but if the observation has been correct, and separate projections are seen forming an envelopment around the nucellus, the fact remains the same, independent from the interpretation attached to this organs.

In an other case viz. in *Cupressus lusitanica* he describes a monstruosity, that is to say a metamorphosis of the integument into leaves. This abnormity was to be seen in different grades, some ovules being transformed wholly into leaves, others probably bearing at their base the rudiment of a nucellus.

Lateron I will discuss these observations in connection with the other facts.

§ 21. *Juniperus.*

Literature: Kubart (82), Nichols (97), Renner (121).

Material:	*Jun. phoenica* L.	Bot. Gard.	Lisbon
	„ *sabina* L.	„ „	Lausanne *.
	„ *Oxycedrus* L.	„ „	Groningen *.
	„ *communis* L.	„ „	Rome.

The female strobilus of *Juniperus* is composed of 1—5 whorls of bracts or sporophylls of which usually the middle one only is fertile. This fertile whorl contains about three sporophylls bearing one or two ovules at their uppersurface or sometimes on their sides.

In *Jun. communis* there are three ovules alternating with the three sporophylls. This case has given rise to much discussion, for it was accepted by most botanists that the ovules belonged to the sporophylls, but others amongst whom Sachs and von Mohl, regarded those ovules to be metamorphosed bracts.

It was Bayer (9) and later on Renner, who observed the following case. Around the central axis he found three bracts and four to five corresponding ovules, meanwhile a ring of three superposed bracts alternating with the first. From which may be concluded that it is impossible to suppose the ovules to be transformed bracts. It is evident that the ovules, belonging to the sporophylls have changed of position in order to obtain a better place of development.

When ripe, the sporophylls and bracts become fused with one another, forming mostly a round fleshy berry, in which the seeds are entirely enclosed.

There is a well developed integument round the nucellus, quite free from it, and built up of a thin exotesta, a thick sclerotesta and a thin fleshy endotesta.

On the ripe seeds two, three or four well-marked ribs are to be found and on transverse sections through those ribs, the sutures can be clearly seen.

The seeds of *Jun. phoenicea* bear small wings on two opposite ribs, sometimes on three, reaching from halfway up the height to near the micropyle.

§ 22. *Callitris.*

Material: *C. quadrivalvis* Vent. Bot. Gard. Lisbon.
C. calcarata R.Br. „ „ Rome.

The female strobilus is formed at the end of short shoots and is generally composed of four pairs of decussate bracts or sporophylls, which continue the phyllotaxis of the sterile leaves. The two lower pairs of bracts are very small, like the trophophylls and with regard to the uppermost ones, which form the fructification properly, they are hardly to be observed. The sporophylls are placed nearly on the same level with one another, so that they give the impression of forming a whorl of four bracts. They are large and soon become lignified closing together and forming a berry-like structure as in all *Cupressaceae*, the apices of which are replaced on the dorsal side.

On its apical surface each sporophyll bears two to numerous erect ovules, which in mature condition are provided with two broad wings and become free by the separation of the sporophylls like four valves.

In *Callitris* the integument has not been differentiated in the three layers, but remains thin and membranous, forming the above mentioned wings on either sides. Probably to increase the capacity of the dispersion of the seed, large cavities filled with air, are found within the membrane.

The nucellus is fused to halfway its height with the integument and is composed of a solid mass of cells, the beak of the pollenchamber pointing into the micropylar tube.

In connection with the reducement of the differentiation of the testa, the vascular supply has been modified and remains as a tracheal plate at the base of the ovule.

In the ripe seed a far developed embryo is enclosed within the soft nucellar tissue.

§ 23. *Thuya occidentalis* L.

Material: Bot. Gard. Lisbon.
„ „ Palermo.

As in the female fructification of *Callitris* the megastrobilus of *Thuya* is built up of four to five pairs of decussate bracts, which, however, are not sharply separated from the sterile leaves, but pass over into them gradually. Only in the middle region of the strobilus itself the sporophylls are fertile, the uppermost pair being sterile and fused, forming a columella-like structure. One or two ovules are borne on their apical side, with their micropyle directed towards the axis of the strobilus.

In a young stage of development, two lips can be seen at the micropyle, but they are not always clearly marked.

The ripe seeds have an oblong shape and are round in transverse sections. Their integument again is differentiated in the three layers, surrounding the entirely free nucellus.

Both the outer layer and the endotesta are thin and only represented by dry papery membranes, whereas the sclerotesta is very hard and occupies the greater part of the testa.

Of the 46 examined seeds 30 were triangular in their upper portion, having like the other lenticular ones small membranous wings on the ribs.

In transverse sections just below the micropylar region, sutures are to be seen corresponding with the angles on the outer surface. In the mature condition the nucellus, contrary to *Callitris*, is represented by a thin dry envelopment only, surrounding the embryo.

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§ 24. *Pinus*.

Literature: Baillon (10, 11), Bessey (22), Brogniart (26), Caspary (32), Čelakovský (39, 42, 44), Delpino (54), Eichler (62), Herzfeld (71), Parlatore (108, 109), Schumann (131), Stenzel (143), Tubeuf (160), Velenovský (163), Willkomm (172), Worsdell (175).

Material: *Pinus Laricio* Poir. Bot. Gard. Groningen.
„ *ponderosa* Dougl. „ „ Kew, *
„ *Banksiana* Lamb. „ „ Rome.
„ *Pumilio* Haenke. „ „ Rome.
„ *Pinea* L. „ „ Montpellier. *

The female fructification is composed of numeral bracts, standing in regular parastichs. The bracts, however, are very small and already in the first year of the development of the strobilus covered and entirely enclosed by the ovuliferous scales. In *Abies* and *Tsuga* the bracts remain large and project between the fertile scales.

There has been a good deal of discussion about the value of this structure and several authors (51. 165. 175.) have given an abridgment of the different views, uttered on this subject.

So I will only mention these views, without giving in extenso the argumentation on which they are based.

Rob. Brown (28) looked for the ovuliferous scale as an independent leaf in the axil of the bract, van Tieghem (157) too takes it for a leaf but this was borne on a short axillary shoot. Schleiden (129) called it a flattened axis or placenta, lateron Strasburger, Baillon a.o. accepted this opinion though a little altered, Kubart (82) comes to the conclusion that it must be an aril and Bessey (22) thinks it is formed as a chalazal outgrowth. Čelakovský (37a, 39, 42, 44) persisting in his thesis that the integuments are leaves gave the theory in which he regarded the ovuliferous scale as two fused integuments, accepting thus, though in an other form, its foliar origin. Sachs (124) an after him Eichler (58) explained it to be a simple outgrowth of the bract, thus being something like a ligular structure. Finely most botanists: A. Braun (24),. Caspary (32), Parlatore (109), Oersted, Stenzel (143). Willkomm (172), Englemann (65), von Mohl, Velenovský (88) a.o. on account of different proliferations found in *Picea excelsa, Tsuga canadensis, Pinus Pinaster, Larix europaea* etc., regard the ovuliferous scale as being formed by the fusion of two lateral leaves of an axillary shoot, standing in the axil of the bract.

As concerns these different theories, I can not agree with Coulter and Chamberlain (51) when they say: „To select amongst these views is more difficult than important" (p. 250), for to solve the question about the position of the ovule and the value of the integuments it is of great importance to know the origin and nature of the organs bearing the ovules.

Though Eichler (62) has given many arguments against the opinion that the strobilus in the *Pinaceae* is a compound one, and in favour to his view of the ligular character, he doesnot give a decisive explanation as to the nature of the monstruosities mentioned above.

It is Delpino (54) who has given a very original idea, to regard the ovuliferous scale as homologous to the strobilus of *Ginkgo* but he explains them both as fused lateral lobes of an excrescenz of the bract. Though his conclusion is not correct, I am inclined to accept the base of his idea, in comparing the female brachyblast of *Ginkgo* with the macrostrobilus of one of the *Pinaceae*. And lead by this comparison, it seems to me most probable to regard the ovuliferous scale to be a reduced axillary shoot. If we keep in mind that, as we have already seen, the strobilus of *Ginkgo biloba*, arising in the axil of a scale or a leaf on a short shoot, is reduced from an axis with several sporophylls to a simple flat stalklet with two ovules, surrounded by a small aril, a further reduction to the case represented by the ovuliferous scale in *Pinus* is not too exorbitant.

After all it is an explanation most in accordance with the observations in other Gymnosperms where compound strobili are to be found.

At the base of the ovuliferous scale on the upper surface two ovules are borne, the micropyle of which points towards the axis of the strobilus.

In a very young ovule the micropyle has on both lateral sides two rather long slips, always corresponding with the place, where the two ribs are to be seen later on.

The integument is composed of the three characteristic layers, which are of equal size in the beginning, but soon the sclerotesta gets the greater development and is the most conspicuous one. In the mature seed the outer soft layer is reduced to a thin dry membrane, which has often disappeared already, but in *Pin. canariensis* for example it still remains as a definite layer, in other cases as in *Pin. sylvestris* a. o. it is prolonged in the well-known thin wing.

The endotesta too becomes reduced to a thin brown layer covering the inner surface of the testa.

In an early stage nucellus and integument are completely free from one another but further growth takes place in the chalazal region, so that in the mature condition they are only separated in their apical portion.

On the sclerotesta two ribs are distinct, according to their corresponding sutures the scale splits easily when pressed.

The integument originates often as two separate protrusions (Eichler, 64).

The vascular supply has disappeared in connection with the less developed outer and inner layer of the testa, remaining only as a tracheal plate at the base of the seed.

§ 25. *Podocarpus.*

Literature: Brooks and Stiles (27), Gibbs, (67), Norén (98), Pilger (117), Sinnott (137), Thomson (156), Tison (159), Young (183).

Material: *Pod.*	*elongata*	Carr.	Bot.	Gard.	Rome.
„	*neriifolius*	Don.*	„	„	„
„	*Nageia*	R.Br.*	„	„	Tokio.
„	*màcrophylla*	Wall*	„	„	„

The female strobilus of *Podocarpus* stands terminal to long or short shoots or in the axil of leaves borne by long or short shoots. It is very different in shape according to the subdivisions of the genus or the various species and also the general form and size of the sporophylls may differ considerably.

In *Pod. macrophylla* the axis bears at its apex three pairs of decussate bracts the lower one of which is small and pointed, the second pair is fleshy and grows out into the receptacle, of which one of the two fleshy scales bears the ovule, finely the third pair does exist in a young stage, but is not developed further.

In *Pod. elongata* the lowermost pair of sporophylls too is large and becomes fleshy in the mature condition, forming with the other pair the receptacle.

With the ripening of the seed the receptacle develops into a round bullet-like berry of crimson colour, in which the original bracts are to be distinguished. A. Braun has indicated that the fleshy receptacle has been formed out of the fused bracts, as he has found abnormous specimens of *Pod. macrophyllus* subsp. *maki* in which the bases of the ordinary leaves were swollen, as is the case with a receptacle. In a young stage the free leave tops are clearly to be seen as small slips on the thickened basalportions.

On the sporophyll only one ovule is present, its micropyle being directed towards the base of the subtending bract. Nucellus and integument are fused together, whereas around this an outer envelopment is found, having already several names and to which different meanings are attributed.

According to Pilger (117) this organ is an epimatium „ein Excrescenz des Carpides" (p. 16); others Brooks and Stiles (27), Coulter and Chamberlain (51), Schumann (131), Worsdell (175) call it a second integument, whilst a third view has been given by Bertrand (21) and Gibbs (67), in comparing it with the ovuliferous scale of the *Pinaceae*. Bertrand (21) says of this „Des Abiétinées propement dites aux *Taxinées* proprement dites en passant par les *Saxe-Gothea* et les *Podocarpus*, nous avous pu suivre une tendance générale de l'écaille ovulifère à embrasser, en le recouvrant comme un capuchon, l'ovule ou les ovules qu'elle porte, à leur adhérer de plus en plus, et finalement à se confondre avec le tégument ovulaire dans les *Torreya* et les *Cephalotaxus*" (p. 68).

For the present I will use here the name epimatium, this being the most neutral one, lateron in the discussion I will return to it. So the epimatium is entirely bent round the ovule and for a short distance in the apical region free from the integument.

According to Pilger there is a scale of gradual transition amongst the *Podocarpoideae* as regards the coalescence of sporophyll, epimatium and ovule.

In *Microcachrys* and *Saxegothaea* the ovule hangs on the sporophyll, with the micropyle directed towards the base of it and the outside is loosely enveloped by the epimatium. Both ovule and epimatium are fixed independently on the sporophyll.

Various species of *Dacrydium* form an intermediate stage towards the case of *Podocarpus*, the ovule namely has been replaced here from the sporophyll to the epimatium, which for the rest is bent freely around the ovule and is fixed with a broad base on the carpel.

Finely *Dacrydium Bidwillii* represents a last transitional stage in which the epimatium encloses the ovule entirely, out of which the micropyle projects only through a small aperture. Epimatium and integument, however, are not yet fused.

As is mentioned already the ovule is composed of a nucellus enclosed by an integument, which is fused with it for two-thirds of the height from the base. In the ripe seed the integument is differentiated in an inner membranaceous endotesta and an outer hard sclerotesta, whereas the epimatium which is often hardly to be separated from the sclerotesta forms a tough fleshy sarcotesta, as an outermost envelopment.

On the sclerotesta, three ribs are clearly to be distinguished running from the micropyle to about the level of separation of nucellus and integument. The stony coat splits entirely according to those ribs when pressed, and in transverse sections sutures are to be seen on those places.

The vascular system consists of two bundles running in the epimatium. According to Gibbs (67) they have a inverse orientation, affected by the rotation of the two bundles as they descend the scale.

§ 26. *Cephalotaxus drupacea.* Sieb et Zucc.

Literature: Pilger (117), Spiess (141), Worsdell (176, 177)

Material:	*Ceph. drupacea*	Bot. Gard	Rome.
	„ „ *	„ „	Kew.
	„ „ *	„ „	Tokio.
	Ceph. Fortunei *	„ „	Rome.
	„ „ *	„ „	Kew.
	„ „ *	„ „	Lausanne.
	Ceph. follicularis *	„ „	Palermo.
	Ceph. pedunculata	„ „	Rome.

The female fructification arises in the axil of the lowermost leaves on young shoots. The axis of the strobilus bears three, four or five pairs of decussate sporophylls, being thick and fleshy as the axis itself, which protrudes above the uppermost sporophylls as a fleshy irregularly curved mass of tissue. On each sporophyll two ovules are formed, originating at its base near the axis, which has become hollow by this and forms between both ovules a thick cushionlike partition, fused with the sporophyll.

When fertilization has taken place, which occurs fourteen months after pollination, the seed soon becomes mature, and the integument first being composed entirely of parenchymatous cells is differentiated now in the three common layers.

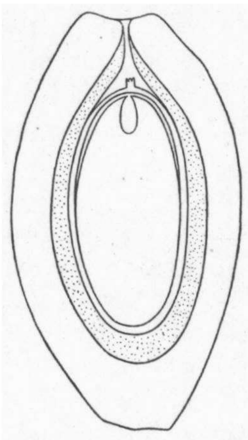

Fig. 7. *Cephalotaxus drupacea*; longitudinal section trough the ovule, sarcotesta, sclerotesta dotted, endotesta with a short micropylar tube, nucellus and one archegonium.

The outer fleshy coat is a very conspicuous-one and forms the greater part of the testa, being broad in its upper portion with a flat top, in the centre of which the entrance to the micropylar tube is found, whereas the lowermost portion of the ovule is rather pointed. Its outer surface is covered by a thick-celled epidermis.

The sclerotesta is in the mature seed about, 1 mM. thick and has a general shape being just the reverse of that of the entire ovule, at its base it is broadest whereas at its top it is pointed, entirely enveloping the micropylar tube.

Inside the stony layer an endotesta is developed, composed of five to six layers of elongated cells, in its upper part becoming free from the sclerotesta and provided with a curious lobed cylindrical micropylar beak, pointing into the cavity between itself and the sclerotesta.

The nucellus is fused to halfway its height with the endotesta and is covered in its upper free part with a well defined epidermis and cuticula, except in its apex above the embryosac, where a way of communication must be left between the latter and the pollenchamber, lying above in the endotesta.

This case is a very remarkable one, for as far as we know amongst the Pteridosperms, the nucellus is always provided in its apical region with a beak in which the pollenchamber, whereas the endotesta is entirely concrescent with the stony coat and covers the innerside of the micropylar tube. Here the endotesta has the function, otherwise performed by the nucellus itself to cover the thin nucellar tissue and to receive and to preserve the pollen by the formation of a pollenchamber.

To be sure of the origin and nature of the different layers, and in order to examine whether it is possible that the endotesta should be an original free envelope, like an inner integument, I investigated the presence of cuticulae. For if two layers, though concrescent, are lined by a conspicuous cuticula, their origin must have been separate, and when no cuticula is to be seen, it may be possible that both layers are formed by the division of a single one.

Cuticulae are best indicated by the reaction of van Wisselingh (173). A microscopical preparate covered by a cover is heated with nitric acid and potassium chlorate, by which the cuticulae become more and more visible and the cellulose and the lignified cell-walls become translucent. To distingiush the cuticulae from the adjacent cell-layers I used potassium iodide-iodine and sulphuric acid, after having washed the preparate with water.

Now I could observe a cuticular-lining on the places which I have indicated for *Torreya* in fig. 9. Below the level of separation of endotesta and sclerotesta no trace of it could be seen and in the upperpart the cells composing the epidermis were coloured very faint in their outer walls. Therefore it is not evident that both layers are fused separate ones, but it is more reasonable that the innermost layer of one integument has become free in its upperpart to cover the nucellus.

This feature is also established as we will see later on by the other Taxads viz. *Torreya* and *Taxus*, and therefore it is an other caracteristic of this group contrary to the other Gymnosperms.

In the ripe seeds two ribs are found on the sclerotesta and accordingly the seed splits open when pressed. Within the stony coat the nucellus is lying entirely free, enveloped by a papery membrane, representing the inner fleshy layer, which has become entirely separated from the testa.

Some authors amongst whom Čelakovský and Worsdell supposed the outer fleshy sarcotesta to be homologuous with the arillus of *Taxus*. Whether it is allowed to make this comparison, I will discuss in the following chapter.

On both sides of the seed, just above the ribs on the stony coat two vascular bundles are running in the sarcotesta, their structure being investigated by Strasburger (147) and Worsdell (176). The former has found that the orientation of the vascular bundles is inverted, the xylem lying outside, whereas the phloem is situated in close proximity to the sclerotesta. The same inverted orientation is present in the ligule of the *Selaginellaceae* and the *Isoetaceae*, and in comparison with this, he supposes the outer fleshy layer to be a ligular structure.

Worsdell has amplified this investigation, and has indicated, that there is a well-developed centripetal xylem extending along the whole tangential face of the centrifugal xylem, besides there are two sets of protoxylem, one attached to the centrifugal, the other to the centripetal xylem. According to this the author regards *Cephalotaxus* as the most ancient of the coniferous genera and says that it is to be expected that it will exhibit in its most primitive organs similar characteristics as those we find in Cycads and in *Ginkgo*. And then he continues „Now the most primitive foliar organs of any plant are, to my mind, the *cotyledon* and the *ovular integument*" (p. 318).

Whether we may agree with this opinion, and as to the comparison with *Ginkgo* and the Cycads I will speak about in the discussion.

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§ 27. *Torreya nucifera* Sieb. et Zucc.

Literature: Coulter and Land (52), Oliver (100), Pilger (117).
Material: Bot. Gard. Rome.
„ „ Tokio.

The female strobili of *Torreya* are borne in the axils of the lowermost leaves of short shoots and usually they occur in pairs on very short axillary branches. The number of them is different and varies from two to six on one strobiliferous shoot, but the upper pairs never come to maturity and only the lowest one produces the large plum-like seeds.

The branch on which the strobili arise is much reduced and bears only a few pairs of leaves; in the axil of one or more of them a strobilus occurs. This is composed of two pairs of decussate bracts surrounding the terminal ovule, which in a young stage is provided with one integument only and an annular wall at its base, but soon the latter develops and envelops the whole ovule as a thick fleshy cupule, or second integument as it is called by some authors.

This outer envelopment overtops the inner-one in a mature condition with two m.M. leaving a free cavity between them in the upper region, lower-down near their base both integument and cupule are concrescent, a well-defined cuticula marking the line of their fusion. The cells composing this outer coat are soft and parenchymatous, a great number of large resin-cavities lying between them.

According to Oliver (100) nucellus and inner integument are completely free at first, but soon by an extensive intercalary growth, beginning in the chalazal region, the free portion between them begins to vanish more and more, till in the mature condition it may represent only one-twentieth of the entire length of the seed.

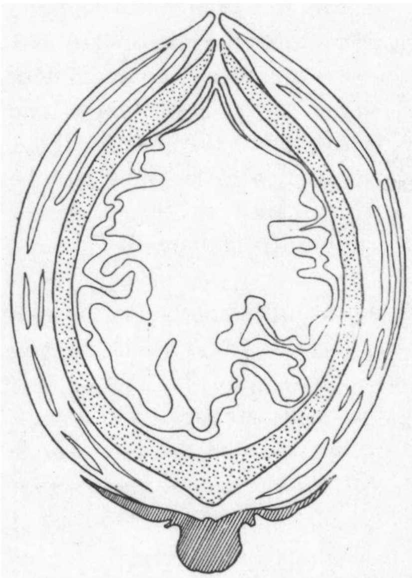

Fig. 8. *Torreya nucifera*; longitudinal section through the ovule: cupule with mucilage cavities, stony layer dotted, inner fleshy layer and nucellus, „ruminating' nucellar tissue.

The inner integument is differentiated into two distinct layers, an outer stony layer and an inner fleshy one. As is the case in *Cephalotaxus* both layers become free from one another in the micropylar-region of the seed, and are rather clearly to be distinguished lowerdown also when the hardening of the sclerotesta has not yet taken place, for this layer is composed of small isodiametrical cells, sharply marked from the lange elongated ones of the endotesta.

Above the level of separation of the stony coat and the endotesta, the latter becomes free from the nucellus, which in its turn points with its sharp apical portion into the cavity formed by the innermost layer. In this way three cavities are formed one above the other, respectively by the cupule, the sclerotesta and the endotesta, and into which are pointing by turns the micropylar beak of the stony coat, that of the inner fleshy layer and the top of the nucellus. Thus the micropylar tube may be compared to three funnels, shoved one on the other with their narrowest opening turned upwards.

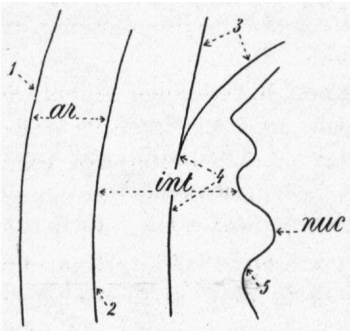

Fig. 9. *Torreya nucifera;* part of longitudinal section through the ovule to indicate the places where a cuticula was found;
1, 2 and 5 very distinct cuticulae, lining the arillus, integument and nucellus. 3. cuticulae very faint, 4 no cuticula, 3 and 4 place of separation of sclerotesta and endotesta.

To distinguish the limits of the different layers, I used the cuticula reaction of van Wisselingh (171) already described for *Cephalotaxus*.

A very peculiar behaviour, characteristic of *Torreya*, is what we may call the „rumination of the nucellus, a very irregular invasion of the endotesta by the nucellar tissue. For a more detailed treatment of this progress, I may refer to (52) or (53).

At the base of the seed two vascular bundles enter the arillus, running upwards close to the woody integument. The orientation of xylem and phloem is normal, the xylem lying at the innerside, the phloem outside. They often divide but then the different branches always reunite at the level of separation of the integument and cupule.

Here at opposite sides of the seed, both bundles traverse the stony coat and the soft endotesta where they fork and encircle the base of the free apex of the nucellus till they meet forming a closed ring.

In a ripe condition the stony coat is circular in outline, at any rate lacks any indication of angles or ribs. The apical region of the seed is a very remarkable one (see: Oliver 101, pl. 14, fig. 13). The micropyle lies in the centre of a ridge, below which on both sides of the seed, two shield-like areas are to be seen, covered by a thin translucent membrane representing the outer surface of the integument, where it is free from the cupule. A few millimetres below the top of the seed in the plane of the micropylar-ridge, two projecting papillae are present on the stony coat, indicating the place where the vascular bundles broke through the testa.

§ 28. *Taxus*.

Literature: Dupler (56), Pilger (117), Robertson (123), Sahni (124a).
Material: see table p. 283.

The ovule bearing organ of *Taxus* consists of a primary shoot and a secondary one. The primary shoot arises in the axil of an ordinary leave and bears a number of little brown coloured scales in spiral order; in the axils of one or two of the uppermost ones the secondary shoot is borne. In the latter case, when there are two, the primary shoot ends as a little knob between them. The secondary shoot, developing a season later than the primary one, bears three pairs of decussate bracts or scales, larger than those of the primary one and green through the existence of chlorophyl in their cells; the first pair of those bracts standing transversely to the fertile scale of the primary shoot. At the top of the secondary shoot between the uppermost scales the ovule develops.

Whether the ovule is borne by one of the scales, functioning as megasporophyl, so that ist is a lateral structure, or it is standing terminal at the top of the axis, is an unsolved question, as the megasporophyl is not clearly to be distinguished. The morphological position has been much discussed by different authors, but I will not repeat their views here, a summary of them being lately given by Dupler (56).

The ripe ovule consists of a thick, fleshy, red coloured arillus or cupule, surrounding a central part formed by the nucellus and the integument. In a young condition the arill is not yet to be seen, but about the time of pollination, the arill begins to develop as an annular wall round the base of the ovule. First it is green coloured and thin, but when the seed becomes mature it enlarges rapidly, forming a mass of large delicate walled, succulent cells, covered by a small-celled, pigmented epidermis, containing numerous stomata.

Amongst a great many seeds I examined, I found two, of which this arill was split, thus giving the impression of being two lobes, fused at their base. The arillus in *Taxus tardiva*, also in the ripe condition, remains very short and appears to be a dishlike swelling at the base of the seed.

The integument, being wholly free from the arillus, is composed of four layers: an outer very thin leathery membrane, a fleshy layer very thin too and a rather thick stony layer, at the innerside of which a papery membrane is to be seen.

The thin fleshy layer covered by the leathery membrane I regard as a real, though very reduced sarcotesta covered by a hypoderma and epidermus.

It has been supposed, that these layers belong to the sclerotesta the cells not having developed the stony character (Dupler, 56). „It would not be necessary to regard a layer or two of cells overlying it (the hard coat) as representing the outer fleshy layer". (Coulter and Chamberlain, 51). In comparison however, with other already described seeds, I am inclined to maintain my opinion.

The other two layers, the stony coat and the papery one are homologous with the sclerotesta and endotesta of the other gymnospermous seeds.

Outside distinctly pronounced ribs are to be distinguished, running from the micropyle till half way down the height. Their number varies and amounts two, three or four. At the micropyle sutures underlying the ribs are to be seen in transverse sections. The form at the base of the seed where it is attached to the axil agrees with the number of ribs in the micropylar region, and is oval, triangular or square, according respectively to the number of ribs; being two, three or four. The following table indicates the number of ribs, for the examined species and varieties. (See page 65). The number of seeds with two ribs hardly dominates over which have three, and those with four ribs too are very frequent.

At the micropyle there are often some lips to be observed as in *Ginkgo*, mostly two in number, but they are not always to be seen and when present do not correspond with the ribs.

In a young stage of development the nucellus is entirely free from the integument, but after fertilization, when the chalazal region has its greatest activity of growth, nucellus and integument become united in their lower part.

Name.	Botanical Garden.	total number of seeds.	2 ribs.	3 ribs.	4 ribs.
Taxus baccata var. *pyramidalis**	Madrid	23		10	13
„ „ „ *horizontalis**	Groningen	122	83	38	3
„ „ „ *adpressa**	Wurzburg	68	34	34	
„ „ „ *fastigiata**	Rome	68	7	40	21
„ „ „ *elegantissima**	Groningen	41	29	12	
„ „ „ *hibernica**	Groningen	128	83	34	11
„ „ „ *pendula**	Bonn	30	13	13	4
„ „ „ *Dovastoni**	Bonn	36	22	13	1
„ „ „ *Dovastoni**	Edinburgh	24	18	6	
*Taxus cuspidata**	Sapporo (Japan)	31	23	8	
„ *disticha*	Groningen	152	99	53	
„ *tardiva*	Rome	46	13	23	10
		769	424	284	63

As in *Cephalotaxus* and *Torreya* the endotesta becomes free in its upperpart from the stony layer and covers the nucellus, without being fused with it.

The nucellus itself is bordered by a well differentiated epidermis. The embryosak within enlarges very rapidly after fertilisation, so that when the seed is mature, the nucellar tissue is only represented by a thin membrane.

The micropyle after pollination „becomes closed by the centripetal radial growth of a portion of the inner epidermis of two sides" (56).

At the base two to four vascular bundles enter the ovule at opposite sides, running through the integument almost to the micropyle. Their course corresponds to the ridges on the testa, sometimes the number being three or four. The two vascular bundles are formed by fusion out of four bundles in the axis, beneath the base of the seed, in cases when there are three or four the fusion of one or both pairs does not take place.

The axil and nucellus are both lacking vascular supply.

Gnetales.

§ 29. *Ephedra americana*. Humb. et Bonpl.

Literature: Land (83), Lignier et Tison (88), Thoday and Berridge (155).
Material: Bot. Gard. Groningen.

The female strobilus of *Ephedra* stands in the axil of the ordinary scale-like leaves, which are decussate on the nodes of the main axis. Sometimes the axis bearing the cone is branched, as is mostly the case with the staminiferous ones where are two lateral strobili with a terminal one standing between them. The strobilus is formed by an axis with, as a rule, three pairs of decussate bracts, the uppermost pair of which is fertile only. Each pair is more or less connâte, forming three cups above each other, the lowest one being small, the upper one very large. Within this uppermost cup mostly two ovules are placed, arising in the axils of each of the bracts, with the apex of the axis between them. Sometimes both ovules are fused with their integuments, two nucelli being present within, but it also often occurs that only one normal ovule is found, standing in the midst of the surrounding fused bracts.

When ripe the bracts become succulent and of a red colour, the composing bracts hardly being to be distinguished. In the tribe *Alatae*, is a greater number of opposite standing bracts, which are not fused, and become membranous instead of succulent when the seed ripens.

Thoday and Berridge (155) suggest that it is probable that formerly more than a single whorl of bracts were fertile, having found a cone of *E. altissima* with small masses of abortive tissue in the axils of the bracts next below the fertile ones, suggestive of undeveloped sporangiophores.

Occasionally a female flower is found in a staminate strobilus.

The ovule is composed of two coverings, an outer and an inner one, and a nucellus.

The outer integument, or perianth as it is called by some authors, is entirely free from the central part and is connate with the inner one at its base only. It contains two, three or four ribs and according to Coulter and Chamberlain (51) „appears first in two distinct parts" (p. 378). It is built up of two layers, an inner fibrous one, comparable with a sclerotesta and an outer layer, composed of great brown cells covered by an epidermis which may be homologous with a sarcotesta.

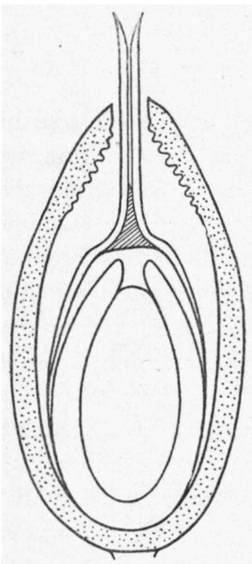

Fig. 10. *Ephedra americana*; longitudinal section through the ovule: outer integument, inner integument with a long micropylar tube closed by a prop of mucilage, nucellus with pollenchamber and large prothallium within.

The inner integument is never more than two cells thick, which are thin walled and parenchymatous, and in its upper part is prolonged in a very long micropylar tube, reaching far beyond the strobilus. At its inner side the micropyle is cuticularised.

The nucellus, concrescent for two thirds of its height with the inner integument is sharply demarcated with its large empty cells from the smaller ones of the integument. Within the nucellus is a large embryosak, and at the top a characteristic deep pollenchamber is formed. After fertilization, when the embryo enlarges, the nucellar tissue becomes thin and in the ripe seed it remains as a papery membrane.

The outer integument bears on its inner surface in the micropylar region several papillae, serving to close the cavity between the micropylar tube and the outer covering. In the micropyle itself a drop of mucilage is segregated, which becomes a hardened mass after pollination, closing the entrance to the pollenchamber.

At the base a ring of vascular bundles enters the ovule and divides into two systems, one running in the outer integument, towards its apex, agreeing in number with the ribs on the stony coat, and one in the inner integument as far below as the level of separation of nucellus and integument and consisting of two rudimentary vascular bundles.

There are many different views about the value of the two coverings of the ovule. Strasburger (147) regards the outer coat as equivalent to a pair of leaves but in (150) he changes his opinion and calls it outer integument. Lignier (58) says that the outer covering is composed of a whorl of three leaves, the outer one of which is more or less abortive, whilst the inner envelope consists of three carpels, of which one only is developed and the others rudimental. Van Tieghem too regards the outer investment as a fusion of two leaves. Finely there are many botanists, who consider them integuments both, but in the discussion I will return to this.

§ 30. *Gnetum.*

Literature: Beccari (12), Berridge (19, 20), Karsten (76, 77, 78), Lignier et Tison (90), Lotsy (92) Pearson (114, 115), Thoday (153, 154).

Material: *Gnetum funiculare* Blume. Bot. Gard. Buitenzorg.
„ *moluccense* Karst. „ „ „
„ *Gnemon* L. „ „ „

The female strobilus of *Gnetum* consists of a long spike-like axis bearing at intervals on the nodes connate decussate bracts, having in their axils a ringshaped swelling of the axis. On this cushion the ovules are developed by localized growth of the tissue (Thoday, 153). In each axil five to eight ovules or „flowers" are present, which consist of a nucellus invested by three envelopes.

As in *Ephedra* there are two kinds of female flowers, those borne on an ovuliferous strobilus and those occurring in the upper portion of the staminate cones. The latter ones are different from the former in lacking the middle of the three coverings. Usually these incomplete flowers have no function, but when in rare cases they are fertile, the three envelopes are developed (Lotsy, 92). It is said (Karsten, 77) that the middle one in a young condition is always to be found, but gradualy disappears during the development.

The outer envelopment or „perianth" becomes very succulent when ripe and is orange, red or green coloured. It encloses the whole of the seed, but from the base it is free from the central part for its greater portion, except in *Gnetum scandens* where it becomes fused with it. The composing tissue is formed of great parenchymatous cells, and resembles that of the cushion bearing the ovuliferous structures.

The middle and inner coverings are real integuments and are therefore called the outer and inner integument.

The outer integument arises from the undifferentiated mass of tissue at the base of the ovule just above the perianth, and is free from the two other coverings, except in the above mentioned case of *Gnetum scandens*, where it is fused with the outermost envelope. At the top it expands, forming a thick wall round the lower part of the micropylar tube. The outer integument is composed of several layers, which are more or less differentiated in the several species. The innermost zone contains many sclerotic fibres, which become lignified and form the sclerotesta. The other layers, which are more fleshy, but in some species as in *Gn. scandens* become lignified too, may be distinguished, as Thoday (153) does, in an outer fibrous zone, a hypodermal strand and a palisade layer, but as a whole are comparable with a sarcotesta. In its upper part the sclerotesta is angular and in transverse section is star-like, thus giving the impression of being composed of four or five valves.

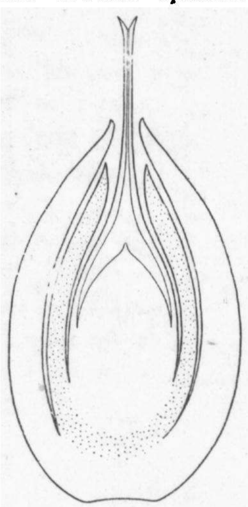

Fig. 11. *Gnetum Gnemon:* longitudinal section through the ovule; cupule, outer integument, inner integument with a long micropylar tube and the nucellus.

The inner integument is a thin layer, in the ripe seed represented by a shrivelled papery membrane, upwards it projects as a long micropylar-tube far beyond the ovulum. At its apex the micropyle ends in four or five slips, agreeing in number and position with the angles on the sclerotesta.

After fertilization has taken place the micropylar tube is closed by a remarkable blocking-tissue at its base, formed by a secondary growth of the tissue of the walls, which becomes lignified.

The nucellus is concrescent for its greater part with the inner integument and ends in a sharp nucellar beak pointing in the cavity formed by the inner integument.

The vascular supply is composed of three systems one in each of the envelops. For *Gnetum Gnemon* it is described by Berridge (20) and for the *Gnetaceae* in general by Worsdell (178).

Each of the 12—14 bundles entering the base of the female flower, at the level of insertion of the perianth give off two traces in this covering and then continue their way to supply the two integuments. All these bundles are well developed and branch often, running in the perianth and outer integument to the top, and in the inner one till reaching the level of separation of this and the nucellus, But also one or more can be traced in the base of the free part of the integument [1]).

There has been a good deal of discussion as to the three coverings; they have been considered as three integuments (Strasburger, 147), as a perianth and two integuments (Beccari, 12) and as two perianths and one integument (Lotsy, 92). In the discussion I shall say more about this.

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[1]) Above the level at which the branches in the perianth are given off, a curious complex of vascular tissue is to be seen. It has been supposed bij Miss Berridge (20) that these tracheids are „the vestiges of a vascular supply of some whorl of organs, which was situated between the outermost covering and the outer integument of the ovule" (p. 990). It „may indicate that the ovule was primitively surrounded by a whorl of male flowers. If this were the case the female inflorescence of *Gnetum* would have been originally compound and bisexual and from such a form the existing male inflorescence can easily be derived." (p. 992).

§ 31. *Welwitschia mirabilis* Hook f.

Literature: Church (48), Hooker (72), Lignier et Tison (89), van der Meulen (94), Mc Nab (96), Pearson (112, 113), Strasburger (147), Sykes (152).
Material: collected by N. Barends in Pforte near Swakopmünd (Z. W. Africa) and present in the Botanical Laboratorium of Groningen.

Since the first discovery of *Welwitschia mirabilis* in 1860 a good deal has been written about this strange plant and especially about the morphology of the „flower". Apart from the many opinions expressed as to the systematic position and the possible connexion with either the *Bennettitales* or the *Angiosperms*, there exists a rather extensive literature about the construction and the morphological value of the different parts of the female fructification.

And especially in this domain of the morphology it seems to be actually the rule that each new investigator gets an other insight in the matter and gives other names to the different parts accordingly. So it is not possible for me, as I always tried to do in these descriptions to render the real conditions in a purily objective manner, without take with the names part once more of some inductive or deductive qualification of the „flower" organs. Therefore it seems best to me to mention a few descriptions from the literature and then to try to find the right interpretation with the help of my own observations.

The female strobili are monosporangiate but the male strobili are morphologically bisporangiate, namely in this case female organs occur between the microsporophylls, but then they do not function. We cannot yet speak here of macrosporophylls on account of a reason to be mentioned later on.

Both specimens of strobili are found on separate plants, *Welwitschia* therefore is dioecious.

The female strobilus is ± 7 c.m. long and consists of four regular orthostichies of bracts, owing to which a more or less square shape is formed. At the base and also at the top these bracts are sterile, but in the middle they bear in their axils, „in the accurate median line, what are regarded as the ovuliferous or carpellary flowers, as definite stalked axillary formations, the whole cone being a bi-axial structure" (48 p. 120).

It is generally accepted that the strobilus is compound except by Sykes (152), who regards it as being a monaxial structure. The figures of Church (48 pl. 9—13) explain his point of view sufficiently to my opinion and he rightly observes besides: „The bi-axial hypothesis holds because there is no real evidence against it, that is to say it is the simplest statement of the facts of observation" (p. 120). Later on we shall see that this opinion is strengthened by other arguments.

The structure of the flower or better of the strobilus of the second order, is quite simple. It is composed of an outer envelopment, being flattened in the tangential plane, parallel to that of the bracts. Lateron it elongates still more also in the tangential direction, and then forms a broad, membranous wing around the seed, serving for the dispersion. Inside we find a terminal ovule enclosed by a distinct integument.

When maturing, the seed becomes oblong and is filled for the greater part with endosperm. The perisperm (the nucellar-wall and the integument) remains only as a thin membrane, whereas the nucellar apex, which reaches here a considerable length, is still attached to the top as a shrivelled mass of tissue. Miss van der Meulen (94) who publishes her opinion about this subject says „Het door het bloemdek ingesloten zaad is langwerpig en bestaat voor het grootste gedeelte uit endosperm, waaromheen het perisperm zit in den vorm van een vliesje, dat aan de top tot een kegelvormig mutsje verdikt is. *Het integument wordt bij het rijpen opgeheven en omgeeft alleen maar het bovenste derde deel van het zaad*" (p. 14) [1].

This is not correct, the membrane surrounding the endosperm, splits as to say in two, at one third from the micropyle, it being out of question that one of the two membranes should be freely attached to the other, like for example the calyptra on a sporogone of the mosses. Here also the nucellus is concrescent with the integument to „shoulderheight" as is the case in nearly all Gymnospermous seeds. The membrane surrounding the endosperm is formed by a narrow fusion of the nucellar wall and the integument, wheras both remain free from one another at their apex, even in the ripe condition of the seed.

Lignier et Tison (89) mention the occasional occurrence of bracts at the base of the outer envelopment. „Exceptionnellement, dans cinq fleurs qui toutes se trouvaient près de la base des cônes, nous avous observé, au-dessous de l'enveloppe ailée, *deux petites bractées situées dans le plan tangentiel*" (p. 129).

The occurrence of these bracts in the lowermost part of the strobilus, where generally, as I have pointed out in *Ginkgo*, the possibility is greatest to observe a more primitive stage, may perhaps indicate that the absence of these bracts in other cases is a secondary feature. In this way they strengthen the opinion, to regard the strobilus as a compound one, for these bracts must necessarily be borne on an axis of the second order.

To form a clear idea about the structure of the female strobilus, and the value of the different segments, we now have to pay our attention to the male strobilus.

This consists of an axis with four rows of decussate bracts like the ovulate one does, but it is smaller, the

[1] I cursivied.

total length varying from 2—4 cM. The lower and upper bracts are mostly sterile, in the axil of the middle ones two pairs of decussate bracts of second order are borne by a short axillary branch. The first pair stands in the transverse plane and is formed by two keeled membranous scales, flattened in the same plane. These are followed by the median pair which is fused in its lower part and forms a bowl-shaped envelopment with two short round lobes. This pair encloses the innermost organs of the bud entirely and may be compared with a true perianth. For now two whorls of organs succeed, which may be called by the names of androecium and gynaecium. The former consists of a series of six, seldom four or five, stamens, which are fused at their base forming a tube, and each one ending at their top in a terminal peltate synange composed of three sporanges. I will not enter into details, whether we have here a whorl of six segments (Hooker, 72), or two lower stamens and four higher ones (Strasburger, 147), or two decussate stamens bearing each three anthers (Lignier et Tison, 89; Mc Nab, 96; Pearson, 112, 113), for this would lead me away from my proper subject. There are no convincing arguments to prefer the second and third interpretation to the first one, which is undoubtedly the simplest statement of the facts.

The gynaecium looks equally simple, and at first sight it would not be supposed, that there is so much difference of opinion about it. A central cone-like mass of tissue, the nucellus, is surrounded by a thin integument, which protrudes into a tube above the nucellar-apex, reaching the level of the tops of the stamens, and ending there in something like a stigma, a flat disk covered with papillae.

It is evident that a superficial contemplator takes this organ to be a pistil with stigma, as it gives entirely the impression of it, but also investigators, who made a more serious study of the flowers of *Welwitschia* have been temped by the external appearance. Mc Nab (96) calls it an ovarium, consisting of two median carpels, where as Lignier et Tison (89) speek of four carpels, of which two are lying in the median plane and two in the transverse one.

The reason why they take these organs for carpels is probably to be found in the fact previously mentioned, that there is a strong resemblance between the gynaecium and a pistil and also in the desire to regard the flower of *Welwitschia* as an angiospermous type. If we could speak here of a pistil, an organ formed by carpellary leaves, the integument would have disappeared entirely, whereas also the nucellus has been reduced to a conform parenchymatous mass of tissue filled up with starch. However, it would be rather strange if an organ as the integument, which has such an important function in the Pteridosperms and Gymnosperms and has attained such a high degree of development, would have suddenly disappeared without leaving a trace behind, whereas a quite different organ like a pistil has come in its place, in a defined angiospermous type, and then even in a functionless organ!

In the fertile ovule of the female flower, a normal integument is undoubtedly present, there being no question about a pistil. And it cannot be accepted that in a functionless organ, representing doubtlessly a reduced state, a higher degree of development should have been acquired, than in the same organ, on the same plant, which really has its function.

The gynaecium in the male flower may be regarded as consisting of a reduced sterile nucellus, invested by an integument originating at its base, and being quite homologous with the integument of the female flower. The stigma-like apex gives certainly rise to some wonderment, but it should be in no case an objection to this interpretation.

Church (48) says of it; „the flattened stigma head, at first sight a new departure, is only an enlarged funnel with closed aperture, the essential and special feature of which consists in the remarkable specialisation of the epidermal cells of the expanded lips. The large rounded papillose cells, the outer walls of which are strongly thickened and pitted, the lumen being almost obliterated in the papillae, are certainly not secretory, but indicate a marked xerophytic structural adaptation, the papillae being restricted to the disk surface, and the edges of the lips, so far as to exactly close over the aperture to the tube". (p. 135.)

Sofar the description of the female and male strobili, the next will be a comparison between both and a determination of the morphological value of the various organs, which has not yet been given in the description.

It is evident that we must try to find a same foundation for both kinds of strobili, but immediately there are a great many difficulties. The best way to make this clear will be in discussing the comparison made by Lignier et Tison (89).

The first cyclus of organs we see are the two small transverse bracts in the male strobilus of the second order and with these, both bracts correspond, which have been found a few times at the base of the female strobilus of the second order. The second whorl, the perianth of the male flower has entirely disappeared in the female one. So far there is not much difficulty in comparing the two(!) but now comes a less acceptable homologization. The staminal series in the male flower should be equivalent to the winged envelopment in the female one. „Le verticille III qui produit l'enveloppe ailée, malgré sa différenciation si spéciale ne peut être assimilé qu'au verticille staminal. Le nombre des faisceaux sortants n'est, il est vrai, pas le même dans les deux cas; mais il ne semble pas douteux que cela provienne d'une adaptation tardive intervenant probablement au cours d'une réduction considérable de l'appareil staminal tout entier" (p. 150). This is still rather acceptable according to Lignier, but now he begins to hesitate himself: „Où les difficultés commencent à devenir sérieuses, c'est dans l'interprétation des parties supérieures de la fleur" (p. 151).

As it is said formerly, Lignier regards the integument of the male flower to be a pistil composed of four carpels and this he supposed to be homologous with the „ovary" of the female flower: „il semble bien que l'enveloppe interne (ovaire) de la fleur femelle corresponde encore à l'enveloppe interne de la fleur mâle et de même pour le nucelle" (p. 151).

In the latter case he compares two organs, which are to my opinion homologous indeed, but as he starts from a wrong supposition, he is obliged to give a rather forced interpretation for the whole. Namely as he has accepted that the „pistil" of the male flower consists of four carpels, he will demonstrate that the thin membrane around the nucellus in the female flower is also built up of four carpels, which doubtlessly represents a true integument: „En somme, nous croyons que dans la fleur femelle, comme dans la fleur mâle, il existe un ovaire uniloculaire formé de quatres carpelles coalescents" (p. 155).

In the preceding part I have already pointed out that it is more reasonable to regard the envelopment, surrounding the nucellus to be an integument both in the male and in the female flower.

There is still one feature worth considering, which, though having little value of its own may probably be important in the connection in which we have treated the integument. Pearson (112) says: „The integument next appears as an equal ring, eventually becomes slightly and unequally lobed in the antero-posterior plane, each lobe being further incised" (p. 284). Lignier (89) has controled this but has not seen a clear lobing in this plane, though present in the tangential one: „une fois, dans une fleur âgée le tube stylaire [1]) semblait se terminer par quatres lobes, deux moins courts dans le plan tangentiel et deux à peine indiqués dans le plan radial" (p. 130).

How far this lobing stands in connection with eventual sutures, as up-to-now we have observed in nearly all gymnospermous seeds is not mentioned and I have not been able myself to examine this, through lach of material of the required age. Therefore we may not attach much value to it, though the presence of lobes may be noticed yet.

There is still the question as to the value of the outer envelopment of the female flower. To homologize this organ with the androecium of the male flower as Lignier does, seems to me rather far-fetched and is not proved by any argument. His only intention is to explain both strobili according to one fundamental plane, but the difficulties we meet with here are too great to accept this without more. Hooker (72) and many others after him call it „perianth", a whorl of sterile bracts, surrounding the fertile ones. Miss Sykes (152) regards it to be an outer integument and has been induced to this, on account of the place of the embryosac. In *Welwitschia* this lies on the same level with the outer envelopment as the embryosac in *Lagenostoma* with regards to the cupule and in the other gymnospermous seeds with regards to the integument. It seems to me that this is not a very strong argumentation, but in the next chapter I will explain my view on this subject.

[1]) Here the integument of the female flower.

CHAPTER III.

Discussion.

In the first place we have seen that the organs which in some cases envelop the macrosporanges of the Isoetales, Lycopodiales and Filicales [1]) are thin membranous outgrowths of the sporophyll. Their function is not yet very important and probably they serve to strengthen the wall of the sporange. A differentiation of the cellular tissue or an other characteristic, indicating a more important task is still absent. Therefore they are distinctly marked off from the testa of the pteridospermous seeds, which immediately show an other feature. The thin membrane investing the sporanges of the Pteridophytes, with no trace of composing units, is replaced here by a solid tissue, several layers thick, provided with a vascular system and exhibiting the indications of a multiple origin in several ways.

On account of this we may accept that the indusia are not homologous with the integuments of the higher developed plants and therefore we may exclude them from a further comparison.

Now we come to the pteridospermous seeds and it will be my intention to compare them in the first place mutually. Afterwards I will discuss the results obtained from my

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[1]) From the Filicales I have described no specimens, because the features exhibited there are well known, and I could not add any new observations.

investigations upon the seeds of the Cycadales, Ginkgoales, Coniferales and Gnetales in connection with the insight we get here about the integumental origin.

The seeds I have described, and which represent the most characteristic specimens of the discovered fossil seeds, are easily to range in a series, suggesting a possible line of evolution. I do not mean to say that they have originated from an other, but that the tendency of investing the macrosporange, has developed in one seed a higher and more differentiated and specialized organ than in the other. So that the supposition arises that the highest developed organ has not been formed all at once, but has passed through the lower stages.

The most primitive stage is probably represented by *Physostoma*. The testa clearly indicates an origin from several segments, which are entirely free at the top, and though connate at their base, they also show there distinctly their original separation. A differentiation of the tissue has not yet taken place, but an attempt for more protection has been disclosed by the formation of a thick hair covering at the outerside.

Lagenostoma and *Sphaerostoma* are higher developed. In both the units, composing the integument are more closely fused and are recognizable only by the ring of loculi around the micropyle, and the vascular bundles, ending in them. A cupule is present in both seeds and probably in connection herewith the differentiation of the testal-tissue is not much advanced. In *Lagenostoma* a palisade layer is present, corresponding with the hypoderma in *Sphaerostoma*, which consists of a layer of sclerotic cells. These layers are apparently the first indications of the later sclerotesta.

Finely *Trigonocarpus* and *Mitrospermum* have reached the highest degree amongst the Pteridospermae. In the integument of both there is a much slighter markation of the units. Traces of them are principally pointed out by the main-ribs, and as in *Trigonocarpus* by three small sutures at the micropyle. The testa is composed of the three characteristic layers, which appear in nearly all Gymnospermous seeds and are here already present in the most differentiated condition.

Externally a very striking difference between *Trigonocarpus* and *Mitrospermum* is the round shape of the former in transverse sections, contrary to the flat shape of the latter seed. Both types the threemeric and the twomeric occur among the gymnospermous seeds.

Though the number of integumental units is not a constant one, and there is always a good deal of fluctuation in it, it varies around a middle-worth, characteristic for each genus. It is suggested by Oliver (104 p. 102) that a great number of units or slips represents a more primitive stage, and he composes a series of them, in which *Physostoma* with about ten tentacles stands highest then coming *Lagenostoma* with nine, *Sphaerostoma* with eight a. s. o. Amongst the Trigonocarpeae this variability seems to be less fluctuant according to Salisbury (126 p. 71).

These series show us that there is a gradual transition between a primitive stage of the testa in which it is composed of a great number of units to that one of their entirely fusion with only slight indications of their multiple origin.

The ovules are always borne on leaves, slightly different from the ordinary trophophylls and bearing resemblance to the fertile fernleaves. Strobili are not formed.

The value we may attribute to the cupule of *Lagenostoma* and *Sphaerostoma* is of great importance. And though this is still uncertain, it may be quite possible for the present, that those cupules are formed by the pinnae of the sporophyll bent around the integument. When in

Sphaerostoma a plane of dehiscence is formed between cupule and integument, preparing the shedding of the seed, and in *Gnetopsis* (135) a similar envelopment encloses two to four seeds [1]), this may be a proof for the supposition that the cupule is not homologous with an outer integument. An integument is always a permanent investment around the nucellus, therefore the cupule may be regarded somewhat as a modified sporophyll or a part of it. The protecting influence, of the cupule, during the connection of the seed to the motherplant is well pronounced by the lack of differentiation of the integument.

The free position of the nucellus within the testa is a primitive state, mostly the case in the young ovules also. By a subsequent growth in the chalazal region, the fusion of nucellus and integument is accomplished. This coherence in the fossil seeds is difficult to control, as the soft tissues of the nucellus have loosened and are collapsed. In all cases the top remains free and then forms the lagenostome or pollenchamber.

A real micropylar tube is not yet formed in *Physostoma*, because the tentacles have not closed and fused. In *Lagenostoma* and *Sphaerostoma* also it is still less developed, the nucellar-apex being on the same level with the surrounding lobes of the canopy. At first in *Trigonocarpus* and *Mitrospermum* the tube becomes longer and also in this respect we get more the gymnospermous type.

A second group of plants, to which we now have to pay attention are the Cycads. Amongst them the genus *Cycas* is distinctly characterized as concerns the place and the structure of the ovule. A single sporophyll is still present here, whereas in the other genera a strobilus

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[1]) The seed of *Gnetopsis* I have not described, because the mentioned feature excepted, it is not much different from *Lagenostoma* and *Sphaerostoma*.

occurs. The ovule is bilateral symmetrical and shows no trace of a multiple origin of the integument, contrary to that of *Macrozamia*, *Ceratozamia*, *Encephalartos* a.o. where distinct slips or lobes on the sclerotesta around the micropyle are to be seen, the number of which may be different variing from 7—16. The ribs on the stony coat correspond with the grooves between the lobes in the apical region, but they are not always very distinct and often secondary ribs occur between the principal ones as is the case in *Trigonocarpus*. They correspond with the vascular bundles running in close proximity to them in the sarcotesta. Though we may not attribute too much significance to the ribs and vascular bundles alone, they are of much value, when they correspond with lobes around the micropyle.

Here the testa is undoubtedly composed of units and from the pteridospermous seeds, *Lagenostoma* represents the type to which the Cycadean seeds resemble most. A further comparison, however, is not to be made.

In what connection *Cycas* stands to the other genera is difficult to say, and whether its ovule represents a reduced structure, the two vascular bundles in the sarcotesta being the remnants of an originally composed system, according to Miss Stopes (145), is not to be determined. Her comparison of the ovules of *Cycas* with *Lagenostoma*, from which she concludes that the integument of the Cycadean ovules should be of double origin is rather risky. In the first place *Cycas* does not exhibit the most characteristic type of Cycadean ovules, so that it should be better to take for example *Macrozamia*, which resembles *Lagenostoma* most. And secondly she bases her theory entirely on the probably accidental similarity of the vascular system in cupule and testa of *Lagenostoma* on one hand, and that in sarcotesta and endotesta of *Cycas* on the other. She concludes from this that the sarcotesta of

Cycas should be homologous with the cupule of *Lagenostoma*, and that the testa of the Cycads should be composed of two originally free layers accordingly. And as the sarcotesta of *Cycas* belongs to a true integument she calls the cupule of *Lagenostoma* an outer integument. We have seen that the cupule of *Lagenostoma* does not appear to be an integument, but as long as we do not know this accurately, we may certainly not homologize it with an organ, that is much higher specialized and give it the same name. Besides, the differentiation into the three layers, occurring in those organs too, which have arisen undoubtedly from a single whorl of units, as in *Trigonocarpus*, *Ginkgo* a. o., there is no reason to speak of a double origin, only on account of a probable resemblance in orientation of the vascular bundles.

Salisbury (127) has already published about the relation between *Ginkgo* and *Trigonocarpus*. Here I may add a point of apparent resemblance, which Salisbury did not notice, viz. the clearly visible sutures at the places of the ribs in the apical region in a young stage of development of the ovule of *Ginkgo* (fig. 6). These sutures support the view of possible connection between the seeds of *Ginkgo* and *Trigonocarpus*, which had been supposed by the great frequention of three-angular seeds, investigated by Affourtit and La Rivière (1).

This feature is also exhibited more or less in all the other gymnospermous seeds. The occurrence of two, three, four or five ribs on the stony coat is a very common thing. For *Cupressus* (140), *Pinus* (64) and *Ephedra* (51) it has been observed that the integument originates as two separate papillae between which a third one, the nucellus. Undoubtedly it occurs also that the integument is formed of three or more projections, but till now no great attention has been paid to it, otherwise it would not have been possible that hardly anywhere the great number of triangular seeds has been mentioned.

Sometimes as is the case in *Callitris* the layers in the integument have not been differentiated, probably in connection with adaptations to the dispersion of the seed. Here the testa is dry and membranous, whereas the nucellar tissue is soft and well developed, in *Thuya*, however, having a differentiated testa, the nucellus on the other hand becomes dry and papery. Thus it is obvious that the differentiation of the integument has a clearly physiological meaning, it is the leading tendency amonst all seeds. The dense haircovering in *Physostoma* forms the first indication of a better enclosure and protection of the germinating macrospore. The cupules of *Lagenostoma* and *Sphaerostoma* accomplish the function elsewhere performed by the differentiation of a sarcotesta, which is also the case with the cupules of *Torreya* and *Gnetum*.

The arillus of *Taxus* is homologous to all appearances with the cupule of *Torreya*. The first is less developed in comparison to the latter and in connection herewith the testa in *Taxus* is still differentiated in the three layers, whilst in *Torreya* the cupule has performed the function of the sarcotesta, an outer fleshy layer not being formed by the integument. In both cases the megasporophyll is not to be observed, whereas in *Cephalotaxus*, having no cupule, it is very distinct. Therefore the suggestion may be ventured that both enveloping organs have been formed by two decussate sporophylls, each bearing originally one ovule. One of the ovules has been reduced and suppressed, so that the other has become terminal, invested by the two fusing sporophylls.

The two opposite vascular bundles in the cupule of *Torreya* (having a normal orientation in contrast with those in the sarcotesta of *Cephalotaxus*) and the case I found in *Taxus*, in which the aril was divided into two lobes, may strengthen this view. In the normal strobilus of *Ephedra* we may observe the same thing; generally there are two uppermost bracts fused together for the greater part and still bearing one ovule each, but often it occurs that the latter are fused with their integuments and finally it is found that only one ovule, then being terminal, remained.

In *Gnetum* also, no trace of a megasporophyll can be observed but a thick cupule envelops the terminal ovule. It is most probable that this outer investment represents the two fused upper sporophylls, from which only one ovule has developed.

In *Welwitschia* we have the same thing, here also a conspicuous megasporophyll is absent. But it seems to me most acceptable to regard the winged envelopment in the female flower as consisting of two fused sporophylls. They stand in the median plane and alternate with the transverse scales, which are observed in few cases. Also Strasburger (147) and Eichler (64) were of the opinion that the winged membrane was composed of two carpels, but according to them, they should stand in the transverse plane.

On account herewith the megastrobilus of *Gnetum* and that of *Welwitschia* are compound. The ovules of *Ephedra* and *Gnetum* are provided with two integuments, whereas the gynaecium of *Welwitschia* in the male as well as in the female strobilus consists of a nucellus enveloped by one integument.

Now I have come to the solution of the questions put forth in the first chapter, and the first thing to be done is to determine, what we may understand by the name „integument." As the result of my investigation the envelopment around the nucellus always seems to consist of units. The inner investment of *Lagenostoma* and *Sphaerostoma* of *Taxus, Torreya, Podocarpus* and *Wel-*

witschia and the entire coat of *Physostoma*, *Trigonocarpus*, *Mitrospermum*, *Bennettites*, of the Cycadean seeds, of *Ginkgo*, and of the seeds of the *Pinàceae* and *Cupressaceae* are homologous organs, always showing traces of units. These organs only (about the integuments of *Ephedra* and *Gnetum* I will speak presently) I should like to entitle with the name integument.

We may not yet fully determine the value of the cupule of *Lagenostoma* and *Sphaerostoma*, but it is most probable that they represent entire sporophylls, at least fused pinnae of it, like the disk of *Bennettites* and the arillus of *Ginkgo*. The cupule of *Taxus* and *Torreya*, as well as the perianth of *Gnetum* and *Welwitschia* consist of two fused sporophylls as is the case in *Ephedra*. Finally the epimatium of *Podocarpus* is an entirely new formation without any connecting link in other fructifications. Perhaps we find a homologous case in the outgrowth of the sporophyll at the base of the ovule in some Cycads. But as long as no better explanation can be given, the name epimatium „Excreszenz des Carpides" (117 p. 16), is the best term we can use.

We have seen that in the ovules of the Taxads the endotesta is loosened from the stony coat in its upper part, and there forms a distinct layer on the nucellus. This may be a transitional stage to the case represented by *Ephedra* and *Gnetum*, where two integuments exsist. The outer integument consists of a sarcotesta and a stony layer, whereas the inner one is very thin and may be compared with the endotesta in other seeds.

It always has been supposed that amongst the Gnetales at once a second integument has appeared which has been persistent in the Angiosperms. But now there has become a closer relation between the ovules with one- and those with two integuments, on account of this connecting link, the ovules of the Taxads. However, we meet here with a great difficully, if we will explain the origin of this second integument. Three ways are possible, having led to this double structure.

A first explanation, which would be most acceptable, is the formation of one integument by the fusion of an outer and an inner one. Miss Stopes has put forwards this theory, as I already mentioned, when she called the cupule of *Lagenostoma* an outer integument, and the testa of the Cycads a double one. The objections to be made against her theory I have dissussed, but now I will add an other one, namely the fact, that if an organ once has been reduced or has disappeared it afterwards never comes back again under the same circumstances and with the same function. So that if two originally free whorls of integumental-units have fused, they lateron do not return to this condition by any means. Unless some fossil seeds become discovered, in which two distinctly separate integuments can be distinguished, we have to accept that the formation of a second envelopment is a proces of more recent date.

In the second place it may be possible that a second whorl of organs is formed around the nucellus in the ancestors of the Taxads and Gnetales. Both cycli are fused for the greater part amongst the Taxads, whereas they have remained free in *Ephedra* and *Gnetum*. *Welwitschia* with only one integument stands entirely apart, here the formation of a second integument has never taken place or it has again disappeared.

The critic of this opinion is especially that nothing is known of these supposed ancestors, and no indications point in this direction. Besides it should be rather accidental if the organs of both cycli, always originated in the same number as is the case in *Ephedra* and *Gnetum*.

Finely a third interpretation is possible, which, however, is not without objection either. Both integuments could have originated by a division of a single one. The separation between the endotesta en sclerotesta, the first indications of which are observed amongst the Taxads, is accomplished in *Ephedra* and *Gnetum*, but has not taken place in *Welwitschia*. Though at first sight this seems a very simple explanation, it is still rather risky, as a regular splitting of one homogenous organ into two is a very uncommon feature.

A tangential dédoublement, which happens with the stamina of some of the *Rosaceae*, also is observed sometimes in the petals of Crucifers (Velenovský, 165). Though it is possible that here we have the same phenomenon, the question about the origin of the second integument is not to be solved entirely, and for the present we have to wait till perhaps more data are obtained from the investigations in palaeobotany.

When the sporophylls enclose the ovule entirely and take over the function which has been performed by the sarcotesta and sclerotesta, the differentiation in the integument may be left out. This case we find in the Angiosperms, where both integuments are thin and indifferentiated, functioning as a endotesta. Owing to this an investigation upon a multiple origin in the ovules of the Angiosperms is encluded, because we have no starting-point here through the absence of layers as a sclerotesta on which ribs and sutures are most distincly to be seen. Also slips at the micropyle are wanting. It seems to me, however, that the integument of the Angiosperms is homologous yet with that of the Gymnosperms, though we have no true demonstration. The probably connecting links as the inner integument of *Ephedra* and *Gnetum* and that of *Welwitschia* which have exhibited an angiospermous type give this opinion a base of surety. On the other hand the ovule of *Myrica Gale* shows a feature resembling that of the pteridospermous seeds, the nucellus stands free within a single integument and the latter is provided with a vascular system. On account of this Kershaw (79) made a comparison between the ovules of *Myrica Gale* and *Trigonocarpus*. Though this may be too far-fetched, it proves that there are indications, which make the homology of the integuments possible.

For the present it has not yet been determined what the exact value of the integumental-units is. The synangial theory, mentioned in the introduction gives a possibility which is not to be rejected, but not to be wholly accepted either. More convincing proofs must be recorded than only a few resemblances as those between *Lagenostoma* and *Telangium*, observed by Miss Benson (15), and before her by Lang (84) between the micro- and mega-sporanges of *Stangeria*. I shall only mention some cases which may support this theory.

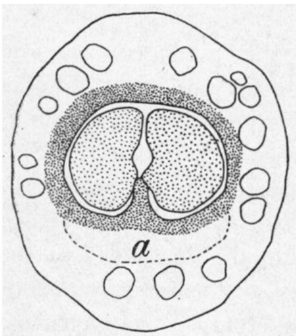

Fig. 12. *Ginkgo biloba;* two nucelli within one integument, sarcotesta with mucilage canals, sclerotesta dotted strongest. *a*. lysigen cavity.

It occurs occasionally that two nucelli are present in one integument, which is observed for *Thuya* (49, p. 210), and which I have found twice in *Ginkgo* (fig. 12). Here it is possible that more sporanges of the original sorus, in casu two, have developed, and the others, remaining sterile have formed the integument. This is not a convincing argument at all, but this may be supplied, when more of these cases are published.

In order to solve in short the questions put in the beginning, my conclusions are as follows:

1. The integuments of the Pteridosperms and Gym-

nosperms are homologous and most probably also with those of the Angiosperms.

2. The integuments are not homologous with the indusia of the Ferns and Lycopods, and the first name may not be used for these organs.

3. The integument is originally composed of units.

4. The value of the units is not yet quite certain.

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