DEVELOPMENT OF OVULE AND EMBRYO SAC OF COCOS NUCIFERA[1]

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(WITH THIRTEEN FIGURES)

Introduction

It seems strange that a plant so interesting and economically important as the coco palm has received so little attention morphologically. Our knowledge of the morphology is fragmentary and limited. The agronomy of the coco palm has been studied extensively; and lately the development of the inflorescence, the female flower, and the stony layer has been investigated (15). The present paper is intended to give only a description of the development of the ovule and the embryo sac at the time of fertilization, and later it is hoped to give a full account of fertilization and the development of the endosperm and embryo.

While, as might be expected, the results of this study do not show wide deviation from the usual series of events in monocotyledons, they have value in indicating the extent of variation within a given order. RADERMACHER (18), studying *Nipa fruticans*, found that the archesporial cell functions directly as the embryo sac mother cell, which divides into a "dyade." The chalazal cell enlarges and becomes the macrospore of the sac. The mature embryo sac possesses eight nuclei. This writer also investigated *Actinophloeus macarthurii* (*Ptychosperma macarthurii* H. Wendl.), and although his series is incomplete, found that the embryo sac mother cell is deep seated, with eight nuclei.

BAUCH (1) observed the 2-nucleate embryo sac of *Phoenix* with three complete degenerated cells as remains of the tetrad cells. According to this investigator *Licuala* has an 8-nucleate embryo sac, and *Sabal* and *Zalacca* possess a widened one. The development of the embryo sac of *Dypsis*, which is 8-nucleate, is similar to that of

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[1] College of Agriculture, University of the Philippines, Experiment Station Contribution, no. 459.

Calyptrocalyx. He also saw the embryo sac of *Heterospathe. Nephrosperma* and *Verschaffeltia* have antipodals which remain long in the sac as an inward prominence of the nucellus. *Ptychococcus* and *Areca* show the remains of the tetrads in their embryo sacs, the former possessing only two, the latter three. BAUCH[1] states:

> The embryo sac mother cell is formed in the first and second row of cells of the nucellus. There may be also formed two embryo sac mother cells, but only one develops, the other degenerates. In *Cocos*, also, the remnants of the tetrahedral cells, which are located near the micropyle, are evident. It is therefore apparent that the cell which is near the chalazal develops into the primary embryo sac mother cell.

So far as the writers know, no work on the ovule or embryo sac of *Cocos nucifera*, except that of BAUCH cited by RADERMACHER (18), is on record.

Material and methods

The material used in this study was gathered between March and April, 1925, from twenty trees growing in the Bacomo Coconut Plantation of the College of Agriculture, University of the Philippines. Two of the trees were killed, and all unopened spadices in which the female flowers could be differentiated by the unaided eye were fixed. Twelve inflorescences were selected, and their dates of opening carefully noted. Inflorescences were gathered at intervals of 3, 4, 6, 9, 12, 15, 19, and 22 days respectively after they opened, until the stigmas were exposed. All female flowers from the inflorescences were then fixed. Slabs were cut from the two sides of the younger pistils and from the four sides of the older ones, and then fixed *in toto* with their perianth segments on or removed.

Only formo-aceto-alcohol (4) and formo-alcohol were used to kill and fix. After fixing the material was washed in 70 per cent alcohol, dehydrated by passing through successive grades of alcohol, dealcoholized in several ascending series of xylols, imbedded in paraffin, and cut with the Spencer rotary microtome into sections 5–7 μ. The appearance of large vacuoles in the sac and the presence of tannin idioblasts in the pericarp made cutting the material rather difficult. Flemming's triple stain was used in some cases. Haidenhain's iron-alum with Orange Gold dissolved in clove oil as background was used throughout, and proved to be very satisfactory.

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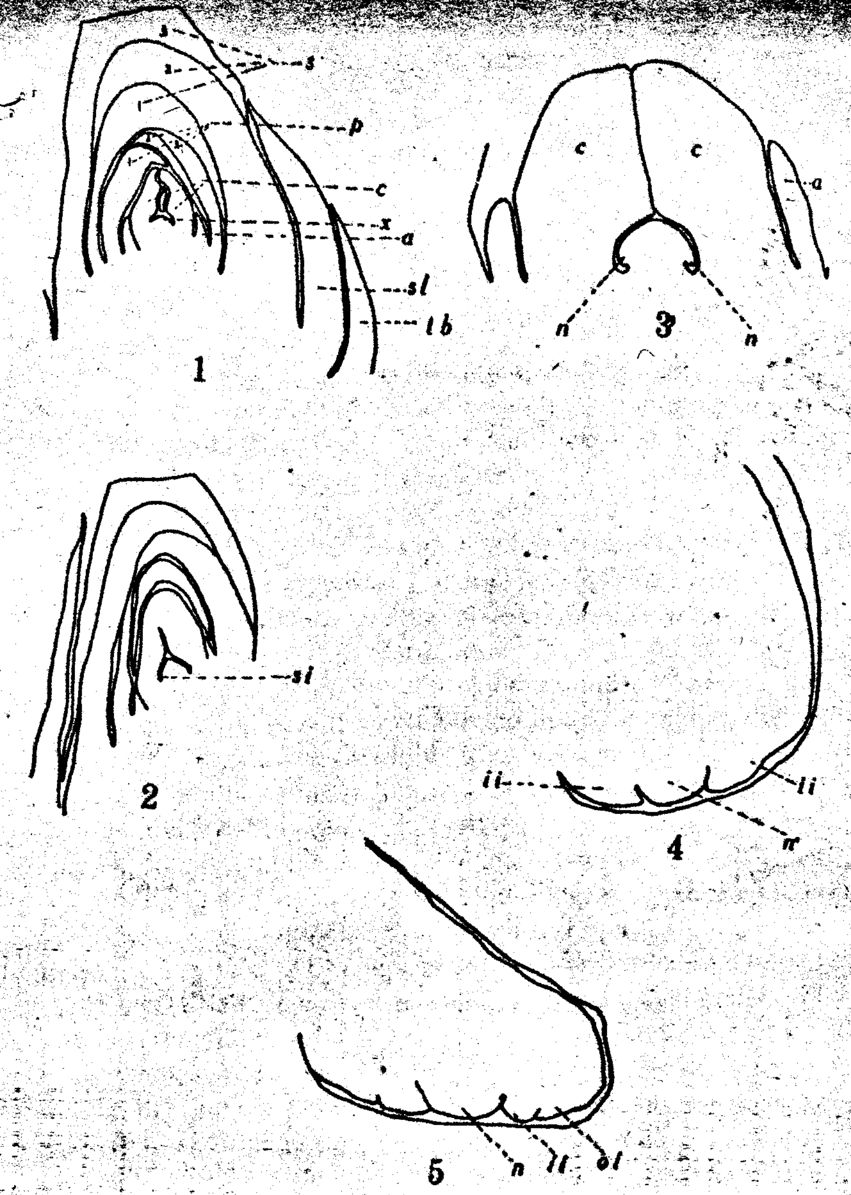
[1] Cited by RADERMACHER; original article of BAUCH not procurable.

Ovule

The development of the spadix and the floral segments of the female flower has been investigated (15). The centripetal appearance of the floral organs is as follows: (1) scaly leaves or "braceteoles," (2) sepals, (3) petals, (4) aril, and (5) carpels. When all the floral envelops and carpel walls have been formed and differentiated, the main axis of the flower starts as a papilla and commences to enlarge, gradually becoming prominent at the basal portion of the ovarial cavity (fig. 1). This protuberance consists of an epidermal layer of cells, most of which are squarish to rectangular, with their long axes tangential to the periphery. The hypodermal cells are isodiametric, filled with plenty of protoplasm and large nuclei. Their growth keeps pace with that of the carpel walls. As the main axis enlarges, the epidermal and hypodermal cells divide and elongate periclinally, and their cytoplasmic contents become less thick than those at the side. This gives the axis a pyramidal appearance (fig. 2). Simultaneously with the elongation of the cells at the apex, the basal cells at the sides (*s*) divide periclinally at first, and division rather than elongation is their first activity. By repeated periclinal divisions of the cells at the sides, and radial elongation and enlargement of the cells at the apex of the axis of the flower, the basal lateral sides are pushed into the three loculi of the carpel walls. These protuberances, which at first are slight, constitute the nucellus (fig. 3*n*) of the ovules. By one-sided growth each primordium becomes bent toward the base of the ovary, developing into the anatropous ovules. It is interesting to note, however, that in the coco palm the usual development of the anatropous ovules as shown in *Lilium philaselphicum* (7) is not closely followed. The nucellus appears first as a few-celled papilla, with projections from which the integuments develop (figs. 4, 5).

The hypodermal cells of the nucellus then divide periclinally and anticlinally. The activity of that mass of tissue is responsible for the enlargement of the nucellus, rather than the epidermal. The epidermal cells remain squarish and become comparatively smaller than the hypodermal cells, which in their juvenile stages are nearly identical in size. Anticlinal division of the epidermal cells enables it to keep pace with the increasing nucellar tissue.

The integuments do not begin to appear until after the inflorescence has attained a maximum circumference of 15–18 cm. (meas-



Figs. 1–5.*—Fig. 1, median longitudinal section of female flower showing tertiary bract (*tb*), scaly leaves or "bracteoles" (*sl*), sepals (*s*), petals (*p*), aril (*a*), carpels (*c*), and floral axis (*x*); ×11.5. Fig. 2, median longitudinal section of older flower showing pyramidal appearance of floral axis; *si*, sides of axis where nucellus of ovule is developed; ×11.5. Fig. 3, median longitudinal section of ovary showing beginnings of nucellus (*n*) of ovules, within carpel walls (*c*); ×53. Fig. 4, longitudinal section of anatropous ovule with inner integument (*ii*) already developed; ×235. Fig. 5, longitudinal section of much older ovule with two integuments, inner (*ii*) and outer (*oi*), appearance of latter being belated; ×235.

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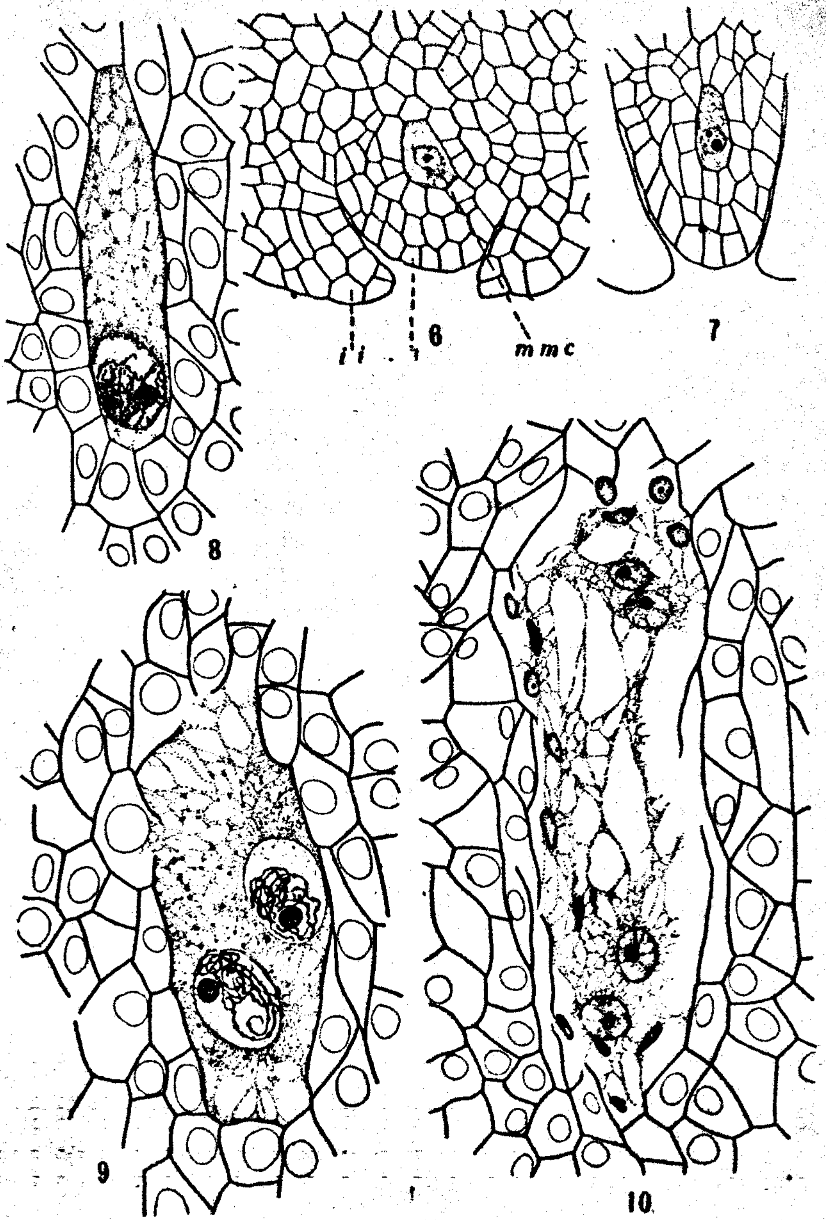
* All drawings were made with the Spencer microscope, Bausch and Lomb lucida, bar length 110, and the mirror at an angle of 55°.

ured with the inner spathe still attached). The inner integument (fig. 4) is the first to develop, followed by the outer (fig. 5).

Embryo sac

The ovule attains a considerable size, with its integuments fully differentiated before the archesporial cell becomes evident. The archesporial cell becomes the megaspore mother cell, and enters synapsis after the two integuments have long been evident. At first the megaspore mother cell is apparently undifferentiated from the surrounding cells, but soon it becomes grumous and is then readily distinguishable (figs. 6, 7). It can easily be recognized from the rest of the nucellar tissue by its size and great staining power. The presence of a large nucleus and its richness in cytoplasm make the megaspore mother cell more prominent. The megaspore mother cell is apparent after the inflorescence has emerged from the outer spathe, and while still enveloped by the inner spathe. It is more or less squarish, with the nucleus at the center of the embryo sac (fig. 6) to begin with, but soon elongates with its micropylar porti[illegible] The mother cell usually appears at the third layer [illegible] of the nucellar tip, but may sometimes be deep seated at the fourth or fifth layer. As the cell enlarges and elongates, there seems to be a definite migration of the nucleus to the micropylar end. Vacuolation of the one-celled embryo sac becomes apparent and progresses as the sac enlarges. The cytoplasm is denser toward the [illegible] portion of the cell and vacuolated at the chalazal region. The [illegible] have failed to find more than one archesporial cell developing, but BAUCH maintains that he found two, only one of which became functional.

The archesporial cell elongates and increases in size, always maintaining the bulbous and bulging appearance, wider at the micropylar end, with the chalazal end somewhat narrow. More granular bodies seem to accompany the enlargement of the nucleus. The vacuoles enlarge in the nucleus, and granular bodies appear in the network of protoplasm. Later, within the nuclear membrane a network of fine dotted threads is partially meshed by granular substance. The first stage which can be identified as indicating approaching division is the slender spireme (fig. 8). The threads become thicker and their dots larger, the nucleolus still remaining prominent. Before



FIGS. 6–10.—Fig. 6, longitudinal section of ovule with archesporial cell already differentiated, which functions as megaspore mother cell (*mmc*); ×540. Fig. 7, megaspore mother cell beginning to elongate; ×540. Fig. 8, megaspore mother cell at synaptic stage; ×890. Fig. 9, dinucleate stage of embryo sac; daughter nuclei at synaptic stage; note absorption of nucellar tissue beginning at chalazal end; ×890. Fig. 10, quadrinucleate stage of embryo sac, two nuclei at micropylar end and two at chalazal end; note destruction of nucellar tissue; ×890.

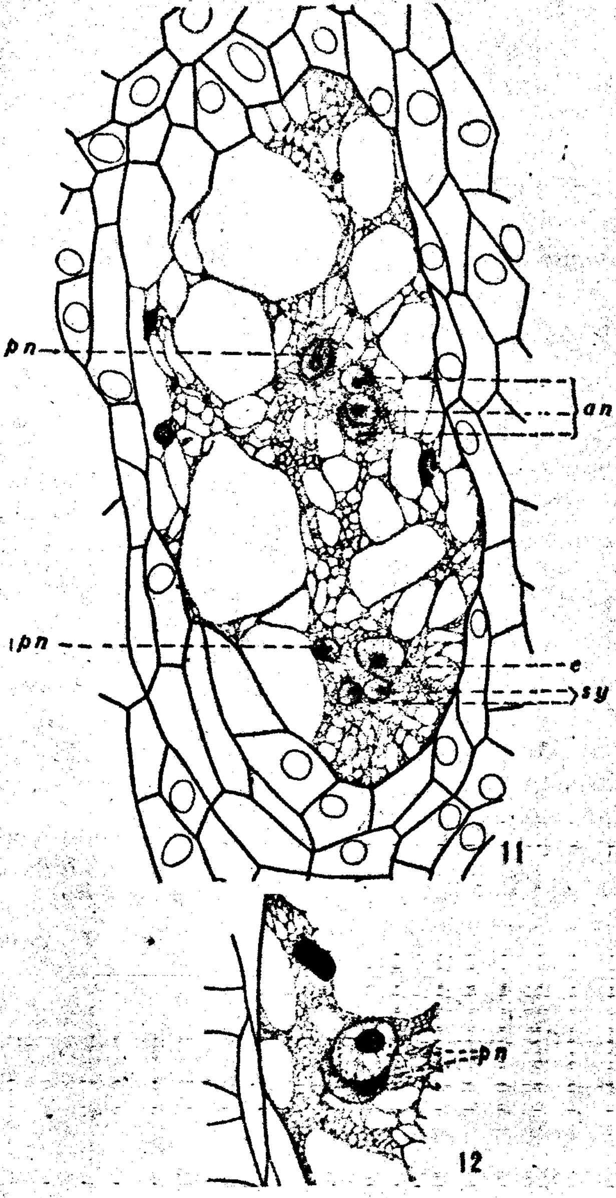
finally passing into the contracted state, the ribbon just described begins to close round the nucleolus. The nucleus now enters the period of synapsis, in which it remains for some time.

The nucleus of the megaspore mother cell of the embryo sac next divides into two, more or less unequal in size, without wall formation (fig. 9). This takes place before the emergence of the inflorescence from the envelope of the inner spathe. In the coco palm the formation of the tapetal cell and the four megaspores is eliminated, the two daughter nuclei lying side by side. They are vacuolated, and in the early synaptic stage of division. More granules are present in the cytoplasm of the sac. At this stage the sac shows signs of disintegration and absorption of the nucellar cells, which begins at the chalazal region (figs. 9, 10). Since the formation of the tetrad is eliminated, this first division of the megaspore mother cell must be heterotypic in nature. In the first division of the megaspore mother cell it was not possible to count the number of chromosomes.

At the binucleate stage of the sac no polarity is evident. Vacuolation begins at the micropylar and chalazal ends, and the daughter nuclei are at the center of the sac. Both chalazal nucleus and micropylar nucleus are commonly similar in shape and age, although the chalazal nucleus seems more advanced in development (fig. 9).

At the quadrinucleate stage of the sac polarity is in full display (fig. 10). The four daughter nuclei are at the ends of the sac, two at the micropylar and two at the chalazal end, the micropylar nuclei being larger than the chalazal. The two chalazal nuclei are unlike in size, the one near the center of the sac being slightly larger. The surrounding nucellar cells undergo disintegration, and their nuclei are freely liberated in the sac. Vacuoles are larger at the center of the sac, and cytoplasm thickest at the two ends. The nuclei apparently rest at this period.

When the sac reaches the octonucleate stage, it seems that the enlargement of the sac has gone far enough. All the chalazal cells show great depletion, almost to the micropylar end (fig. 11). This therefore makes the nuclei appear to be at the center of the sac. The micropylar group consists of three nuclei of the same size, one of which is the polar nucleus (*pn*). The larger one is the egg (*e*); the two similar ones are the synergids (*sy*). The chalazal group consists of



FIGS. 11, 12.—Fig. 11, octonucleate stage of embryo sac before final orientation of nuclei: *e*, egg; *sy*, synergids; *pn*, polar nuclei; *an*, antipodals; ×890. Fig. 12, fusion of polar nuclei; ×1060.

three congregated antipodals (*an*) and the elongated polar nucleus. It seems evident that the polar nucleus from the chalazal region is much larger than that from the micropylar region. The antipodals migrate to the chalazal pole, and before the fusion of the polar nuclei begin to disintegrate. The union of the two polar nuclei (fig. 12) is accomplished by the motility of the two nuclei approaching each other, and meeting and coalescing near the center of the embryo sac. The polar nucleus of the chalazal region apparently is at rest and the micropylar one appears more motile. This same condition occurs in *Luzula*, *Alisma*, *Carex*, *Triglochin*, *Orchis*, *Ornithogalum*, and *Nothiscordum* (22). Coalescence takes place before fertilization and before the pollen tube tip has reached the embryo sac.

At the final orientation of the component parts of the sac, it tapers at both ends and becomes more enlarged at the middle. This is not a general rule, however, as other shapes may also be round, depending on the amount of absorption and destruction of the nucellar tissues by the developing sac. Fig. 13 shows a mature embryo sac, at the chalazal end of which are the three antipodals, which are faintly recognizable. They are surrounded by thick protoplasm, and connection with the rest of the contents of the sac seems lost.

At the micropylar end is the egg apparatus, which is derived from the nuclei at the micropylar group. Prior to the migration of the polar nucleus, the egg is already differentiated from the two synergids in size (fig. 11). It becomes greatly vacuolated and enlarged, and is inserted somewhat lower down in the walls of the embryo sac.

A complete *Cocos* embryo sac is pictured in fig. 13. The antipodals (*an*) have gone into progressive degeneration. The endosperm nucleus (*en*) has assumed a central position, with a massive nucleolus, and with a spherical form. The egg apparatus, consisting of a very prominent egg (*e*) and two synergids (*sy*), has approached maturity. At this stage the synergids begin to show signs of degeneration.

In the development of the ovule and embryo sac of *Cocos nucifera* much time is involved The internal growth of the axis of the flower must have begun long before the inflorescence has emerged from the outer spathe. The ovules differentiate and attain their natural position when the inflorescence has escaped from the outer spathe and

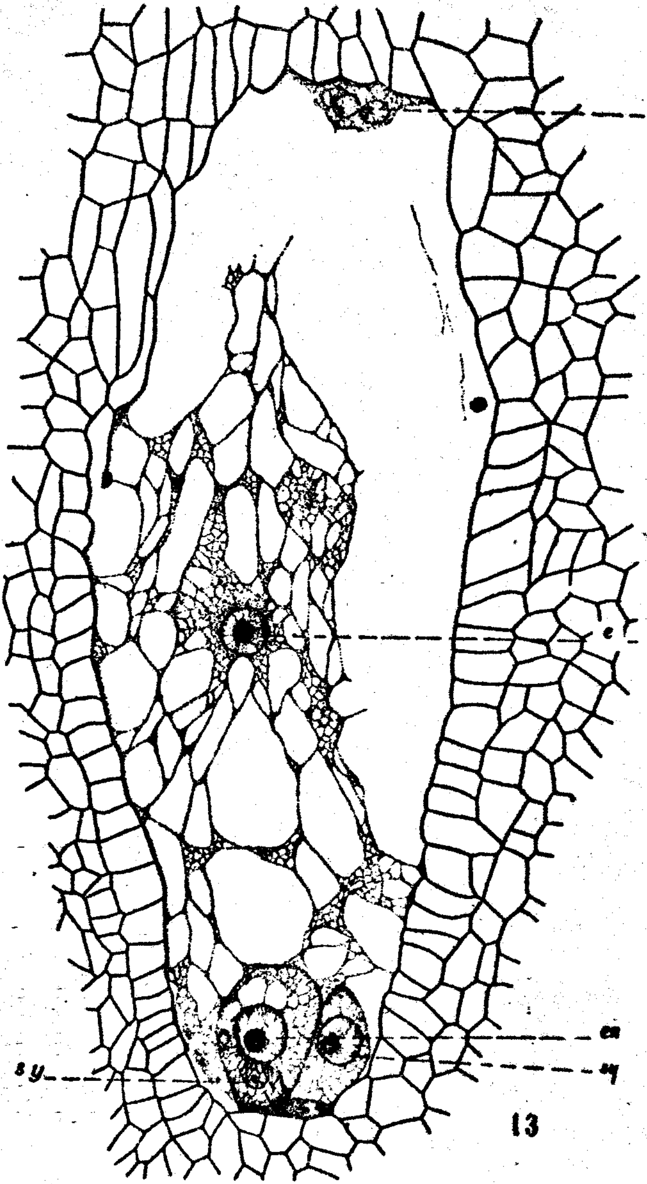


FIG. 13.—Mature embryo sac showing antipodals (*an*) at process of degeneration, endosperm nucleus (*en*) already formed, and synergids (*sy*) of egg apparatus at stage of degeneration; ×540.

made appearance from the axil of the clasping petiole. At this time the integuments are already formed.

INFLORESCENCE	MEGASPORANGIUM AND OOGENESIS
Inflorescence still inside of petiole, with outer spathe and inner spathe; 52 cm. long, and 15.3 cm. circumference*	Axil of the pistil already differentiated, bulging and initiation of ovules
Inflorescence out of outer spathe; circumference 14.3 cm.	Anatropous situation of ovules prominent
Inflorescence out of outer spathe; circumference 15.8 cm.	Outer and inner integuments formed
Inflorescence out of outer spathe; length 40 cm., circumference 18 cm.	Archesporial cell differentiated
	First division of megaspore mother cell
Inflorescence out of outer spathe; length 66.5 cm., circumference 27.2 cm.	Second division of megaspore mother cell
	Third division of megaspore mother cell
Just after opening of inflorescence	Fusion of polar nuclei and disintegration of antipodals
Emergence of stigmas (in receptive condition)	Disappearance of synergids and enlargement of egg and endosperm nucleus

*Length measured from base of lowest rachilla to tip of spathe; circumference based at largest portion of spadix.

Discussion

It has been the constant attempt of botanists to unravel, by a comparative study of the development of their gametophytes, that complicated fabric of phylogenetic relationships existing among plants. Unless a thorough study of nearly all the species known is carried out, no fair comparison can be made. It must be understood, however, that it is not within the scope of this investigation to offer any solution of this question.

The female flower arises as an emergence in the axil of the tertiary bract of the rachilla. At the axil of the tertiary bract and the floral cone, small papillate protrusions appear, which elongate, bend, and cover the juvenile flower. As soon as these scale leaves develop, the three sepals appear simultaneously from the basal portion of the flower primordium, one overlapping the other at the apex. The petals, alternating with the sepals, next emerge simultaneously, first as rudimentary papillae, and soon differentiating like the sepals. The next to the last structure to emerge is the aril. The carpel walls are the last to develop.

The ovules may be considered cauline, as they arise from the central axis of the flower. In *Balanophora* and *Loranthus* (7) several writers found a similar situation, where a structure (or "mamelon") arises at the bottom of each sporangial chamber and grows until it completely fills it. *Rhopalocnemis phalloides* exhibits similar growth of the floral axis, especially before the appearance of the archesporium. The floral axis of *Cocos nucifera* enlarges, and toward each loculus is produced a papilla which serves as nucellus of the ovule. In other words, the nucellus of the nascent ovule is directed toward the receptacle. This case, where the usual development of the anatropous ovule is not followed, is an exception to the rule. The integuments are two, inner and outer.

Only one cell constitutes the archesporium, which according to our observation functions as a megaspore mother cell, and develops into the sac direct. According to RADERMACHER, *Nipa fruticans* also possesses an archesporium of one cell.

The cells of the archesporium, whether they be one or more, may by transverse division give rise to a primary parietal cell and a primary sporogenous cell. In *Cocos*, however, the archesporium, which is one-celled, never cuts any parietal cell. COULTER and CHAMBERLAIN (7) quote that *Avena fatua*, *Allium*, *Hemerocallis*, *Lilium*, *Erythronium*, *Tricyrtis*, *Sisyrinchium iridifolium*, *Gymnadenia conopsea*, *Orchis pallens*, and also *Commelina stricta* and *Iris stylosa* (10) do not develop any parietal cell. *Canna indica* (10) sometimes develops a parietal cell and sometimes does not.

The archesporial cell functions directly as the megaspore mother cell similar to *Lilium*, *Fritillaria*, *Funkia*, *Tulipa*, *Convallaria* (23), and *Erythronium* (19). Among the primitive aquatic plants, COULTER and CHAMBERLAIN give *Typha* and *Alisma* as exhibiting similar development of the megaspore mother cell. HALL (11) cites *Limnocharis* as possessing parallel development of the megaspore mother cell. CALDWELL (3) reports that the mother cell does not divide in *Lemna*. Among the higher families *Narcissus* (10) and *Costus* (12) possess an undividing mother cell. *Nipa* (18) also shows an undividing megaspore mother cell, similar to that of *Cocos*.

BAUCH stated that a sign of degeneration of megaspores was found by him. Unfortunately the original article of BAUCH could not be obtained, so a fair comparison could not be made. However, judging from his statement[3] he seems to believe that the megaspore mother cell must have divided to form the two daughter megaspores, the chalazal becoming functional. This is contrary to what is reported in this paper. This discrepancy and divergence of interpretation is not uncommon; the case of *Richardia africana*, where MICHELL and GOW (16) seem not to agree as to the origin of its sac, is an example of differences of this kind. GOW found its origin to be a duplicate of *Cocos nucifera*, but MITCHELL found that four megaspores were produced. We base our conclusion on observations in the examination of hundreds of slides, and believe that the production of the megaspores or the tetrad in the normal development of the sac is entirely suppressed. Signs of disintegration of the megaspores were observed by BAUCH at the micropylar region of the sac. In many of our preparations we have found remains of nuclei from the nucellar cells undergoing absorption by the developing sac at the micropylar end (fig. 10). Two, three, or more nuclei may be crushed together and stain deeply so as to give an appearance of distintegration, or what BAUCH might have termed daughter megaspores experiencing disintegration or degeneration. These nuclei are plentiful, especially at the quadrinucleate stage of the sac.

The development of the megaspore mother cell into the embryo sac direct is not only found among the monocotyledons, but also in the dicotyledons. COOK (6) on *Rhytidophyllum*, CHAUVEAUD (5) on *Vincetoxicum*, YOUNG (24) on *Melilotus alba*, DASTUR (8) on *Hydnora africana*, and D'HUBERT (9) on *Opuntia* report cases of undividing mother cells. *Peperomia*, *Piper*, and *Heckeria*, as mentioned by JOHNSON (13, 14), also develop undividing mother cells.

The regular division from the megaspore mother cell (or 1-nucleate stage of the embryo sac) to the octonucleate sac, follows the usual

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[3] Cited by RADERMACHER.

situation common in *Calopogon* (17), *Epipactis* (2), and in *Epidendrum variegatum*, *E. cochleatum*, *E. verrucosum*, *E. globosum*, *Coelogyne massangeana*, *Pogonia macrophylla* (20), and others.

The early degeneration of the antipodals, previous to the fusion of the polar nuclei, seems to indicate that they are ephemeral and do not persist long, as in *Nephrosperma* and *Vershaffeltia* (1). Typhaceae, Naiadaceae (*Potamogeton*), Alismaceae, Pontederiaceae, Liliaceae (except *Ornithogalum*), Scitamineae, and Orchidaceae (10) show ephemeral antipodals.

It is evident, as with *Eichornia* (21) and *Lilium* (7), that the fusion of the polar nuclei forms the endosperm nucleus.

Summary

1. The axis of the flower must have developed long before the emergence of the inflorescence from the outer spathe, and develops the ovules after it has escaped from the spathe. The development of the embryo sac continues and proceeds up to about the receptive stage of the stigma.

2. The ovules are cauline, arising from the central axis of the flower. The floral axis bulges out, and papillae which serve as the nucellus of the nascent ovules are pushed toward each loculus of the ovary. The inner and outer integuments develop in succession.

3. The archesporium is one-celled, which does not cut off any parietal cell, but functions directly as the megaspore mother cell, which develops the embryo sac.

4. The megaspore mother cell divides in the usual manner, and produces the octonucleate sac, hence upon maturity we have the egg, two synergids, two polar nuclei, and three antipodals.

5. The polar nuclei fuse just after the opening of the inflorescence and before the degeneration of the antipodals and synergids. The polar nuclei migrate toward the center of the sac, where they fuse.

6. The synergids begin to disappear just before the time when the ovary becomes receptive.

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[*Accepted for publication February 27, 1927*]

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seem that oxygen deficiency must present serious difficulties. The growth of roots of any ordinary land plants, whose seeds might in any way be carried into the bog, or whose vegetative parts might begin to grow forward into the bog from any bordering association, would be either greatly retarded or entirely prevented.

The presence of methane in bogs that have developed by forming a floating mat on open bodies of water correlates with the well known fact that large amounts of methane are produced by the decay of masses of organic matter at some depth in undisturbed waters. It seems to follow naturally that the amount of methane would be greater in the deeper layers than in the upper, due to its formation and solubility. The presence of the methane decreases the partial pressure of the other gases, and thus reduces their solubilities. This is shown by the smaller amount of nitrogen, the least soluble of the gases, dissolved in the waters of the wet bogs, and by the high concentration of nitrogen in the gases liberated in Esperance Bog. The presence of methane may also correlate with the earlier stage of development found in the wet bogs. No work on the effects of this gas on the growth of roots has come to the attention of the writers.

Summary

1. The differentiation between wet bogs and dry bogs appears to be characterized by the gases dissolved in the waters of the bogs.
2. Wet bogs contain methane while dry bogs do not.
3. Wet bogs contain greater concentrations of carbonic acid than the dry bogs.
4. The presence of methane causes the liberation of nitrogen from solution, and thus wet bogs contain smaller dissolved quantities of this gas.
5. The oxygen content in all samples of bog water examined is practically nil. This marked oxygen deficiency when viewed in the light of the effects of such conditions on ordinary land plants, found by other workers, leads to the inference that this condition must be a large factor in the inhibition of non-bog plants from bogs of the Puget Sound region, and that bog plants are more tolerant of these conditions.

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[*Accepted for publication March 29, 1927*]