The Morphology of *Agathis australis*.¹

BY

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With Plates I-IV and 92 Figures in the Text.

BECAUSE of fame as a timber-tree, *Agathis australis*, (Lamb.) Steud., the Kauri-Pine, has probably become the best-known species of the genus. Endemic in New Zealand, it inhabits the region from the North Cape nearly to 30° South latitude, thus being distinctly sub-tropical as compared with the remaining species, which inhabit the East Indian region. Throughout most of its distribution the Kauri is abundant, forming forests of magnificent trees. In youth its habit is strongly spire-like, much resembling that of many other Conifers; but in full maturity a form is developed which is quite different. The central shaft is lost above. A huge columnar trunk, quite free of branch or knot—a condition secured through the function of a ramular absciss-layer—bears a crown of stout, broad-spreading branches. When still quite young the trees begin to bear ovuliferous cones, and when full-grown fruit freely. Opportunity for the collection of material for an investigation of the life-history of this araucarian genus was afforded the writer while collecting and studying in Australasia as a Sheldon Travelling Fellow of Harvard University.

The structure of the gametophytes and the embryo of the Araucarineae has been almost unknown thus far, chiefly because of the inaccessibility of the group; and a knowledge of the morphological and cytological details of the development of these structures is greatly to be desired, inasmuch as it is now clear that the Araucarians form a group somewhat apart from other Conifers. Their phylogenetic position, therefore, is one of unusual interest, and, further, is at present very much in discussion. Hence it is hoped that such details of structure and development of the sexual generation and of the early stages in sporophyte formation as are brought out by this investigation may aid in the solution of relationships among the Conifers.

Collections of the strobili of the Kauri were made at Puru Creek and at Puriri, near Thames, N.Z., and in the Waitakere Hills, near Auckland,

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N.Z., in late October and in November, 1910, and again, at the last station, in February, 1911.

The individuals from which material was taken were strictly monoecious, bearing freely cones of both sexes (Pl. I, Fig. 1), whereas the genus as a whole is dioecious. The male cones are cylindrical, three to six centimetres long, and about one centimetre in diameter. They are borne solitary, erect, and slightly peduncled in the axils of normal leaves. The microsporophylls, spirally arranged, bear eight to twelve sporangia attached to the lower side of the peltate tip, projecting adaxially. The pollen is shed from late September to the middle or last of October. The earliest date available for collection was October 28, and the pollen was then found to have been nearly all shed. The only material obtained was from an individual retarded in development. In this only ungerminated microspores were found. Hence a study of the early history of the male gametophyte could not be made. However, Jeffrey and Chrysler (4) have described its early development in this species, and Thomson (14 and 15) has published some notes on the germination of the pollen and the behaviour of the nuclei at this time. Two prothallial cells are cut off as in many Gymnosperms. These cells not only persist, but divide further to form a complex of several cells within the pollen-grain. Evidently a considerable proliferation of this tissue occurs, followed by the freeing of its many nuclei, since Thomson reports as many as forty nuclei within the young pollen-tube. Similarly, a large number of supernumerary nuclei form in the pollen of *Araucaria*, as Lopriore (8) has shown for *A. Bidwillii*. The method of pollination in these genera is unique among Gymnosperms. Germination occurs upon the ligule in *Araucaria*, and on the surface of the cone scale nearer the ovule in *Agathis*. Thence the pollen-tubes pass towards the micropyle. Thomson, who made this discovery, has designated such a method of fertilization as 'protosiphonogamic'. In the placing of the pollen the Araucarineae thus differ from all other Conifers where the grains are conveyed to the micropyle; and their proliferation of male prothallial tissue is paralleled only in the Podocarpineae.

In the study of his material the writer has not seen pollen-grains germinating upon the scale. They are found chiefly deep in the axil of the scale. Often the grains have become embedded in the cortical tissue of the cone axis, or of the nucellus by the growth of the latter against the former. In this position the tubes are sent out as described below.

The female cones terminate short stout branches. In October three stages are found: very young cones, about 1 cm. in diameter, just breaking from bud-scales; small, obovoid cones, about 2 cm. in diameter, with loose scales,—the flowering stage; and large, almost spherical cones, from 4 to 6 cm. in diameter. Fertilization occurs in the last mentioned from the end of October to the middle of November, and the seeds are

mature and fall about the first of the following March. Thus here, as in many other Conifers, a long period intervenes between the appearance of the ovulate strobilus and the ripening of the seed. A year is required to develop the cone from its appearance to pollination; about thirteen months pass between pollination and fertilization; and four more are taken to complete the growth. The history of the male cone is, as with other Conifers, apparently much shorter, less than a year, since no evidence of young strobili is found at this time.

The female cone is made up of close spirals of scales, each bearing a single median ovule. These scales are broad, thin-winged proximally, with stout, short, up-turned tip. They have the simple appearance well known in the genus *Agathis*, and there is no external evidence of a double nature such as appears in most Conifers.

In strobili just appearing from the bud ovular growth has not yet begun. The ovule is first recognizable, according to Dickson (1), who investigated young cones from greenhouse plants as early as 1863, as a small swelling at the base of the scale. At pollination well-marked projections of the general form of ovules are developed. But at this time there is no differentiation either of integument or of archesporial tissue. This condition is in contrast to that commonly found in Gymnosperms where there is at least sufficient differentiation to form a micropyle to receive the pollen. And this suggests a cause for the germination of the pollen at other points. Progress in development must be rapid from this time on, since in February the integument is set off, and the embryo-sac has enlarged considerably. Fig. 5 presents this stage. The nucellus is well formed. Embedded in 'spongy tissue' in its centre lies the embryo-sac, still in the free nuclear stage, the nuclei arranged in the customary parietal layer. The nucellus is free from the integument, and each is bounded by an epidermis-like layer of cells.

Ovules just previous to fertilization were the next stage available. At this time they resemble somewhat in form and size the ripe seed. The character of the micropyle varies much, especially among ovules from different cones. The surface of the nucellus is exposed above and below by large V-shaped openings in the integument, the ventral being considerably the larger in most cases. Huge micropyles were found occasionally where the opening reached down half the extent of the embryo-sac. This condition is probably correlated in some way with the peculiar basal margins of the cone scale, where auricles leave small sinuses in the wing. One of these openings lies directly over the ovule of the scale below. This arrangement may be concerned with the peculiar germination of the pollen-grain.

The nucellus is clearly set off from the surrounding tissue. The separation extends far down, always to the base of the gametophyte, and

often so far below as to create a stipitate appearance (Figs. 2 and 3). It is bounded externally by the above-mentioned layer of larger cells with mucilaginous, deeply staining contents. Inwardly is found the megaspore membrane. Adjacent to the latter the innermost layers of cells show signs of disintegration, and bounding these inwardly are frequently the remains of cells absorbed in the development of the gametophyte. The tip of the nucellus is at times enlarged, though not greatly, the swelling, perhaps in many cases, being limited by the proximity of the micropyle to the cone axis, against which the nucellar tissue is frequently firmly pressed. In ovules of the age of the vacuolated embryo-sac the nucellar cells largely contain starch. This disappears irregularly, for at the time of fertilization the upper portions of some nucelli contain much starch, though many have none. The presence of this seems to have no effect upon the behaviour of the pollen-tube as it passes through.

Thomson (16), in a comparative study of the megaspore membrane in the Gymnosperms, has shown that the latter in the Araucarians is very poorly differentiated structurally. With this statement the writer agrees so far as *Agathis australis* is concerned. In most Conifers this coat becomes thin, or is quite lacking at the apex of the gametophyte. Thus the pollen-tube is given free access to the archegonia, which are in most cases apical. But in *A. australis* almost reverse conditions prevail: the membrane is not thin or lacking below the micropyle, but, on the contrary, its thickness is usually increased there to a considerable extent. The regions where the membrane is thin or absent lie lower down on the gametophyte. Thus a marked cap is formed over the apex of the archegoniate prothallium. Fig. 7 shows this thickened terminal portion of the megaspore membrane, and suggests also to some extent its function. The tip of the gametophyte is shown in longitudinal section with the nucellus, much eroded, surrounding it. Portions of the integument are seen on the sides. The very dark line externally bounding the nucellus is the epidermis-like layer above mentioned. The nucellar tissue is almost entirely destroyed by the pollen-tubes, some of the contents of which may be seen on the right. The dark irregular lines at the internal boundary of the nucellus are the remains of its destroyed cells and pollen-tube walls. Lying against these on the inside is a homogeneous layer, the megaspore membrane. It is thick above, and thins away rapidly in the lower part of the photograph. Its cap-like nature is evident. The pollen-tubes have been prevented by its presence from destroying the upper portion of the gametophyte. Contrast this condition with that in Fig. 9, where the pollen-tubes have broken through, as they do at times. Much of the upper section of the gametophyte has been eroded. This protective function will be seen below to have a definite relation to the position and order of development of the archegonia, as well as to the nature of the pollen-tube.

The formation and germination of the megaspore were not seen, nor was material available to determine the method of wall formation within the embryo-sac. The definite arrangement of the cells, especially at the micropylar end, points clearly to a centripetal growth not different from that of other Conifers. The mature gametophyte is distinctly club-shaped, the upper larger portion bearing the archegonia (Fig. 2). The cells of this latter portion are elongated radially and arranged rather symmetrically, strongly suggesting the huge elongated cells, the 'alveoli', of endosperm formation. In the basal portion there is much less regularity, and the cells are smaller. At this stage, just before the maturity of the egg, the cells of the gametophyte are not rich in cytoplasm, though they are multinucleate, especially those of the central portion.

The archegonia are numerous and arranged irregularly, many of them being deep-seated. They occur only upon the upper third or half of the gametophyte. The number is variable, from three to twenty-five in the ovules studied, eight to fifteen being the commonest numbers. Though in general the method of placing is indefinite, there is often a noticeable tendency to assemble them in three groups: a small terminal cluster, and two uneven encircling crowns at short intervals below. Within these groups no order is distinguishable; in fact, all transitions are found from the solitary archegonium to a sort of archegonial complex. Some difference in age is discernible, indicating an acropetal development. When fertilization is occurring in lower archegonia the ventral canal nucleus may not as yet have been cut off in the apical archegonia. The megaspore-membrane cap protects these young archegonia, which are not ready for fertilization at the time the first male cells come down, shunting the latter off and down to the thinner lower regions of the megaspore membrane, under which are situated the greater number of archegonia and the more mature eggs. Fig. 10 shows the course taken by pollen-tubes, how they have passed by one of the nearest upper archegonia and fertilized those below. The two lower archegonia contain proembryos distinguishable in the figure by their dark hue.

The archegonia vary much in position in the gametophyte; some are very deep-seated, others superficial. The majority are embedded beneath several to many cells. That some of the archegonia are derived from peripheral cells seems apparent, and it is doubtful if any are actually deep-seated in origin. In those of shallow position the neck-cells, as seen in vertical section, lie in the unbroken line of the outermost layer of cells; in the more deeply situated a narrow canal reaches to the surface from the neck, and evidence of overgrowth by the surrounding cells is suggested. Where the canal is completely closed, its former position may often be discerned, so that its existence at one time is probable in all cases. The complete burial of the archegonium is compensated for by the unusually strong erosive capacity of the pollen-tube. Fig. 11 presents a fairly

typical mature archegonium, deep-seated, with a canal from the neck to the surface of the gametophyte. The shape and size vary considerably, dependent upon position and relation to other archegonia. The usual form is that most common in the Coniferae, sub-ovoid, somewhat elongated and unsymmetrical (Pl. I, Figs. 11, 12, and Pl. II, Fig. 14).

The scattered distribution of the archegonia offers various resemblances to the archegonial complex of the Taxodineae and the Cupressineae. The arrangement of the archegonia is almost exactly that of *Sequoia*. Small groups of closely placed archegonia occur frequently; between these no endosperm cells are found, and at times the separating jacket cells are partly lacking also,—a close approach to the perfect complex. An abnormal compacting of egg-cells also occurs frequently. From two to four central cells develop within a normal jacket—the latter may be distorted a little in some cases by the extra cells. These additional egg-cells lie radially above each other; one or two are usually very small, and may resemble a ventral canal cell. In all cases eggs, normal except in size, are formed. The ventral canal nuclei were seen in some cases, but naturally development must occur without the cutting off of a neck-cell initial, except in the outermost. Fertilization was found in one case to have occurred in each of two cells enclosed in an archegonium, though the proembryo formed in the smaller was much distorted.

There are two points in which the archegonium of *Agathis* is in strong contrast with the common condition: a discontinuance of the jacket near the neck-cells, and the peculiar arrangement and permanency of the latter.

The jacket cells are sharply differentiated from those of the gametophyte surrounding them. They are irregular in size and shape, and in rare cases become two tiers deep. A bi- or multinucleate condition is common, particularly in the upper portion, the nuclei being large with often two or more nucleoli. The interruption at the neck is clearly visible in Pl. I, Figs. 11, 12, Pl. II, Fig. 14, and Pl. IV, Fig. 39.

The neck-cells form a rounded, somewhat pyramidal mass, the individuals radiating outward and downward from the top. In number they vary from twelve to twenty, the smaller numbers occurring most frequently. Pl. IV, Fig. 40 shows the group in transverse section. There is but a single tier—compare Figs. 11, 12, 14, 39—though an unsymmetrical arrangement places some cells partly above others. Displacement may thus form a falsely two- or three-tiered neck. This cap of cells becomes firmly bound together, and the walls considerably thickened (Figs. 12, 14, 40, and especially 39). In no case was a passage-way found through them to the egg. They do not, as in many Gymnosperms, serve to attract or nourish the pollen-tube; on the contrary, they resist its entry strongly, and are never destroyed or torn from one another. The pollen-tube is unable to disrupt them and must pass to one side to enter the archegonium. The result of such resis-

tance to the entrance of the pollen-tube is well shown in Fig. 38. This is a transverse section of a neck and the surrounding tissue. The tip of the pollen-tube has eroded the gametophytic cells around the neck completely, leaving the latter entirely unaffected. On this account the neck complex is frequently freed as a whole when the male cells break through, and is thrust aside, in some instances being even carried with the male cytoplasm into the centre of the archegonium.

The central cell in the youngest stage studied presents the condition shown in Fig. 12: cytoplasm thin and strongly vacuolate—as usual in the coniferous archegonium at this time; a small nucleus with little chromatin, and a brilliant nucleolus. The position of the nucleus is upper central, though it is not rarely found towards the base of the cell. An upward migration must occur before the cutting-off of the ventral canal nucleus.

The formation of the latter occurs in the uppermost portion of the cell, and nearly always well to one side, instead of below the neck-cells. Figs. 13 and 14 show the ventral canal nucleus and the young egg nucleus soon after formation. Fig. 13 is a somewhat tangential section of the archegonium and does not show the neck-cells. But there is no question as to the identity of the nuclei presented, as the series reveals the archegonium unruptured, and further, the male nucleus is very different in size and appearance. In two or three cases the mitosis was found to occur centrally, and Fig. 14 shows a rare case of median position of the ventral canal nucleus. In all the many cases where the latter was cut off to one side, that which may be called the abaxial side of the archegonium was chosen—referring of course to the oblique, lateral archegonia. One can see no significance in this fact, however.

Immediately after division the two nuclei are about equal in size—perhaps exactly so—and cannot at first be told apart except in position. The egg nucleus grows rapidly, retreating towards the centre of the cell; the ventral canal nucleus immediately begins to disorganize, disappearing completely in a short time. No evidence of wall formation, or of differentiation in the surrounding cytoplasm suggestive of cell limitation, was seen. So rapid is the disintegration of the canal nucleus that normally it is not to be found when the egg nucleus is half-grown, and no trace exists when maturation is complete. In Figs. 13 and 14 the nucleus is already beginning to disorganize.

Immediately after the central cell nucleus has divided the vacuoles largely disappear from the central portions of the cytoplasm (Figs. 13 and 14). Pl. II, Fig. 19 shows the young egg nucleus and the condition of the cytoplasm at this time, under considerable magnification. The nucleus develops rapidly. The mature egg nucleus is represented in Fig. 20; the nature of the surrounding cytoplasm is also indicated. (The sections of archegonia shown in Figs. 19 and 20 are nearly transverse.) Large vacuoles are found

occasionally in the mature egg, but their occurrence or position is not constant, as is the case in some Abietineae. The ripe egg nucleus may be found in any part of the cell, but its position is normally upper central.

The germination of the pollen was not observed, but the behaviour of the tubes is even more unusual than reported by Thomson (15) in this genus and in *Araucaria*. The latter has described them passing along the cone scale, penetrating its tissue and that of the integuments. In *Agathis australis* the pollen-grain from its position in or near the axil of the scale sends tube-branches in various directions—into the nucellus and also away from the ovule into the cortex of the cone axis and into the basal portions of adjacent scales. The courses of those leading away from the ovule are very peculiar. Their direction is often apparently purposeless: some wander just beneath the epidermis and may pass to the micropyle of adjacent ovules; others push directly inward, reaching the central cylinder of the cone. These in their course often follow the scale traces, running along or into the phloem, and even entering the xylem! All the tissues of the cone may be penetrated; only large resin canals prove obstacles. When a pollen-tube enters one of the latter it promptly retreats and takes a new direction. Penetration of the xylem of the scale trace by the pollen-tube is not constant in *Agathis australis*; some cones show many instances, others none at all. The tube branches which behave in this strange way are usually small, and follow an irregular course—in and out from cortex to fibro-vascular bundle, dying out as tapering tips in either tissue.

Among spiral and scalariform tracheides fragmentation occurs during the passage of the tube. Pitted xylem is probably only entered before lignification is complete. Pl. IV, Fig. 41 shows a cross-section of a scale trace (within the cortex of the cone), the xylem of which has been entered by a pollen-tube. The latter seems to have penetrated while the xylem was in a plastic state, since the tracheides have arranged themselves smoothly about it. The shrunken pollen-tube wall is visible. The tube entered the trace from the side near the base of the cone scale, passed some distance through the phloem, entered the xylem, which it traversed for a few millimetres, and returned to the cortex. Three other tubes are seen in the phloem on the lower side of the figure.

This odd feature was observed in other species of *Agathis* during the study of the anatomy of the cone scale. It was not found in *A. vitiensis*, (Seem.) Benth. and Hook. f., perhaps because the cones examined were almost sterile. But the scale traces and even the axial cone bundles of *A. alba*, Rumph., and of *A. Bidwillii* (specific name as placed on material sent from Botanic Gardens, Buitenzorg, Java) show pollen-tubes traversing them, even more frequently than does *A. australis*, and those of *A. borneënsis*, Warb., are very much eroded by them. In the latter species so serious is the attack in some cases that wonder is caused as to how the

bundles continue to function. Fig. 37 is a photograph of a transverse section of an axial bundle from a part-grown cone. Tubes are seen throughout the bundle, the older ones full of a mucilaginous substance and the younger ones appearing white and empty. The tubes reach the central cylinder either through the cortex or along the scale traces. Within the axial bundles they seem to pass chiefly downward and depart only with the traces. They may accompany the branches of the latter well out into the scale.

These tubes of so strong haustorial nature appear in many cases to be the most rapidly growing branches. The time of approach of the male tubes to the embryo-sac is probably very variable. In *A. australis*, Thomson (14) has found tubes beside the very young embryo-sac; the writer's material of this stage did not show them. Many ovules ready for fertilization show tubes just entering, and in others the erosion of the embryo-sac—by a single unbranching tube—has clearly occurred only since the maturity of the latter. Thus apparently the fertile branches of the tubes reach the ovule at widely different times, a fact due either to varying times of departure from the pollen-grain or to greater or less amounts of meandering in sterile tissue. Perhaps at times the first branches enter the nucellus, at others the cone axis.

Tube branches pass from the cone axis and from the base of the adjacent scales to the nucellus, crossing the space that exists between them in those cases where nucellar enlargement is not great. Whether the space at this time is filled with fluid or with air is not known. Thus another Angiosperm-like feature is added to so-called 'protosiphonogamic' fertilization.

The great exposure of nucellus by the large micropyle, and the sinus in the wing of the cone scale directly over the ovule, are probably means of providing readier access to the ovule for the pollen-tubes. The openings in the scales suggest that the fertile tube branches may come from pollen deposited on other scales than that bearing the ovule.

Entering the nucellus a tube may continue to branch and cause much erosion, or its course may be straight down to the gametophyte. After that point is reached, the course is normally downward between the nucellus and the megaspore membrane. This is followed, often without erosion, until the thinner portions of the megaspore membrane are reached. Then these advance tube-tips—the fertile nuclei are not yet within the ovule—erode the tissue about the necks of the archegonia, forming depressions or cavities above them (Pl. I, Fig. 9—the archegonium on the left). Pl. IV, Fig. 38 shows a transverse section of this cavity. After one archegonium has been thus prepared for fertilization, the tube passes on to others.

The male elements follow down the pathway so well prepared beforehand. The latter were not found within the ovule in any case until just

before fertilization, and their downward progress seems to be rapid. The body-cell was found in a few cases. It is large, with much cytoplasm, a huge nucleus, and a thin wall (Pl. II, Fig. 16). It is accompanied by varying amounts of cytoplasm from the tube—being either almost naked or surrounded by several times its volume of dense, coarsely granular cytoplasm. A correspondingly variable number of small nuclei are found connected with it. These contain little chromatin and a prominent nucleolus, thus resembling the stalk and tube nuclei of other Conifers. (Two are seen in advance of a male cell in Fig. 18.) It seems probable from their appearance and behaviour that these represent the stalk and tube nuclei, but since as many as six and eight occur at times, some of them, at least, must be of the great number of supernumerary nuclei, unless the stalk and tube nuclei have shared in the tendency to proliferate.

The division of the body-cell was not seen. It clearly may occur before the descent through the nucellus is finished, perhaps even without the ovule, or so late as the arrival at the archegonium. The male elements thus formed are two large nuclei with close reticulum, surrounded by the dense cytoplasm of the body-cell and of the tube. At first no delimitation is visible within the mass. Later the cytoplasm belonging to each of the nuclei becomes clearly defined, and is finally bounded by a membrane which remains very delicate. The two nuclei are usually elongate and somewhat unequal in size. Fig. 17 shows rather typical nuclei at this stage, the difference in size being exaggerated somewhat by different planes of section. The extent of the cytoplasm connected with each can be faintly made out, though the membrane is not visible in the photograph. A slight amount of tube cytoplasm surrounds them. Ordinarily these two cells do not separate until the entrance to the archegonium is reached, but in Fig. 18 complete separation has occurred. One of the male cells with distinctly limited cytoplasm is seen, preceded by two of the usual accompanying nuclei. The large nucleus is cut tangentially. The other male cell is above and lies outside the plane of section.

Entrance to the archegonium is evidently not secured readily despite the preparation made therefor. This is shown by the heaping-up of the male cytoplasm in a mound of concentric layers over the male cells as they lie against the top of the archegonium; by the disturbance of the cytoplasm of the egg throughout its extent by the entrance; by the breaking away of the resistant neck-cells and their frequent transportation into the egg during the inrush. A considerable amount of male cytoplasm always passes in with the male cell as in all other Conifers, and with it sometimes the other male cell and the small nuclei. In such a case the sterile nuclei remain in the top of the archegonium and rapidly go to pieces there. Rarely the smaller male cell can be distinguished when proembryonic development is complete, and two cases were noted where the extra male nucleus persisted

unchanged until three or four divisions had taken place in the proembryo. More frequently the smaller nuclei are left outside, and the second male cell is entrapped at the entrance, disorganization occurring in these positions. No cases were found of division, mitotic or amitotic, among these nuclei.

That the second male nucleus has potential fertilizing capacity is possible. A remarkable instance of its activity was observed. Both male cells entered an archegonium, the larger effecting fusion with the egg nucleus. The second broke its way laterally through a single layer of jacket cells into an unfertilized archegonium situated just below and beside the first entered egg-cell. Whether fertilization would have occurred is doubtful in view of the somewhat disorganized appearance of the nucleus on its arrival. A possible case of fertilization by both male cells is the above-mentioned instance of the development of proembryos by two eggs enclosed in a single archegonium.

The male nucleus that is to accomplish fusion passes to the egg nucleus, which maintains its station. It takes position beside it, and the two while fusing are slowly and unevenly surrounded by the male cytoplasm. Thus a sort of loose kinoplasmic sheath is formed (Pl. III, Fig. 27). In the Conifers generally this investment of the fusion nucleus by male cytoplasm does not occur, although it is reported in the genera *Torreya*, *Taxodium*, and *Juniperus*. No preparations were secured showing clearly the male and female nuclei in process of fusion, but Figs. 25 and 26 show the condition just previous to this. The nuclei lie side by side; the plane of section, however, is such that both cannot well be seen at once. Fig. 26 displays a median section of the male nucleus; the dense nature of its contents is noticeable. The egg nucleus lies just below and to the left, as Fig. 26, a photograph of a section just below, discloses. Here a portion of the egg nucleus appears, somewhat flattened by the approach of the male, a small tangential section of which is discernible to the right. Sections still farther on show the remainder of the egg nucleus.

The remarkably large size of the male nucleus is probably the most noteworthy feature of fertilization. Because of a frequently elliptical outline its actual size is difficult to judge, but it is approximately that of the egg nucleus, and possibly even surpasses it. Such a state is surely unusual. In the Conifers the male nucleus is in nearly all cases very much smaller than the female. But according to Lawson (5 and 6) in *Cryptomeria* the latter is nearly as large, and in *Sequoia sempervirens*, Endl., 'at the time of their fusion the male and female nuclei are of equal size.' Hence the unusual lack of contrast in size is not without parallel in the group. Further, Seward and Ford (10) show in *Araucaria imbricata* (Fig. 28, E and F) two large nuclei of approximately equal size in the archegonium, and these they consider to be the male and female nuclei.

A sort of pseudo-fertilization occurs to some extent in ovules which

escape pollination. The jacket cells break down in part. Their contents pass into the cytoplasm of the egg as angular, dense fragments. These fuse more or less and migrate towards the egg nucleus. In this condition they form densely granular, reticulate masses, often with narrow clear zones surrounding them. In some cases these bodies were seen deeply indenting the nuclear membrane, as in Pl. II, Fig. 15. It seems doubtful if actual fusion occurs, as in the cases where penetration is noticed the egg nucleus is beginning to disorganize. Probably no significance can be attached to this phenomenon, although a suggestion is perhaps given of parthenogenesis, or of double fertilization. This condition is found only in archegonia that have not been approached by male cells, and no evidence appeared of the migration of nuclei, or of large portions of the contents of the jacket cells under normal conditions.

As shown in Pl. III, Fig. 27 the fusion nucleus has a marked nuclear membrane, and is loosely invested by a prominent sheath of kinoplasm. It maintains its position near the centre of the archegonium, and there gives rise rapidly to a large proembryo. This behaviour in the early history of proembryonic development is in great contrast to the conditions in other groups of Conifers where the fusion nucleus or its division products, two, four, or eight nuclei, sink to the bottom of the archegonium, and there continue the growth of the proembryo.

The spindle of the first division is small and intranuclear, as Pl. II, Fig. 21 shows. The two daughter nuclei (Fig. 22) are of good size. They are still free from the kinoplasmic sheath. But with the division into four the kinoplasm is invaded, and the nuclei become distributed throughout a uniform mass of dense cytoplasm. Pl. III, Fig. 29 exhibits this spherical mass with its nuclei (two only of the four visible) suspended near the centre of the archegonium. Another rapid simultaneous division forms eight nuclei of good size. These are distributed uniformly throughout the proembryo—compare Fig. 30, four nuclei showing. In the continuation of the free nuclear division the mitoses resulting in the formation of sixteen and thirty-two nuclei do not occur so rapidly, and are not always simultaneous within the group—some divisions being quite complete when others are only beginning.

After the fifth consecutive division in the proembryo free nuclear mitosis frequently ceases, and wall-formation soon occurs; but a sixth complete division of this sort was found in a few cases, and an irregular increase in nuclei may take place at this time. Thus the proembryo in its final stage before wall-formation may possess anywhere from thirty-two to sixty-four nuclei, thirty-two being most common. Fig. 36 represents the sixteen-, and Fig. 23 the thirty-two-nuclear stage. The nuclei are large, rounded, and frequently binucleolate. At this time they are evenly distributed throughout the entire mass, those parietally situated often causing

tubercle-like swellings on the surface, and even projecting almost free from the cytoplasm. A period of rest from mitosis then intervenes, during which a rearrangement of the nuclei and cytoplasm ensues. Even while the last divisions are occurring some beginning of this is made. A thin layer of cytoplasm—definitely distinguishable from that of the globose mass—forms over the upper portion of the proembryo. Whether this is secured from the cytoplasm of the egg, which is being constantly absorbed by the growing sporophyte, or is withdrawn from among the nuclei of the proembryo, could not be ascertained. As the nuclei begin to take definite position this cap increases greatly in thickness, and extends down over the upper half or two-thirds of the rounded mass. A somewhat similar region is set off on the opposite side—but within the original sphere—by a nuclear retreat. These two features are well shown in Fig. 28. A median transverse section of the proembryo at just this stage is shown in Fig. 23. It is evident that the cap of dense cytoplasm extends completely around the upper portion of the proembryo. Meanwhile enlargement occurs; the spherical form is lost, and the mass becomes broadly top-shaped, the cap increasing this appearance. Orientation at this time is by no means constant. The proembryo points usually slightly obliquely or straight downward, but the apex may be turned at right angles to that. The nuclei group themselves in three tiers,—the first evidence of those into which the mature proembryo is so sharply differentiated. In their new position they become somewhat flattened and angular by mutual compression. The nucleoli become two to several. Fig. 24 shows all these features clearly. The three tiers are recognizable: the uppermost, a cap of a single layer of large, radially elongated nuclei; the median, a cluster of a few smaller rounded nuclei; and the apical, another cap of elongated nuclei, smaller than those on the opposite side. The size, shape, and position of the cells soon to be formed are foretold at this time by the nuclei. The upper peripheral nuclei, while maintaining their relative position, push slowly out into the cap of cytoplasm under which they lie, and the latter is finally entirely occupied by them, the line of separation from the section beneath being lost.

The purpose of the cap clearly is to nourish the uppermost layer during its formation of large nuclei. The lesser zone of cytoplasm free of nuclei at the opposite pole, though of different derivation, also serves to build up a tier of nuclei on that side in a very similar manner.

As soon as these processes are complete wall formation occurs. This first becomes evident by lines of demarcation in the cytoplasm, setting off portions about each nucleus (Fig. 24). Then delicate walls appear which become strong only at full maturity of the proembryo.

The median group consists of eight to twelve cubical cells, small but rich in protoplasm, arranged for the most part in two tiers. In these no

further change occurs until the descending embryo attains its final position. It is this rather insignificant portion of the proembryo which forms the embryo proper. The terminal groups are concerned only in the transfer of this central section to the centre of the endosperm. Growth in the embryo proper goes on rapidly after that.

The upper group, which is to form suspensors, elongates distally, reaching out in long tube-like processes through the upper section of the archegonium (Fig. 31), at times even out through the ruptured top.

The lower group becomes more specialized, forming a cap that fits over and protects in a remarkable way the initials of the true embryo above. This cap consists of a terminal, conical cluster of firm-walled, tightly fitted cells elongated backward from the apex, somewhat like the neck-cell complex. The cap form is secured by smoothly 'stepping' the cells one upon the other. A circular rim of cells is placed upon the edge of the cap, extending upward and sheathing the embryonic tier (which is partially sunken in the hollow of the cap) and the base of the suspensors. Fig. 31, a proembryo nearly mature, exhibits all these features. The cap and embryo proper may be better seen in Fig. 32, which illustrates a later stage.

Among Gymnosperms there are two other instances known where the terminal cells of the proembryo do not become embryo proper but form a cap—*Cephalotaxus* (7) and some species of *Podocarpus* (11). But in these genera the cap is very simple—a large terminal cell, and one to several smaller ones placed irregularly between it and the young embryo behind.

When the cap is perfected and distal elongation ceases in the suspensor tier, the proembryo has acquired a shuttlecock-like form (Fig. 31). It has now attained maturity.

There are three distinct tiers, as in the proembryos of other Conifers, but their functions are very different. In this case the central tier is fertile, whereas generally this becomes suspensors. The lower tier, which usually is fertile, becomes a sterile tip, and the suspensors in this case correspond to the rosette tier of many others. The tier of naked nuclei above the rosette layer finds no homologous portion in the araucarian proembryo.

The total number of cells at this stage is found to vary from thirty to seventy. The greatest variation is among the suspensors; a range of eleven to thirty-eight was found, fourteen and twenty-six being most common. From eight to fifteen cells compose the embryo proper. The cells of the protective cap number from ten to twenty.

In that region of the gametophyte into which the descending embryos are to penetrate a marked change takes place at an early stage. This is in the form of preparation to supply greater nourishment for their development, and also for the suspensors during the descent. The cells so situated as to be likely of absorption become richer in content. The change can

usually be detected even before the eggs are mature, and after fertilization it goes on rapidly. One large central area usually suffices for all the archegonia, but where two crowns of eggs are well separated such a region is formed for both. The changes are these: the cytoplasm becomes more dense; the nuclei, of which there may already be several, increase in number, often forming clusters of three to eight. Division is amitotic, the small nuclei becoming elongate and then fragmenting. Great increase in size follows. Then starch grains appear. In the cell contents of the rest of the endosperm no change has occurred at this time.

Elongation of the suspensors forces the embryo and its cap downward, as usual in the Conifers. The course taken is not direct. The path of least resistance—that along the radial rows of endosperm cells—is followed until the central line of the gametophyte is attained. Then the core of suspensors coils, forming a close spiral. This also is a common feature of coniferous embryonic development. It may be due to increased resistance to progress, or to the food-supply stored in this region, the coils of the suspensors becoming absorptive, and causing widespread cell destruction, since behind them in the archegonium they have no supply of nourishment for their growth. Beyond this point the suspensors extend straight down to the final position of the embryo. Fig. 6 shows the complete course followed by the suspensors; the remains of the archegonium—very dark—on the upper right side; the first section of the suspensors, the coils of the central spiral loose in a large eroded cavity, and the straight lower section tipped with the embryo.

The suspensors form a fascicle, cylindrical or somewhat angular, and are generally firmly compacted. Fig. 8 shows transverse sections of the bundle in the spiral region. The firm walls are noticeable. No evidence was seen of any splitting within the bundle such as results in polyembryony in *Cephalotaxus*, *Dacrydium*, *Cryptomeria*, and perhaps other genera. The cap would naturally hinder any budding of this sort from the embryo. Only a single embryo ever develops from the egg. But frequently several archegonia are fertilized, and as a result a number of embryos may start downward. Their suspensor coils snarl together, and that with the strongest bundle is alone able to pass directly down to the central situation. The others lose their courses and pass out laterally or even back upon their track, slowly going to pieces.

The embryonic cap remains wholly unchanged from the time of its maturity until the growth of the suspensors is complete. During its transportation the cells of the true embryo are also dormant, but immediately upon arrival at the end of the course rapid development ensues. The cap and the base of the suspensor core give up their contents, probably being absorbed as nutriment together with the surrounding cells. Fig. 32 shows the tip of the suspensors forcing the cap and the embryonic tier

down through the endosperm. In Figs. 33, 34, and 35 are seen progressive stages in the growth of the embryo and the disappearance of the cap. The latter is spread out and flattened by the enlarging embryo. In Fig. 35 all traces are lost. This figure also represents the latest stage in embryo development obtained. The embryo must be left as a small, somewhat spherical mass in the lower central section of the endosperm.

Soon after embryos begin to pass down into the endosperm the entire upper portion of the ovule inside the integument begins to shrivel, all of the archegonium-bearing section being concerned. This destruction of gametophytic tissue is very extensive, including as it does nearly or quite all of the larger upper section of the mature gametophyte. Fig. 3 shows the beginning of this: all that section above the centre of the suspensor coil gives evidence of disintegration. The lower portion has already increased in diameter, thus reversing the club-like shape of earlier stages, the basal portion being now the larger. The archegonial region in all gymnospermous ovules is destroyed during the development of the embryo, but the destruction is naturally not great owing to the limited distribution of the archegonia. The ripe endosperm of *Agathis* thus consists in large part of the *smaller* portion of the mature gametophyte. Fig. 4 shows a longitudinal section of a ripe seed. Embedded in the endosperm is a distinctly large embryo with two cotyledons. The embryo extends nearly throughout its length. A dry beak of collapsed tissue represents the fertile section of the gametophyte. The shrivelled nucellus is still conspicuous, free from the integument. The endosperm shows no signs of the 'ruminating' outline reported to occur in the Araucarineae. Neither was such a condition found in the large seeds of *Agathis vitiensis*, which were also examined. Erosion by the voracious pollen-tubes in regions which become permanent endosperm would doubtless cause a condition simulating that in the ruminated seeds of the Taxaceae, and it is possible that such is the condition in *Araucaria*.

AFFINITIES.

There have been presented above, in the history of the gametophyte and of the embryo of *Agathis*, a number of features sufficiently striking in their contrast to those known to obtain in other Conifers to justify from this standpoint—as well as from that of the anatomy and morphology of the mature sporophyte—the isolated position of the Araucarineae. The important question then arises—what is the phylogenetic relation of this group to the other Conifers? Are these features indicative of a primitive condition, as those already known have led some to believe, or is some other explanation more consistent with the facts? The writer believes that they are certainly not primitive—that though at first glance they may suggest the conditions prevailing in the more primitive Gymnosperms, the

resemblances are superficial, not underlying. These very features bespeak not primitive conditions, but strong specialization. Consider the supernumerary nuclei supplied for the long, branching pollen-tubes; a megaspore membrane cap to protect young archegonia; a pollen-tube tip that prepares access to *several* deep-seated archegonia; the lack of jacket cells at the top of the archegonium to give readier access to the male cells since the neck has become impenetrable; a ventral canal nucleus that is ephemeral, and about which no wall is formed; in proembryo formation five or six consecutive free nuclear divisions in a *restricted* central area,—not *throughout* the egg-cell as in Cycadales and Ginkgoales; a mature proembryo far more complex than any other known; an embryonic cap of remarkably elaborate nature for protection and penetration; and suspensors with a double elongation, the first to secure a holdfast from which to thrust in the opposite direction an embryo suspended freely in the archegonium.

As possibly primitive features in the history of the male gametophyte the large number of microsporangia and the many supernumerary nuclei of the pollen-tube have been cited. As concerns the sporangia, the Abietineae and the Podocarpaceae are the only tribes in which the number is strictly two. The Taxineae and the Araucarineae universally have more. Among the Taxodineae and the Cupressineae several genera, clearly among the more specialized within the groups, have three to several microsporangia; for example, *Sequoia*, *Taxodium*, *Widdringtonia*, *Juniperus*. The two last-mentioned tribes are now generally admitted to be recent and specialized. Mr. Sinnott (11), in a paper contemporaneous with this, shows the primitive character of the Podocarpaceae, emphasizing from a study of their gametophytes and strobilar morphology their abietinean affinities and their close relation to the Taxineae, which he considers a specialized branch from the group. This presents another instance of multiplication of sporangia,—the two of the Podocarps becoming several in their recent branch the Taxads. Further, the microsporangia of the primitive *Ginkgo* are two. Hence the occurrence of microsporangia in greater number than two among the Conifers seems to be a feature of recent specialization, and the Araucarians cannot on that account be considered primitive.

The excessive amount of prothallial tissue of the araucarian pollen-grain has been compared with that found in palaeozoic Gymnosperms. In the pollen of the Cycadofilicales and the Cordaitales a number of internal cells exist. Is this internal tissue vegetative or spermatogenous? We cannot say at present. Coulter and Chamberlain in their recent text-book (p. 178) believe it 'a safe inference' that these cells are in part, if not entirely, spermatogenous. The primitive living Gymnosperms, the Cycads and *Ginkgo*, form but one or two prothallial cells; in the Araucarians and the Podocarps the larger number is the result of proliferation of these. The cells within the palaeozoic pollen-grains are not situated at one pole, nor

does their arrangement suggest an origin from two primary cells—rather that each is itself an original cell of the prothallus. Thus, if the two prothallial cells of most of our Conifers are a reduction from an original complex, wherever a larger number occurs the mode of origin at least seems recent. There would seem to be in the extensive running and branching tubes of *Agathis* a demand for a considerable supply of nuclei. The derivation of these would be most naturally from pre-existing prothallial nuclei. Thus the evidence seems to favour the belief that the tissue in question is cenogenetic and not palingenetic.

Another feature of palaeozoic seeds which it has been suggested the Araucarians have retained is the great freedom of the nucellus from the integuments. This condition has been demonstrated above for *Agathis*. However, no systematic significance can be attached to this character, since Fujii (2) has recently shown it to be very variable even within a genus. Complete freedom of the nucellus exists in scattered genera among the Coniferae—*Callitris*, *Araucaria*, *Cunninghamia*, *Juniperus*.

The large number of archegonia and their scattered positions are suggestive of some lower forms. But the archegonia of the heterosporous Pteridophytes are few and terminal. In the Cycadofilicales and the Cordaitales very little is known of the archegonia, but they were apical (beneath the pollen chamber) and surely not numerous. *Ginkgo* has two or three terminal archegonia. The number in the Cycads, with the exception of *Microcycas*, is ten at the most. Among the Conifers the large numbers are found in the recent tribes—as many as 60 in the Taxodineae and 100 in the Cupressineae. To be sure many of these are found in complexes, but *Agathis* shows how many scattered archegonia may be brought together. And the parallelism with *Sequoia* must be emphasized again. This genus also has many irregularly placed archegonia, and some are deep-seated. Further, in both genera there are the same transitions between a single archegonium and a complex. Thus the few terminal archegonia of the Abietineae seem more likely to be primitive, and specialization to have taken the form of multiplication.

The haustorial nature of the pollen-tubes far exceeds that of any others known. That the cone axis and its bundles, even the xylem, should be invaded is remarkable indeed. A cause for such behaviour cannot now be suggested; far too little is known of the early history of the tubes. But there is the probable reason for the germination of the pollen on the cone scales, that no micropyle is ready to receive it. The seeds of the lower Gymnosperms have given no evidence of pollen-tubes. In the Cycads, though, the haustorial nature of the pollen-tubes is well known. But the section which is concerned with carrying the fertile elements is not at all extensive and can hardly be compared with like portions in *Araucaria* and *Agathis*. If comparisons are to be made of any feature of this so-called

'protosiphonogamic' type of fertilization, the penetration by the pollen-tube of tissues about the ovule and of the integument, with the passage of a space in the attainment of the nucellus, is suggestive of angiospermous conditions and not of primitiveness.

In the Gymnosperms generally the pollen-tube erodes a passage only to one archegonium—except in the case of the complex. In *Agathis* the tube goes from archegonium to archegonium. Is this a more simple condition than the common one?

The neck cells have lost their normal function, that of providing entrance to the egg-cell. They have become instead a serious obstacle to the advance of the male cells. Partial recompense is secured by eliminating the jacket cells contiguous to the neck, leaving normal, somewhat less resistant gametophytic cells. This is not a step in the reduction of the archegonium as a whole, that evolutionary tendency which results in the free egg of the higher Gnetales. Aside from the break at the top the jacket shows no signs of reduction. It is merely a little more complex than that of the Cycadales, *Ginkgo*, and the Abietineae.

In the history of the female gametophyte probably the most prominent evolutionary tendency apparent in the series from the Pteridophytes to the Angiosperms is the reduction of the complex archegonium of the lower forms. The final result is the complete freedom of the egg nucleus. In the lower Gymnosperms the neck canal cells no longer appear. The ventral canal cell is next in line for elimination. This is completely accomplished within the Conifers themselves. The Abietineae form a definite cell; in *Taxus* and *Torreya* even the nucleus has disappeared. In the Araucarineae the condition is that of most Conifers—a ventral canal nucleus is cut off, but no wall is formed. The nucleus itself disintegrates very rapidly. Certainly in this respect the Araucarineae are less primitive than the Abietineae, and on an equal footing with some of the higher Conifers.

The method of fertilization does not suggest resemblances to the lower Gymnosperms any more than to the Conifers as a whole, unless the very large male cell be compared with the sperms of the Cycads. But the ovule of *Agathis* gives no evidence of that ancient feature the pollen-chamber, nor do the male nuclei show signs of motility. A male nucleus of equal size with that of the egg occurs in *Sequoia*, another feature to add to the several in which parallelism has been emphasized.

In the Cycadales and the Ginkgoales the extensive proembryo stands out as a presumably primitive feature. Since the proembryo of the Araucarineae also sometimes fills the egg, Thomson (14) has noted a close resemblance. In all three groups free nuclear division proceeds to a stage well beyond that known in other Gymnosperms, at least eight consecutive divisions taking place in the first two and five or six in the third. But these are of an absolutely different character. In the Cycads and *Ginkgo* the

free nuclei are scattered *throughout the cytoplasm of the egg*, and when wall-formation occurs the entire egg is segmented. In *Agathis* the free nuclear division invades only *a small differentiated portion of the egg*. Further, the cytoplasm of that mass is largely male in origin and not chiefly that of the egg. The only period when the egg-cell is wholly occupied by the proembryo is at the maturity of the latter, and then the filling has been accomplished in a quite different manner—by the growth of cells that originally occupied only a small portion of the archegonium. That the proembryos are distinctly different in character is clear.

In development and structure the proembryo of *Agathis* is unique among Gymnosperms (excepting, of course, the sister genus *Araucaria*, which from the little already known is undoubtedly closely similar). In other Conifers the preliminary proembryonic tissue is few-celled and situated in the base of the egg, where it has been formed from the products of a fusion nucleus which settled to that point. The few cells of this simple proembryo are very likely the reduced form of the similarly situated, more extensive structure of the Cycads and *Ginkgo*. In that only a small portion of the egg is selected for proembryonic development, *Agathis* is different from the lower forms and like its fellow Conifers. But from the time this method of reduction was chosen, the Araucarians have apparently followed a different path from that taken by the others. Effectiveness has been secured in the latter by great simplicity, in the former by great specialization. A position in the bottom of the egg would not make readily available the supply of nourishment in the egg for the elaboration of the terminal cap. Hence possibly the fusion nucleus was retained in the centre of the archegonium. The embryonic cap need not be discussed further; the perfection of its structure speaks for itself.

The suspensor cells of the Cycadales and the Ginkgoales, since derived from entire sections of the egg, form broad massive cylinders; those of the Conifers, excepting the Araucarians, are more slender, but just as simple bundles. The suspensor group of *Agathis* differs from both these in having a double elongation, first in the direction opposite to that in which later expansion is to lead. Strasburger (12) has shown in *Araucaria* even greater specialization. The suspensor cells during their first elongation develop tubercle-like swellings or 'shoulders' which it is suggested aid in anchoring the base of the proembryo.

Can the foregoing facts be considered as indications of a 'non-specialized embryogeny', as Thomson (15) has suggested? All in all the morphology of the gametophyte and of the embryo proclaims for the Araucarineae a great amount of specialization, and strongly emphasizes the isolated position so generally conceded from the morphological and anatomical study of their mature sporophytes. Certainly on this evidence alone no close relation exists between them and the Cycadales and Gink-

goales. They stand off, likewise, sharply from the other Conifers. Yet in essential underlying features they clearly belong to the latter. Starting with some ancient coniferous stock specialization has followed rather different lines in the araucarian branch from that taken in others. Yet many of the same tendencies have prevailed in both, as an attempt has been made to show above by comparing some characters of the recent groups Taxodineae and Cupressineae, especially of the genus *Sequoia*.

If then this tribe, though somewhat apart from other Conifers, yet distinctly goes together with them on the ground of gametophytic morphology and of embryology, what additional evidence of this position does its mature sporophyte afford? In anatomy, perhaps the most critical features pointing to a distinctness of the Araucarians from other Conifers are the lack of xylar resin canals and of bars of Sanio; and in morphology the question of the underlying structure of the megasporophyll is of the greatest importance. Professor Jeffrey is about to announce the discovery of bars of Sanio and of resin canals, as well as of abietineous pitting in the xylem of araucarian cones. Thus the most conservative region of the sporophyte in this tribe proclaims its origin from a stock possessing characters which have been retained by the Abietineae.

The morphology of the ovulate strobilus of the Coniferales has been a much debated subject. It is apparently now clear, however, that the megasporophyll of the Abietineae represents a modified axillary branch, homologous with the 'short shoot', placed in the axil of a bract. The relations of the two structures are very nearly the same as those of their homologues upon vegetative branches. The vascular supply is similar. The bract, as in all Conifers, receives a bundle from the axis with xylem and phloem arranged as in any leaf. The vascular supply to the sporophyll has the position of the xylem and phloem inverted. It arises like that of an axillary structure,—that is, it is formed by the immediate fusion of two strands departing separately from the central cylinder of the cone above the origin of the bract bundle. Text-figs. 75 to 78 are diagrams to show the condition common to the Abietineae, 75 giving the method of origin of the two strands found in 76. Text-fig. 77, at the very base of the scale, shows the bract, slightly fused, and the bundle of the upper series dividing into three; 78 shows the small free bract, and the scale with its strong series, also the ovular supply bundles passing to the two ovules.

Within the Abietineae these two companion structures have undergone very little change, both retaining their identity. The bract is less prominent in some genera, and is slightly fused at its base to the scale (Text-fig. 77). The vascular supplies of the two are quite distinct throughout. Fusion of these two elements, which is only suggested in this tribe, becomes a prominent feature of the Taxodineae and Cupressineae. In their evolution from abietinean stock the double nature of the elements of the ovuliferous cone

has been somewhat obscured by simplification through fusion. Yet such a condition is evident in the presence of the two series of vascular strands—the lower normally oriented, the upper with reversed xylem and phloem—and by the two free apices on the fertile structure. Both ways in which coalescence and reduction can occur have been seized upon. The resulting strobilar element is in one case composed chiefly of the tissue of the fertile scale, the bract having nearly disappeared; and in the other of that of the bract, the scale being barely represented. The former is much more commonly found. *Sequoia* forms a good example. In this genus the scale has enlarged and folded down, enclosing and obscuring the small bract. This is evident externally by the position of the bract tip, which projects like an umbo centrally from the scale, internally by the vascular supply (Text-figs. 79–81). The entire supply arises together as a cylinder. Soon the two series are formed. That for the bract is a small median bundle. The strong inverted series almost surrounding it is that of the fertile scale. Lateral portions of a false lower series are formed by upfolding from the wings of the enlarged scale.

As examples of bracteal enlargement at the expense of the scale, *Cunninghamia* and two species of *Athrotaxis* may be cited. Externally the presence of the seminiferous scale is evinced in *Cunninghamia* only by a collar-like projection from the region of ovular attachment (Text-fig. 85). In *Athrotaxis laxifolia*, Hook., it is represented by a rounded cushion-like mass upon the prominent bract (Text-fig. 83), whereas in *A. selaginoides* all external evidence of a scale has disappeared. That these vestiges must represent the ovuliferous scale of the Abietineae is evident from the undoubted origin of the Taxodineae, from the occurrence within the tribe of all transitional stages, as well as from the evidence of vascular anatomy given below.

Only in the Araucarians and the Podocarps has the double nature of the female strobilar scale been questioned. Some investigators claim that the megasporophylls in these groups are simple in nature, being merely fertile bracts, strictly homologous with the microsporophylls—and therefore not at all of the same nature as those of the Abietineae. If such is the case, both simple and compound strobili occur in the Coniferales. This is a vital point and concerns deeply the unity of a group which otherwise seems to be clearly a natural one.

The writer will try to show that the strobili of the Abietineae and the Araucarineae are homologous—that those appearances suggesting a simpler origin of the fertile scale are due to nearly or quite complete coalescence and great reduction.

Even within themselves the Araucarineae show a complete series from a form with strobilar units of a distinctly double nature to one most simple through reduction. Further, exactly parallel evolution has taken place in the Taxodineae. The apparently simple sporophyll of the Podocarpineae

is also the result of similar fusion, as Mr. Sinnott is clearly demonstrating in the above-mentioned paper—a complete series existing from forms of *Podocarpus* with free bract and scale to the *Agathis*-like cone scales of *Saxegothaea* and of *Microcachrys*. Too little comparative work has been done on the cone scales of the many genera of the Conifers. On looking over the entire field, the conditions obtaining in the different tribes cannot be interpreted otherwise than as indicating the origin of the araucarian condition. Leaving the discussion of the Podocarpaceae to Mr. Sinnott, the Taxodineae give us *Cunninghamia*, with sporophylls closely similar to those of *Agathis*, and *Athrotaxis*, not only with the species *A. selaginoides*, D. Don., having cone scales internally as well as externally the counterpart of those of *Agathis*, but demonstrating in its other species the origin of such a very reduced scale. *A. cupressoides*, D. Don., has dominant scale and weak bract; *A. laxifolia*, Hook., scale and bract of nearly equal prominence.

The genus *Araucaria* itself must be considered in detail. Its cone scales possess a ventral structure, the ligule, in contrast with those of *Agathis*, which have no outgrowths on the apparently very simple scale. By those who consider the araucarian cone scale to be of double origin, the ligule is generally believed to be the remnant of the fertile scale; by others it is supposed to be merely a ventral outgrowth of the sporophyll. This ligule is found in all species of the genus, but in varying degrees of development—from the stout, prominent structure of *A. Bidwillii*, Hook., to the thin, almost indistinguishable projection in *A. brasiliana*, A. Rich. The vascular supply of the cone-scales varies in like proportion. The anatomy of these structures divides the genus into three distinct groups which show stages in reduction from the abietineous type of vascular supply to that of *Agathis*.

Group I. The vascular supply originates as two entirely separate strands which, though later brought close together and somewhat interlaced below the huge embedded ovule, maintain their independence. The upper forms an inverted series supplying the ovule and the ligule, and the lower a strong bracteal series.

Group II. The vascular supply arises as a single strand, which immediately divides to form two opposed bundles. The upper supplies the ovule and the ligule (whenever the latter has a supply); and the lower, the bract as usual.

Group III. The vascular supply arises as in Group II, but does not divide to form two opposed series, its behaviour being exactly that of the lower primary bundle of Groups I and II.

These three groups, as defined by differences of anatomical structure, correspond in part to the systematic subdivisions of the genus. The section Eutacta, so far as its members have been studied, forms Group II, and Groups I and III fall into the section Colymbea. The latter section thus contains the most primitive and the most specialized forms. The geo-

graphical distribution of the species corresponds to the grouping suggested above: Groups I and II are Australasian, Group III South American.

A. Bidwillii is the only species, so far as known, that falls within Group I. Text-figs. 1–15 demonstrate the course of the bundles supplying the cone-scale. (Note.—All references to figures below are to text-figures, unless otherwise stated.) Fig. 1, a tangential section of a portion of the xylem of the cone-axis, shows the mode of origin of the two strands. The lower, vertically elongated bundle is that of the bract; above, on either side of the gap in the cylinder caused by the exit of this trace, are the two bundles which by immediate union form the primary strand of the upper series. Worsdell (19) has noted this double origin of the vascular supply, and like the writer considers it strong evidence for the double nature of the araucarian sporophyll. However, he states that both the bundles are of compound origin. With this the writer cannot agree. The method of derivation of the bract and megasporophyll in *A. Bidwillii* is exactly that found in the Abietineae. Compare Figs. 75 and 76. Continuing with *A. Bidwillii*, Figs. 2, 3, and 4 follow these two primary strands in their early course. The upper is at first the stronger, but the lower rapidly surpasses it in size. Figs. 5, 6, 7, and 8 show the divisions that occur while still within the cortex of the cone. Each forms a strong series. After they pass into the free scale, the upper is forced downward in the centre by the embedded ovule (Figs. 9 and 10). A median group of small bundles is definitely set off as ovular supply. Figs. 11–15—on a much reduced scale—show the later course taken by the bundles. Those below the ovule disappear in the chalazal region. The rest of the upper series, portions of which have passed along the sides of the ovule as crowded twisted groups, come together behind the ovule in a horizontal series and pass on into the free ligule as strong bundles. The lower group continues its straight course to the end of the structure. Thus we have a vascular supply clearly abietinean—two series of bundles, arising separately from the axial strands of the cone, and completely free from each other throughout. The upper, of double origin, supplies the ovules and the upper section of the scale; the lower furnishes the stout lower section, differing from that of the ordinary bract only in its great development. Fusion has not affected the vascular tissues in any way, and the megasporophyll, though smaller than the huge bract, is free therefrom to a considerable extent, and its bundles have not been reduced.

To the second group belong *Araucaria excelsa*, R. Br.,¹ *A. Cunninghamii*, Sweet., *A. Rulei*, F. Muell., and *A. Cookii*, R. Br. Among these species the ligule is short and small, with a very weak vascular supply, or none at all. Though in the various species the details of the bundle-course are rather

¹ The anatomy of the cone scale in the cases of *A. excelsa* and *A. brasiliana* is as given by Radais (9), Strasburger (12), and Worsdell (19); in all other cases the writer has made his own studies.

Diagrams illustrating the mode of origin, course, and orientation of vascular supply of the cone scale and ovule. Xylem black, phloem unshaded. (Transverse.) Figs. 1-15, *Araucaria Bidwillii*.

different, the essential features are the same. *A. Cunninghamii* has been chosen to represent the section in the diagrams. Fusion has gone on to such an extent that the vascular system is affected, the two series being brought together in their origin (Fig. 16). Immediately, in part while the

bundle is yet within the cortex of the cone, the two series are formed. The upper is entirely given over to supply the ovule. It consists of a series of four to six bundles, all of which pass beneath the ovule and enter its base. The lateral portions of the series, so prominent in *A. Bidwillii*, which pass on into the scale have entirely disappeared. Beyond the ovule no upper series is visible, and the ligule has no supply. The lower series is normal.

A. Cookii from this group is also figured to show features transitional to Group I. An upper series is formed from the single normally oriented bundle, as in *A. Cunninghamii* (Figs. 24–8). As in *A. Bidwillii*, only the central portion of this becomes ovular supply. The lateral portions continue *beyond the ovule* into the distal part of the scale (Fig. 30)—a more primitive state than in *A. Cunninghamii*—but do not reach the ligule as in *A. Bidwillii*. *A. Rulei* closely resembles the former species in this respect: a weak series of upper bundles is formed, some of which tend to be lateral, but all enter the ovule. The inverted series in *A. excelsa*, which consists of a few small bundles, dies out midway beneath the ovule, and the ovular supply is derived entirely from lateral bundles of the lower series.

The third group consists of *A. brasiliانا*, A. Rich, and *A. imbricata*, Pav. Here no upper series at all is formed, and the ovular supply is derived from the lower series very near the base of the ovule, passing directly in. See figures of *A. brasiliانا*, Nos. 32–8. This species represents the greatest reduction in the genus. *A. imbricata* is closely similar. Even external evidence of the ligule has almost disappeared.

Thus the genus *Araucaria* itself presents a type of cone scale—that of Group III—the vascular supply of which is very greatly simplified. And it displays the method and steps of this reduction from a type distinctly abietinean, at least in the origin of its supply.

Further comparisons emphasize the mode of origin of the cone scale of *Agathis*. It has been stated above that the genus *Athrotaxis* displays stages of fusion and reduction of importance in this respect. Figs. 39–59 illustrate this. The longitudinal sections (Figs. 82–4) show the external features and the general plan of the bundle system. *A. cupressoides* (Fig. 82) has a prominent fertile scale which in its expansion has nearly absorbed the bract, the latter projecting as a tiny tongue from the tissue of the former. In *A. laxifolia* (Fig. 83) the two members are about equally developed, the scale resting upon the well-developed bract as a large cushion with rounded end—a very blunt ligule. In the third species, *A. selaginoides* (Fig. 84), all external evidence of a scale has disappeared, the fertile structure having a ventral surface as free of outgrowths as that of *Agathis* or *Saxegothaea*. The change in the bundle systems takes place *pari passu* with that of the external structures. Transverse serial sections demonstrate this. The vascular supply in *A. cupressoides* leaves the stele of the cone as a cylinder (Fig. 39). The latter breaks up immediately on

Diagrams illustrating the mode of origin, course, and orientation of the vascular supply of the cone scale and ovule. (Transverse.) Figs. 16-23, *Araucaria Cunninghamii*; Figs. 24-31, *A. Cookii*; Figs. 32-38, *A. brasiliana*.

entering the scale, and the normal opposed series are formed. The lower series is considerably weaker, and is almost surrounded by the upper (Figs. 43-5). This is a case of strong dominance of the scale series. It is to be compared with *Sequoia*, in which the scale is still more prominent, the

Diagrams illustrating the mode of origin, course, and orientation of the vascular supply of the cone scale and ovules. (Transverse.) Figs. 39-45, *Athrotaxis cupressoides*; Figs. 46-52, *A. laxifolia*; Figs. 53-59, *A. selaginoides*.

bract being represented only by the single median bundle of the lower series (Figs. 79-81).

Passing to the next species, *A. laxifolia*, two series of bundles of about

equal strength are found (Figs. 49 and 50). This means that reduction has occurred in the scale, which is normally far the larger member, and perhaps enlargement in the bract. The bundle originates as a broken cylinder (Fig. 46). The upper series arises from this a short distance out in the scale. Further, the upper series, though well developed, supplies *only the ovules*. Here fusion of the two series has progressed out into the scale, and the upper series has still further disappeared, in that its distal portion is lost—a condition like that found in Group II of *Araucaria*. Compare Figs. 17–23 with Figs. 48–52. Exactly parallel conditions obtain.

A long step towards simplification has been made in *A. selaginoides*. The sporophyll supply arises as a single normally oriented bundle—clearly a remnant of the stronger strand of the other two species. Compare Figs. 39, 46, 53. About one-third the distance out along the scale, a weak upper series of two bundles arises (Figs. 55 and 56). These are ovular supply, and represent the upper series. The lower series continues without change towards the tip.

Another genus of the Taxodineae shows great coalescence and reduction—*Cunninghamia*. Fig. 85, a longitudinal diagram, suggests the extent to which external changes have occurred. A small projection, ligule-like, without vascular supply, situated beyond the attachment of the ovules, is the only vestige of the fertile scale. The bract is much enlarged, with strong bundle system. The upper series, though fairly strong, is ovular supply only. These features are further exemplified in the transverse series diagrams. A single bundle arises from the axis (Fig. 60) as in *Agathis*, *Saxegothaea*, *Athrotaxis selaginoides*, &c. Near the base of the scale this throws off a weak bundle, which inverts itself (Figs. 61 and 62). It immediately divides into three, each of which supplies an ovule (Figs. 63–5). Thus another example is presented of the almost complete dominance of the bract.

The study of these three genera—*Araucaria*, *Athrotaxis*, and *Cunninghamia*, makes intelligible the condition found in *Agathis*. In this genus simplification has reached a very high degree—absolute coalescence of bract and ovuliferous scale, the latter being fused into the former and obliterated. The upper xylem is also extremely reduced, only Group III of the genus *Araucaria* having progressed further in this direction. The former presence of the scale can be detected only by comparisons. Figs. 67–74 and 86 demonstrate the anatomy of the cone scale of *Agathis australis*. A single bundle, normally oriented, leaves the central cylinder of the cone (Fig. 67, and also Pl. IV, Fig. 41), and divides into three (Fig. 68) just before entering the scale base. The median bundle remains undivided throughout its course, though diminishing in size; the lateral bundles divide repeatedly, forming a fan-shaped series of as many as twenty. About half-way out under the ovule the median bundle gives rise to a smaller

Diagrams illustrating the mode of origin, course, and orientation of the vascular supply of the cone scale and ovules. (Transverse.) Figs. 60-66, *Cunninghamia sinensis*; Figs. 67-74, *Agathis australis*; Figs. 75-78, the abietinean type; Figs. 79-81, *Sequoia sempervirens*.

bundle (Fig. 70), which immediately becomes inversely oriented (Fig. 71). This soon divides into two weak strands (Fig. 72) which pass out into the base of the ovule (Fig. 73). Beyond this point only the strong lower series is found (Fig. 74). This will be seen to be almost exactly the structure of *Cunninghamia*, and of *Athrotaxis selaginoides*. In these two plants, however, there is more than one ovule, a feature which causes a slightly less simple arrangement.

In the study of the cone scale of *Agathis*, several species besides *A. australis* were investigated. These in general display a closely similar anatomy. *A. vitiensis* only is divergent. Its upper series has not entirely disappeared. Figs. 87-92 are diagrams to show the origin and position of all bundles of this series. In its proximal portion the vascular series is essentially the same as that of *A. australis*, and has not been represented. The ovular supply consists of many more bundles than in the Kauri, and, further, is drawn from the five or seven median bundles (Figs. 87-9). (The vertical lines limit laterally the ovular supply bundles and those of the lower series from which these arise.) Each of these may divide once or twice, and ten or fifteen bundles enter the ovule. The latter is attached along the edge of a horseshoe-shaped swelling, the curve extending down between the wing-shoulders to the base of the ovule proper. Along this line the bundles pass out (Figs. 90 and 91). Very weak branches pass on from some of these bundles into the scale beyond for a short distance (Fig. 91). Not only do the seven median bundles give off an upper series, but all members of the lower series also divide in this manner. The division of these bundles begins soon after the ovular group has been formed (Fig. 89), and passes progressively outward laterally until each has formed opposite to it an inverted bundle. All of the latter persist to the end of the scale. The appearance given (Figs. 91 and 92) is that of an upper series formed by the folding over of the lower, in the manner in which in *Sequoia* a false lower is formed from the upper. This effect is given by the removal of the central portion by the ovule. The origin of the series is clear. The definite inverse orientation shows that the double series cannot be accounted for merely by the large size of the scale. Thus even in the genus *Agathis* remnants of the double series occur. In *A. Bidwillii* and *A. alba* ten to twelve traces supply the ovule, being derived from the three median traces; in *A. borneënsis* there are six to eight, and in *A. spinulosa* four to eight traces, also all derived from the three median bundles. Thus in the reduction of its ovular supply to two weak strands, and the derivation of those from the median bundle only, *A. australis* seems to be the least primitive.

The Araucarineae and the Podocarpaceae, having simple sporophylls, have been supposed by some to form one section of the Coniferales, and all others with compound strobili another. Thomson (17) has termed the first

Diagrams illustrating the origin and course of the vascular supply of the cone scale. (Figs. 82-6, longitudinal; Figs. 87-92, transverse.) Fig. 82, *Athrotaxis cupressoides*; Fig. 83, *A. laxifolia*; Fig. 84, *A. selaginoides*; Fig. 85, *Cunninghamia sinensis*; Fig. 86, *Agathis australis*; Figs. 87-92, *A. vitiensis*.

forms 'aplosporophyllous' and the second 'diplosporophyllous'. It is evident from the above figures and descriptions that in a 'diplosporophyllous' group, the Taxodineae, we find an 'aplosporophyllous' genus,

Cunninghamia, and further, another genus, *Athrotaxis*, containing both an 'aplosporophyllous' and a 'diplosporophyllous' species. Such fundamental differences could hardly occur even within a natural family, much less within the limits of a genus. In the Araucarineae, a so-called 'aplosporophyllous' tribe, one species, *Araucaria Bidwillii*, is found, the 'diplosporophyllous' nature of which can hardly be questioned. Even in *Agathis* itself there remains a species possessing a cone scale with a double series of bundles. Further, Hollick and Jeffrey (3) have demonstrated a double series of bundles in the cone scales of Mesozoic Araucarians. Apparently the strobili of the Conifers are strictly homologous, and hence the terms 'aplo-' and 'diplosporophyllous' may appropriately be abandoned.

Much of the evidence on which the conclusion was drawn that the fertile structure in the Araucarians and the Podocarps is of simple nature, is related to the orientation of the ovular supply. Thomson (17) has announced that in some Abietineae the ovular supply is inversely oriented, thus a double inversion occurring in the ovuliferous scale. The conclusion is then drawn that, since in *Saxegothaea* and *Microcachrys* the inverted series is very weak, and supplies only the ovules, it is merely ovular supply. This must likewise apply to the Araucarineae. Hence the sporophyll in these forms must be simple. But under these conditions so would be those of *Cunninghamia*, *Athrotaxis laxifolia*, and *A. selaginoides*, which certainly are not of a simple nature. In such cases as *Saxegothaea*, *Agathis*, *Cunninghamia*, *Microcachrys*, and the two above-named species of *Athrotaxis*, the upper series is not merely ovular supply morphologically, though that may be chiefly its physiological function. Naturally the extreme distal portions are, however. These bundles are the last vestige of the upper series, retained to supply the ovules. There is clear evidence of this. These supposedly strictly ovular supply bundles in *Agathis australis* and *A. vitiensis* give off, as they turn into the ovule base, branches which continue the course of the original bundle—a scale supply branch. Further, strands departing to ovules in forms where the upper series is not reduced are not freed until the immediate vicinity of their destination is reached. Why, even if the sporophyll is simple, should an ovular supply be set off far back at the base of the cone scale as in *Saxegothaea* and *Cunninghamia*, or part way out in the scale as in *Agathis* and *Athrotaxis selaginoides*? *Athrotaxis cupressoides* (Fig. 82) suggests the normal point of origin and short course of ovular bundles in that genus. Compare with *A. selaginoides* (Fig. 84). In *Araucaria brasiliiana*, where fusion has undoubtedly gone even farther than in *Agathis*, the ovular supply is derived almost directly beneath the base of the ovule (Figs. 35 and 36). Finally, the ovular supply bundle is not generally inverted. Compare the statements of Radais (9), Van Tieghem (18), and Strasburger (13). It may be oriented normally or laterally, but is most frequently concentric. The orientation may change during the

course. This variable condition might be expected in a minute bundle that follows the short twisting reversed course it usually follows. Hence it is believed that no sound argument can be based on the inversion of the ovular supply.

From comparative and structural evidence it seems, therefore, that the apparently simple cone scale of *Agathis* is really of compound nature, and represents the double structure of the abietinean cone. The Araucarians are thus *Conifers*, even though they have progressed far along a different line from that followed by the other groups. With Mr. Sinnott's (11) demonstration of the similar nature of the cone scale of the Podocarpaceae, it becomes evident that the female cones of all the Conifers are strictly homologous. And hence, since those forms in which the twofold nature is hidden are either—as the Taxodineae—admittedly recent, specialized derivatives of such a double-unit stock, or seem clearly to be such when all evidence is carefully considered, the primitive Conifers must have possessed this type of cone. And the Abietineae in retaining it are thus representatives of ancient, ancestral forms. The unity of the Coniferales as a natural group seems to be established, and the writer cannot too strongly dissent from the opinion expressed by Seward and Ford (10), that the living and extinct Araucarians should form a subdivision of the Gymnosperms, the 'Araucariales'.

From the evidence presented by the study of the morphology of the female cone, the Araucarians occupy the same phylogenetic position as is suggested by their gametophytes and embryos—a highly specialized branch of the Conifers derived far back from some stock possessing abietinean characters. Vestiges of features possessed by this primitive stock are still to be found—the bars of Sanio, opposite pitting, and xylar resin canals recently discovered by Dr. Jeffrey, as well as the double nature of the megasporophyll. All these features have not unnaturally been almost lost during the long period of separation and divergent development of the araucarian stock. Meanwhile, as is clear from the evidence of fossils, this group flourished, a great series of widely variable forms inhabiting much of the world during the Mesozoic. Under such circumstances the few surviving members might well be highly specialized forms. That the same general evolutionary tendencies have prevailed, however, as in all Conifers, is evident from the similar results brought about in forms admittedly at the extreme end of another branch from the primitive stock—in the genera *Cunninghamia*, *Athrotaxis*, *Sequoia*.

As between the two genera, *Agathis* and *Araucaria*, the latter, as regards the morphology of the ovulate strobilus, is the more primitive on the whole, though it contains species (*A. brasiliensis* and *A. imbricata*) which have progressed further than any species of *Agathis*. Too little is yet known of the early life-history of *Araucaria* to determine from that stand-

point what relation it may bear to *Agathis*. It seems evident that within the latter genus the species selected for this investigation, *A. australis*, is the least primitive.

SUMMARY.

1. *Agathis australis* is monoecious. Ovulate strobili appear about October first; pollination occurs one year later, and fertilization thirteen months after pollination.

2. The mature gametophyte is club-shaped, the larger upper section bearing numerous scattered archegonia.

3. The archegonial jacket is incomplete near the neck, the cells of which are thick walled and form a complex which resists the entrance of the pollen-tube.

4. The pollen germinates in the axil of the cone scale, no micropyle being differentiated at that time. Long, branching haustorial pollen-tubes penetrate the cone axis, also the phloem and even the xylem of the scale traces. In other species of *Agathis* they also invade the axial bundles.

5. The two male elements are cells, somewhat unequal in size, limited by delicate walls. The nucleus equals in size that of the egg.

6. The fusion nucleus maintains a central position in the archegonium, and five or six consecutive free nuclear divisions ensue.

7. The mature proembryo is complex. Of its three tiers the median is the embryo proper, the upper forms suspensors, and the lower is an elaborate penetrative and protective cap.

8. The cone scale of *Agathis* is double in nature, homologous with the bract and megasporophyll of the Abietineae. Exactly parallel fusion and reduction have taken place in the Taxodineae.

9. The morphology of the gametophyte, of the embryo, and of the ovulate strobilus bespeaks strong specialization.

10. The Araucarineae represent a highly specialized divergent branch of the Coniferales. Those features which at first glance seem to relate them to more primitive Gymnosperms are the result of specialization and reduction.

11. The two genera, *Araucaria* and *Agathis*, are closely related; *Agathis* is probably the more recent, and within the genus *A. australis* the highest type.

METHODS.

In preparing the ovules both sides were cut off, the embryo-sac being freely exposed or sectioned. A chrom-acetic solution—1.0 per cent. chromic acid and 0.8 per cent. acetic acid—was used as a killing and fixing agent. This was allowed to act at least twenty-four hours, and even three to five days in some cases. The long immersions produced equally

good, if not better results, and the material was considerably bleached. The usual methods of dehydrating and embedding in paraffin were employed. Sections were cut five and ten micra thick, and stained with Haidenhain's haematoxylin and safranin.

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DESCRIPTION OF PLATES I TO IV.

Illustrating Mr. Eames's paper on *Agathis australis*.

Note: The figures are of *Agathis australis*, with the exception of Nos. 37 and 42.

PLATE I.

- Fig. 1. Habit; showing mature male cones, and female cones at time of pollination and of fertilization. $\times \frac{1}{3}$.
- Fig. 2. Longitudinal section of ovule just before fertilization; showing distribution of archegonia and freedom of nucellus. $\times 7$.
- Fig. 3. The same; after fertilization. The suspensors have thrust the embryo down into the lower portion of the endosperm. $\times 7$.
- Fig. 4. Longitudinal section of the ripe seed; showing the large embryo and the dry beak. $\times 6$.
- Fig. 5. Longitudinal section of young ovule; showing developing embryo-sac and 'spongy tissue'. $\times 500$.
- Fig. 6. Portion of Fig. 3 enlarged to show course of suspensors. $\times 25$.
- Fig. 7. Longitudinal section of tip of mature gametophyte and surrounding tissue; showing the cap of the megaspore membrane. $\times 80$.
- Fig. 8. Longitudinal section of suspensor coil with embryo. $\times 80$.
- Fig. 9. Longitudinal section of upper portion of nucellus and gametophyte; showing erosion of the latter by pollen-tubes. $\times 80$.
- Fig. 10. The same; showing course of pollen-tubes. $\times 80$.
- Fig. 11. A typical mature archegonium. $\times 125$.
- Fig. 12. The archegonium with mature central cell. $\times 250$.

PLATE II.

- Fig. 13. Archegonium (sectioned somewhat obliquely); showing young egg nucleus and ventral canal nucleus, the latter at the side and beginning to disorganize. $\times 250$.
- Fig. 14. Archegonium with young egg nucleus and ventral canal nucleus in median position. $\times 200$.
- Fig. 15. Archegonium showing 'pseudo-fertilization'. $\times 500$.
- Fig. 16. Body cell just before division, passing down between nucellus and embryo-sac. $\times 500$.
- Fig. 17. The male cells passing down between the nucellus and the gametophyte; the large nuclei are prominent, the limitation of the cytoplasm about each can faintly be seen. $\times 500$.
- Fig. 18. A male cell with tube cytoplasm and two accompanying nuclei. $\times 500$.
- Fig. 19. The young egg nucleus and surrounding cytoplasm, seen in transverse section of the archegonium. $\times 1,000$.
- Fig. 20. The mature egg nucleus with surrounding cytoplasm, seen in transverse section of the archegonium. $\times 1,000$.
- Fig. 21. The fusion nucleus and its kinoplasmic sheath with the intranuclear spindle of the first division. $\times 1,350$.
- Fig. 22. The proembryo: two-nuclear stage, the nuclei large and free from the kinoplasmic sheath. $\times 1,200$.

Fig. 23. The same; thirty-two-nuclear stage, transverse section; showing lower part of young suspensor cap. $\times 800$.

Fig. 24. The same; vertical section at time of first wall formation. Three tiers of cells are evident: the upper, suspensor initials; the median, the embryo proper; the lower, the undifferentiated embryonic cap. $\times 800$.

PLATE III.

Fig. 25. The archegonium at time of fertilization; showing the large male nucleus in the centre. $\times 500$.

Fig. 26. The same archegonium, a section just below Fig. 25; the egg nucleus is seen, and a small tangential section of the male nucleus. $\times 500$.

Fig. 27. The fusion nucleus surrounded by the kinoplasmic sheath. $\times 700$.

Fig. 28. The proembryo; thirty-two-nuclear stage with suspensor cap of cytoplasm. $\times 600$.

Fig. 29. The proembryo in the archegonium; four-nuclear stage. $\times 300$.

Fig. 30. The same; eight-nuclear stage. $\times 300$.

Fig. 31. The proembryo almost mature; showing the suspensors elongating distally, the embryo proper, and the penetrative cap. $\times 350$.

Fig. 32. The embryo proper with its penetrative cap and the base of its suspensors penetrating the endosperm. $\times 700$.

Fig. 33. The embryo enlarging, the cap disintegrating. $\times 700$.

Fig. 34. The same; a slightly later stage. $\times 700$.

Fig. 35. The same; a still later stage; the cap has disappeared. $\times 700$.

Fig. 36. The proembryo; thirty-two-nuclear stage, before suspensor-cap formation. $\times 800$.

PLATE IV.

Fig. 37. *Agathis borneensis*; transverse section of axial bundle of the cone; showing invasion by pollen-tubes. $\times 125$.

Fig. 38. Transverse section of archegonium neck and surrounding tissue; showing erosion by pollen-tube around the resistant neck cells. $\times 250$.

Fig. 39. Top of archegonium with thick-walled neck cells. $\times 800$.

Fig. 40. Transverse section of archegonium neck. $\times 500$.

Fig. 41. The trace of the megasporophyll within the cortex of the cone; showing a pollen-tube in the xylem, also three in the phloem at the lower side of the figure. $\times 250$.

Fig. 42. *Araucaria Bidwillii*; transverse section of the vascular supply of the megasporophyll close to the cone axis; showing the two original bundles, the upper inverted. $\times 40$.

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