On the Gametophytes and Embryo of *Pseudolarix*.

BY

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With Plate XLVIII.

ALTHOUGH the gametophytes, fertilization, and embryogeny of the Abietineae may, at present, be said to be the best known among the Coniferales, there remain still some genera of which the gametophytic structures are entirely untouched by investigators. Among the existing nine genera of the Abietineae, the genus *Pinus* has been most thoroughly investigated. We have also more or less complete records of the gametophytes of *Picea*, *Abies*, *Tsuga*, *Pseudotsuga*, and *Larix*.¹ But, in the remaining three genera—*Cedrus*, *Pseudolarix*, and *Keetleria*—this phase of life-history is entirely unknown. In light of the accumulating evidence in support of the view that the Abietineae is a very ancient group of the Coniferales,² it has been thought very desirable that the gametophytic phase of all the genera of the group should thoroughly be worked out. The present study has been undertaken with this object in view and to fill up one of the gaps in our knowledge of the life-history of the Abietineae.

Pseudolarix Kaempferi, the only species of the genus, is a native of China and seems to thrive quite well in Southern Europe. The material for the present study has been secured from Northern Italy, through the kindness of Dr. R. Rovelli in Pallanza, in whose garden a beautiful specimen of this tree is growing, and to whom we are very much indebted. During the years 1903 and 1904, it was sent from there to Bonn, Germany, where one of us (K. M.) was staying at the time. The living male or female cones with part of the attached branches were sent two or three times a month

¹ Chief contributions to our knowledge of the gametophytes and embryo of the Abietineae are those of Hofmeister ('51, '58), Strasburger ('69, '72, '78, '79, '84, '92), Goroschankin ('80, '83a, '83b), Sokolowa ('90), Mottier ('92), Belajeff ('93), Dixon ('94), Coulter ('97), Blackman ('98), Chamberlain ('99), Cavara ('00), Murrill ('00), Arnoldi ('00), Coulter and Chamberlain ('01, '10), Ferguson ('01a, '01b, '04), Miyake ('03a, '03b), Thomson ('05), Stopes and Fujii ('06), Kildahl ('07), and Lawson ('09).

² Concerning the anatomical and palaeontological evidences, see Jeffrey ('05, '08) and Hollick and Jeffrey ('09).

during April to July. Part of the material was always fixed immediately after being received, and the remainder put in a moist chamber to be fixed later. The cone-bearing twigs were usually inserted into water under a bell-jar, and it was found that the cones showed normal development at least for several days.

The fixing was done usually with Flemming's chromosmo-acetic acid solution, chrom-acetic acid mixture being occasionally employed. After being embedded in paraffin in the usual way, the material was cut 5–10 μ in thickness. For staining, Flemming's triple combination or Heidenhain's iron-alum haematoxylin were used.

On account of the insufficiency of the material our results are not quite so complete as we had wished, but they show distinctly that the gametophytes and embryogeny of *Pseudolarix* closely follow the normal Abietinous type.

THE MALE GAMETOPHYTE.

The microspore seems to be quite mature at the end of March. In the male cones received early in April, the microspores were already fully formed, with well-developed wings, and many of them were found in the process of division. In fact, in cones of the same date we may find various stages of division which are described in the following paragraphs.

The nucleus of the mature microspore soon divides to form the first prothallial cell (Pl. XLVIII, Figs. 1–3). The first prothallial cell shows signs of disintegration soon after its formation and is at first found as a lenticular cell at the dorsal side of the microspore (Fig. 4). It, however, disorganizes quite rapidly and sooner or later becomes flattened against the spore wall (Figs. 5, 7). The second division follows immediately, and the second prothallial cell is organized, which soon shares the same fate as that of the first (Figs. 5, 7, 8–11). Fig. 6 shows a polar view of a spindle of one of these divisions and the number of chromosomes is seen to be distinctly twelve.

As the third division, resulting in the formation of the generative and tube cells, is completed, the two prothallial cells are seen as thin darkly staining bodies pressed against the dorsal wall of the pollen-grain (Fig. 8). The generative cell soon divides, and the so-called body and stalk cells are formed (Figs. 9–11). Now the pollen is ready for pollination. The number of cells in the mature pollen-grain of *Pseudolarix* is the same as in *Larix* (Strasburger '72, '92) and *Picea* (Strasburger '92, Miyake '03 a), while it differs from that of *Pinus*. In the latter the generative cell does not divide until some time after pollination (Strasburger '92, Ferguson '04).

Pollination seems to take place in Northern Italy about the middle or the latter part of April. It seems to occur somewhat later in Southern Germany; for, judging from the male cones received from Baden-Baden

on May 13, 1904, which were in the last stage of pollination, the latter had probably begun at the beginning of the same month.

The further development of the male gametophyte after pollination has not been investigated.

THE FEMALE GAMETOPHYTE.

The division in the formation of the megaspores seems to occur about the time of pollination, the megaspore mother-cell being as a rule solitary in each ovule. Stages of the division were not observed, nor has the number of potential megaspores been determined. The lowest of the megaspores soon begins to enlarge and develops into the female prothallium, while the upper sister cells gradually disintegrate and are crowded to the upper corner of the growing gametophyte. Fig. 12 shows a young female gametophyte with two free nuclei which are embedded in the parietal layer of cytoplasm surrounding a large central vacuole, and the disorganizing remains of the sterile megaspores are seen at the upper part of it. It is probable that the parietal layer of cytoplasm is organized at one-nuclear stage, as has already been reported in *Pinus* (Ferguson '04) and *Cunninghamia* (Miyake '10). The free nuclear division in the megasporic sac takes place hand in hand with the enlargement of the latter as in other Conifers.

Fig. 13 shows the condition of a young female prothallium about four weeks after that of Fig. 12. It is surrounded by several layers of well-developed tapetal cells. After much enlargement and more nuclear divisions, the walls are formed between the nuclei, and finally the entire megasporic sac is filled up with compact prothallial tissue. At this time the tapetum is much compressed by the growing prothallium, and shows signs of disintegration.

The so-called megaspore membrane enclosing the female prothallium is at first thin and delicate. During the growth of the prothallium the membrane becomes thicker and more conspicuous. Its structure and thickness are on the whole similar to those described for other Abietineae (Thomson '05, Lawson '09). Fig. 14 is drawn from the lateral basal region of a mature prothallium, showing the well-developed megaspore membrane, which measures about 4.5μ in thickness. The exosporium shows characteristic radial striations, and is several times as thick as the homogeneous endosporium. Thomson ('05), who has studied the megaspore membrane in five genera of the Abietineae, states that in this group 'the coat is thick in the chalazal region, and thins out gradually towards the micropylar portion of the prothallium, being not more than one-third as thick at the apex as at the base of the macrospore'. He found, however, that in *Larix* 'there is scarcely a trace of the megaspore coat in the archegonial region'. Lawson ('09) also found a similar thing in *Pseudotsuga*, and says that 'at a plane

almost level with the base of the archegonia the membrane thins out rather abruptly, and from this region to the very apex of the prothallium no trace of the membrane could be detected'. In *Pseudolarix*, as in the majority of the Abietineae studied by Thomson, the megaspore membrane is present in the micropylar region of the prothallium, where it is much thinner than at the basal portion.

As soon as the female gametophyte is filled with solid prothallial tissue, archegonial initials appear at the micropylar end of the prothallium. This seems to take place early in June. One of the earliest stages of the young archegonia observed is shown in Pl. XLVIII, Fig. 15. This is figured from the material received on June 6. The archegonial initial has already divided once, and the primary neck-cell is cut off from the central cell.

The primary neck-cell is soon divided into two cells by an anticlinal wall (Fig. 16). The two cells then divide again by walls perpendicular to the first. The four cells thus formed usually divide once more by periclinal walls, and two tiers of four cells each are formed (Fig. 22). These constitute what may be called the normal neck of the mature archegonium. In some archegonia, however, the neck was found in a longitudinal section to consist of two tiers of four cells each, suggesting that there may be eight cells in each tier.

The central cell increases in size quite rapidly, and in about three weeks after the formation it reaches the full size. In the early stages of development it contains a large vacuole occupying the greater part of the cell (Figs. 15, 16). The presence of a similar vacuole has been observed in the young archegonia of *Tsuga* (Murrill '00), *Taxodium* (Coker '03), *Cunninghamia* (Miyake '10), *Dioon* (Chamberlain '06), and several Cupressineae (Strasburger '79, Land '02, Norén '07, Lawson '07), and may probably represent the normal condition in the young central cell of the Gymnosperms. The formation of the central vacuole may be considered as a result of the growth of a cell without a corresponding increase of its cytoplasm, as in the case of the young female gametophyte. Later, the vacuole gradually decreases in size, and the cell is gradually filled up with cytoplasm. The cytoplasm is at first vacuolate, but later it becomes more dense and granular. The nucleus is, from the first, always situated at the apex of the cell just beneath the neck (Figs. 15-17).

Enveloping the central cell is a layer of sheath or jacket cells, which are scarcely distinguishable from the adjacent cells of the prothallium in the early stage of development (Fig. 15). But later the cytoplasmic contents become more dense and the nuclei much larger, and in the mature archegonium they are well differentiated (Figs. 22, 23).

The number of archegonia in a single ovule varies from four to seven, the more usual number being five or six. As in other Abietineae the archegonia are arranged quite separate from one another, and they may

come in contact in the middle region where they are widest. Even there the egg-cells never come into direct contact as in the Cupressineae and some of the Taxodineae, but they are always separated by one or two layers of jacket cells (Fig. 23). Each archegonium has its own archegonial chamber, and this more or less funnel-shaped depression above the neck is not so deep as that in *Pinus* (Ferguson '04) and *Tsuga* (Murrill '00) (Figs. 22, 25, 30).

As the central cell of the archegonium reaches its full size, the nucleus prepares for division. Figs. 18 and 19 show the early prophase of the division, and we can see that the chromatic contents of the nucleus accumulate near the centre of the cavity in a condition suggesting the synapsis of the reduction division, as has already been observed in various other Abietineae (Murrill '00, Miyake '03 *a*, '03 *b*). The first indication of the spindle formation is the appearance of a fibrous cytoplasmic cap at the lower side of the nucleus (Fig. 19). The process of the division does not seem to differ from that of other Abietineae. Fig. 20 shows the metaphase of the division; the spindle is more or less pointed at the lower end and somewhat blunt on the upper side, as has often been observed in *Pinus* (Ferguson '04) and *Picea* (Miyake '03).

The result of the division is the formation of the ventral canal-cell. The cell shows, however, signs of disintegration as soon as it is formed (Fig. 21). In the mature archegonium ready for fertilization, the ventral canal-cell usually appears as a deeply-staining lenticular or crescent-shaped cap over the top of the egg (Figs. 22, 24).

The egg nucleus begins to enlarge soon after its formation, and moves down towards the centre of the egg. The mature egg nucleus situated near the centre of the archegonium is more or less spherical or elliptical and usually contains a nucleolus (Fig. 22). It has often been observed that the chromatic substance arranged in more or less irregular reticulum does not fill up the entire nuclear cavity, but is somewhat contracted on one side (Figs. 22, 24). This condition has been quite frequently found in apparently well-fixed eggs, but we have not been able to determine whether this is a normal structure or an artifact caused by reagents.

After the division of the central cell, the number and size of the vacuoles in the cytoplasm gradually decrease, and in the mature egg there are usually found a few smaller vacuoles. The number of so-called proteid vacuoles seem to be not so numerous as in some other Abietineae (Figs. 17-22).

In the mature archegonium previous to fertilization we have sometimes found an extra nucleus at the upper part of the egg (Fig. 24, *x*). A similar nucleus has been observed in the mature archegonium of *Tsuga* (Murrill '00) and *Abies* (Miyake '03 *b*). Murrill calls such a nucleus in *Tsuga* the nuclear vacuole. The origin and fate of the nucleus have not been followed.

THE EMBRYO FORMATION.

Fertilization takes place about the end of June. The actual fusion of the sexual nuclei was not observed. But various stages of the embryo formation were followed. The process does not differ from the usual *Abietineae* type. The result of the division of the fusion nucleus is shown in Pl. XLVIII, Fig. 25. The two daughter nuclei soon divide, and the four free nuclei of the proembryo now move down towards the base of the archegonium (Fig. 26). Upon reaching the base of the egg, the four nuclei arrange themselves in a plane, as shown in Fig. 27. They then undergo further division, and the walls are formed between the eight daughter nuclei. Thus a tier of four completely walled cells is cut off below, and the upper four nuclei being separated from one another by walls are exposed above to the rest of the egg cytoplasm (Fig. 28).

The eight nuclei divide once more, and eventually there are formed four tiers of cells of four cells each, the upper tier being incompletely walled, since the nuclei are separated from one another by walls, but freely exposed above to the unsegmented part of the egg (Figs. 29, 30). The lowest tier forms the embryo proper, the tier above is elongated to form the suspensor, and the uppermost of the completely walled tiers constitutes the rosette (Fig. 31). The young embryo in Fig. 31 is apparently in eight-cell stage.

SUMMARY.

The mature pollen-grain has wings and contains the large tube cell, smaller generative and stalk cells, besides the disintegrated remains of two prothallial cells. The stages of division in the formation of these cells were observed. The number of chromosomes was found to be twelve.

Pollination takes place in Northern Italy about the middle or the end of April, and it seems to be somewhat later in Southern Germany. The further development of the male gametophyte after pollination has not been investigated.

The formation of the megaspores seems to occur about the time of pollination, the megaspore mother-cell being usually solitary in each ovule. The lowest of a row of megaspores develops into the female gametophyte.

The large central vacuole of the young female prothallium seems to be formed already at one-cell stage. The enlargement of the functional megaspore goes hand in hand with the free nuclear division.

The young female gametophyte is surrounded by several layers of well-developed tapetal cells, which later show signs of disintegration.

The megaspore membrane is well developed in the mature prothallium and has about the same structure and thickness as that of other *Abietineae*. It is quite thick in the basal region and thins out gradually towards the micropylar region of the prothallium.

The female gametophyte is filled with solid tissue early in June, and soon the archegonial initials appear at the micropylar end of the prothallium. The archegonia reach the mature size in about three weeks.

The development and structure of the archegonium do not seem to differ much from those of other Abietineae. The number of archegonia in a single ovule varies from four to seven, the more usual number being five or six. The neck consists usually of eight cells, arranged in two tiers of four cells each.

In the division of the central cell of the archegonium, the chromatic contents of the nucleus at first accumulate near the centre of the cavity as in synapsis. The ventral canal-cell is formed as a result of the division, and it shows immediately signs of disorganization. The egg nucleus increases in size soon after its formation, and moves down towards the centre of the egg.

Fertilization takes place about the end of June. The actual fusion of the sexual nuclei was not observed. The first two divisions of the fertilized egg nucleus take place near the centre of the egg, and the four free nuclei of the proembryo move down to the base of the archegonium. The four nuclei now divide again, and the walls are then formed between eight free nuclei, which are arranged in two tiers.

The nuclei of both tiers divide once more, and eventually the proembryo consists of four tiers of four cells each, the uppermost of which is open at the top. The lowest of the tiers becomes the embryo proper, the next tier above elongates to form the suspensor, and the uppermost of the completely walled tiers constitutes the rosette.

The structure and development of the gametophytes and embryogeny of *Pseudolarix* follow the normal Abietinous type.

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EXPLANATION OF FIGURES IN PLATE XLVIII.

Illustrating Dr. Miyake and Miss Yasui's paper on *Pseudolarix*.

All figures were drawn with the aid of a camera lucida.

- Figs. 1-3. Stages in the first division of the microspore. $\times 1,400$. April 2.
- Fig. 4. The first prothallial cell is formed. $\times 1,400$.
- Fig. 5. Division in the formation of the second prothallial cell. Disorganized first prothallial cell is seen as a thin deeply staining body. $\times 1,400$.
- Fig. 6. A polar view of a spindle of one of the first two divisions of germinating microspore, showing twelve chromosomes. $\times 1,400$.
- Fig. 7. The second prothallial cell is formed. $\times 1,400$.
- Fig. 8. The third division is completed. The generative cell, the tube cell, and the remnants of two degenerating prothallial cells are shown. $\times 1,400$.
- Figs. 9, 10. Stages in the division of the generative cell. $\times 1,400$.
- Fig. 11. Mature pollen-grain just before pollination, showing the tube cell, the body and stalk cells, besides two degenerating prothallial cells. $\times 1,400$.
- Fig. 12. The two-nucleated stage of the female gametophyte. One of the two nuclei, outline of which is shown here, appears in next section. $\times 480$.
- Fig. 13. Young female prothallium surrounded by several layers of tapetal cells. $\times 90$. May 22.
- Fig. 14. A lateral basal portion of the periphery of a mature female prothallium, showing the structure of the megaspore membrane. $\times 480$.
- Fig. 15. Young archegonium with a single primary neck-cell. $\times 160$. June 6.
- Fig. 16. A later stage with two neck-cells. $\times 160$. June 13.
- Fig. 17. Upper portion of a full-grown central cell shortly before division. $\times 310$.
- Figs. 18, 19. Prophase in the division of the central cell. $\times 310$.
- Fig. 20. Metaphase of the division. $\times 310$.
- Fig. 21. The division is almost completed. $\times 310$.
- Fig. 22. Mature archegonium. $\times 105$. June 26.
- Fig. 23. Cross-section of a mature prothallium showing seven archegonia. $\times 80$.
- Fig. 24. Upper half of a mature egg, showing an extra nucleus (*x*) just below the disintegrating ventral canal-cell (*v.c.c.*). $\times 160$.
- Fig. 25. The two daughter nuclei resulting from the first division after fertilization. $\times 105$.
- Fig. 26. A later stage, with the four free nuclei of the proembryo. $\times 105$.
- Fig. 27. The four nuclei at the base of the archegonium. Only two of them are shown. $\times 105$.
- Fig. 28. The eight-nuclear stage, showing the formation of walls between the nuclei. $\times 105$.
- Figs. 29, 30. Formation of the proembryo is completed. $\times 105$.
- Fig. 31. A later stage, showing the elongating suspensor. $\times 105$.

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