EMBRYOGENY (Figs. 13.37, 13.38)

The zygote immediately germinates. It undergoes a series of divisions still enclosed within the ovule, to form a relatively elaborate **Pro-embryo**. Before divisions, the nucleus of the zygote is in central position. It divides twice to form four nuclei, which migrate to the chalazal

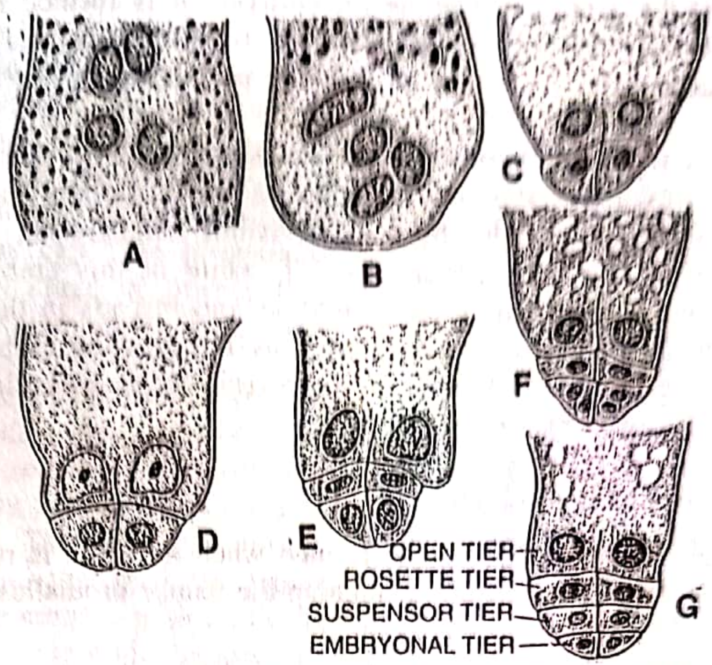

Fig. 13.37 Early stages in the development of embryo in *Pinus wallichiana* (After Konar)

end of the archegonium. They divide again. The resultant eight nuclei arrange themselves in two tiers of four each. Walls appear between the four basal nuclei. The upper four nuclei take no further part in the development of the embryo. Each of the four small cells of the basal tier divides once by a transverse wall to form two tiers of four cells each. The cells of the lower tier divide again. In this way three tiers of four cells each are formed. The fourth uppermost tier is formed by the four free nuclei which as stated above take no share in the development of the embryo and are separated by imperfect walls. They form an open upper tier without walls on one side. This symmetrical group of sixteen cells is called the **pro-embryo**. The four lowermost cells farthest from the micropylar end constitute the **embryo tier**. Each of these may develop into an embryo. The cells next above the embryonal cells constitute **suspensor tier**. The third tier from below is called the **rosette** tier. The suspensor cells elongate considerably and push the embryonal cell out of the archegonium and deep into the tissue of the female prothallus, at the expense of which they grow. The four suspensor cells undergo cleavage on fourth elongation and separate from each other. Each suspensor cell has a rapidly dividing embryonal cell at its tip. As division continues in the embryonal cell, it passes through the quadrant and then an

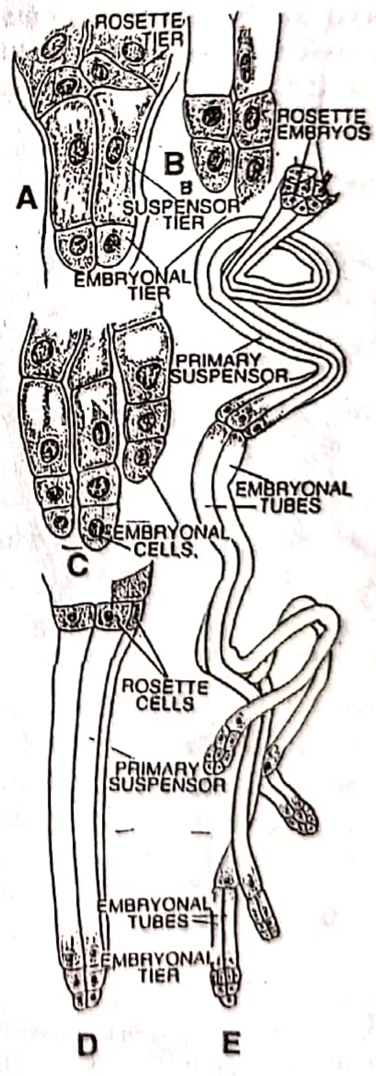

Fig. 13.38. Later stages in development of embryo in *Pinus wallichiana*. (After Konar)

octant stage. Each of the octants is a **potential embryo**. It is formed from one embryonal cell only. There are thus four potential embryos formed from one fertilized egg. This curious feature of **embryogeny** is termed as **cleavage polyembryony** in contra-distinction to the similar condition which may be the result of fertilization of more than one archegonium. This is **simple polyembryony**. In the course of further deveopment of the potential embryos, one takes the lead and grows more rapidly than the others. The actively growing potential embryo by cell division, cell growth and differentiation becomes the embryo of the seed, others die off, while in this embryo development is taking place. The female prothallus grows, enlarges and inroads in the nucellus. Its cells become packed with food material which is used by the growing embryo and also serves a reserve in the seed. Sometimes the cells of the rosette tier also develop into embryos and this is called **rosette polyembryony**.

Formation of Seed (Figs. 13.39—13.42)

It is rather complicated structure and is formed when the cone is running into its third year. It is formed from the mature ovule (containing the female prothallus and embryo) which with its contents falls from the tree as a seed.

The growing embryo feeds on the central tissue of the female prothallus. The space so formed is filled with the folds of the massive suspensor. As the embryo matures the suspensor eventually dries to form a coiled thread towards the root end of the embryo. The embryo at this stage becomes dormant. The outer unused layers of the female prothallus tissue persist in the mature seed and function as a nutritive tissue surrounding the embryo. It is the so called **endosperm**. It is different in origin from the endosperm of

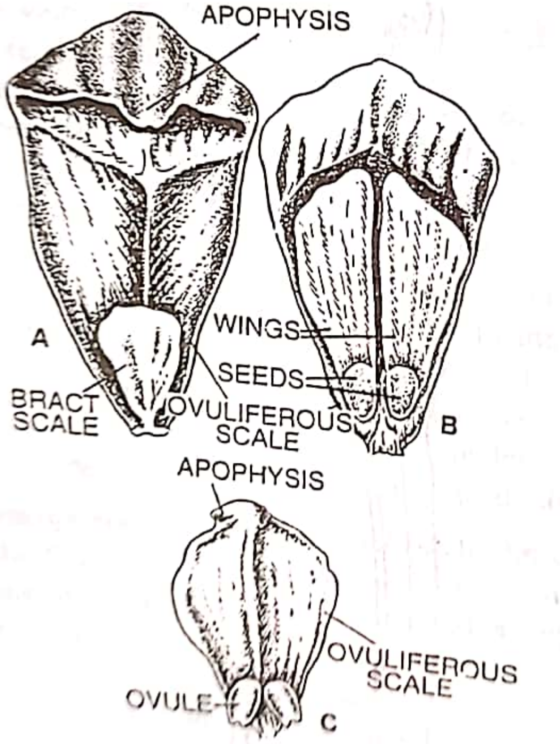

Fig. 13.39. A—C. Mature megasporophyll of *P. roxburghii* as seen from ventral side. B. Megasporophyll bearing two seeds. C. Megasporophyll bearing two ovules.

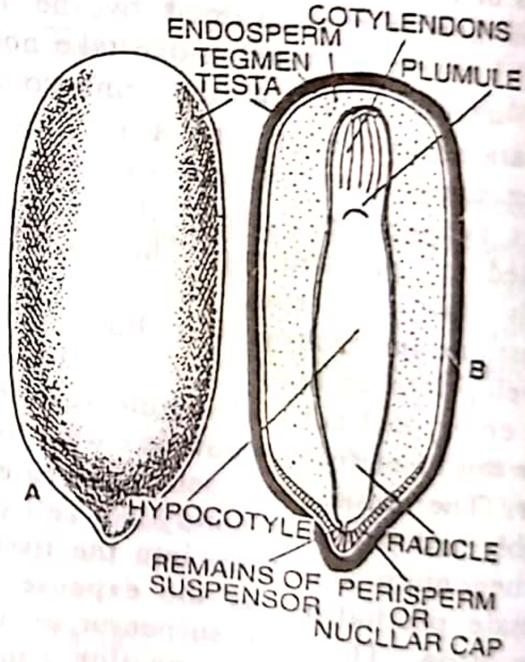

Fig. 13.40. A—B. A. Seed of *P. gerardian.* B. L.S. of seed.

angiospermic seeds but has the same function. It will be recalled that as the female prothallus enlarges and becomes laden with food materials, it invaded the surrounding nucellar tissue which is invariably crushed except for a thin cap-like structure at the micropylar end of the endosperm. It is called the **nucellar cap**. The integument, which at an early stage of development consists of a median stony layer with inner and outer layers of soft cells, dries up. The outer layer of the soft cells disappears, the middle stony layer hardens to form the **testa** and the inner soft layer forms a thin brown membranous covering called the tegmen. The seed now consists of the hard testa, the papery tegmen, endosperm and the embryo with a nucellar cap at the micropylar end. As the seed matures a thin layer of tissue from the upper surface of the ovuliferous scale separates as a membranous wing which is attached to the testa and aids in seed dispersal. The pine seed is now ready to be liberated. At this stage the female cone is in its third year. It is large, dry, brown and woody. Under dry atmospheric conditions the ovuliferous scales spring apart and the winged seeds, as they escape from the cones, are blown away by the wind. The opened out ovuliferous scale is a large, thick woody structure with two seed pits at its base and well marked wing impressions on its upper surface in continuation with the seed cavities.

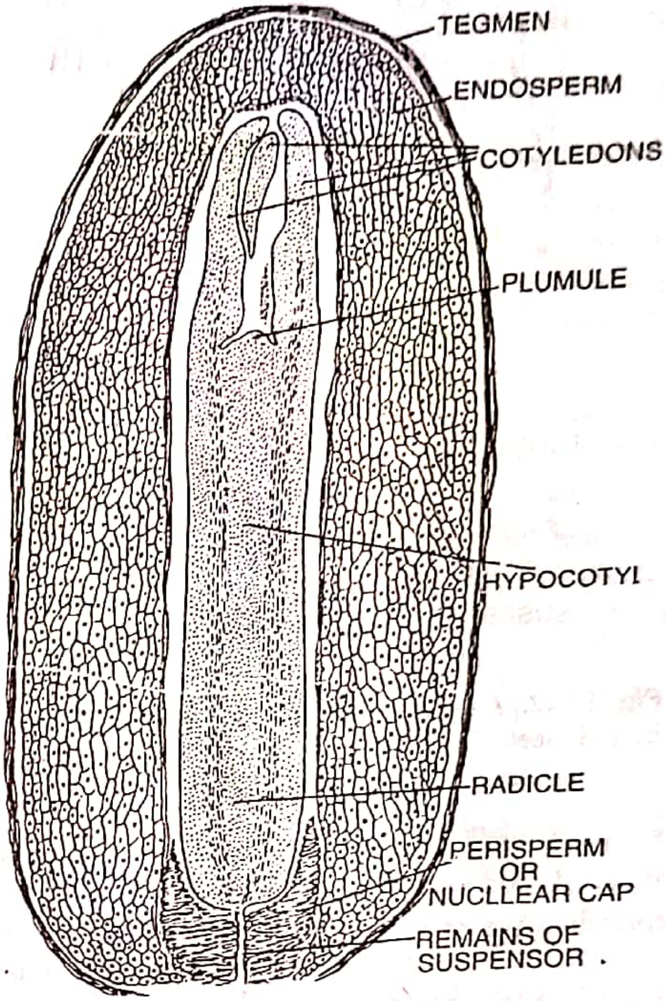

Fig. 13.41. L.S. seed of *Pinus roxburghii*.

The seeds of *Pinus gerardiana*, which are commonly known as chilgoza, are fairly large and used as human food.

Structure of the Seed

There is the outer hard shell or seed coat called the **testa**. It protects the inner delicate parts of the seed from drying and mechanical injury. Within the testa is the brown papery inner seed coat called the **tegmen**. The latter surrounds a white fleshy kernel which on analogy with angiospermic seeds is often called the **endosperm**. Towards the pointed end of the endosperm is the nucellar cap which represents the remains of the nucellus. In the centre of the endosperm is a distinct central cavity in which lies the embryo. The embryo is straight and consists of a short axis bearing a ring of about ten slender, yellow cotyledons at the end, away from the micropylar end. The axis is differentiated into the radicle towards the micropylar end, the **hypocopyl** forming a major portion of the axis below the cotyledons and the tiny conical stem apex or **plumule** (epicotyl) which is surrounded by the cotyledons. The tip of the radicle is attached to a dry, coiled, thread-like structure, the dried up **suspensor** (suspensor can be better seen if the kernels are soaked in a solution of alcohol and glycerine before examination).

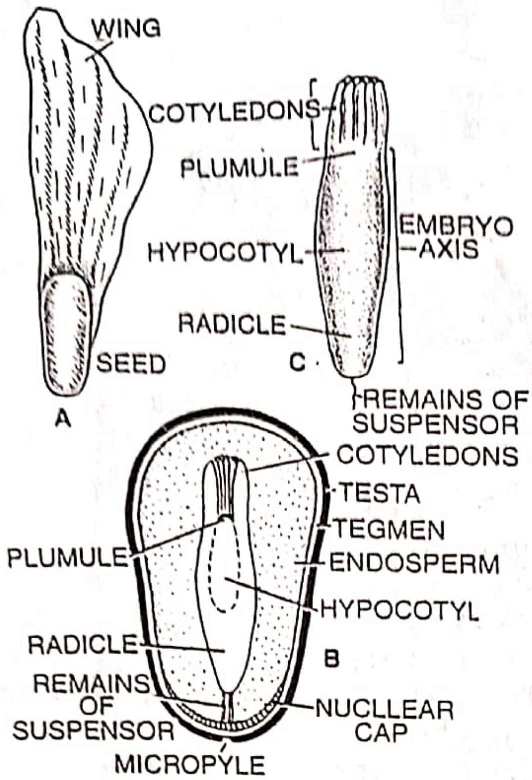

Fig. 13.42. A—C. A. Winged seed of *P. roxburghii.* B. L.S. seed. C. The embryo after taking it out from the seed.

Morphology of the Seed

From the detailed description of the structure of the seed it is evident that the seed of *Pinus* or other gymnosperms is not a single structure. It is made up of tissues which do not belong to the same generation. It represents three generations as follows :

The testa or seed coat which is the matured integument and the nucellar cap, which represents the remains of the nucellus (megasporangium) are parts of the old sporophyte (pine tree) ; the food storage tissue of the female prothallus which is often called the endosperm and surrounds the embryo represents the next generation, the **female gametophyte.** The third generation is an immediate offspring of the pine tree sporophyte which may develop into a new tree. This is the embryo and is for the time being dependent for its nutrition (parasitic) upon its parent, the female gametophyte represented by endosperm, which in its turn is protected by the seed coats and is dependent on the old sporophyte. The pine seed is, therefore, a representative of three generations.

Origin of the Seed

The formation of this important reproductive organ, **the seed,** in the spermatophytes, is the result of three conditions : heterospory and its further specialization, retention and germination of the megaspore within the nucellus of ovules, and formation of the dormant embryo.

(*i*) **Heterospory.** It ocurs in a number of lower vascular plants such as *Selaginella, Marsilia,* etc., in which the two kinds of spores, the microspores and the megaspores are produced in separate sporangia. On germination they give rise to reduced and endosporic male and female gametophytes respectively. In the spermatophytes the male gametophyte is further reduced but it is the female gemetophyte which has undergone remarkable changes.

(*ii*) **Retention of Megaspore.** In the spermatophytes the megaspore is not at all discharged from the parent plant, because the nucellus which encloses it never opens. The megaspore thus germinates *In situ,* to give rise to the female prothallus representing the female gametophyte. The latter in the gymnosperms produces female gametes (eggs) in archegonia. The female prothallus and the enclosing nucellus are surrounded by a protective covering the integument. This whole structure is called the ovule. This ovule is the potential seed. The ovule remains attached to the parent plant till it is matured. The maturity of the ovule is dependent upon the transfer of the microspores, containing little microgametophytes within them through the air, in a position near the female gametophyte which is buried in the nucellar tissue and eventually the carriage of the microgametes through nucellar tissue to the egg in the archegonium. A new structure, the **pollen tube**, develops from the male gametophyte. It helps in accomplishing fertilization by carrying the male gamete to the egg in the archegonium.

(*iii*) **Formation of dormant embryo**. The fertilized egg immediately develops into the embryo which, as it grows, feeds on the surrounding tissue of female gametophyte. The rest of the tissue of the female gametophyte whose cells are gorged with food, functions as the endosperm. The integument hardens to form the seed coat. The ovule is now mature, and ready to fall from the tree as a seed. As pointed out above the seed is a reproductive structure containing a dormant embryo—the future sporophyte, well supplied with food reserve in the form of endosperm and heavily protected against drying and mechanical injury by the hard seed coat or testa. The formation of seed thus involves the nutrition of embryo sporophyte, through the much reduced female gametophyte, by the parent sporophyte of the previous generation. The gametophyte, therefore, merely functions to transfer food. It is not a supplier of food.

Biological Importance of Seed

The seed is a special structure linked with the adaptation of land habits. As a matter of fact perfect adaptation to life on land and subsequent successful distribution on the surface of the globe has much to do with the formation of seed in the spermatophytes. The bryophytes and pteridophytes suffer from two great handicaps in their successful adaptation to life on land. These are the presence of the external water at the time of fertilization as their sperms are motile and the forced germination of their embryos in external conditions whether they are favourable or not. In the spermatophytes the seed overcomes both these handicaps. The first handicap, *i.e.*, presence of external water at the time of fertilization is eliminated by the formation of non-motile male gametes in the male gametophyte. The latter in a state of partial development in the pollen grain is transported through the air to the micropyle of the ovule and from there on to the top of the nucellus. Here the pollen grain puts out a pollen tube which carries the male gametes, and traverses through the nucellus to reach the archegonia on the female gametophyte. This makes fertilization more certain. The second difficulty has been overcome by the formation of a dormant embryo, well supplied with food materials and protected by a heavy seed coat which enables it to live in a state of dormancy until the external conditions become favourable for its growth.

Advantages of Seed

The seed has many advantages over similar reproductive structures such as the spores, the zygotes and the like. Its heavy often hard and impervious seed coat protects the innermost delicate parts from drying and mechanical injury. Owing to a very low percentage of water within it, the seed is able to withstand a long period of low temperature. The reserve food within the seed enables the embryo to remain dormant but alive until the external conditions are favourable for growth. The food stored within the seed supplies a requisite amount of energy at the time of germination. The differentiation of the dormant embryo in advance of dormancy into the radicle, the plumule and the cotyledons hastens the establishment of the primary root and the primary leaf at the time of germination. The seeds of pine and many angiosperms develop structures like wings, plumes or hair etc., which help in their dissemination away from the parent plant to more suitable localities. This leads to the distribution of the species over a wide area.

Germination of the Seed (Fig. 13.43)

The seed may germinate at once if it falls on a suitable soil where it can get moisture. The resting period if any, is not long. The hypocotyl elongates absorbing food from the endosperm and the testa splits open. The micropylar end of the hypocotyl emerges first through the crack. Its tip-radicle grows downwards and penetrates the soil to become the primary root. This is followed by the elongation of the rest of the hypocotyl which may at first be arched as it lifts the seed out of the soil because its one end (radicle) is anchored in the soil and the other (epicotyl) is put in the seed. The arched hypocotyl then straigthens out pushing the cracked testa, remains of nucellus if any and what is left of the endosperm through the ground ahead of the cotyledons. As the germination proceeds cotyledons become green, their tips absorbing what is left of the endosperm. Finally a thin film of the latter is left which dries and breaks away as the cotyledons unfold and eventually drop off and decay along with the testa. The tiny plumule is very slow to show any signs of growth and practically no difference is seen in it until the cotyledons are unfolded. The green unfolded cotyledons begin to manufacture food. The embryo seedling is now an independent plant. The cotyledons eventually wither and fall off. The plumule grows into a shoot of unlimited growth. It bears only green needle-like leaves in a spiral manner. When the seedling is about 3 to 4 inches in height, first foliar spurs appear in the axils of the green needle-like leaves. As the seedling grows the green needles become progressively smaller in size until they gradually merge into the scale leaves characteristic of the pine tree. After a long period of growth the seedling gradually develops into a mature sporophyte consisting of a stem, branches, leaves and cones. The life cycle of *Pinus* is graphically represented in Fig. 13.44.

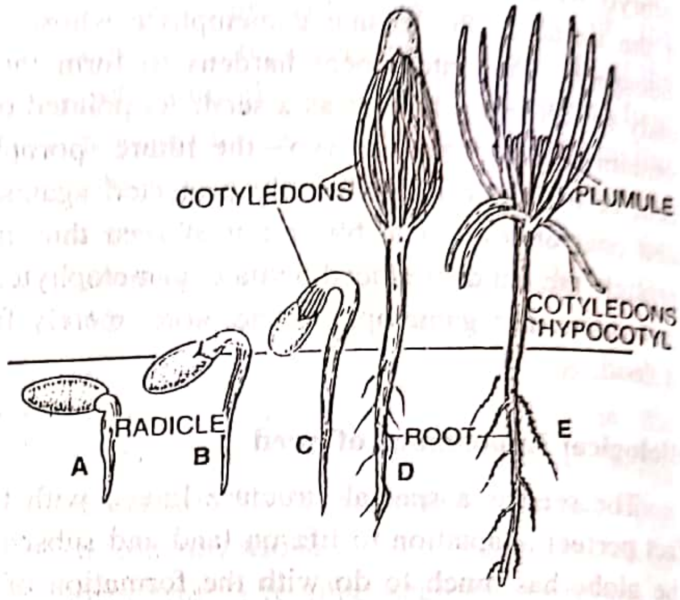

Fig. 13.43. A—E. Stages in the germination of seed of *P. roxburghii*

Alternations of Generations

The life cycle of *Pinus* displays the same alternation of generations as we have seen in other types lower in organisation than the gymnosperms. The sporophyte phase is of long duration and is represented by the huge pine tree which bears the staminate and ovulate cones. The staminate cone produces pollen grains in pollen sacs on the microsporophylls. The female cone produces megaspores one in each ovule borne on the upper surface of the ovuliferous scale. Since meiotic divisions occur at the time of the differentiation of the pollen grains and megaspores, the latter structures represent the first cells of the second generation—the gametophytes. Both the gametophytes (male and female) in *Pinus* are further reduced and are parasitic upon the sporophyte. They are retained within the respective spores. The vegetative or sterile phase of the male gametophyte is represented by the prothallus cells. The female gametophyte, no doubt, consists of an extensive tissue forming the female prothallus but its chief function is to provide nutrition to the embryo. It obtains the food for this purpose from the sporophyte plant. It has neither chlorophyll nor rhizoids, hence it is unable to carry on independent assimilation. The most remarkable feature is that it is retained within the sporophyte tissue—the nucellus and not discharged. The little microgametophyte is carried by the wind to a position in the vicinity of the ovule from where, it is shifted on to the apex of the nucellus. It then puts out a pollen tube which carries the male gametes on to the archegonia developed at the micropylar end of the female prothallus. The male gametes unite with the egg in the archegonium to effect fertilization. The fertilized egg is a diploid structure. It is the first cell of the future sporophyte. It develops into the embryo which is the new sporophyte.

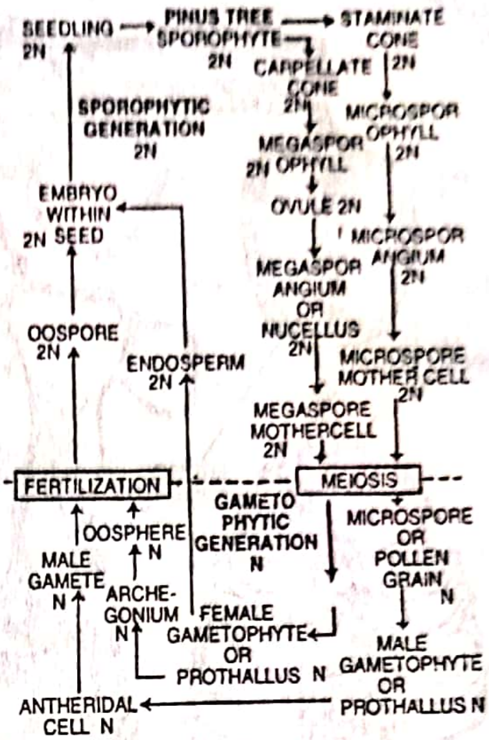

Fig. 13.44. Graphic life cycle of *Pinus.*

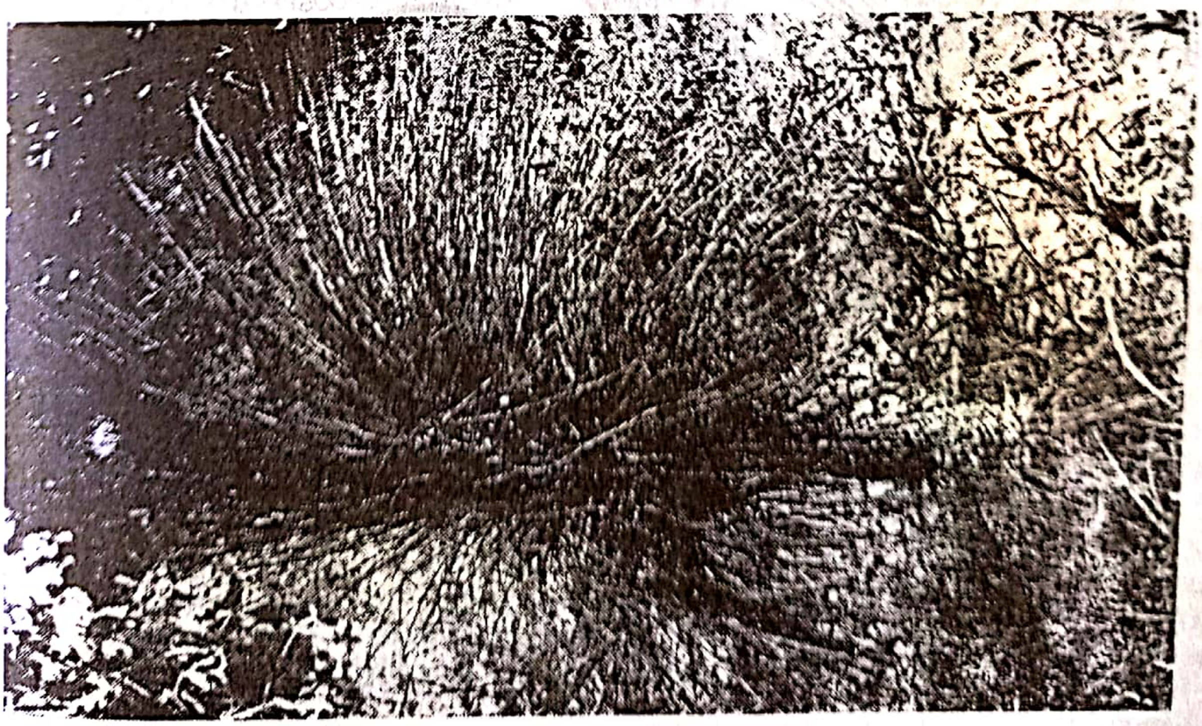

Plate XVII. A young plant of *Pinus roxburghii.*

Scanned with CamScanner

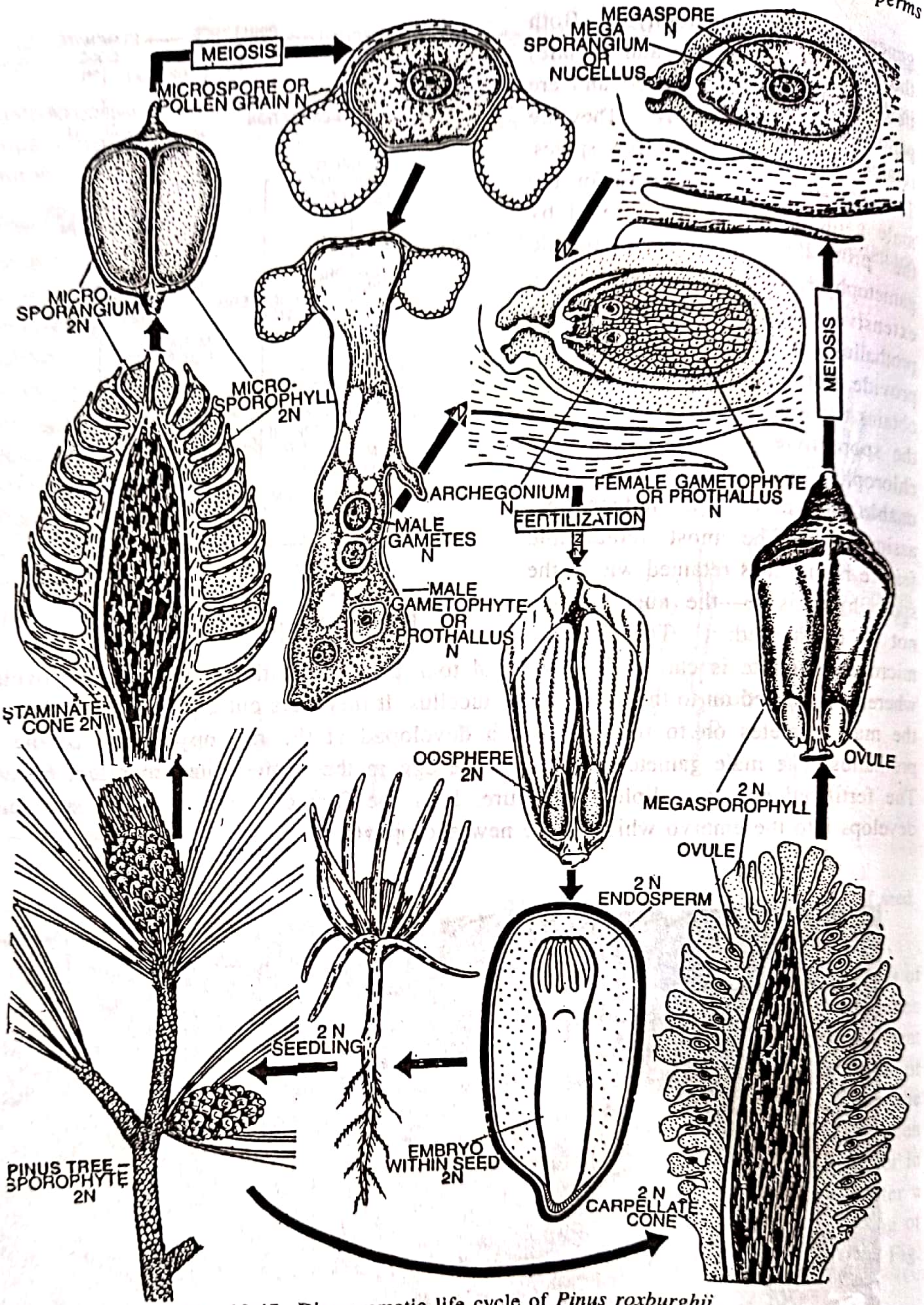

Fig. 13.45. Diagrammatic life cycle of *Pinus roxburghii*.