Zusammenfassung

Eine Untersuchung an 19 kartierten und periodisch gemessenen Probeflächen von Kiefer und Fichte hatte folgende Ergebnisse:

1. Zwischen der Stammgrundfläche der Bäume und der mit dem Abstand gewogenen Summe der Grundflächen der Nachbarn besteht eine negative Korrelation.
2. Diese Korrelation nimmt mit dem Alter zu.
3. Sie ist anfangs geringer und nimmt langsamer zu in nicht durchforsteten Beständen.
4. Eine korrekte Deutung der Korrelation ist nicht möglich. obgleich sie sicherlich als Ergebnis der zwischen benachbarten Bäumen stattfindenden Konkurrenz gewertet werden kann.
5. Auch bei Durchforstiungsverfahren mit extremer Konkurrenzregulierung, wie dem Lichtwuchsbetrieb, ist sie nachweisbar und nicht geringer als in anders durchforsteten Beständen.
6. Eine Schätzung des Konkurrenzanteils an der phänotypischen Varianz im Bestand unter Verwendung dieser Korrelation 'dürfte allenfalls eine Schätzung der unteren Grenze liefern.

Summary

An investigation on 19 permanent yield plots in stands of Scotch pine and Norway spruce indicated the following results:

1. There is a negative correlation between basal area of single trees and sum of basal areas of neighbouring trees the latter weighted adequately by distance.
2. This correlation becomes stronger with increasing age.
3. It starts with lower values and increases more slowly in unthinned stands.
4. It seems not to be possible to interpret the correlation unambiguously, though it certainly results from competition between neighbouring trees.
5. The correlation exists, and is by no means weaker, even if heavy thinning is applied which minimizes competition effects, like in "Gehrhardts Lichtwuchsbetrieb" in Norway spruce.
6. An estimate of the competitional part of phenotypic variance in a stand by means of this correlation gives probably an estimate of the lower limit of competitional variance.

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Observations on Abies pindrow with a Discussion on the Question of Occurrence of Apomixis in Gymnosperms

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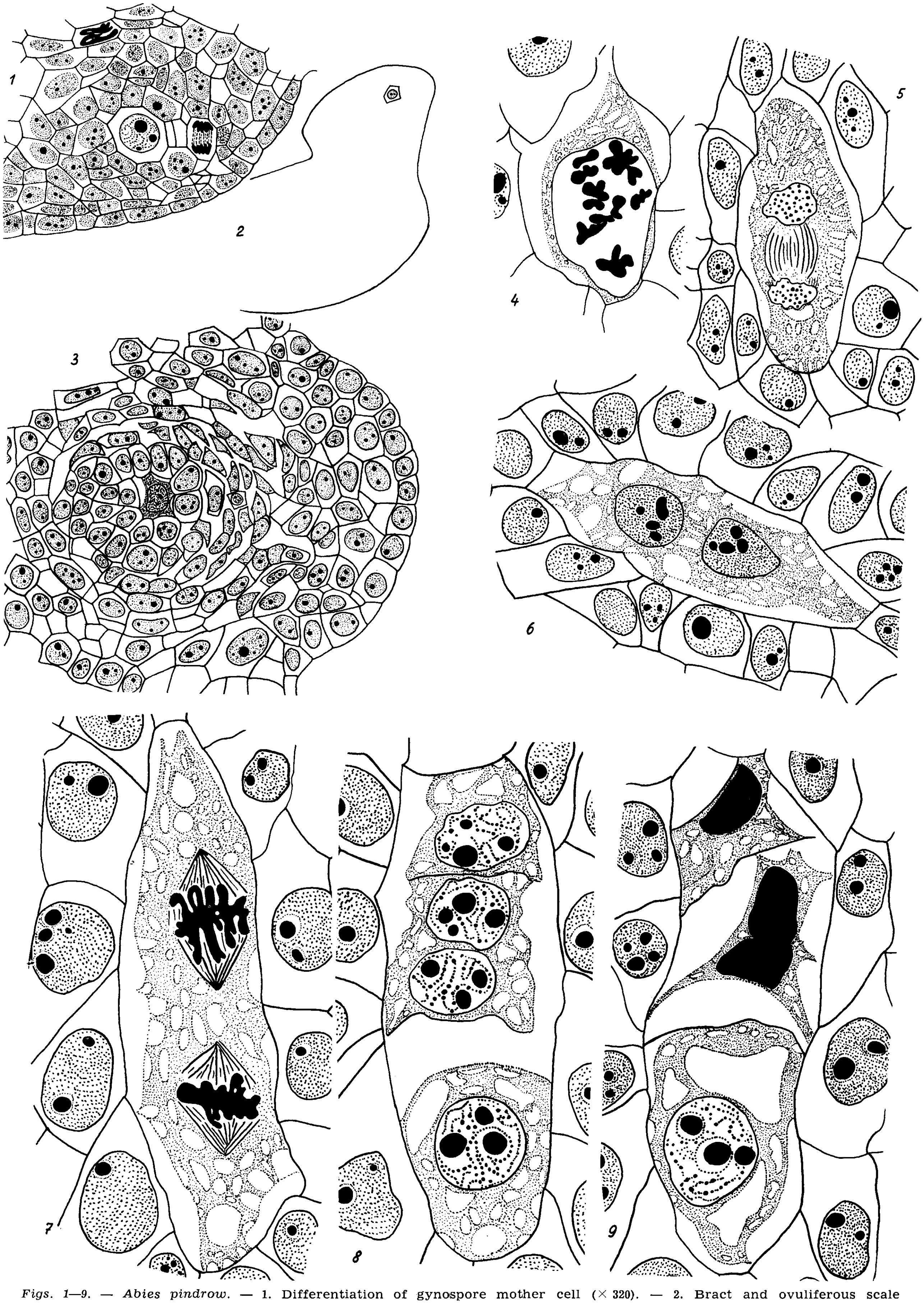
According to GUSTAFSSON (1947a), the term apomixis in general covers all types of asexual reproduction which tend to replace or act as substitutes for the sexual method. The phenomenon is well known in pteridophytes and angiosperms. In angiosperms it has been reviewed by ROSENBERG (1930), STEBBINS (1941, 1950), GUSTAFSSON (1946, 1947a, b), MAHESHWARI (1950), and BATTAGLIA (1963).

In gymnosperms the embryological literature contains several reports regarding processes apparently suggestive of occurrence of apomictic phenomenon. Of interest are the reports of probable embryo formation in the unpollinated ovules of *Pseudotsuga menziesii* by ALLEN (1942) and ORR-EWING (1957). Keeping these interesting observations in view, the writer undertook an embryological investigation of the naturally unpollinated and pollinated ovules of Abies pindrow (ROYLE) SPACH. The results of this investigation are reported in the present paper. Based on these data, the occurrence and nature of this phenomenon have been critically reviewed from an embryological point of view.

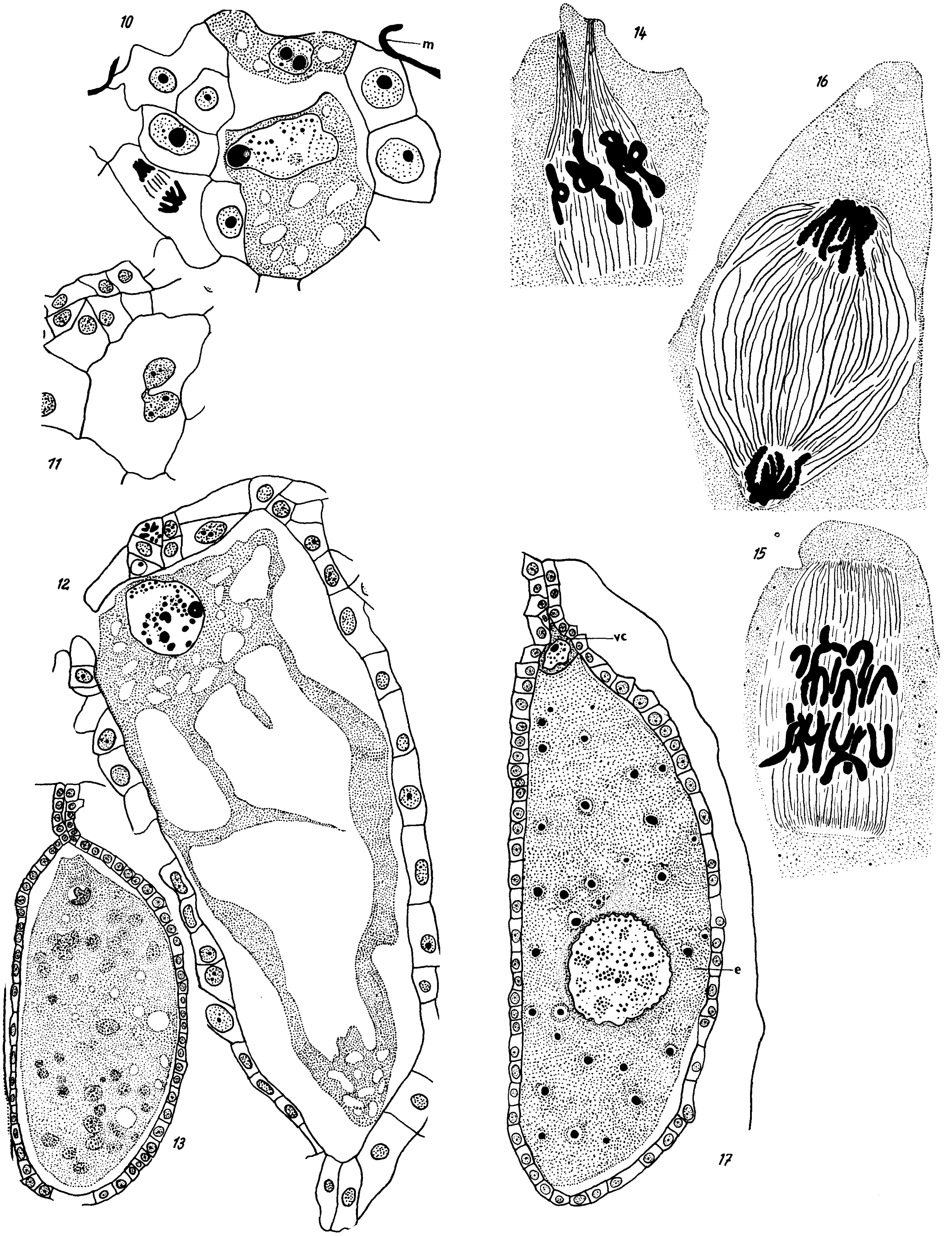
Material and Method

The material was taken from an isolated population of about fifty trees growing near Simla (Northwest Himalayas) at an altitude of about 2286 m. The peculiar feature of this population is that the usual male and female cone formation was interrupted by the production of exclusively female cones in 1954. The reason of such behaviour of this population poses an important physiological problem which may be of value for mass hybridization work.

Abies *pindrow* completes its life history in one year. The ovules studied consist of two separate batches: (1) unpol-



Figs. 1—9. — *Abies pindrow.* — 1. Differentiation of gynospore mother cell (× 320). — 2. Bract and ovuliferous scale primordia showing gynospore mother cell (×82). — 3. Later position of gynospore mother cell lying under several layers of nourishing cells (×320). — 4. Gynospore mother cell during first meiotic division, diakinesis stage (×1160). — 5, 6. Telophase of first meiotic division showing absence of wall formation (×750). — 7. Division of dyad nuclei (×1160). — 8, 9. Three celled tetrad, central cell contains two free nuclei, lowermost cell enlarges upper two degenerate (×1160).



Figs. 10—17. — *Abies pindrow.* — 10. Divided archegonial initial, gynospore membrane (m) broken to expose micropylar end of prothallus (×480). — 11. Fusion of two nuclei of a prothallial cell (×320). — 12. Developing archegonium, broad at upper end pointed at base, showing vacuolated central cell (×1160). — 13. Developing archegonium showing 4-cell long neck and densely granular central cell (×82). — 14, 15, 16. Divisional phase of central nucleus forming egg and ventral canal nuclei (×1160). — 17. Mature archegonium with ventral canal (vc) and egg (e) cells (×130).

linated ovules collected in June and July during the exceptional year when no male cones were borne by this small population of trees, and (2) normally pollinated ovules collected during the following year. The material was fixed in 1 : 3 acetic acid and alcohol and preserved in 75 per cent alcohol. Sections 15 − 25 μ in thickness were cut from the paraffin embedded material and stained with safranin-fast green combination.

Unpollinated ovules

In *Abies pindrow* the unpollinated cones develop in the same way as the normal pollinated ones. In *Pseudotsuga* and other conifers this phenomenon has been referred to as parthenocarpy (Allen, 1942, Orr-Ewing, 1957). The ovules can be sectioned till early July when the integuments harden, the gametophytes shrivel, and its place is filled by the inward expansion of the stony integuments. These ovules look like the normal fertile ones and most of them sink in water. Bulk dissections of these ovules from several trees failed to show embryo formation.

Development of prothallus: — The gynospore mother cell lies embedded below three to four layers of the hypodermis *(Fig. 1)*. It is pushed down by further growth of the tissue *(Fig. 2)*. The ovuliferous scale primordium grows from the rear side and the integuments get differentiated. In mid-March the nourishing layers develop into a spongy tissue *(Fig. 3)*. In early April the enlarged mother cell undergoes a reduction division *(Figs. 4, 5)*. A scrutiny of early, mid, and late telophase shows an absence of wall formation and two free nuclei are formed *(Fig. 6)*. These divide simultaneously and in this division cytokinesis gives rise to three linear cells of which the central cell contains two free nuclei *(Figs. 7, 8)* as also reported in *Sciadopitys verticillata* (Lawson, 1910, Tahara, 1940). The upper and the middle cells degenerate; the lowermost cell enlarges *(Fig. 9)*. The surrounding tissue nourishes this cell, and after the free nuclear and the wall formation stages the female gametophyte is formed. A thick spore membrane covers the gametophyte. The spore membrane is thinner towards the micropylar region where it usually breaks to expose the archegonial region *(Fig. 10)*. The cells of the female gametophyte sometimes show irregular patterns owing to the presence of large polyploid cells formed by fusions of the adjacent nuclei *(Fig. 11)*.

Development of the archegonium: — The archegonial initial divides by a periclinal wall into a small upper primary neck cell and a lower central cell *(Fig. 10)*. The lower cell enlarges considerably. The upper cell divides anticlinaly to give rise to neck cells *(Fig. 12)*. At this stage the archegonium elongates, becoming pointed towards the base but broad towards the neck and resembles the podocarp archegonium. The neck cells divide to give rise to a 4-celled long neck similar to the one seen in *Keteleeria evelyniana* and *K. davidiana* (Sugihara, 1943, Wang, 1948). Gradually the vacuolated cytoplasm becomes dense and granular and the proteid bodies are organized. The jacket layer becomes distinct and the mature archegonium now becomes long, narrow, and rounded at the base *(Fig. 13)*. The central nucleus divides but the shape of the spindle of this division is variable *(Fig. 14)*. The spindle becomes truncated at the poles during anaphase *(Fig. 15)*. Cytokinesis follows and a wall is formed by thickenings on the spindle fibres which fill the ventral canal *(Fig. 16)*. A ventral canal nucleus is thus cut off by the formation of a thick and well developed wall *(Figs. 17, 18)*. The nucleus of the ventral canal cell is much larger in proportion to the cell cytoplasm. The egg nucleus moves down to occupy a central position in the egg.

The behaviour of the neck cells on maturation and prior to entrance of the pollen tube is worth noting. These are rich in starch grains and show signs of considerable physiological activity. They have vacuolated cytoplasm and often become binucleated probably by the dissolution of the intervening walls *(Fig. 18)*. At this time an exudate fills the neck. Such exudation has been reported in *Zamia umbrosa* (Bryan and Evans, 1957). The neck cells degenerate ultimately and a passage is formed *(Fig. 19)*, which is also shown in *Abies balsamea* by Miyake (1903), and Hutchinson (1915).

Several conditions are exhibited by the archegonia:

1) In the developmental stages some of the archegonial initials contain polyploid nuclei in a state of fusion *(Fig. 20)*. Sometimes such initials give rise to 3 to 4 archegonia joined together *(Fig. 21)*.

2) In many cases the adjacent archegonia fuse, perhaps by the dissolution of the intervening prothallial tissue. The fused archegonia may have a common neck. The adjacent eggs fuse and their nuclei come close together as if about to fuse *(Fig. 22)*. The two ventral canal nuclei are

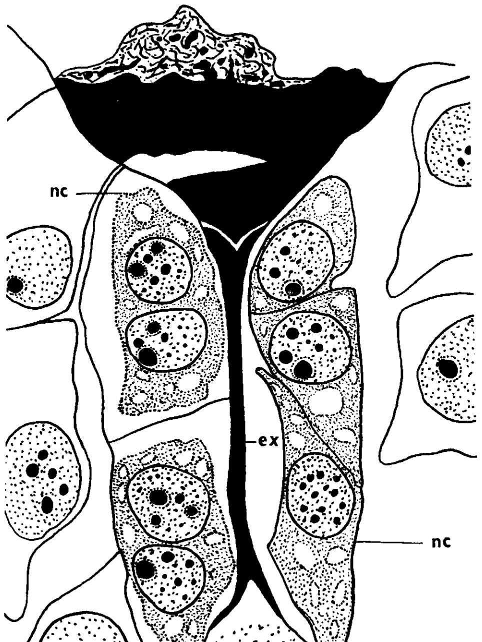


Fig. 18. — *Abies pindrow.* — Archegonial neck prior to pollen tube entry. Exudate *(ex)* fills neck passage above ventral canal cell *(vc)*. Neck cells *(nc)* are binucleate and physiologically active (×1160).

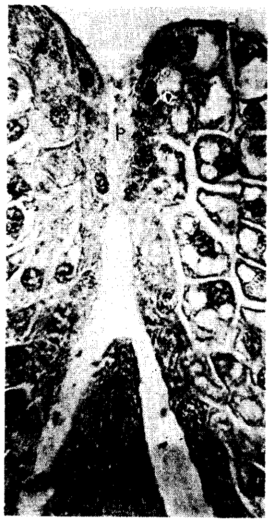


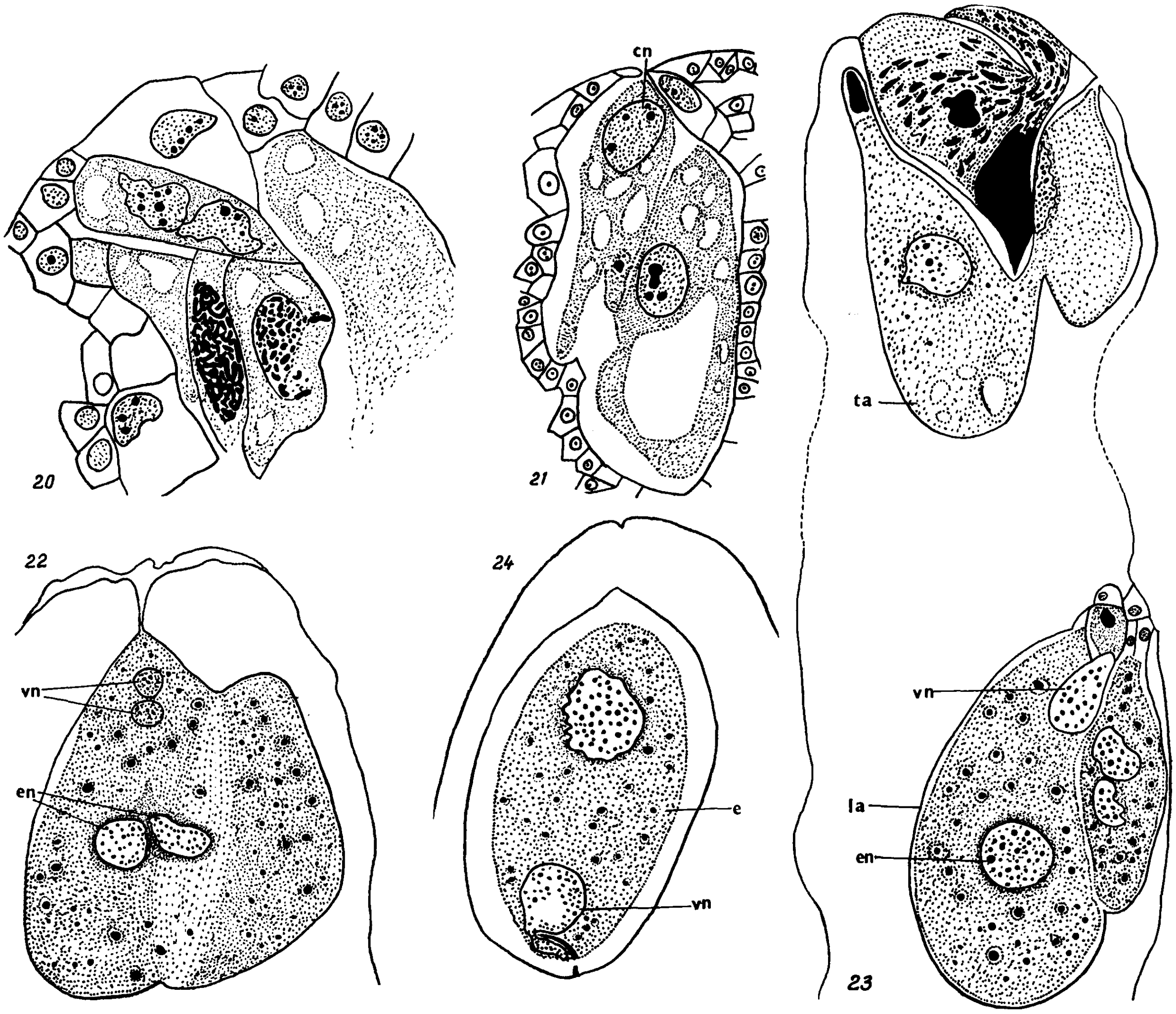
Fig. 19. — Abies pindrow. — Photomicrograph of archegonial neck before pollen tube entry, showing a long canal-like passage *(p)* (×225).

also seen to be closely situated. In addition to the terminal archegonia, two to three lateral archegonia enclosed in a common jacket are also seen *(Fig. 23)*. Most of these fused archegonia degenerate.

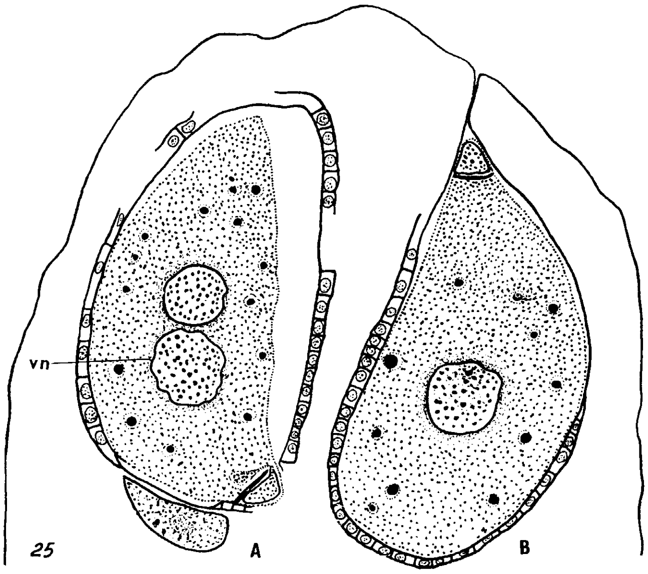
3) Some inverted archegonia were also seen at the micropylar end along with the normally orientated ones *(Figs. 24, 25)*.

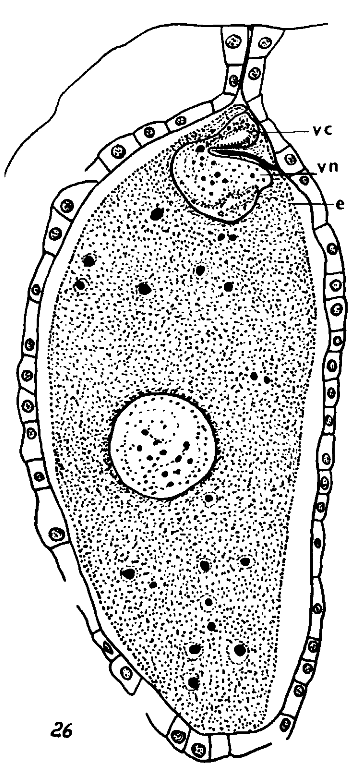
The ventral canal nucleus and its behaviour: — The behaviour of the ventral canal nucleus is variable. Usually it slips out of its cell from a side opening and grows to the size of the egg nucleus within the egg *(Figs. 26, 27, 28)*. Sometimes when the opening is very narrow, the nucleus in the process of emergence can be seen partly within the ventral canal cell and partly in the egg with a narrow isthmus-like connection between the two. The chromatin flows through this narrow channel into the outer portion of the nucleus. Occasionally the isthmus-like portion thins out to the extent of breaking and two nuclei are formed *(Fig. 29)*, of these the nucleus within the egg often enlarges to look like the egg nucleus; the nucleus remaining within the ventral canal cell either degenerates or may get further fragmented forming additional nuclei *(Fig. 30)*.

This behaviour of the ventral canal nucleus has also been noticed in the inverted archegonia *(Figs. 24, 25)*.



Figs. 20—24. — Abies pindrow. — 20. Archegonial initials showing nuclear fusions and nuclei of polyploid constitution (×320). — 21. Archegonia with central cell nuclei *(cn)* of polyploid constitution (×130). — 22. Fused archegonia with paired ventral canal *(vn)* and egg nuclei *(en)* (×82). — 23. Prothallus showing terminal *(ta)* and lateral*(la)* archegonia. Lateral archegonia show free ventral canal *(vn)* and egg *(en)* nuclei (×82). — 24. Micropylar region of prothallus showing abnormal inverted archegonium. Ventral canal nucleus *(vn)* is flowing out of its cell into egg *(e)* (×82).





Figs. 25—26. — *Abies pindrow.* — Inverted (A) and normally orientated archegonia (B); — *vn,* fragmented ventral canal nucleus. — 26. Archegonium showing ventral canal nucleus *(vn)* flowing from its cell into the egg region *(e)* (×130).

Sometimes the ventral canal cell develops a weak or incomplete wall *(Fig. 31)* which easily dissolves and the ventral canal nucleus comes to lie freely in the egg.

Two or more free nuclei in the egg are formed by any of the above methods. However, the nuclei formed by fragmentation usually degenerate and their further behaviour is unimportant. The free ventral canal and the egg nuclei need further mention.

In unpollinated ovules the ventral canal nucleus is sometimes seen to approach the egg nucleus and both may come to lie in close proximity. The egg nucleus now, forms a deep depression, similar to the one formed during normal sexual fusion, except that in this case it is larger and the two fusing nuclei are almost equal in size *(Figs. 32, 33)*. The ventral canal nucleus flattens considerably on the side facing the egg nucleus. The two nuclei fuse and the separating wall gradually vanishes *(Figs. 34, 35)*. It must, however, be mentioned that during this fusion the syngametic stages of chromatin behaviour, seen in the fusion of male and female nuclei, were not observed. Bulk dissections of these ovules failed to show any embryo formation.

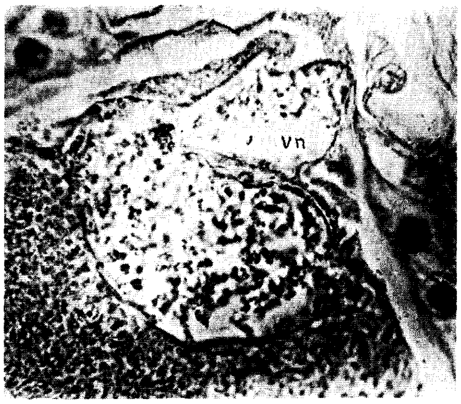


Fig. 27. — *Abies pindrow.* — Photomicrograph of the archegonial region below neck showing ventral canal nucleus *(vn)* flowing out of its cell into the egg through an opening in the separating wall (×345).

Normally pollinated ovules

The pollen tube usually releases two male nuclei in the egg one of which fuses with the egg the other degenerates. The proembryogeny is like that of *Pinus* (Mehra and Dogra, MS, b). Dissections showed presence of polycotyledonous embryo in 70 per cent of seeds.

In several cases the second male nucleus was seen in contact with the ventral canal nucleus *(Fig. 36)* as in the process of fusion. Two and four free nuclei were observed near the neck in addition to the normal proembryo at the base *(Figs. 37, 38)*. It is thought that these free nuclei and the cells are formed after the fusion of the ventral nucleus and the second male nucleus. Cells partly and completely walled were seen in this part of the archegonium in addition to the normal proembryo at the base as shown in a better preparation of *Picea smithiana (Fig. 39)* and is also recorded for *Thuja occidentalis* (Land, 1902), *Ephedra trifurca* (Land, 1907), and in *A. balsamea* (Hutchinson, 1915). Some of the phenomena described for unpollinated may also occur in pollinated ovules.

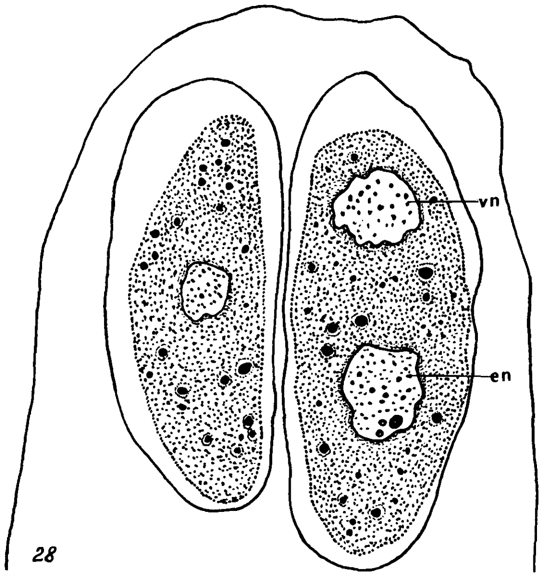
Discussion

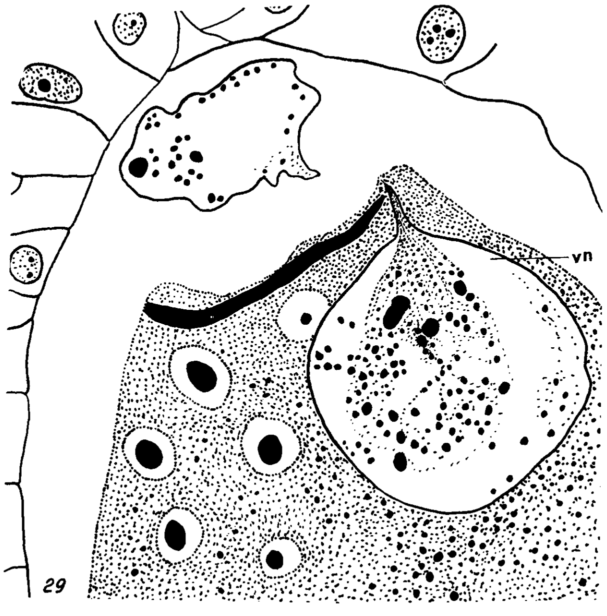
Apomixis is of two types: agamospermy, where reproduction is by seeds formed without the fusion of male and female nuclei, and, multiplication or vegetative reproduction where seeds do not participate. In gymnosperms apomixis, if present, is in the form of agamospermy. Vegetative reproduction, except in cycads, is not common. For a proper appraisal of the present observations, it is essential to review briefly the observations of the earlier workers pertinent to the present theme.

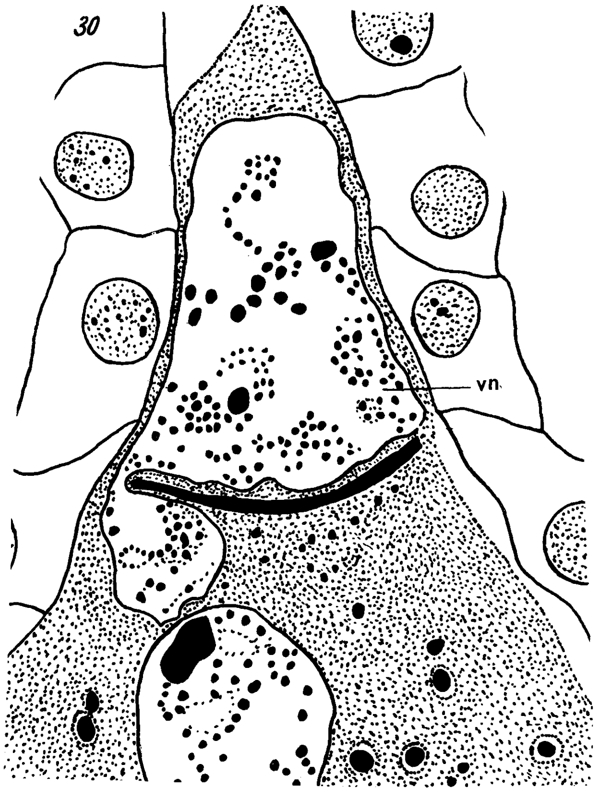
Chamberlain (1935) reports embryo formation in conservatory material of cycads where male cones are absent. He attributes the formation of seeds in these plants to fertilization by the ventral canal nucleus, a feature recorded in *Encephalartos villosus* by SEDGEWICK (1924).

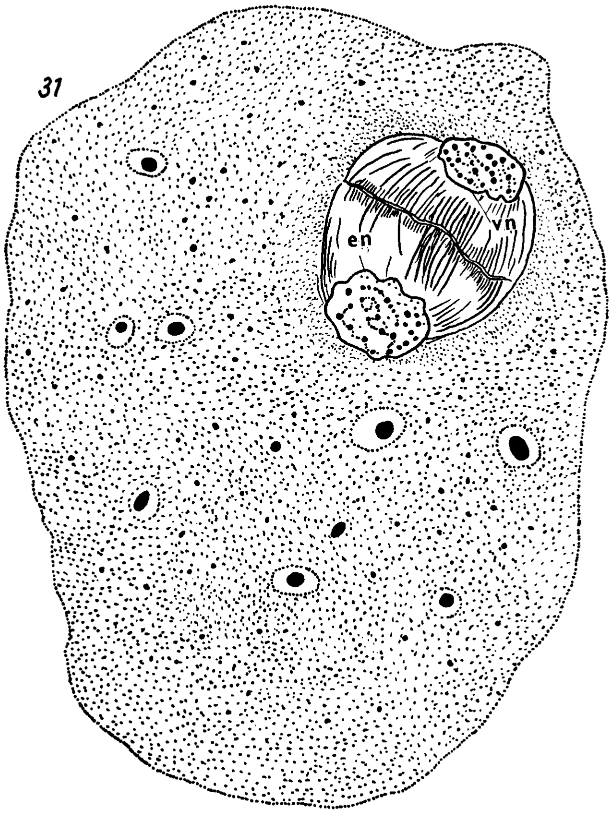
DUCHARTRE (1888) discovered roots on female gametophytes of *Cycas thouarsii* (cf. LA RUE, 1954). LA RUE (1948, 1950, 1954) believed that in gymnosperms one generation of life cycle can be reproduced from the other by direct regeneration from the tissue without sexual intervention. He demonstrated this by *in vitro* cultures of female gametophyte of *Zamia floridana* and *Cycas revoluta* where a small percentage (less than 1 per cent) of cases directly gave rise to roots and shoots and a few of these stems bore roots and leaves. Such miniature plants were said to be haploids and they survived (LA RUE, 1954). Similar trials by LA RUE on other gymnosperms like *Ginkgo, Abies, Picea, Pseudotsuga, Larix, Chamaecyparis, Juniperus, Thuja, Podocarpus,* and *Ephedra* failed to yield such results. In this connection it is of interest to point out that though the female gametophyte of *Zamia* and perhaps also of *Cycas* has been shown to have inherent capacity for embryo formation given suitable conditions, yet it is not the case in several other conifers tried by him.

IKENO (1901) described rare cases in *Ginkgo* where the ventral canal nucleus enlarged to the size of the egg nu-









Figs. 28—31. — *Abies pindrow.* — Ventral canal *(vn)* and egg nuclei *(en)* lying free in the archegonium on right hand side (×82). — 29, 30. Ventral canal nucleus *(vn)* fragmenting as it flows out of its cell (×480). — 31. Formation of incomplete separating wall between egg *(en)* and ventral canal nuclei *(vn)* (×480).

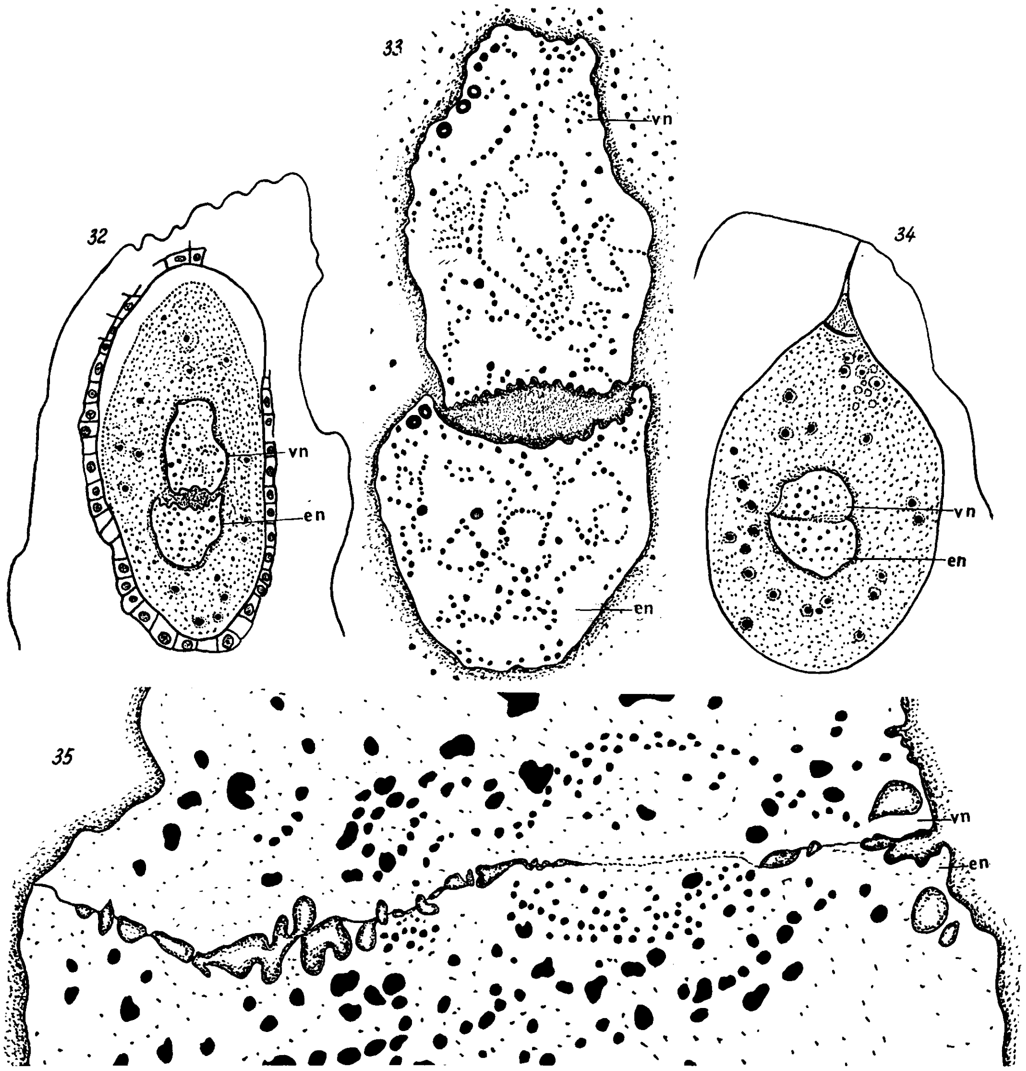
cleus and it was assumed that it fused with the egg nucleus (see Coulter and Chamberlain, 1917; Chamberlain, 1935). As far as the present writer is aware, there has been as yet no clear demonstration in *Ginkgo biloba* of formation of fertile seeds without the help of pollen.

The fusion of ventral canal nucleus and egg nucleus is recorded in *Picea vulgaris* by Strasburger, in *Pinus laricio* by Coulter (cf. Coulter and Chamberlain, 1917; Chamberlain, 1935) and in *Abies balsamea* by Hutchinson (1915). It has been suggested that such fusion could result in embryo and seed formation.

Two cases of probable apomixis in *Pseudotsuga menziesii* in the field are reported by Allen (1942) and Orr-Ewing (1957). Pollination was prevented in these cases by bagging the female cones. Allen reports three viable seeds from two trees. Orr-Ewing (1956, 1957) has attempted to confirm Allen's results by careful bagging techniques and he reports 22 seeds containing embryos from 11 cones. Twelve seeds germinated to produce diploid seedlings of which 7 survived. The seedlings were less vigorous in growth and did not show any variation in height and form. The possibility of pollen contamination, though not ruled out, is considered to be remote. Orr-Ewing (1957) says that agamospermy is of rare occurrence in *Pseudotsuga* but when present, it is probably due to adventitious embryony or to the fusion of two large nuclei (possibly the egg and ventral canal nuclei) observed in unpollinated ovules.

Mehra and Dogra (MS, a) record 10 per cent cases in *Pinus wallichiana* and 5 per cent in *P. nigra* var. *austriaca* where the egg nucleus divided parthenogenetically without participation of the male nucleus. A haploid chromosome number (twelve) and only one chromatin net-work instead of two (normal male and female) were recorded during the first division of the egg nucleus. Saxton (1909) reports similar parthenogenetic division of the egg nucleus in *Pinus pinaster*. Beyond the demonstration of haploid nature of the division little can be said as regards embryo formation from it. If such a division was to give rise to embryo formation it could perhaps be classified as non-recurrent haploid parthenogenesis (cf. Maheshwari, 1950). As far as writer's observations on conifer embryogeny go, the possibility of survival of such embryos if formed is remote. However, diploid embryos can be formed by failure of the first division and consequent doubling of chromosome number. There is, however, no direct evidence available which could suggest such a possibility.

It may be emphasized that all the above cases do not represent a regular feature of the taxa concerned. Embryo



Figs. 32—35. — *Abies pindrow*. — 32, 33. Ventral canal *(vn)* and egg nuclei *(en)* in process of fusion (32 ×82; 33 ×320). — 34, 35. Fusion of ventral canal *(vn)* and egg nuclei *(en)*(34 ×82; 35 ×1160).

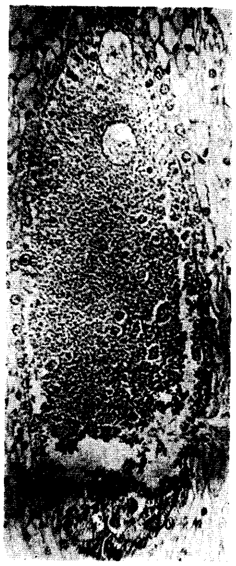
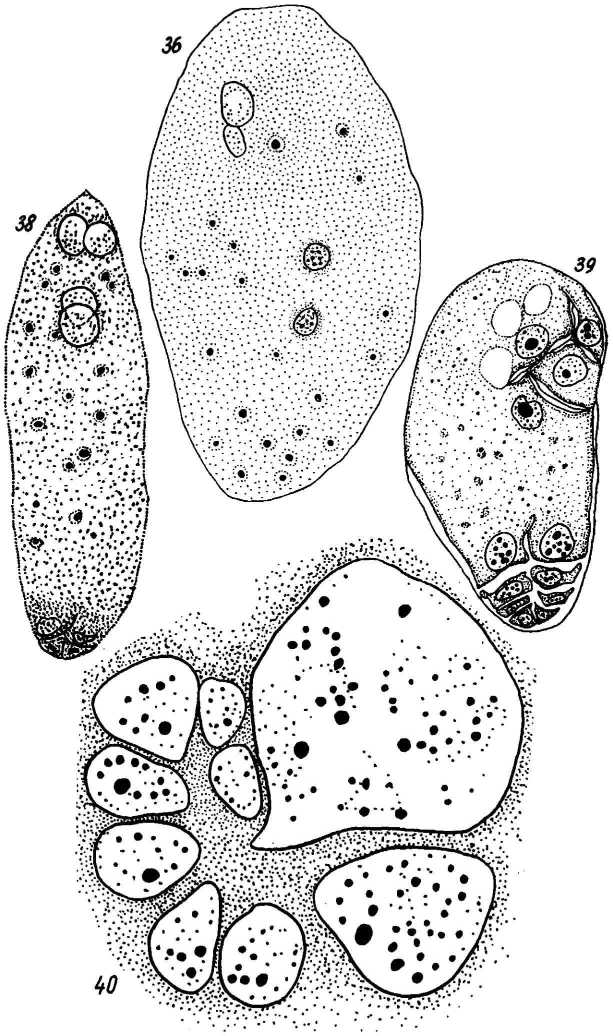


Fig. 37. — *Abies pindrow.* — Photomicrograph of archegonium showing two free proembryonal-type of nuclei near neck region in addition to normal proembryo (seen in next section) at base (×345).

formation, if present, in all such cases would evidently be the result of apomixis, more precisely may be due to some form of agamospermy. Two principal classes of agamospermy are known, namely adventitious embryony and gametophytic apomixis (cf. STEBBINS, 1950). As already pointed out, there is no clear cut case of adventive embryony reported so far except in the form of a suggestion by ORR-EWING (1957). Regarding gametophytic apomixis there is again no conclusive evidence but the present work on *Abies pindrow* has shown that there could be at least three mechanisms by which diploid chromosome number could be restored. These are: (1) Fusion of nuclei from adjacent cells or in free nuclear state. (2) Fusion of two adjacent archegonia and their respective ventral canal and egg nuclei (also recorded in *Abies balsamea* by MIYAKE, 1903). (3) Fusion of the ventral canal and the egg nuclei. The ventral canal nucleus is sometimes seen near the egg nucleus. It may come to lie in the egg by incomplete formation and disappearance of the wall of the ventral canal cell, or it may migrate from the ventral canal cell, sometimes fragmenting into two or more nuclei. The fragmentation of the egg nucleus is known to occur in several conifers (DOGRA, 1961) e. g. *Cunninghamia lanceolata (Fig. 40)*. The fragmentation of ventral canal and egg nuclei is also reported in *Zamia umbrosa* (BRYAN and EVANS, 1957). Hence reports of one or more nuclei in addition to the egg nucleus in gymnosperm archegonia, even if they look similar in size, need not be a matter of special significance. In *Abies pindrow* the ventral canal nucleus fuses with the egg nucleus in a manner akin to sexual fusion, with the difference that the fusing nuclei are not only equal in size but are also isogenic. However, the syngametic stages of chromatin behaviour are not observed.

Although a large number of unpollinated mature ovules of *A. pindrow* were dissected no embryo formation was seen. This was in spite of frequent occurrence of the nuclear fusions described above, and the so-called fertilization by the ventral canal nucleus. This is not fertilization in the normal sense as it occurs between two isogenic nuclei in the female tissue. On the other hand, observations of the normally pollinated ovules of the same population



Figs. 36, 38—40. — 36. *Abies pindrow;* second male nucleus in contact with ventral nucleus in the upper half and two proembryonal nuclei in the centre of the egg (×130). — 38. *Abies pindrow;* four free nuclei, in appearence similar to those of proembryo, near neck with normal proembryo at base (×82). — 39. *Picea smithiana;* cell formation amongst nuclei near neck and normal proembryo at base (×90). — 40. *Cunninghamia lanceolata;* fragmented egg nucleus (×900).

showed 70 per cent of seeds containing mature embryos. Writer's findings on *A. pindrow* agree with those of ORR-EWING (1957, table, 2) on *Pseudotsuga menziesii* where seeds from parthenocarpic cones show 100 per cent sterility. The study of embryogeny of 24 conifer species including *Taxodiaceae, Cupressaceae,* and *Pinaceae* (DOGRA, 1961) fails to give any direct evidence of apomixis.

More often agamospermy entails circumvention of meiosis, but to date there has not been recorded any such case either in *Abies pindrow* or in any other gymnosperm.

From the above data, it is apparent that there is no clear cut evidence of embryo formation in the unpollinated ovules in gymnosperms, at any rate it can be categorically denied in the case of *Abies pindrow* even though ventral canal nucleus and egg nucleus come together and involve themselves in an act of near fertilization. Furthermore even if embryo formation occurs, it has to be noted that *it takes place in a non-recurrent fashion and is not a fixed and a regular feature in any gymnosperms,* although considerable embryological work has been done. This is an important point particularly because apomixis (both agamospermy and vegetative reproduction) is an important evolutionary mechanism in pteridophytes and angiosperms. Khoshoo (1963, 1964) has tried to explain the total lack of this process in gymnosperms on the basis of the properties of the genetic system of the group.

In conclusion it may be stated that experiments utilising the bagging techniques of Allen (1942) and Orr-Ewing (1957) were not tried by the writer. The occurrence or otherwise of apomixis in gymnosperms can be proved only by large scale experiments employing strict pollination preventive methods. Apomixis as a regular phenomenon seems to be absent in gymnosperms and the sexual method is the only method of seed formation. Fusions of nuclei in the prothallial tissue, in the archegonia, or parthenogenetic division of the egg nucleus need not indicate agamospermy, though they may show an incipient tendency for embryo formation in unpollinated ovules which has failed to establish it self.

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Summary

Observations on pollinated and unpollinated ovules and on some stages of life history of an isolated population of *Abies pindrow* are given. A linear tetrad of three cells with two nuclei in the middle cell, a physiologically active neck of archegonium before entry of pollen tube, possible fusion of the second male and ventral canal nuclei, resulting in formation of nuclei and their segmentation near the neck are recorded. In the unpollinated ovules various phenomena which could possibly lead to agamospermy such as nuclear fusions in the prothallus cells, fusion of archegonia and eggs, and fusion of ventral canal and egg nuclei are described. Bulk dissections of these ovules, however, show 100 per cent sterility. Normally pollinated ovules of the same population had 75 per cent fertility. The possibility of occurrence of apomixis in gymnosperms is discussed and it is concluded that apomixis as a regular phenomena seems to be absent in gymnosperms and sexual method is the only regular method of seed formation.

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