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Mixoploidy of tannin coenocytes in *Sambucus racemosa* L.

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Abstract

In young lateral shoots and seedlings of *Sambucus racemosa* L. the ontogenesis of elongated tannin coenocytes was investigated with particular reference to their karyology. In these tannin containers both small nuclei and giant ones are present. The DNA content in the particular nuclei was determined by the cytophotometric method after the Feulgen reaction. The ploidy of the nuclei was concluded on the basis of the DNA level. It was found that in multinuclear tannin coenocytes there are diploid nuclei as well as others with various degrees of ploidy. Thus, tannin coenocytes are mixoploidal. On the basis of karyological investigations it was attempted to elucidate the mechanism leading to the formation of polynuclear and mixoploid coenocytes.

INTRODUCTION

In 1935 Küster advanced the supposition that the elongated tubes with tannin observed by him in *Sambucus nigra* shoots are polynuclear. Szuleta (1937, 1938) proved their polynuclear character and demonstrated that it was the consequence of synchronic karyokineses occurring within these tubes, followed by no cytokineses. The elongated tannin-containing tubes are thus coenocytes.

Synchronous divisions have been also observed in tannin coenocytes of other species of the genus *Sambucus* — *S. ebulus* and *S. nigra* var. *laciniata* (Stopa, 1971). Since both small and giant nuclei with numerous nucleoli were observed in coenocytes, it would seem that these nuclei represent various degrees of ploidy, and that in coenocytes we are dealing with mixoploidy.

The aim of the present work was to study the degree of ploidy of tannin coenocyte nuclei in *Sambucus racemosa* L. and to elucidate the mechanism by which nuclei of various ploidy (mixoploidal), are formed.

Polyploidy may be the result of:

— fusion of nuclei after karyokineses without cytokineses (Mechelke, 1952; Mahlberg, 1959a and b; Pogan, 1964; Titz, 1965).
— formation of restitution nuclei after disturbed karyokinesis (Skalińska, 1958).
— endomitoses (Geitler, 1953; Bajer and Molé-Bajer, 1955; Turała, 1958, 1963, 1966, 1971b; Turała-Szybowska, 1974).
— after endomitosis and subsequent mitosis there may occur fusion of the derivate nuclei. This rare phenomenon has been observed in the endosperm of some plants (Enzenberg, 1961; Jankun, 1970; Turała, 1971a).

MATERIAL AND METHODS

The growth apexes and upper internodes of lateral shoots were examined on mature individuals and on four- and eight-month-old seedlings of *Sambucus racemosa* L. Shoots of *S. racemosa* L. were collected from wild plants and seedlings grown in the garden and in a glasshouse, as well as the shoots growing from the axillary buds at the winter time in the glasshouse, were fixed in chrome-aceto-formalin (Cr AF) 0.5 : 1 : 20 (per cent ratio), in aceto-alcohol (AA) 1 : 3 (vol. by vol.) or in Carnoy solution. Part of the preparations for karyological analysis was stained with iron hematoxylin after Heidenhain.

Preliminary karyological observations show that in tannin coenocytes we are dealing with diploid nuclei and polyploid ones of various degrees. On longitudinal sections the volume of the nuclei was measured, since it usually increases with the rise of DNA content (Carniel, 1952; Tschermak-Woess and Hasitschka, 1953; Bradley, 1954; Turała, 1958; Nagl, 1962; Erbrich, 1965) and logarithms of this volume were calculated in view of the logarithmic increase in volume in relation to the degree of polyploidy (Hasitschka, 1965). For calculation of the volume of spherical nuclei the formula $V = {}^4/_3 \Pi r^3$ was used (Carniel, 1952; Tschernak-Woess and Hasitschka 1953) and for ellipsoid ones the formula $V = {}^4/_3 r_1^2 r_2$ (Bregnard and Ruch, 1974) where r_1 is the shorter radius and r_2 the longer one. Two diameters were taken into account, since orientational measurements on cross and longitudinal sections demonstrated that the dimensions of the two shorter radii of ellipsloid nuclei are very similar.

The number of nucleoli was also counted. In some cases it is used as index of polyploidy (Moll, 1928; Geitler, 1932; Trela, 1963). The basic number of nucleoli in a diploid nucleus of *Sambucus racemosa* is four. In tannin coenocyte nuclei during their elongation, the nucleoli frequently fuse, therefore it is only when more nucleoli than four are noted that we may be sure that the nucleus is polyploid, but the degree of its ploidy is

not known. The nucleoli were counted in preparations stained with iron hematoxylin and on diagrams obtained by connection of a scriber to the cytophotometer.

Then the cytophotometric method was applied (Wied, 1966; Wied and Bahr, 1970). Microtome 15-μm sections were subjected by the Feulgen reaction according to Kasten (1960), after Hiraoka, 1973). For measurement two different cytophotometers were used in the two steps of investigation. In both cases the measurements were taken at light wavelength 5500 Å.

In the preliminary step of measurement a Reichert type Zetopan cytophotometer was used for DNA content measurement, with 20 point readings on one nucleus. Extinction obtained in this way was multiplied by the surface area computed by means of a planimeter. The DNA content was obtained in Arbitrary Units (AU). At the same time on the same nuclei the longer and shorter diameter were measured in order to calculate the nucleus volume the results were obtained in μm^3. The degree of ploidy of the given nucleus was concluded from the DNA content in it and, separately, from its volume.

In the second step a Stroud and Bahr type GN-2 cytophotometer was used in which nuclear DNA was read automatically. The results were expressed in arbitrary units (AU).

Only those nuclei were examined which lay in the cytoplasm and were not covered with tannin. The error in the first measurements did not exceed 7, and in the automatic measurements 5 per cent (Wied, 1966).

RESULTS

Karyological analysis of the preparations stained with iron hematoxylin showed that even the mononuclear tannin cells which are the mother cells of the elongated tannin elements, contain nuclei twice as large as those in the surrounding parenchyma (Plate I, fig. 3). In such cells karyokinesis occurs without cytokinesis (Plate I, fig. 4). A binuclear cell arises (Plate II, fig. 5) in which the nucleoi (still diploid) may further divide (Plate II, fig. 6). The division of the nuclei is synchronous without cytokinesis, this leads to the formation of an elongated four-nuclear coenocyte. If these nuclei lie close together fusion may occur. A proof of fusion of the nuclei in a four-nuclear tannin coenocyte is the fact of occurrence of some few three-nuclear cells (Plate II, fig. 7). One of these nuclei, as shown in cytophotometric investigations contains twice as much DNA as each of the remaining ones.

In the further development of the tannin coenocyte, karyokineses are very frequent, as proved by the fact of occurrence already in the second internode of very long multinuclear tannin coenocytes at a small distance

from the mononuclear tannin cell (Plate I, fig. 1). Division of eight-and more-nuclear coenocytes was observed, leading to the formation of a very long polynuclear tubes the nuclei of which are all of equal size (Plate II, fig. 9). The observed frequent cases of polyploid and diploid division in the same coenocyte (Plate II, fig. 8) indicate that fusion of the nuclei has occurred earlier and the derivate nuclei do not lose their ability of dividing.

In the course of growth of the tannin coenocyte the nuclei are pushed back to the cell wall into cytoplasm bays or into the ends of the coenocyte (Plate II, fig. 10). At these sites the nuclei lying very close to each other may fuse. This is confirmed by the cytophotometric graph of the DNA amount in two neighbouring nuclei (Plate III, fig. 13). Between the first diploid nucleus and the next giant one there is not enough deep bend of the transmission curve which would be evidence of separation of the nuclei. Owing to the fusion process of various numbers of nuclei there arise elongated coenocytes with mixoploid nuclei (Plate III, fig. 11).

The karyological studies were confronted with cytophotometric examinations. In the preliminary stage of cytophotometric investigations the volume of the nuclei in the tannin coenocytes and neighbouring parenchyma cells was measured and amount of DNA in the same nuclei was measured, too. The degree of ploidy of the given nucleus was concluded separately from its volume and from the DNA level in it (Table 1).

This Table indicates that the data concerning ploidy, resulting from the volume of the nuclei and the logarithm of their volume agree (only in the case of high ploidy of the nucleus its degree resulting from the volume is 22 C and from the volume logarithm 24 C), but they differ in reference to the degree of ploidy resulting from DNA content.

The degree of ploidy resulting from the volume or the logarithm of volume is always higher than that concluded from the DNA content. For instance in a coenocyte with nuclei of various size four large nuclei are present, the volume of which suggests that they are polyploid (Table 1, 16 C), on the other hand, DNA content is the same as in other parenchymal nuclei. It would seem that the giant nucleus in another coenocyte (the only one I was able to measure) may contain 22 C as concluded from its volume. Actually, however, measurement of DNA indicated only 12 C. The volume of nuclei in the parenchyma surrounding the mononuclear tannin cells and the volume of these nuclei would indicate an equal degree of ploidy. It appeared, however, that the DNA content in the parenchymal cell was almast twice as high (Table 1 — 22.7 in parenchyma, 11.6 in tannin cells).

A GN-2 Stroud and Bahr cytophotometer was used for measurements in the second step of the investigations. Nuclei from parenchyma cells and tannin containers were compared on the same section. The results were

Table 1

Kind of cells	No. of cells examined	Mean volume of nucleus μm^3	Degree of ploidy from volume	Logarithm of mean volume	Degree of ploidy from logarithm	Mean DNA content (AU)	Degree of ploidy from DNA content
telophase in parenchyma cell	4	73.8	2C	1.869	2C	8.95	2C
undividing parenchyma	35	161.6	4C	2.275	4C	22,7	2C i 4C
mononuclear tannin cell (coenocyte mother cell)	4	164.2	4C	2.2154	4C	11.64	2C—4C
Coenocyte with nuclei of equal size	4	707.3	16C	2.850	16C	18.22	2C—4C
coenocyte with nuclei of various size (mixoploid)	1	987.0	22C	2.995	24C	70.2	12C

Table 2

Kind of cells	No. of nuclei examined	Mean DNA content (AU)	Range of DNA content (AU	(AU) Degree of ploidy resulting from DNA content
parenchyma	506	84.4	50—175	2C—4C
tannin mononuclear	18	82.8	55—120	2C+synthesis
tannin binuclear	14	85.6	65—140	2C+synthesis
tannin four-nuclear	12	98.0	90—120	2C+synthesis
tannin three-nuclear	3	65, 65, 125		2C i 4C
coenocytes with nuclei of equal size	53	78.9	55—120	2C+synthesis
mixoploid coenocytes	50		70—1290	2C—34C

obtained automatically in Arbitrary Units (AU). They are shown in Table 2 which gives the mean DNA values in the nuclei of tannin elements containing various numbers of nuclei of various ploidy degree according to the nuclear DNA content.

It results from Table 2 that in mononuclear tannin cells (tannin coenocyte mother cells) localized close to the promeristem (Plate I, fig. 2) the amount of nuclear DNA may be lower or equal to that in nuclei of the neighbouring parenchyma and within the range of DNA content characteristic for meristematic cells.

During division of a mononuclear tannin cell and after it the DNA content in the newly formed nuclei is not higher than in the parenchyma cells. A binuclear tannin cell has nuclei each of which contains as much DNA as the nuclei of the neighbouring parenchyma.

In four-nuclear tannin coenocytes each nucleus has DNA amount characteristic for the nucleus of a binuclear cell. Some few three-nuclear coenocytes were also observed in which one nucleus contained twice as much DNA as the remaining two. In the coenocytes of the second and further internodes (Plate I, fig. 1) the nuclei differ widely in DNA content (Plate III, fig. 11). Some coenocytes exhibit uniform diploid nuclei, but most, particularly the farther ones (2nd and 3rd internode) also contain, beside diploid ones (up to 34 C).

It may be concluded from the graph of DNA content obtained by connecting the cytophotometer with a scriber that two of the three neighbouring nuclei of a tannin coenocyte are polyploid (there are 5 pits on the diagram indicating the existence of at least 5 nucleoli), and one nucleus is diploid (Plate III, fig. 12), and that the border between one giant nucleus and the diploid one at the graph is obliterated what indicats the existence of junctions between them (Plate III, fig. 13).

A number of nucleoli higher than four proves that we are dealing with a polyploid nucleus. The highest number of nucleoli observed was 20 and was found in a giant nucleus. The number of nucleoli in a tannin coenocyte mother cell does not exceed four, and it seldom exceeded two. Fusion of nucleoli occurs here more frequently than in the nuclei of the neighbouring parenchyma cells.

DISCUSSION AND CONCLUSIONS

The method of nucleus volume measurement as index of the degree of ploidy proved good for most tissues. An increase in DNA content proportional to the increase of the nuclear volume was noted in: the tapetum of various plants (Skalińska, 1958; Trela, 1958; Turała, 1958, 1963), the parenchyma of *Vicia faba* roots (Grzycka, 1967), the hairs of *Cucumis* (Turała, 1960), the endosperm of *Pedicularis palustris* (Stef-

fen, 1956), the cells of haustoria of numerous plants (Erbrich, 1965), bean suspensors (Nagl, 1962), antipodes of numerous plants (Hasitschka, 1956; Tschermak-Woess, 1956), various tissues of angiospermous plants (Tschermak-Woess and Hasitschka, 1953; Hasitschka-Jenschke, 1962) and tissues of numerous plants and animals (Tschermak-Woess, 1963).

It results from the present investigations, however, that the volume method may be used in the case of *Sambucus racemosa* for concluding as to the degree of ploidy only in application to parenchyma cells. The DNA content in mononuclear tannin cells is not higher than in parenchyma cells, although their volume is almost twice that of the latter.

This phenomenon is in contrast to that observed by Beermann (1962) in secretory tissues of *Drosophila melanogaster*. This author found that the nuclei of secretory tissue contain larger amounts of DNA and that a doubling of DNA content does not cause a twofold increase of the volume of the nucleus. In the case of mononuclear tannin cells it is the nucleus volume that increases without a rise of the DNA level, meaning that the chromatin becomes diluted. Therefore some of the nuclei in Table 1 may represent nuclei in which DNA synthesis had only just started, while their volume was larger than that of nuclei of parenchyma cells. It is probable that DNA synthesis leading to nucleus division (Table 2) in mononuclear tannin cells occurs later, but their DNA content does not exceed that in the nuclei of parenchyma cells.

The method of counting nucleoli (Moll, 1928; Geitler, 1932; Trela, 1963) cannot be applied here since in the course of tannin coenocyte elongation, and thus of elongation of nuclei, fusion of the nucleoli often occurs. This fusion occurs much earlier in the tannin cell nucleus than in the nucleus of parenchyma cells.

The cytophotometric method allowed to establish that in mononuclear tannin cells the nuclei are diploid and their volume is increased. Synchronous karyokineses without cytokineses lead to the formation of tannin coenocytes which become mixoploid only later owing to the fusion of nuclei of different ploidy. A similar mechanism of polyploid nuclei formation was observed by Mahlberg (1959a, b) in the laticiferous ducts of *Euphorbia* and *Nerium*. The process of fusion of nuclei occurs in polynuclear cells. Even the partly forming cell wall does not prevent fusion of nuclei as found by Olszewska (1952) in *Narcissus*. In the shoots of *Sambucus racemosa* typical endomitotic nuclei were not observed, neither was postendomitotic division which occurs in the roots of this plant where tannin coenocytes have not been found. The absence of endomitosis in tannin coenocytes is also indicated by the fact that the contents of DNA in tannin nuclei as for instance 12 C, 34 C are not the expected multiples for the corresponding levels of endomitotic polyploidy.

The above discussed results allow the following conclusions:

1. Tannin coenocytes in *Sambucus racemosa* L. shoots arise from mononuclear cells (coenocyte mother cells) by the way of successive synchronous karyokineses without cytokinesis.

2. Tannin mononuclear cells (coenocyte mother cells) differentiate already in the first internode.

3. The nucleus of the mononuclear tannin cell, although much larger than the neighbouring nuclei of parenchyma cells, is diploid.

4. Tannin coenocytes may be classified to two types: those in which the nuclei are of equal ploidy and those with both polyploid and diploid nuclei.

5. Giant nuclei are formed in polynuclear tannin coenocytes by way of fusion of diploid and polyploid nuclei.

6. Both diploid and polyploid (giant) nuclei within the same coenocyte can divide by mitosis.

7. In tannin containers polyploidisation was found not to occur by way of endomitosis.

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Miksoploidalność cenocytów garbnikowych u Sambucus racemosa L.

Streszczenie

Metodą cytometryczną wykonano pomiary poziomu DNA jądrowego w miksoploidalnych komórkach garbnikowych u *Sambucus racemosa* L. W tym celu młode pędy boczne oraz siewki dzikiego bzu koralowego utrwalono w płynie CrAF, AA lub Carnoy. W preparatach mikrotomowych grubości 15 μm, po reakcji Feulgena, wykonano pomiary zawartości DNA jądrowego w komórkach garbnikowych oraz otaczających je komórkach miękiszowych. Pomiary wykonano przy λ = 5500 Å cytofometrem Stroud i Bahr GN — 2.

Jednojądrowa komórka garbnikowa znajdująca się w pierwszym międzywęźlu zawiera jądro duże, ale z rozrzedzoną chromatyną. Przy diploidalnej zawartości DNA jądro takie jest prawie dwukrotnie większe od jąder w sąsiadujących komórkach miękiszowych. W trakcie dalszego rozwoju w takiej komórce odbywają się kolejne synchroniczne kariokinezy bez cytokinez, które prowadzą do powstania kolejno komórki czterojądrowej, ośmiojądrowej itd. W komórkach wielojądrowych (komórczakach), występujących już w drugim międzywęźlu, często zachodzi proces fuzji jąder prowadzący do powstania jąder olbrzymich, poliploidalnych obok jąder diploidalnych. W takim cenocycie miksoploidalnym przez pewien czas wszystkie jądra zdolne są do podziałów.

PLATE I

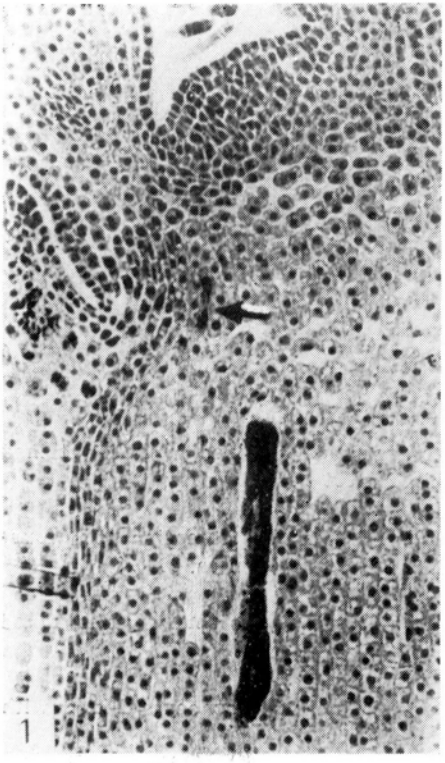
Fig. 1. Longitudinal section through upper internodes of young lateral shoot of *Sambucus racemosa* L. In first internode tannin mononuclear cell (arrow). In second internode tannin coenocyte. Fixed in CrAF, stained with iron hematoxylin, ca 150 ×

Fig. 2. Longitudinal section through first internode of young lateral shoot of *Sambucus racemosa* L. Mononuclear tannin cell (coenocyte mother cell) marked with arrow. Fixed in CrAF, stained with iron hematoxylin, ca 600 ×

Fig. 3. Mononuclear tannin cell (coenocyte mother cell). Large nucleus visible. Tannin in two vacuoles. Fixed in CrAF, stained with iron hematoxylin, ca. 800 ×

Fig. 4. Telophase without phragmoplast in mononuclear tannin cell. Fixed with CrAF, Feulgen reaction, ca. 500

Plate I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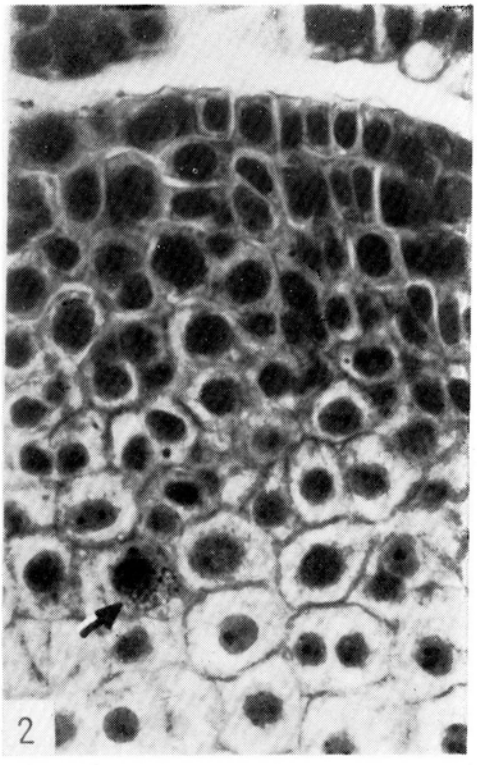
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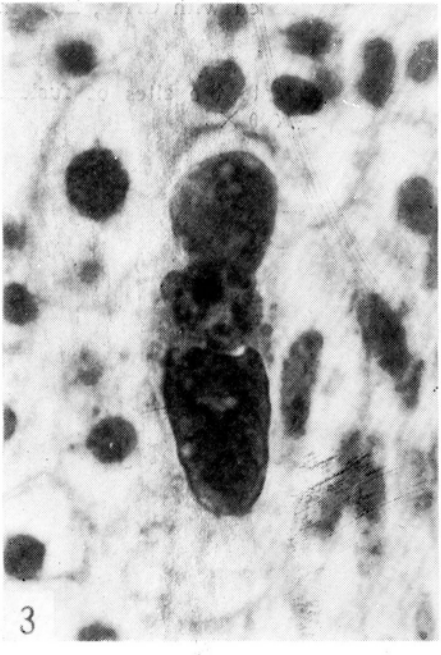
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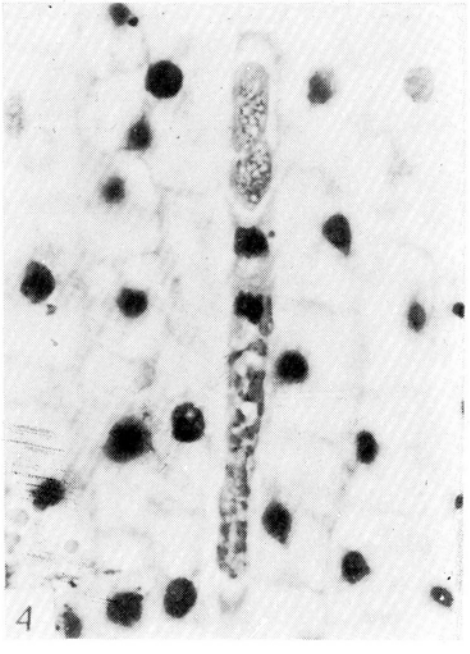

4

PLATE II

Fig. 5. Binuclear cell with nuclei lying close to one another. Fixed in CrAF, stained with iron hematoxylin, ca. 800 ×

Fig. 6. Synchronous division in binuclear cell leading to the formation of a four-nuclear coenocyte. Fixed with CrAF, Feulgen reaction ca. 600 ×

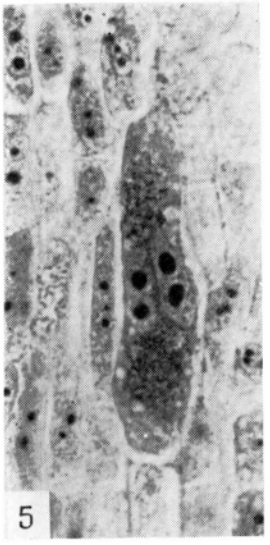
Fig. 7. Three-nuclear cell. Lower nucleus larger, formed of two smaller ones. Fixed with CrAF, Feulgen reaction, ca. 600 ×

Fig. 8. Division of polyploid and diploid nuclei in mixoploid coenocyte. Fixed with CrAF, Feulgen reaction, ca. 600 ×

Fig. 9. Division of diploid nuclei. Phragmoplast lacking. Fixed with CrAF, Feulgen reaction, ca. 600 ×

Fig. 10. Fusing nuclei in tannin coenocyte. Arrows indicate the sites of fusion. Fixed with CrAF, Feulgen reaction, ca. 600 ×

Plate II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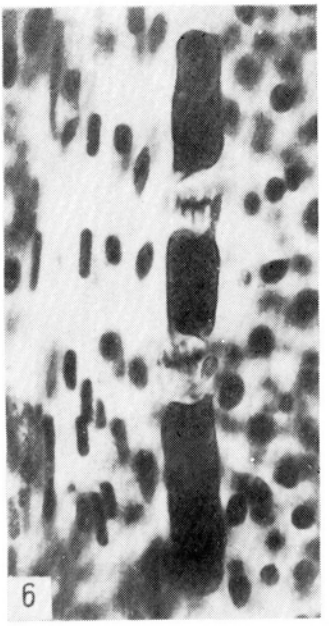
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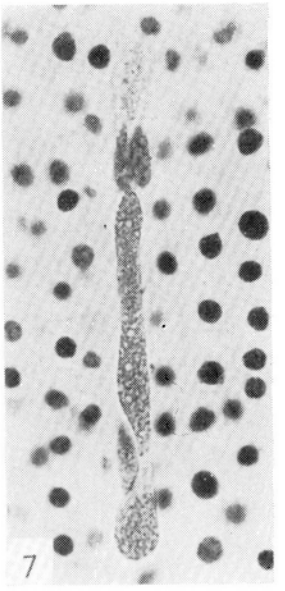
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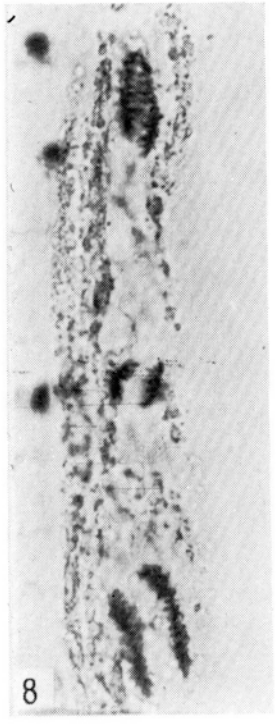
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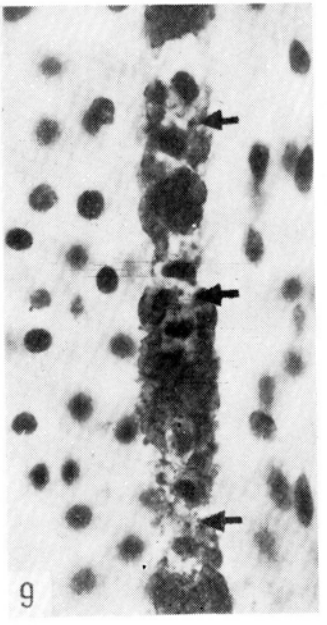
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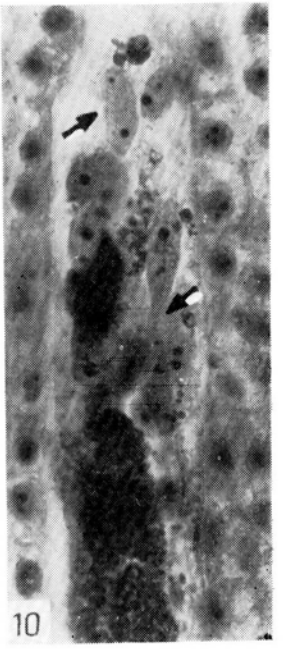
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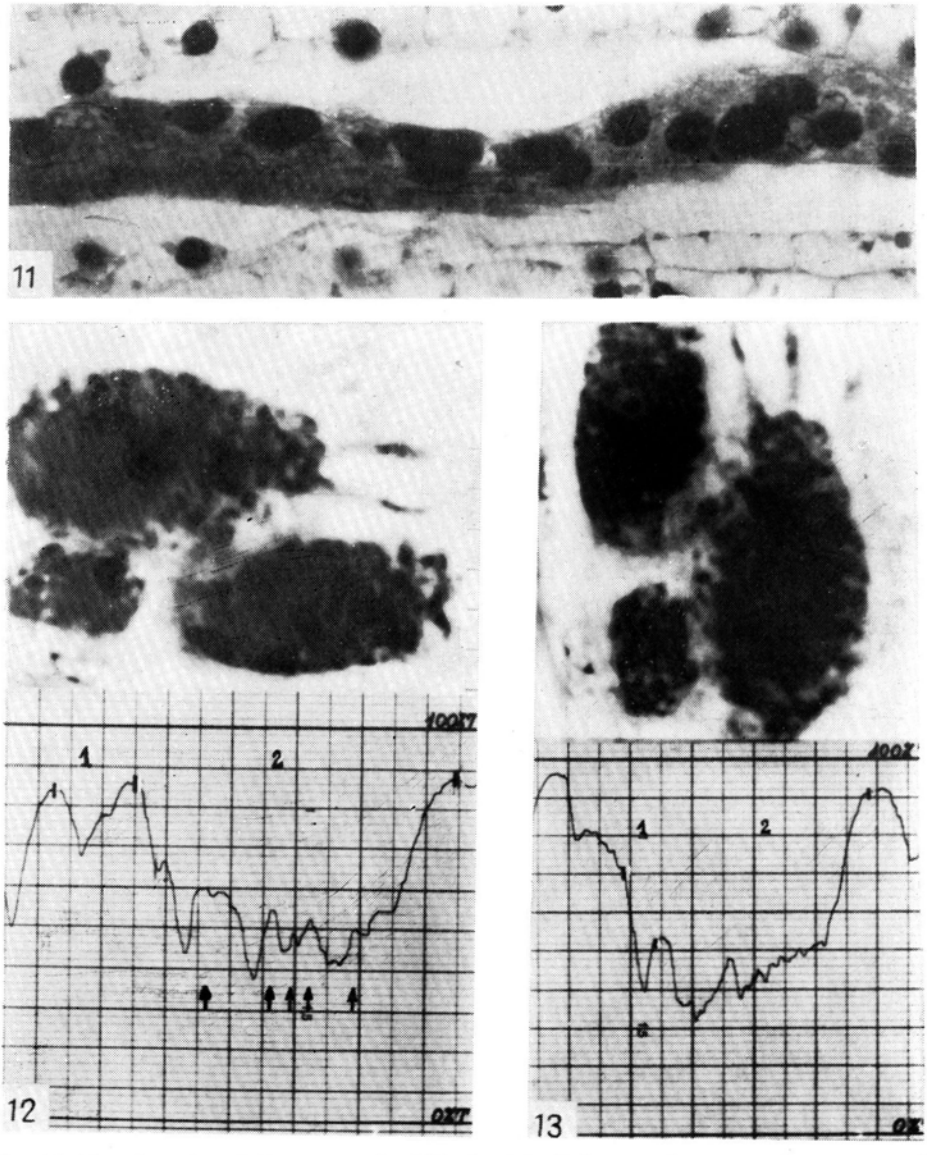

Fig. 11. Tannin mixoploid coenocyte. Fixed with CrAF, Feulgen reaction, ca. 600 ×
Fig. 12. Graph of DNA content in diploid (1) and polyploid (2) nucleus in horizontal line. In polyploid nucleus arrows indicate 5 nucleoli. Fixed with CrAF, Feulgen reaction, ca. 2 000 ×
Fig. 13. Record of DNA content in diploid (1) and polyploid (2) nucleus in horizontal line. Between these nuclei enhanced transmission does not take place, this indicates the occurrence of junctions between other nuclei. Fixed with CrAF, Feulgen reaction, ca. 2 000 ×