Cyto-histological processes during the differentiation
of the tapetal cells in the anthers of *Anthemis tinctoria* L.,
Erigeron annuus (L.) Pers. and *E. canadensis* L.

K. BIJOK, B. KREŃSKA, AND T. PAWLAK

Institute of Biology, University of Gdańsk, Gdynia

ABSTRACT

Tapetal cells in the anthers of *Anthemis tinctoria*, *Erigeron annuus* and *E. canadensis* were uninucleate in the premeiotic stage of the PMC's. Tapetum differentiation with inhibited cytokinesis took place during the period of meiotic divisions. In *E. canadensis* both mitoses were normal, whereas in *A. tinctoria* and *E. canadensis* after both first and second mitotic divisions as a result of numerous disturbances polyploid nuclei were formed.

INTRODUCTION

The present investigations aimed to establish the cytological processes during tapetal cells differentiation in the three species studied with special emphasis on the number of nuclei in the cells and of their ploidy degree was studied.

MATERIAL AND METHODS

The plants were collected from natural habitats in Poland (Table 1).

Young flowers buds were fixed in the field with 50% Nawashin fixative. The fixed material was embedded in paraffine and cut on microtome into 15 μ m thick sections. The preparations were stained with 1% gentian violet and differentiated in phenol solution in xylene (1:3). The drawings were done with Zeiss apparatus from Amplival microscope with 100 $\times$ objective and K 20 $\times$ Zeiss eye piece.

Table 1

List of habitats of *Anthemis tinctoria* L., *Erigeron annuus* (L.) Pers. and *Erigeron canadensis* L.

Species	Place of origin	
<i>Anthemis tinctoria</i>	Koniaków	district Cieszyn
	Ustroń	" "
	Czechowice-Dziedzice	" Bielsko
	Częstochowa	" Częstochowa
	Działdowo	" Działdowo
	Olsztyn-Kortowo	" Olsztyn
	Puszcza Piska	" Pisz
<i>Erigeron annuus</i>	Kończyce Wielkie	district Cieszyn
	Wisła	" "
	Pszczyna	" Pszczyna
	Olsztyn-Kortowo	" Olsztyn
	Puszcza Piska	" Pisz
<i>Erigeron canadensis</i>	Kończyce Małe	district Cieszyn
	Istebna	" "
	Działdowo	" Działdowo
	Olsztyn-Kortowo	" Olsztyn
	Puszcza Piska	" Pisz

RESULTS

Tapetal cells layer on premeiotic stage of PMC's

The tapetal cells layer at the premeiotic stage of PMC's was quite distinct from PMC's (Fig. 1). At the time PMC's were polygonal and tightly adjacent to each other (Fig. 1a) whereas the tapetal cells in the longitudinal section of the anther were of nearly the same size and formed an unilayer tissue (Fig. 1b). The tapetal cells had granular cytoplasm and both cytoplasm and nuclei were strongly stained. In the premeiotic stage of PMC's no mitotic divisions in tapetal cells were observed. They were always uninuclear in all three species studied.

The tapetal cells at the time from zygotene to first metaphase in PMC's and their ploidy degree

The ploidy degree was established not on the analysis of metaphase plates as the chromosomes were very crowded, but on the nuclear diameter. As the nuclei were more or less elongated both the length the breadth of the nuclei were measured (Tab. 2). The obtained values were divided in three categories: diploid, tetraploid and octoploid nuclei (Tab. 2).

Figs 1—2. *Anthemis tinctoria* L.
1a — P.M.C's, 1b — tapetal cells, 2 — degenerated tapetal cells ($\times 1200$)

The frequency of mitotic divisions in T.C's of the species studied was the highest at the stage between zygotene to diakinesis in PMC's (Tab. 3). In earlier or later stages no mitotic divisions were observed. The maximum frequency of mitotic divisions in all three species was during pachytene stage, was decreasing in later stages and mitoses were completely disappearing at the first metaphase stage of PMC's.

At the time in tapetal cells big changes in their size and shape as well in the number of nuclei in individual cells took place.

In all three species only two mitotic divisions in tapetal cells occurred with inhibited cytokinesis. As a results of the first mitotic division two diploid nuclei were formed in tapetal cells (Figs 3—5, 16—18, 28—31). After second mitosis in tapetal cells four diploid nuclei were formed (Figs 3, 6, 7, 19, 20, 32). In this case they were most often arranged linearly (Figs 7, 20, 33), rarely and some angle within the cells. Both after the first and second mitotic division the tapetal cells elongated strongly parallel to the logitudinal axis of the anther (Figs 3—7, 16—20, 28—33).

In *Erigeron canadensis* during the first and second division with inhibited cytokinesis no disturbances in tapetal cells were observed.

Table 2
Diameter measurements of nuclei of *Anthemis tinctoria* L., *Erigeron annuus* (L.) Pers. and *Erigeron canadensis* L.

Species	2n oval		4n oval		4n elongated		8n oval	
	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length
<i>Anthemis tinctoria</i>	7.3—7.6	9.0—9.9	7.2—8.5	12.6—13.9	5.8—7.2	20.7—22.5	13.0—14.1	13.9—15.3
<i>Erigeron annuus</i>	7.6—8.1	7.9—8.2	10.3—10.9	11.0—11.5	7.3—7.6	21.0—23.4	15.7—15.9	16.2—16.8
<i>Erigeron canadensis</i>	5.5—5.8	9.5—9.9	—	—	—	—	—	—

Table 3

The course of the first and second mitoses in 100 investigated tapetal cells of *Anthemis tinctoria* *Erigeron annuus* and *Erigeron canadensis* during successive meiotic stages

Meiotic stages in P.M.C's	Tapetal cells																																	
	<i>Anthemis tinctoria</i>										<i>Erigeron annuus</i> (L.) Pers										<i>Erigeron canadensis</i> L.													
	Uninucleate	Binucleate	Four nucleate	Uninucleate in division	Binucleate in division	1 tetraploid nucleus in division	With 1 tetraploid restitution nucleus	With 2 tetraploid restitution nuclei	With 1 tetraploid and 2 diploid nuclei	With 1 octoploid restitution nucleus	With 1 octoploid fusion-nucleus	Uninucleate	Binucleate	Fournucleate	Uninucleate in division	Binucleate in division	1 tetraploid nucleus in division	With 1 tetraploid restitution nucleus	With 2 tetraploid restitution nuclei	With 1 tetraploid and 2 diploid nuclei	With 1 octoploid restitution nucleus	With 1 octoploid fusion-nucleus	Uninucleate	Binucleate	Fournucleate	Uninucleate in division	Binucleate in division	1 tetraploid nucleus in division	With 1 tetraploid restitution nucleus	With 2 tetraploid restitution nuclei	With 1 tetraploid and 2 diploid nuclei	With 1 octoploid restitution nucleus	With 1 octoploid fusion-nucleus	
Premeiotic stage	100	—	—	—	—	—	—	—	—	—	—	100	—	—	—	—	—	—	—	—	—	—	100	—	—	—	—	—	—	—	—	—	—	—
Zygotene	61	8	6	10	10	—	5	—	—	—	—	30	10	5	15	25	—	10	5	—	—	—	43	7	20	25	—	—	—	—	—	—	—	
Pachytene to diakinesis	—	15	20	5	6	15	7	20	8	4	—	—	20	20	6	5	10	5	9	15	5	5	—	27	50	8	15	—	—	—	—	—	—	
First metaphase in P.M.C.'s	—	—	41	—	—	—	20	20	—	19	—	—	—	46	—	—	—	15	14	10	10	5	—	35	65	—	—	—	—	—	—	—	—

Figs 3—15

After first mitotic division the tapetal cells had two diploid nuclei and after the second division — four diploid nuclei (Table 3, Figs 28—33).

In T.C's of *Erigeron annuus* disturbances during the second mitotic division with inhibited cytokinesis were observed. Probably as a result of incomplete of spindle formation the metaphase from two nuclei fused (Fig. 25) and in the tapetal cells two tetraploid nuclei with strongly elongated shape were formed (Fig. 26). The T.C's with one restitutional octoploid nucleus were formed if the chromosomes from two fused metaphase plates formed bridges during the chromosomes separation (Fig. 28).

In *E. annuus* octoploid nucleus of tapetal cell might also arose by fusion of two tetraploid nuclei (Fig. 27).

If the axes of kariokinetic spindles of two dividing nuclei were some angle to each other (Fig. 21) tapetal cells with three nuclei of different ploidy degree were formed: one restitutional tetraploid nucleus and two diploid nuclei (Fig. 22).

In *Anthemis tinctoria* as in *Erigeron canadensis* and *E. annuus* only two mitotic divisions with inhibited cytokinesis were observed and thus the tapetal cells with two or four diploid nuclei occurred (Fig. 3—7).

Disturbances were observed both in first and second mitotic divisions.

During the first mitotic division in *A. tinctoria*, like in the second division in *E. annuus*, as a result of bridges formation at anaphase one restitutional tetraploid nucleus was formed (Fig. 8, 9). Whereas the formation of anaphase bridges leded to formation of one, restitutional octoploid nucleus (Fig. 10, 11).

The normal division of that restitutional, tetraploid nucleus resulted in the formation of tapetal cells with two tetraploid nuclei (Figs. 12—13).

Other disturbances during the second mitotic division in tapetal cells of *A. tinctoria* consisted of the fusion of two chromosome groups at anaphase at both poles (Fig. 19). The resulting tapetal cells had two elongated tetraploid nuclei (Fig. 15).

Figs 3—7. First and second mitoses with inhibited cytokinesis in tapetal cells of *Anthemis tinctoria* L.

3 — cell with one diploid nucleus, 4 — anaphase of first mitosis, 5 — tapetal cell with two diploid nuclei, 6 — anaphase of second mitosis, 7 — tapetal cell with four diploid nuclei ($\times 1000$)

Figs 8—15. Disturbances during the first and second mitoses with inhibited cytokinesis in tapetal cells of *Anthemis tinctoria* L.

8 — abnormal first mitosis responsible for the development of tetraploid restitution nucleus, 9 — tapetal cell with one tetraploid restitution nucleus, 10 — abnormal mitosis in restitution tetraploid nucleus, responsible for the development of one restitution octoploid nucleus, 11 — tapetal cell with one octoploid restitution nucleus, 12 — anaphase tetraploid restitution nucleus, 13 — tapetal cell with two tetraploid nuclei, 14 — abnormal second mitosis in cell with two diploid nuclei, responsible for the development of two tetraploid restitution nuclei, 15 — tapetal cell with two restitution tetraploid nuclei ($\times 1000$)

Figs 16—27

28 — tapetal cell with one diploid nucleus, 29 — metaphase of first mitosis, 30 — anaphase of

Erigeron canadensis L.

28 — tapetal cell with one diploid nucleus, 29 — metaphase of first mitosis, 30 — anaphase of first mitosis, 31 — tapetal cell with two diploid nuclei, 32 — anaphase of second mitosis, 33 — tapetal cell with four diploid nuclei ($\times 2400$)

Table 3 contains the data on the course of first and second mitosis with inhibited cytokinesis from 100 studied cells for each species. As we see in the first metaphase stage in PMC's only in *Erigeron canadensis* 35% of T.C's had two diploid nuclei, they were absent completely in *A. tinctoria* and *E. annuus*. Cells with four diploid nuclei appeared in 41% of T. C's of *A. tinctoria*, in 46% of T.C's of *E. annuus* and in 65% of T. C's of *E. canadensis*. Cells with one and two tetraploid nuclei appeared in 40% of T.C's of *A. tinctoria*, and in 29% of T.C's of

Figs 16—20. First and second mitoses with inhibited cytokinesis in tapetal cells of *Erigeron annuus* (L.) Pers.

16 — cell with one diploid nucleus, 17 — anaphase of first mitosis, 18 — tapetal cell with two diploid nuclei, 19 — anaphase of second mitosis, 20 — tapetal cell with four diploid nuclei ($\times 750$)

Figs 21—27. Disturbances during the second mitosis with inhibited cytokinesis in tapetal cells of *Erigeron annuus* (L.) Pers.

21 — abnormal second mitosis in two diploid nuclei, 22 — tapetal cell with one tetraploid restitution nucleus and two diploid nuclei, 23 — abnormal second mitosis in two diploid nuclei, responsible for the development of one octoploid restitution nucleus, 24 — tapetal cell with one octoploid restitution nucleus, 25 — abnormal second mitosis in two diploid nuclei, 26 — tapetal cell with two tetraploid restitution nuclei, 27 — tapetal cell with one octoploid nucleus which was formed after the fusion of two tetraploid nuclei ($\times 750$)

E. annuus but were absent completely in T.C's of *E. canadensis*. In *E. annuus* occurred also tapetal cells with one tetra- and two diploid nuclei, thus 10% of octoploid cells.

Cells with one octoploid nucleus occurred in 19% of T.C's of *A. tinctoria* and in 15% of T.C's of *E. annuus*.

At the time of formation of primary pollen grains processes connected with the beginning degeneration of the tapetal tissue took place. They proceeded very slowly, the cells were elongating and the whole tissue lost gradually its compact structure. A vacuolization of the cytoplasm was observed and the nuclei lost early their stainability and their boundaries become less distinct. At the same time the cell walls desintegrated (Fig. 2).

The processes of degeneration were simultaneous in all tapetal cells (Fig. 2). The tapetal tissue in all three species maintained its cellular character.

DISCUSSION

The cyto-histological differentiation of the tapetal tissue in the anthers of *Anthemis tinctoria*, *Erigeron annuus* and *E. canadensis* were studied.

The development of tapetal cells was especially studied by Carniel (1952, 1954) in many of angiospermous species.

Only very rarely tapetal cells remain uninucleate. Their nuclei can be at different levels of ploidy as a result of endomitosis (Carniel, 1952, 1954; Turała, 1958). More often the differentiation of tapetal cells occur through one to four mitoses without cytokinesis. This leads in many cases to the formation of cells with two or many nuclei. This development is often complicated by disturbances in mitotic divisions in these cells.

Uninucleate T.C's were found in *Delphinium ajacis* (Cooper, 1933), *D. villosum*, *Helleborus foetidus* (Carniel, 1952), *Melilotus albus*, *M. officinalis*, *Trigonella coerulea* (Bijok, 1962), *Trifolium hybridum*, *T. repens* and in their artificial polyploids (Bijok, Góral and Góral, 1970). *T. pratense* var. *spontaneum* and its artificial polyploid (Bijok, Góral and Góral 1970).

In species studied by Carniel (1952) and Turała (1958) in uninucleate T.C's polyploid nuclei formed by endomitosis were found.

In *Ranunculus fascicularis* (Cooper, 1933), *Crambe abyssinica*, *C. maritima*, *Brassica napus*, *B. rapa*, *B. juncea*, *B. nigra* (Bijok 1962, 1963, 1964, 1966 a, b, 1967) tapetal cells are with two nuclei and in *R. ficaria* are four-nucleate (Carniel 1952). Wunderlich (1954), Trela (1958)

in *Aconitum variegatum* and *A. vulparia*, and Smith (1933) in *Galtonia candicans* have found binucleate T.C's and Carniel (1952) in *A. vulparia* also multinucleate tapetal cells.

In *Hyoscyamus niger* var. *annuus* Bijok, Sulma and Tokarz (1968) have observed binucleate tapetal cells with diploid nuclei and also binucleate cells with tetraploid nuclei, as well as multinucleate cells with nuclei at different levels of ploidy. Bijok (1960) and Adamkiewicz (1966) got similar results with *Chrysanthemum segetum*, *Ch. subcorymbosum*, *Ch. corymbosum* and *Ch. parthenifolium*. In *Valeriana officinalis* Skalińska (1958) has found tapetal cells with 8 diploid nuclei.

In the present study in the premeiotic stage of PMC's only unicleate tapetal cells were found. As a result of two mitotic division without cytokinesis these cells were transformed in bi- or four nucleate cells with diploid nuclei.

In *Erigeron canadensis* this stage was the final one.

In *Anthemis tinctoria* after first mitosis which on the whole was quite normal binucleate cells were formed. The disturbances in the course of anaphase and telophase caused the formation of tetraploid restitution nuclei. This was never observed in *Erigeron annuus*.

The course of second mitotic division in tapetal cells of *A. tinctoria* and *E. annuus* was often irregular. During the restitution divisions of tetraploid nuclei in *A. tinctoria* uninucleate tapetal cells with octoploid nuclei were formed, or if the course of mitosis was normal binucleate tapetal cells with tetraploid nuclei appeared. This kind of disturbances in several species from the families *Compositae*, *Scrophulariaceae* and *Solanaceae* was observed by Mayer (1925), Gentscheff, Gustafsson (1940), Mechelke (1952), Bijok (1960), Bijok, Sulma, Tokarz (1968), Adamkiewicz (1966) and Małecka (1971).

In cells with parallel orientation of karyokinetic spindles in *Erigeron annuus* the fusion of metaphasal plates from two nuclei occurred. In case of the occurrence of additional anaphasal bridges octoploid restitutional nuclei were formed. When the spindle axes were at some angle during the second mitotic division T.C's arose with three nuclei — two diploid and one tetraploid. This kind of disturbances was observed in *Chrysanthemum segetum*, *Ch. subcorymbosum*, *Ch. corymbosum* by Bijok (1960), in *Ch. parthenium* by Adamkiewicz (1966) and in *Hyoscyamus niger* var. *annuus* by Bijok, Sulma and Tokarz (1968).

In some species as *Hieracium amplexicaule* (Gentscheff, Gustafsson 1949), *Leontodon autumnalis* (Mayer 1925), *Valeriana officinalis* (Skalińska 1958), *Cichorium intybus* (Jaworska 1963), in the genus *Taraxacum* (Małecka 1971), *Sonchus asper* and *S. oleraceus* (Walter and Kuta 1971) three or even four mitotic divisions

in tapetal cells were described. Thus, the above mentioned authors have found in these plants tapetal cells with eight or sixteen diploid nuclei.

The nuclear fusion like in *Erigeron annuus* was also observed by Poddubnaja-Arnoldi (1931), Genscheff and Gustafsson (1940) and Skalińska (1958) in *Carduus* sp., *Hieracium* and *Valeriana*.

Like in *Anthemis tinctoria*, *Erigeron annuus* and *E. canadensis* many authors have observed the highest frequency of mitotic divisions in tapetal cells at the stage of prophase of first meiotic division in PMC's. After the first meiotic division of PMC's no further mitotic divisions without cytokinesis were observed in T.C's. Exceptionally in *Ranunculus ficaria* (Carniel 1952) the maximum of mitotic divisions in tapetal cells was observed in the stage of the second meiotic division in PMC's.

In *Aconitum variegatum* the process of tapetal cells degeneration started in uninucleate diploid cells and gradually spreaded to binucleate cells and later appeared in tetra- and octoploid T.C's. In *Anthemis tinctoria*, *Erigeron annuus* and *E. canadensis* this process was simultaneous in all kinds of tapetal cells with no relation to the degree of ploidy and number of nuclei.

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Authors' address:

Prof. dr. Karol Bijok,
Mgr. T. Pawlak, and Mgr. B. Kreńska
Institute of Biology, University of Gdańsk,
Czołgistów Str. 46; 01-378 Gdynia; Poland

*Procesy cyto-histologiczne w czasie różnicowania się tapetum pylników
Anthemis tinctoria L., Erigeron annuus (L.) Pers. i E. canadensis L.*

Streszczenie

Komórki tapetum u *Anthemis tinctoria* L., *Erigeron annuus* (L.) Pers. i *E. canadensis* w stadium premejotycznym komórek macierzystych pyłku były jednojądrowe. Różnicowanie warstwy tapetum w pylnikach u tych gatunków zachodziło przez dwa podziały mitotyczne z zahamowaniem cytokinezy. Podziały jąder komórek tapetum zachodziły w stadiach od zygotenu do diakinezy w komórkach macierzystych pyłku.

U *E. canadensis* obydwie mitozy miały przebieg normalny, dając dwu- i czterojądrowe komórki tapetum o jądrach diploidalnych.

U *Anthemis tinctoria* i *E. annuus* w większości przebiegu pierwszego i drugiego podziału mitotycznego w komórkach tapetum zachodziły zaburzenia, które prowadziły do powstania poliploidalnych jąder. U *A. tinctoria* obserwowano więc komórki tapetum jedno- i dwujądrowe o jądrach tetraploidalnych oraz jednojądrowe o jądrach oktoploidalnych. U *E. annuus* obserwowano poza tym komórki o trzech jądrach, z których dwa były diploidalne, a trzecie tetraploidalne. U *E. annuus* stwierdzono ponadto w komórkach tapetum fuzję jąder tetraploidalnych w jądro oktoploidalne.

U badanych gatunków tapetum było typu komórkowego.

Proces degeneracji warstwy komórek tapetum rozpoczynał się od stadium kształtowania się pierwotnych ziarn pyłku i miał przebieg jednoczesny we wszystkich komórkach, niezależnie od ich stopnia poliploidalności.