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Studies in the biology of reproduction and embryology of *Homogyne alpina* (L.) Cass.

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INTRODUCTION

The present paper deals with the mode of reproduction of *Homogyne alpina* (L.) Cass., a high polyploid species of the *Compositae* frequently occurring in Carpathians and Sudetes, as well as in the Tatra Mts, from the higher mountain layer up to the alpine layer.

Langlet (1936) gives for *Homogyne alpina* the approximate haploid chromosome number n = 70. Root-tip metaphases of plants from the Tatra Mts studied on slides kindly put at my disposal by Dr. H. Wcisło also proved the presence of a very high number of chromosomes, crowded in the plates. A precise counting was very difficult, but the chromosome number seemed to approach that given by Langlet.

Embryological investigations of *Homogyne alpina* have not been carried out hitherto. The problem of reproduction of this species is interesting in view of the frequent occurrence of apomixis among *Compositae*. As it has been shown by the investigations on *Hieracium* (Rosenberg 1907, Gustafsson 1935), *Antennaria* (Juel 1900, Stebbins 1932a, b, Bergman 1951) and *Taraxacum* (Osawa 1913, Gustafsson 1932), particular species within the genus may differ from one another in the mode of reproduction. Besides sexual species with lower chromosome numbers there occur polyploid apomictic species. On the other hand, in other genera some high polyploids may have a normal sexual reproduction e. g. *Doronicum Clusii* (Wcisło 1952) with the chromosome number, 2n = 120.

The present investigations have shown that *Homogyne alpina* represents likewise a high polyploid species with a sexual reproduction.

Table 1

No of habitat	Place of origin	Altitude over sea level(m)
12	Bieszczady Mts — Połonina Caryńska	c. 1250
11	Gorce Mts — Mogielica	c. 1140
	Tatra Mts.	
	a. Higher mountain layer:	
24	Kuźnice — road to Valley Olczyska	c. 1020
23, 31	Wood in the lower part of Valley Jaworzynka	c. 1050
26	Boczań — path to Hala Gąsienicowa	c. 1240
16, 17, 18	surroundings of the Valley Roztoka	c. 1250
	b. Layer of subalpine forests:	
25, 27	slopes over Valley Jaworzynka	1300 — 1400
8	Valley of the lake Morskie Oko — in neighbourhood of the tourists-house	c. 1400
9, 10	border of the lake Morskie Oko and path to Czarny Staw over Morskie Oko	1393 — 1400
33, 29	Hala Gąsienicowa — in a spruce wood	c. 1500
22	road from Hala Gąsienicowa to Brzeziny	c. 1470
	c. Layer of *Pinus montana*:	
13, 28, 35	Hala Gąsienicowa	1500 — 1530
37, 38	Hala Gąsienicowa — „old" track to Czarny Staw Gąsienicowy	c. 1530
30	western slope of Mały Kościelec	c. 1550
7	middle part of the road from Hala Gąsienicowa to Czarny Staw Gąsienicowy	c. 1550
5	northern slope of Mały Kościelec	c. 1580
6	eastern slope of Mały Kościelec	c. 1600
3, 4	path from Kasprowy Wierch to Hala Gąsienicowa	c. 1700
20, 21, 39	Valley of Stawy Gąsienicowe	c. 1700
32	Kopa Magury — near the peak	c. 1700
19	Valley of the Five Polish Lakes — border of the lake Wielki Staw	c. 1665
34	peak of Mały Kościelec	c. 1780
	d. Alpine layer:	
2	northeastern slope of Beskid	c. 1800
1	eastern slope of Kasprowy Wierch	c. 1800
15	near the lake Zmarzły Staw below Zawrat	c. 1800
36	Uhrocie Kasprowe — northern slope	c. 1830
14	Valley Kozia Dolinka	c. 1900

MATERIALS AND METHODS

The material in the form of flower buds and inflorescences in various stages of development originated from the Tatra Mts, Gorce and Bieszczady Mts. Table 1 gives the list of the particular habitats.

The fixation has been always carried out on the spot, in the years 1953, 1954 and 1955. The first lot of materials was fixed in the Tatra Mts in the spring 1953 by Prof. Dr. Skalińska (n. 1, 2, 3, 8, 9). The

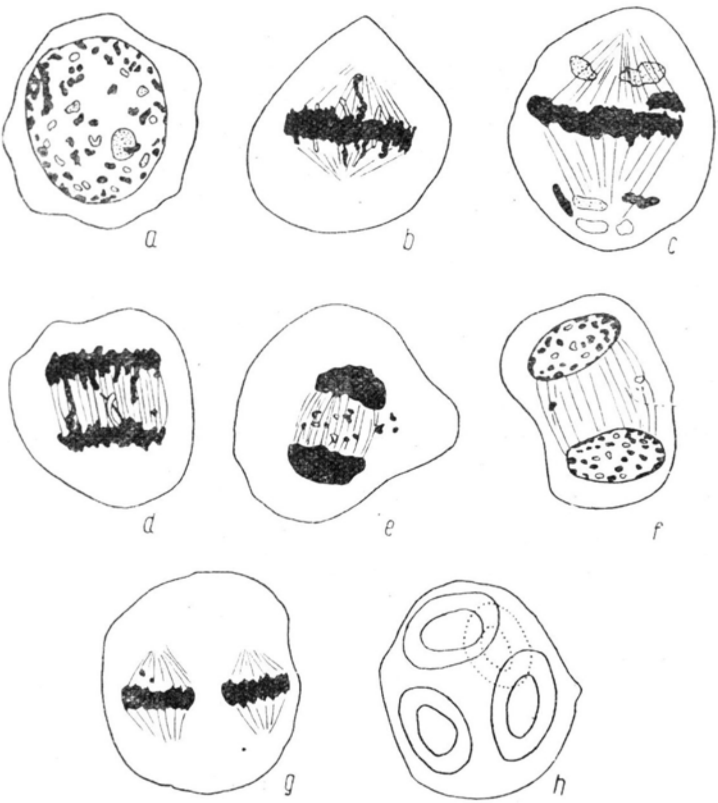

Fig. 1. *Homogyne alpina*, meiosis in PMC's: a, Diakinesis. b, I Metaphase with polyvalents. c, I Metaphase in side view: groups of chromosomes outside the equatorial plate. d, abnormal I Anaphase in side view. e, I Telophase with lagging chromosomes. f, Interkinesis with lost chromosomes. g, II Metaphase. h, tetrad (1500 ×).

material was fixed in acetic alcohol. The microtome sections 10 μ thick were stained with Heidenhain's hematoxylin; for older stages Meyer's hematoxylin was used with good results.

Drawings were made under a Leitz's microscope with the aid of Leitz's camera lucida. Their magnification is given with the explanation of the respective figures.

OBSERVATIONS IN THE BIOLOGY OF REPRODUCTION AND THE FIRST STAGES OF DEVELOPMENT OF FLOWER BUDS

The anthers of the first flower buds fixed in spring 1953 (15 June 1953) contained pollen grains with a wholly developed exine. This fact suggested that flower buds are formed already in the previous season. Subsequent observations permit me to establish, that their development really begins in mid-summer, immediately after the dispersal of the achenes.

Hibernating flower buds of *Homogyne* develop among the basal leaves; they attain in the autumn a maximal diameter of 4—6 mm. The young heads are covered with two scales and a sheath-like petiole, and are therefore difficult to discern. Abundantly developed covering hairs provide a thermal isolation.

In the flower buds fixed in the mountains in late autumn, almost immediately before snow fall (18 Nov. 1954), the anthers contained already developed PMC's. The ovules in the oldest flower buds possessed a differentiated unicellular archesporium. The observed differences in the stages of development of the ovules were probably due to the position of the particular flowers in the heads.

These observations explain the fact that meiotic divisions take place very early in spring. Probably a very slight increase of temperature induces the beginning of meiosis in PMC's. In the first inflorescences fixed in spring (15 April 1955) meioses were found in the anthers in spite of the fact that the buds were covered with snow.

Hibernating flower buds with differentiated PMC's are known in early-flowering plants. This was shown for instance by F a v a r g e r (1952) for *Gentiana verna*, and by D a h l g r e n (1915) for *Populus tremula* and *Salix purpurea*.

MICROSPOROGENESIS

As has been previously noted, the winter buds of *Homogyne alpina* have already differentiated PMC's. I succeded in finding the first stages of meiosis in the material from the Tatra Mts fixed early in spring (April 1955). At that time the buds frequently still remained under the snow cover.

According to L a n g l e t (1936), *Homogyne alpina* possesses a high chromosome number (n = c. 70). The same is true also of the biotypes from the Tatra Mts. At Diakinesis the chromosomes are evenly distributed just under the surface of the nucleus. Besides bivalents the occurrence of univalents in a varying number and also of polyvalents (Fig. 1) could be established.

The I Metaphase appeared as a rather regular stage, though occasionally irregular plates could be also observed; univalents were frequent, sometimes they were found in a large number outside the equatorial plate

Table 2

Dates of the various stages of development found in the ovules

Stage	No of habitats*	Dates of the fixation **
Younger stages of development of the ovules	13, 14, 15, 16, 17 18, 19, 20, 21	28 Aug. 9 Sept. 19 Sept. 23 Sept. 31 Sept. 1 Oct. 12 Oct. 14 Nov.
Ovules with the archesperial cell	22	18 Nov.
EMC (resting stage and I meiotic division)	8, 23, 24, 25, 26	14 June, 13 Apr. 15 Apr. 6 May, 14 June.
Il meiotic division	8, 28	14 June, 15 May.
Tetrad (polyad)	8, 28, 27	14 June, 15 May, 13 May.
uninuclear ES	5, 8, 9, 10	13 June, 14 June. 15 June.
I mitosis in ES	5	13 June.
binuclear ES	5, 6, 7, 9, 10, 29, 30	13 June, 14 June, 15 June. 15 May, 26 May.
II mitosis in ES	—	—
four-nuclear ES	5, 7, 9, 10, 29, 30, 31, 32, 33, 34, 35	13 June, 14 June, 15 June. 15 May, 26 May, 29 May. 31 May, 1 June, 15 June. 16 June.
III mitosis in ES	5, 9	13 June, 15 June.
13-15 nuclear ES	1, 2, 35, 36, 37, 38, 39	14 Jul. 16 June, 24 June. 25 June, 30 June, 6 Jul.
ES containing embryolike structures at the chalazal end	38, 39	30 June, 6 Jul.
Typical embryo surrounded by endosperm	3. 4, 11, 12,	14 Jul. 12 Jul. 29 June.

* see Table 1

** the sequence of the fixation dates corresponds to that of the habitats in the second vertical column.

(Fig. 1). In I Metaphase spindles in side view it was possible to discern some polyvalents which differed distinctly in length from bivalents grouped in the equatorial plate. In polar view the Metaphase plates showed a high number of crowded chromosomes; the counting was extremely difficult. In two plates in which the chromosomes were somewhat better spaced, about 70 units could be counted.

The I Anaphase was found in a relatively small number of PMC's. In some cells an irregular distribution of the chromosomes could be observed. In a number of cells a large number of chromosomes was scattered beyond the spindle. Some anthers containing PMC's in these stages manifested signs of degeneration.

In the I Telophase a varying number of scattered chromosomes was stated almost in all cells.

On the whole, the Interkinesis had a normal appearance. However in addition to the two daughter nuclei small supernumerary nuclei or lagging chromosomes (Fig. 1) could be found rather frequently. In one pollen sac, besides normal cells at the I Telophase, some PMC's with only one nucleus were found; such a nucleus with its elongated, rather irregular shape may represent a restitution nucleus. Thus, the respective cells possibly correspond to an abnormal uninucleate interkinesis.

The II Metaphase had a rather typical appearance. In the II Telophase the presence of sporadically appearing microcytes could be stated.

The majority of the tetrads were normal and the mature pollen consisted of well filled fertile grains with sculptured exines.

MACROSPOROGENESIS

As is was already noted, the ovules of the hibernating flower buds of *Homogyne* possess already a differentiated unicellular archesporium. In this stage the integument does not surround totally the nucellus, reaching approximately to two thirds of its height. In the buds fixed in spring (15 April 1955) the EMC's were in early stages of the meiotic Prophase (leptotene, pachytene). In comparison with the autumn stages the integument shows an increase in size. The top of the nucellus, however, is enclosed by the integument at the time, when the EMC reaches I Metaphase. The dates of the particular stages of development are grouped in Table 2.

On the whole, the beginning of the meiotic divisions in EMC's coincides with the end of the meiotic divisions in the anthers or sometimes with the tetrad stage. Only rarely some deviations were observed.

In the course of a further development, the stalks bearing the heads at their tops stretch gradually. Initially they are bent down, but prior to the beginning of flowering they assume a upright position.

The investigated material consists of 296 ovaries containing ovules in stages ranging from the EMC to an embryo of several cells. The frequency of the stages is shown in Table 3.

The following course of meiosis was observed: in pachytene a double structure of the threads could be stated and in some portions of the nuclei pairs of chromomeres were discernible. In the I Metaphase the spindle was orientated regularly, parallel to the axis of the ovule (Fig. 2). The two daughter nuclei after the Ist division were separated by a distinct cell wall. The observed stages of the Interkinesis, the II Metaphase and that of the II Anaphase had a normal appearance (Fig. 2).

In the tetrad stage, however, some deviations were stated. Of a total of 14 ovules, polyads instead of tetrads were found in 9 ovules. In a group

Table 3

Frequency of the stages in 296 ovules

Stage of development	Number of the ovules
Twin ovules containing EMC's in Prophase	2
I meiotic division in EMC (Prophase, I Metaphase)	19
II meiotic division in EMC	3
Tetrad (polyad)	14
one-nucleate ES	37
I mitosis in ES	1
two-nucleate ES	29
II mitosis in ES	—
four-nucleate ES	33
III mitosis in ES	2
13-14 nucleate ES (number of antipodals increased to 8 or 9)	73
ES with polar fusion nucleus	42
ES containing an egg cell, a polar fusion nucleus and embryolike structures at the chalazal end	9
ES containing egg cell, developing endosperm and embryolike structures at the chalazal end	1
ES with developing endosperm and embryolike structures at the chalazal end	1
ES at the basis of which an additional cell with a dividing nucleus (Telophase)	1
Typical embryo surrounded by endosperm	17

of macrospores composed of three cells (a triad) the micropylar cell was much larger than the remaining ones and it possessed a large nucleus; presumably the second division of the top cell of the dyad did not take place. In a tetrad (Fig. 2) two cells, the micropylar and the chalazal cell, were notably enlarged. In another ovule a group composed of as many as 8 cells (Fig. 3) was found: two cells situated nearest to the micropyle had a normal appearance, while the next 4 cells manifested signs of degeneration. It may be noted, that the arrangement of these cells was not strictly linear, two cells lying side by side. The two remaining cells near the chalazal end probably did not represent real macrospores, but addi-

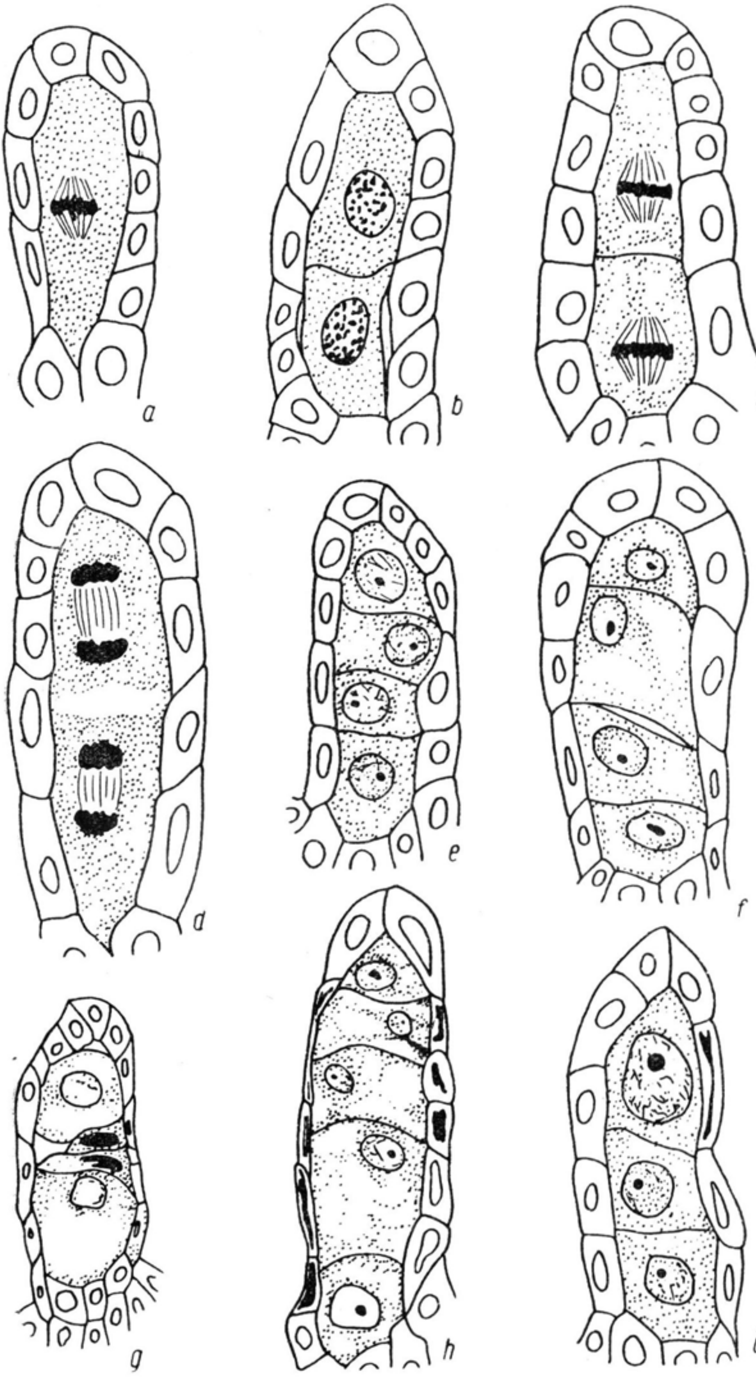

Fig. 2. *Homogyne alpina*, macrosporogenesis: a, I Metaphase in EMC. b, Interkinesis. c, II Metaphase. d, II Anaphase. e, f — tetrads. g, tetrad with enlarged micropylar and chalazal macrospore. h, pentad. i, triad. (c. 700 ×).

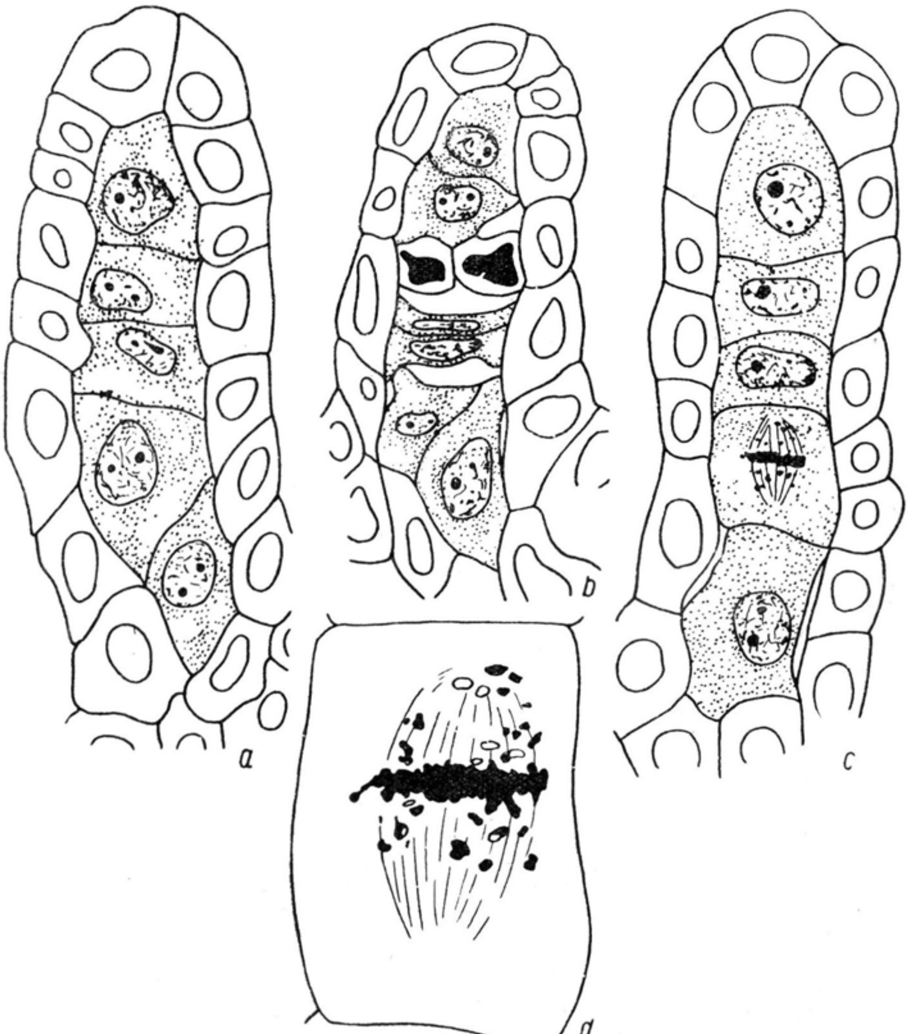

Fig. 3. *Homogyne alpina:* a, tetrad with one additional cell. b, polyad. c, a group of macrospores: probably a triad and two additional cell, — in one of them probably a meiotic metaphase. (980 ×). d, the same cell at higher magnification (3500 ×).

tional (somatic) cells; they were notably enlarged. In one of the pentads observed the largest cell was found at the chalazal end. Another group composed of five cells (Fig. 3 c, d) deserves a special mention. In this group the cell lying near the micropyle was larger than two next cells. The fourth cell was seized in the stage of Metaphase showing, however, the characteristics of a meiotic division. The configuration of the chromosomes as well as the occurrence of a considerable number of chromosomes scattered outside the equatorial plate (Fig. 3d) favour this assumption. This phenomenon will be considered later in the discussion.

The observations of changes going on in the nucellus and integument facilitated the identification of the particular developmental stages after meiosis. The nucellus consisting of a single layer of cells is still visible in the tetrad stage. Later on, at the time of the germination of the macrospore, it becomes gradually crushed by the growing gametophyte and undergoes a degeneration. The remnants of its cells were latest seen in the stage of the III embryosac division (Fig. 4).

At this time, the adjacent tissue representing the inner epidermis of the integument differentiates histologically and gives the so called "nutritive jacket". This layer which may be seen already around the two-nucleate embryosac, forms a compact tissue composed of a single layer of flat, large, densely staining cells.

THE DEVELOPMENT OF THE FEMALE GAMETOPHYTE

In the material investigated it is not always the chalazal macrospore which develops into the embryosac. Sometimes it is the second cell from the micropyle, which may show developmental tendencies. In other cases both the micropylar and the chalazal cell of the tetrad enlarge simultaneously, while the two remaining cells lying between them have already degenerated. More such examples could be given.

The first macrospore division proceeded regularly. The polarisation of the young embryosac takes place already after the first division. In this stage a distinct vacuolization of the cytoplasm could be observed; in the two-nucleate embryosac the nuclei were connected only with a thin strand of cytoplasm.

The two nuclei resulting from the I division divide twice more without any formation of cell walls (Fig. 4). In this way the stage of an eight-nucleate embryosac is attained. The differentiated embryosac, however, contains not 8, but 13—15 nuclei, as a result of the increased number of the antipodal cells. From the arrangement of the spindles during the III division it may be inferred that this increase is due to secondary divisions in the antipodal cells (as in *Antennaria*) rather than to an irregular distribution of the nuclei after the second division, as in *Fritillaria*. I did not, however, succeed in observing such secondary divisions.

The differentiated embryosac appears as a pyriform body enlarged near the micropylar pole and narrowed on the chalazal pole. By this shape it differs from the younger stages with spindle-like outlines. The synergids in the mature embryosac are approximately triangular. Vacuoles are present in their enlarged part turned towards the chalazal pole. Their

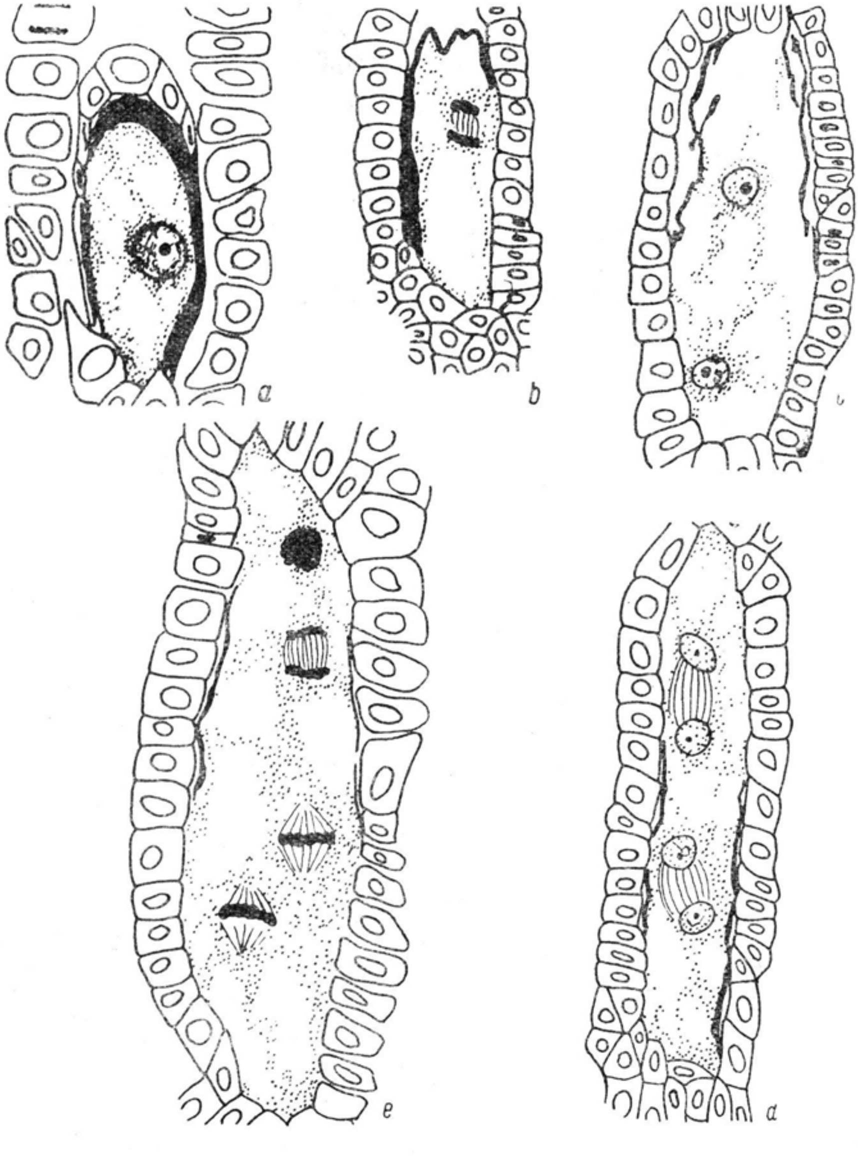

Fig. 4. *Homogyne alpina:* development of the female gametophyte; a, enlarged basal macrospore (406 ×). b, first mitosis in embryosac (357 ×). c, two-nucleate embryosac. d, four-nucleate embryosac. e, III mitosis in embryosac. (700 ×).

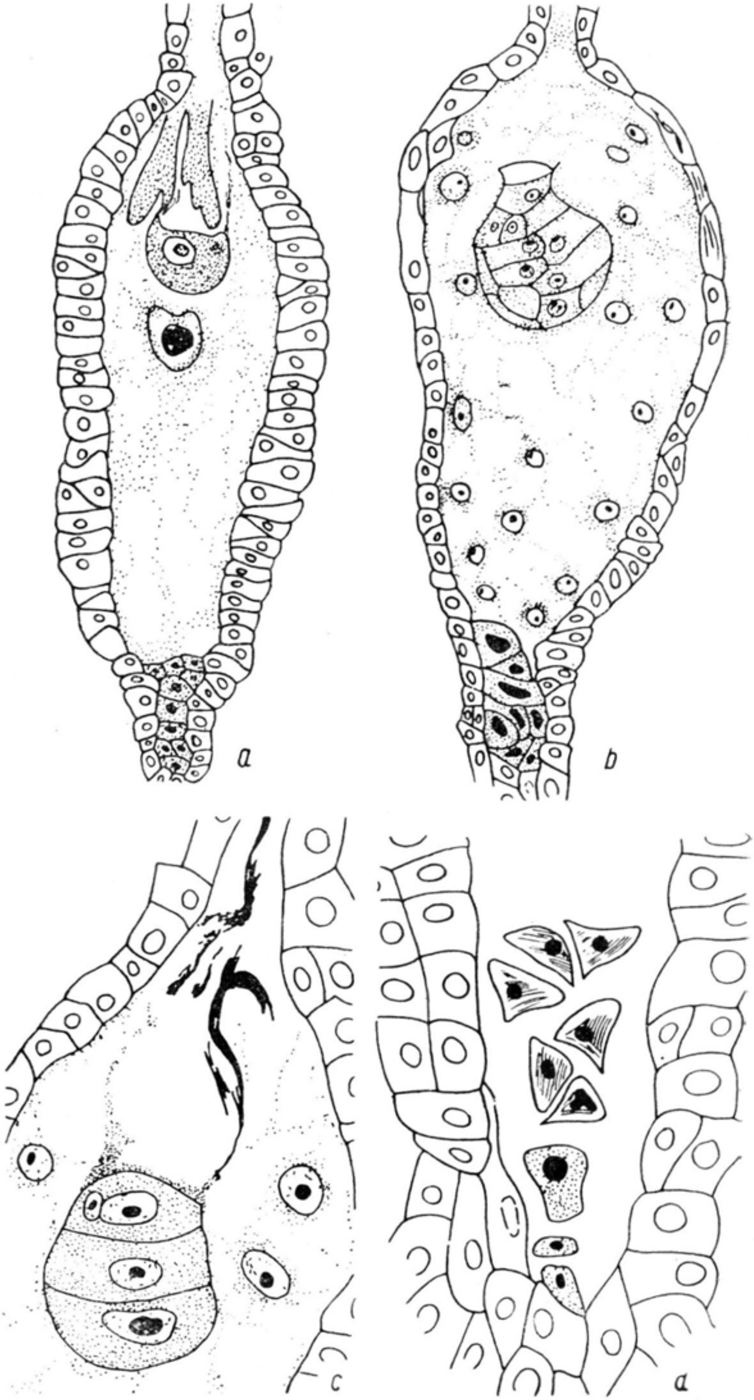

Fig. 5. *Homogyne alpina*. a, normal mature embryosac. In its central part the polar fusion nucleus (c. 220 ×). b, typical embryo surrounded by endosperm (c. 220 ×). c, the micropylar end of an embryosac: typical embryo and the remnants of a pollen tube (615 ×), d, chalazal end of an embryosac: degenerating antipodal cells (c. 700 ×).

nuclei placed nearer to the micropyle are rather small, somewhat elongated.

The egg cell has its cytoplasm accumulated mainly around the nucleus. Over it, in its narrower micropylar part, there is a large vacuole. The nucleus of the egg cell is large, oval; it contains a distinctly stainable nucleolus. In the majority of the embryosacs a large polar fusion nucleus, placed below the egg cell was observed. Apparently the fusion of the polar nuclei takes place relatively early (Fig. 5a).

The number of antipodal cells is considerably increased; it ranges from 8 to 10. The antipodal cells are mostly uninucleate, though occasionally two nuclei were observed in some of them.

The "nutritive jacket" attains in this stage its typical histological differentiation; many divisions observable in its cells lead to the growth of this tissue resulting in the enlargement of the cavity of the embryosac.

THE FIRST STAGES OF DEVELOPMENT OF THE EMBRYO AND ENDOSPERM

The observations of later stages proved that *Homogyne alpina* is a species with a sexual reproduction. In the ovules of wholly expanded and of older flowers pollen tubes could be detected rather frequently; they appeared as strands of dense, deeply stained cytoplasm in the micropylar part of the embryosac. In this stage the synergids begin to degenerate.

In one ovule in which the egg cell was still undivided probably a sperm could be observed; it appeared as a rather thick, slightly bent rod lying in a close contact with the polar fusion nucleus.

The first divisions of the egg cell were not found in the material investigated. The embryos observed consisted already of several or more cells. The development of an embryo always coincided with the development of the endosperm (Fig. 5 b, c).

The antipodal cells appeared in these stages as cells with somewhat collapsing walls — a sign of the beginning degeneration. They did not lie close to one another, being arranged rather loosely (Fig. 5 d).

The morphology of the embryos (the developed suspensor) and their position in the region of the micropyle show that they had developed from egg cells. The occurrence of pollen tubes observed in many sacs indicates that their development was preceded by fertilization.

EMBRYOLIKE STRUCTURES ON THE CHALAZAL POLE

In the material from two different populations in the Tatra Mts (n. 38 and 39), in some embryosacs some anomalies on the chalazal pole could be detected. In about a dozen sacs some kind of differentiation

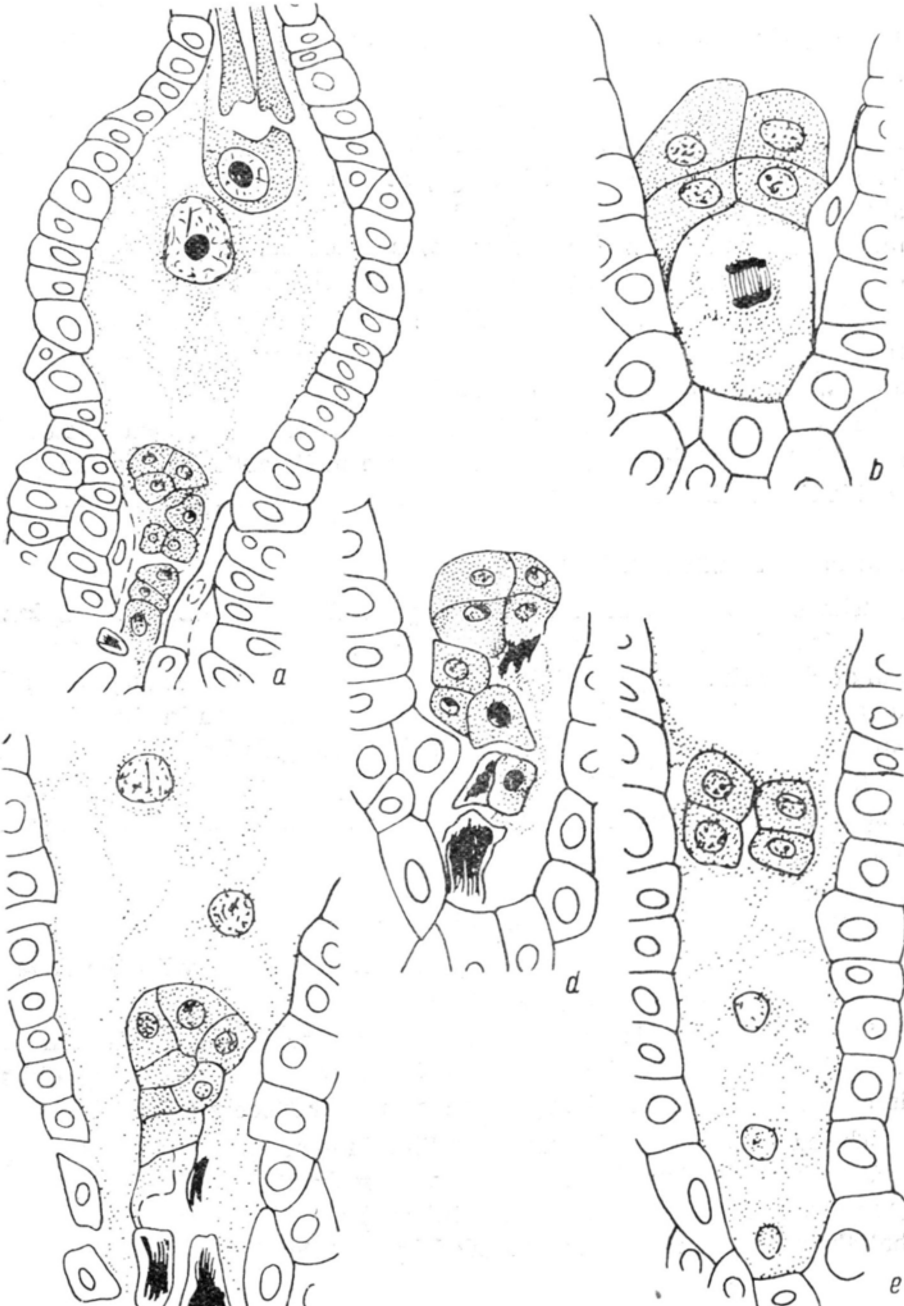

Fig. 6. *Homogyne alpina:* a, c, d, e — embryolike structures in the chalazal ends of three embryosacs: a — the polar fusion nucleus and the egg cell still undivided (406 ×). c — the first stages of development of the endosperm. b — chalazal end of an embryosac: enlarged, distinctly hydrated cell with a dividing nucleus (telophase) (c. 700 ×).

within the antipodal cells was observed in a stage in which normally a degeneration of these cells should begin. Some of them, as expected, had collapsed walls and were faintly stained; their living contents was degenerating (Fig. 5 d); others, however, did not show any signs of abortion. They were well-filled with cytoplasm and their nuclei had a quite normal appearance. Sometimes such cells were arranged in compact groups without intercellular spaces (Fig. 6). The top surface of such groups protruded into the cavity of the embryosac, unlike the usual arrangement of the antipodal cells. On the whole, the shape of these structures was somewhat similar to developing embryos.

It may be interesting to note that such phenomena were found chiefly in embryosacs with egg cells displaying a deficient viability. In spite of the occasional occurrence of endosperm no embryo was found in any of these ovules. Such a group of cells has been found once in a sac containing an egg cell which did not develop in spite of the presence of a pollen tube in the micropylar region. The occurrence of several endosperm nuclei in this embryosac shows that fertilization of the polar fusion nucleus had taken place (Fig. 6 c).

Another type of abnormal structures was observed only once in an embryosac containing still unfused polar nuclei. On its chalazal pole, beneath a group composed of four proliferating antipodal cells, a much larger cell with a strongly vacuolated cytoplasm was seen (Fig. 6 b). Its nucleus was in the stage of Telophase. This phenomenon is similar to the pictures described by E s a u (1946) in *Parthenium*. These phenomena will be considered later on in the discussion.

DISCUSSION

The problem of the connection of polyploidy with the apomictic mode of reproduction has been repeatedly discussed in literature (G u s t a f s s o n 1946—47). Studies in the embryology of *Homogyne alpina* permitted to state that it is not an apomictic, but a sexual species despite its high polyploidy.

Observations in microsporogenesis showed some deviations from the typical course of meiosis. In PMC's besides bivalents and polyvalents the occurrence of univalents lying outside the spindle was also stated. In the I Anaphase a delayed separation of some chromosomes was noticed and in later stages microcytes from the eliminated chromosomes were occasionally observed.

The meiotic disturbances were probably induced by sudden changes of temperature, since the fixing of the material in spring was interrupted by several unexpected snow falls.

Similar irregularities in PMC's of *Soldanella* were observed by K. Satczek (1951). According to this author such disturbances belong to the category of phenomena bound with thermal shocks.

It should be noted, however, that in meiosis of high polyploids also disturbances of another kind may appear in connection with an irregular division of polyvalents (Meurman 1929).

After meiosis in the ovules, in addition to normal tetrads relatively often polyads were observed. The formation of three macrospores instead of a tetrads (a triad), is probably due to the failure of a division in the top cell of the dyad; this explanation is suggested by the large size of its nucleus. A similar picture was described in *Poa* by Nygren (1950).

More frequently, however, there is an increase of the number of the macrospores. This leads to the formation of polyads. Similar phenomena were described by Stebbins (1932) in some apomictic species of *Antennaria*. Polyads are formed here in consequence of disturbances in meiotic divisions. It may be assumed that some of the polyads observed in *Homogyne* were formed in a similar way; the arrangement of the polyad cells, shown in Fig. 3 suggests that one of the spindles was orientated perpendicularly and not parallel to the axis of the ovule.

Some cells in the polyads, however, have probably a different origin. They seem to represent additional somatic cells, developed from the chalazal part of the ovule and showing some tendency to an apomictic development. Such an explanation may be applied to a group of macrospores in Fig. 3c. The three macrospores lying near the micropyle probably represented a triad in which the top cell failed to divide; the two remaining, however, should be regarded as additional cells in view of the fact that in one of them a Metaphase of the meiotic type was found.

A similar phenomenon was described by Bergman (1951) in *Antennaria carpatica*. It should be added that according to this author it is considered as "...a somatic cell, the division of which has been meiotisized for some reason or other" (p. 508). Such phenomena seem to be extremely rare.

The meiotic division taking place in an additional cell of *Homogyne* points to its developmental tendency; thus, if Bergman's interpretation is correct it seems that a certain tendency to apospory comes here to light.

In this connection also the occurrence of a cell found on the chalazal pole of a mature embryosac should be discussed; this cell was notably enlarged and it contained a nucleus in the stage of Telophase (Fig. 6 b). Its cytoplasm was vacuolated, unlike that of the adjacent antipodal cells. This phenomenon shows a striking similarity to some structures described in *Parthenium* by Esau (1946). This scientist considers them as initials of additional embryosacs and emphazises that such "...aposporic cells are characterized by a high degree of hydration" (p. 96). In her ample material Esau found also pictures which seemed to constitute earlier and later developmental stages of such structures. Although I observed only once such a phenomenon in *Homogyne*, it seems probable that this cell, likewise, may be regarded as an early stage of an exceptionally developing aposporic embryosac.

In spite of such deviations which do take place only sporadically, in the majority of the ovules a typical embryosac with the reduced chromosome number develops. The reproduction of *Homogyne alpina* is sexual; pollen tubes were found in about a dozen sacs. Embryos without endosperm occurring in some apomictic species (*Potentilla, Poa*) were never observed in the present material.

The peculiar groups of antipodal cells found in some ovules remain to be discussed. They manifested an increased viability, their shapes showing some similarity to embryos. Their appearance is particularly characteristic in embryosacs in which the egg cell did not yet start its divisions but the development of the endosperm was initiated.

Antipodal cells stimulated to a further development and forming an additional egg apparatus were described by Håkansson (1951) for tetraploid races of *Allium odorum;* their embryosacs, however, frequently have a non-reduced chromosome number. Thus, such an additional antipodal embryo would possess the somatic chromosome number like an embryo developing parthenogenetically from the egg cell. In *Homogyne,* however, the proliferating antipodal cells have a reduced chromosome number, thus they have little chance of a further development. They could be observed in embryosacs with developing endosperm but without an embryo.

In general the development of an embryo from antipodal cells is a very rare phenomenon; the greater part of the cases given were querried. Johansen (1950) emphazises this and points to the necessity "...to distinguish between mere proliferation of the antipodal cells into embryo-like structures and true antipodal embryos" (p. 208). It may be possible that in the ovules observed in the course of the present work, the development of these structures is causally connected with the lack of fertilization of the egg cell; as a consequence the nutrients accumulating for the embryo stimulate some antipodal cells, which proliferate into embryolike structures. A uniform interpretation of these phenomena, however, seems difficult.

SUMMARY

The present investigations deal with the biology of reproduction and the embryology of *Homogyne alpina* (L.) C a s s., a high polyploid monuntain species (n = c. 70).

1. The development of its flower buds begins in August after the dispersal of the achenes. In the hibernating buds the anthers remain in the stage of PMC's from the late autumn to spring; the meiotic divisions start early in spring. The ovules attain in autumn the stage of a differentiated archesporium cell. In spring the meioses begin somewhat later in EMC's than in PMC's.

2. Some disturbances observed in the microsporogenesis (a delayed separation of some chromosomes, the occurrence of univalents) were probably caused by sudden temperature changes during meiosis; some irregularities, however, may be connected with the high degree of polyploidy of *Homogyne alpina*.

3. The meiotic divisions in EMC's lead to the formation of groups of macrospores which represent either normal tetrads or polyads. The developing embryosac possesses a reduced chromosome number.

4. In some ovules, besides macrospores the occurrence of additional cells of somatic origin was also stated; such somatic cells reveal sometimes developmental tendencies. Exceptionally such cells may be observed also in a later stage, when the normal embryosac is already totally differentiated. They may be considered as initials of aposporic embryosacs.

5. *Homogyne alpina* is a sexual species, this being indicated by the presence of pollen tubes in several sacs some of which already contain typically developed embryos surrounded by endosperm.

6. Embryolike structures on the chalazal pole are probably proliferating antipodal cells which manifest an increased viability; the possibility of their further development seems dubious.

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