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Embryo sac development of *Carex praecox* Schreb.

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INTRODUCTION

The type of embryo sac present and its developmental pattern are constant for any given species. Modern systematics frequently makes use of embryological and embryogenic characters to provide additional criteria for the separation of taxonomic units. Such characters have not only proved useful in the formation of species boundaries but also in the allocation of families to orders and in the separation of related genera into distinct units (Krupko 1960).

Maheshwari is of the opinion that there is a sound basis for considering a number of characters in microspore and macrospore and embryo development to be useful criteria for the demarcation of taxonomic boundaries. He gives a list of twelve embryological characters of importance in systematics and evolution (Maheshwari 1950). Two of these, No. 7 and No. 8 concern the shape and internal structure of the ovule. The present work contains the description of several phases of embryo sac development in *Carex praecox* Schreb., which are included in above mentioned two characters.

The literature concerning embryo sac development in *Carex* is not extensive. Schnarf (1929) reviews some of the older works. Hofmeister (1871) describes embryo sac development in *Carex panicea*, *Carex hirta* and *Carex arenaria*, Vesque (1879) in *Carex vesicaria*, Fischer (1880) very short and superficialy in *Carex praecox*, Jonsson (1881) in *Carex acuta*, Heilborn (1918) in *Carex pilulifera*, *Carex digitata*, *Carex caryophyllea* and *Carex panicea*. Last, Grężicka (1964) describes megasporogenesis and embryo sac development in *Carex aristata*. The chief characteristics of macrosporogenesis in this genus given below are based on this type of data. The nucellus of young ovules consists of an epidermis and several cells immediately underneath it lying parallel to the long axis of the ovule. The middle row of nucellus cells grows faster than the others giving rise to the archesporial cell which divides forming primary parietal cell and megaspore mother cell. The parietal cell divides before tetrad formation. The cells so formed pile up above the megaspore mother cell giving rise to the impresion that the embryo sac has been pushed down into the nucellus. Fischer (1880) formed the mistaken opinion that it is the embryo sac which deve-

lops deeper down into nucellus. He observed in one case the megaspore mother cell arising deep in nucellus and he noted that the megaspore mother cell formation and embryo sac development in *Carex praecox should* be deeply investigated. The chalazal part of nucellus develops normally. The megaspore mother cell gives rise to the usual tetrad. The cell at chalazal end and the cell at the micropylar end of this tetrad grow faster and squash the two middle cells. The embryo sac always arises from the chalazal cell. Its further development is normal i.e. of the *Polygonum* type (Schurhoff 1926). There is generally much variability in the type of antipodal cells developed. In *Carex* there are three, very small antipodal cells which degenerate early (Heilborn 1918). The egg cell nucleus and the primary endosperm nucleus lie close together after fertilization and other nuclei degenerate. The next stage is the division of the endosperm nucleus giving rise to many free nuclei. These nuclei hold together in groups of two or three. Walls are formed later giving rise to various polynucleate cells (Schurhoff 1926). The formation of nuclear endosperm has been reported by Sussenguth (1919) for *Cyperus nataliensis*, by Heilborn (1918) for *Carex ericetorum*, *Carex caryophyllea*, *Carex pilulifera*, *Carex panicea* and *Carex digitata*. The characteristics of the mature embryo in some *Cyperaceae* are described by Wettstein (1935). One end of the embryo forms cotyledon initials, the oposite end forms plumule initials, while radicle initials arise towards the middle of the embryo and towards one side. There is usually one embryo per seed in the *Cyperaceae*, but some exceptions have been noted by Mirbel (cited by Braun 1860). There are often twin embryos in the seeds of *Carex maxima* (Schnarf 1929). The presence of a group of cells known as the obturator is frequent in the *Cyperaceae*. The obturator includes inner cells of the outer integument.

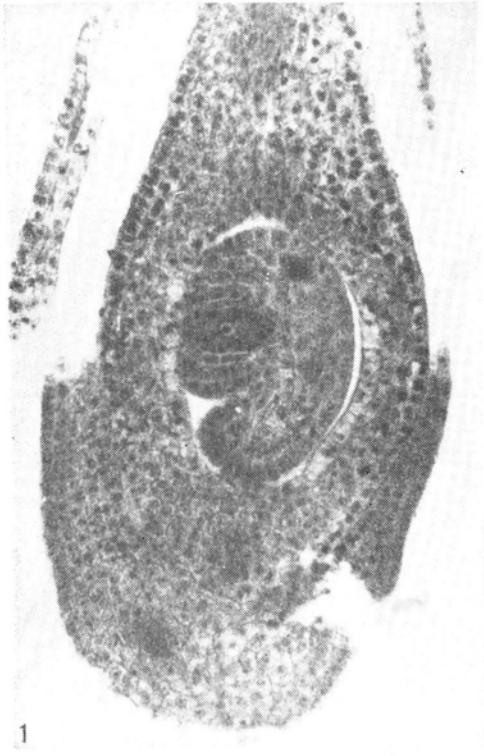
Plate I

1. A hemianatropous ovule, the archesporial cell fully developed.
2. Anatropous ovule. Outer integuments still not adhering.
3. Ovary with ovule inhibited in development through fungal infection.
4. Bulging of inner integuments. Long cells of the obturator clearly visible.
5. The orthotropous ovule bulging and breaking out of the outer integuments. Fungal infection at the top of the nucellus.

Plate II

6. Megaspore mother cell.
7. Linear tetrad.
8. One nucleate embryo sac.
9. Division in the one nucleate embryo sac. Late anaphase.

Plate I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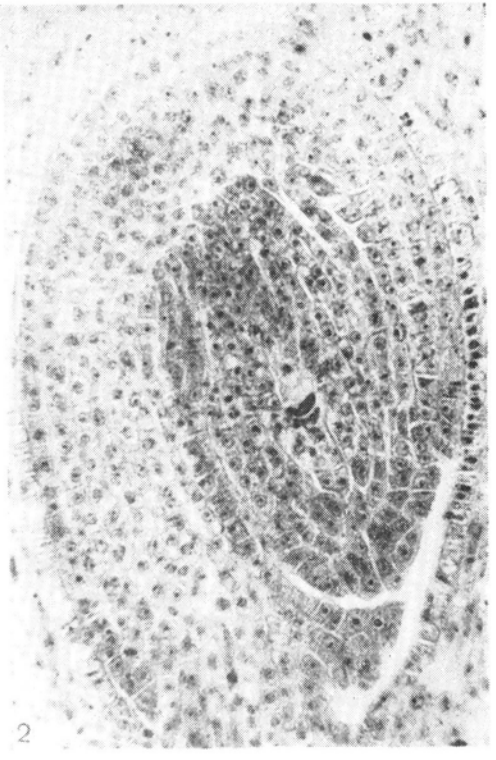
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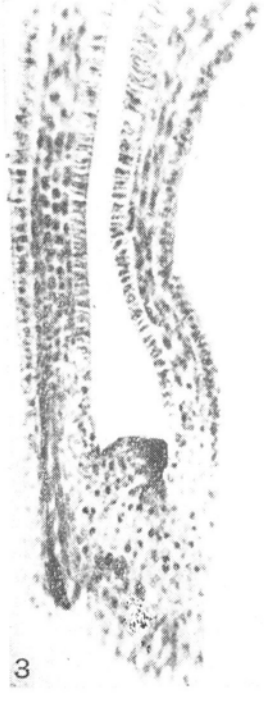
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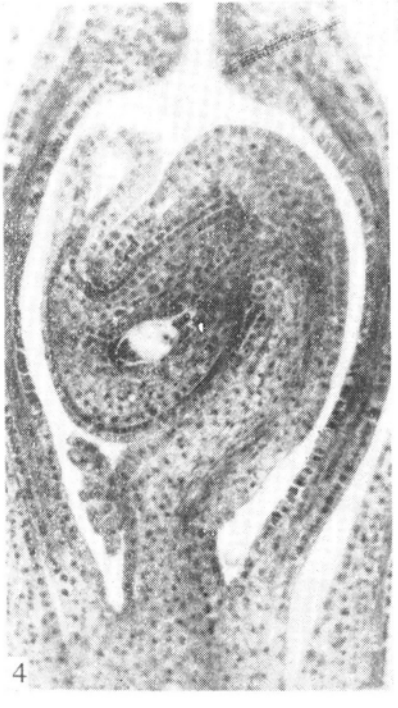
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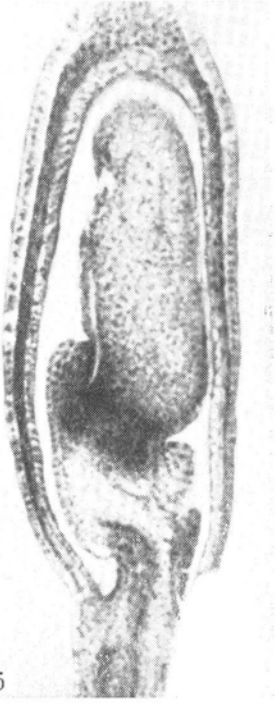
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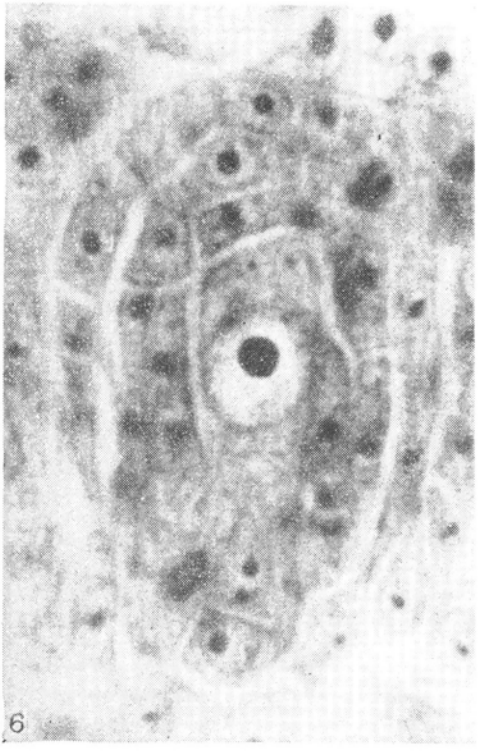
Plate II



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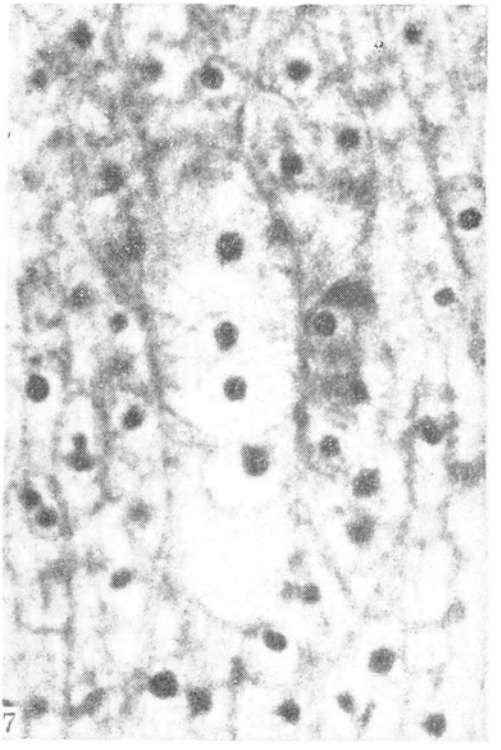

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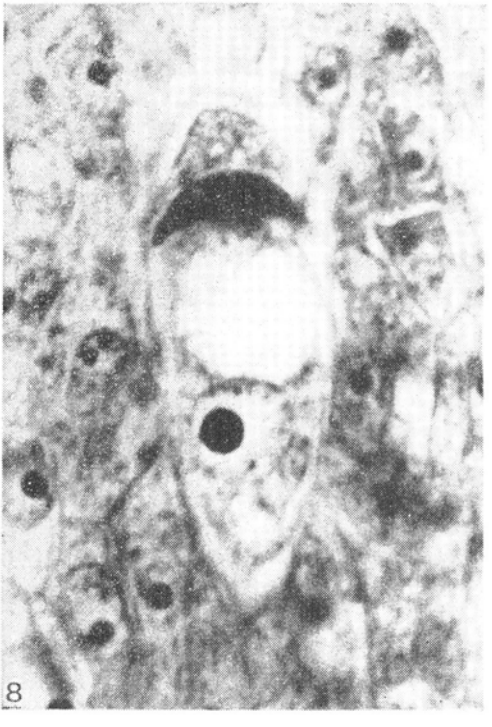

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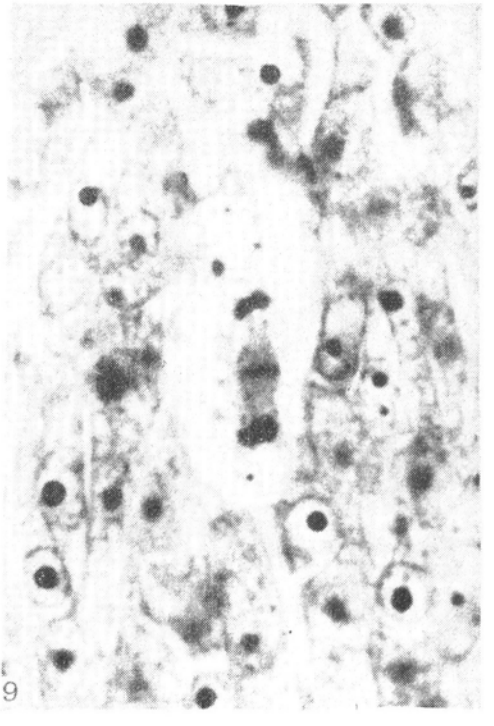

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MATERIAL AND METHODS

Like other members of *Cyperaceae*, *Carex praecox* Schreb. has solid, three-cornered stems with few internodes. Underground rhizomes are formed. Flowers are born in spikelets. The distended, barrel shaped pistil contains one anatropous ovule. The fruit is an achene. The site of plants investigated lies on the edge of a dry scarp which forms the original bed of the Vistula (Wisła), at Przyłubie in Bydgoszcz province. Buds of various development stages were collected on 27th May and June 17th in 1960 and on April 13th, May 4th, and July 27th in 1961. The spikelets were cut up and fixed in Navashin (Stocholm modification) or in F.A.A. (Johansen 1940) immediately, in the field. The fixed material was divided into groups according to the maturity of the buds or even of single ovaries and embedded in 55°C parafine wax. The ovary sections were cut 8, 12 and 20 μ thick. A total of 245 permanent slides were prepared. Permanent preparations were enclosed in canada balsam. A total of 330 ovaries was used. Sections were stained with iron hematoxylin (after Heidenhein) and counter stained with fast-green. A part of the material was stained with crystal violet (after Newton). The microphotographs and drawings were done using a Zeiss LgOB microscope and a Reichert Zetopan.

RESULTS

The male and female flowers occur on the same spike. Their respective position on the inflorescence is arbitrary but some cases were found in which male flowers predominated towards the top of the inflorescences. Male flowers consist of three stamens situated in the corner of the bract. The female flowers have a single pistil in the same position. The pistil has two or three stigmas growing on a long style. The ovary is superior and one chambered. It is covered with a thin membranous covering forming the utricle. The ovaries change their shape from elongate and unibilateral to swollen and barrel-shaped in the course of development (Plate I, Phots. 1—5). One, or very rarely two ovules develop in each ovary and they change from orthotropous to anatropous during development. The ovules are carried on a funiculus, which grows out of the placenta. The young funiculus, (Phot. 2) is shorter than the older one (Phot. 4). Ovules which were underdeveloped due to fungal infection, were frequently encountered (Phot. 3). In such cases the ovary grew normally forming a good deal of free space around the ovule whose development was inhibited. Fungal mycelium was also observed in the nucellus cells of a fully formed ovule. The ovules of *Carex praecox* Schreb. are crassinucellate and the epidermis is distinct. The nucellus

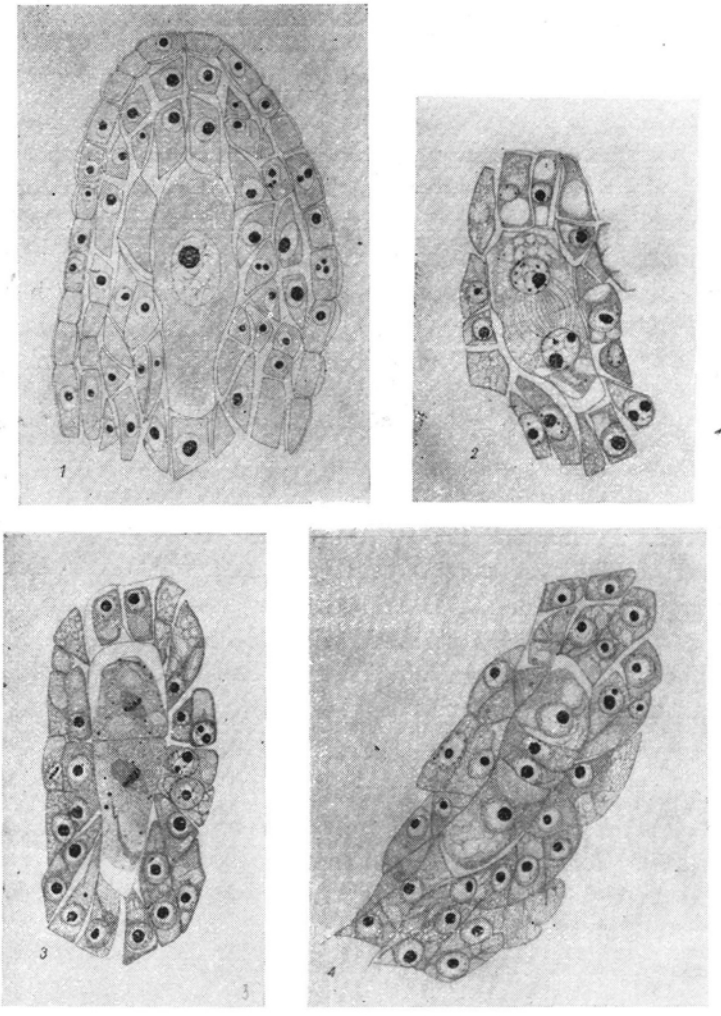


Fig. 1—4. *1* — Archesporium; *2* — Diad formation. Spindle fibres shown; *3* — Diads dividing. Metaphase; *4* — Tetrad. The two middle cells have started to degenerate due to the strong development of the chalazal cell and the micropylar cell. Magn. 885 ×

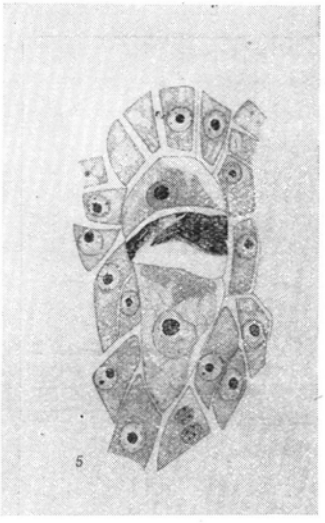
is surrounded by two integuments both of which take part in the formation of the micropyle. The micropylar canal is straight. The state of differentiation of the integuments is specific for a given ovule developmental stage. The inner integument usually consists of two layers of cells and the outer integument of three layers of cells. These two were often found to adhere so closely that a clear boundary between them could not be observed. The cleft between the two integuments is only clearly visible at the micropylar end (Phot. 2). The inside of the external integument is poorly developed. It consists of a single layer of cells. This layer did not form a normally shaped integument due to lack of space.

At the micropylar end this layer forms a tissue known as the obturator. The individual cells of this layer grow from the funiculus towards the micropyle. They are longer and larger than usual nucellus cells (Phot. 4). This layer of closely packed cells, provides something like bridge for the passage of the pollen grain tube. After penetration by the growing pollen grain tube the cells in this layer are markedly loosened. This pattern of events was observed in only one ovule but seems feasible since endosperm formation was noted in the same ovule. The obturator may have a part as conducting tissue for food supply to the ovule. The cells walls of the obturator are not lignified. In young ovules the nucellus consists of an epidermis and several rows of cells underneath it which lie parallel to the ovule long axis (Phot. 2, 6). The middle row of cells gives rise to the megaspore mother cell. It is much larger than all the surrounding cells (Phot. 6, Fig. 1). The cytoplasm in this cell is denser and the nucleus 6—7 times larger than the cytoplasm of the surrounding nucellus cells. Measurements of over 100 ovules show the megaspore mother cells have the largest nuclei. The average diameter of the megaspore mother cell nucleus is 9,1 μ. The following measurements refer to the diameters of various other nuclei at different stages in the embryo sac development.

	Average diameter
diad nuclei	6,5 μ
tetrad nuclei at the stage of equal nuclear size	4,4 μ
greatest size attained by the embryo sac nucleus	6,5 μ
nuclei in the two-nucleate embryo sac	5,6 μ
nuclei in the four-nucleate embryo sac	4,5 μ
nuclei at the free nuclei stage of the eight-nucleate embryo sac	4,0 μ

In the embryo sac differentiation stages which follow, the size of the nuclei increases. This refers to the eight nucleate embryo sac, and its differentiation into an egg apparatus, antipodals and polar nuclei.

There is always one archesporial cell. Of the 12 cells found in the sections examined only two had formed parietal cells. Both of these parietal cells underwent periclinal division (Fig. 1, Phot. 6). The archesporial cells in the rest of the sectioned material did not show parietal cell formation. The groups of cells visible above such archesporial cells arose as a result of division in the cells of the nucellus epidermis. Cells in these groups are arranged one above the other in a ladder-like formation and may be considered as constituting common developmental rows with the corresponding cells of the nucellus epidermis (Fig. 1). One case of a one nucleate embryo sac lying separated from the archesporial cell by two layers of cells was observed. This indicates that instants of the formation of two archesporial cells in one nucellus do



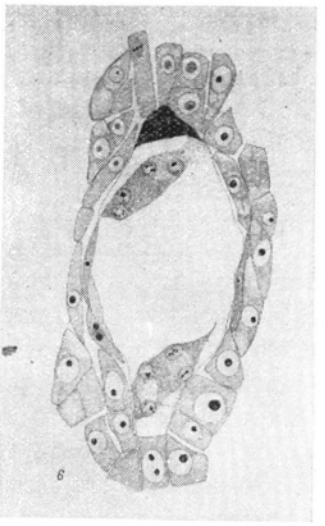


Fig. 5 Tetrad. Chalazal cell developing. Two middle cells have degenerated. Visible as roll strongly stained with hematoxylin. (885 ×)
Fig. 6 — Eight nucleate embryo sac (687 ×)

occur. This pattern of events might perhaps be considered one of the reasons for the future development of twin embryos, inspite of the fact that the usual manner in which such embryos arise is from two macrospores of a single tetrad. The ovule at the megaspore mother cell formation stage of development is usually hemianatropous and fills most of the space within the ovary (Phot. 1). At this stage the outer integuments do not adhere too closely and the inner integument only reaches as far as the nucellus epidermis. One instant of a reduction division metaphase was observed in one archesporial cell. Diad formation and conspicuous spindle fibres are shown in Fig. 2.

The lower of two diad cells i.e. the chalazal one is larger and has a larger nucleus. On one occasion unsynchronized diad division was found. In that instant the nucleus in the chalazal cell divided. The course of normal division of the diads was observed on a sequence of preparations. Diads in metaphase are shown in Fig. 3. Macrospore tetrads had a linear arrangement and that was the only type of tetrad found (Phot. 7, Fig. 8). The inner integuments grow fast at the tetrad stage and form an empty space between them and the nucellus in the course of this growth. This space disappears at the one nucleate embryo sac due the growth of the nucellus. The outer integuments begin to fuse at about this time. At the beginning all the tetrad cells are equal in size but in time the two central cells are squashed due to the intensive growth of the chalazal and micropylar cells and degenerate (Fig. 4). The

remains of these cells may then be observed as a roll shaped, dense piece of tissue, staining very dark with hematoxylin (Fig. 5). At the one nucleate embryo sac stage another similar roll of tissue is visible. This represents the remains of the degenerated micropylar tetrad cell.

All the tetrad stages examined indicate that the embryo sac always develops from the chalazal macrospore. The one nucleate embryo sac is trapeze shaped and narrow and the nucleus which usually lies at the centre of the cell is large (Phot. 8). The ovule is completely anatropous by this time. The integuments adhere closely and the ovule forms a single uniform mass of tissue filling up the entire ovary. The three consecutive mitotic divisions in the embryo sac mother cell give rise to the eight nucleate embryo sac. The first of these divisions gives rise to the two nucleate embryo sac (Phot. 9). The embryo sac at this stage is elongate at first and of equal width throughout. The nuclei lie at its two poles separated by a vacuole. In time the two nucleate embryo sac becomes distinctly racket shaped. The chalazal end forms the racket handle (Phot. 10). The remains of the three tetrad cells form a mass of tissue at micropylar end of the embryo sac. The observed nuclei in two nucleate embryo sacs were equal in size. One abnormally shaped 2 nucleate embryo sac was found. Instead of the usual racket shape it is forshortened. On a few occasions three nucleate embryo sacs were observed. These arise as a result of unsynchronised division in the two nucleate embryo sac. The majority of the four nucleate embryo sacs is racket shaped (Phot. 11). The position of the nuclei at the micropylar end of the embryo sac at this phase of development is horizontal in relation to the embryo sac long axis. The nuclei at the chalazal end of the embryo sac are placed parallel to the embryo sac long axis. Several instances were noted of the assumption of a linear arrangement by the four nuclei i.e. all of them lying in a straight line parallel to the embryo sac long axis (Phot. 12). The nuclei at the micropylar end of the four nucleate embryo sac are on the average larger than the nuclei at the chalazal end. The usual position of the four nucleate embryo sac is six layers of cells below the nucellus epidermis. There was only one instant recorded in which there were two layers of cells separating the four nucleate embryo sac from the epidermis. The integuments are pressed close together at the four nucleate embryo sac stage. This observation does not exclude the possibility of exceptions and in isolated instants the integuments may not adhere to one another.

The third mitotic division leads to the eight nucleate embryo sac stage. To begin with the nuclei lie in cytoplasmic strands in two groups of four, one at each of the opposite poles of the embryo sac (Fig. 6). These nuclei enlarge uniformaly. Three of the nuclei at the micropylar end of the embryo sac give rise to the egg apparatus. Three nuclei at the

chalazal end give rise to the antipodals. The two remaining nuclei are the polar nuclei. A very young stage of the eight nucleate embryo sac is shown in Phot. 13 a, b. These photographs were based on two separate sections from the same embryo sac. In this case the cell walls around the nuclei of the egg apparatus and the antipodals have already formed. The two polar nuclei which are free are approching the centre of the embryo sac. Cells in the embryo sac at this stage are all alike and have not yet formed vacuoles. Nuclei in these cells are of equal size. This is a transitional stage in development towards maturity.

The egg apparatus consists of three cells i.e. the two synergids and the egg cell. The synergids are triangular at first becoming pear-shaped later on. The nuclei lie in the narrower upper portion of the synergids above the vacuoles. The vacuoles fill the lower portion of the synergids. The egg cell is sac shaped and lies between the two synergids. It is also frequent for the synergids to be found lying one on another, while the egg cell lies towards one side of one of them. The egg cell nucleus lies in the lower enlarged portion of the cell, surrounded by a strand of cytoplasm. The upper part of this cell contains the vacuole. The egg cell nucleus is always larger than the synergid nuclei.

The central cell of the embryo sac is lined with cytoplasm. Cytoplasmic bridges connect the egg apparatus and the antipodals (Fig. 7) as well as the polar nuclei or the secondary nucleus. There are vacuoles in between the cytoplasmic strands.

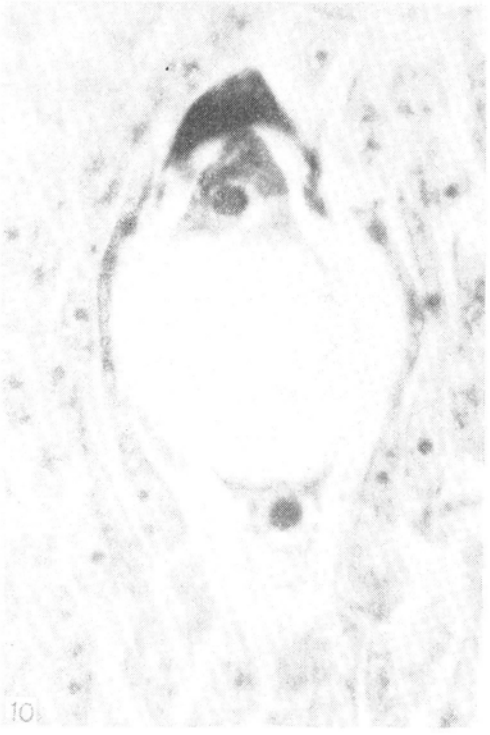
The three antipodals are always distinct. They lie in the "handle" of racket shaped embryo sac (Phot. 7). They are arranged in a row or in a T shaped figure. The antipodals persist for a long time since they only begin degenerating after fertilization. Their cytoplasm absorbs stains readily which accounts for the fact that they are clearly visible even after they have begun degenerating.

Plate III

10. Two nucleate embryo sac, racked shaped.
11. Four nucleate embryo sac.
12. Four nucleate embryo sac — all nuclei linear order.
13a. Young eight — nucleate embryo sac.

Plate IV

13b. Young eight — nucleate embryo sac.
14. Mature embryo sac. Two synergids and their nuclei visible. The egg cell nucleus faint but visible. Embryo sac secondary nucleus cospicuous next to the egg cell. Degenerating antipodal cells.
15a, b. Mature twin ovules. Wall separating the two ovules clearly defined. Antipodal cells have degenerated.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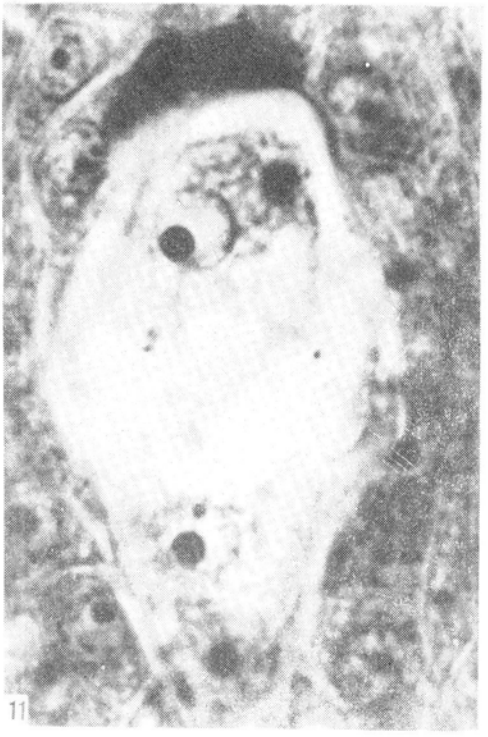
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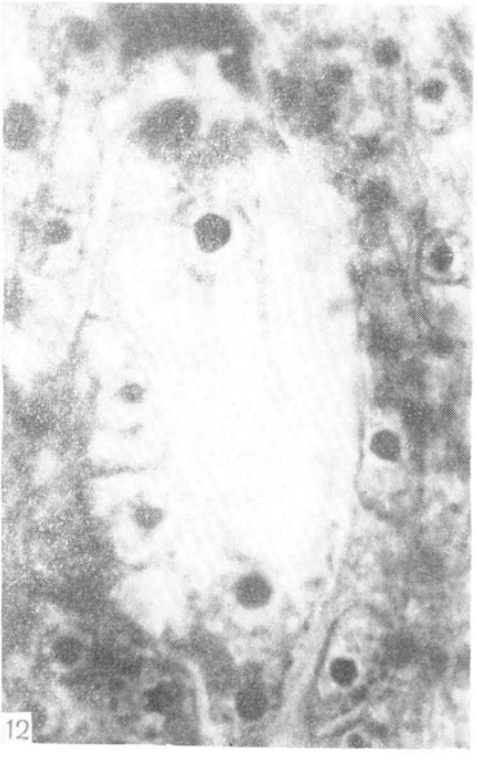
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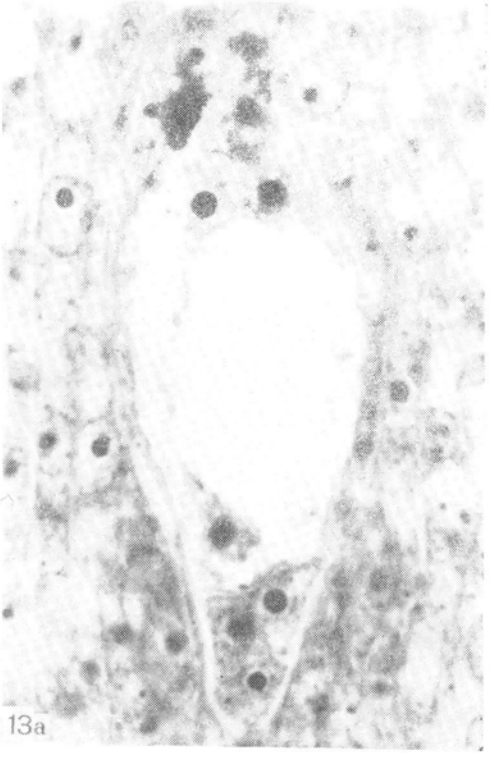
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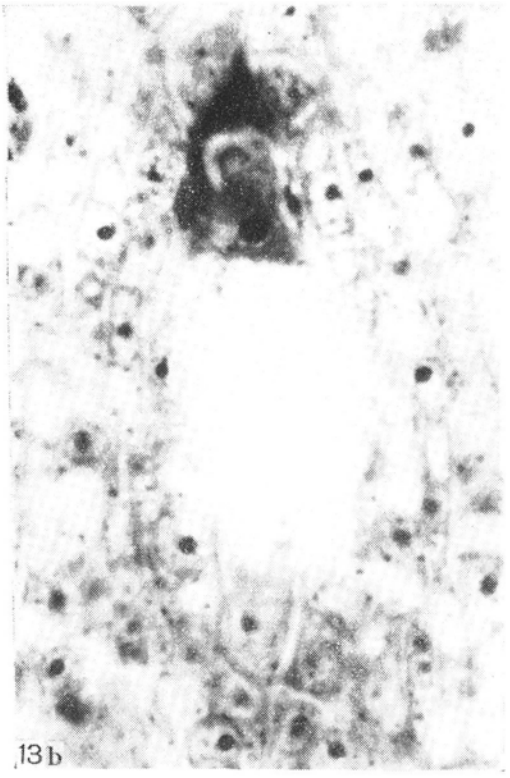
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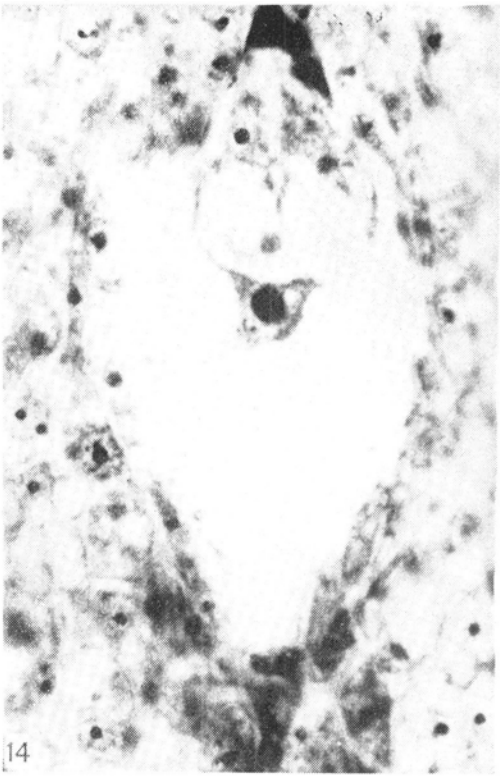
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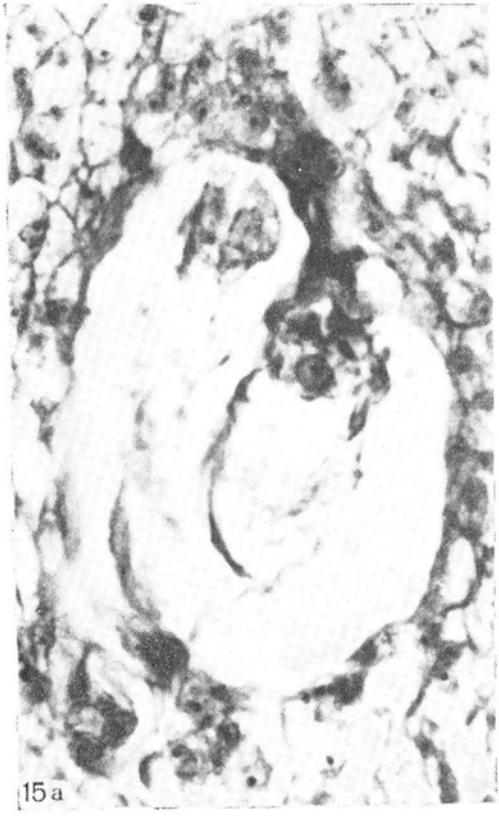
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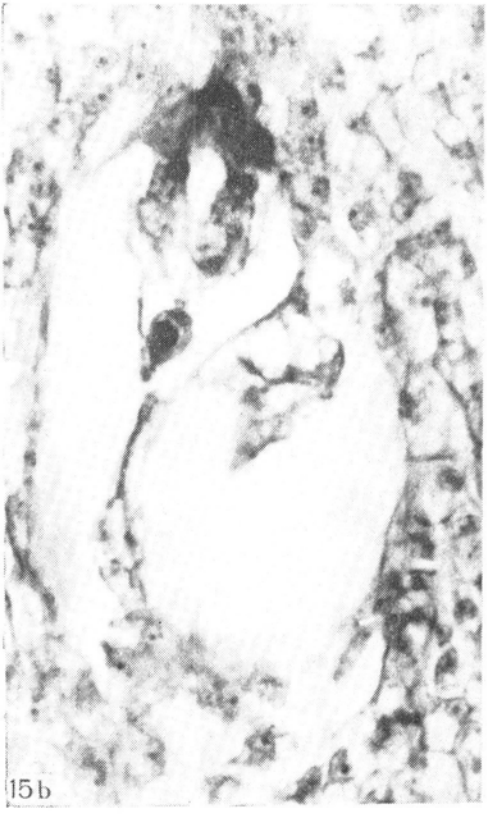
15b

The polar nuclei fuse to form the diploid secondary nucleus which gives rise to the endosperm after fertilization. Fusion usually takes place at the centre of the embryo sac. When it occurs next to the antipodals the micropylar polar nucleus is presumed to have travelled faster than the chalazal one. Fusion of the polar nuclei takes place quickly. Most of the mature embryo sacs found were at the 7 nuclei stage.

The mature embryo sac is large and rounded. As the developing embryo sac grows in size, surrounding nucellus cells are destroyed (Fig. 7). It is possible that the contents of these cells are absorbed by the embryo sac. Tetrad remains persist a long time as thin strand lying over the egg apparatus (Fig. 7). They only finally disappear after the first division of the endosperm nucleus (Fig. 8).

The ovule is large at the age when it contains a mature embryo sac, but does not fill all the space inside the ovary.

No clear fertilization image was found. The pollen grain tube is probably absorbed by the embryo sac too quickly after fertilization. One preparation did show the union of the sperm nucleus and the secondary nucleus (Fig. 7). The other sperm nucleus and the egg cell nucleus had probably already fused. The triploid endosperm primary nucleus arises directly from the fertilization of the secondary nucleus. It moves towards the egg cell and lies in close contact with it (Phot. 14). The antipodals and the synergids begin to degenerate at this time. They are partially destroyed by the entrence of the pollen grain tube. The synergids shrivel and degenerate often producing cellulose which collects forming a cap over them, just below the strand of degenerating tetrads (Fig. 7). This was never found at the younger stages in embryo sac development.

A slide showing a stage in endosperm development was taken as proof that fertilization had taken place. The primary endosperm nucleus had divided into two endosperm nuclei while the egg cell had not yet divided (Fig. 8). A cell wall is visible between the endosperm nuclei. This is not expected in the *Cyperaceae* family where the endosperm is nuclear and the nuclei are free at first, cell walls forming later. Since the first division of the endosperm nucleus in *Carex praecox* Schreb. is followed by wall formation it seems probable that the endosperm development in this species belongs to the *Helobium* type which occurs in the *Juncaceae*. This endosperm may also be supposed to be of the cellular type. Since no other slides showing division in endosperm nuclei were found it is impossible to reach a sound decision in this matter. Fertilization was probably not very frequent, since many dried and shrivelled ovules were found in the older developmental stages.

Some cases of twin embryo sacs in a single ovule were found. To record this abnormality photographs of two neighbouring sections were taken (Phot. 15 a, b). The cell wall separating the two embryo sacs is clearly visible. The one embryo sac has synergids and nuclei, an egg cell

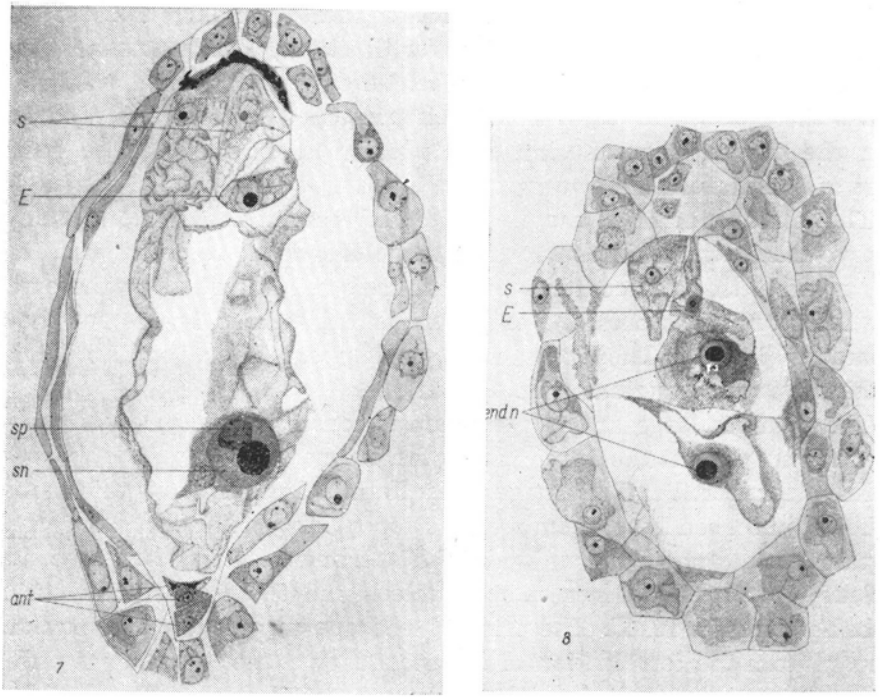

Fig. 7 — Fertilization in the mature embryo sac. Synergids and antipodals degenerating, sperm visible in the secondary nucleus (567 ×)

Fig. 8 — Endosperm formation. Primary endosperm nucleus has divided into two nuclei. A wall separates the new nuclei ((567 ×)

E — egg cell; *s* — synergids; *sp* — spermatozoon; *sn* — secondary nucleus; *ant* — antipodals; *end n* — endosperm nucleus.

and a secondary nucleus. In the other embryo sac the egg cell nucleus is larger and the secondary nucleus is enormous. It is visible on the next serial section. The synergids have degenerated due perhaps to the entrence of the pollen grain tube. The antipodals have degenerated in both embryo sacs. An example of an early stage in the development of twin embryo sacs has already been described. Ovules are usually anatropous. Some orthotropous ovules have been found. They are attached to a long funiculus and the micropyle is formed by the inner integuments only. The outer integuments only reach the top of the nucellus epidermis. There were usually no embryo sacs in the orthotropous ovules. This may have been due to fungal infection (Phot. 5). Fungal infection is shown in the cells on the left. In this case the embryo sac is bulging out of the outer integuments. A bulging of the inner integuments leading to a looped structure occured in one anatropous ovule (Phot. 4). A tendency to form this type of abnormal structure was observed in four nucleated embryo sacs of some of the anatropous ovules.

It was quite frequently noted that new small ovules were formed in ovaries in which the orthotropous ovules present had not formed embryo sacs.

Some examples of proliferation were found. These are a result of the continued growth of the base of an ovary in which neither ovules nor embryo sacs had developed. The above incidents of abnormal growth were found in the oldest ovaries.

SUMMARY

The following embryological characteristics have been established for *Carex praecox* Schreb.:

1. The anatropous ovule is crassinucellate. There are two integuments and the funiculus is short.
2. The mature embryo sac is 8-nucleate and belongs to the *Polygonum* type.
3. The polar nuclei lie at the centre of the embryo sac. After fertilization the secondary nucleus lies near the egg cell.
4. The three small antipodals degenerate very late.
5. The remains of the three degenerating tetrads persist until the first division of the primary endosperm nucleus.
6. One of the slides was found to show cellular endosperm. Two cells were present after the formation of the first endosperm nuclei.
7. An obturator tissue was present. It consisted of a densely packed layer of large cells, growing out of the funiculus and forming a roof over the micropyle.
8. There were frequent instants of abnormal, overvigorous growth in ovule tissues after fungal infection.

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Rozwój woreczka zalążkowego u Carex praecox Schreb.

Streszczenie

Praca niniejsza zawiera opis budowy wewnętrznej i poszczególnych faz rozwoju woreczka zalążkowego u *Carex praecox* Schreb. Wewnątrz zalążni powstaje jeden, rzadko dwa zalążki, przechodzące w trakcie rozwoju z kształtu ortotropowego w anatropowy. Zalążek osadzony jest na krótkim funikulusie. Stwierdzono występowanie obturatora w postaci zwartej masy komórek o większych rozmiarach, wyrastających z funikulusa i zasłaniających mikropyle w postaci okapu. Ściany komórek obturatora nie są zdrewniałe. Nucellus jest gruboośrodkowy. W nielicznych przypadkach stwierdzono, że archespor oddziela komórkę przykrywkową. Tetrada megaspor ułożona jest liniowo. Woreczek zalążkowy rozwija się z megaspory chalazalnej. Dojrzały woreczek zalążkowy jest jednosporowy, ośmiojądrowy, typu *Polygonum*. Jądra polarne zlewają się w centralnej części woreczka zalążkowego, a po zapłodnieniu leżą blisko komórki jajowej. Antypody degenerują bardzo późno, dopiero po powstaniu triploidalnego jądra bielmowego pierwotnego. W jednym przypadku znaleziono bielmo celularne dwukomórkowe. Obraz ten jest nietypowy dla rodziny *Cyperaceae*. W zalążniach starszych częste jest nienormalne rozrastanie się tkanek zalążka.