

Megasporogenesis, ovule and embryo sac development in *Carex aristata* R. Br. var. *cujavica*

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INTRODUCTION

The genus *Carex* has been comparatively little investigated embryologically. The description of every additional species belonging to this group provides data necessary for clarifying its phylogenetic relationships.

The sedge investigated, *Carex aristata* var. *cujavica* has a number of characters which distinguish it from other members of this genus.

Carex aristata R. Br. is a member of the subgenus *Eucarex* group *Dontostomae*, section *Hirtae*. The subgenus was first described by Robert Brown 1823 from North America.

The geographical distribution range of this species occupies the Northern regions of North America, Europe and Asia. In Central Europe it is of local occurrence forming infrequent islets of distribution. It was reported by Siegert (1851, cf. Ascherson 1888) from Lower Silesia and by Spribille (1887 cf. Wilkoń-Michalska 1960) from Balin surroundings near Inowrocław. The plant formed a fairly abundant stand on a marshy meadow. Ascherson gave Spribille's plant the status of a new variety. It was later reported from the same locality by Szulczewski (1925 cf. Wilkoń-Michalska 1960) and Michnikówna 1927. It grew in a water collecting ditch on the road from Balin to Latkowo. These sites mark the South Western boundaries of the distribution of this species.

Kulczyński (1927) prepared a map of *Carex aristata* distribution in Central Europe. This map was further augmented by stations reported from Finland by Hulten (1950).

Kulczyński considers this sedge to be a young boreal-dilluvial arrival in Europe. He thinks that it spread from the Altaic part of Siberia across Southern Ural together with a group of other lowland, peat-bog genera. It is a Northern, historical element of the flora. This particular member of the genus *Carex* is considered to be rare in Europe. The variety *cujavica* is considered to be endemic or more precisely neo-endemic to the Polish flora. The plant is under protection as a curiosity in the typical flora of the Polish lowland.

MATERIALS AND METHODS

The material was collected at Balin near Inowrocław over two vegetation seasons. In 1960 the material was fixed and collected in May and June. The plants were taken from a ditch of standing water on a farm (site A). In the 1961 season this site was flooded out due to abundant rainfall and a new site was found 300 meters distant from the first (site B). This new site was also a water collecting ditch. The plants found here grew more abundantly and individual specimens were larger, taller and had thicker and stiffer stems.

The material was fixed in Navashin (Stockholm modification) and in F.A.A. The subsequent staining procedure used were: — 1) 1% Iron hematoxylin followed by Fast Green. 2) Crystal violet (after Newton) followed by Orange G in clove oil.

RESULTS

Carex aristata var. *cujavica* has the characteristic reduced flowers, common to all sedges. Flowers of both sexes occur on one plant, but in different spikes. In the female flowers the pistil is subtended by a bract. It is hidden in an utriculus which is rectangular when young and egg-shaped at later stages. The pistil is superior, composed of one, uniloculate carpel. It is slightly swollen and bears a long style and three long stigmas. The ovary is oval in shape, one chambered and contains one or more rarely two ovules borne on a basal placenta.

Megasporogenesis and embryo-sac development are normal. Considerable differences have been found in ovule structure and development in the material originating from the two separate sites.

Ovule structure

In plants originating from site A ovule development is normal but there are considerable abnormalities in the material from site B. The abnormalities arise in the structure of the ovary, the position of the ovule, integument development and structure of the funiculus. Ovaries in the material from site B are several times larger than the ovaries in the material from site A. In the site A material with the smaller ovaries, the ovule fills almost the entire space within the ovary. In the site B material the ovary wall epidermis consists of closely adhering cells with large nuclei and little cytoplasm. These cells are plate shaped. In material from both sources, the beginning of ovule differentiation, at the base of the ovary, is the same. A group of cells growing up, out of the placenta, into the ovary, gives rise to a funiculus and an ovule. In the site A material the development and positioning of the ovule are normal. Turning occurs at the time when the megaspore mother cell is

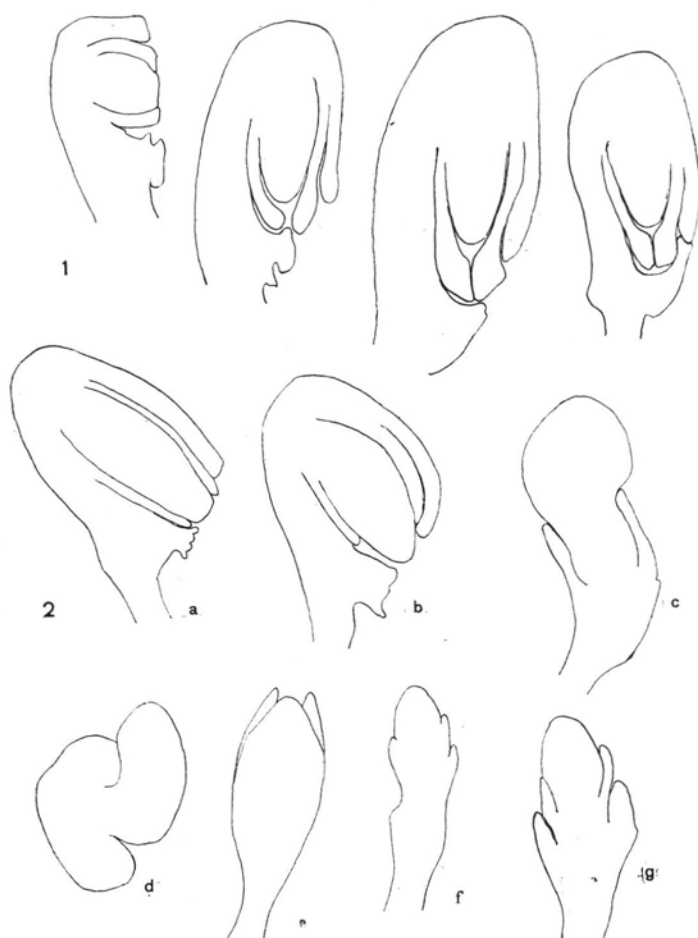
differentiating. Ovules at the megaspore mother cell stage are usually hemianatropous. The integuments are well developed by this time. The outer integument consists of 3 layers and the inner integument consists of two layers. The inner integument is longer. The micropyle is not yet formed. At the tetrad stage the ovule is just about completely turned. The inner integument grows further, becoming thicker at the ends and the micropyle is formed. At later stages (two nucleate embryo sacs) the thickening at the ends of the inner integument is more conspicuous. It is through the extra growth in these cells that the micropyle is finally closed. At this time the ends of the outer integument also become two layered. The outer integument does not develop on the funiculus side. A group of cells forming a structure growing out of the funiculus right underneath the ovule is probably the obturator. The cells of the obturator have a function in the closure of the micropyle. They enlarge to eventually meet the outer integument lying on the other side of the placenta. This process usually takes place at the stage of the four nucleate embryo sac some times as early as the two nucleate embryo sac stage. At the eight nucleate embryo sac stage, the micropyle is completely closed. The free space present between the inner integument and the placenta at younger stages has also disappeared. The turning of the ovule into the anatropous position and integument development are shown in Plate I, 1 and Plate II fig. 1. The course of development is quite different in the site B material. There is seemingly no regularity and no order in the positioning of the ovule, in the development of the integuments and in the structure of the funiculus. A good deal of variation and many abnormalities were the rule.

There were almost as many anatropous ovules as there were orthotropous ones. When the ovules were anatropous the process of turning into that position was normal. Sometimes the positioning was a little late as compared with the same process in the site A material. There were some hemianatropous ovules at the two nucleate embryo sac stage. Integument development is different in the site B material. The inner integument is shorter than the outer integument. Micropyle formation takes place later due to this. It is the outer integument and the obturator tissue, mentioned previously, which form the micropyle. It is fairly frequent for the nucellus not to be covered by the integuments. It was also frequently found that the integuments were not sufficiently long for the micropyle to be formed (Plate I, 2 a b). The orthotropous ovules usually have only one integument. The integument covers the nucellus to a greater or lesser extent since it is often half uncovered (Plate I, 2 g and Plate II, fig. 2). It would seem that the ovule shown in Plate II, fig. 2 was once hemianatropous and was subsequently bent back to the orthotropous position. The free space visible between the inner integument

and the outgrowth supports this supposition. In this particular case the nucellus is much elongated.

In one case the integuments were found to form a thick fold at the base of the nucellus which was not covered (Plate II, fig. 3). In many cases no integuments developed and the nucellus was completely naked and grew out of the side of a bent funiculus. In some cases a part of the nucellus forms a part of the same thick fold, which it is difficult to distinguish as the integument tissue. In two instances (Plate II, fig. 4)

Plate I



Diagrams of ovule structure

Fig. 1 — Site A. Turning of the ovule and integument development. Magn. $\times 140$

Fig. 2 — Site B. a, b: differences in the degree of integument development; c, d, e, f, g: abnormalities in ovule development. Magn. $\times 95$

the outer integument bends backwards on one side and grows backwards, alongside the funiculus, towards the bottom of the ovary, instead of covering the nucellus.

There are further abnormalities in the development of the funiculus. It was frequently unusually elongated. In one case it appeared to have twisted into a type of spiral (Plate II, fig. 5). The commonest abnormality is for the constituent cells to multiply and grow to such an extent that the thickness and the size of the funiculus (Plate II, fig. 4) outstrips the proportions of the ovule itself (Plate II, fig. 6). A section was found in which the funiculus had bent backwards so that an ovule with orthotropous characteristics became anatropous again (Plate II, fig. 7).

There was a marked tendency in the plants from site B to have ovaries containing two ovules. About 1/3 of the young ovaries examined was found to contain two ovules. To begin with the rate of development is about the same in both ovules. The first signs of competition may be observed at an early stage, before the integuments have formed. At older stages the ovule which has been outstripped in development has the appearance of an outgrowth of the ovary base (Plate II, fig. 9). Instances of equal development in both ovules and the formation of two normal ovules have nevertheless been encountered (Plate II, fig. 8). Embryo sacs at the eight nuclei stage have been found in both these ovules. These ovules had a common funiculus and a common integument which partially covered them.

Two or three megaspore mother cells per ovule were also frequently encountered in the site B material. These were either adjacent and touching (Plate IV, fig. 1, 2) or separated by cells of the nucellus (Plate IV, fig. 3). They do not develop at an equal rate. E.g. one ovule was found to contain a one nucleate embryo sac, a two nucleate embryo sac and a megaspore mother cell all adjacent to each other. Some investigations of the rate of ovule growth were carried out. It was found that the most intense rate of growth occurs between the stage of the megaspore mother cell and the tetrad stage. The ovule enlarges four times in the period of development between the megaspore mother cell stage and the eight nucleate embryo sac stage.

Megasporogenesis and embryo sac development

In plants collected from both sites, mentioned above, megasporogenesis and embryo sac development were normal. The pattern of development belongs to the *Polygonum* type. The embryo sac is monosporic and eight nucleate.

Development begins with the differentiation of the megaspore mother cell in the nucellus (Plate III, fig. 1). This occurs sooner in the site B material and in material from both sites the nucellus and the integu-

ments are already fully formed at that stage. Megaspore mother cells were observed in the site B material when the nucellus was still naked and the integuments at the beginning of their development. Although many very young ovules were examined successive stages of megaspore mother cell differentiation were not encountered. In the present material this cell was either fully differentiated or else it was not visible at all and only uniform cells of the nucellus could be seen. It was concluded that the megaspore mother cell rate of development from the moment of its initiation onwards is too fast to allow isolated stages of its enlargement to be distinguished. Its cytoplasm is not dense and it is light coloured. There is a large nucleus at the centre of the cell and the nucleolus is the same size as the nuclei of the surrounding nucellus cells. The most frequently encountered and the earliest stage in the development of this nucleus is the leptotene. At the preleptotene stage the megaspore mother cell is separated from the epidermis by 4 to 6 layers of nucellus cells. The telophase stage in the division of the megaspore mother cell is shown in Plate III, 2. The linear tetrad is the result of the next division. Two instances of a T-shaped arrangement of the tetrad were encountered. In one of these instances a diad cell at the micropyle end underwent longitudinal division in the other instance a diad cell at the chalazal end underwent longitudinal division (Plate IV, fig. 2). Of the four resultant megaspores the two outer are much larger and have larger nuclei than the others. The two central megaspores degenerate sooner. The chalazal megaspore gives rise to the embryo sac. In the course of enlargement the chalazal megaspore displaces and squashes the other megaspores. Its nucleus reaches a size over twice that of the tetrad nuclei and directly before division its size is $\frac{2}{3}$ the size of the megaspore mother cell nucleus. The position of this nucleus varies but it is usually central (Plate III, fig. 4; Plate IV, fig. 2). One nucleate

Explanation of Plate II

- Fig. 1. Hemianatropous ovule. Inner integument — 2 layers; outer integument --- 3 layers
- Fig. 2. An ovule returned to the orthotropous position. Elongated nucellus
- Fig. 3. Nucellus not covered by integuments. Inner integument short and massive; outer integument in the course of being formed
- Fig. 4. Integument bent back towards the bottom of the ovary
- Fig. 5. Much enlarged, twisted funiculus
- Fig. 6. Over enlargement of the funiculus. Integuments poorly developed
- Fig. 7. Non typical anatropous ovule with a single integument
- Fig. 8. Two equally developed ovules in a single ovary
- Fig. 9. Two ovules in a single ovary. One ovule retarded in development. Magnification: $\times 120$

Plate II

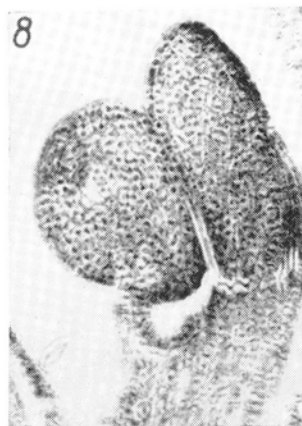


Plate III

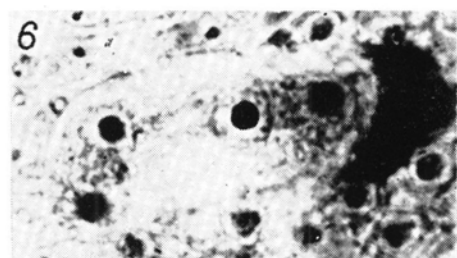
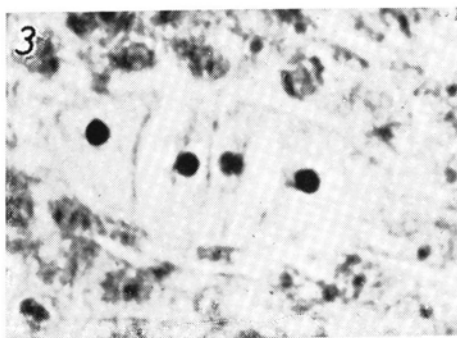
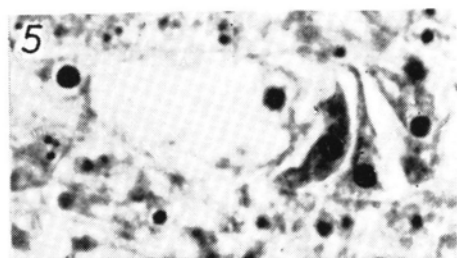
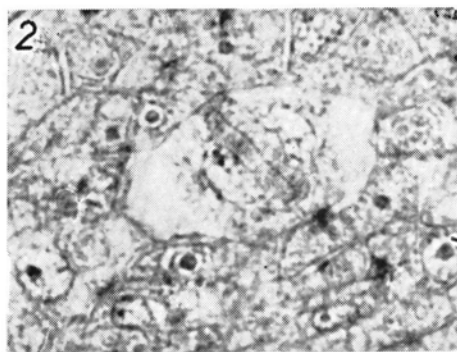
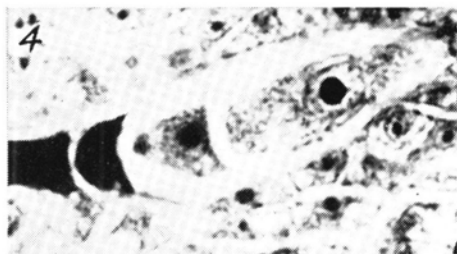
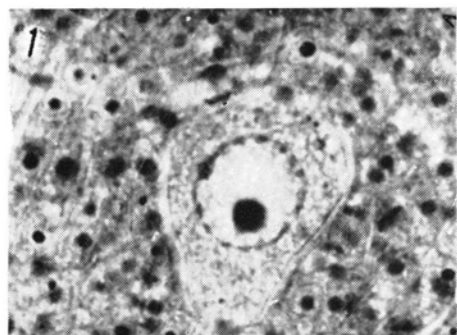


Fig. 1. Megaspore mother cell (preleptotene)
 Fig. 2. Early diad stage
 Fig. 3. Typical liner tetrad
 Fig. 4. One nucleate embryo sac.
 Fig. 5. Two nucleate embryo sac. Well preserved tetrad remains
 Fig. 6. Four nucleate embryo sac. Rhomboid shape
 Fig. 7. Typical synergids. Magnification $\times 1500$

embryo sacs have an approximately triangular shape, the base of the triangle touching the degenerating megaspores. Two nucleate embryo sacs have the shape of an elongate ellipse. A large vacuole arises between the nuclei. The nuclei are about $1/4$ smaller than the mother nucleus. Tetrad remains at this stage are very distinct (Plate III, fig. 5).

The planes of division of the 2 nuclei are usually different in the next division (Plate III, fig. 6). This division leads to the formation of the four nucleate embryo sac. The size of the nuclei decreases further. The cytoplasm continues to concentrate at the poles. Its greatest concentration is between the twin nuclei. The vacuole shape becomes even more irregular. The embryo sac enlarges and acquires a rhomboid shape (Plate III, fig. 6). Certain deviations in embryo sac shape do occur e.g. oval or "racket" shaped embryo sacs. The tetrad remains are by now a compact black mass covering the micropyle end of the embryo sac.

In the eight nucleate embryo sac, the nuclei are arranged in two groups of four, one at either end of the embryo sac (Plate V, fig. 1). At later stages only 3 nuclei remain at each pole, since one nucleus from the micropylar end moves to a position below the egg apparatus while one nucleus from the chalazal end moves across the embryo sac towards the micropylar end (Plate V, fig. 2). These are the two polar nuclei, which fuse just next to the egg apparatus, giving the secondary nucleus. The secondary nucleus sometimes moves towards the centre of the embryo sac (Plate V, fig. 3). Fusion of the polar nuclei occurs at a comparatively late stage since it was only observed in four cases out of the 46 mature embryo sacs examined. Fusion takes place at the time when the egg apparatus has begun degenerating. The border lines between cells vanish and the cytoplasm becomes denser (Plate V, fig. 3). The antipodals are still well preserved at this time. The secondary nucleus is very large. Its nucleolus is larger than the egg cell nucleus.

The position of the egg cell is usually at the centre of the egg apparatus. The synergids cover it. The egg cell is smaller than the synergids and its nucleus is smaller. It has the shape of a swollen drop.

Synergids are sac shaped and rounded towards the chalazal end. They frequently contain a vacuole. The nuclei lie at the centre of the synergids.

The position of the three antipodals at the chalazal end of the embryo sac varies. They may be placed irregularly, in a triangle or in linear order. Their shape also varies. They are filled with dense cytoplasm. The size of their nuclei approaches the size of the egg cell nucleus. They are fairly long-lived structures being still in good condition in the mature embryo sac after the fusion of the polar nuclei. (Plate V, fig. 3). They shrink in the course of degeneration. Their cytoplasm stains strongly and gaps arise between them.

In mature embryo sacs the nuclei are smaller than the nuclei of all the preceding stages. Even polar nuclei very rarely approach the size of the nuclei at the 4 nucleate embryo sac stage. The secondary nucleus exceeds all other nuclei except the megaspore mother cell nucleus in size. There is relatively little cytoplasm in the embryo sac. It is concentrated around the polar nuclei. Cytoplasmic strands extend across the embryo sac, from the egg apparatus towards the antipodals.

The embryo sac markedly increases in size after the fusion of the polar nuclei. Due to its enlargement surrounding nucellus cells are squashed. Its shape is still elongate and oval but it is often swollen at the position of the egg apparatus and thinner towards the lower end. There is a cap of megaspore remains over the micropylar end. These stain strongly and decrease, vanishing gradually as the embryo sac ages.

Only one pollen grain tube was found in the material examined. It was pushing its way in between the ovary wall and the integuments (Plate IV, fig. 4). The sperm nuclei and the vegetative nucleus are clearly visible. The male gametes are at the tip of the pollen grain tube. They have the shape of short, bent rods, slightly thicker at one of their ends. The nuclear membrane is more distinct in the vegetative nucleus. There is a lighter coloured space visible around the sperm nuclei. Navashin and Finn (1912) consider this to be the degenerating remains of the generative cell cytoplasm. The cytoplasm surrounding the gametes has in no way been found to be different from the cytoplasm filling the rest of the pollen grain tube. It is thought that the male gametes are but naked nuclei.

Lack of sections showing fertilization naturally follows on the lack of pollen grain tubes in this material. There was only one case in which a structure noted close to the synergid nucleus may have been a sperm nucleus on its way to the egg cell (Plate V, fig. 3). It can not be considered to be a sperm nucleus with certainty due to the lack of a pollen

Explanation of Plate IV

Fig. 1. Tetrad and archesporial cell in the same ovule. They are not separated by nucellus cells

Fig. 2. An archespore and a tetrad in T-shaped formation in a single ovule separated from each other by a single layer of nucellus cells

Fig. 3. Two one nucleate embryo sacs in a single ovule

Fig. 4. Germination of the pollen grain tube. Two rod-shaped sperms nuclei and vegetative nucleus. Magnification $\times 1310$

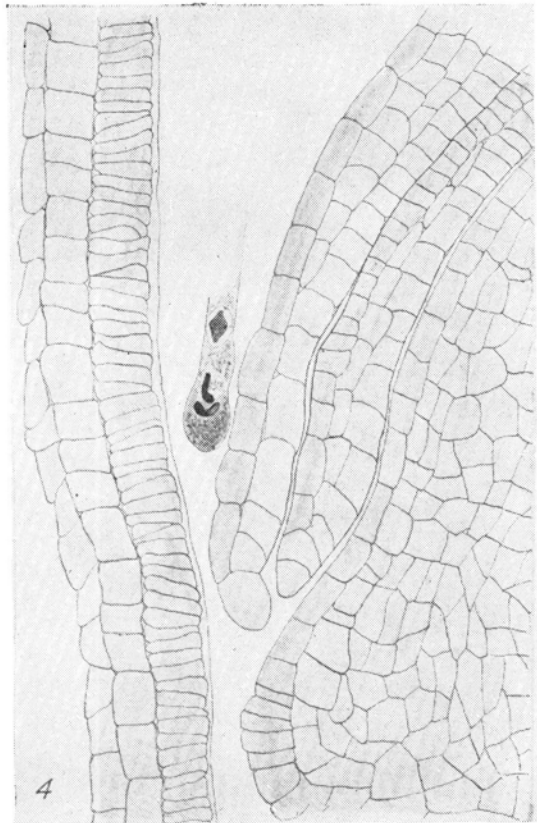
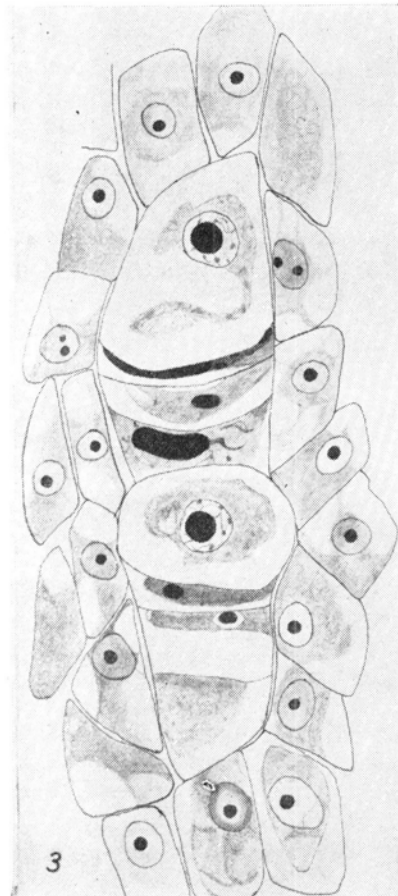
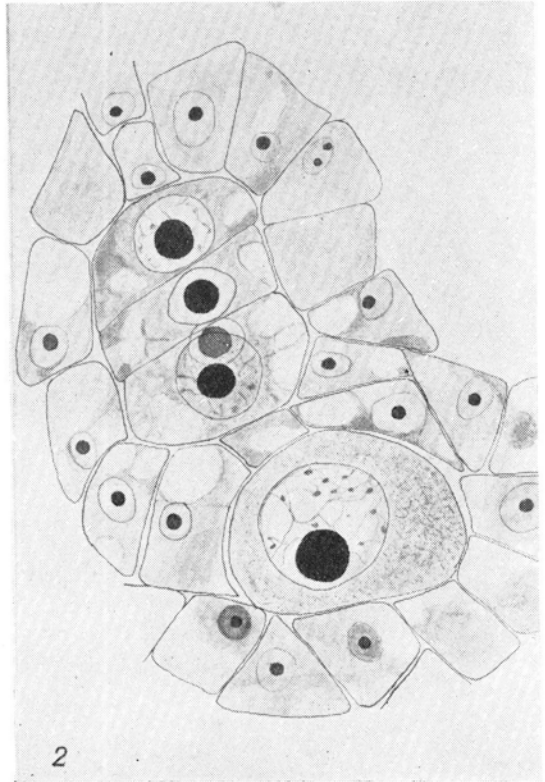
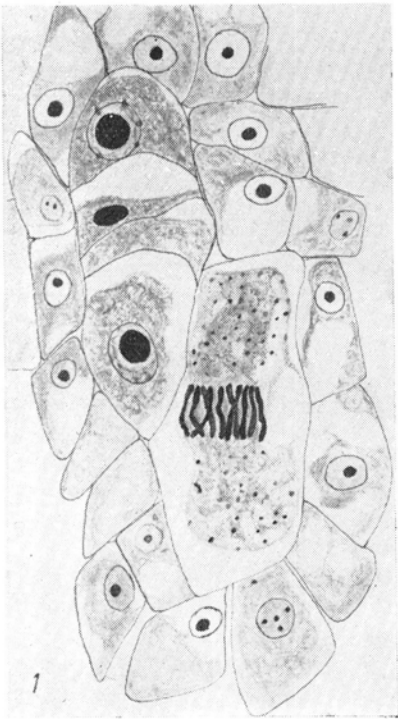
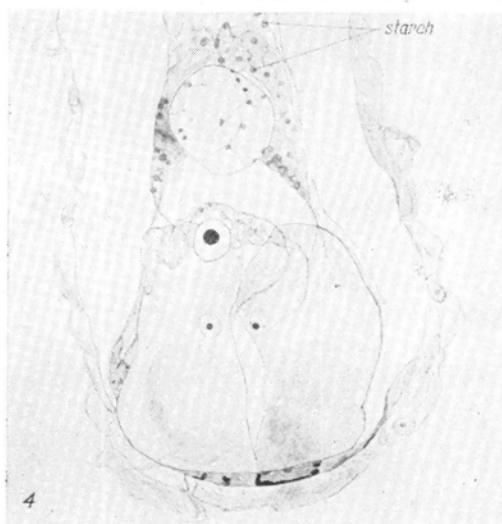
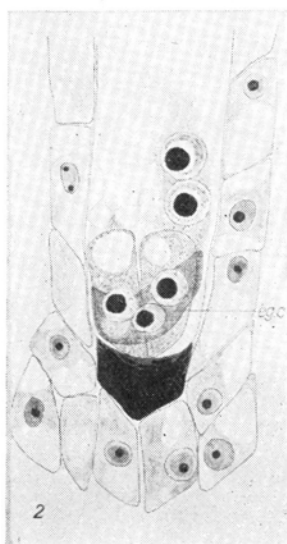
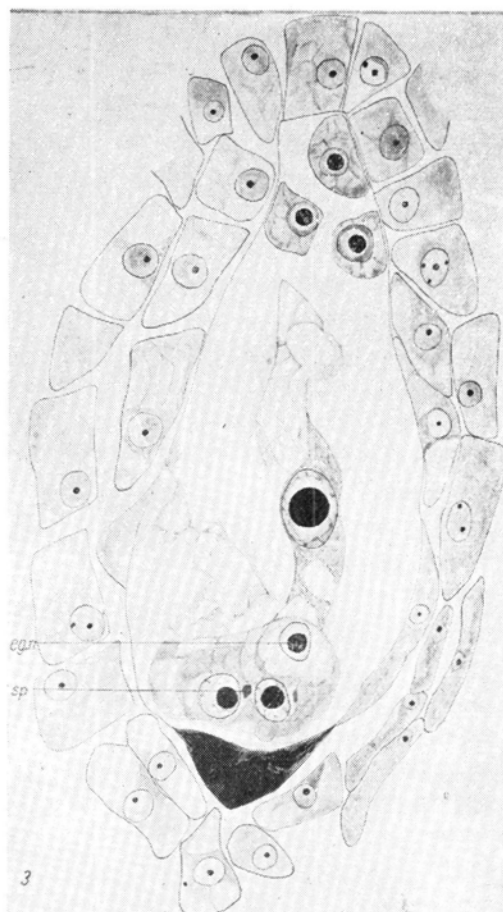
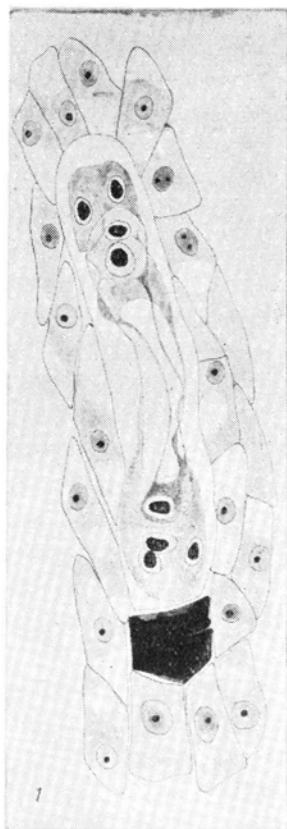


Plate V



grain tube. The presence of degenerating embryo sacs bears out the supposition that fertilization is rare. These degenerating embryo sacs are abnormally enlarged. They are 2 to 3 times larger than the eight nucleate embryo sacs. The contents of these embryo sacs enlarge also (Plate V, fig. 4). The size of the synergids increases most and their characteristic shape is obliterated. The size of their nuclei decreases while the nuclear membranes become very indistinct and only the tiny nucleoli are clearly visible. The egg cell nucleus persists for a much longer time even though the egg cell cytoplasm is simultaneously disappearing. Only the area immediately surrounding the nucleus has a greater cytoplasm content. The secondary nucleus with a large nucleolus is the best preserved. The antipodals disappear completely. Only one case was found in which they did not disappear and they had enlarged proportionately to the size of the rest of the embryo sac. The megaspore remains are still visible as thin strips above the egg apparatus. Starch storage substances begin to collect within the embryo sac. The starch mostly collects around the secondary nucleus. Nucellus cells surrounding the embryo sac are completely destroyed. Alternatively free spaces form around the embryo sac. It is possible that these cells were used up as nutritive substances during embryo sac enlargement.

Degenerating embryo sacs were observed in site A material. They were noted at the stage when the spike contains fully formed nutlet. The base of such a mature nutlet is filled up by a large ovule. The size of this ovule is 2 to 3 times the size of an ovule with an eight nucleate embryo sac. This ovule only fills 1/3 of the nutlet space while the remainder is empty. It is not known whether seeds form in a nutlet of this type at a later stage. Observations on site B material only went as far as the mature eight nucleate embryo sac stage.

DISCUSSION

As a result of the investigations on *Carex aristata* var. *cujavica* it may be concluded that the species is unstable and very susceptible to variation and formation of abnormalities. These abnormalities concern morphological as well as anatomical characters. Already Wilkoń-Mi-

Explanation of Plate V

Fig. 1. Very early stage of an eight nucleate embryo sac.

Fig. 2. Typical egg-apparatus and polar nuclei

Fig. 3. Mature embryo sac. Probably a sperm nucleus next to one of the synergids

Fig. 4. Degenerating embryo sac. Typical features of degenerating synergids.

Magnification $\times 1050$.

chalska (1960) reported a good deal of variation in certain of the individuals. It is interesting that plants from two neighbouring though separate sites should have shown such large developmental differences. Even though the morphological differences are to an extent understandable if one argues that plants on site B had better environmental conditions for development, the abnormalities and the variation in internal structure were striking. The cause of the irregularities encountered is unknown. The fact that *Carex aristata* R. Br. is probably a hybrid of the cross *C. vesicaria* \times *C. hirta* (Siegert 1851 — cf. Ascherson 1888 and Wimmer 1853 — cf. Krawiecowa, Kuczyńska 1959) may be of significance in seeking for an explanation of the abnormalities in the development of different organs. One might equally well suspect the variation to be the result of a genetic mutation.

Similar abnormalities have been known to occur in *C. praecox* as a result of a fungal infection. This is not the case in the present material.

In spite of the many differences, plants from the two sites under discussion had many common characters. These can be listed as typical for *Carex aristata*.

The ovule arises at the base of the ovary. It is supported on a rather long funiculus. The anatropous position of the ovule is typical for this variety and it is the position listed as characteristic for sedges by Schnarf (1929). The ovules are crassinucellate. The integuments develop when the nucellus is already fully formed. Warming (1879) studied several groups of plants in order to construct a system of nucellus and integuments classification on the basis of primitive or more advanced attributes of these tissues. He recognizes three classes:

1. The nucellus is formed in advance of the integuments. This is the case when subepidermal cells develop to form the nucellus before integument initials are recognizable (*Ribes*, *Helianthemum*, *Convallaria*, *Iris*, *Senecio*).

2. The nucellus and the integuments develop simultaneously (*Sedum*, *Epilobium*, *Primula*, *Ficaria*).

3. Integument is formed in advance of the nucellus (*Cuphea*).

According to this classification *Carex aristata* would belong to the first group in which the nucellus itself initiates the formation of the integuments.

Observations carried out on young ovules show that in *Carex* and in other plants the inner integument is formed first. A fold of the outer integument covers the outer part of the ovule only. On rare occasions plants belonging to one family may have either one or two integuments. The occurrence of only one integument is the result either of an inhibi-

tion in the development of the other one or its subsequent disappearance. Netolitzky (1923) states that the disappearance of one integument does occur. This remark does not refer to members of the family *Cyperaceae* but data reported for *C. aristata* may nevertheless support his findings. Schürhoff (1926) states in a discussion on the structure of *Carex* ovules that the outer integument develops into a structure very rich in cytoplasm on the inward side of the anatropous ovule. It is possible that this tissue functions as an obturator. The present investigation and that of Dunajská (1964) on *Carex praecox*, provide confirmation of Schürhoff's observations. Braun mentions instances of the formation of two ovules per ovary found by Mirbel for *C. pendula (maxima)*, cited by Schnarf (1929). Schnarf regards this as an abnormality. The development of one of these ovules is frequently arrested.

Warming (1913) considers the underdeveloped, extra ovules sometimes found in ovaries, to be sterile. He finds no explanation for their presence.

Macrosporogenesis and embryo sac development are normal in *C. aristata*. Nevertheless characters which distinguish this species from other sedges are present. The formation of the first archesporial cell was not observed in the present material. This cell on division gives rise outwards to a smaller parietal cell called the tapete cell by Schürhoff and the cover cell by Schnarf. In the present material the megaspore mother cell is formed directly deep down in the nucellus (4 to 6 cell layers below the epidermis). If a parietal cell was ever formed rows of cells originating from it should be visible in the nucellus. Neither do the rows of nucellus cells above the megaspore mother cell show any trace of previous division in the epidermis. The nucellus cells are small and irregularly arranged. There were 42 ovules at megaspore mother cell stage in the present material. In most of these it is certain that the sections were cut correctly and were not skew. All these sections support the view that no parietal cell is formed. This contradicts Schürhoff's observations, who concluded that a cover cell is formed and its subsequent divisions push the developing embryo sac down into the nucellus. There is no parietal cell formed in *C. praecox* as reported by Fischer (1880). It seems possible that Schnarf was too quick to generalize on the basis of his own findings for all *Carex* species. Nevertheless the formation of a deep-seated archesporial cell and the lack of a parietal cell must be regarded as a rare occurrence for angiosperms.

In general, megaspore remains are known to vanish early, while in the present material they are still present in mature degenerating embryo sacs. According to Schürhoff, Heilborn and Fischer antipodals are three small cells which disappear soon. In *C. aristata* the

antipodals are large, sometimes as large as the synergids. They persist a long time. It is interesting that the egg cell nucleus is smaller than the synergid nuclei. It persists longer than the latter. In degenerating embryo sacs the egg cell nucleus and the secondary nucleus are both distinct. The persistence of these nuclei at the time when the synergids are undergoing degeneration and the antipodals have already degenerated is of interest. It suggests that in spite of appearances fertilization has taken place, but the two nuclei subsequently undergo a long resting stage. It is unfortunate that more pollen grain tubes were not found since a greater measure of certainty as to the occurrence of fertilization might then be attained. In the one pollen grain tube observed the sperm nuclei were naked. If for the sake of argument, this be considered typical for *C. aristata* then according to Navashin and Finn the species is a young form, phylogenetically very advanced in its development.

Since fertilization, embryo and endosperm formation have not been proved to take place, it may be supposed that the species propagates vegetatively through a vigorously branched rhizome system.

The chromosome number of some sedge species has been recorded. The largest number of species was studied by Heilborn (1918). The haploid chromosome number in various species ranges from 8 to 52 chromosomes. It is frequently observed that chromosome number and chromosome size are inversely proportional. There are some indications of the chromosome number in *C. aristata* var. *cujavica* in this material. A metaphase I stage of division in the megaspore mother cell was found once. This is shown in Plate IV, fig. 1. The homologous pairs, closely in contact along their whole lengths were distinct. The magnification is $1500\times$. Ten pairs of chromosomes are visible. Unfortunately this count could not be confirmed by a larger number of observations.

SUMMARY OF OWN RESULTS

Sites A and B on which the material was collected

The embryo sac is monosporic, eight nucleate, of the Polygonum type. Embryo sac development is normal. The egg cell nucleus is smaller than the synergid nuclei. The antipodals persist a long time. Megaspore remains also persist forming a black cap over the embryo sac.

Site A. Ovule development is normal. It is anatropous. There are two integuments. Development is normal up to the mature, eight nucleate stage of the embryo sac. From then on embryo sacs degenerate and enlarge abnormally, probably as a result of the lack of fertilization. Megaspore remains persist in degenerating embryo sacs.

Site B. Abnormalities in ovule and funiculus development are present. Ovules are usually orthotropous and there is frequently only one

integument. Integument development is often arrested (the nucellus is then uncovered). Other developmental irregularities include integument growth in thickness instead of in length, a bending back of the integument, straightening out of the ovules, back into the orthotropous position, overenlargement and proliferation of the funiculus.

The occurrence of two ovules per ovary, one of which is often underdeveloped was frequent.

Two or even three megaspore mother cells per ovule were often observed (e.g. single ovule containing a megaspore mother cell, a one nucleate embryo sac and a two nucleate embryo sac).

I offer my sincere thanks to Professor Stefan Krupko for valuable suggestions and assistance received in the course of this work.

Thanks are due to Doc. A. Szweykowska the Head of the Department, for the facilities provided during the course of this work.

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(Entered: 12.VII.1963)

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Budowa zalążka, megasporogeneza i rozwój woreczka zalążkowego u Carex aristata R. Br. var. cujavica

Streszczenie

Stanowisko A i B

Woreczek zalążkowy jest jednosporowy, ośmiojądrowy, typu *Polygonum*. Rozwój woreczka jest normalny. Jądro komórki jajowej mniejsze od jąder synergid. Długowieczność antypod. Długie utrzymywanie się resztek megaspor w postaci czarnej czapy nad woreczkiem zalążkowym.

Stanowisko A

Rozwój zalążka normalny. Jest on anatropowy, dwuintegumentowy. Normalny rozwój woreczka zalążkowego trwa do stadium dojrzałego, 8-jądrowego. Później rozrastanie i degeneracja woreczków zalążkowych — prawdopodobnie wynik braku zapłodnienia. Obecność resztek megaspor w degenerującym woreczku.

Stanowisko B

Nienormalności w rozwoju zalążka i funikulusa. Zalążki przeważnie są ortotropowe i bardzo często jedointegumentowe. Widoczny również niedorozwój integumentów (ośrodek jest wtedy nieosłonięty). Inne nienormalności rozwojowe to: wzrost integumentu na grubość, a nie na długość, odgięcie integumentu, powtórne wyprostowanie zalążka, bujanie funikulusa, przerost funikulusa.

Powstawanie w zalążni dwóch zalążków, z których jeden najczęściej jest niedorozwinięty, oglądano na wielu obiektach. Obserwowano wypadki zakładania się dwóch, a nawet trzech komórek macierzystych megaspor w jednym zalążku (np. komórka macierzysta megaspor, woreczek jednojądrowy i dwujądrowy).