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Development of *Cladium mariscus* (L.) Pohl. fruit

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Abstract

The ovule and ovary development was investigated with the aim to establish from what is the scleroid cover of the *Cladium mariscus* fruit derived. It was proved, that like in other members of the *Cyperaceae* family, it derives from the ovary.

INTRODUCTION

The only, scanty data on the *Cladium* fruit development can be found in the paper by Chlewińska-Karpowiczowa (1929). The authoress believed that the scleroid cover of *Cladium mariscus* seed had originated from the ovule integument.

It was established beyond a doubt, that in other taxons of the *Cyperaceae* family the thick, woody seed cover derives from the ovary (Wilczek 1892, Marek 1958, Shah 1968). That is why it was decided to determine finally from what structure the hard cover of the *Cladium mariscus* seed develops.

MATERIAL AND METHOD

The material included young inflorescences in the leaf axils collected in the Sława Śląska neighbourhood in May 1975 and florescences collected in the Poznań environs owing to the courtesy of Prof. Waldemar Żukowski in the second part of June 1975. Series of microtome slides approximately 8 μm thick were made from the material fixed in Navashin's fixative. Sections were stained with safranin and fast green, dehydrated in isopropyl alcohol, cleared in xylene, and embedded in Canadian balsam. Material including ovules with embryo sacs ready for fertilization and completely

formed, mature seeds was chosen as most suitable for resolving the problem. Photographic documentation concerns these two stages.

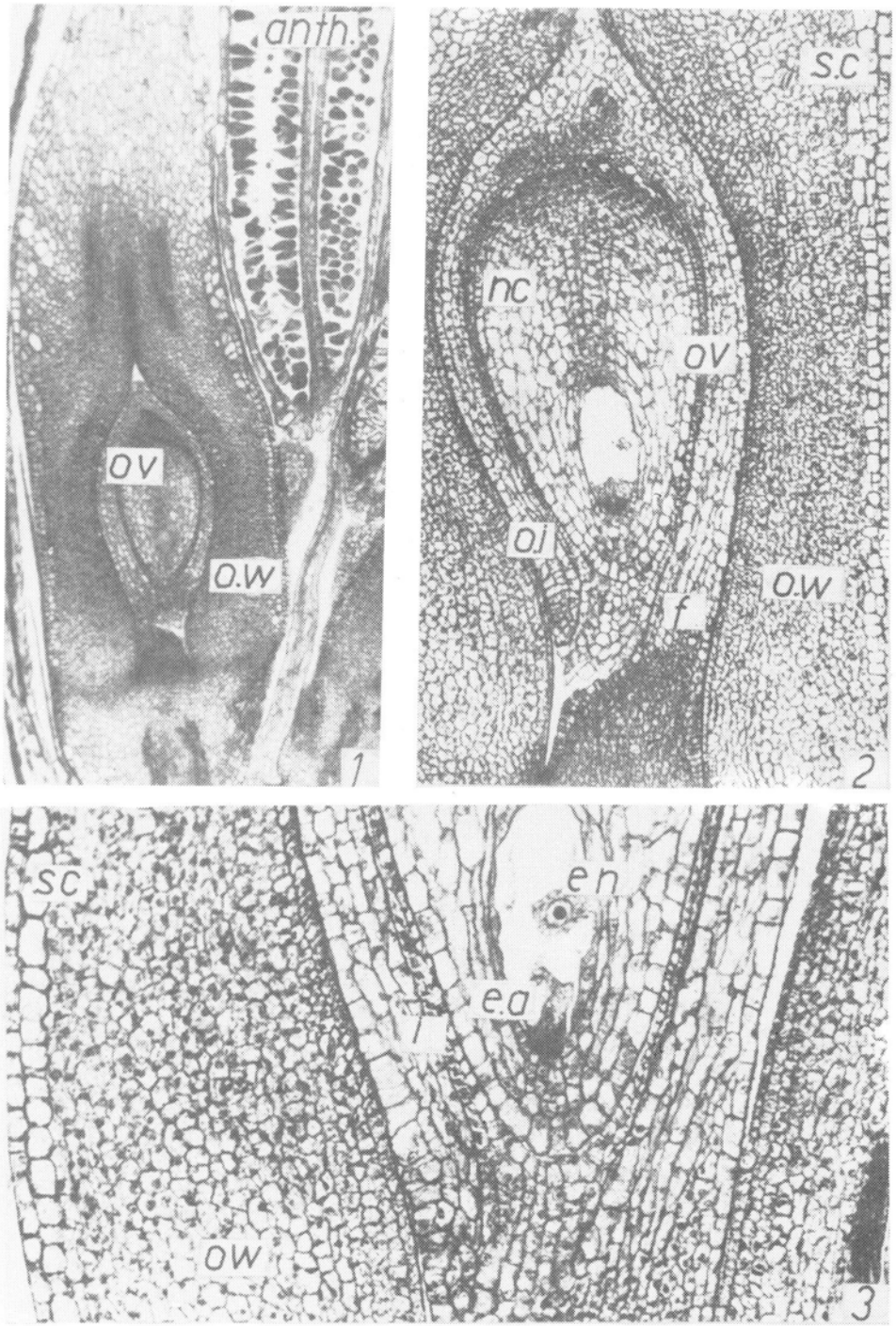
RESULTS

OVULE DEVELOPMENT

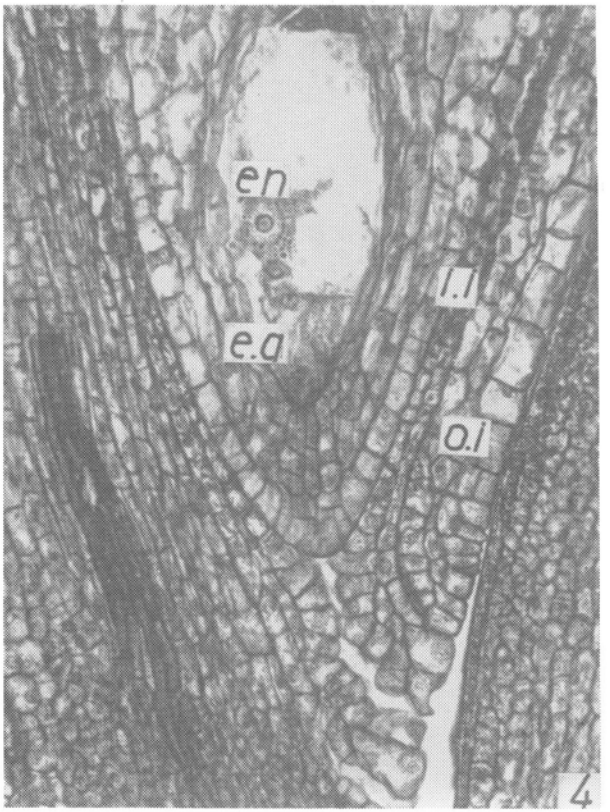
The ovule projection borne on the placenta at the base of the developed paracarpous ovary is a simple structure, growing apically till the appearance of archesporial cell. The spore mother-cell differentiation and the beginning of inner integument differentiation occur together. Then at the base of the developing inner integument the outer integument primordium appears. The spore mother-cell differentiation and the developement of the integument primordium occur simultanously with the process of ovule bending. The latter becomes an anatropous ovule at the stage ready for double fertilization. During this process meiosis and macrospore formation occur. Only one spore mother-cell appears. The developed ovule is anatropous (Fig. 2), with two integuments (Figs. 2, 3, 4, 6) and crassinucellar (Fig. 2). Embryo sac development is of the *Polygonum* type. It consists of a three-cell egg apparatus (Figs. 3, 4), a definitive nucleus (Fig. 3) and three gradually disintegrating antipodal cells (Fig. 4). The *Cladium mariscus* endosperm is of nuclear type. The inner integument is a two-cell-layer structure (Figs. 3, 4, 6). In the micropylar part these cells increase and bulge (Figs. 4, 6). The integument is separated from the nucellus by a distinct cuticle layer (Figs. 4, 6). The cuticle layer and different biochemical character of the integument and the nucellus epidermal cells permit for coloured differentiation of these layers. The outer integument is formed by 3-6, mostly 4 cell layers (Figs. 2, 3, 4, 6). In the micropylar part the nucellus divides periclinally and a layered pattern of cells is formed (Fig. 4).

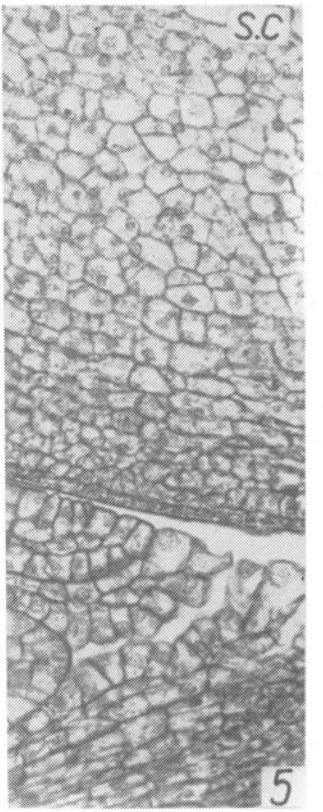
PERICARP DEVELOPMENT

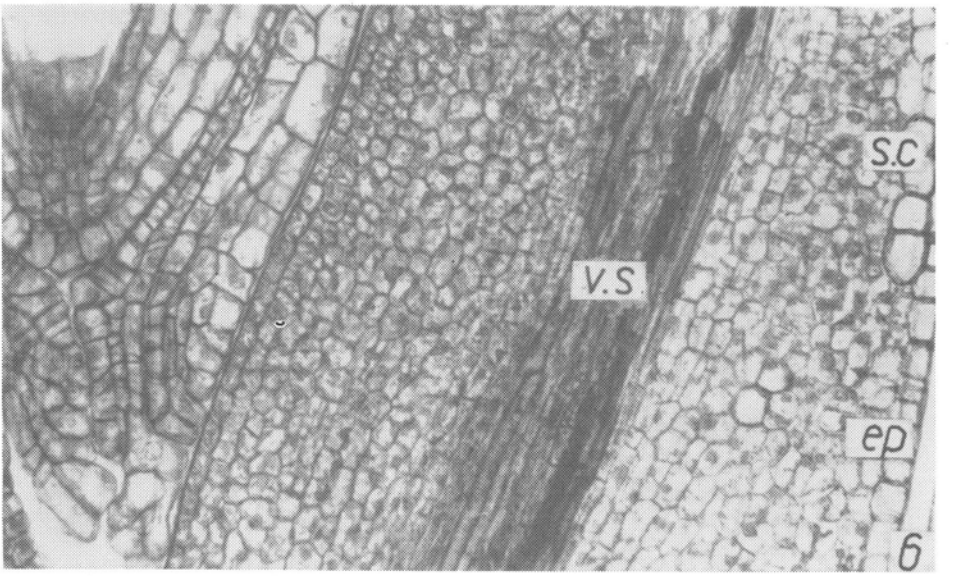
When the embryo sac development is nearly finished and it is ready for double fertilization, all the typical ovary layers are already formed. The unilocular ovary originates from three carpels—so it is of paracarpous type. There are 2-5 layers of big cells of sub-epidermal origin under the outer epidermis (Figs. 1, 2, 3, 6, 7, 8). The number of the cells increases in the apical part of the ovary (Fig. 1). Sub-epidermal cells are parenchymatous. They become dry and filled with air in the course of fruit maturation. This enables the fruit to keep on the water surface and to disperse over great distances. There are approximately 20 layers of cells gradually differentiating into sclereids between the parenchyma and inner epidermis layer. The secondary growth of the pericarp is due to cell



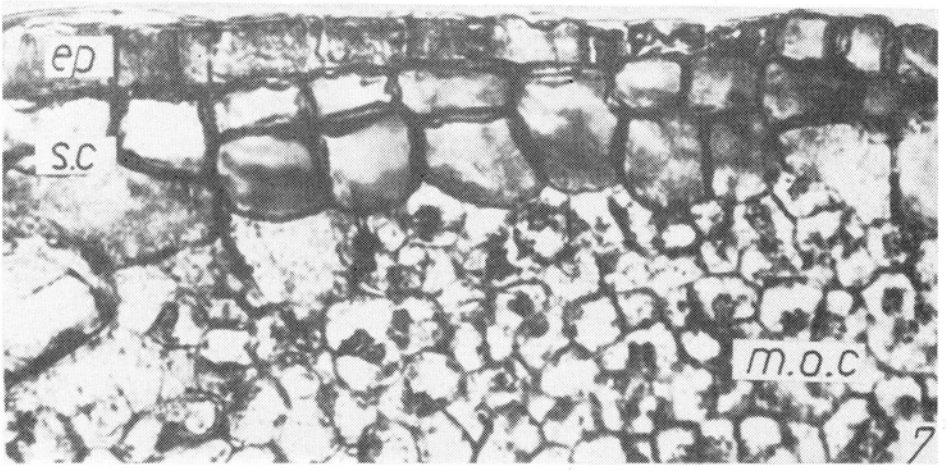
Figs. 1-3. Longitudinal, central section of the ovary at mature stage of the embryo sac showing distinct border between ovary wall and bitegmic, crassinucellate ovulus. Anticlinar and periclinal divisions in subepidermal cells of the ovary are evident. Differentiation in the ovary wall into subepidermal, parenchymic part and scleroid one is seen. anth. —anthers, e.a—egg apparatus, f—funicle, en—endosperm nucleus, i—integuments, nc—nucellus, o.i—outer integument, ov—ovule, o.w—ovary wall, s.c—sub-epidermal cells. Fig. 1—75 x, Fig. 2—200 x, Fig. 3—400 x

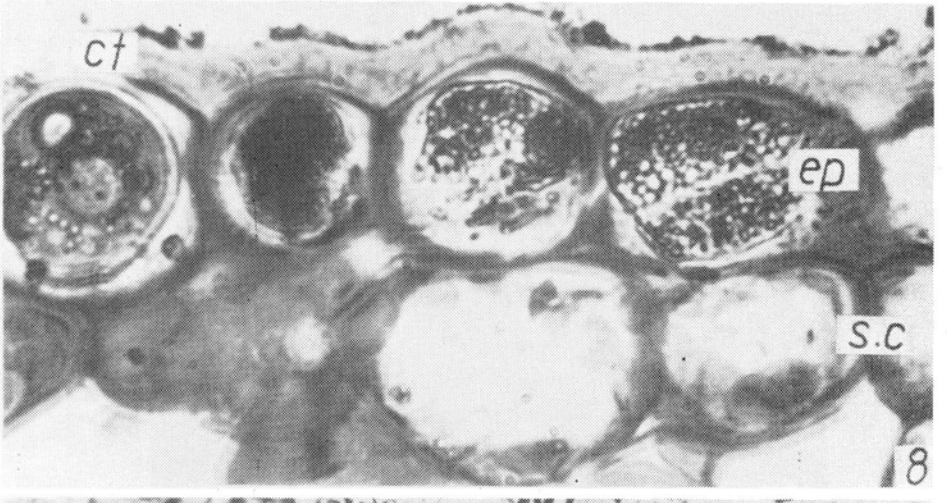






Figs. 4-6. Longitudinal section in micropylar region of the ovulus and ovary wall in its neighbourhood. On Fig. 4 embryo sac with antipods, egg apparatus and polar nuclei. Distinct border between nucellus, inner integument, outer integument and fissure separating outer integument from the ovary wall. Fig. 6 shows the proportion of the integuments and the ovary wall in an early stage of sclereids, differentiation. Subepidermal parenchymic cells are also seen. e.a—egg apparatus, en—endosperm nucleus, ep—epidermis, i.i—inner integument, o.i—outer integument, s.c—sub-epidermal cells, v.s—vascular supply. 550 x





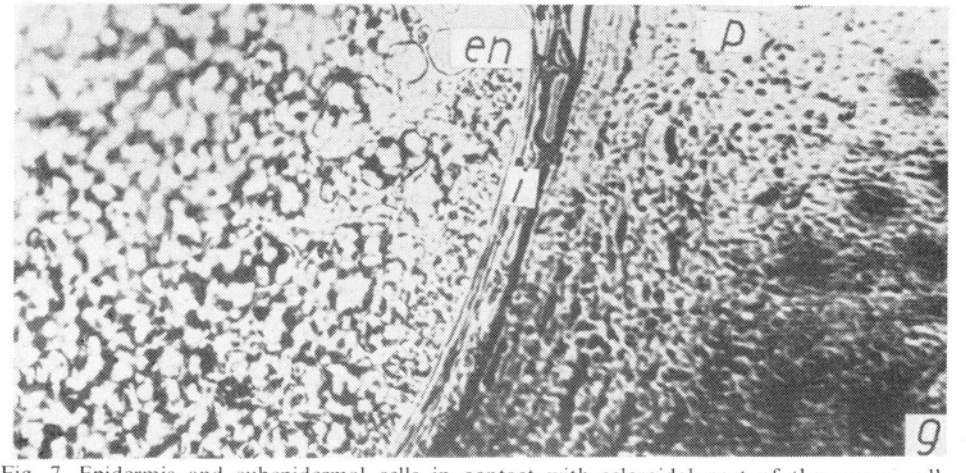


Fig. 7. Epidermis and subepidermal cells in contact with scleroidal part of the ovary wall. Periclinal division in subepidermal cells is seen. 1000 x

Fig. 8. Thick, cutinized outher walls of epidermal cells with tannins in contact with subepidermal parenchyma. 2000 x

Fig. 9. Cross section of the mature fruit of *Cladium mariscus*. Endosperm, seed coat, interguments and scleroidal part of the pericarp. The border between endosperm, seed coat and pericarp is well expressed. Look at the thickness of seed coat and that of pericarp. 1000 x ct—cuticle, en—endosperm, ep—epidermis, i—integuments, m.o.c—middle ovary wall cells, p—pericarp, s.c—sub-epidermal cells

divisions of "mesocarp". The inner epidermis consists of cells elongated crosswise to the long axis of fruit. In the course of maturation it also differentiates into sclereids. The developed *Cladium mariscus* pericarp consists of two parts: a) an outer epidermis of cells with thickened, cutinized walls and parenchyma of sub-epidermal origin (Figs. 7, 8), b) an inner epidermis and approximately 20 sclereid layers. During observation of the ovule and ovary development it can be noticed that the ovule cells get mature later than the ovary cells do.

The growing and differentiating ovule fills gradually the ovary locus till its outer surface comes into the contact with the inner surface of the ovary wall—inner epidermis of the developing pericarp. The two, however, do not fuse into one. The outer integument does not coalesce with the pericarp and can be easily separated from it (Figs. 3, 4, 6, 9). Integument cells do not differentiate into sclereids and do not form a thick mechanical cover around the seed (Fig. 9). They develop into a thin seed coat, clearly defined and distinguished from the endosperm and pericarp sclereids (Fig. 9). It consists usually of 3-5 layers of crushed thim-walled cells. Therefore, the pericarp and particularly its scleroid part forms the thick seed cover (Figs. 2, 5, 6, 9), owing to such a structure the fruits of *Cladium mariscus* are being well preserved in Holocene materials (Kowal 1958, Marek 1958, 1965).

DISCUSSION

In the evaluation of the anatomical description of *Cyperaceae* family fruits, particularly fruits of genera belonging to the *Scirpoideae* and *Rhynchosporoideae* subfamilies, the features of mature *Cladium* fruits were given (Marek 1958). As the author had only mature fruits, the thick scleroid *Cladium* seed cover was assumed, by analogy to the *Carex* pericarp formed from sclerenchyma, to have been a structure connected in its development with the ovary, contrary to Chlewińska-Karpowiczowa's (1929) interpretation. Now, it can be stated beyond a doubt that the scleroid cover of the *Cladium* seed derives from the ovary. The scleroid seed cover also develops from the ovary in *Rhynchospora*, *Schoenus*, *Bulboschoenus*, *Dichostylis*, *Blysmus*, *Eriophorum*, *Trichophorum*, *Isolepis*, *Holoschoenus*, *Schoenoplectus*, *Scirpus* (Marek 1958), *Carex* (Wilczek 1892), *Cyperus*, *Carex*, *Kyligia* (Shah 1968) genera. Hence, the structure of *Cladium* fruits does not differ from the structure scheme common in the whole *Cyperaceae* family. According to Winkler's classification (1939) they belong to the group of the simple paracarpous fruits derived from upper ovary.

Like the ovules of other members of the *Cyperaceae* family the *Cladium mariscus* ovule is anatropous, with two integuments, crassinucellar, borne on the basal placenta, with embryo sac developing according to the normal type, and nuclear endosperm. Similarly to other members of the *Cyperaceae*

family the seed coat is a delicate structure, derived from two integuments, that does not coalesce with the ovary. The inner integument develops earlier than the outer, the latter differentiates at the base of the inner integument. Integument cells never differentiate into sclereids. Thus, the developing seed coat is a delicate structure, composed of crushed, thin-walled cells and does not form a sufficient cover for the endosperm and embryo. The scleroid layer, connected in its development with the ovary, represents the main, mechanical cover of *Cladium mariscus* seed. The mature *Cladium* pericarp consists of two parts: a) an outer—epidermic-parenchymatous, treated by Chlewińska-Karpowiczowa (1929) as a pericarp and b) an inner—scleroid considered by her as a structure, developing from the outer integument. The outer, epidermic-parenchymatous part of the pericarp, although rarely preserved in subfossil materials, plays an important role in fruit dispersal by water.

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Rozwój owoców Cladium mariscus (L.) Pohl.

Streszczenie

Zbadano rozwój zalążka i wocni. Stwierdzono, że z obu integumentów powstaje dość jednolita i delikatna łupina nasienna zbudowana z cienkościennych komórek, wyraźnie wyodrębniona od bielma i zalążni. W przekształcającej się w owocnię zalążni różnicują się dwie odrębne strukturalnie części: 1) część wewnętrzna, składająca się ze zgrubiałej i zdrewniałej wewnętrznej epidermy i z około 20 warstw sklereidów; oraz 2) część zewnętrzna, w skład której wchodzi zewnętrzna epiderma i miękisz głównie subepidermalnego pochodzenia, który w czasie dojrzewania owocu wysycha i wypełnia się powietrzem. Plan budowy owoców *Cladium mariscus* jest podobny do planu budowy owoców innych przedstawicieli rodziny *Cyperaceae*. Owoce te można łącznie zmieścić w grupie owoców pojedynczych, jednonasiennych, powstałych z górnej, parakarpowej zalążni.