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Activation of embryo during rape (*Brassica napus* L.) seed germination

I. Structure of embryo and organization of root apical meristem

MIECZYSŁAW KURAŚ

Laboratory of Electron Microscopy, Institute of Botany
Warsaw University

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Abstract

The structure of the mature rape embryo was examined on longitudinal microtome sections, and its developmental interpretation is given, based on the author's own studies and literature data.
The boundaries between the epicotyl, hypocotyl and radicle are recognized and identified with the limits between the proembryo segments. The radicle structure and root apical meristem organization are described. In the dermatogen and periblem cell patterns four segments are distinguished, separated successively from the initial cells. Their position is recognized as almost the same on both sides of the root axis and in different embryos. The easily discernible limits between the dermatogen sectors are to be utilized as reference points in studies on the root apical meristem activation and growth during rape seed germination.

INTRODUCTION

Germinating embryos are a very convenient and widely used object for investigation on initiation of metabolic processes in dormant tissues.

Among the studies on the course of germination, biochemical investigations prevail. Their aim is to establish the sequence of processes leading to the resumption of growth by the embryo, and particularly of nucleic acids, proteins and enzymes syntheses, and to find the causes of deep dormancy of seeds. Papers on the morphological symptoms of activation of the dormant embryo are scarce. Precise data concerning the distribution of growth in the germinating embryo are not available. An

exception here is the paper by Miller and Wetmore (1945a and b, 1946) who studied the course of growth of the axis of young *Phlox Drummondii* seedlings. Data on the resumption of mitotic activity are not numerous and fragmentary. They are only analysed as far as this was connected with the establishment of the course of germination as a consequence of the resumed cell division and growth. Most studies from this field concern the sequence in which growth initiation and cell division occur (Toole, 1924; Caldecott and Smith, 1952; Picklum, 1953; Wolf, 1954; Evenari et al., 1957; Haber and Luippold, 1960; Mayer and Poljakoff-Maybor, 1963) and the possibility of separation of these two processes (Haber and Luippold, 1960 Haber et al., 1961; Haber and Foard, 1964; Haber, 1968). These papers, however, lack information on the distribution of the first mitoses and their spread in germinating embryos. In the literature available to date precise data are also lacking on the course of activation of the apical meristem of the embryo.

In view of this the Group of Plant Morphogenesis of the Warsaw University, under the guidance of professor Henryk Teleżyński started a few years ago studies on the course of activation of dormant rape embryos. The choice of this species was decided for several reasons, the most important of which was the extremely regular development of the embryo, particularly of its radicle which makes possible the recognition and comparison of homologous segments of the embryo axis in the successive steps of its development, germination and growth of the young seedling. The possibility of recognition of the limits of the homologous segments in successive phases of embryogenesis and germination has allowed developmental analysis of the structure of the mature embryo and investigation of the spatial course of activation and axis growth. The successive steps of this research will be the subject of separate publications. The first of them is the present paper on the structure of the mature embryo with particular reference to the organization of the radicle apical meristem.

Descriptions of mature embryos can be found in many taxonomic monographs and numerous manuals with general data concerning the size of the embryo and number of cotyledons. The structure of the mature embryo has also been the subject of numerous studies, most of which concern gymnosperms (Schleiden, 1849; Strasburger 1872, Hutchinson, 1917; Clare and Johstone, 1931; Buchholtz and Old, 1933, Schopf, 1943; Allen, 1946, 1947 a, b; Spurr, 1949; Berlyn, 1972; Stockey, 1975). Mature embryos of angiosperms have been described in detail among others by Nast, (1941); Miller and Wetmore (1945 a, b, 1946); Reeve (1948); Berlyn, 1972). A description of the development of the mature embryo may be found in only few papers (Reeve, 1948; Miller and Wet-

more, 1945 a, b; Allen, 1946, 1947 a, b; Spurr, 1949). Mostly it is a description of the mature embryo without reference to embryogenesis. Therefore, most of the detailed descriptions of the anatomical structure of embryos is burdened with serious errors and but little useful in investigations on the anatomical changes occurring during seed germination. In this situation the seeds of Cruciferae with an extremely regular embryo structure and exceptionally well known embryogenesis are a very convenient object for investigations (Hanstein, 1870; Soueges, 1916, 1919, 1936, 1939; Schnarf, 1929; Lebègue, 1952; Creté, 1963), and among these particularly rape seeds (Kavetskaya, 1958; Tykarska, 1976).

MATERIAL and METHODS

The investigations were performed on mature embryo axes of winter rape (*Brassica napus* L.,), variety Górczańska, prepared out from dry seeds. The axes of embryos were prepared out intact and fixed in chromacetoformalin (CrAF), percentual composition 0.5-1-20. After fixation the material was washed repeatedly with distilled water, dehydrated with ethanol and, after passing through xylene, embedded in paraffin. Longitudinal and cross section 5 μm thick were cut on a Reichert microtome. The slides were stained with safranin and fast green according to Sass (1940) or with alcian blue after Benes (1968).

The structure of the axis of mature embryos was analysed on microtome longitudinal sections with particular attention to the organization of the root apical meristem. Measurements of the length of the whole embryonal axis and of the radicle, hypocotyl and epicotyl were performed. The limits between them are defined below. The measurements were taken in two ways: along the central axis from the shoot apex to the end of the root cap and along the boundary between the dermatogen and the cortex on the convex and concave sides of the bent axis. In the latter case the measurements were performed from the columella to the boundary between the hypocotyl and the cotyledons. The data for the radicle obtained by measurement along the dermatogen do not, therefore, include the columella. All measurements were taken with a micrometric ocular on central longitudinal sections of 10 roots and the arithmetic means were calculated.

RESULTS

General structure of the embryo

The mature rape embryo axis is characteristically bent like in other *Cruciferae* species, and the well developed cotyledons cover it almost completely (Plate I). The axis consists mainly of the hypocotyl. In its

upper part it ends by the hardly protruding shoot apex with the primordium of the first leaf, and in its lower part by the radicle apical meristem.

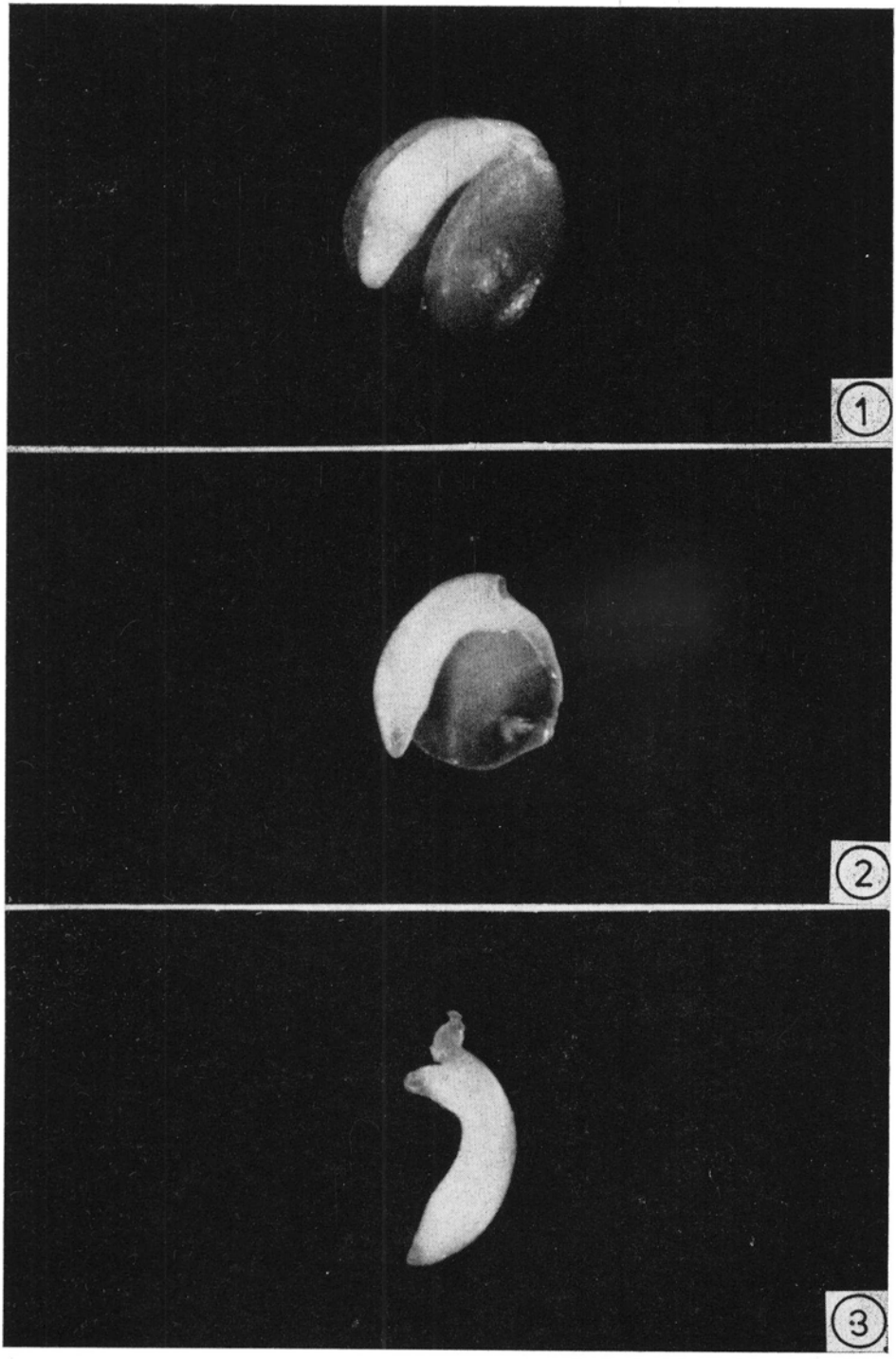
The boundary between the hypocotyl and the cotyledonary node does not show in the outer shape of the embryo. Distinction of the radicle from the hypocotyl on the basis of the external morphological features is usually easier. In the lower part of the embryo axis a distinct constriction is visible (Plate I). The beginning of the zone of tapering may be assumed as the morphological boundary between the hypocotyl and the radicle.

A more precise distinction of the parts of the embryo is possible on the central longitudinal sections. Here the boundary between the hypocotyl and the radicle is most pronounced. In the zone of tapering of the embryo axis a sudden change occurs in the number of cortex cell layers and the first layer of the root cap stands out. The upper border of the first root cap cell layer is assumed as the boundary between the hypocotyl and the radicle. Owing to the discontinuity in the arrangement of the cell files, a transverse developmental boundary separating the root part from the hypocotyl one is distinctly outlined in the cortex at this level (Plates II—IV). This boundary corresponds to the second transverse segmentation boundary in the periblem of the globular embryo (T y k a r s k a, 1976).

Much more difficult is the recognition in the mature embryo of the upper developmental boundary between the hypocotyl and the epicotyl. On longitudinal sections of many mature embryos, however, its course is well distinguishable immediately above the forking of the procambium. In the peripheral part of the embryo axis it runs lower than in the central part (Plate III). This boundary, discernible in the cell pattern of a mature embryo, is a natural developmental boundary as well, corresponding to the boundary of segments in the early stage of embryo development. It, namely, results from investigations on the embryogenesis of rape (T y k a r s k a, 1976) that the cotyledons with the cotyledonary node and shoot primordium are derived from the upper tier of cells of the apical part of the proembryo (tier 1), whereas the hypocotyl with the radicle arise from the lower cell tier (l').

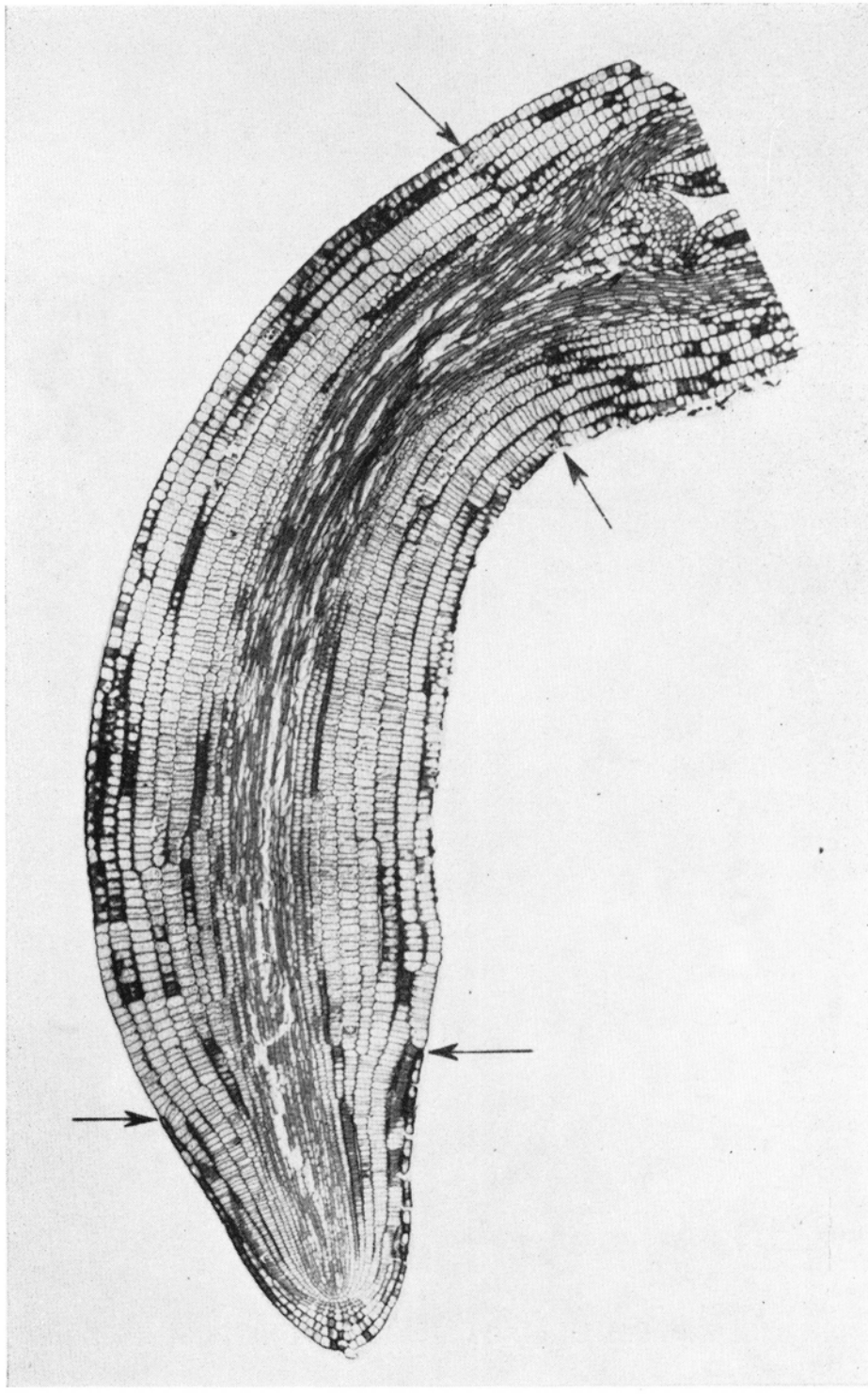
Thus, it appeared that in most embryos the natural developmental boundaries between the hypocotyl and the radicle, and the hypocotyl and the cotyledons, corresponding to the boundaries of the segments in the early stages of embryonic development can be distinguished on longitudinal microtome sections.

Owing to the identification of these boundaries, it was possible to perform measurements of the radicle and hypocotyl length in mature embryos and later, during germination and the first stages of seedling development. It results from these measurements (Fig. 1) that the mean

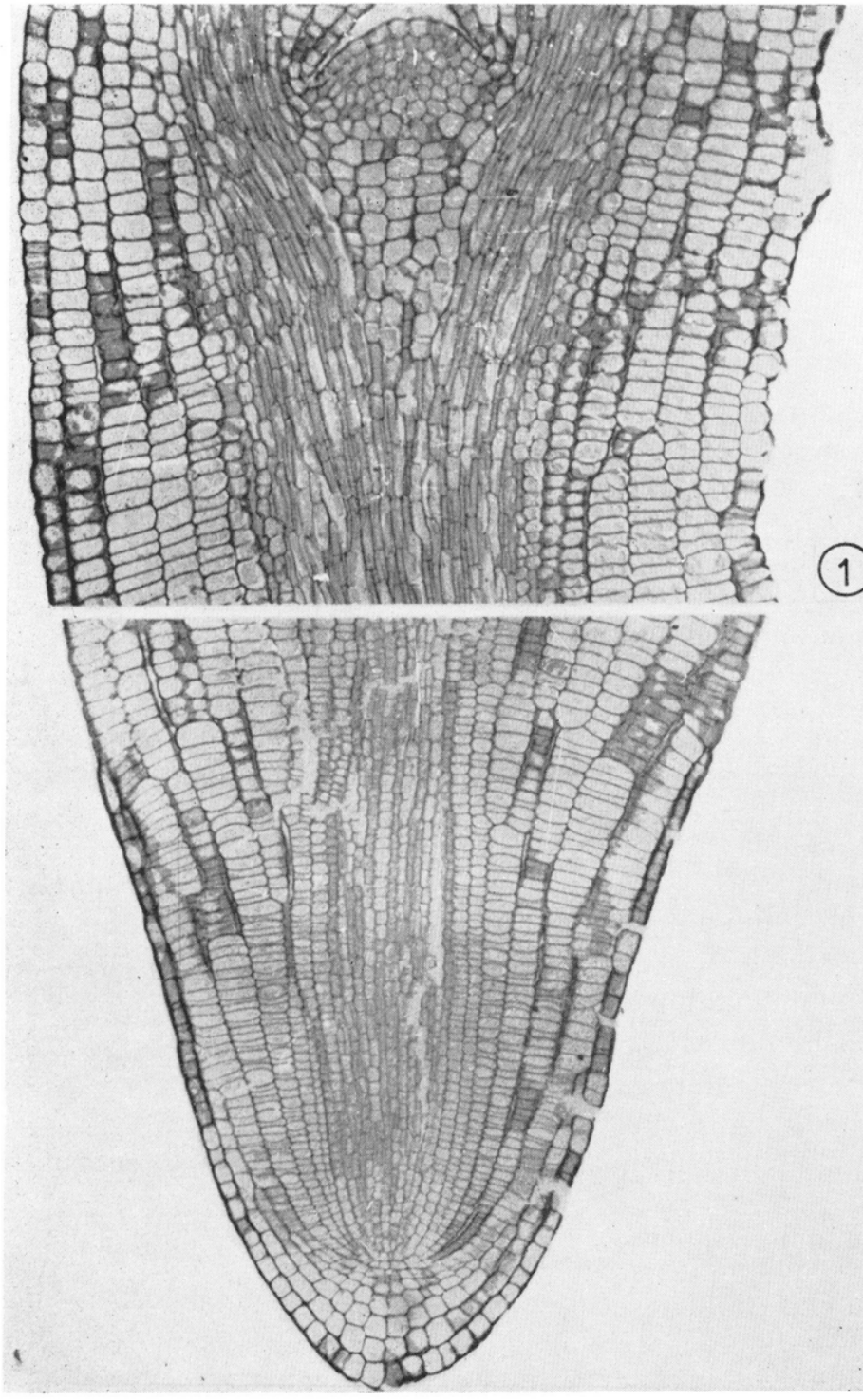


Mature rape embryo prepared out from swollen seed

1 — whole embryo, 2 — embryo with one cotyledon, 3 — embryo axis. Mag. 10×

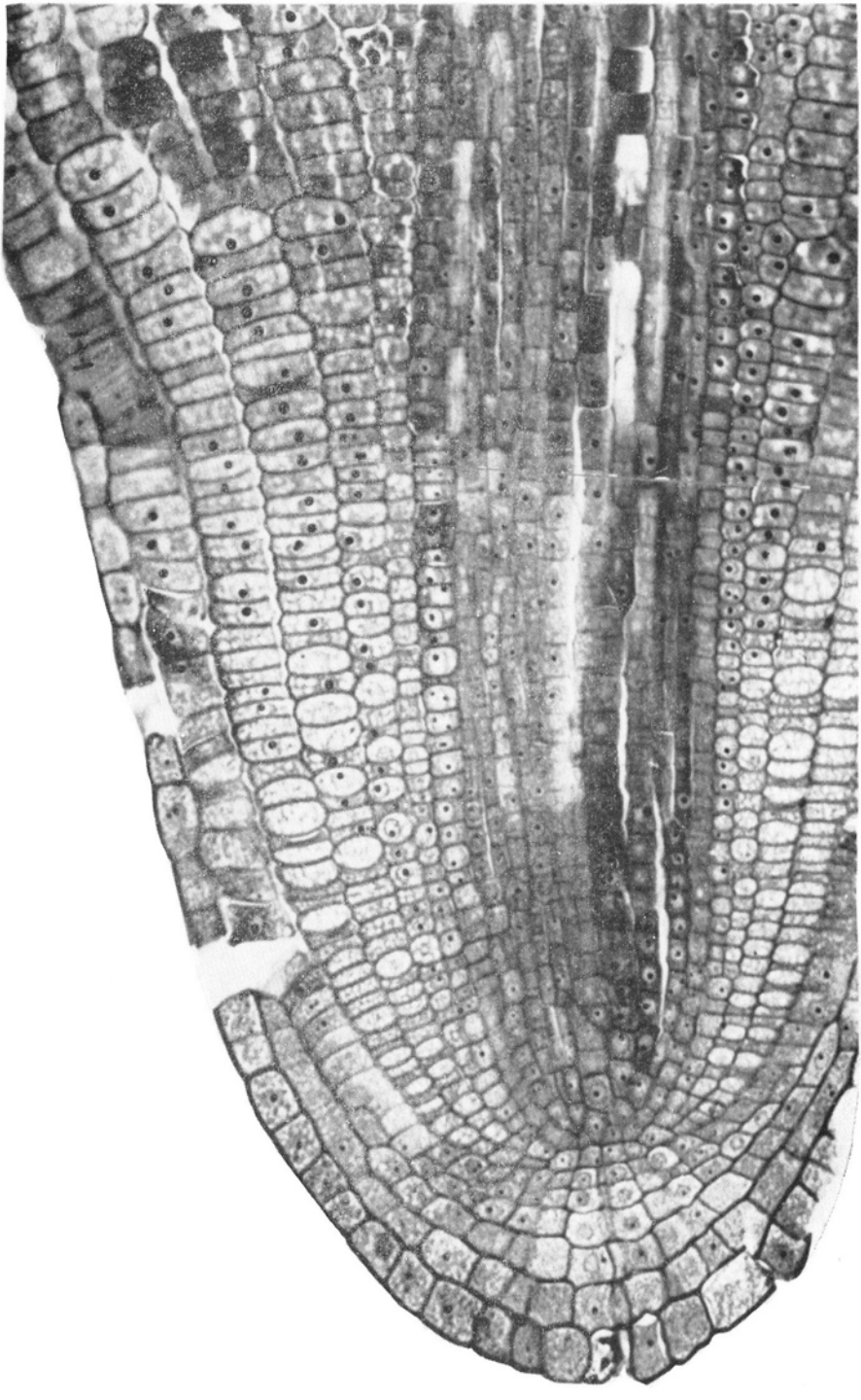


Longitudinal section through rape embryo axis. Upper arrows denote boundary between hypocotyl and cotyledons and shoot primordium, lower arrows indicate lower boundary between hypocotyl and radicle. Mag. 120×

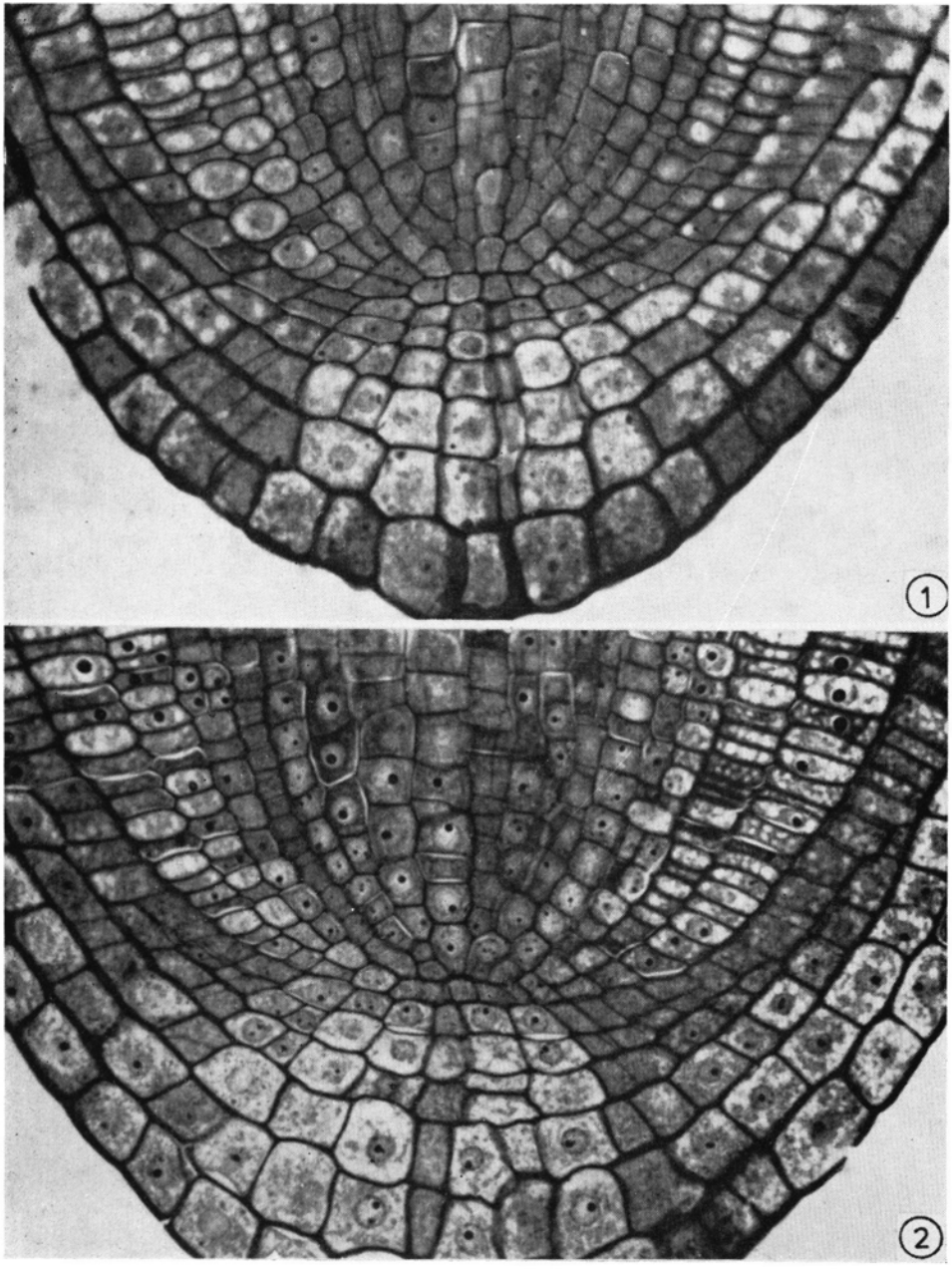


Longitudinal section through apical parts of axis of dormant rape embryo

1 — shoot primordium and base of cotyledons, arrow indicates boudary of hypocotyl. 2 — apical meristem of radicle. Mag. 250 ×



Longitudinal section through rape radicle. Mag. 350×



Longitudinal sections through root promeristem of dormant embryo. Mag. 400×

length of the axis of a mature embryo is 2.6 mm. Almost 4/5 of the axis length are occupied by the hypocotyl (1.9 mm). The radicle is as long as 1/4 of the hypocotyl (0.5 mm) and the part of the axis above the hypocotyl is twice shorter (0.2 mm). The apical meristem of the shoot includes as little as 1/4 of the length of the shoot primordium (ca. 50 μm, Fig. 1).

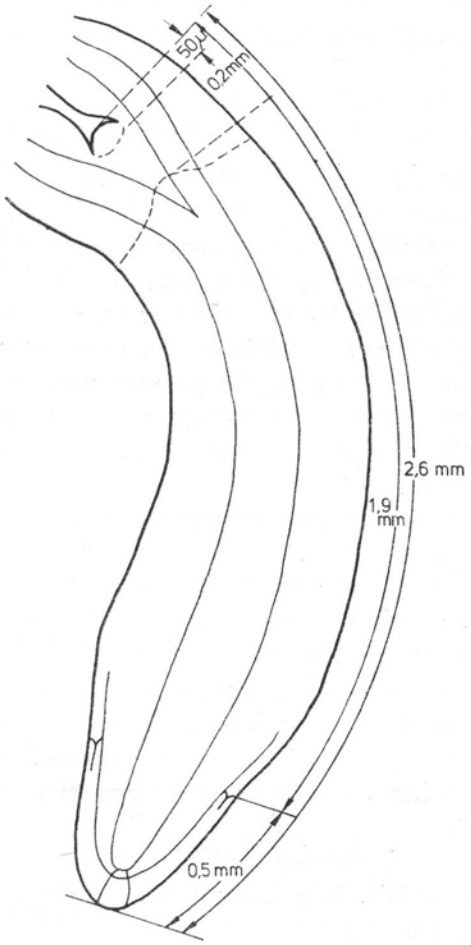


Fig. 1. Diagram of situation of natural boundaries in mature embryo axis and mean length of its parts

The hypocotyl is curved. The almost 50 per cent difference in the length of the dermatogen on both sides of the curvature is due to the different length of the cells, their number being almost the same.

Organization of the radicle apical meristem

In spite of the bending of the embryo axis the root primordium is built symmetrically. It has the shape of a cone with height equal to the diameter of its base. The root cap occupies 1/5 of its length. The primordium is formed of nothing but apical meristem and consists of not very numerous cells. The mean number of cells in one dermatogen file is 48.0. The radicle apical meristem organization is very regular and dependent on the constantly 3-tier promeristem (Plates III (2), IV and V). Thus, the apical meristem of rape root is closed.

Promeristem

In the constructional centre of the meristem three tiers of initial cells can be distinguished. The upper tier is formed of initials of the central cylinder. The middle tier is composed of central binding cells — Verbindungszellen (Guttenberg, 1960) and of the cortex initials surrounding them from outside. The lowest tier consists of columella initials and the surrounding common initials of the protoderm and lateral parts of the root cap. These 3 tiers of the promeristem correspond, thus, to 3 histogens: plerome, periblem and dermatocaliptrogen (Plates III (2), IV and V). The cells composing each of the 3 promeristem tiers are distinctly differentiated.

In the initial plerome tier the marginal cells, initials of the pericycle, can be distinguished.

Among the internal cells which initiate the middle part of the central cylinder, one or two initials of the central metaxylem vessel stand out by their size and position (Plates III (2) and IV).

In the middle tier there is a central group of binding cells which constitute the intermediate layer between the plerome initials and columella initials. This layer consists, on the central longitudinal section, of 3 or 4 cells standing out distinctly among the surrounding initials (Plate III (2), IV and V).

The group of central binding cells is surrounded from outside by a ring of periblem initials. The latter are sometimes periclinally divided into two initials. The inner one of these functions as initial of inner cortex and the one adjacent to the dermatogen as initial of the outer cortex layer.

The central binding cells forming the intermediate layer between the plerome and columella initials cannot be considered as initials of the radicle cortex, since they do not take part in the renewal of periblem initials over the entire period of embryogenesis, as indicated by the results of analysis of the longitudinal and cross sections. The setting off of this group of cells is also indicated by the sustained characteristic

arrangement of the cells and the thickness of the cell walls separating this layer from the cortex initials (Plates IV and V).

The lowest tier of the promeristem initials is also differentiated, giving rise to the protoderm and root cap. The central part of this tier consists of columella initials. On the central longitudinal sections they are usually four in number. The number of columella initials corresponds to the number of cell files forming the columella. The central group of columella initials is surrounded by initials of the dermatocalyptrogen.

The external cell files of the columella sometimes can be well distinguished on longitudinal sections from the lateral parts of the root cap (e.g. Plate V (1)). It is obvious in those cases that the cells of the columella did not undergo longitudinal division from the moment of formation of the 4-cell files visible on longitudinal sections. Neither did these cells take part in the development of the lateral parts of the root cap. In many cases, however, the setting off of the columella from the lateral parts of the root cap is not so pronounced. This might indicate the possibility of renewal of these parts by the cells of the external columella cell files, and of dermatocalyptrogen initials by columella initials (Plate V (2)). Analysis of the cross sections seems to suggest, however, unequivocally a developmental separatness of the columella during embryogenesis.

Longitudinal sections of the embryo show an unquestionable separatness of the particular initial cell tiers and their genetic continuity with the corresponding histogens. What is more, analysis of the cell pattern allows the reconstruction in many cases of the course of growth of these histogens, owing to the possibility of recognition of the cell complexes, that is cell groups of common origin or cell families. The growth of the root apical meristem during embryogenesis occurs, by way of growth and division of initials and their direct derivatives in the apical part and by way of growth and division of earlier formed segments situated in the basal part of the radicle.

Analysis of the cell pattern in the part adjacent to the promeristem may, therefore, elucidate the role of initials in meristem development and reveal a regularity in the sequence of divisions during the growth of segments of various histogens.

Plerome

The course of growth and differentiation of plerome during embryogenesis is difficult to reconstruct on the basis of cell arrangement in the mature embryo. Investigations on the course of embryogenesis in rape (Tykarska, 1976) demonstrated that, similarly as in other Cruciferae (Soueges, 1916; Lebègue, 1952), the initial cells of the

plerome and periblem of the hypocotyl and radicle separate in the first step of development of the globular embryo, that is soon after the formation of dermatogen, by periclinal division of the 4 internal cells of the first cell tier Soon afterwards the pericycle and internal plerome initials separate, and in turn the metaxylem initials separate from these in a later stage of embryogenesis. The initial plerome tier in the mature embryo consists of about 15-20 cells, five of which are usually visible on the central longitudinal section. The pericycle, owing to the early separating out of its initials, forms a layer of cells sharply cut off from the remaing plerome. The cell file of the central metaxylem vessel is separated out similarly in the apical part of the root primordium. The main part of the plerome lies between the pericycle and the central metaxylem cell file. It is initiated by its own initials and rapidly grows in width owing to periclinal centrifugal divisions. In the basal part of the radicle there already are about 15 cell files in the plerome on longitudinal sections and the plerome diameter is 1/3 of that of the root (Plates II and III).

The radicle plerome in rape has a diarchic structure. A plate of several files of incipient metaxylem cells runs across the root axis through its middle (Plate V-2). The number of these cell files on longitudinal sections varies in dependence on the position of the transection plane in relation to the symmetry plane of the plerome. Usually, the large cell file of an incipient central metaxylem vessel can be distinguished on longitudinal sections. It runs continuously from the initial to the upper parts of the hypocotyl.

There are no mature sieve tubes nor differentiated protoxylem vessels in the mature rape embryo.

Periblem

The common periblem mother cell of the hypocotyl and of the radicle becomes set off in embryogenesis simultaneously with the plerome mother cell by periclinal division. The first division of periblem primary cells is always anticlinal. Two successive anticlinal divisions of the periblem primary cells lead to the formation of 4 cells, the upper three constituting the hypocotyl periblem segments and the lower cell becoming the primary initial of the radicle cortex. The periblem initial cells usually divide anticlinally 4 times during embryogenesis, forming 4 segments of the radicle cortex. Each segment gives rise to a different cell family (T y k a r s k a, 1976). The first division in each segment is always periclinal. It leads to the separation of a cell initiating the outer cortex layer (subdermatogen) and a cell initiating the inner cortex. Owing to this, the outer periblem layer of the radicle is set off in each

segment at once in its whole length in its first division (Fig. 2). The inconsistent cell pattern in this layer indicates, therefore, the boundary of the segments. The directions and sequence of divisions in the inner cell may differ, they always, however, lead to the singling out in the subapical part of the meristem of 3 cell layers. The inner cortex layers are usually formed in each segment after one or two anticlinal divisions of their mother cell. The disagreement in the cell pattern in the inner periblem layers may then occur, not only on the boundary of the segments, but inside them. It is, therefore, difficult, on the basis of analysis of the cell pattern in the mature embryo, to reconstruct the whole course of periblem development. As basis in the description, the pattern of periblem layering shown in fig. 2 may be adopted. The periblem layering may, namely, be described as the result of

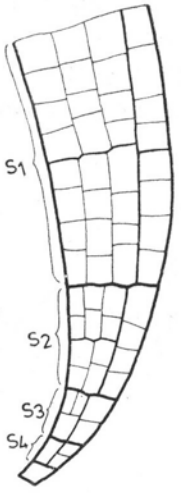


Fig. 2. Diagram of periblem development in radicle primordium I — initial cell, S_1—S_4 — succesive segments

separation of the successive cell layers, owing to splitting of the deepest cell layer by periclinal walls at an increasing distance from the apex. In mature embryos all the 4 layers are already separated at a distance of several (5-10) cells from the periblem initials. The first splitting, separating the external periblem layer comprises frequently the initial cells themselves.

Dermatogen and the lateral parts of the root cap

The radicle dermatogen is of common origin with the protoderm of the hypocotyl. Their common ancestral cells are the primary protoderm cells becoming set off in the first octant division in tier 1'.

After two successive anticlinal divisions of these cells their II order derivatives bordering on the hypophysis sometimes divide periclinally forming a dermatocalyptrogen initial and a mother cell of the external root cap layer. More frequently, however, the periclinal divisions of dermatogen mother cells occur only as late as after the third anticlinal division. Even then, however, the separation of the external root cap layer occurs usually on the same area as in the preceding case, since both the III order derivatives divide then periclinally. The position of the upper, that is basal, boundary of the first dermatogen sector is, therefore, relatively constant in the embryo axis. This position usually coincides with the boundary between the third hypocotyl periblem segment and the first segment of radicle periblem.

Mother cells of the deeper root cap layers are formed in embryogenesis by way of successive periclinal divisions of dermatocalyptrogen initials formed concurrently with the outer cap layer. This usually occurs immediately after the first anticlinal division of initial cells, that is after separation of dermatogen segments from them (Figs 3 and 4A).

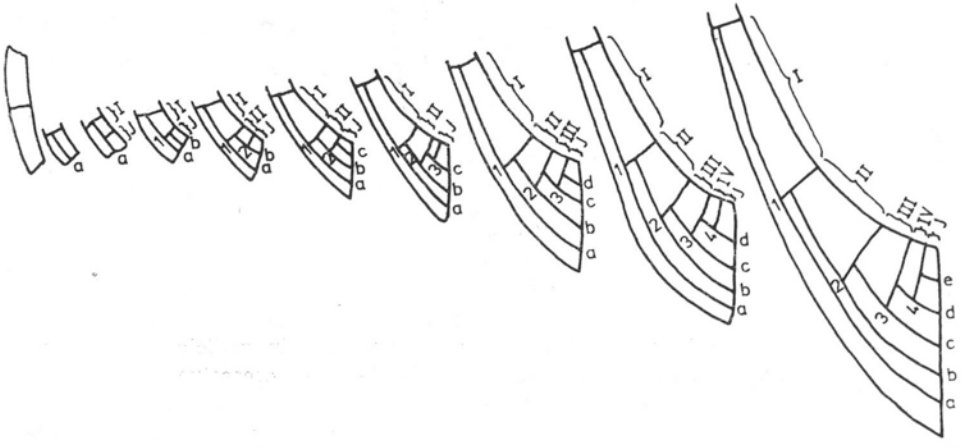


Fig. 3. Diagram of successive development of dermatogen segments (I—IV) in embryogenesis by anticlinal division (1 — 4) of the dermatocaliptrogen initial and development of root cap layers by successive periclinal divisions (a — e) of the dermatocaliptrogen initial

The cells of each root cap layer only divide anticlinally. The number of root cap layers lying under the outer layer indicates, therefore, the number of periclinal divisions of the dermatocalyptrogen initial and the equal number of dermatogen segments formed from the dermatocalyptrogen initial by anticlinal division preceding separation of the mother cells of the successive root layer.

In the mature rape embryo the lateral parts of the root cap have at

the boundary with the columella 5 cell layers and 6th dermatocalyptrogen initial layer.

It seems, therefore, that the dermatocalyptrogen initials have formed 4 dermatogen segments and 4 root cap layers by a regular sequence of anticlinal and periclinal divisions (Fig. 3, Plates III (2) and IV).

Such an interpretation of the root cap development was assumed at the beginning of the present investigations. It appeared, however, later that the boundaries of the last dermatogen sectors in the mature embryo do not usually strictly correspond to the primary boundaries of the dermatogen segments. During late embryogenesis there occur, namely, additional periclinal division of the distal dermatogen cells in the last segments, which shift their boundaries in basal direction.

In this way the initial range of the successive root cap layers is increased. Usually it is the range of the deepest root cap layers that

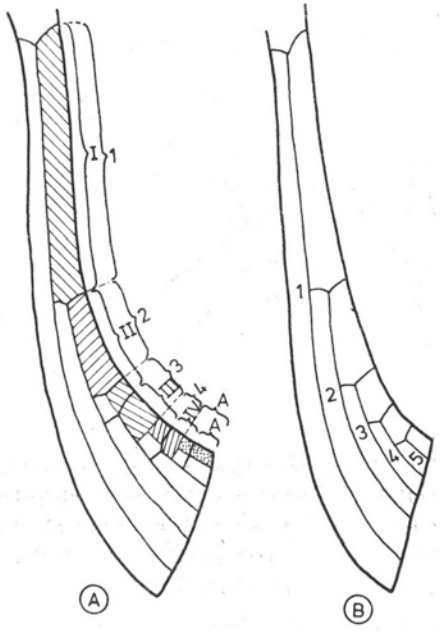


Fig. 4. A. Situation of dermatogen sectors (1 — 4) in mature embryo in relation to primary segments (I — IV). B. pattern of root cap layering

changes — of the 4th and 5th one — and least frequently of the 1st and 2nd layer. The boundaries of the corresponding dermatogen segments undergo of course parallel changes. Additional periclinal divisions in the dermatogen lead, therefore, to the formation of structural units different from the initial segments. These units have been termed sectors (Fig. 4A).

Under the outer root cap layer, in the mature embryo, there lie in diminishing distances from the columella 4 successive dermatogen sectors and 4 subsequent root cap layers corresponding to them, as well as the last sector which is the initial dermatocalyptrogen layer.

The upper boundaries of the successive dermatogen sectors do not, therefore, usually correspond to the boundaries of the initial dermatogen segments. They are, however, very similarly distributed on both sides of the radicle on the longitudinal sections and occupy an almost constant position in relation to the dermatogen and periblem segments.

This suggested the idea of utilizing these easily noticeable natural boundaries of dermatogen sectors as reference points in studies on the growth of the rape root apex during germination which is the main subject of the present work.

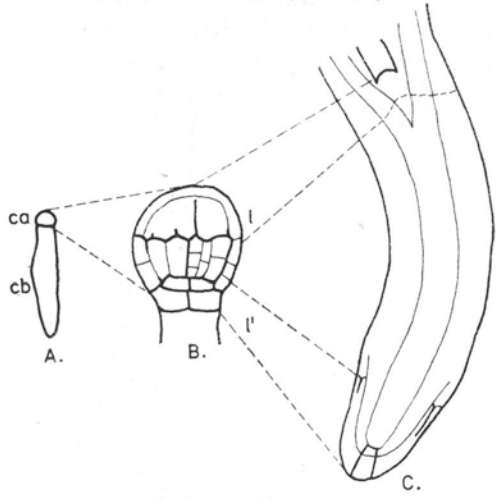


Fig. 5. Segmentation cell walls in bicellular proembryo (A) and globular embryo (B) preserved as natural developmental boundaries in mature embryo (C)

The occurrence of supplementary periclinal divisions makes difficult the recognition of the initial boundaries of the successive dermatogen segments. This does not, however, change the general pattern of layering of the lateral parts of the root cap (Fig. 4B), which may serve as basis for the description of the root cap in the mature embryo. The layering of the lateral root cap parts may, namely, be described as separation by periclinal cell walls of its successive layers from dermatogen at diminishing distances from the dermatocalyptrogen. The external root cap layer is of course the longest, each subsequent one is shorter. The same is true for the dermatogen sectors. Each of the 4 successive sectors

is usually shorter than the preceding one and consists of a smaller number of cells. The last, 5th sector is the dermatocalyptrogen sector.

Columella

The columella is of common origin with the central binding cells. Its mother cell is formed in embryogenesis the latest of all histogens by periclinal division of the hypophysis simultaneously with the mother cell of the central binding cells (Tykarska, 1976).

The growth of the incipient columella in width, that is in direction perpendicular to the embryo axis, is correlated symplastically with the growth of the intermediate tier of central binding cells. It is limited, and rapidly leads through several anticlinal divisions to a definitive stabilization of the initials forming the cell files of the columella.

The growth of the columella along the embryo axis is correlated with the growth of the lateral root cap parts. New layers of columella cells and lateral root cap layers arise as the result of partly synchronized periclinal division of their initials and their cells never undergo later periclinal divisions. This gives a uniform layered cell pattern in the columella and lateral parts of the root cap (Plates IV and V).

DISCUSSION

Anatomical investigations are usually limited to definite phases of the plant life cycle. Some of these studies are devoted to the structure of the mature embryo. Many descriptions of the mature embryo concern gymnosperms. Schleiden (1849) was the first to describe the pine embryo parts in the stage of ripe seed distinguishing: the root apex, the shoot apex and cotyledons. Some yeras later Strasburger (1872, 1887) gave a description of mature embryos and root and shoot apical meristems of numerous gymnosperms such as *Ephedra altissima, Picea vulgaris, Pinus pumila, Thuja occidentalis, Taxus baccata.* Descriptions of mature embryos of many coniferous species are known from the extensive comparative studies of Hill and De Fraine (1908). Hutchinson (1917) described the structure of the mature and germinating embryo of *Keteleeria fortunei.* Clare and Johnstone (1931) described the external appearance of embryos prepared out from ripe seeds of several pine species. The pine *(Pinus strobus)* embryo was examined by Spurr (1949) with particular reference to the organization of tissue systems in late embryogenesis. Recently Berlyn (1972) examined thoroughly the developmental anatomy of the pine *(Pinus lambertiana)* embryo and seedling and Stockey (1975) described the structure of the seed and embryo of *Araucaria mirabilis.* However, the descriptions of the structure of mature embryos of angiosperms are given in much less detail. Here may be quoted above all the studies of Reeve (1948) concerning late histogenesis and the structure of the mature embryo

of *Pisum sativum* and the studies of Miller and Wetmore (1945) on the embryogenesis and structure of the mature embryo of *Phlox Drummondii*. Noteworthy are also the results of Berlyn (1972) concerning the developmental anatomy of the embryo and seedling of maize.

In contrast to the relatively scarce and fragmentary descriptions of the structure of the mature embryo, early stages of embryo development are discussed in great detail in the botanical literature (Johanson, 1950; Schnarf, 1929; Souèges, 1916, 1919, 1939). It results from the data of Eams (1961) that up to 1961 the embryogenesis of about 1800 angiosperm species has been established, nevertheless there still remain wide discrepancies in the interpretation of the nature of some parts, terminological confusion and unprecise definitions. This is mainly due to the fact that, in contrast to the already well known early embryogenesis, studies devoted to the later stages of embryogeny, particularly as regards organization of the apical meristems are not numerous and unprecise. Investigations of early embryogenesis are but of little importance for histogenesis if they are not continued up to the end of embryo development. Developmental studies of seed plants should start from the beginning of embryogenesis and continue through the stage of mature embryo and seedling to the development of the mature plant. In the present literature, however, there is a striking lack of information as regards the late stages of embryogenesis, and particularly the histogenetic origin of the cotyledons, the development of shoot and root apices, and time and rate of development of these structures. Doubtlessly investigations on dormancy and germination should comprise full embryogenesis. In the present situation it is, therefore, necessary to gain wider information concerning the end stages of embryo development. Without this, a correct interpretation of the dormant embryo structure and the changes in it during germination is quite impossible.

The postulate of developmental investigation of plant structure, proclaimed more than a 100 years ago (Nägeli, 1859; Sachs, 1868; Hanstein, 1868, 1873) and repeatedly stressed by later botanists (Buchholtz, 1933; Esau, 1943; Miller and Wetmore, 1945, 1946; Allen, 1946, 1947; Reeve, 1948; Spurr, 1949, Eams, 1961; Hejnowicz, 1973) has not found full expression to this day in the results of investigations on early stages of plant development. Closest to the realization of this concept were Allen (1946, 1947) and Miller and Wetmore (1945, 1946), since their studies comprised the development of plants from early embryogenesis to the apical meristems of mature plants. Their data concerning histogenesis are, however, highly unprecise and fragmentary. Others, as for instance those of Reeve (1948)

and Spurr (1949) whose work is frequently quoted as an example of appropriate histogenetic investigation, are not acceptable as such because they do not include early embryogenesis and were carried out on plants *(Pisum sativum* and *Pinus strobus)* in which it is particularly difficult to follow the course of histogenesis on account of the transveral type of the root apical meristem. Therefore, it is preferable to perform such investigations on objects with regular embryogenesis and closed type of root apical meristem. It is rape that is such a suitable object. The accurately known (Tykarska, 1976) and very regular in its course embryogenesis allowed to establish precisely the sequence of segmentation divisions, in which segments become set off and can be distinguished in the successive stages of development of the embryo and in mature embryos. Owing to this, it is easy to establish in successive stages of embryonic development the boundary between the hypocotyl and radicle and between the hypocotyl and the incipient shoot and to ascertain that these boundaries coincide with the primary limits of segments in the proembryo. The course of these boundaries in three stages of embryo development is shown in Fig. 5.

The results of Tykarska concerning the course of embryogenesis in rape and the present author's studies on the course of radicle development in the last stages of embryogenesis also allowed a better knowledge of the root apical meristem structure. Its description was based in the first place on analysis of the cell pattern on longitudinal sections through the root apical meristem in the mature embryo. The organization of this meristem is very regular. It is an example of a closed type of meristem with a 3-tier promeristem. Separate permanent promeristem initials give rise to longitudinal sectors. Each of these consists of several transverse segments formed successively by the initial cell of the sector. Almost one half of the length of the whole longitudinal dermatogen sector is occupied by the oldest segment in which the last division cycle occurs during germination. The initials divide seldom, less frequently than their sister segments. The rarely dividing initials are however, the primary source of all the cells of the meristem. Owing to symplastic growth, there is an equal number of segmentation divisions of the periblem and dermatogen initials in the radicle, the number of segments in these histogens is also equal, and the boundaries between them coincide in most cases.

The successive dermatogen sectors are similarly distributed in radicles of the rape seeds and easily noticeable on longitudinal sections. Basing on this, professor H. Teleżyński suggested a new method — the analysis of homologous root sectors in investigations on the activation and growth of the root apical meristem during germination of rape seeds. The results of these studies as well as analysis of the apical

meristem structure in the radicle, based on a series of cross sections, will be the subject of forthcoming publications.

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Author's address:
Dr Mieczysław Kuraś
Institute of Botany, Warsaw University;
Al. Krakowskie Przedmieście 26/28; 00-927 Warszawa; Poland

Aktywacja zarodka podczas kiełkowania nasion rzepaku
I. Budowa zarodka i organizacja merystemu wierzchołkowego korzenia

Streszczenie

Na mikrotomowych skrawkach podłużnych przez oś dojrzałego zarodka rzepaku można rozpoznać naturalne granice rozwojowe między zawiązkiem pędu i hypokotylem oraz między hypokotylem a merystemem wierzchołkowym korzenia zarodkowego. Przebieg górnej granicy korzenia zarodkowego zaznaczający się na skrawkach podłużnych w nieciągłości słupów kory zbiega się z zasięgiem pierwszej warstwy czapeczki.

Merystem wierzchołkowy korzenia ma bardzo regularną organizację zapoczątkowaną przez trzypiętrowy promerystem (merystem zamknięty), dający początek trzem histogenom.

Piętro górne składa się z pierścienia inicjałów perycyklu otaczających inicjały wewnętrznego pleromu. W środku inicjałów pleromu jest jedna lub dwie komórki inicjalne centralnych naczyń metaksylemu. Piętro pośrednie utworzone jest z pierścienia inicjałów peryblemu otaczających centralne komórki wiążące. Centralne komórki wiążące uważane powszechnie za komórki inicjalne peryblemu, nie biorą udziału w rozwoju peryblemu korzenia zarodkowego i są odpowiednikiem centrum spoczynkowego. Piętro dolne składa się z pierścienia inicjałów dermatokaliptrogenu, otaczających inicjały kolumelli.

Wzrost merystemu wierzchołkowego korzenia w okresie embriogenezy polega na rozroście i rozczłonkowaniu przez kilkakrotne podziały kolejnych segmentów oddzielonych od komórek inicjalnych. Cały peryblem i dermatogen korzenia zarodkowego utworzony jest zwykle z czterech homologicznych segmentów oddzielonych od komórek inicjalnych. Granice zasięgu tych naturalnych segmentów zbieżne są z granicami zasięgu kolejnych warstw czapeczki. Łatwe do rozpoznania granice sektorów dermatogenu można wykorzystać jako stałe punkty odniesienia w badaniach nad przebiegiem wzrostu korzenia zarodkowego w czasie kiełkowania.