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Rape embryogenesis. II. Development of embryo proper

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Abstract

It was found in the continued studies on rape embryogenesis, started by the description of the proembryo (T y k a r s k a, 1976) that the development of embryo is extremely regular and based on differentiating divisions.

It appeared that the transverse segmentation boundary and cell walls separating the mother cells of the histogens in the proembryo can be distinguished in all the later stages of the embryo.

The border between the cytoledons and epicotyl part of the embryonal axis, and the hypocotyl corresponds to the segmentation boundary between layer *l* and layer *l'* at the octant stage.

As border between the hypocotyl and radicle was assumed the upper boundary of the root cap reaching usually to the level of the boundary between segments II and III of dermatogen and periblem.

The apical meristem of the shoot forms from dermatogen and the peri-axial cells of the globular embryo subepidermis.

The promeristem of the radicle constists of 3 layers of initial cells surrounding on all sides the inactive layer of central binding cells.

INTRODUCTION

The development of the rape proembryo has been described in detail in the preceding paper (T y k a r s k a, 1976). It was followed from the zygote to the young globular embryo containing the mother cells of all the root histogens: dermatogen, periblem, plerome, as well as mother cells of the columella and the central binding cells ("*iec*"). It was found that the direction and successive divisions of the first blastomeres of the proembryo are determined by the mode of growth and shape of the cells (vertical division of apical cells, horizontal division of quadrants, dermatogen formation, divisions in layer *l*, division of internal cells of *l'* differentiating plerome and periblem).

The present paper is a continuation of these investigations concerning the embryo body development from the globular stage to the end of embryogenesis.

This period of embryo development is but little known even in the so well described embryologically uniform family *Cruciferae* to which rape belongs. In the literature usually only a description of the particular stages, may be found (Kavetskaya, 1958 — *Brassica napus;* Ahuja and Bhaduri, 1956 — *B. campestris*; Joffe, 1957 — *Raphanus sativus*; Schaffner, 1906 — and Rijven, 1952 — *Capsella bursa-pastoris*).

In the present study the further development of the parts distinguished in the proembryo and the regularities in histogen formation were followed.

In each stage of embryo development measurements were performed of its length and breadth and of the length of both parts of the axis originating from layers *l* and *l'* of the proembryo, in order to establish the growth dynamics of the particular parts of the embryo proper.

MATERIAL AND METHODS

The material and fixation methods, preparation and staining are described in the previous paper (Tykarska, 1976).

Analysis of embryo development was performed on central longitudinal sections. The length was measured along the central axis and its breadth at the level of boundary *O'* between layers *l* and *l'*.

RESULTS

1. Globular stage

In this stage of development the embryo shows a distinct axial symmetry (Plate I photos 1, 2, and Figs 1—19).

At the beginning of this stage it is easy to distinguish in the embryo two layers, *l* and *l'*, formed as the result of division of quadrants to octants. In the upper layer *l* at least 4 cells are visible on the section under the dermatogen (Fig. 1), and in the lower layer periblem and plerome mother cells can be seen. The hypophysis is divided into two derivatives: a lenticular mother cell of the "*iec*" layer and a lower lying columella mother cell *co*.

Owing to the numerous divisions, the spherical embryo increases distinctly in size, but its lower layer *l'* grows faster than the upper one *l*. Therefore the developmental segmentation boundary *O'* dividing these layers moves upwards (Figs 1—19).

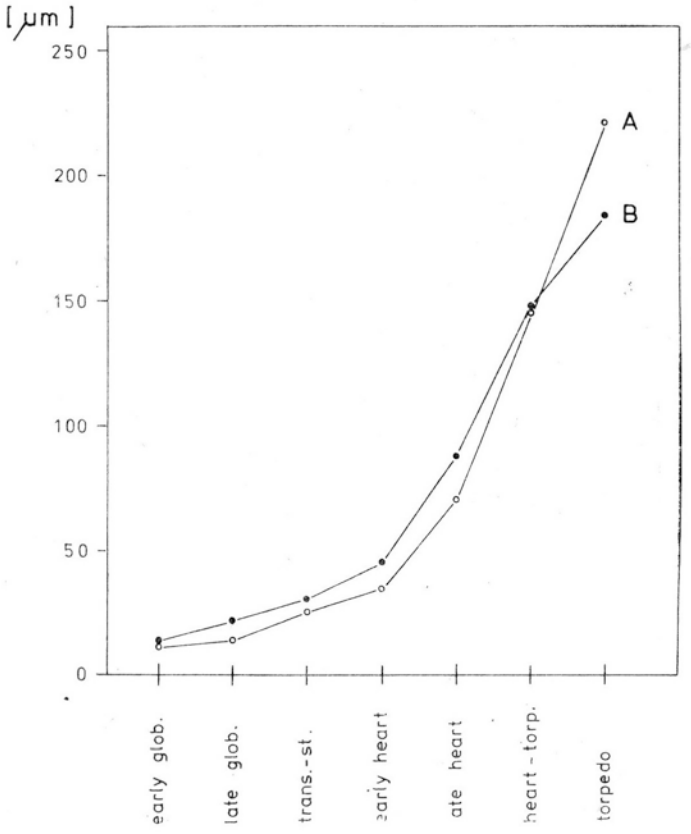


Diagram 1. Comparison of height of first periblem segment (A) and of the remaining part of the *l'* layer (B) in the successive stages of embyogenesis (measured at the epiderm) subepiderm boundary)

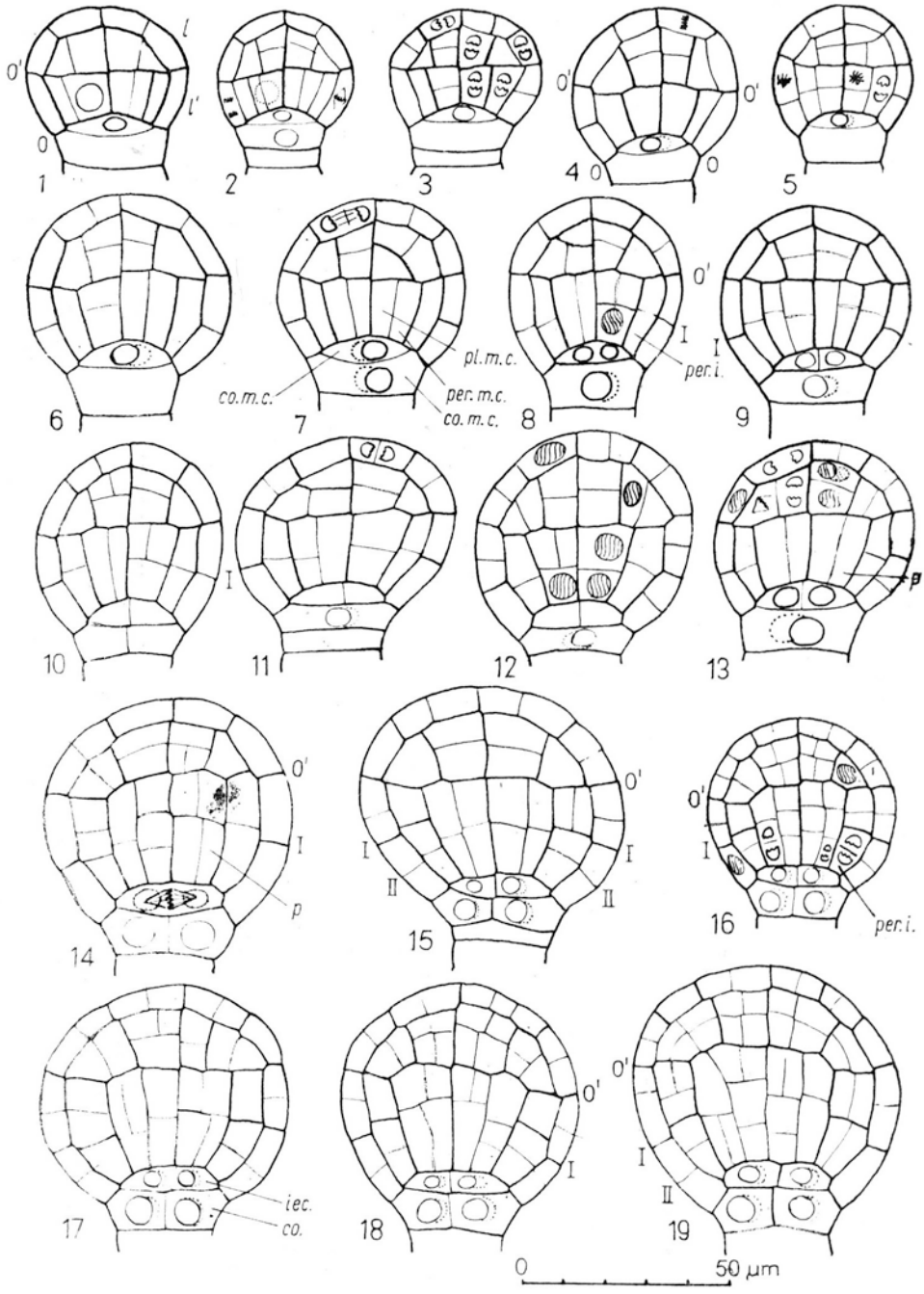
Two periods can be distinguished in the globular stage: an early and a late one. In the former cell divisions occur mostly in the lower layer. The plerome and periblem mother cells divide for the first time and the first vertical division of the hypophysis derivatives takes place (Plate I photo 1 and Figs 1—8).

In the second period there appear successive divisons of the inner cells of layer *l* and further divisions occur in the lower layer. At this time the second vertical division of the derivatives of the hypophysis takes place (Plate I photo 2 and Figs 8—19).

1.1. Young globular embryo

1.1.1. Upper embryo layer *l*

The upper embryo layer in the globular stage develops rather slowly. At first it is higher than the lower one. In time their heights become



Figs 1—19. Globular stage. Young globular embryos figs 1—9. Older globular embryos figs 10—19:

pl.m.c. — plerome mother cell, *per.m.c.* — periblem mother cell, *iec.m.c.* — *iec* layer mother cells, *co.m.c.* — columella mother cell, *per.i.* periblem initial, *p.* — pericycle, *iec.* — intermediate cell layer cells, *co* — columella, *O* — segmentation boundary separating part formed from apical cell of 2-cell proembryo from suspensor formed from basal cell, *l* and *l'* upper and lower layer of embryo formed as the result of division of quadrants to octants, *O'* — boundary separating layers *l* and *l'*, *I* — segmentation boundary in dermatogen and periblem, separating first generation of mother cells of these histogens, *II* — segmentation boundary separating second generation of dermatogen and periblem

equal and towards the end of the first period the lower layer is already taller (Table 2 No. 1—3).

In the upper embryo layer there arises under the dermatogen a system of 6 cells visible on the longitudinal section: 4 periaxial ones in two cell layers and 2 lateral ones (Plate I photo 1 and Figs 2—9).

Dermatogen consisting of 4 cells (Figs 1, 2, 4, 5, 9) begins to divide asynchronously into 8 cells (Figs 3, 4). Usually (61 cases of 70) the apical cells divide first (Plate I photo 1 and Figs 4, 6, 7), as if the extension growth began from the central axis of the embryo to the sides. This is confirmed by the next dermatogen division.

1.1.2. Lower embryo layer *l'*

P l e r o m e. Among the histogen mother cells in layer *l'*, the plerome mother cells are the first to divide.

Vertical divisions prevail. Thirty six vertical devisions and 10 transversal ones were observed, both directions are to be found in the same embryo (Figs 6, 8). These divisions are not always synchronised (Figs 1—3).

P e r i b l e m. The periblem mother cells usually divide only after division of the dermatogen mother cell (Fig. 5). Their division is always transversal, owing to the elongated cell shape (mean length 13.1 μm breadth 5 μm). As the result of this division the periblem initial (*per.i.*) and segment 1 of the periblem are formed. The wall dividing the two cells is the 1st segmentation boundary periblem (Figs 8, 9).

The first division of the periblem mother cells is a characteristic moment in the development of the embryo. It is, namely, connected with the change in the proportions of the height of both the embryo layers. Before division of the periblem mother cell the upper layer is higher than the lower one, in the course of division the two layers become equal, and after division the lower layer is taller (Table 2 No. 1—3).

D e r m a t o g e n. Divisions of the dermatogen mother cells (Figs 1—4), lead to the differentiation of the initials and 1st dermatogen segments. After the end of these divisions there appear segmentation boundaries denoted by the symbol *I*, running across the dermatogen and periblem (Figs 8, 9). The fragmoplasts in both mother cells are usually disposed more or less at the same level. Frequently, however, the shift of both walls is already considerable at this stage (Figs 5, 9, 12, 18, 19). In the periblem boundary *I* lies usually somewhat higher than in the dermatogen (Figs 5, 9, 11, 15, 16, 18, 19). Sometimes the reverse may occur (Figs 12, 13). In 28 young globular embryos, where we considered both halves of the embryo, this border ran more or less convergently 25 times, higher in the periblem 21 times anl lower 10 times.

The increased cell number in both histogens, and particularly the asynchrony of dermatogen cell divisions, makes it difficult to recognise boundary *I* in older stages. In mature embryos this boundary may be only distinguished in the periblem.

1.1.3. Hypophysis derivatives

After the first division of plerome mother cells (in some few cases before it — Fig. 4) both the hypophysis derivatives divide. Their division is always vertical (Figs 4—13). The division planes of these cells are independent and may be perpendicular to one another (Figs 9, 11, 13).

1.2. Older globular embryo

1.2.1. Upper embryo layer *l*

The subdermatogenic marginal cells divide anticlinally, joining by the division wall the dermatogen and the plerome (Figs 12—14, 17).

The periaxial cells divide in turn (sometimes earlier — Figs 10, 16) in both cell layers (Figs 13, 14). These divisions are always vertical. In this way two cell layers are formed in the upper embryo layer: one of subepidermal cells of almost cubic shape and a second one apposed to boundary *O'* of cells somewhat elongated in vertical direction (Figs 16, 18, 19).

The second division cycle in the dermatogen starts usually in the periaxial cells. The remaining cells of the apical part of the embryo follow them (Figs 7, 16—19). These divisions are not synchronised, thus, the number of cells formed varies. The increase in the number of these cells runs parallel with the increase in volume of the whole embryo, but the cells are smaller as compared with those of the preceding stage.

1.2.2. Lower embryo layer *l'*

P l e r o m e. The first division (vertical or horizontal) of plerome mother cells has taken place in the young globular embryo. The next runs perpendicular to the first one (Figs 9, 12). As the result of these divisions, initials of the pericycle — *p* and of the inner plerome differentiate (Figs 9, 13, 14, 15). In further embryo development the pericycle initials and their derivatives divide as a rule transversally (Figs 16, 18). Periclinal divisions of these calls are very rare (Figs 17, 19). They were noted in only 4 embryos from among the 98 analysed. In such cases the pericycle develops from the outer cells.

The periclinal division of one or two opposite initials of the inner plerome leads to the differentiation of one or two initial cells of the central metaxylem vessels. From this moment the layer of plerome initials is composed on the longitudinal section across the embryo of 5 or 6 cells.

The central metaxylem vessels initials *m* begin to differentiate already in the late globular embryo (Fig. 20). They may, however, still be absent event in the mature embryo. Four plerome initials in 17.1, five in 54.3 and six in 28,6 per cent were found in longitudinal sections through 35 mature embryos.

P e r i b l e m a n d d e r m a t o g e n. Periblem develops slower than plerome in the globular embryo. The primary periblem initial (*per.i.*), elongated in the course of growth of layer *l'* (1st generation of mother cell), divides transversally (Fig. 16). The dividing wall arises on the prolongation of the corresponding anticlinal wall in the dermatogen which in the meantime divides in layer *l'* into 4 cells on both sides of the embryo (Fig. 17, 18). Then a segmentation boundary *II* is formed (Figs 15—19). Sometimes, similarly as in the case of boundary *I*, shifts occur (Figs 18, 19). After this division, periblem initiation is taken over by its lower derivative which also divides horizontally. In most cases each further *per.i.* will take the same direction.

The above mentioned primary *per.i.* may exceptionally divide periclinally (Fig. 19). Among the 97 examined embryos only one cell underwent such a division, this leading to a premature differentiation of the initial cell of the outer periblem layer and the inner periblem initial usually occurring in the last phase of embryogenesis. In heart-shaped, torpedo--shaped and mature embryos 18.9, 38.7 and 45.7 per cent, respectively, of periblem initials are periclinally divided.

The first periblem segment, that is the upper cell formed after the division of the periblem mother cell, usually divides periclinally (69.4% of 72 cases). When divisions are anticlinal, boundary *II'* is formed (Figs 16, 17). Further dividing walls of both the sister cells formed are usually perpendicular to the earlier arising ones (Figs 19 and 21).

1.2.3. Hypophysis derivatives

The second vertical division of the hypophysis derivatives takes place after formation of the pericycle mother cells. The directions of division in these two layers are independent of one another as in the first division.

1.3. Recapitulation

In the globular embryo two phases may be distinguished: the first called "young globular embryo" in which all the histogen mother cells

divide in the lower layer of the embryo and the second, called "older globular embryo", in which the second generation of histogen mother cells is formed.

In the young, globular embryo the proportions of the heights of both embryo layers change. From the moment of the first anticlinal histogen mother cells division in the lower embryo layer, the latter is taller.

At the end stage of development of the globular embryo we find in the upper embryo layer:

— in the dermatogen — the third generation of the primary dermatogen cells,
— in the central part two cell layers,
— in the lateral parts at least two cells on each side;

The lower embryo layer has:

— in the plerome a differentiated pericycle with its own initials different from those of the inner plerome,
— in the periblem two generations of periblem mother cells forming two successive segments and initial cells,
— in the dermatogen — the second generation of the dermatogen mother cells,

The hypophysis is divided into two layers: "*iec*" and *co*, each consisting of 4 cells.

2. Transition stage

This is the period of embryo development in which axial symmetry changes to bilateral. In the course of this transformation the embryo continues to enlarge, growing above all in width. Its width increases by 28.8 and its length by 18.5 per cent. The lower layer still grows faster than the upper one. At the end stage it is twice the length of the upper layer (Figs 23—25, Plate I photo 3, Table 2).

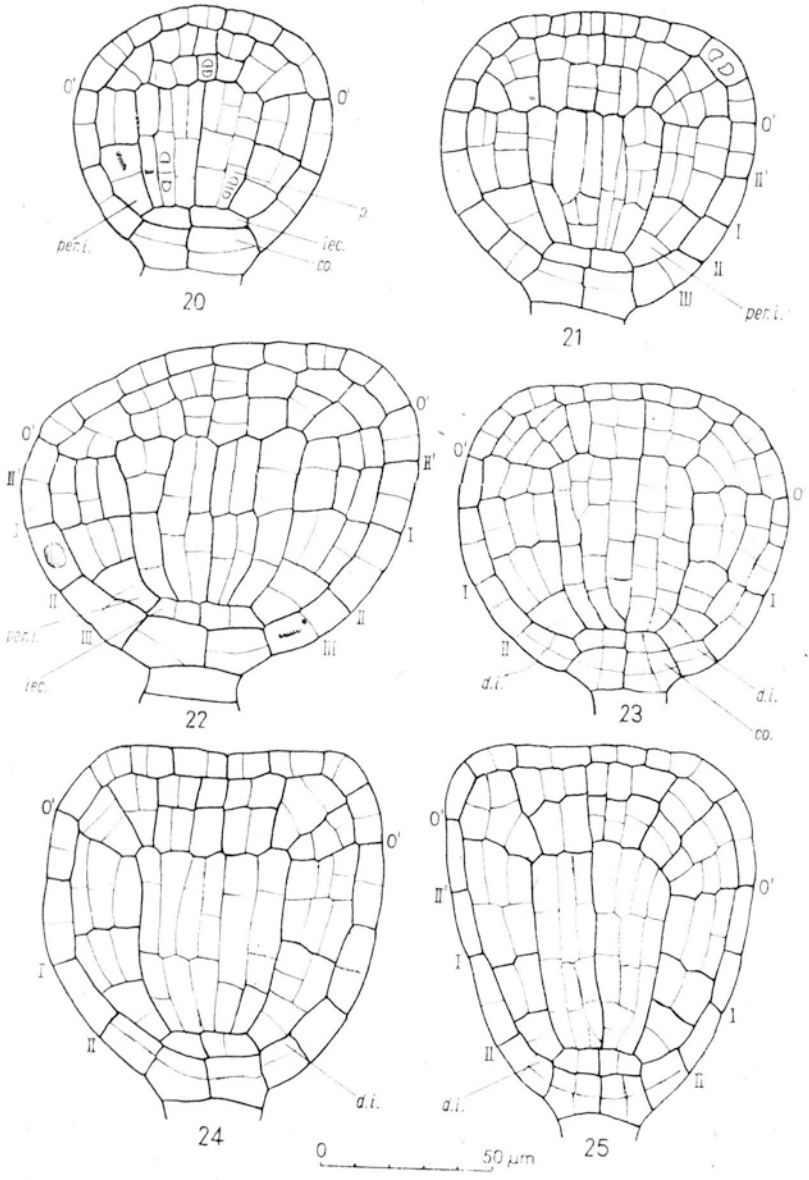
2.1. Upper embryo layer *l*

In the transition stage the upper layer of the embryo mainly extends in width. In the cells of the cotyledonary parts there appear divisions parallel to the surface and the cotyledons develop buttresses (Plate I photo 3 and Figs 19—25).

This is the moment of transition from axial to bilateral symmetry.

In the central part the cells of the layer joining the subepidermis with the hypocotyl, elongated parallelly, to the embryo axis, begin to divide anticlinally (Figs 20—22, 25, Plate I photo 3).

The divisions in the dermatogen shift from the embryo apex towards the cotyledonary parts which now begin to grow vigorously (Fig. 21).



Figs 20—25. Transition stage

m — initial of central mataxylem vessel (the middle cell of plerome, it is adhering to the *iec* layer) — at the figs 20, 22, 24, *di* — initial of dermatocalyptrogen, I, II, III — successive segmentation boundary in periblem and dermatogen. Other notations as in figs 1—19

2.2. Lower embryo layer *l'*

The lower layer extends regularly in width (by 28.8%) and in length (by 29.8%).

Plerome. The plerome increases in thickness owing to vertical periclinal division of the inner cells limited by the pericycle. All plerome cells undergo anticlinal division in the embryo. Owing to divisions of the initials adherent to the "*iec*" layer, new plerome segments arise.

Periblem. In the transition stage the periblem consists at first of two segments and a periblem initial, visible on both sides of the longitudinal sections.

Segment II (between boundaries *I* and *II*) adjacent to the *per.i.* consists at first of one cell. The latter always divides periclinally (Fig. 20), cutting off on the outside the subdermatogen mother cell, and on the inner side, the inner periblem mother cell. The subdermatogen mother cells divide in further development only anticlinally (Figs 22, 26—29). Divisions in the inner periblem mother cell may run in both directions (Figs 22—24), but most frequently they are periclinal. The development of further segments occurs in the same way. The situation is similar in the upper part of the periblem, that is in segment I, between *O'* and *I*. In this way the subepidermal layer is formed running along the whole periblem (Figs 21—23, 26—29, Plate I photos 3—5, Plate 2).

The number of periblem layers increases, owing to periclinal divisions of the cells adhering to the plerome. In the transition stage the upper part of the periblem is formed of 3 cell layers (Figs 21—25). The periblem (on longitudinal section of the embryo) has the form of a wedge ending by a tapering initial cell *(per.i.)* (Figs 20—25).

In the transition stage a 3rd periblem segment separates from the initial cells (Figs 22—25), which may arise even as early as the end phase of the globular embryo.

Dermatogen. In the older globular embryo a second dermatogen mother cell generation has arisen (4 cells on each side of the embryo) in the dermatogen of layer *l'*. A third successive division of dermatogen cells occurs in the transition stage. Before this division the columella mother cells elongate and divide periclinally, and the lower dermatogen cells adjacent at the time to the two-layer columella grow symplastically. This has a decisive influence on the direction of division in the dermatogen in the lower embryo layer. The 3 upper dermatogen cells always divide anticlinally, whereas the cell contacting the columella may divide anticlinally (Fig. 21), giving rise to the third segmentation boundary (*III*), or periclinally (Figs 23—25). In the material examined 43 anticlinal and 19 periclinal divisions were recorded. After anticlinal division the dermatogen cells adhering to the columella always divide periclinally (Fig. 22).

Periclinal division of the dermatogen cell adhering to the columella results in both cases in two cells. The outer one gives rise to the lateral cell layer of the cap, the prolongation of which is the outer cell layer

of the columella, and the inner one is the initial of dermatocalyptrogen (*d.i.*) (Figs 23—25).

The dermatocalyptrogen initials first divide anticlinally giving rise, to new dermatogen segments, and then periclinally, initiating a new lateral cell layer of the cap.

The outer cap layer reaches usually to segmentation boundary *II* of dermatogen, owing to supplementary periclinal divisions in the dermatogen in these cases, whereas primarily it reaches segmentation boundary *III*.

A detailed analysis of cap development in the rape radicle and of dermatocalyptrogen initials division is given by K u r a ś (1974).

2.3. Hypophysis derivatives

In the young transition embryo the columella mother cells divide periclinally giving rise to the columella initials and the outer columella cell layer. There are sporadic cases (1 per 100 cells) when the dividing wall joins the dermatogen to the suspensor (Figs 22 and 33).

In the same stage all cells originating from the hypophysis may divide vertically. Then in each layer 4 cells may be seen in the central longitudinal section (Figs 23, 25). These divisions usually start in layer "*iec*" (Figs 22, 24).

2.4. Recapitulation

In the transition stage the following changes occur:

in embryo layer *l:*

— change of embryo symmetry caused by development of cotyledon buttresses with marginal cell divisions parallel to the surface,

— periclinal divisions of periaxial cells in the second subepidermal layer;

in embryo layer *l'*:

— separation from initials of new periblem and dermatogen segments forming segmentation boundary *III*,

— periclinal divisions of primary columella mother cells and dermatogen cells adjacent to them, leading to the formation of columella initials and dermatocalyptrogen initials and of the first root cap cell layer.

3. Heart stage

The emerging cotyledon primordia rise gradually above the embryo axis (Figs 26—29). The remaining part of the embryo at first grows uniformly in all directions. Very soon, however, divisions along the axis and

perpendicular to it begin to predominate. The embryo now enters the phase of elongation (Plate II photo 1, Figs 28, 29), which will last to the end of embryonal development. Therefore, it is rather difficult to establish the boundary between the heart stage and the next one. It is assumed here that the heart stage will include embryos with not more than 3 cell layers in the columella (Fig, 29 and Plate II photo 1).

The differences in the size and shape of the heart-shaped embryo from the time of emergence of the cotyledons to the end phase of this stage are very wide. Therefore, for measurements the heart-shaped embryos were divided into 3 groups, according to the number of cell layers in the columella and the shape and length of the embryo. Thus, the following groups were distinguished:

(1) young heart-shaped embryos with two columella cell layers (Figs 26, 27),
(2) older heart-shaped (embryos with 3 columella cell layers and cotyledons shorter than one half of axis) (Fig. 28),
(3) heart-torpedo shaped embryos with longer cotyledons and a 3-layer columella (Fig. 29). The mean dimensions are given in Table 2.

During these transformations, that is from the transition to the heart--torpedo stage, the embryo axis length increases by 305.2 per cent, that is fourfold, and the width by 86.3 per cent. The increase in height of layer l' is more than 10 times that of layer l (437.2 and 40.9%).

3.1. Upper embryo layer l

In the central part of embryo layer l, under the dermatogen, a third layer of subepidermal cells appears which was started as the result of horizontal division of the cells, adherent to O' in the transition stage (Figs 25—29). The subepidermal cell layer in the cotyledons is the prolongation of the first subepidermal cell layer of the central part of layer l (Figs 26—29). The remaining two cell layers of the central part contact in the cotyledonary base the cell layer situated under the subepidermis (Figs 27—29).

3.2. Lower embryo layer l'

Elongation of the embryo in the heart stage occurs mainly owing to growth and anticlinal division in layer l'. The height of this layer increases from 58 μm in the youngest heart-shaped embryo to 274 μm in the heart-torpedo embryo, that is more than four times. The course of this growth can be best followed in the periblem by comparing the lengths of homologous segments.

P l e r o m e. Within the whole plerome, according to the direction of growth, there occur mainly anticlinal divisions (Figs 26, 28). The increase

of plerome in width is small. At the beginning of the heart stage the plerome width at the level of border *O′* is on the average 59.8 μm, and in older heart-shaped embryos 65.0 μm and consists jointly with the pericycle of 8—10 cells (in transition stage 6—7 cells).

Periblem in the young heart-shaped embryo is formed of 3 segments separated from the initial cells. These segments lie between boundaries *O′/I*, *I/II* and *II/III* (Figs 26, 27).

The development of the first segment bordering on the cotyledonary bases is much less regular than that of the subsequent segments in which the sequence and directions of divisions are very similar. In spite of these differences, in the first stage of the heart-shaped embryo the growth of all segments occurs similarly, owing to similar elongation (Table 1).

Table 1

Number of subdermatogen cells in the successive periblem segments and height of these segments in heart-shaped and torpedo-shaped embryos

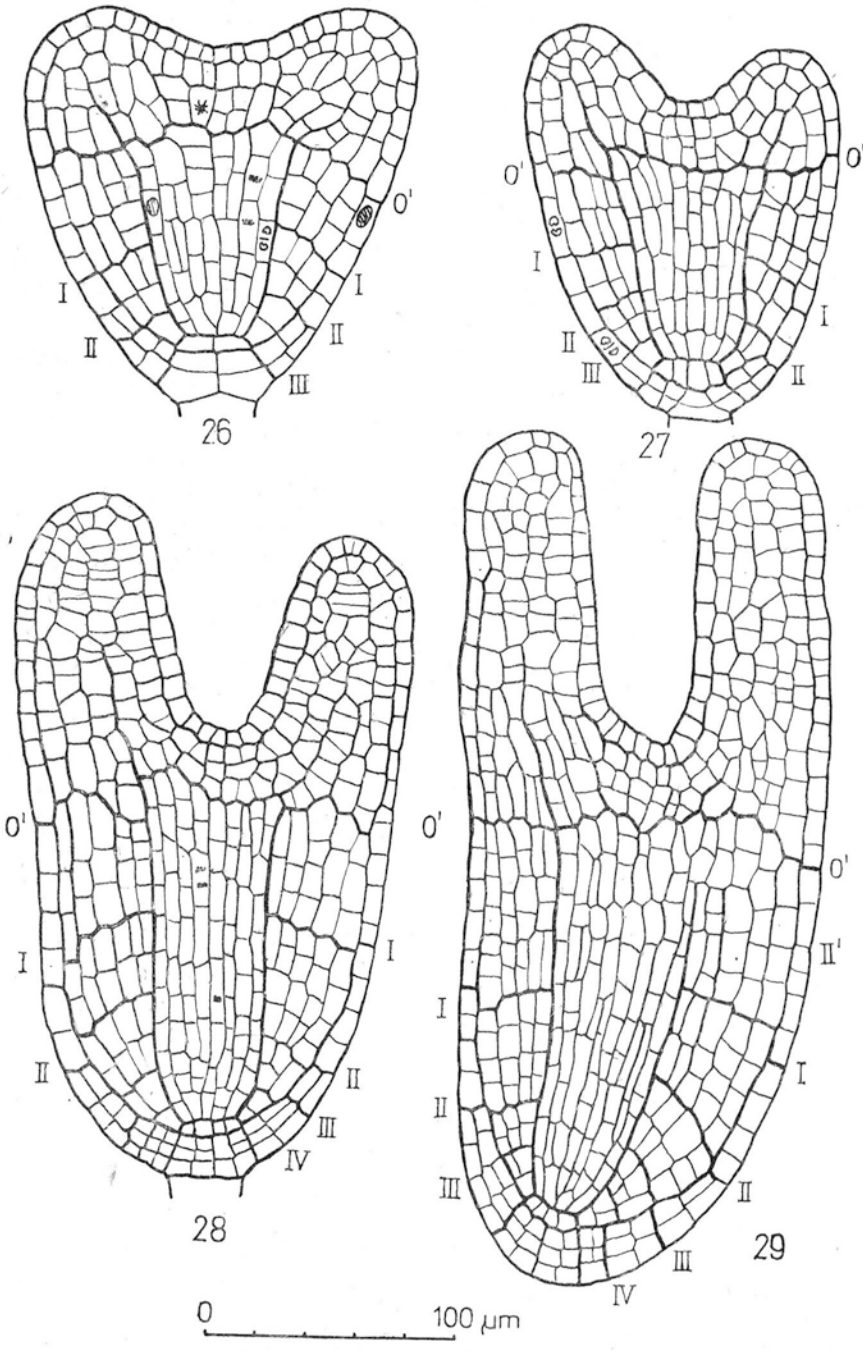
Part of embryo axis	Segment	Heart young	Heart older	Heart-torpedo	Torpedo	Grown up
Hypocotyl	1 (0′—I)	2—3 cells 34 μm	5—7 cells 70 μm	6—8 cells 138 μm	8—16 c. 221,7 μm	70—80 c.
	2 (I—II)	2 cells 20.3 μm	2—4 cells 41 μm	3—4 c. 65 μm	4—8 c.	ca 32 c.
Root	3 (II—III)	1 cells 13,1 μm	2—3 cells 30 μm	2—4 c. 39 μm	3—5 c.	15—33 c.
	4 (III—IV)	— —	1 cells segment	1—2 c.	2—4 c.	8—18 c.
	5 (IV—V)	— —	— —	0 or 1 c.	1—2 c.	4—9 c.
	6 (V—VI)	— —	— —	— —	0 or 1 c. segment	2—5 c.
	7 (VI—VII)	—	—	—	—	0 or 1—2 c.

In the second stage growth is fastest in the first segment (relative increment 97%) and weakest in the third one.

In the heart stage there occur, thus, changes in the growth rate of the same segments and in the distribution of growth along the embryo axis. They seem to be correlated with cell division.

In the older heart-shaped embryo a 4th periblem segment forms, and in the heart-torpedo-shape one the 5th segment begins to separate.

The increase in the number of periblem layers occurs by way of periclinal division of the cells of the layer adjacent to the plerome.



Figs 26—29. Heart stage

O' — boundary seperating layers *l* and *l'*, I—IV — successive segmentation boundary in periblem and dermatogen.

A 5th cell layer (Figs 28, 29) arises in older heart-shaped embryos in the upper part of the periblem. The number of periblem cell layers diminishes acropetally. As a rule the successive periblem segment has one cell layer less than the preceding one (Fig. 29). This is also true for late stages. Sometimes neighbouring segments differ not by one but by two layers (Fig. 28 — left side of embryo). This occurs mainly in segments lying closer to the radicle tip. The two highest segments separated by boundary *I* generally have the same number of cell layers (Figs 28, 29 — right side of embryo, and Figs 35, 37). This makes it difficult to detect this boundary in later stages.

3.3. Hypophysis and dermatogen derivatives

The last vertical division of hypophysis derivatives occurs in the heart stage. It leads to the formation of a 4 cell file columella. This division may occur earlier, in the transition stage (Fig. 25).

Soon after the division of the periblem initials, differentiating segment 4, the columella initial *(co)* and dermatocalyptrogen initial *(d.i.)* give rise to the second root cap cell layer by dividing periclinally. The new root cap cell layer reaches to the lower third segmentation boundary (Figs 28, 29). Further layers of the root cap form similarly, each one shorter than the previous one (Figs 33, 34).

3.4. Recapitulation

Characteristic for the heart stage are:

— the ending of uniform growth in all directions and prevalence of growth along the embryo axis,
— rapid growth of the cotyledons,
— more than 4-fold elongation of embryo layer *l'* with minimal growth of embryo layer *l*,
— formation of a 3rd cell layer from subdermatogen derivatives in the central part of embryo layer *l*,
— the arising of a 4th and sometimes 5th periblem segment in embryo layer *l'*,
— separation of the 2nd root cap cell layer from the layer of dermatocalyptrogen and columella initials (3-layer root cap).

4. Torpedo stage

The typical torpedo-shaped embryo has a straight axis and rather short spatular cotyledons. This stage is characterised by elongation growth of the whole embryo (Plate II, Photo 2).

In the end phase of this stage the cotyledons begin to curve, growing into the bent part of the embryo sac. As anatomical feature distinguishing the torpedo stage was assumed a 4-layer columella.

4.1. Upper embryo layer *l*

The growth of cotyledons and their arrangement in the embryo have been earlier described in *Capsella bursa-pastoris* by R i j v e n (1952) and in *Brassica napus* by K a v e t s k a y a (1958). Therefore, the changes in their shape will only be noted here in the characteristic of the particular stages.

In the torpedo-shaped embryo the beginning of differentiation of the shoot apical meristem is observed.

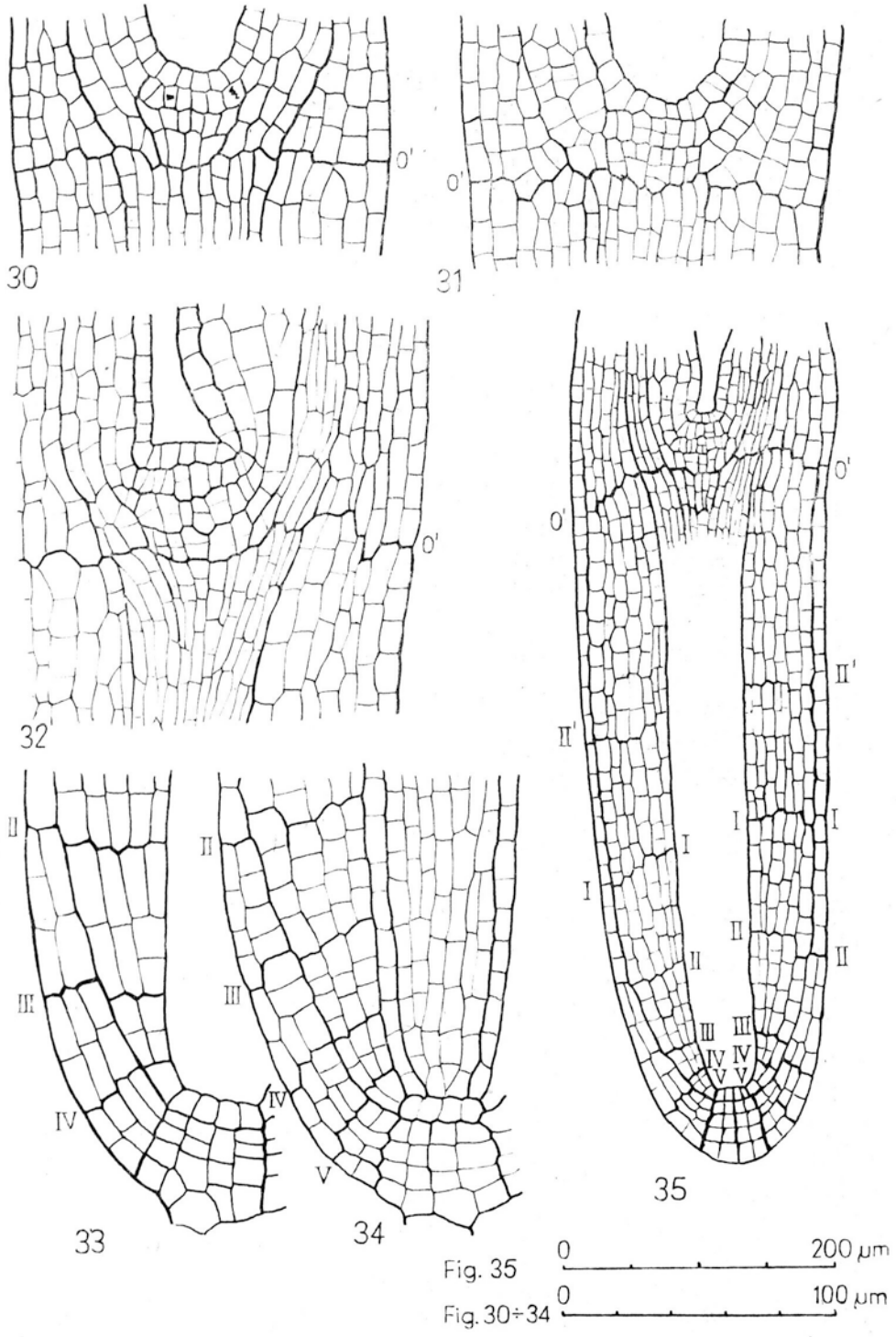
Three subepidermal cell layers formed in the heart stage, the central part of layer *l*. The cells undergo periclinal division in the torpedo stage. In this stage they divide periclinally. The cells of the 1st subepidermal layer divide first (Fig. 30). In turn, divisions occur in the elongated cells of the 3rd layer adjacent to the hypocotyl (Fig. 31). In the end phase of the torpedo stage the central cell layer als divides. In the fully grown torpedo-shaped embryo the central part of upper layer *l* lying under the protoderm will consist, therefore, of 6 cell layers (Fig. 32).

4.2. Lower embryo layer *l'*

In the young torpedo-shaped embryo the procambium bundles spreading to the cotyledons are already differentiated. Between these procambium bundles a group of poorly-staining vacuolised cells can be distinguished. It is formed of 4—6 short files, each of 2—3 cells (Plate III photo 1).

The growth of the embryo axis is nonuniform. At present the upper part of the hypocotyl (segment I, and particularly its upper part between boundaries *II* and *O'*, Fig. 35) grows fastest, whereas in heart-shaped embryos the lower part of the embryo axis grows most rapidly (Diagram 1, page 393).

P e r i b l e m and p l e r o m e. In the young torpedo-shaped embryo the periblem initial cells *(per.i.)* divide forming the new 5th periblem segment (5th generation of periblem mother cell). These divisions may sometimes occur earlier at the end of the heart stage (Fig. 29). Anticlinal division in the basal periblem segments doubles the number of cells formed in the heart-shaped embryo (Figs 28 and 35). In older torpedo-shaped embryos the number of cells in the apical part of the radicle also doubles (Table 1).



Figs 26—29. Heart stage
figs 30—32 — fragments of embryos with shoot apex, figs 33,34 — fragments of radicle tips. The notations as in figs 26—29.

During rapid elongation of the torpedo-shaped embryo the number of periblem and plerome cell layers increases only slightly. In the upper part of the hypocotyl it increases by one (to 6 layers) and in the plerome usually by 4 layers (to 12—14 layers).

Root cap. In young torpedo-shaped embryos a new root cap layer arises (Figs 33, 34), started by periclinal division of columella initials.

4.3. Recapitulation

- In the periaxial part of the upper embryo layer the number of subepidermal cell layers increases to six by periclinal divisions in the 3 cell layers formed in the heart stage.
- Elongation of the embryo axis in the torpedo stage is above all the consequence of hypocotyl and radicle growth which originates from the lower proembryo layer.
- The twofold elongation of the hypocotyl and radicle is associated with a doubling of the cell number, observed in the periblem cell files in all segments.
- In the upper part of the hypocotyl two bundles of procambium spreading to the cotyledons and a group of ground meristem cells between them can be distinguished.
- In the periblem a new 5th segment is formed.
- In the columella and lateral parts of the cap a 4th cell layer arises.

5. Growing up embryo and end of embryogenesis

The last step of embryogenesis comprises the final formation of the embryo, that is the final formation of the cotyledons and the end of embryonal axis development.

In mature seed the embryo axis is archwise bent, and the bilobed fleshy cotyledons encompass it tightly on 3 sides, giving the seed a spherical shape.

The development of cotyledons is correlated with that of the embryo axis. In the torpedo stage the cotyledons have at first the shape of flat spatules. In older embryos of this stage they split and begin to bend archwise along the axis.

In growing up embryos the bent cotyledonary blades grow rapidly. The embryo axis grows also rapidly and curves.

The last cell divisions occur in the embryo axis when the cotyledons loosely surround the embryo axis, and the whole embryo is already spherical. This end stage is called "the end of embryogenesis".

In the growing up embryo it is mainly the derivatives of the octants lower embryo layer l' that elongate. From the moment of formation of

two octant layers to the end of embryogenesis the upper layer elongates about 11 times, while the lower layer 290 times. The growth of the embryo axis is illustrated in table 2.

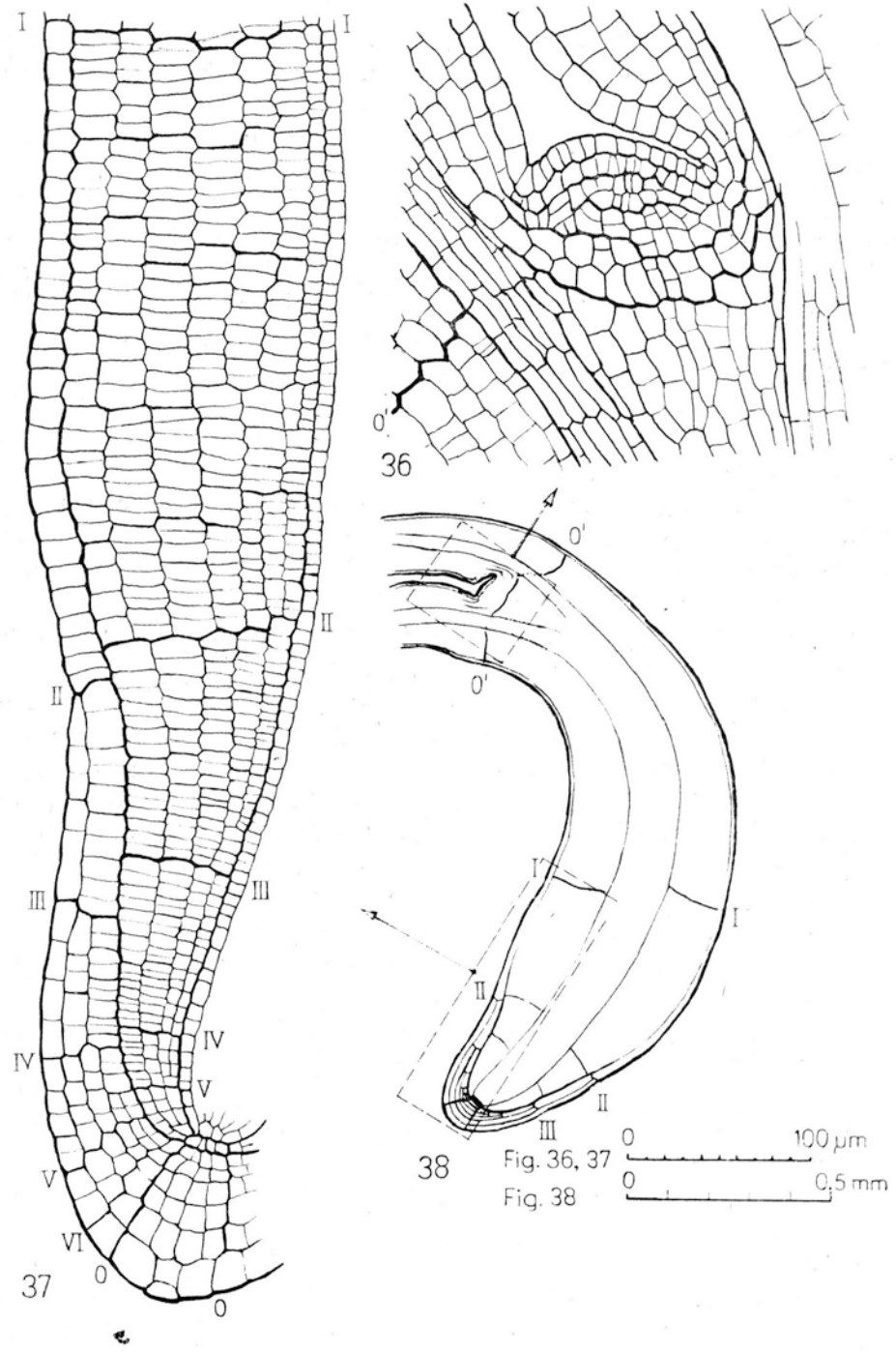
The last mitotic divisions occur in the intensively green embryo very easy to prepare out from the equally green ovule. The full grown embryo just after the end of embryogenesis exhibits cotyledons still standing away somewhat from the embryo axis. These growing up embryos and those in the stage of last mitotic divisions are classified to a common measurement group (Table 2 No. 11). To the next group belong the already maturing green embryos more difficult to prepare out and closely adhering to the seed coat.

5.1. Upper embryo layer *l*

In the growing up embryo a shoot primordium is formed finally. Between the cotyledons a group of strongly staining meristematic cells can be distinguished which form a bulge protruding outside (Plate II photo 3 and Plate III photo 3).

At the end of embryogenesis the shoot apical meristem builds the primordium of the first leaf (Plate III photo 4).

The shoot apical meristem is formed from dermatogen and the subepidermal cells of the globular embryo. In the torpedo stage the primary subepidermal cell layer divides horizontally into two. During further development only anticlinal divisions occur in the new subepidermis, leading to an extension of the meristem. The subepidermis divides when a leaf primordium is formed. On the other hand, its sister layer, by periclinal division of the periaxial cells and their derivatives, causes a protrusion of the apex (Fig. 36, Plate III photo 3). There is no sharp border between the meristem proper and the surrounding cells. The transition consists of cells which absorb the dye less intensively (Plate III photo 3 and Fig. 36). These cells originate from the middle layer which in the torpedo-shaped embryo are separated into two (this layer arose in the heart-shaped embryo from cells adjacent to the hypocotyl). In further development some of these cells in both layers may divide horizontally (Fig. 36). Both these layers join the meristem proper of the shoot apex with the cells adhering to the boundary of the hypocotyl. The latter also divide into two layers in the torpedo-shaped embryo (Fig. 32). In the mature embryo, therefore, there are 2 to 4 layers between boundary *O'* and the shoot apical meristem. These cells are highly vacuolated, they stain poorly, are rather large, frequently characteristically flattened and widened at the base. Boundary *O'* between embryo layers *l* and *l'* is slightly sunken into the hypocotyl (Fig. 36) and it is rather easy to find it in this part of the embryo. In the lateral part this boundary runs more or less at the same level, but it is more difficult to identify.



Figs 36—38. Mature embryo

O — segmentation boundary separating part formed from apical cell of 2-cell proembryo from suspensor formed from basal cell, *O'* — boundary separating layers *I* and *I'*, I-VI — successive segmentation boundary in periblem and dermatogen.

5.2. Upper embryo layer *l'*

The derivatives of layer *l'* form the greater part of the embryo axis. In the growing up embryo this part of the axis elongates considerably and widens. In the last stage of embryogenesis the axis is 4 times longer and almost 3 times wider than in the torpedo stage. In the growing up embryo another periblem cell layer appears in the hypocotyl so that now there are 7 periblem cell layers. The plerome has widened by about 6 files of cells and on the longitudinal section it has 18 to 20 files.

The more than fourfold elongation of layer *l'* in the end period of embryogenesis, as compared with the torpedo-shaped embryo, is associated with twofold anticlinal periblem cells divisions. This is indicated by the change in the cell number in the particular segments of the hypocotyl and radicle (Table 1). Particularly instructive are the outer files of cells (Fig. 37). The periblem initials (*per.i.*) divide in this period once or sometimes twice, forming the 6th and sometimes 7th segment (6th and 7th generation of periblem mother cell).

The number of cells also increases fourfold in the ground meristem cell files between the procambium bundles running to the cotyledons. These cells are much larger than the neighbouring ones — derivatives of the upper embryo layer (Plate III photos 3, 4), this being an additional indication for discovering the upper boundary of the hypocotyl *O'*.

Distinction of the segmentation boundary in the periblem of mature embryos is rather difficult. The discontinuity of the cell files, when present, makes it easier.

The easiest to identify is segmentation boundary *II* between periblem segments 2 and 3, owing to:

(1) the different number of periblem cell layers in the two segments (in 2nd segment there are 6 or 7, and in 3rd — five);
(2) the sharply delineated discontinuity of the files;
(3) the neighbourhood of the first root cap cells which reaches usually to the analogous segmentation boundary *II* in the dermatogen;
(4) tapering of the embryo root axis which starts at the root cap border.

In the mature embryo the root cap consists of 6 cell layers (Plate III photo 2), the variety 'Górczańska' may sometimes have seven.

5.3. Recapitulation

In the end step of embryogenesis a further growth and histological differentiation occur and the cotyledons and embryo axis take their definitive shape.

1. In the axis of the full grown embryo the epicotyl, hypocotyl and radicle parts can be distinguished.

The boundary between the cotyledons and the epicotyl part of the axis, and the hypocotyl corresponds to the segmentation boundary between layer *l* and layer *l'* at the octant stage.

As boundary between the hypocotyl and radicle was assumed after K u r a ś (1974, 1978) the upper limit of the cap reaching usually to the level of the boundary between segments II and III of the dermatogen and periblem.

2. The mature rape embryo contains the apical shoot meristem with the primordium of the first leaf. The apical shoot meristem is formed in the end stage of embryogenesis by periclinal division of the subepidermal cell layer of the torpedo-shaped embryo into two cell layers and it is not yet definitively shaped (there is no zonal cytohistological differentiation).

3. The root apical meristem is closed and has 3 initial layers. The plerome initial layer consists of pericycle initials, inner plerome initials and one or two initial cells of metaxylem central vessels.

The intermediate layer is formed of a ring of periblem initials surrounding the central binding cells.

The lower layer consists in its central part of columella initials surrounded by a ring of dermatocalyptrogen initials.

4. The radicle of the mature rape embryo is formed of promeristem and meristem segments separated from the initial cells. It was found that dermatogen, the lateral parts of the cap and columella and the radicle periblem consist in the mature embryo usually of 4 and sometimes 5 segments.

5. The root cap of the mature rape embryo consists usually of 6 cell layers, but in the winter 'Górczańska' variety, the columella sometimes has already 7 layers.

6. In the hypocotyl which elongates fourfold in the last stage of embryogenesis, the periblem cells divide twice perpendicularly to the axis similarly as they do in the radicle and they grow in width, particularly in the outer layers. The number of cells in the dermatogen and plerome increases similarly.

The number of periblem layers increases owing to periclinal division of the inner layer cells.

7. The vascular tissue of the mature embryo is formed in the radicle and hypocotyl from the precambial cylinder which bifurcates just under the upper border of the hypocotyl into two strands entering the cotyledons.

In the shoot primordium there is as yet no provascular tissue.

8. The segmentation boundaries are difficult to distinguish in the mature embryo. Easiest to identify is boundary *II* between the 2nd and 3rd dermatogen segments to which the root cap reaches, and the cor-

Table 2

Dimensions of embryo in the course of embryogenesis (mean values and standard deviations in μm)

No.	Stage		Height of embryo layers measured along central axis			Width of embryo axis at level of O' boundary	No. of measured embryos
			$l+l'$	l	l'		
1.	Globular with histogen mother cells		27±3	16,1±1,9	10,9±1,9	36,3±5,6	17
2.	Young globular during division of periblem MC.		34±4	18,3±2,3	16,1±2,2	47±6	18
3.	Globular early after division of periblem MC.		41±4,5	18,8±2,3	22±3,1	52,5±5,7	11
4.	Globular late		55,9±8,3	23,6±2,6	32,1±6,3	65,6±6,3	27
5.	Transition		77,5±9	26,6±3,4	50,9±8,7	87,3±12	34
6.	Heart early		93,5±12,4	27,2±3,4	66,2±10,8	118,0±14,1	29
7.	Heart late		166,9±30,4	30,4±4,5	136,5±28,0	146,3±16,2	23
8.	Heart-torpedo		311±35	37,5±1,6	274±36	162±13	6
9.	Torpedo		468±102	44,3±3,6	423±99	187±22	12
10.	Growing up		839±80	47,6±4,2	791±79	222±17	8
11.	End of embryogenesis		1190±60	101±11	1888±60	500±65	12
12.	maturing embryos from seeds	green	2200±160	117±13	2082±150	635±45	13
13.		yellowish-green	2200±120	123±13	2078±120	650±40	12
14.		brownish-green	2260±210	123±13	2140±210	660±30	15
15.		brown	2220±160	122±15	2100±150	660±5	10
16.		black	2330±210	120±8	2210±20	720±40	9

responding boundary in the periblem, because a striking discontinuity in the cell files often occurs.

9. The axis of the mature embryo is about 2300 μm long. The derivatives of the proembryo upper layer 1 form as little as 1/20 part and the radicle about 1/5. The rest is occupied by the hypocotyl.

6. Embryo maturation

After the end of embryogenesis the embryo enters the period of maturation. For some time still it remains green. At this time some slight further growth of the whole embryo is observed (Table 2). Its axis and cotyledons become massive, filling the gaps left by the digested endosperm remains, until finally the seed coat adheres to the embryo tightly. At this time the so far intensively green seed coat begins to become paler and its colour gradually changes to brown. This colour darknes with advancing maturation. Rape seeds are black. Simultaneously the embryo changes its green colour to whitish and later yellowish-golden.

During the maturation period storage material is intensively accumulated in the embryo. The starch appearing during embryogenesis disappears, the amount of lipids increases in the cytoplasm of the embryo cells and the vacuoles fill with protein.

Accumulation of storage material is associated with active growth of the embryo cells. This is indicated by the results of measurements of mean cell length in layers I and IV of the hypocotyl cortex, performed on 4 embryos after the end of embryogenesis, 11 mature embryos from green seeds and 9 embryos from brown ones.

Immediately after the end of embryogenesis the cells of the second segment of the embryo axis grow most intensively in the still green seeds, particularly at the site of greatest expansion of the axis in the lower part of the hypocotyl. In this segment the relative increase in cell length on the convex side of the axis is on the average in the subepidermis 13.1, in cortex layer IV 18.4 and on the concave side 5.9 and 24.6 per cent, respectively.

In the seeds turning brown the hypocotyl part now extends on its convex side (increase by 11.8% of subepidermal cells). This leads to a further curving of the embryo axis and a slight reduction of the mean cell length in the cortex on the concave side.

7. Suspensor

The suspensor mother cell in rape *cb*, at the moment when it arises, is elongated with a small cell *ca* at its tip, from which the embryo

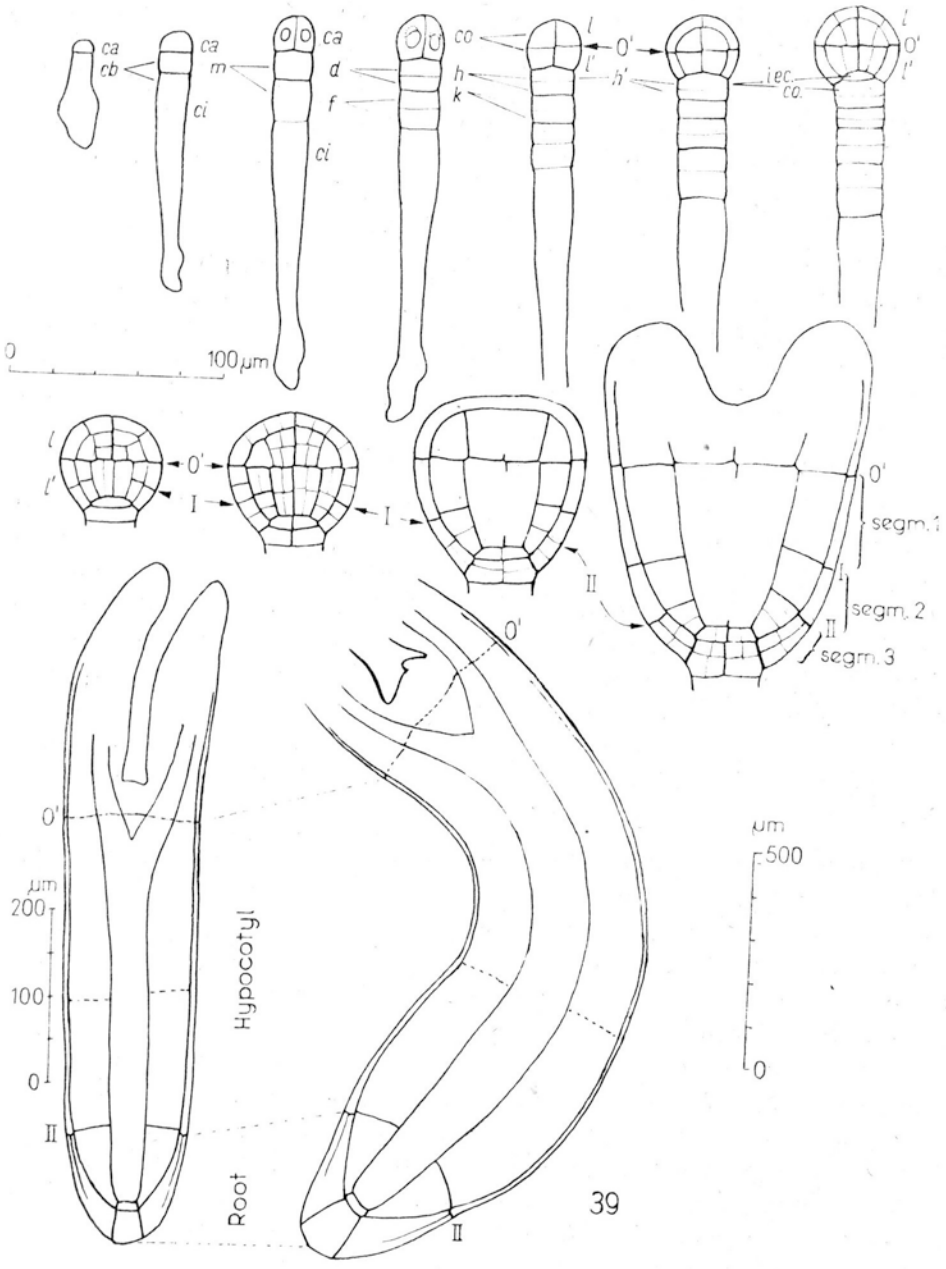


Diagram 2. Diagram of rape embryo development

ca — apical cell, *cb* — basal cell, *m*, *ci*, *d*, *f*, *h*, *k* — suspensor cells formed owing to division of basal cell, *h'* — hypophysis mother cell. Segments 1, 2, 3 — successive periblem segments. Remaining notations as in preceding figures

proper will develop. The widened base of the suspensor (Fig. 39) grows into the micropylar part of the ovary. At the beginning of embryogenesis the suspensor develops faster than the body of the proembryo. By frequent divisions it rapidly elongates carrying deep into the nuclear endosperm the apical cell (*ca*) which transforms to the proembryo.

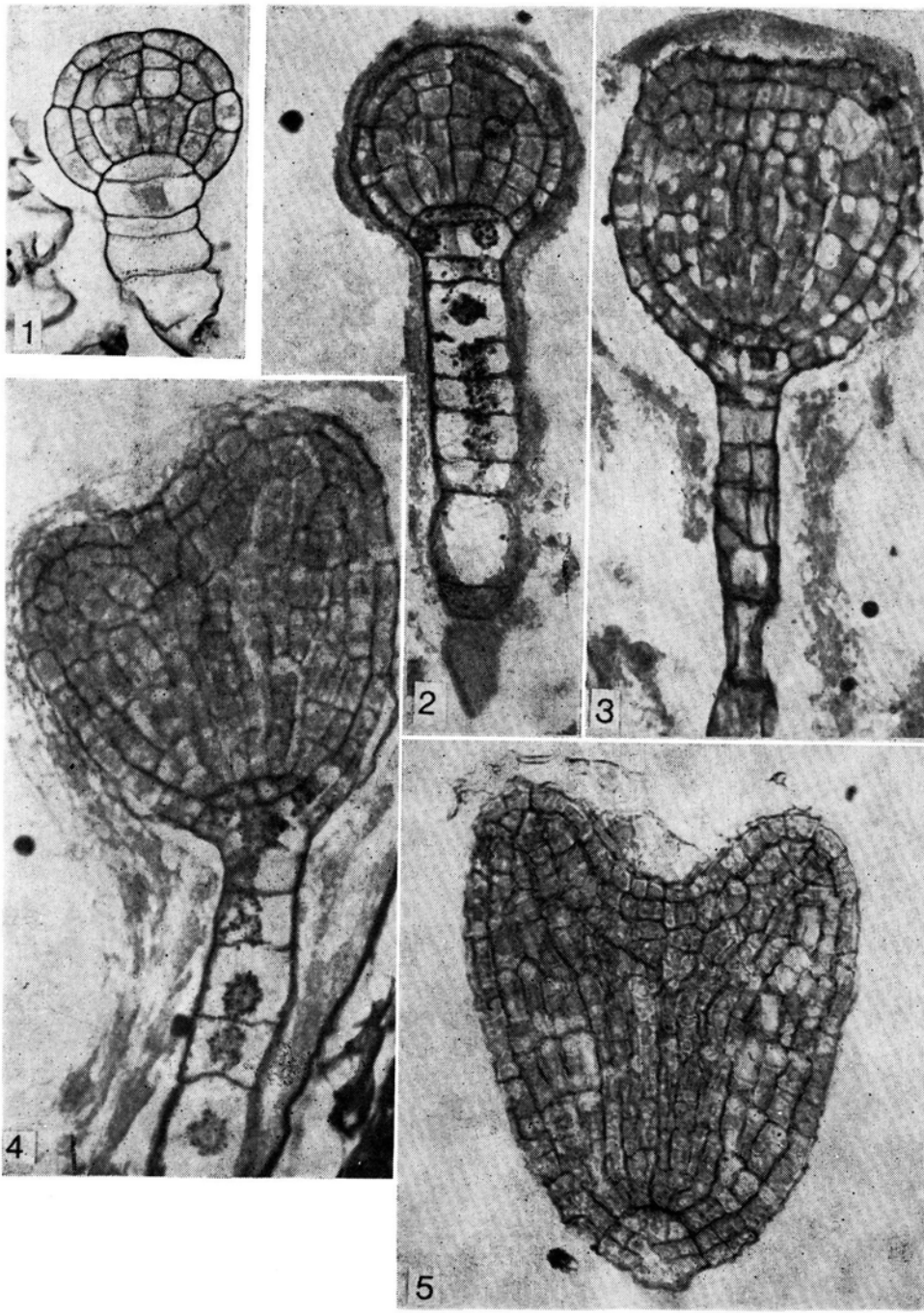
After differentiation of dermatogen (during the first division of cells of the proembryo upper layer) the hypophysis is formed. This is the only cell of the developing suspensor which is included in the embryo proper. The hypophysis is usually the 8th cell of the suspensor and the 5th generation of cell *cb* (Fig. 39). During further development of the embryo the suspensor does not grow so intensively any more, but still in the globular state several divisions may occur in it, so that the number of suspensor cells in rape may increase to 9, 10 or 11. In the 'Górczańska' variety a globular embryo was once found with 14 cells in the suspensor.

After the end of division the suspensor cells continue to grow and mature. This occurs in basifugal direction. The cells are strongly vacuolated, but the central vacuole arises at first only in the basal cell. In the remaining ones there are only numerous minute vacuoles up to the heart stage. The cytoplasm is weakly basophilic. The large spherical nucleus with a small nucleolus is suspended on cytoplasmic bridges, occupying a central position in most suspensor cells (Plate I photos 1, 2, 4). The nucleus of the basal cell lies in its apical end. The micropylar part contains a wide layer of cytoplasm.

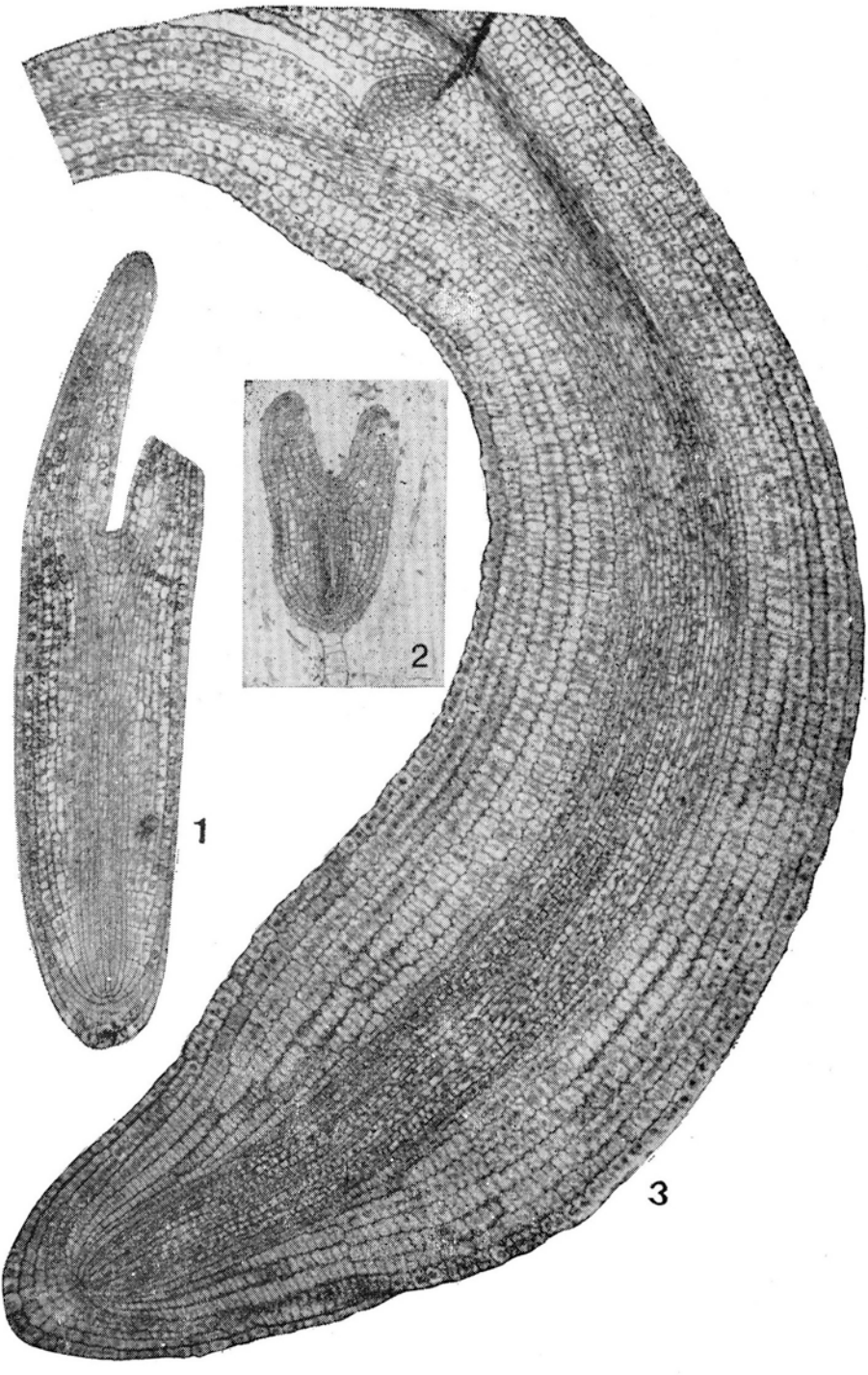
Starch grains are present in the suspensor cells, accumulated mainly around the nucleus (Plate I photos 2, 4). The cells also contain lipid drops.

In maturing suspensor cells transfer outgrowths arise on the walls. They are directed towards the interior of the cells. They first appear in the micropylar basal part of the cell in the young proembryo with a 2-cell apical part, and then in the whole suspensor. They are well visible in the light microscope after intensive staining of the cell walls by the PAS method for instance. Their length is about 0.5—1 μm reaching in the basal cell of torpedo-shaped embryos 2—3 μm. The transfer outgrowths are densely packed next to one another, when seen from above they present a pattern of bent lines. In the proembryo they were only observed in the widened apical part of the basal cell of the suspensor. In the globular stage they may be found in the whole basal cell. Beginning with the transition stage, they are also observed in the central cells of the suspensor.

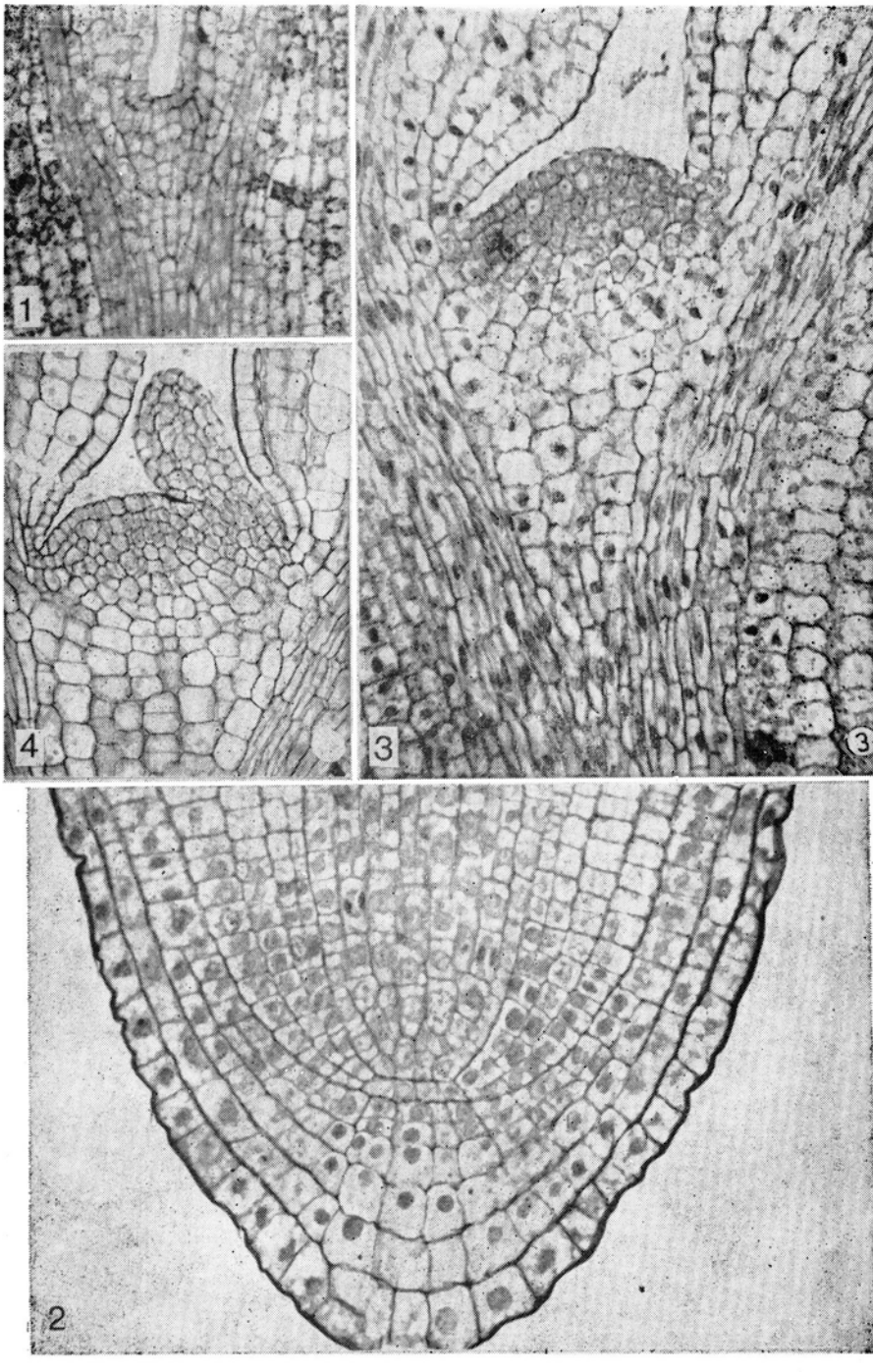
In older heart-shaped embryos the transfer outgrowths can be seen in the whole suspensor with the exception of the hypophysis cells. The cell wall outgrowths are still denser in the basal part. In the torpedo stage, which falls to the period of intensive elongation of the embryo axis, the



Development of embryo proper: photo 1. young globular embryo, Ehrlich haematoxylin, photo 2. older globular embryo, PAS, photo 3. transition stage, PAS, photo 4. Heart-shaped embryo immediately after outgrowth appearance of cotyledons, PAS, photo 5. young heart--shaped embryo with fragment of cellular endosperm, Alcian blue
Material fixed in CrAF 0.5—0.5—10



Development of embryo proper (continued), × 120: older heart-shaped embryo, Alcian blue (photo 2); Torpedo stage, PAS (photo 1); Full grown embryo Ehrlich's hematoxylin (photo 3). Material fixed in CrAF.



Apical meristems: photo 1. shoot apex in torpedo-shaped embryo, PAS, ×300, photo 2. radicle tip in end stage of embryogenesis, Ehrlich's haematoxylin, ×300, photo 3. shoot apex in mature embryo, Ehrlich's hematoxylin, ×300, photo 4. shoot apex with leaf primordium, Alcian blue ×200

outgrowths are markedly larger, but it is mainly their number that increases. Their accumulation in the central part of the suspensor is similar as in the basal cell of the proembryo.

The suspensors are easy to fix up to the heart stage, that is when they are surrounded with nuclear endosperm. They contain at this time abundant cytoplasm and numerous vacuoles. When the endosperm cells form around them and the whole embryo, and particularly when endosperm digestion by the embryo begins, they become very difficult to fix. They have not much cytoplasm left and they shrink. It is, therefore difficult to follow the course of dying back of the whole suspensor. There is no doubt, however, that the suspensor cells adjacent to the embryo can live a long time.

DISCUSSION

1. In this study, it was endeavoured to establish the regularities concerning the directions and sequence of the first cell divisions and the character and frequency of deviations from these regularities. Particular attention was devoted to transverse divisions in the development of the proembryo, which lead to the formation of transverse segmentation boundaries running through the whole proembryo, and to horizontal divisions in the dermatogen and periblem of the lower proembryo layer from which the hypocotyl-root axis arises (T y k a r s k a, 1976, and the present paper). These boundaries at later stages of embryo development delineate the cell families of common origin. They can be recognised and identified on medial longitudinal sections of the embryo in various stages of development.

Owing to this, it was possible to establish that development of the rape embryo is extremely regular and that the destination of the cells formed after these segmentation divisions is from the beginning strictly determined for further development (Fig. 39), similarly as in other *Cruciferae* (S o u è g e s, 1939; L e b è g u e, 1952).

— the body of the embryo arises from the apical cell *ca*, with the exception of the columella and the cells binding it with the plerome,
— the multicellular fusiform suspensor develops from the basal cell — *cb* which divides only transversally and so does the hypophysis — the mother cell of the central binding cells layer "*iec*" and of the columella,
— from the 4 octants of the upper embryo layer *l*, the hypocotyl and the apical shoot meristem are formed with the primordium of the first leaf,
— the 4 octants of layer *l'* give rise to the hypocotyl and radicle (Fig. 39).

Study of the transverse segmentation boundaries in the dermatogen and periblem of embryo layer *l'* showed that the boundary between the radicle and the hypocotyl is determined in the same way. As this boundary was assumed after K u r a ś (1974, 1978) the upper limit of the 1st root cap cell layer reaching up to segmentation boundary *II* between the 2nd and 3rd segment of periblem of the axis.

Owing to the regularities in the direction and sequence of cell division in the proembryo, the origin and succession in formation of histogen mother cells of the radicle can be accurately established.

Dermatogen mother cells of the hypocotyl-root axis differentiate by periclinal division of the lower octant layer. Then the mother cells of periblem and plerome form simultaneously by periclinal division of the inner cells of the embryo lower layer.

The columella mother cell and that of the central cell layer binding promeristem cells are in turn formed and outlined by the arched transverse wall from the hypophysis which is the 5th layer of the basal cell *cb*.

Later, in the older globular embryo, the mother cells of the pericycle and of the inner plerome differentiate by periclinal division of plerome mother cells or their derivatives after transverse division. Finally, in the transition stage to the heart stage, columella initials arise by periclinal division of columella mother cells and dermatocalyptrogen initials as well as mother cells of the first lateral root cap cell layer by periclinal division of the dermatogen cells adherent to the columella (2nd or 3rd generation of dermatogen mother cells in the octants of the lower proembryo layer).

It was found by observing the further development of the radicle that the layer of central binding cells joining the columella with the plerome and generally considered (H a n s t e i n, 1870; S o u è g e s, 1939; M a h e s h w a r i, 1950) as periblem initials (*iec*) does not play any creative role in the course of development of the embryo. Periblem is started by the initial cells differentiated from the periblem mother cells after their first transverse division.

The radicle promeristem of rape thus consists of plerome, periblem, dermatocalyptrogen and columella initials surrounding on all sides the inactive layer of central binding cells.

2. It has been demonstrated in the present paper that the basic mechanism of rape embryo development consists in differentiating divisions which determine the future development fate of sister cells.

The embryos of other *Cruciferae* and related families develop probably in a similar way, the development of the proembryo occurs in them similarly as in rape (L e b è g u e, 1952) and so do embryos classified to other regular embryonomic types in which transverse, longitudinal and

pericilinal cell divisions take place according to a definite sequence, after the transverse division of the distinctly polarly differentiated zygote.

The same does not happen, however, in all angiospermous species. For instance in some *Delphinium* species studied by Babis (1974), the first zygote division is always oblique to the zygote axis and the future embryo axis. In this case the next cell divisions perpendicular to one another cannot be, and are not differentiating divisions. The two superposed parts of the embryo, the one forming the cotyledons and the shoot primordium, and the other forming the hypocotyl and radicle, differentiate in these *Delphinium* species gradually in the pyriform proembryo, without relation to the cell pattern. Determination of the parts of the embryo body thus occurs in these species only after the establishment of morphogenetic gradients in the multicellular proembryo. During embryogenesis in rape and many other angiosperms these gradients must be established much earlier before the differentiating divisions. Owing to this acceleration the first segmentation divisions of the zygote may be differentiating divisions.

2. In the description of embryogenesis in rape in the preceding (Tykarska, 1976) and the present paper the proembryo and embryo proper are distinguished with the assumption as criterion of the moment of differentiation of the histogen mother cells. Globular embryos possessing differentiated plerome, periblem, dermatogen and columella mother cells were classified as embryo proper.

Hofmeister (1849) considered as proembryo (Vorkeim) a file of cells formed by transverse divisions of the zygote up to the moment when the terminal cell enlarges or divides longitudinally. At present as proembryos are usually considered after Souèges (1932) all early stages of embryo development up to the late globular stage, in which the embryo body exhibits axial symmetry, and as embryo proper are assumed all later stages with leaf primordia in which the embryo body has a bilateral symmetry.

The change of symmetry and embryo structure is also associated with a change of its physiology. Hart-shaped embryos of various species can easily be cultured *in vitro* (Cutter, 1971). In the transition period the rape embryo begins to take on a green hue and its growth rate changes (unpublished results of the author).

In the course of development of the rape embryo two crucial happenings can be distinguished. The first is the end of proembryo development and beginning of growth of the embryo proper. At that moment all the basic parts of the mature embryo are already determined and can be identified, namely the upper part forming the cotyledons and shoot primordium, and the lower part forming the hypocotyl and the radicle with the mother cells of the central cylinder (plerome), cortex (periblem)

protoderm (dermatogen), root cap columella, and central binding cells. The second turning point in rape embryogenesis is the change from axial to bilateral symmetry related with the formation of cotyledon primordia.

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Embriogeneza rzepaku. II. Rozwój zarodka właściwego

Streszczenie

Kontynuując badania nad embriogenezą rzepaku, zapoczątkowane przez opis rozwoju prazarodka (Tykarska, 1976), stwierdzono, że rozwój zarodka jest niezwykle regularny i oparty na różnicujących podziałach.

Wykazano, że poprzeczne granice segmentacyjne i ściany komórkowe, rozgraniczające komórki macierzyste histogenów w prazarodku, można zidentyfikować we wszystkich późniejszych stadiach zarodka.

Granica między liścieniami i częścią epikotyledonarną osi zarodka a hypokotylem odpowiada granicy segmentacyjnej między piętrem *l* i piętrem *l'* w stadium oktantów.

Za granicę między hypokotylem a korzeniem przyjęto górną granicę czapeczki, sięgającą zwykle do poziomu granicy między II i III segmentem dermatogenu i peryblemu.

Merystem wierzchołkowy pędu powstaje z dermatogenu i z przyosiowych komórek subepidermy zarodka globularnego.

Promerystem korzenia zarodkowego składa się z trzech pięter komórek inicjalnych, otaczających ze wszystkich stron nieaktywną warstwę centralnych komórek wiążących.