DEVELOPPEMENT DE LA GRAINE

(embryon, albumen, graine, fruit)

1. Embryogenèse descriptive

1.1 Dicotylédones - Arabidopsis
1.2 Monocotylédones
1.3 Suspenseur
1.4 Albumen
1.5 Téguments
1.6 Maturation de la graine
1.7 Embryogenèse somatique
1.8 Réserves des graines

2. Contrôle génétique de l'embryogenèse

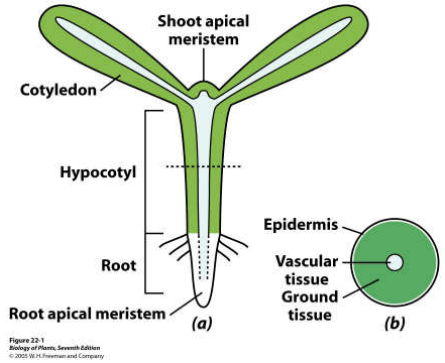
3. Dormance et germination

4. Fruit

1. Embryogenèse descriptive

L'embryon est formé de:

- **cotylédons**
- **axe embryonnaire**
  - méristème apical caulinaire (« Shoot Apical Meristem » - SAM) } épicotyle
  - parfois: ébauches de feuilles
  - hypocotyle
  - radicule
  - méristème racinaire (« Root Apical Meristem » - RAM)



A quoi sert l'embryogenèse puisque le développement est « post-embryonnaire »?

• formation des 3 tissus de base: épiderme, parenchyme, système vasculaire

• établissement de la **polarité** :
  – axe embryon-suspenseur, puis
  – axe tige-racine

• formation des **méristèmes**

• préparation de l'embryon à la phase de **dormance**

→ phase de **maturation** de l'embryon:

  – accumulation de réserves (albumen et/ou cotylédons)
  – déshydratation et arrêt métabolique

1.1 Dicotylédones-Arabidopsis

Notions fondamentales:

-**polarité**
-**symétrie**
-**détermination**

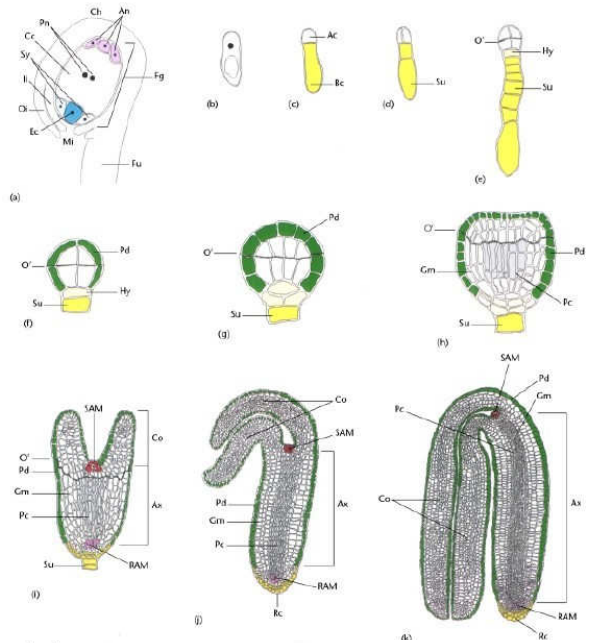


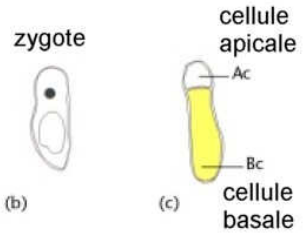
Figure 1 The ovule and representative stages of embryo development.
(a) Ovule, (b) zygote, (d) four-cell embryo proper, (e) octant-stage embryo, (f) 16-cell embryo, (g) globular-stage embryo, (h) transition-stage embryo, (i) torpedo-stage embryo, (j) bent cotyledon-stage embryo, (k) mature-stage embryo. Ac, Apical cell; An, antipodal cells; Ax, axis; Bc, basal cell; Cc, central cell; Ch, chalazal region; Co, cotyledons; Ec, egg cell; Fg, female gametophyte; Fu, funiculus; Gm, ground meristem; Hy, hypophysis; Ii, inner integument; Mi, micropyl region; O′, O′ line; Oi, outer integument; Pc, procambium; Pd, protoderm; Pn, polar nuclei; RAM, root apical meristem; Rc, root cap; SAM, shoot apical meristem; Su, suspensor; Sy, synergid cells.

La polarité est déterminée dès la première division du zygote

→ oosphère asymétrique OU polarisation après fécondation

Résultat: 2 cellules différentes:

- **cellule apicale (terminale)**:
  petite → embryon
- **cellule basale** : grande (vacuole)
  → quelques mitoses → suspenseur



Mitose asymétrique

Donc : polarité du zygote détermine:

1- axe embryon-suspenseur, puis

2- axe tige-racine.

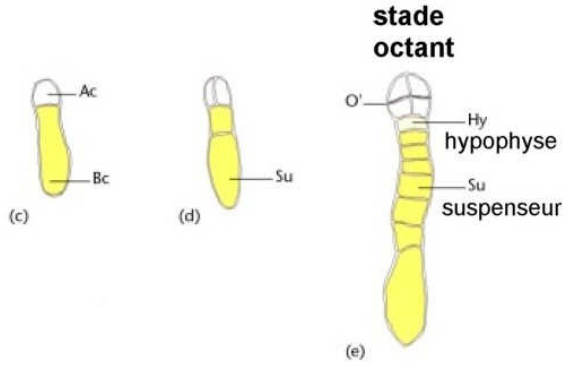
N.B. asymétrie visible au niveau moléculaire: p.e. les ARNm du gène ***ATML1*** ne se retrouvent que dans la cellule apicale. Chaque cellule exprime donc déjà son propre programme génétique (**détermination**).

Entre 12 et 30 HAF (Heures Après la Fécondation):

- cellule terminale: 3 mitoses (1 dans chaque plan-**symétrie**)
  → **stade OCTANT**: **proembryon** sans polarité **apparente**

  ATML1 s'exprime dans les 8 cellules de l'embryon.

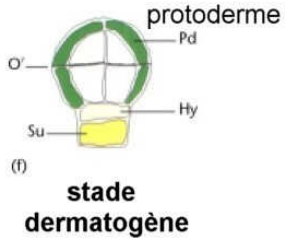
- cellule basale: mitoses dans un seul plan → suspenseur (7-10 cellules)

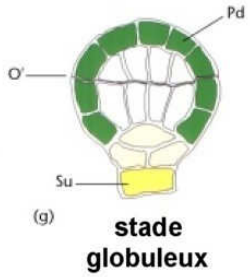


O' : frontière entre régions apicale et centrale de l'embryon **(détermination)**

Entre 30 et 42 HAF: stade **DERMATOGÈNE**

- chaque cellule subit une division **péricline** (parallèle à la surface)
  → 16 cellules:
  - 8 cellules externes: **protoderme** → divisions **anticlines** → épiderme (perpendiculaires à la surface)
  - 8 cellules interne: autres tissus
- Début de **différenciation** cellulaire; premier **patron de développement**
  NB. expression de ***ATML1*** : cellules du protoderme seulement.
- En parallèle: **hypophyse** (cellule du sommet du suspenseur):
  quelques mitoses → cellules à l'origine des tissus externes de la racine.

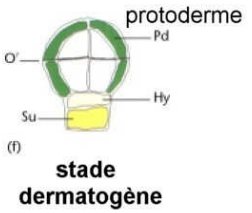


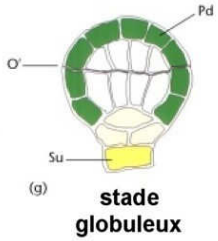


Entre 42 et 60 HAF: stade **GLOBULEUX**

- L'embryon passe de 16 cellules à environ 100 cellules.
- La différenciation cellulaire est visible au niveau de l'expression spécifique de plusieurs gènes :

  → mise en place de patrons de développement qui seront visibles au stade suivant:
  - **axe apical-basal** (axe tige-racine)
  - **symétrie radiale**:





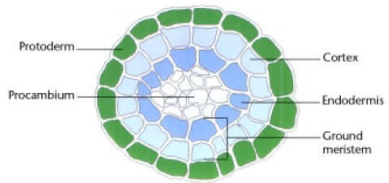


Figure 3 Radial patterning of embryonic tissues. The three embryonic tissue systems are the protoderm, the ground meristem and the procambium. In the embryonic root, the ground meristem gives rise to the cortex and endodermis.

Ground meristem : méristème fondamental

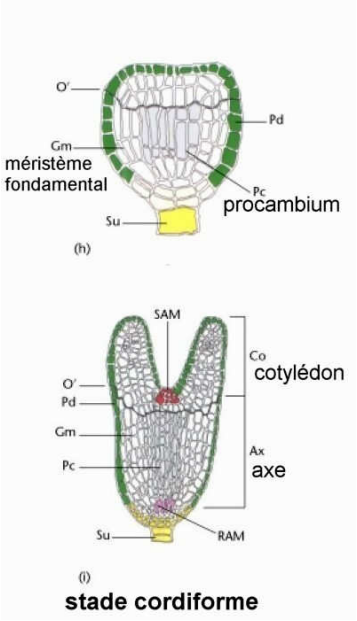
Entre 60 et 84 HAF: stade **CORDIFORME**

- formation des cotylédons: croissance et division cellulaire localement plus rapides (pic d'auxine)
- formation du **méristème racinaire**
- début de différenciation: **procambium**

  → système vasculaire → établissement d'un nouveau patron de développement:

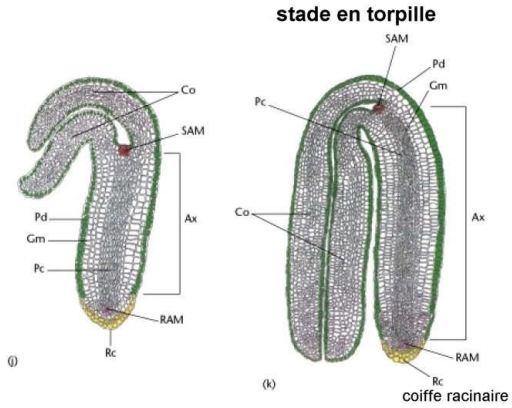
  cellules du xylème-cellules du phloème
- fin du stade cordiforme: début de formation du **méristème apical caulinaire**

  (après les cotylédons)



Entre 84 et 96 HAF: stade "**EN TORPILLE**" ("torpedo")

- Divisions, croissance et différenciation se poursuivent
- L'embryon comporte maintenant environ 20 000 cellules
- A partir de ce stade, on entre dans la **PHASE DE MATURATION**



Entre 4 et 9 JAF (Jours Après la Fécondation):

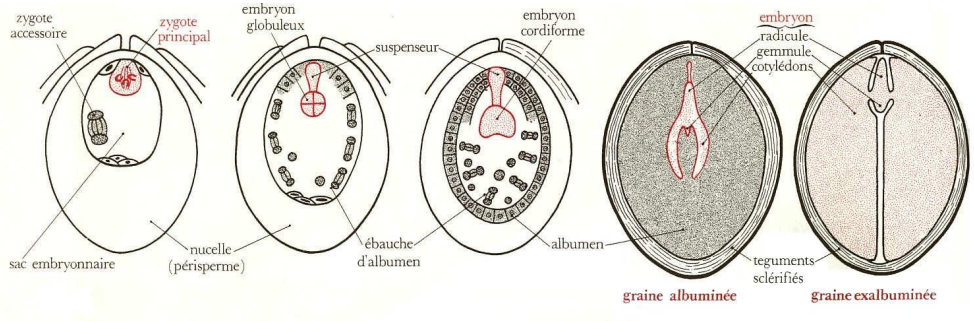
- division cellulaire ralentit puis s'arrête
- augmentation importante de la taille des cellules: accumulation des **réserves**
- augmentation de la taille de l'embryon (aux dépens de l'albumen)

A partir de 9 JAF:

- embryon occupe tout le volume de la graine; il n'y a plus d'albumen

  → graine **exalbuminée**

  NB. Les cotylédons représentent 80% du volume de l'embryon
- déshydratation, arrêt métabolique, **dormance**



Au microscope :

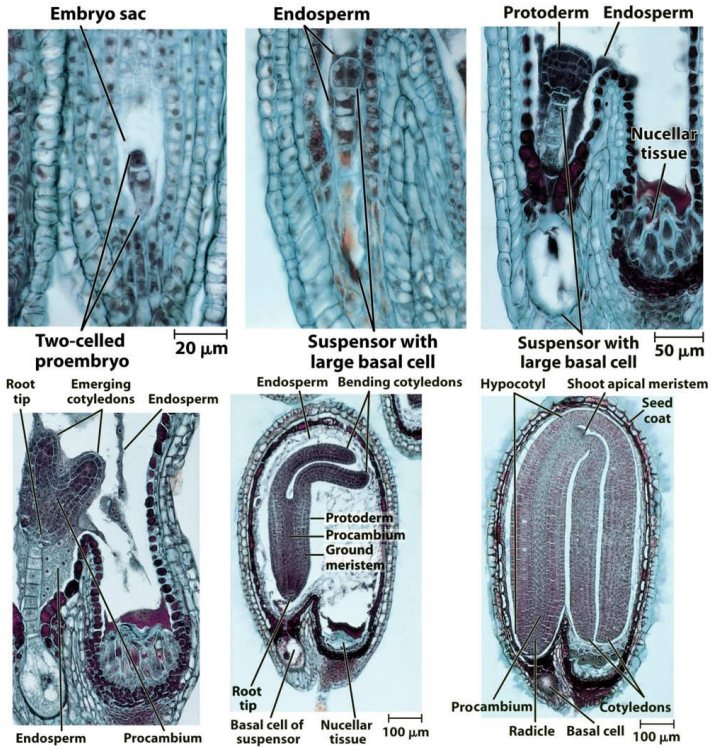


Figure 22-3f
Biology of Plants, Seventh Edition
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Arabidopsis Book: Stages of Arabidopsis embryogenesis

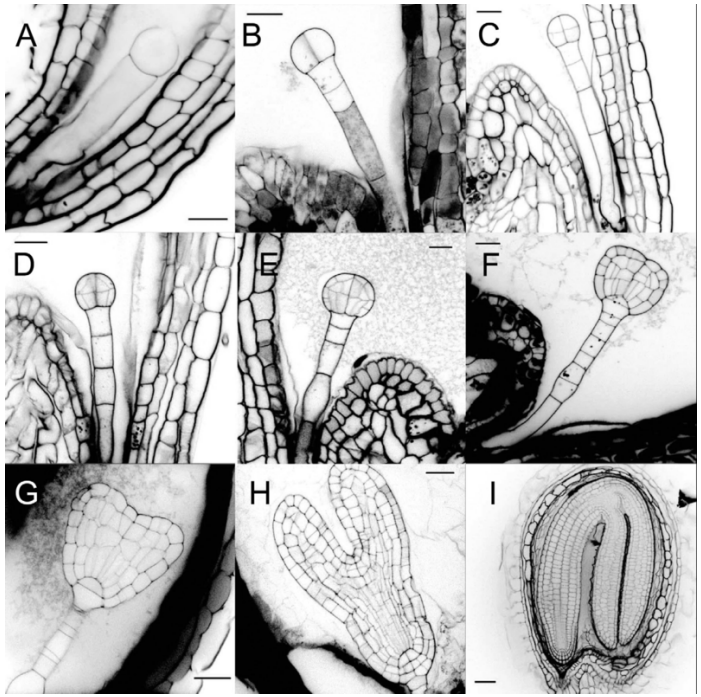


Figure 3. Stages of Arabidopsis embryogenesis.

(A) Early embryo, with a single cell in the embryo proper.
(B) Early embryo with 2 cells in the embryo proper.
(C) Octant stage; four of eight cells in two tiers are visible. Cells of the upper and lower tier (*u.t.* and *l.t.*) of the octant will give rise to specifi c parts of the seedling (see Figure 1). Together with descendants of the uppermost suspensor cell (hypophyseal cell) the eight 'octant' cells will form all the structures of the seedling.
(D) Dermatogen stage. A tangential division of each of the eight 'octant' cells produces inner cells and epidermis (protoderm) cells.
(E) Early globular stage; divisions of the inner cells immediately after the dermatogen stage are oriented in the apical-basal dimension, endowing the embryo with a morphologically recognizable axis.
(F) Triangular stage; now a polarized pattern of major elements is recognizable (see text): *u.t.* cells have generated two symmetrically positioned cotyledon primordia and *l.t.* cells a radially patterned cylinder (comprising epidermis, ground tissue and vascular tissue). Additional divisions distinguish the 'hypophyseal cell' from other suspensor cells. Its descendants will ultimately form the quiescent center of the primary root meristem and the columella initials.
(G) Heart stage; cotyleldon outgrowth. Subsequently, cells between the outgrowing cotyledons initiate the primary shoot meristem.
(H) Mid-torpedo stage; enlargement of cotyledons and hypocotyl and further elaboration of the radial pattern.
(I) Bent cotyledon stage embryo with elaborated radial pattern in different organs. In the cotyledons a single adaxial subepidermal layer of elongated cells (palisade mesophyll) can be distinguished from underlying mesophyll cells. The radial pattern of the hypocotyl is comprised of a single cell layer of epidermal cells, two cortex layers, one endodermis and one pericycle layer enclosing the vascular cylinder.
Bar is 5 µm in **A**, 10 µm in **B**, **G** and **H**, 15 µm in **C** and **E**, 20 µm in **D** and **F**, 50 µm in **I**.
Images kindly provided by J. Runions, are also available at:

https://www.brookes.ac.uk/lifesci/runions/HTMLpages/Embryo%20development.html!

Mise en place du patron apical-basal du développement de l'embryon (1)

→ Détermination de 3 domaines embryonnaires:

-apical : SAM + cotylédons

-central : cotylédons (partie) + hypocotyle + RAM (partie)

-basal: RAM (partie)

Puis: sous-domaines…

(Segmentation)

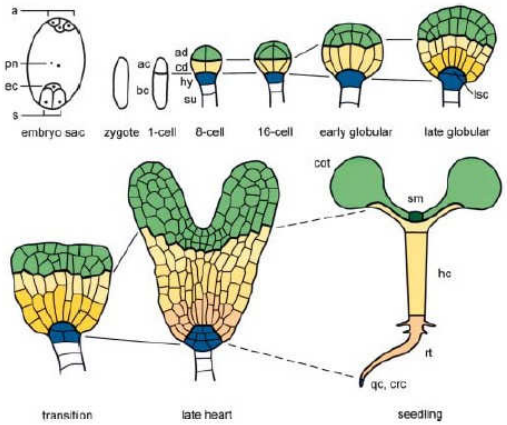
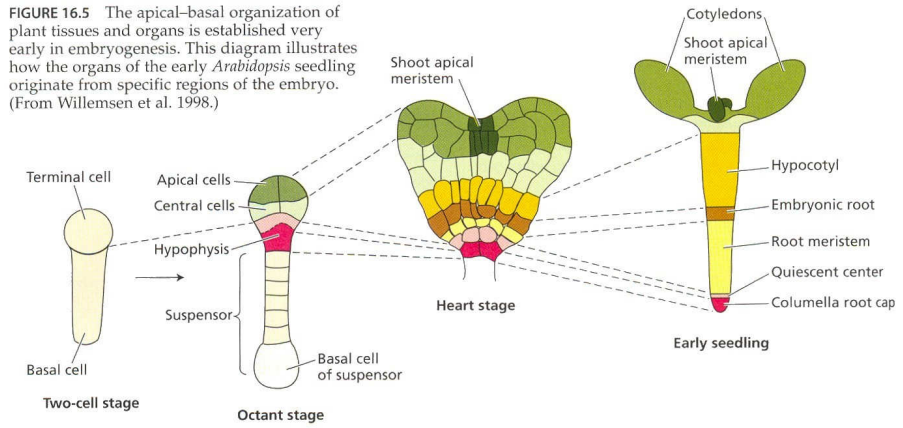


Figure 1. Apical–Basal Arabidopsis Embryo Development.

Schemes of longitudinal median sections. The upper and lower thick lines represent clonal boundaries between the descendants of the apical and basal daughter cells of the zygote and between the apical and central embryo domains, respectively. See text for details. a, antipodes; ac, apical daughter cell; ad, apical embryo domain; bc, basal daughter cell; cd, central embryo domain; cot, cotyledons; crc, central root cap; ec, egg cell; hc, hypocotyl; hy, hypophysis; lsc, lens-shaped cell; pn, polar nuclei; qc, quiescent center; rt, root; s, synergids; sm, shoot meristem; su, suspensor.

Mise en place du patron apical-basal du développement de l'embryon (2)



Columella root cap : coiffe à columelles

Mise en place du patron radial de développement de l'embryon (1)

Détermination de l'identité des cellules des différentes couches: **effet de position**

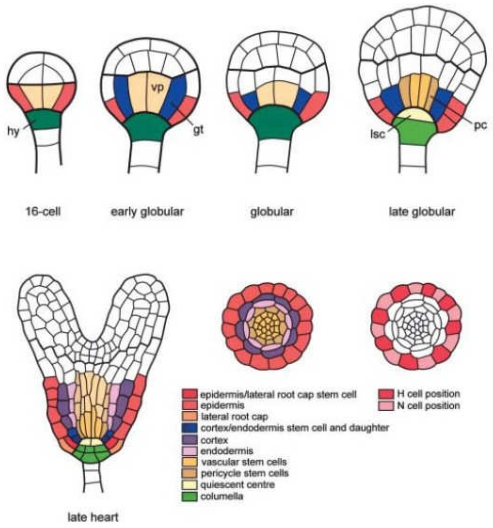


Figure 3. Development of the Radial Pattern.

The top row and the illustration at bottom left show schemes of longitudinal sections; the other illustrations in the bottom row show schemes of cross-sections through a root. The upper and lower thick lines represent clonal boundaries between the descendants of the apical and basal daughter cells of the zygote and between the apical and central embryo domains, respectively. Cell types are shown in color as indicated. Vascular and pericycle cells are shown in lighter colors than stem cells. See text for details. gt, ground tissue; hy, hypophysis; lsc, lens-shaped cell; pc, pericycle; vp, vascular primordium.

Mise en place du patron radial de développement de l'embryon (2)

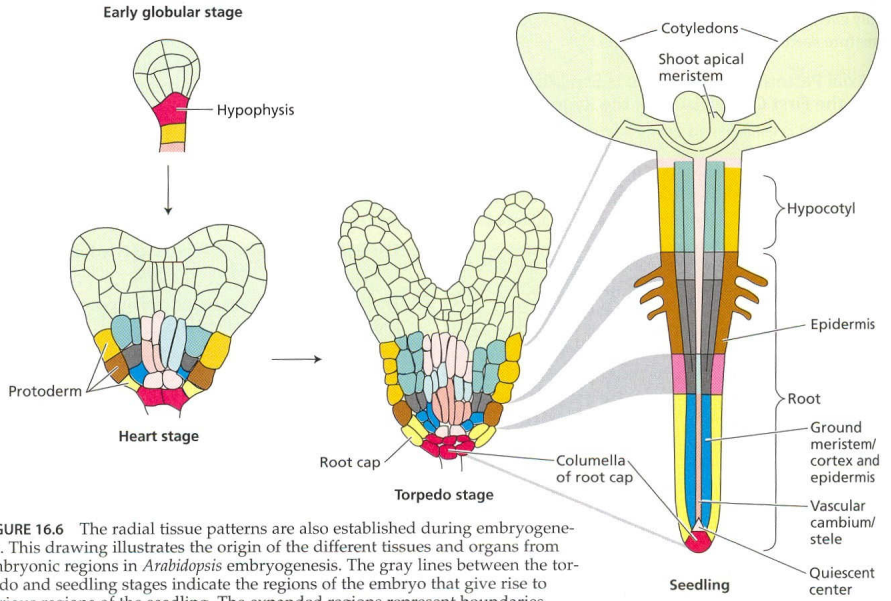
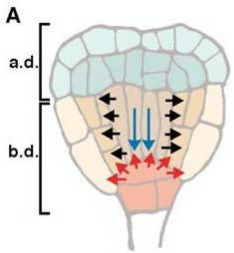


FIGURE 16.6 The radial tissue patterns are also established during embryogenesis. This drawing illustrates the origin of the different tissues and organs from embryonic regions in *Arabidopsis* embryogenesis. The gray lines between the torpedo and seedling stages indicate the regions of the embryo that give rise to various regions of the seedling. The expanded regions represent boundaries where developmental fate is somewhat flexible. (After Van Den Berg et al. 1995.)

Signalisation et effet de position



Flèches bleues: signalisation domaine apical-hypophyse
Flèches noires: cylindre vasculaire- patron radial
Flèches rouges: hypophyse-cellules souches du RAM

Figure 2: Positional references provided by the early embryo pattern
Arrows indicate presumed pattern transmission mechanisms, which are discussed in sections 4 and 5. **A**: Triangular-stage embryo with central vascular cylinder (narrow cells in the center). Black arrows indicate signaling from the vascular cylinder to induce radial patterning in the overlying ground tissue (Section 5.3.); blue arrows indicate the likely dependence of hypophyseal cell fate acquisition on apical signals (Section 4.1.2.). Signals from hypophyseal derivatives (red arrows) confer stem cell identity in the root meristem (a.d. and b.d. = the apical and basal domains respectively. Section 4).

Autres types de développement embryonnaire des Dicotylédones:

- différences dès les premières mitoses

- principe général identique

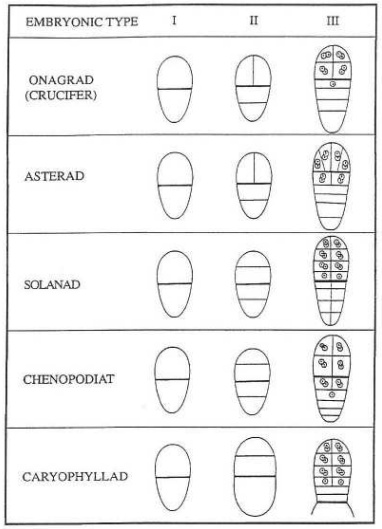


FIGURE 1. Schematic overview of the five different embryonic types displaying a transversal division of the zygote. Representations demonstrate the zygote after the first (I), and the second division (II), and the early proembryo before periclinal divisions give rise to protoderm formation (III). While gray colored cells represent derivatives of the apical cell, white-colored cells represent derivates from the basal cell. Cells containing drawn nuclei (III) will contribute to the embryo, whereas cells not containing drawn nuclei contribute to the suspensor. The presence of two nuclei in one cell indicates that one cell lays above and one beneath the drawing plane. Embryonic types are based on the classification of Schnarf (1929) and Johansen (1945). (Figure adapted from Natesh and Rau (1984) with permission.)

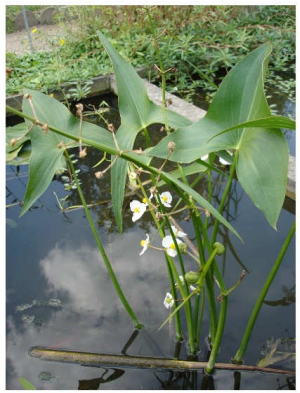
1.2 Embryogenèse chez les Monocotylédones

Mêmes grands principes que chez les Dicotylédones :

- zygote **asymétrique**
- les premières étapes permettent la mise en place des principaux **patrons de développement:**
  - axe suspenseur-embryon puis
  - axe tige-racine
  - symétrie radiale

Mais: beaucoup moins de symétrie **apparente**

Exemple: Sagittaire



Axe embryonnaire

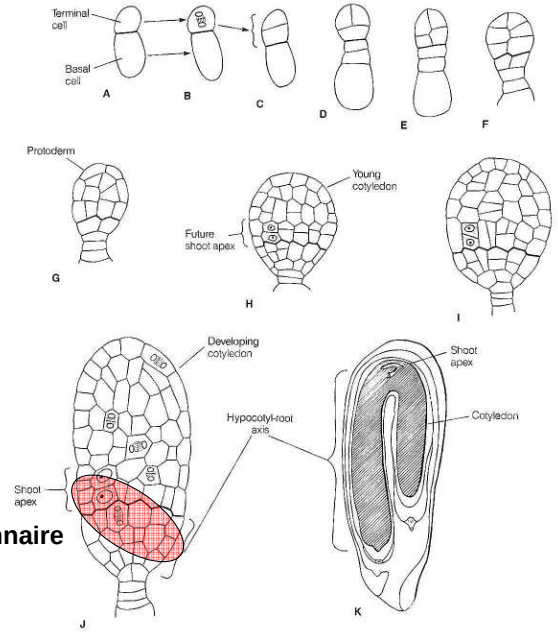


FIGURE 20-34 A–J, early embryogeny in *Sagittaria sagittaefolia;* derivatives of terminal cell and basal cell separated by heavy line; **K,** nearly mature embryo in seed. Note that the shoot apex and single cotyledon are derived from derivatives of the original terminal cell. [**A–J,** redrawn from Swamy, *Phytomorphology* 30:204–212, 1980; **K,** redrawn from Schaffner, *Bot. Gaz.* 23:252, 1897.]

Cas particulier des Poacées. Ex: maïs

- **Entre 0 et 3 JAF:** formation d'un **PROEMBRYON** ovoïde, 12 à 24 cellules:
  - sommet: cellules à cytoplasme dense → embryon
  - base: grandes cellules vacuolisées → suspenseur

  NB. Frontière embryon-suspenseur mal définie.

- **Entre 3 et 8 JAF**: stade de **TRANSITION** (début)
  - allongement important
  - début de différenciation du protoderme, de façon non uniforme

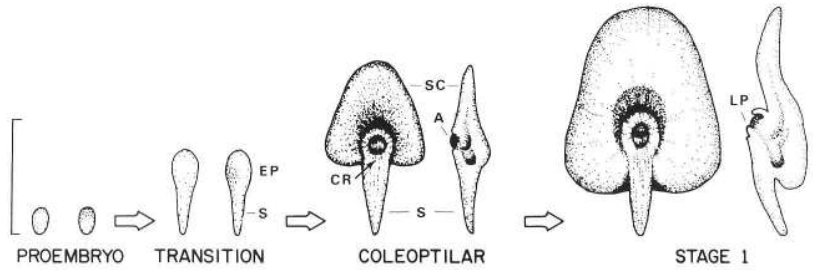
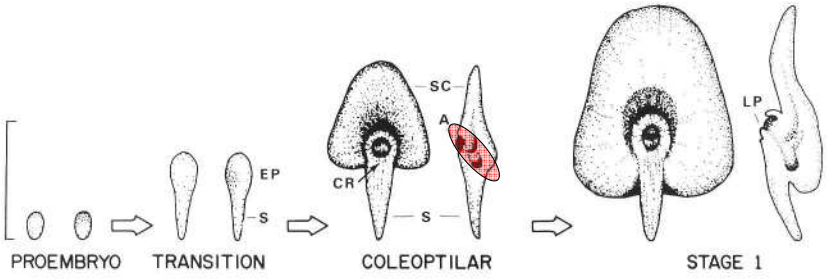


Figure 5. Early Stages of Embryogenesis in Maize.

Each stage is represented by a face view (left) and a longitudinal section (right) with the embryo face at left. The transition embryo contains an embryo proper (EP) and suspensor (S). The scutellum (SC), shoot apex (A), suspensor (S), and coleoptilar ring (CR) are visible at the coleoptilar stage. The first leaf primordium (LP) appears at the base of the shoot apex at stage 1. Bar = 0.5 mm. Figure adapted from Clark and Sheridan (1986). See also Sheridan and Clark (1987).

- **Entre 8 et 12 JAF:** stade de **TRANSITION** (fin)
  - activité mitotique localement intense → axe tige-racine oblique
    → à 12 JAF, formation des **méristèmes**
  - début de développement du **coléoptile** (spécifique aux Graminées)
    → recouvre le méristème apical caulinaire
  - début de développement du **scutellum** ("bouclier"): cotylédon
- **Entre 12 et 16 JAF**: stade **COLEOPTILAIRE**
  - L'embryon atteint 1 mm de longueur



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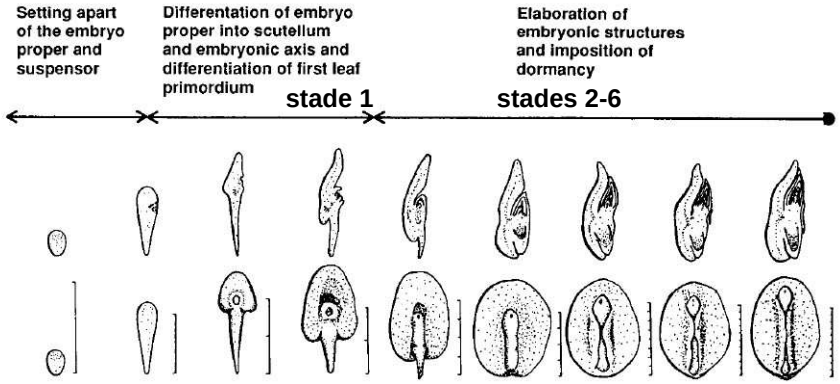
- **16 JAF: STADE 1** (≈ l'embryon mature des Dicotylédones)
  → premier primordium de feuille; coléorhize*
- **30 à 40 jours suivants: STADES 2 à 6**
  - formation d'autres primordia de feuilles (et de racines)
  - ↑ importante de la taille du scutellum: entoure l'embryon
  - accumulation des réserves (**maturation**)



* recouvre la racine; spécifique aux Poacées

Embryogenès - Poacées
niveau cellulaire

→ 4 domaines, démarcations moins marquées que chez les Dicotylédones (**segmentation**)

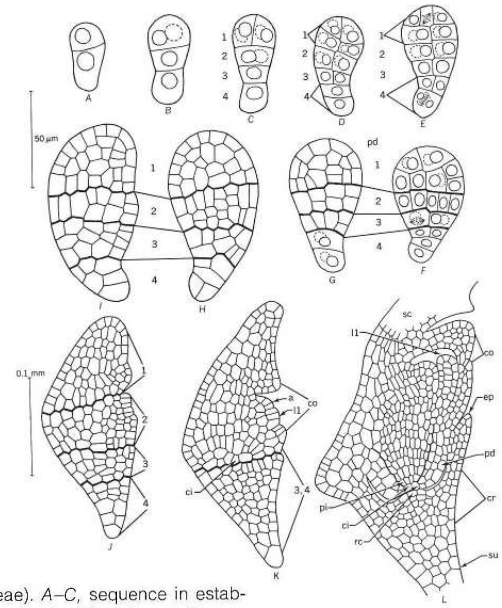
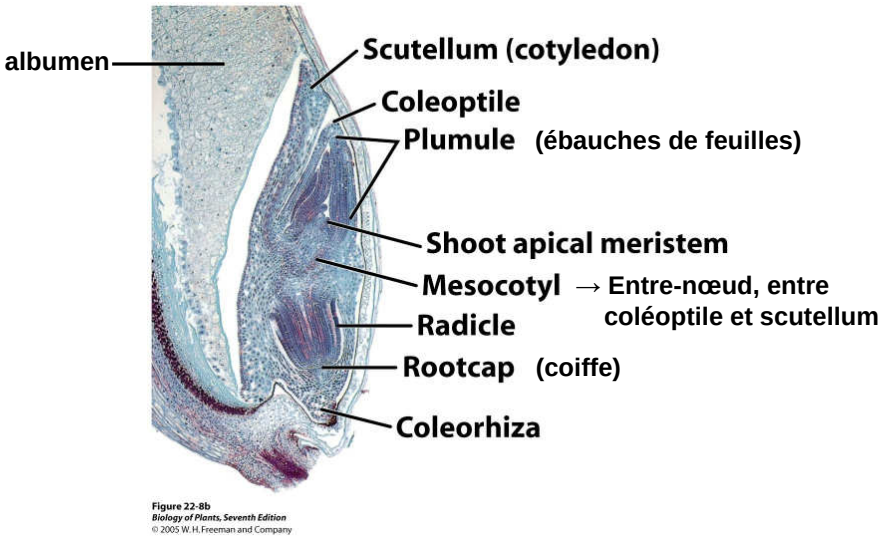


Figure 24.9 Embryo development in *Poa annua* (Poaceae). *A–C*, sequence in establishment of four tiers of cells. *D–H*, multiplication of cells in each of four tiers. *I–K*, continued cell multiplication and beginning of organ differentiation. *L*, growing foliar primordia and evidence of internal organization. Details: numbers, tiers of cells; *a*, apex of epicotyl; *ci*, cortical (periblem) initials; *co*, coleoptile; *cr*, coleorhiza; *ep*, epiblast; *l1*, first leaf; *pd*, protoderm; *pi*, vascular cylinder (plerome) initials; *rc*, rootcap initials; *sc*, scutellum; *su*, suspensor. (Adapted from Souèges.[46])

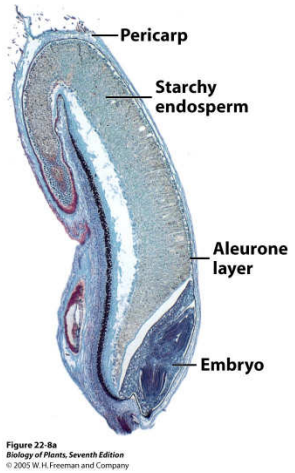
EMBRYON MATURE:

- 5 à 6 ébauches de feuilles
- l'embryon est entouré de l'**albumen** (graine **albuminée**)

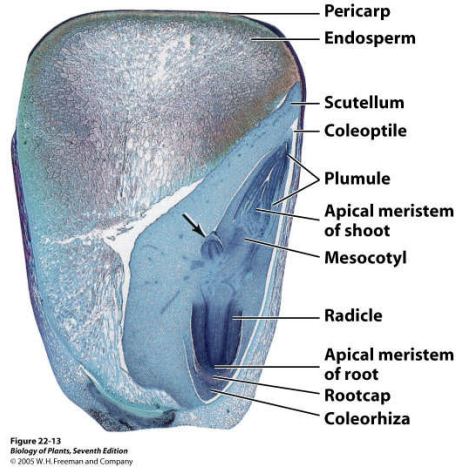


Les caryopses sont des fruits contenant une graine dont les téguments ont été hydrolysés pendant l'embryogenèse: confusion graine-fruit

blé



maïs



flèche: racine adventive