To our limited intelligence, it would seem a simple task to divide a nucleus into equal parts. The cell, manifestly, entertains a very different opinion.

E. B. Wilson, 1923

Cleavage

Rapid cell division without growth
Rate of cell division is unparalleled
Examples:
Early *Drosophila* embryo - mitosis occurs every 10 min for 2 hr (4096 nuclei); 50,000 cells in only 12 hr
*Xenopus* (frog) embryo - 37,000 cells /43 hr

Figure 8.1 Rate of Formation of New Cells During Early Development of the Frog

Cell division rate typically slows at the end of cleavage
Cleavage

Two separable events:
Karyokinesis (mitosis) - nuclear division
Cytokinesis - cell division

Cytoskeletal elements key to these events:
Microtubules (spindle apparatus)
Actin microfilaments (contractile ring)

Figure 8.3 Role of Microtubules and Microfilaments in Cell Division

<table>
<thead>
<tr>
<th>Process</th>
<th>Mechanical agent</th>
<th>Major protein composition</th>
<th>Location</th>
<th>Major disruptive drug</th>
</tr>
</thead>
<tbody>
<tr>
<td>Karyokinesis</td>
<td>Mitotic spindle</td>
<td>Tubulin microtubules</td>
<td>Central cytoplasm</td>
<td>Colchicine, nocodazole</td>
</tr>
<tr>
<td>Cytokinesis</td>
<td>Contractile ring</td>
<td>Actin microfilaments</td>
<td>Cortical cytoplasm</td>
<td>Cytoskeleton B</td>
</tr>
</tbody>
</table>

Protamine subunits have been found to independently mediate several membrane functions, including regulation of the transport of ions and nucleotides. Protamine has been used to inhibit microtubule-mediated processes (Pasquale 1997).
The Cell Cycle

The Cell Cycle - Cleavage

MPF - Mitosis Promoting Factor

- CyclinB
- cdk1

MPF - the key regulator of entry into mitosis
Figure 8.2(1) Cell Cycles of Somatic Cells and Early Blastomeres

cdc2 = cdk1 = p34 kinase

CyclinB

DCCD2 = CDK1 = p34 kinase

PO$_3^-3$

Mitosis

Cyclin degradation

S

Inactive protein kinase

Synthesis

Cyclin synthesis

Active cdc2 protein kinase

M

Nuclear envelope breakdown

CyclinB

cdk1

Histones

- promotes condensation

Chromosome condensation

Cytokinesis

Myosin

- inhibits initiation of cytokinesis

Little or no transcription

RNA Polymerase

- inhibits transcription

cdk1 phosphorylates proteins to alter function

MPF - Mitosis Promoting Factor

Events in Mitosis

Targets of cdk1 phosphorylation

Nuclear envelope breakdown

Nuclear lamins - promotes disassembly

Chromosome condensation

Histones - promotes condensation

Cytokinesis

Myosin - inhibits initiation of cytokinesis

Little or no transcription

RNA Polymerase - inhibits transcription

Target

Protein
Figure 10.3(2) Mitosis and DNA Replication in Xenopus

Figure 8.2(2) Cell Cycles of Somatic Cells and Early Blastomeres

Classification of Eggs and Types of Cleavage

Animal Pole

Less Yolk

Vegetal Pole

More Yolk
Classification of Eggs and Types of Cleavage

Classification by yolk content

Isolecithal - little yolk, evenly distributed
Mesolecithal - moderate yolk
Telolecithal - large amounts of yolk

Yolk content affects how cells divide

Holoblastic cleavage - complete division
Meroblastic cleavage - incomplete division

Figure 8.4(1) Summary of the Main Patterns of Cleavage

1. HOLOBLASTIC CLEAVAGE
   A. Isolecithal
      1. Radial cleavage
         Echinoderms, amphioxus
      2. Spiral cleavage
         Annelids, molluscs, flatworms
      3. Bilateral cleavage
         Tunicates
      4. Rotational cleavage
         Mammals, nematodes

Last classification: Cleavage symmetry
Figure 8.4(2) Summary of the Main Patterns of Cleavage

I. HOLOBLASTIC CLEAVAGE
A. Mesolecithal
   Dispersed radial cleavage
   Amphibians

Figure 8.4(3) Summary of the Main Patterns of Cleavage

II. MEROBLASTIC CLEAVAGE
   A. Tetrahedral
      1. Bilateral cleavage
         Cephalopod molluscs
      2. Discoidal cleavage
         Fish, reptiles, birds
   B. Centrolecithal
      Superficial cleavage
      Most insects

Fig. 8.8 Cleavage in Live Embryos of the Sea Urchin

(A) (B) Fertilization envelope (C)

(D) (E) Micromeres (F) Blastula Blastocoele
Figure 8.26(1) Spiral Cleavage of the Snail Ilyanassa

(A)

Figure 8.27(1) Looking Down on the Animal Pole of (A) Left-Coiling and (B) Right-Coiling Snails

(A) Left-handed coiling

(B) Right-handed coiling

Figure 8.27(2) Looking Down on the Animal Pole of (A) Left-Coiling and (B) Right-Coiling Snails
Maternal effect genes: the genetics of shell-coiling in *Limnaea*

Genotype of mother determines coiling of progeny, regardless of progeny genotype.

**DD, Dd mother:** all right-handed progeny

**dd mother:** all left-handed progeny

Maternal effect makes for atypical genetics:

**DD female** $\times$ **dd male** - all progeny Dd, all right-handed

**dd female** $\times$ **DD male** - all progeny Dd, all left-handed

**Dd female** $\times$ **Dd male** - progeny 1:2:1 DD: Dd: dd, all right-handed

Maternal effect demonstrates fundamental role of egg cytoplasm (vs. zygote nucleus) in early development.

Important general lesson: Early development is regulated by the maternally-provided cytoplasm (egg cytoplasm) vs. the zygote nucleus.
**Fig. 8.36** Bilateral Symmetry in the Egg of the Tunicate Styela partita

![Diagram showing bilateral symmetry in the egg of Styela partita](image)

**Figure 8.4(2)** Summary of the Main Patterns of Cleavage

1. **HOLOBLASTIC CLEAVAGE**
2. **Mesolecithal**
   - Displaced radial cleavage
   - Amphibians

**Figure 10.1** Cleavage of a Frog Egg

![Diagram showing cleavage of a frog egg](image)
Figure 10.2 Scanning Electron Micrographs of Cleavage of Frog Egg

Figure 11.1(1) Zebrafish Development Occurs Very Rapidly

Discoidal Meroblastic Cleavage

Figure 11.4 Discoidal Meroblastic Cleavage in a Zebrafish Egg
Fig. 11.27 Early Cleavage in (a) Echinoderms and Amphibians and (B) Mammals

(A) ECHINODERM AND AMPHIBIAN
(B) MAMMAL

Fig. 11.29 SEMs of (A) Uncompacted and (B) Compacted 8-cell Mouse Embryos

Compaction indicates change in cell-cell adhesion

Figure 11.26 Development of a Human Embryo From Fertilization to Implantation

1. Fertilization typically takes place at the top of the oviduct

2. Implantation takes place in the uterus after 'hatching'
Figure 11.30  Hatching From Zona And Implantation of Mammalian Blastocyst

Blastocyst hatching from zona pellucida

Figure 11.30  Hatching From Zona And Implantation of Mammalian Blastocyst

Trophoblast - extraembryonic tissues (chorion)

Inner cell mass - embryo proper

uterus

Blastocyst implanting into uterine wall

Figure 11.36  Development of a Human Embryo From Fertilization to Implantation

Implantation outside of the uterus

Ectopic pregnancy - very dangerous
**Figure 8.4(3) Summary of the Main Patterns of Cleavage**

<table>
<thead>
<tr>
<th>II. MEROBLASTIC CLEAVAGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>E. Centrospherical</td>
</tr>
<tr>
<td>Superficial cleavage</td>
</tr>
<tr>
<td>Most insects</td>
</tr>
</tbody>
</table>

![Drosophila blastoderm, cycle 13](image)

**Drosophila Syncitial Early Development**

Karyokinesis occurs without cytokinesis to form a **syncitium** - a single cytoplasm with multiple nuclei.

Embryo forms a **syncitial blastoderm**

After 13 rounds of mitosis in a syncitium, nuclei at the surface cellularize to form a **cellular blastoderm**

**Figure 9.1 Laser Confocal Micrographs of Stained Chromatin Showing Superficial Cleavage in a Drosophila Embryo**

![Laser Confocal Micrographs](image)
Figure 9.3(1) Formation of the Cellular Blastoderm in Drosophila

Figure 9.3(2) Formation of the Cellular Blastoderm in Drosophila

Microtubules - Orange  Actin - Green