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

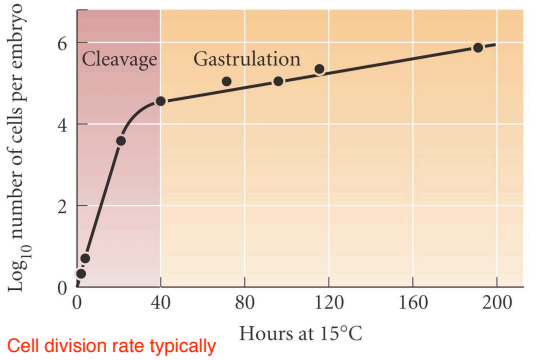
Rate of cell division is unparallelled

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***

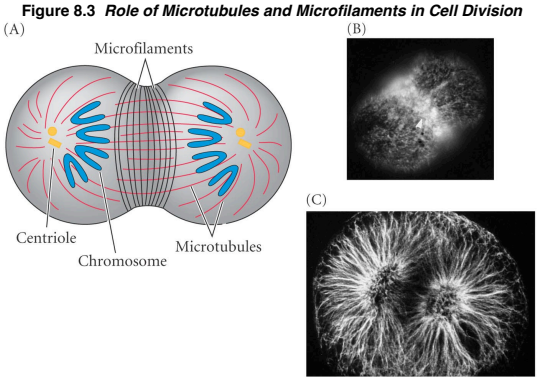
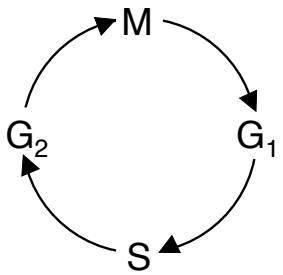


TABLE 8.1 Karyokinesis and cytokinesis

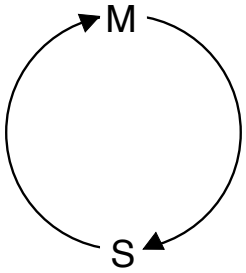
Process	Mechanical agent	Major protein composition	Location	Major disruptive drug
Karyokinesis	Mitotic spindle	Tubulin microtubules	Central cytoplasm	Colchicine, nocodazole[a]
Cytokinesis	Contractile ring	Actin microfilaments	Cortical cytoplasm	Cytochalasin B

[a]Because colchicine has been found to independently inhibit several membrane functions, including osmoregulation and the transport of ions and nucleosides, nocodazole has become the major drug used to inhibit microtubule-mediated processes (see Hardin 1987).

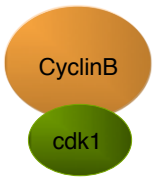
The Cell Cycle



The Cell Cycle - Cleavage

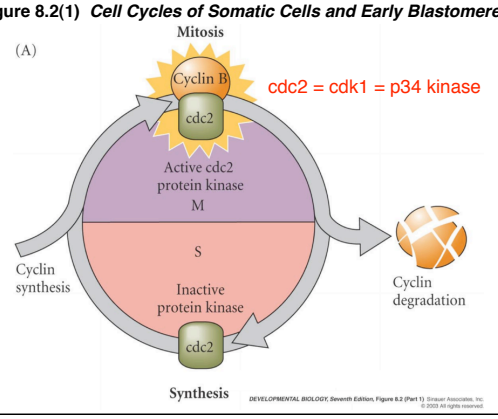


MPF - Mitosis Promoting Factor

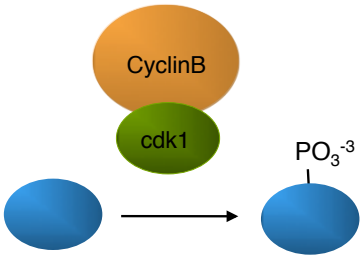


MPF - the key regulator of entry into mitosis

Figure 8.2(1) ***Cell Cycles of Somatic Cells and Early Blastomeres***



MPF - Mitosis Promoting Factor



cdk1 phosphorylates proteins to alter function

Events in Mitosis	Targets of cdk1 phosphorylation
Nuclear envelope breakdown	**Nuclear lamin proteins** - promotes disassembly
Chromosome condensation	**Histones** - promotes condensation
Cytokinesis	**Myosin** - inhibits initation of cytokinesis
Little or no transcription	**RNA Polymerase** - inhibits transcription

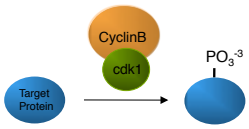
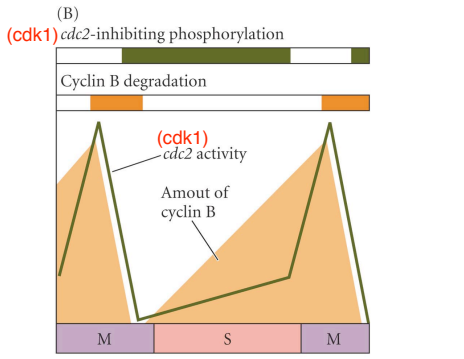
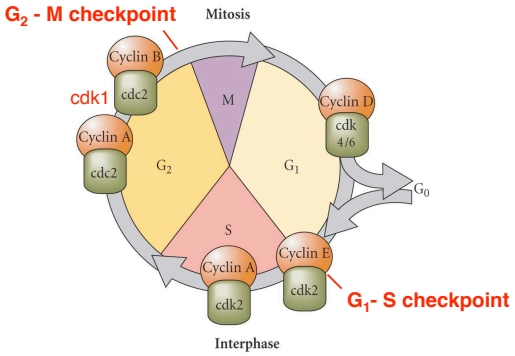


Figure 10.3(2) ***Mitosis and DNA Replication in* Xenopus**

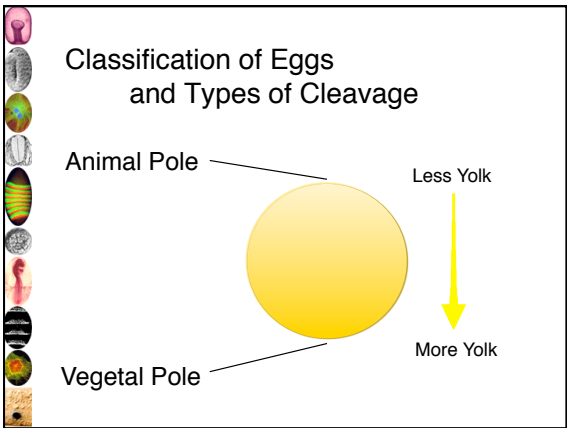


DEVELOPMENTAL BIOLOGY, Seventh Edition, Figure 10.3 (Part 2) Sinauer Associates, Inc. © 2003 All rights reserved.

Fig. 8.2(2) ***Cell Cycles of Somatic Cells and Early Blastomeres***



DEVELOPMENTAL BIOLOGY, Seventh Edition, Figure 6.2 (Part 2) Sinauer Associates, Inc. © 2003 All rights reserved.



Classification of Eggs and Types of Cleavage

Classification by yolk content

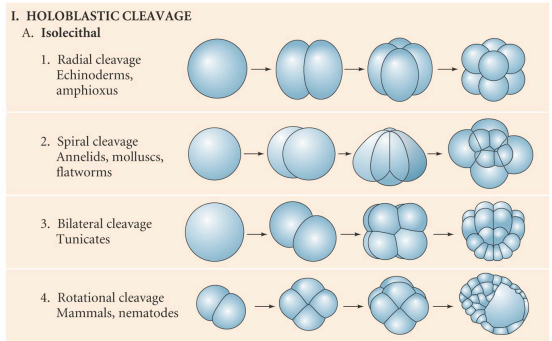
- Isolecithal - little yolk, evenly distributed
- Mesolecithal - moderate yolk
- Telolecithal - large amounts of yolk

Classification of Eggs and Types of Cleavage

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***



Last classification: Cleavage symmetry

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

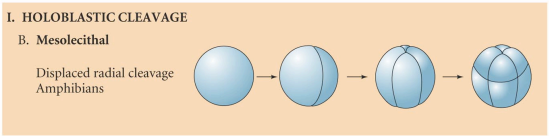


Figure 8.4(3) ***Summary of the Main Patterns of Cleavage***

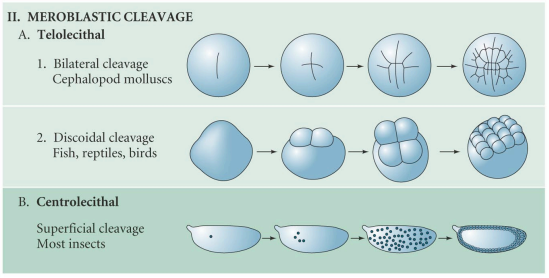


Fig. 8.8 ***Cleavage in Live Embryos of the Sea Urchin***

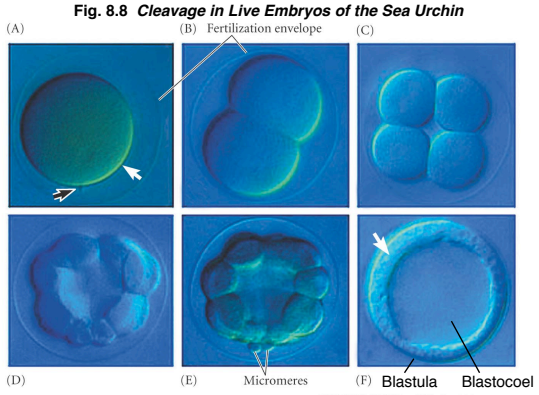


Figure 8.7 ***Cleavage in the Sea Urchin***

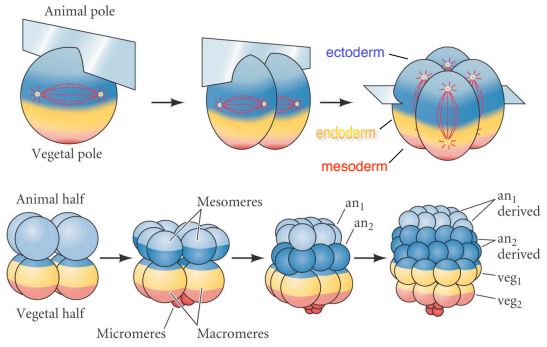


Figure 8.25(1) ***Spiral Cleavage of the Mollusc*** **Trochus**

(A) VIEW FROM ANIMAL POLE

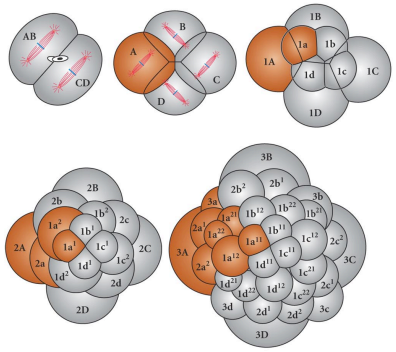
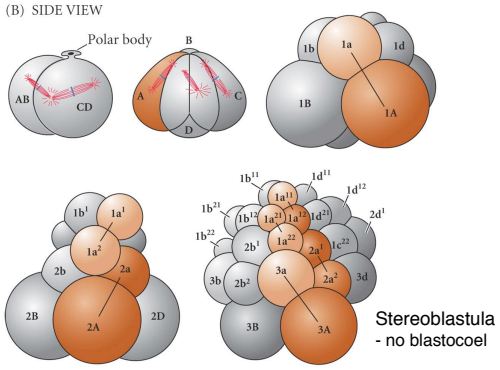


Figure 8.25(2) ***Spiral Cleavage of the Mollusc*** **Trochus**

(B) SIDE VIEW



Stereoblastula
- no blastocoel

Figure 8.26(1) ***Spiral Cleavage of the Snail*** **Ilyanassa**

(A)

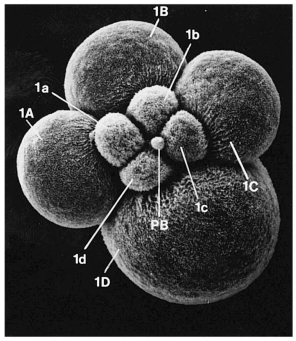


Figure 8.27(1) ***Looking Down on the Animal Pole of (A) Left-Coiling and (B) Right-Coiling Snails***

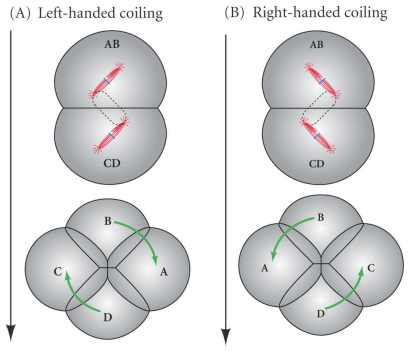
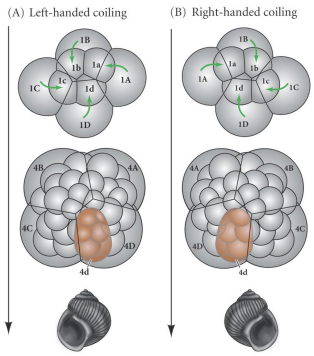
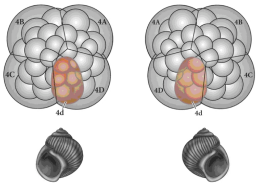


Figure 8.27(2) ***Looking Down on the Animal Pole of (A) Left-Coiling and (B) Right-Coiling Snails***



Maternal effect genes: the genetics of shell-coiling in *Limnaea*

Left-handed snail from *dd* mother



Right-handed snail - from *DD* or *Dd* mother

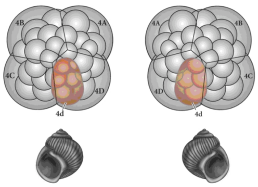
Genotype of mother determines coiling of progeny, regardless of progeny genotype.

DD, Dd mother: all right-handed progeny

dd mother: all left-handed progeny

Maternal effect genes: the genetics of shell-coiling in *Limnaea*

Left-handed snail - genotype could be: *Dd* or *dd* !



Right-handed snail - genotype could be: *DD, Dd* or *dd* !

Maternal effect makes for atypical genetics:

DD female X *dd* male - all progeny *Dd*, all right-handed

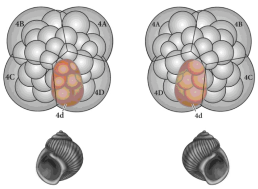
dd female X *DD* male - all progeny *Dd*, all left-handed

Dd female X *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.

Maternal effect genes: the genetics of shell-coiling in *Limnaea*

Left-handed snail - from *dd* mother



Right-handed snail - from *DD* or *Dd* mother

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**

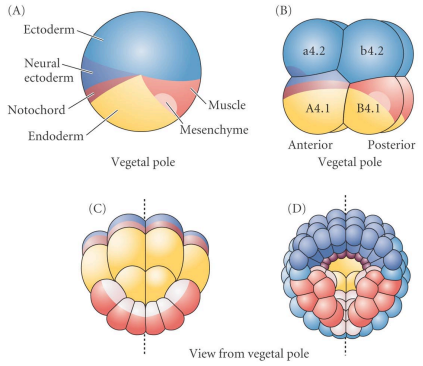


Figure 8.4(2) ***Summary of the Main Patterns of Cleavage***

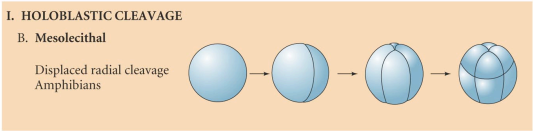


Figure 10.1 ***Cleavage of a Frog Egg***

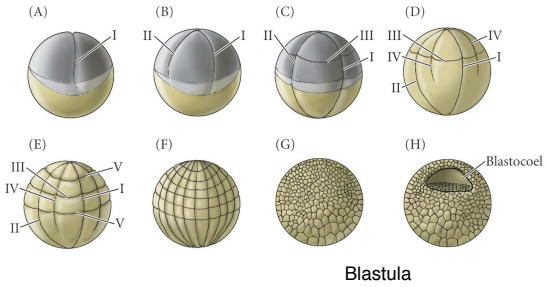


Figure 10.2 ***Scanning Electron Micrographs of Cleavage of Frog Egg***

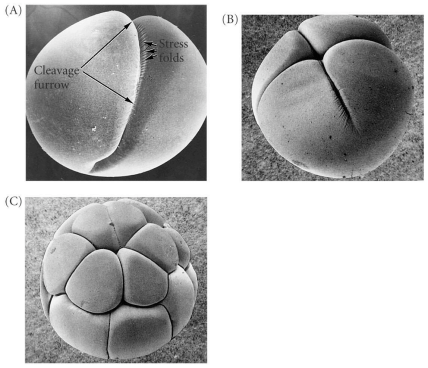
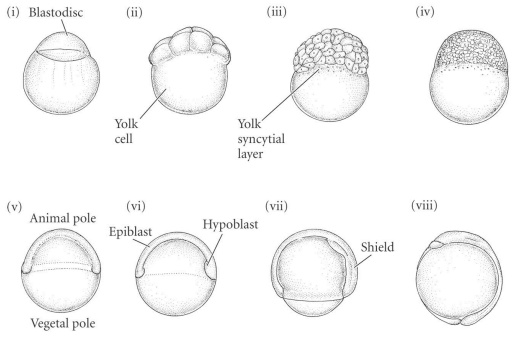


Figure 11.1(1) ***Zebrafish Development Occurs Very Rapidly***



Discoidal Meroblastic Cleavage

Figure 11.4 ***Discoidal Meroblastic Cleavage in a Zebrafish Egg***

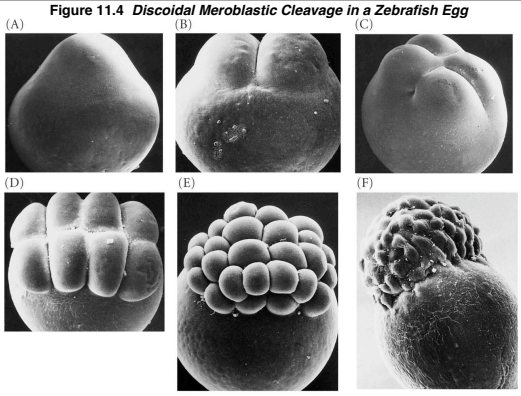


Figure 11.12 ***Discoidal Meroblastic Cleavage in a Chick Egg***

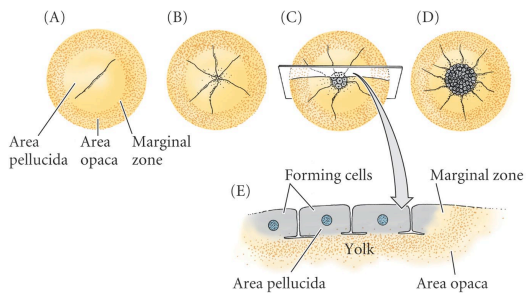


Figure 11.13(A) ***Formation of the Blastoderm of the Chick Embryo (simplified version)***

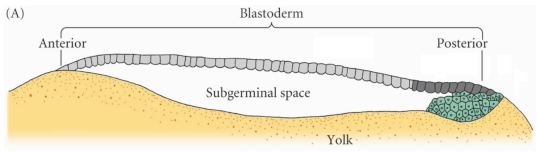
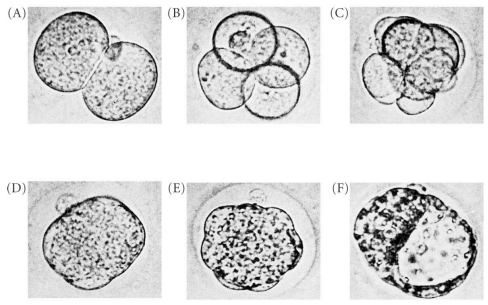


Figure 11.28 ***The Cleavage of a Single Mouse Embryo*** **In Vitro**



Holoblastic Isolecithal Rotational Cleavage

Fig. 11.27 ***Early Cleavage in (a) Echinoderms and Amphibians and (B) Mammals***

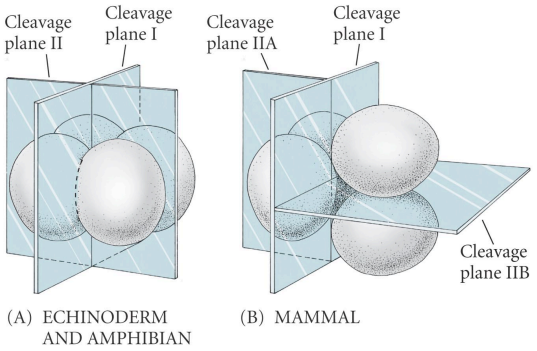
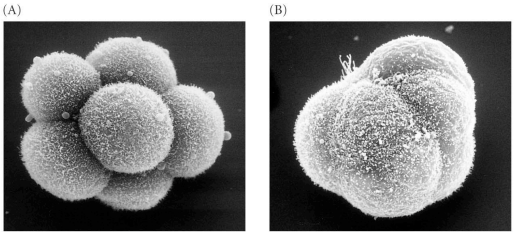


Fig. 11.29 ***SEMs of (A) Uncompacted and (B) Compacted 8-cell Mouse Embryos***



Compaction indicates change in cell-cell adhesion

Figure 11.26 ***Development of a Human Embryo From Fertilization to Implantation***

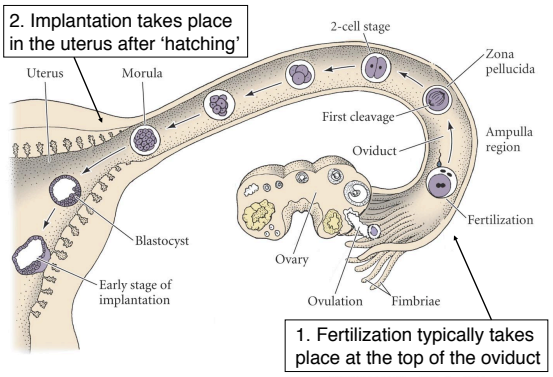
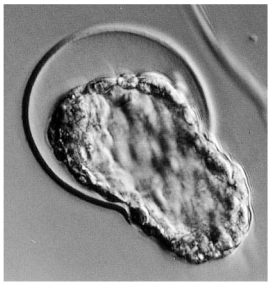
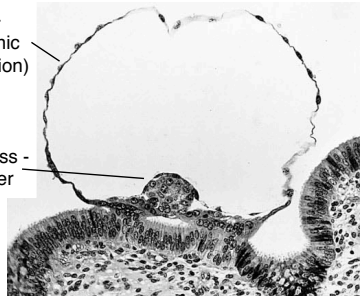


Figure 11.30 ***Hatching From Zona And Implantation of Mammalian Blastocyst***



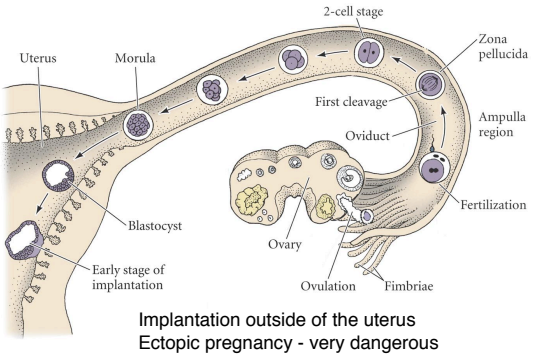
Blastocyst hatching
from zona pellucida

Figure 11.30 ***Hatching From Zona And Implantation of Mammalian Blastocyst***



Blastocyst implanting into uterine wall

Figure 11.26 ***Development of a Human Embryo From Fertilization to Implantation***



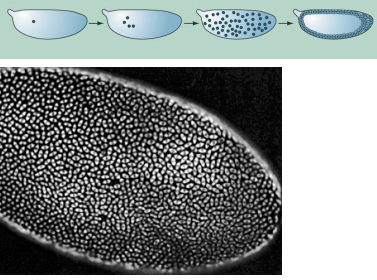
Implantation outside of the uterus
Ectopic pregnancy - very dangerous

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

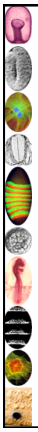
II. MEROBLASTIC CLEAVAGE

B. **Centrolecithal**

Superficial cleavage
Most insects



Drosophila blastoderm, cycle 13



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***

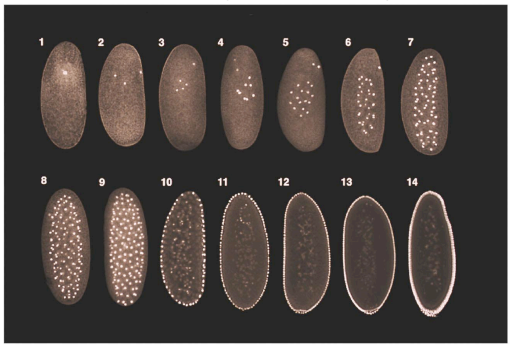


Figure 9.3(1) ***Formation of the Cellular Blastoderm in*** **Drosophila**

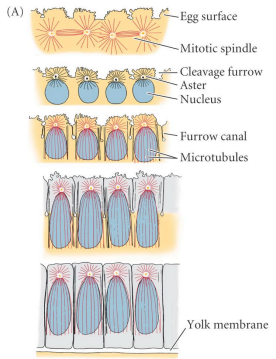
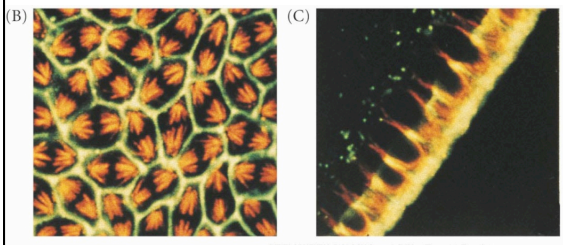


Figure 9.3(2) ***Formation of the Cellular Blastoderm in*** **Drosophila**



Microtubules - Orange Actin - Green