

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

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## Cleavage

Rapid cell division without growth

Rate of cell division in 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

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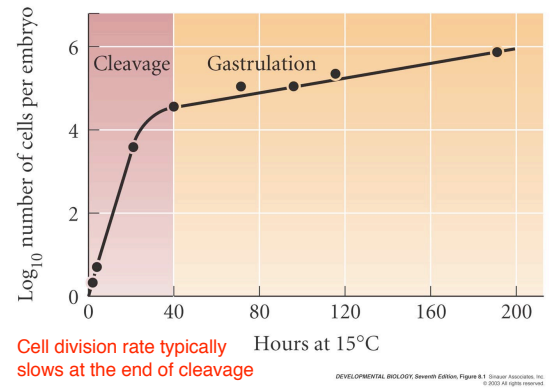
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Figure 8.1 Rate of Formation of New Cells During Early Development of the Frog



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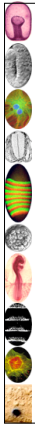
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## Cleavage

Two separable events:

Karyokinesis (mitosis) - nuclear division

Cytokinesis - cell division

Cytoskeletal elements key to these events:

Microtubules (spindle apparatus)

Actin microfilaments (contractile ring)

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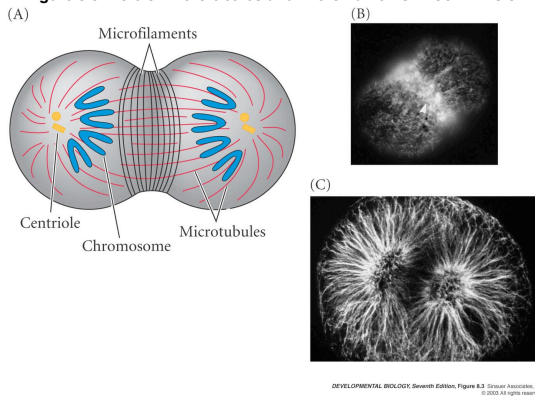
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**Figure 8.3 Role of Microtubules and Microfilaments in Cell Division**



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**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 <sup>a</sup>
Cytokinesis	Contractile ring	Actin microfilaments	Cortical cytoplasm	Cytochalasin B

<sup>a</sup>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).

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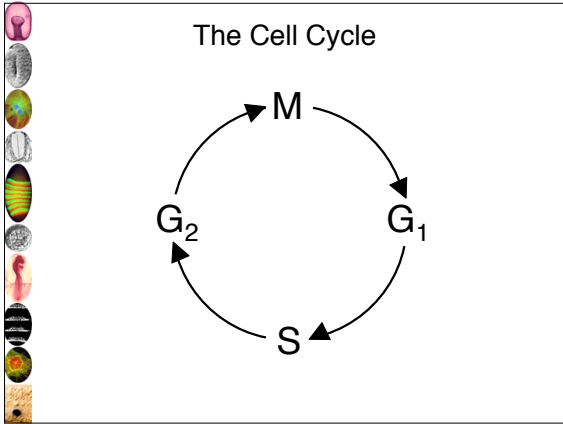
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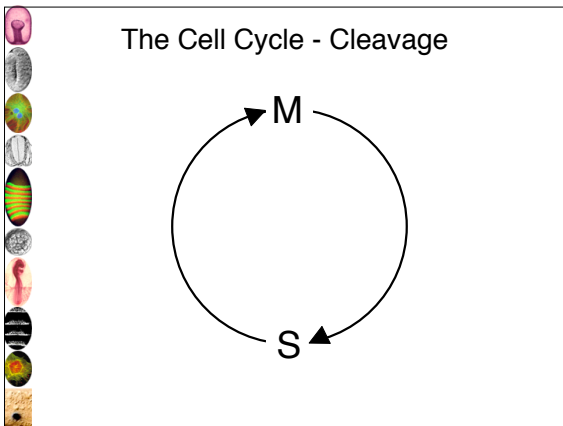
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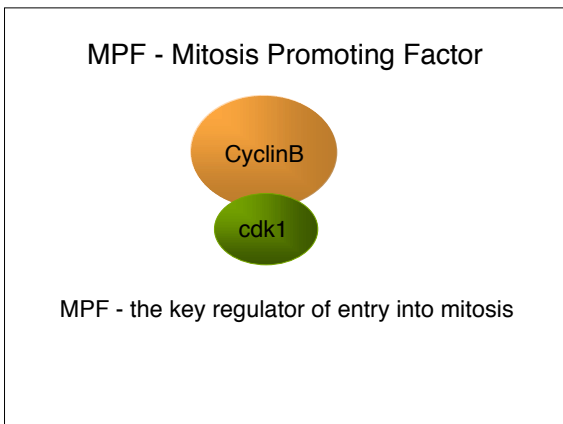
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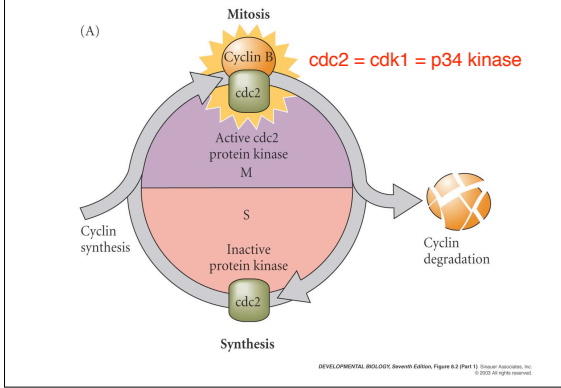


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**Figure 8.2(1) Cell Cycles of Somatic Cells and Early Blastomeres**




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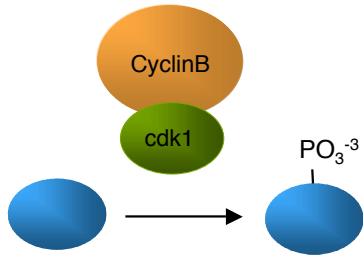
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**MPF - Mitosis Promoting Factor**



cdk1 phosphorylates proteins to alter function

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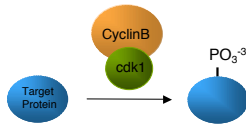
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**Events in Mitosis      Targets of cdk1 phosphorylation**

- |                            |  |
|----------------------------|--|
| Nuclear envelope breakdown | <b>Nuclear lamin proteins</b> - promotes disassembly |
| Chromosome condensation    | <b>Histones</b> - promotes condensation              |
| Cytokinesis                | <b>Myosin</b> - inhibits initiation of cytokinesis   |
| Little or no transcription | <b>RNA Polymerase</b> - inhibits transcription       |




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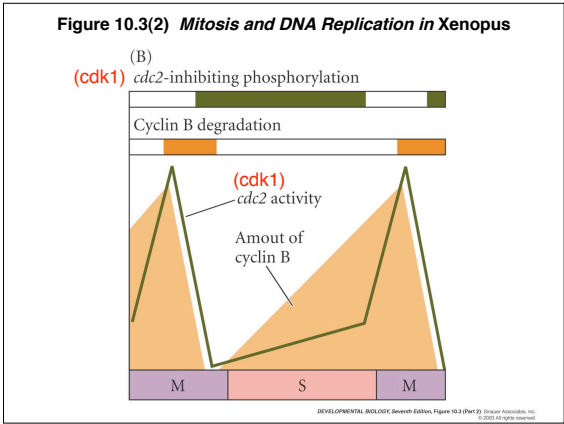
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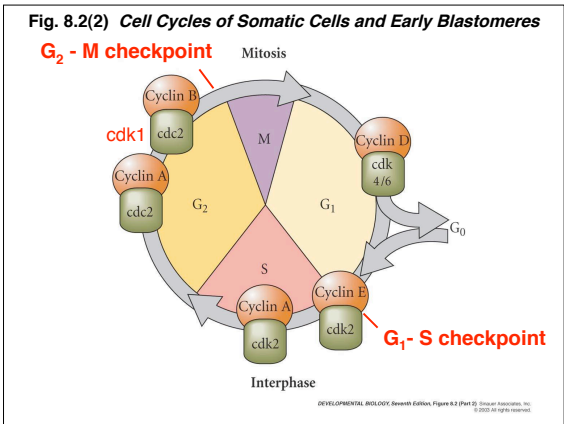
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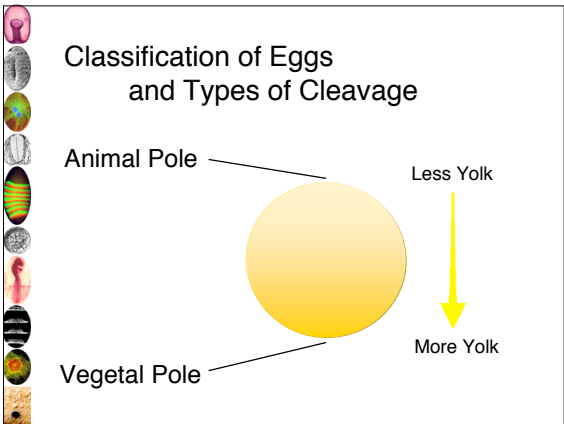
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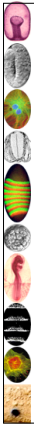
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## Classification of Eggs and Types of Cleavage

### Classification by yolk content

Isolecithal - little yolk, evenly distributed

Mesolecithal - moderate yolk

Telolecithal - large amounts of yolk

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## Classification of Eggs and Types of Cleavage

### Yolk content affects how cells divide

Holoblastic cleavage - complete division

Meroblastic cleavage - incomplete division

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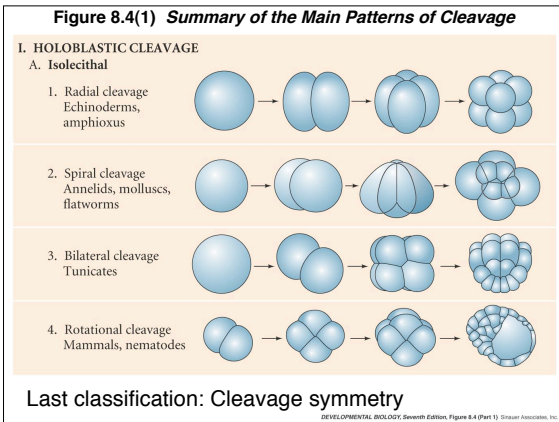
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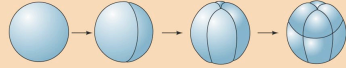
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**Figure 8.4(2) Summary of the Main Patterns of Cleavage**

**I. HOLOBLASTIC CLEAVAGE**

**B. Mesolecithal**

Displaced radial cleavage  
Amphibians



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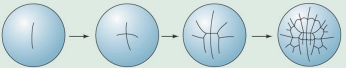
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**Figure 8.4(3) Summary of the Main Patterns of Cleavage**

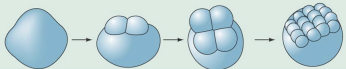
**II. MEROBLASTIC CLEAVAGE**

**A. Telolecithal**

1. Bilateral cleavage  
Cephalopod molluscs

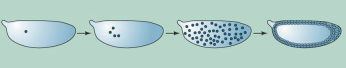


2. Discoidal cleavage  
Fish, reptiles, birds



**B. Centrolecithal**

Superficial cleavage  
Most insects



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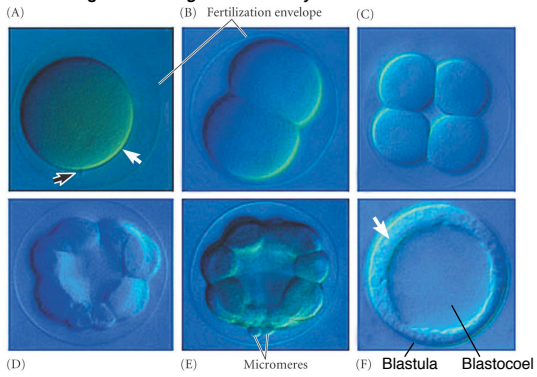
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**Fig. 8.8 Cleavage in Live Embryos of the Sea Urchin**




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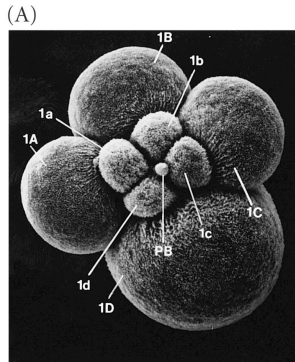
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**Figure 8.26(1) Spiral Cleavage of the Snail Ilyanassa**



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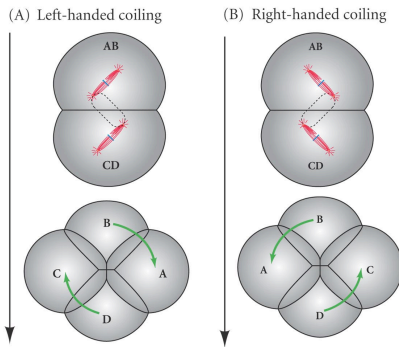
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**Figure 8.27(1) Looking Down on the Animal Pole of (A) Left-Coiling and (B) Right-Coiling Snails**



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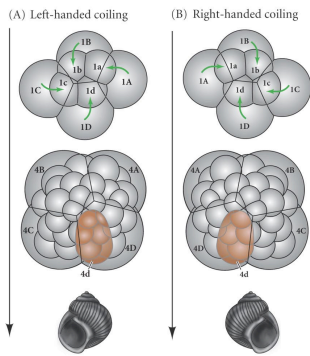
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**Figure 8.27(2) Looking Down on the Animal Pole of (A) Left-Coiling and (B) Right-Coiling Snails**



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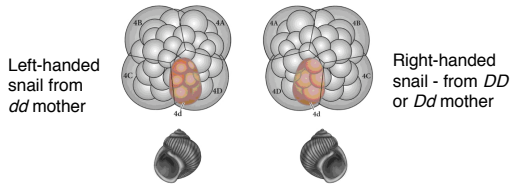
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**Maternal effect genes: the genetics of shell-coiling in *Limnaea***



The genotype of the mother determines the coiling of the progeny, regardless of the progeny genotype.

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

*dd* mother: all left-handed progeny

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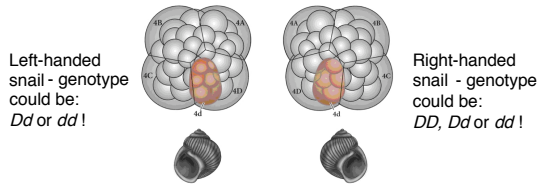
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**Maternal effect genes: the genetics of shell-coiling in *Limnaea***



The 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.

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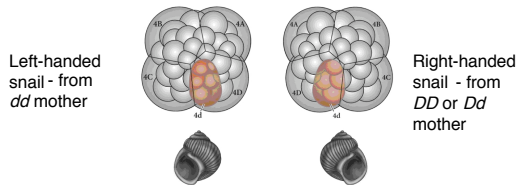
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**Maternal effect genes: the genetics of shell-coiling in *Limnaea***



Important general lesson: Early development is regulated by the maternally-provided cytoplasm (egg cytoplasm) vs. the zygote nucleus.

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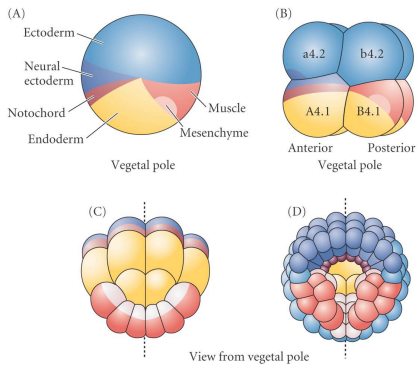
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**Fig. 8.36 Bilateral Symmetry in the Egg of the Tunicate *Styela partita***



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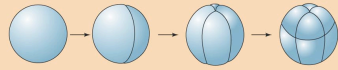
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**Figure 8.4(2) Summary of the Main Patterns of Cleavage**

**I. HOLOBLASTIC CLEAVAGE**

**B. Mesolecithal**

Displaced radial cleavage  
Amphibians



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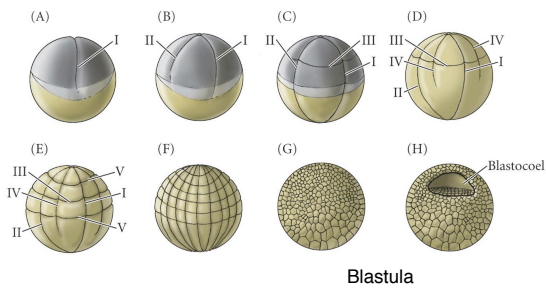
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**Figure 10.1 Cleavage of a Frog Egg**



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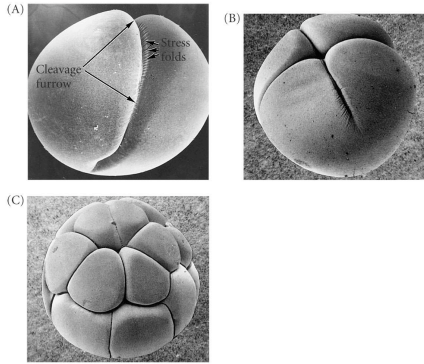
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**Figure 10.2 Scanning Electron Micrographs of Cleavage of Frog Egg**



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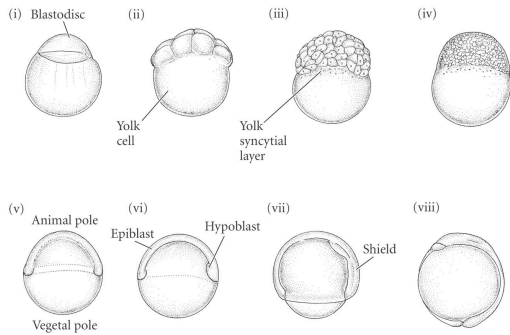
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**Figure 11.1(1) Zebrafish Development Occurs Very Rapidly**



**Discoidal Meroblastic Cleavage**

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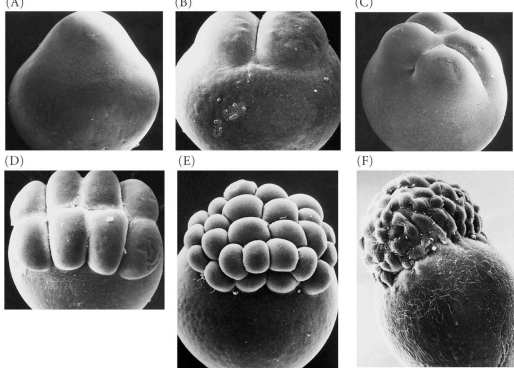
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**Figure 11.4 Discoidal Meroblastic Cleavage in a Zebrafish Egg**



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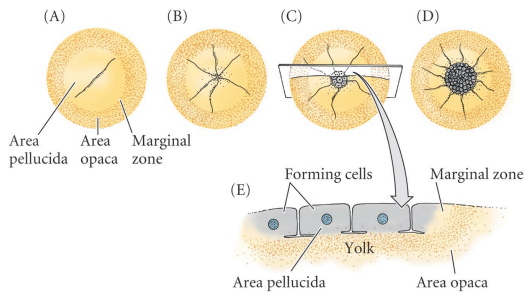
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**Figure 11.12 Discoidal Meroblastic Cleavage in a Chick Egg**



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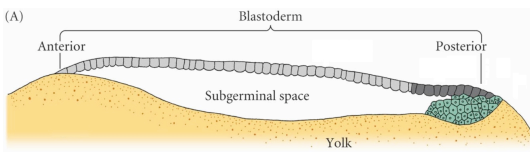
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**Figure 11.13(A) Formation of the Blastoderm of the Chick Embryo (simplified version)**




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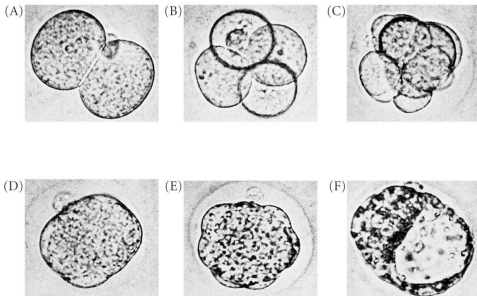
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**Figure 11.28 The Cleavage of a Single Mouse Embryo In Vitro**



**Holoblastic Isolecithal Rotational Cleavage**

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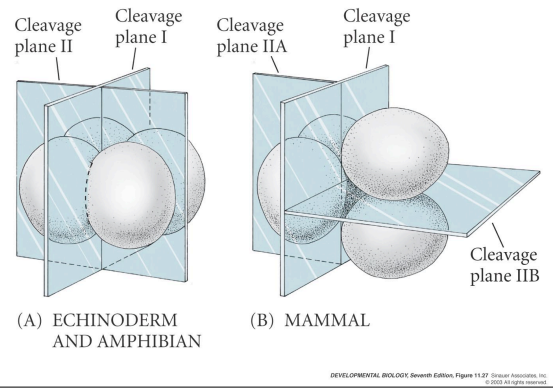
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**Fig. 11.27 Early Cleavage in (a) Echinoderms and Amphibians and (B) Mammals**




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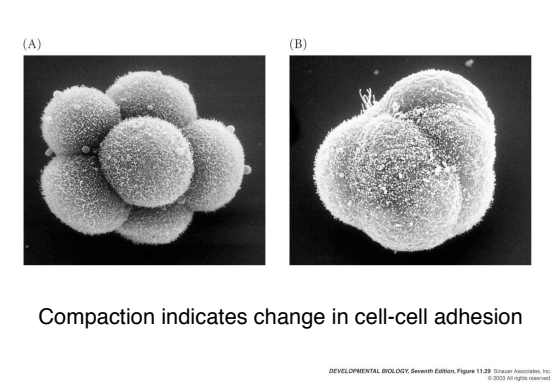
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**Fig. 11.29 SEMs of (A) Uncompacted and (B) Compacted 8-cell Mouse Embryos**




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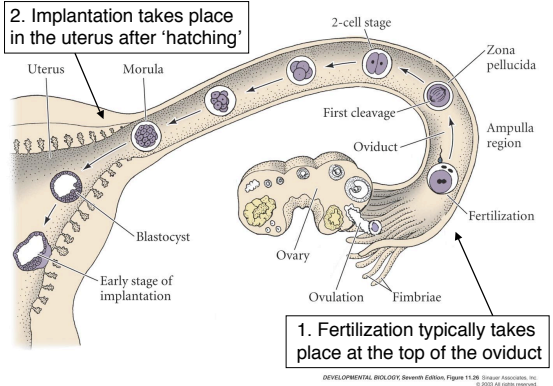
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**Figure 11.26 Development of a Human Embryo From Fertilization to Implantation**




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



Blastocyst hatching from zona pellucida

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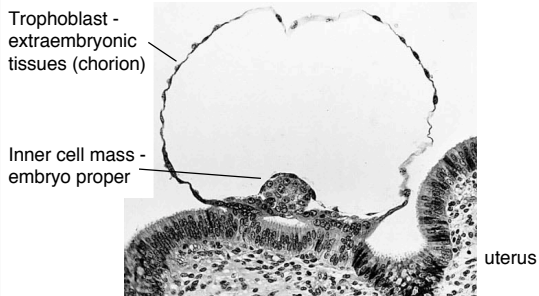
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Figure 11.30 *Hatching From Zona And Implantation of Mammalian Blastocyst*



Blastocyst implanting into uterine wall

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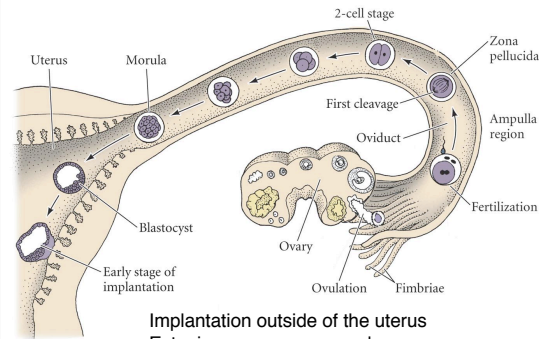
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Figure 11.26 *Development of a Human Embryo From Fertilization to Implantation*



Implantation outside of the uterus  
Ectopic pregnancy - very dangerous

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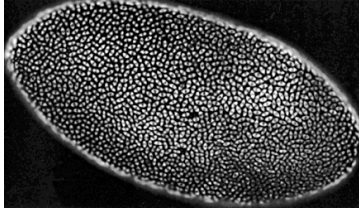
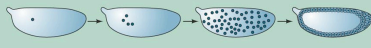
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**Figure 8.4(3) Summary of the Main Patterns of Cleavage**

II. MEROBLASTIC CLEAVAGE

B. Centrolecithal

Superficial cleavage  
Most insects



*Drosophila* blastoderm, cycle 13

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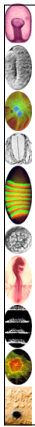
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*Drosophila* Syncitial Early Development

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

Embryo forms a **syncitial blastoderm**

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

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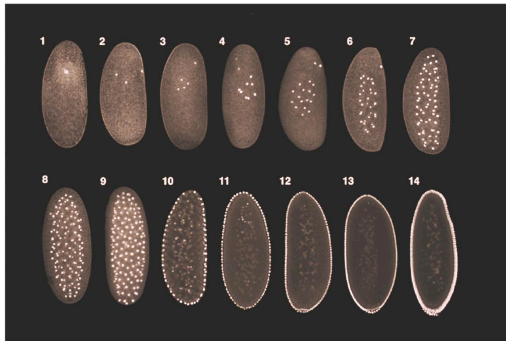
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**Figure 9.1 Laser Confocal Micrographs of Stained Chromatin Showing Superficial Cleavage in a *Drosophila* Embryo**



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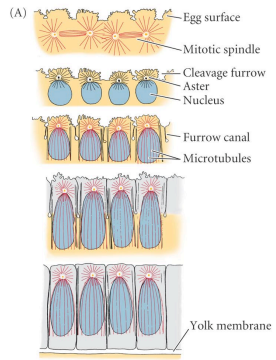
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**Figure 9.3(1) Formation of the Cellular Blastoderm in Drosophila**



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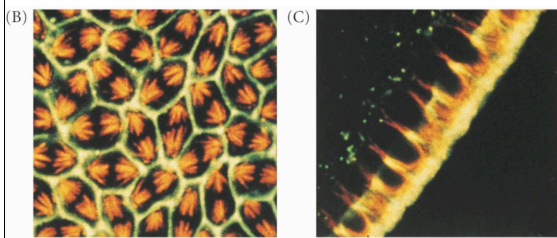
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**Figure 9.3(2) Formation of the Cellular Blastoderm in Drosophila**



Microtubules - Orange    Actin - Green

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