

Cleavage

Cleavage = mitotic cell division of early embryo, eventually forming a blastula or blastodisc.

Cleavage - During the early stages of cleavage, the cells (known as blastomeres) show very little growth (e.g., zygote and blastula are about the same size).

- Egg Types are important in determining the nature of the cleavage process
 1. Microlecithal = little yolk, blastomeres equal in size (Mammals, Amphioxus)
 2. Mesolecithal = somewhat more yolk (moderate amount). Blastomeres are unequal in size (Amphibians, lamprey, lungfish).
 3. Macrolecithal = lots of yolk (Reptiles, Birds, Elasmobranchs)
- There are also terms describing the distribution of yolk within the egg:
 1. Oligolecithal = yolk evenly distributed (microlecithal)
 2. Telolecithal = yolk concentrated in one hemisphere (meso- and macrolecithal)

Cleavage Types

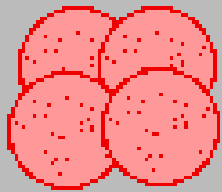
- Holoblastic = total cleavage. The entire egg divides, as do successive blastomeres.
 - Equal = microlecithal eggs; dividing cells are equal in size
 - Unequal = mesolecithal eggs; dividing cells ventrally are larger than those dorsally
- Meroblastic (Discoidal) = division occurs only in a small area at the animal pole (becomes the blastodisc).
- Oligo (Micro) → Holoblastic equal cleavage (Mammals, Amphioxus)
- Telo (Meso) → Holoblastic unequal (Amphibians)
- Telo (Macro) → Discoidal (Reptiles, Birds, Elasmobranchs)

Cleavage Patterns

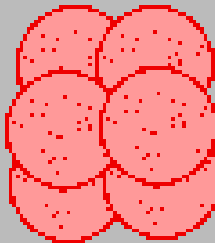
- Regular progression of cleavage divisions:
 - Vertical plane → produces 2 cells
 - Vertical plane, but rotated 90° → 4 cells
 - Horizontal plane → 8 cells
- Position of upper cells relative to lower cells during cleavage is important to classification:
 - *Radial Cleavage* = cleavages are symmetrical to the first (Echinoderms and Chordates – cleavage pattern shows link between these groups, both deuterostomes).
 - *Spiral Cleavage* = cleavages are rotated from the first (Annelids, Molluscs, some other invertebrates → separate evolutionary lineage: Protostomes)
- End product of cleavage is the blastula (micro-, meso-) or blastodisc (macro-).

Radial Cleavage

Four-cell embryo



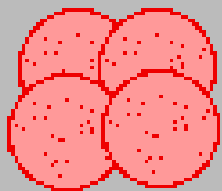
8-cell embryo (2 cells,
hidden behind, can't be seen)



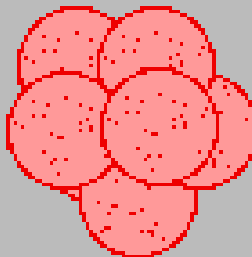
Cell division has occurred so that
the cells are aligned directly over
each other

Spiral Cleavage

Four-cell embryo

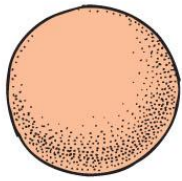


8-cell embryo (2 cells,
hidden behind, can't be seen)

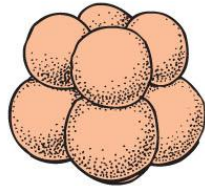


Cell division has occurred so that
the cells are NOT aligned directly
over each other, but rather are
aligned at an angle.

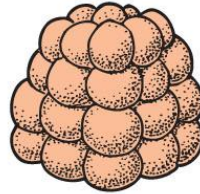
Zygote



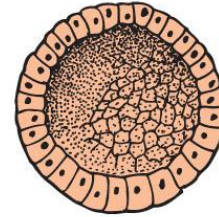
Morula



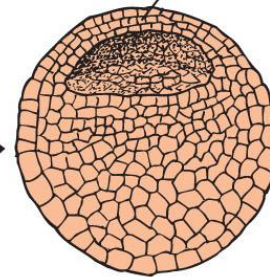
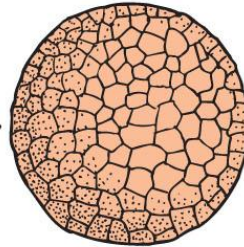
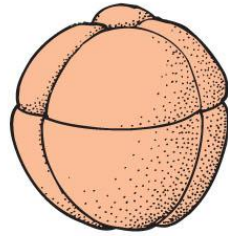
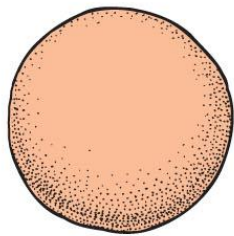
Blastula



Sagittal section of blastula



(a) Amphioxus = holoblastic equal



Blastoderm

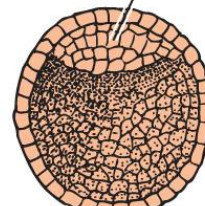
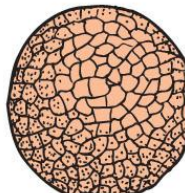
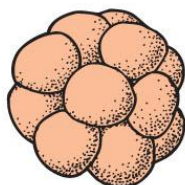
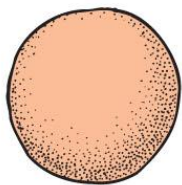
(b) Amphibians = holoblastic unequal



Blastoderm

Subgerminal space

(c) Reptiles/birds = discoidal



Inner cell mass

(d) Mammals (eutherian) = holoblastic equal

Fig 5.2 – Cleavage stages in chordates

Fig 5.3 – Holoblastic unequal cleavage in the bowfin, *Amia*

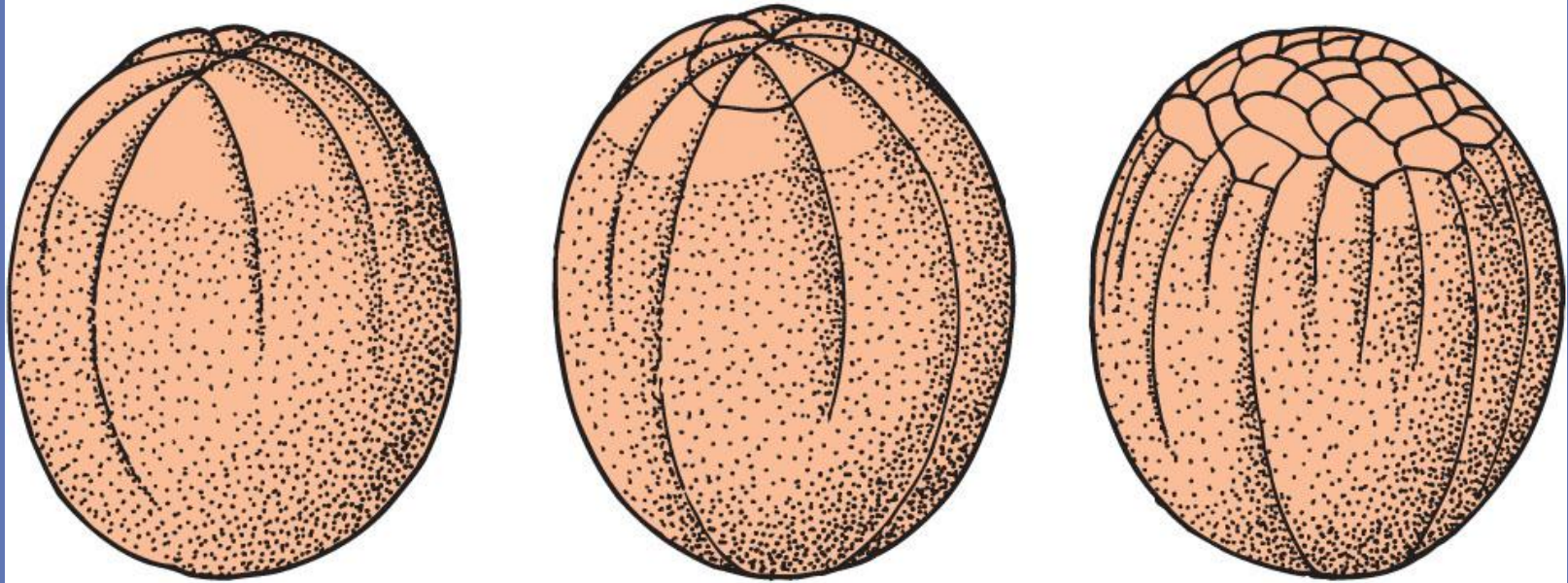
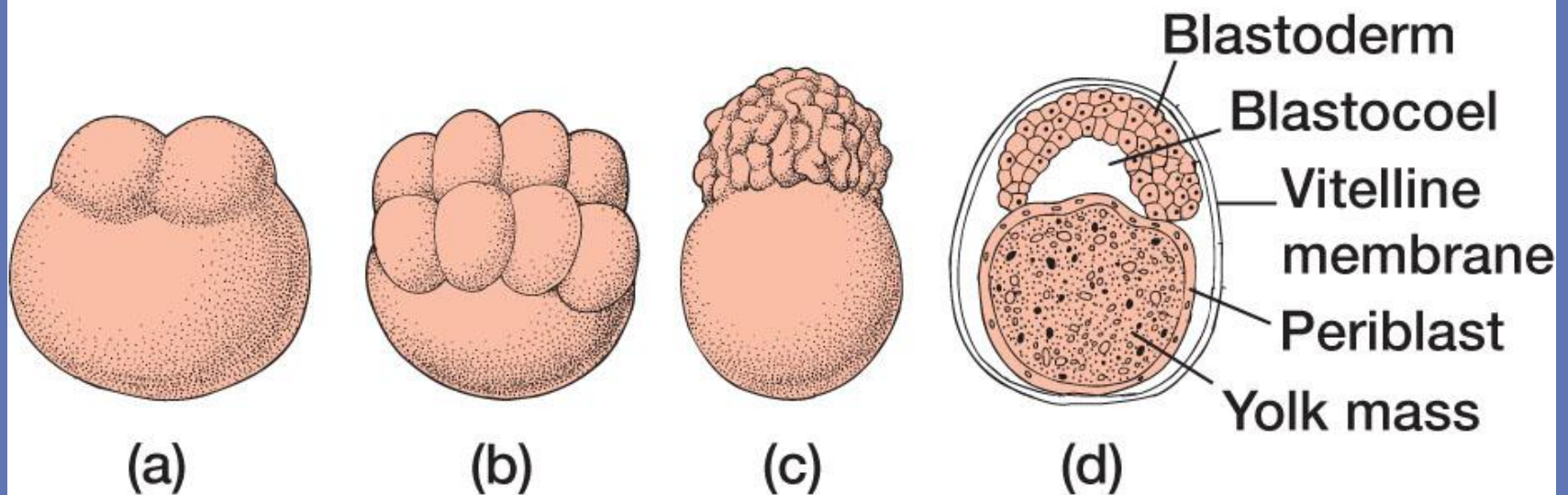
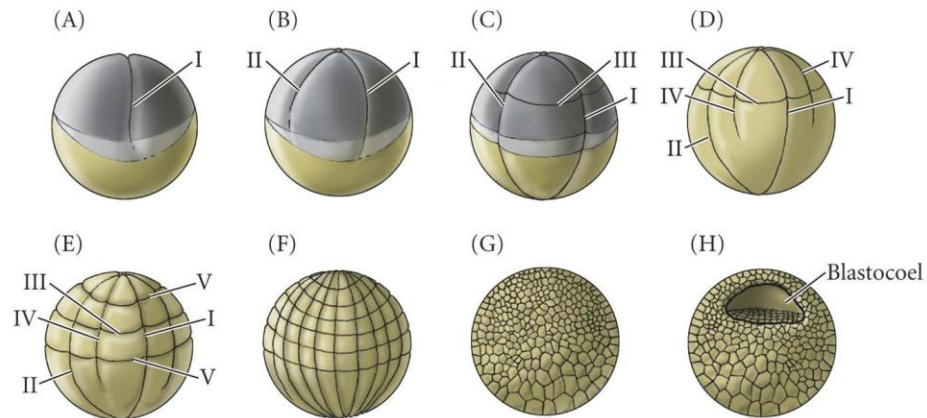


Fig 5.4 – Discoidal cleavage in the Zebrafish, *Danio rara*



Cleavage in a frog

- Describe the progression of events.



Amphibian Cleavage Video

<http://www.luc.edu/faculty/wwasser/dev/cleavage.mov>

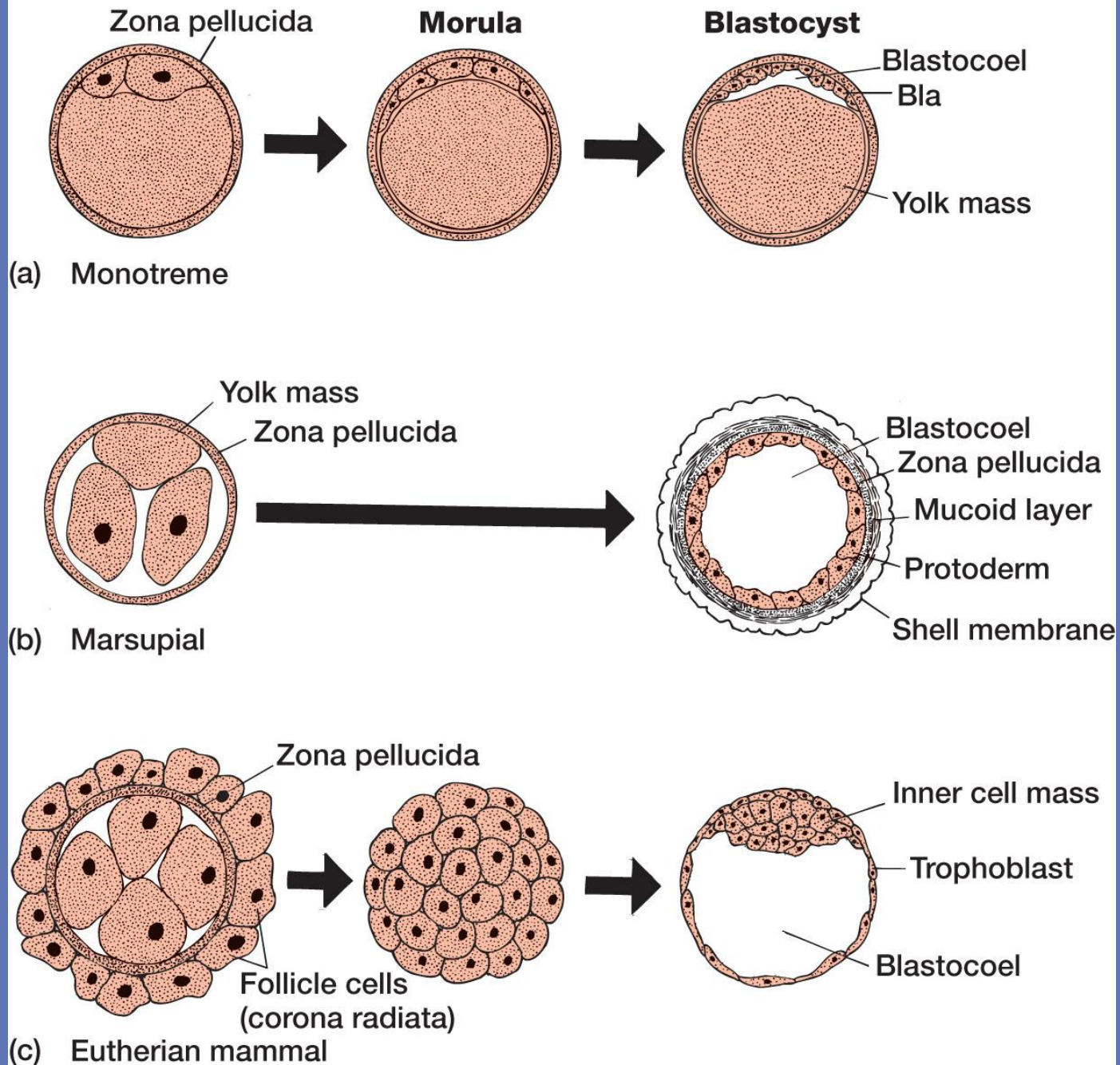
Blastulae

1. Microlecithal (Amphioxus) → hollow sphere
 2. Mesolecithal (Amphibian) → hollow sphere, wall is several layers thick.
 3. Macrolecithal → blastula forms as a plate, several cell layers thick, on top of the yolk mass (blastula termed a blastodisc).
- 2 areas of the blastodisc:
 - Area opaca = peripheral portion of blastodisc
 - attached to the yolk mass
 - involved in digestion of yolk and formation of the extraembryonic membranes.
 - doesn't contribute to the embryo
 - Area pellucida = central part of blastodisc
 - becomes lifted off the yolk mass
 - forms the actual embryo

Blastulae

4. Microlecithal (mammals) → blastula becomes specialized for placental attachment.
- Early division (cleavage) similar to that in Amphioxus, but later 2 distinct groups of cells develop:
 - Trophoblast = expanded sphere of cells (similar to Amphioxus blastula)
 - Inner Cell Mass = mass of cells lying directly on top of blastocoel. Similar to macrolecithal blastodisc.
 - Trophoblast becomes extraembryonic membranes, which form the embryonic side of the placenta.
 - Inner Cell Mass develops into the embryo.

Fig 5.5 – Cleavage and blastulae in living mammals



Chemical Changes During Cleavage

- Ratio of Nuclear (DNA) to Cytoplasmic Material
 - very low in zygote
 - reaches adult cell levels, essentially without growth, by blastula stage.
- Therefore – the amount of DNA in the embryo increases as division (cleavage) proceeds. *Where does this DNA originate?*
 - Czihak et al. (1967) - Experiment: radioactive Uridine was given to early sea urchin embryos → some of it becomes incorporated into DNA (indicates conversion of RNA to DNA). Later research showed that conversion was due to the enzyme ribonuclease reductase, present in the zygote.
 - So ... *one source* of increased DNA is from the RNA, present in the cytoplasm of the zygote, which is converted to DNA.
 - Grant (1958) - Experiment: ^{14}C -glycine injected into zygotes → some becomes incorporated into DNA by serving as a precursor in purine synthesis.
 - *A second source* of DNA are precursors (amino acids) present in the zygote (purines = A,G. pyrimidines = C,T,U).

Chemical Changes During Cleavage

- Protein Synthesis - mostly proteins directly involved in cell multiplication (e.g., histones, tubulin → microtubules, ribonucleotide reductase {RNA→DNA}).
- Experimental:
 - Treat cleaving eggs with puromycin (which inhibits RNA-dependent protein synthesis) → cleavage stops.
 - Treat cleaving eggs with Actinomycin D (which inhibits RNA production) → cleavage proceeds normally.
- Conclusion: Protein synthesis uses RNA (all three varieties) already present in the zygote.

References

- www.smackslide.com-embryology-usd-5ebd349e6b8dd