02 CLEAVAGE

2.1. INTRODUCTION

Soon after fertilization, the fertilized egg resorts to successive cell divisions. The division of cells is spoken of as **cleavage.** In this process there are usual mitotic divisions. But there is a subtle difference between the mitotic divisions in the adult and during cleavage. In the adult, after each mitotic division, the daughter cells regain the original size but in case of cleavage the resulting blastomeres do not increase in size, but are half the size of the orginal cell. The blastomeres have larger nuclei than those present in the somatic cells. This is due to large nuclear sap rather than chromatin mass. In other words, there is a progressive increase in the nucleocytoplasmic ratio during cleavage.

Every time there is a cleavage the DNA duplicates in *s*-period of the interphase. Ribosomal RNA is not synthesized during cleavage. Messenger RNA and transfer RNA are synthesized particularly during the later stages of cleavage. A number of proteins are synthesized during cleavage and these are histones, tubulin, ribonucleotide reductase, DNA polymerase, etc.

2.2. TYPES OF CLEAVAGE

(i) Radial—In this case, the blastomeres of the upper tier lie over the blastomeres of the lower tier, so that the pattern of blastomeres is radially symmetrical.

Ex. eggs of echinoderms.

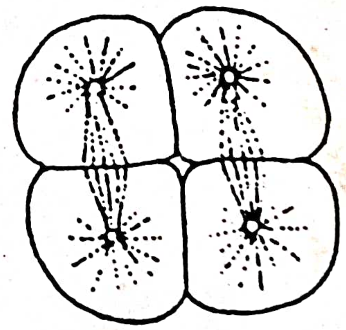

Fig. 2.1. Radial cleavage with equal-sized blastomeres (Viewed from animal pole, 4-cell stage)

(ii) Spiral—In protostomes, the blastomeres of the upper tier shift in the same direction in relation to the blastomeres of the lower tier. The oblique positions of mitotic spindles do not allow the two daughter cells to lie one above the other. Ex. annelids, molluscs, etc.

Depending upon the turn of the spiral, it may be called **dextral** (clockwise), and **sinistral** (anticolckwise).

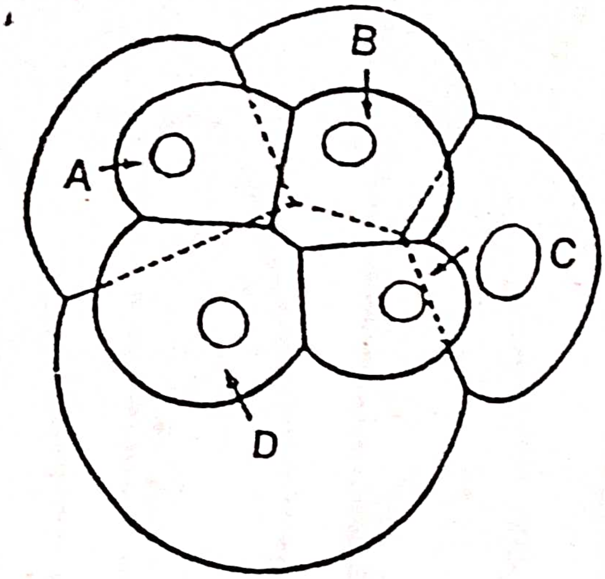

Fig. 2.2. Spiral cleavage in *Unio*. Blastomere D is larger than A, B, C.

(iii) Bilateral—In radial type of cleavage, out of the four blastomeres, two may be larger than the other two. This establishes the plane of bilateral symmetry. Ex. tunicates.

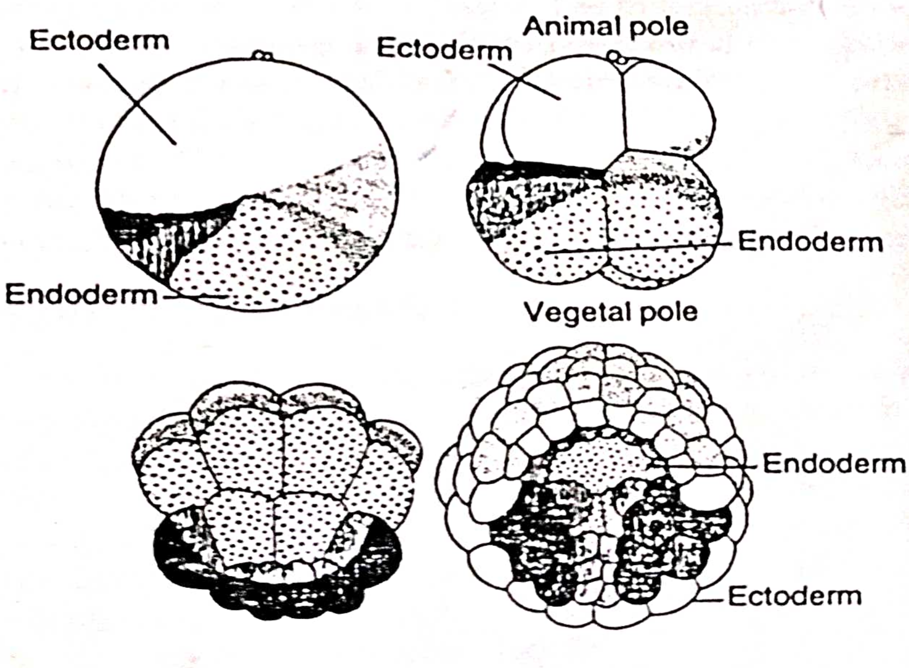

Fig. 2.3. Bilateral cleavages in Ascidian

(iv) Mosaic or determinate—In this type of cleavage, bilateral symmetry is established when the first division produces two unequal cells. The resulting cells then divide at right angles to each other giving rise to *T*-shaped blastomeres. In nematodes each of the blastomeres gives rise to specific parts of the embryo. This is the reason why such a cleavage is known as determinate type. Ex. nematodes.

The cleavage is greatly influenced by the distribution and amount of yolk in the fertilized egg. During the anaphase of the mitotic division, a furrow appears on the surface of the fertilized egg, known as **cytokinesis.** The furrow appears first in the area of the egg where there is little or less yolk. Gradually, there is a deepening of the furrow. But this is slowed down as it reaches the area where the amount of yolk is greater. Further accumulation of yolk in the vegetal hemisphere almost completely blocks the cell fission. In some cases, the cleavage furrow never reaches the vegetal pole so that the vegetal hemisphere remains uncleaved. This is known as **incomplete cleavage.** Ex. reptiles and birds. This type of cleavage is also called **meroblastic cleavage.** The other type of cleavage in which the hindrance is caused by the presence of yolk is not great enough to thwart complete separation of the two cells. In other words, when the two blastomeres become completely divided, the cleavage is called **holoblastic** or **complete.** Ex. *Amphioxus*, Frog.

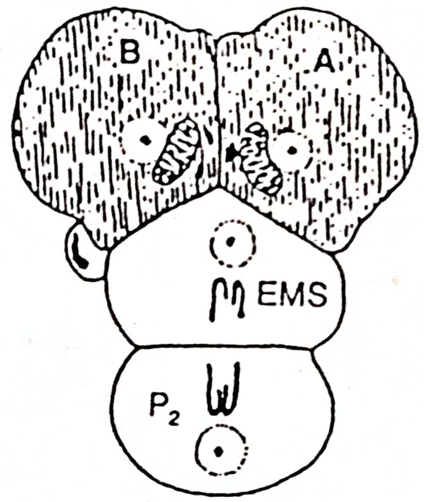

Fig. 2.4. Determinate cleavages in *Ascaris*

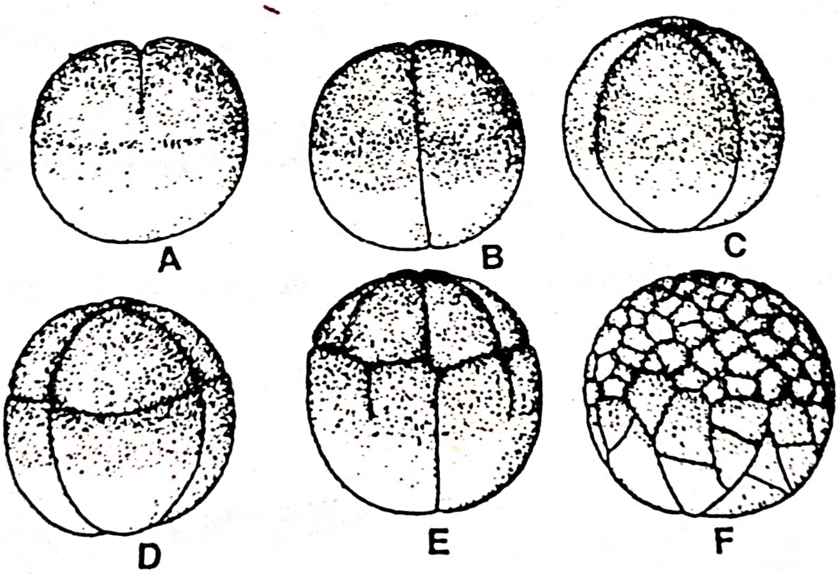

Fig. 2.5. Holoblastic cleavages in Frog egg (Semidiagrammatic)

In **centrolecithal eggs,** the cleavage is incomplete and the nuclei occupy the central position. Subsequently, these nuclei move to the periphery of the embryo. The nuclei are then surrounded by a small portion of the cytoplasm. The surface of the enbryo is syncytium with nuclei embedded in cytoplasm. Later on these cells become completely separated from the central yolk. This type of cleavage is known as **superficial cleavage.** Ex. insects.

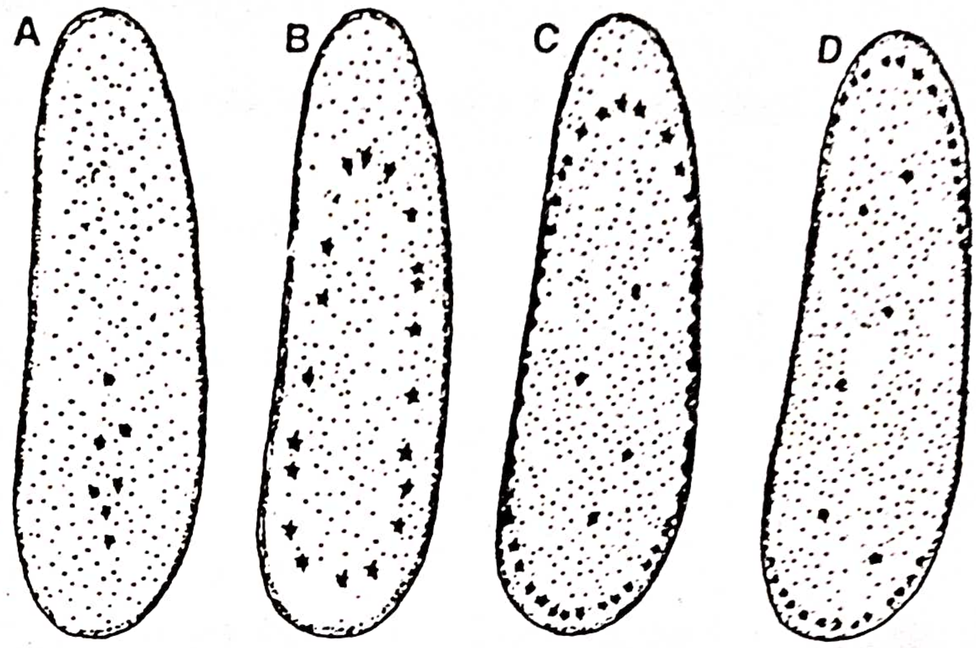

Fig. 2.6. Superficial cleavage in *centrolecithal egg of an insect*

2.3. CLEAVAGE IN AMPHIOXUS

The cleavage in *Amphioxus* is holoblastic. The first cleavage is **meridional** or vertical. The second cleavage is also meridional but at right angle to the first. The third cleavage is horizontal, but this occurs slightly above the equatorial plate, giving rise to four smaller cells called **micromeres** and four larger cells, the **macromeres.** The former occupy the animal pole, whereas the latter, vegetal pole. The fourth and fifth cleavages are meridional and horizontal, respectively. At sixty-four cell stage, the **blastula** becomes pear-shaped.

2.4. CLEAVAGE IN AMPHIBIA

In Frog, the first cleavage is meridional. The cleavage is **holoblastic.** The second cleavage is also meridional but at right angle to the first. This results in the formation of four equal **blastomeres.** The third cleavage is horizontal but slightly displaced towards the animal pole. Thus the four blastomeres are cleaved unequally. This division gives rise to four smaller **micromeres** in the animal hemisphere and four larger **macromeres** in the vegetal hemisphere. The fourth cleavage is also vertical (from animal pole to vegetal pole). The fifth cleavage is somewhat irregular (Fig. 2.5).

2.5. CLEAVAGE IN BIRDS

Since the eggs of birds are heavily laden with yolk, the cleavages are restricted to the blastodisc which is a small protoplasmic area confined to the animal pole. It is meroblastic cleavage. The first cleavage is meridional which occurs at about 4 hours from fertilzation. The second cleavage occurs at right angle to the first, but is vertical. The third cleavage is also vertical but tends to be irregular. The fourth cleavage cuts off the cells into central and peripheral

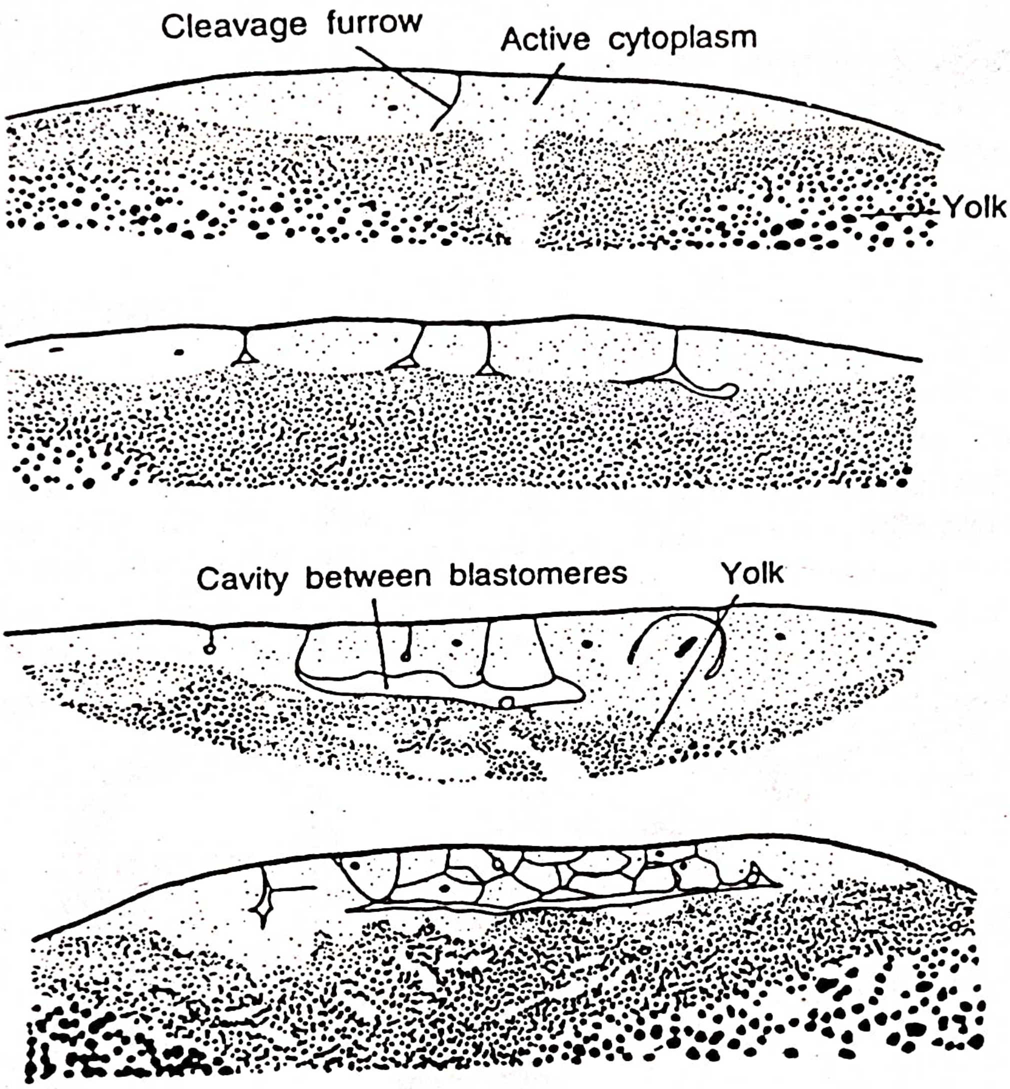

Fig. 2.7. Stages in the cleavage of hen's egg in sections (*A–D*)

parts. In this way, eight central blastomeres and eight marginal blastomeres are formed.

2.6. CLEAVAGE IN MAMMALS

Eutherian eggs have holoblastic cleavage. But there is no synchronization among the blastomeres as far as the timing of cleavage is concerned. Moreover, the speed of cleavage is slower than that of other vertebrates. Two-cell stage is reached after 12 hours of fertilization; one of the two blastomeres is slightly larger than the other. The larger cell divides first. The smaller cells are slower in division. Mitotic spindles of the cleavages are at right angles to one another. There is a good deal of asynchrony and independence among the blastomeres of mammalian morula.

2.7. CLEAVAGE THEORIES

There are several theories to account for the formation and occurrence of cleavage. These are:

(i) Astral growth theory,

(ii) Spindle elongation theory,

(iii) Cortical gel contraction theory,

(iv) Expanding polar membrane theory,

(v) Furrow membrane growth,

(vi) Endoplasmic flow factor.

There are a few working principles behind the formation of cleavage furrows. These have been stated by different workers.

1. Sach's law: According to this law, the successive cleavages occur at right angles to each other and, secondly, the blastomeres tend to be of equal size unless obstructed by yolk.

2. Hertwig's law: In the isolecithal egg spindle is located in the centre whereas in the telolecithal egg it is shifted somewhat towards the animal hemisphere. The axis of the spindle lies in the longest axis of the protoplasmic mass. Thus the plane of the furrow cuts the long axis across.

3. Balfour's law: The cleavage is determined by the yolk in the egg. The amount of yolk is inversely proportional to the speed of cleavage.

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