Planes and Patterns of Cleavage

Dr. R. Prasad
Department of Zoology,
Eastern Karbi Anglong College,
Sarihajan

13.2 CLEAVAGE

Cleavage is a series of cell divisions of the fertilised egg through which it is converted into a multicellular structure, called **blastula**. Practically no growth takes place during cleavage only the large volume of the zygote's cytoplasm is divided into numerous smaller cells called blastomeres. Except for mammals, in most other animals the initial rate of division and the placement of blastomeres in relation to each other is controlled by maternal proteins and mRNAs stored in the oocytes. Only in later stage, the division of cells is under the direct control of the genome of the zygotes. During cleavage the cell division is mitotic and has some striking peculiarities which makes it different from mitotic division in somatic cells. The main characterstic features of cleavage are as follows:

a) All the divisions of the zygote are mitotic and occur in quick succession.

b) Synchronisation of cell divisions of blastomeres: The early blastomeres divide simultaneously (synchronously) producing two blastomeres from zygote followed by 4,8,16.32,64 blastomeres and so on, in most cases. However, such synchronisation is lost, during later cleavage divisions.

c) There is no interphase between two successive cleavage divisions in blastomeres, or the Interphase period in the cleavage divisions is very short and does not involve growth so that the resulting blastomeres becomes smaller in size as their number increases i.e. there is no growth in the amount of cytoplasm in the derived blastomeres with the result that the size of daughter blastomeres continues to decrease during successive cleavages.

d) The size of the nucleus remains practically unchanged. Therefore, the nucleus: cytoplasm ratio, which is very small in the fertilized egg cell or zygote, continues to increase in the blastomeres, derived from successive cleavage divisions.

e) The rate of cell divisions is very rapid and a very large number of cells are produced during cleavage. For example in fast cleaving embryos,

13.2.3 Planes of Cleavage

The ova of most of the animal groups (except some specific cases like insects) are spherical or nearly spherical having their own actual centre which is comparable to the earth shapes. Similar to north and south poles on earth, the egg has animal and vegetal poles (Fig.13.3). The yolk platelets have more density than the active cytoplasm which also contains the nucleus. The yolk platelets are concentrated more towards vegetal hemisphere. Therefore, when the egg lies in any fluid medium (the fundamental feature of most of the eggs even in the apparently terrestrial eggs like those of birds etc.), the vegetal pole tends to face the centre of gravity and animal pole is away from it.

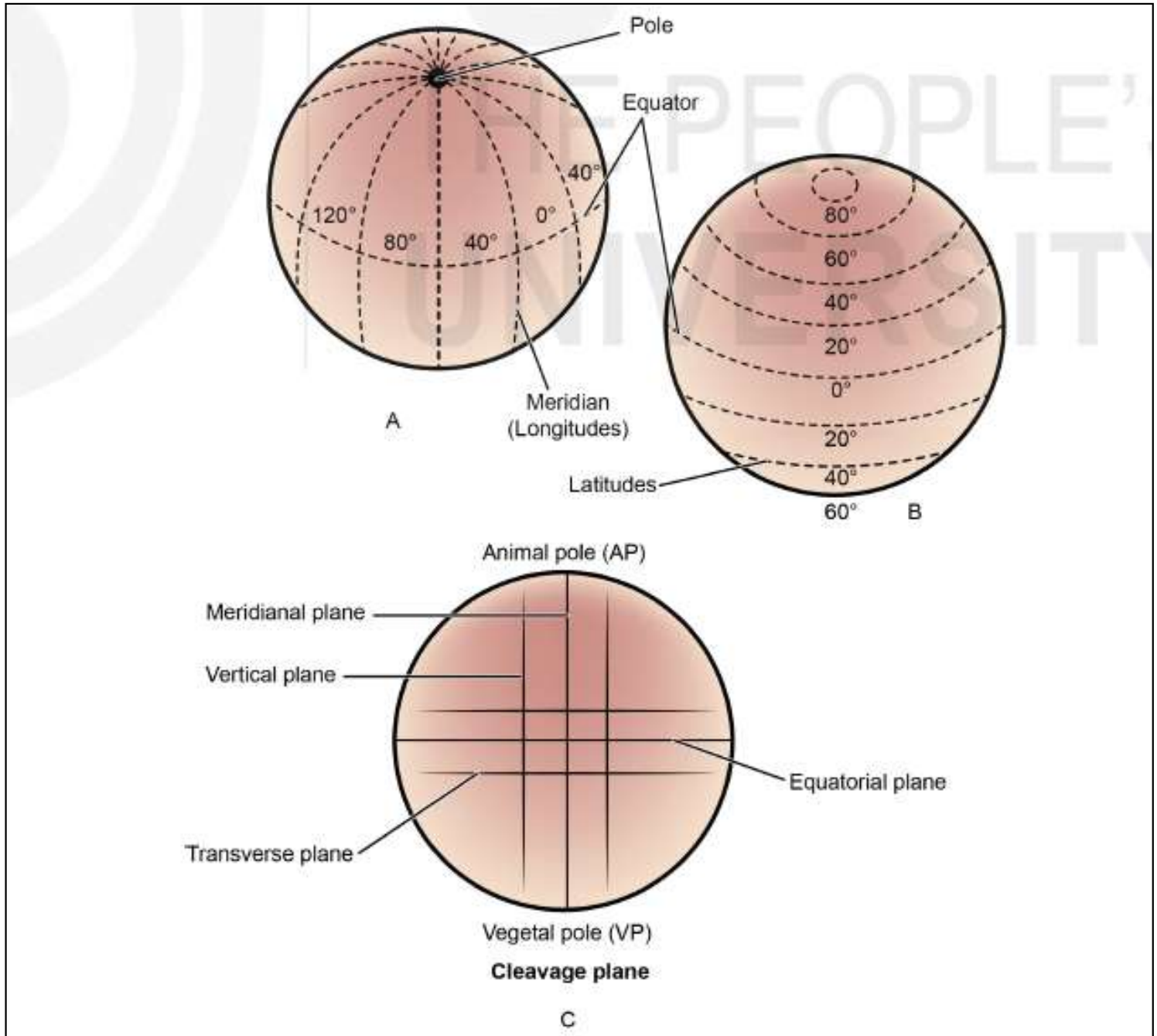

Fig. 13.3: A) Meridians (longitudes); B) Latitudes (imaginary lines on the earth surface which are comparable to the cleavage planes of a spherical egg); and C) Cleavage planes of egg.

With this picture in mind, we can now define the planes of cleavage of zygote or blastomeres, keeping in mind the imaginary lines (latitudes and longitudes) drawn on the earth surface (Fig.13.3).

The basic planes along which the egg and its daughter blastomeres are divided during early cleavage are as follows:

i) **Meridional Plane** – the cleavage furrow passes from the animal pole to the vegetal pole through the centre of the spherical egg or the blastomeres, so as to divide the egg into two equal halves, e.g., first cleavage furrow in the chick and first as well as second cleavage furrow in the frog's egg (Fig.13.4 A, B).

ii) **Vertical Plane** – the cleavage furrow may lie on either side of the central meridonial plane passing through animal-vegetal axis. The cleaved cells may be unequal in size. e.g., (2) **Vertical plane:** When cleavage furrow passes from the animal pole to the vegetal pole, but it does not pass through the median axis of the egg. Example: 3rd cleavage plane of chick (Fig.13.4 C and 13.8 C), Bowfin (*Amia calva*) and Gar fish (*Lepidosteus*). (Fig.13.4 C).

iii) **Equatorial Plane** – the cleavage furrow bisects the egg at right angle to the median axis exactly half way between the animal and vegetal poles. The cleavage furrow appears along the equator of the spherical egg e.g., the third cleavage plane of sea urchin (Fig.13.4 D).

iv) **Latitudinal or transverse or horizontal plane** – it is like equatorial but the cleavage furrow passes through the egg cytoplasm on either side of equator along the latitudes of the egg sphere, e.g., third cleavage plane of amphibian eggs (Fig.13.4 E).

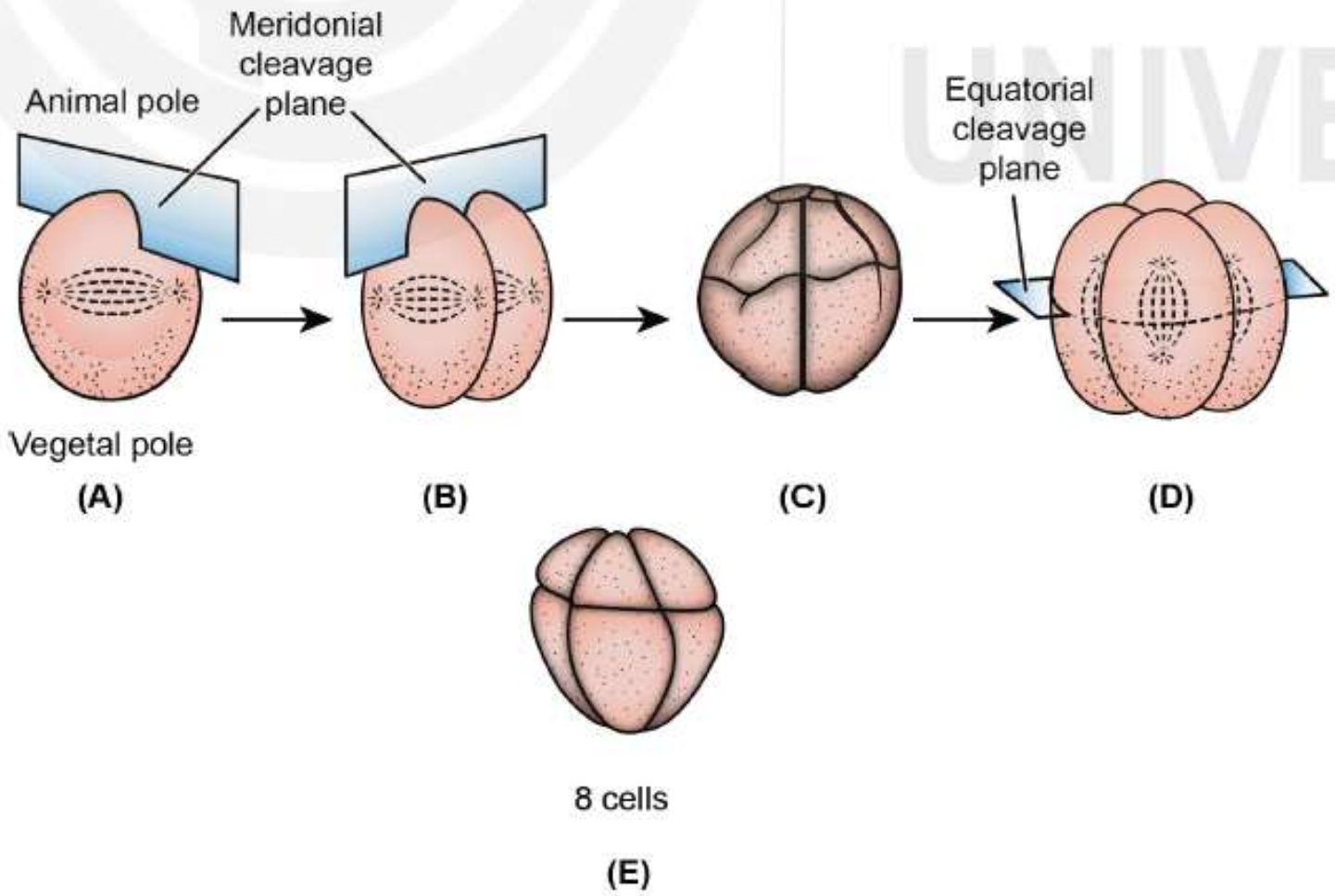

Fig.13.4: Planes of cleavage. A) and B) Meridonial cleavages; C) Vertical cleavage; D) Equatorial cleavage; and E) Latitudinal cleavage plane the upper tier of blastomeres (micromeres) are smaller than the lower tier of cells (macromeres) as there is more yolk in the vegetal pole.

13.2.4 Patterns of Cleavage

The pattern of embryonic cleavage in animals is determined by two major parameters: the amount and distribution of yolk protein within the cytoplasm, and factors in the egg cytoplasm that influence the angle of the mitotic spindle and the timing of its formation.

In most of the animal groups with spherical or almost spherical egg in which yolk is absent (alecithal) or occurs in little or moderate amounts (micro-or mesolecithal eggs), the first and second divisions result in four blastomeres of almost equal size (Fig.13.4, A, B, C). The third cleavage due to greater concentration of yolk platelets in the vegetal hemisphere divides the 4 blastomeres in the latitudinal plane giving rise to 8 cells that are arranged in two tiers of 4 blastomeres each. The first tier consists of 4 small blastomeres (micromeres) and lies in the animal hemisphere while the second tier consists of 4 large blastomeres (macromeres) and lies in the vegetal hemisphere (Refer again to Fig.13.4 E). The arrangement of blastomeres in these two tiers is very distinct and on this basis, the cleavage may be of 4 types (Fig.13.5):

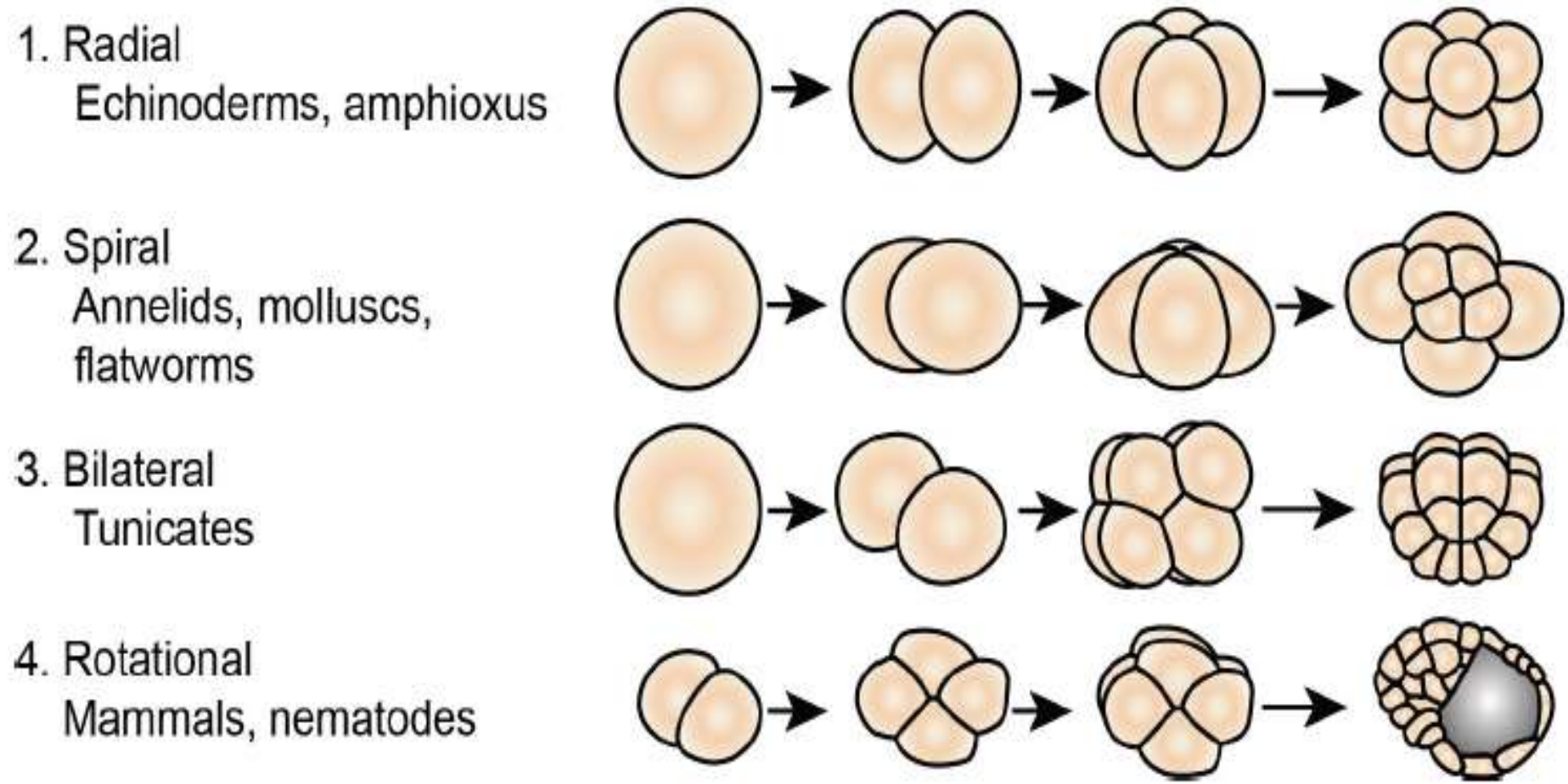

Fig.13.5: The four types of cleavage that occur in microlecithal (A to C) zygotes and D) the fourth type of cleavage that takes place in alecithal egg of nematodes and mammals(except for monotremes).

a) **Radial type:** If each of the blastomeres of upper tier lies exactly over the corresponding blastomeres of the lower tier the pattern of cleavage is radially symmetrical. Radial cleavage is a characteristic of deutrostomes, and results in indeterminant blastomeres (cells that can individually give rise to a complete embryo, and they don't have a determined embryological fate early on during the development of the embryo). In other words, you can take a single cell from a developing embryo, and given the right condition, that single cell can give rise to a whole embryo e.g.echinoderms, *Amphioxus*, amphibians (see again Fig.13.4 E also see Figs.13.7 D-F).

b) **Spiral type:** The upper tier of blastomeres of 8-cell stage embryo may be shifted with respect to the lower tier. They are not located exactly on top of one another; instead, they are located at a slight angle. This position results from the oblique (tilted) position of mitotic spindle so that, from the start, the two daughter blastomeres do not lie one above the other. Spiral cleavage is a characteristic of protostomes (annelids, molluscs, some helminthes) and results in determinant blastomeres (cell that have a determined embryological fate early on during the development of the embryo). In other words, determinant blastomeres are programmed to become a specific type of cell, early on during the process of development. Spiral cleavage is influenced by maternal cytoplasmic determinants. The right handed or clock wise displacement of the micromeres is called dextral spiral cleavage .The left handed or anticlockwise displacement of micromeres is called sinistral spiral cleavage. A good example is the left handed and right handed coiling of the shell in snail which is the result of the spiral cleavage as the direction of cleavage and shell coiling is the same (Fig.13.6)

The turn of spiral in the snail as seen from above may be in a clockwise direction (dextral) or counter clockwise (sinistral) direction, (Fig.13.5 A,B). In many animals such as snails, it is a genetic character.

c) **Bilateral cleavage:** In some animals (e.g., tunicates and nematodes, although in (different manner), the arrangement of 4 blastomeres after second cleavage is almost radially symmetrical as in the radial type of cleavage, but two of these are larger as compared to the other two blastomeres establishing a plane of bilateral symmetry in the developing embryo. During subsequent cleavages the bilateral arrangement of blastomeres may be still more obvious.

d) **Rotational cleavage:** Zygote of mammals display rotational cleavage. Rotational cleavage involves a normal first division along the meridonial axis, which gives rise to two daughter cells. The way in which this cleavage differs is that one of the daughter cells divides meridionally, whilst the other divides equatorially.

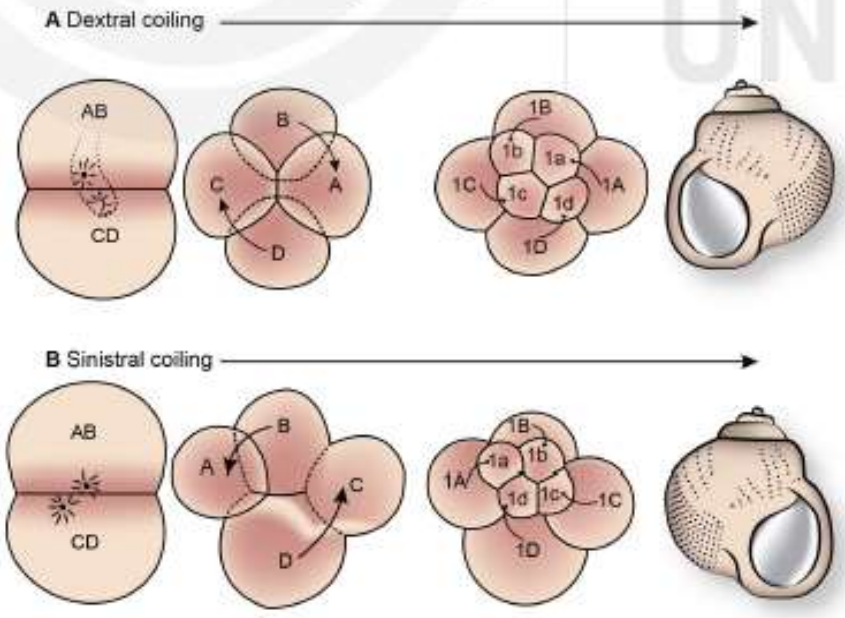

Fig. 13.6: Spiral cleavage in mollusc snails. Looking down upon the animal pole, the blastomeres are arranged either: A) clockwise (dextral) or B) anti-clock wise (sinistral). It happens to be a genetic character resulting in dextral or sinistral coiling of the shell of snails.

Furthermore, based on whether a particular cleavage furrow may divide the egg completely or partially, cleavage has been described as:

A) **Holoblastic or complete cleavage:** Each cleavage furrow divides the entire egg completely in a particular plane. Holoblastic cleavage may be:

i) **Equal holoblastic cleavage:** It occurs in alecithal (eutherian mammals) or microlecithal (*Amphioxus*, echinoderms) eggs where each cleavage furrow divides the egg so as to produce blastomeres of approximately equal size (Fig.13.7 A to G).

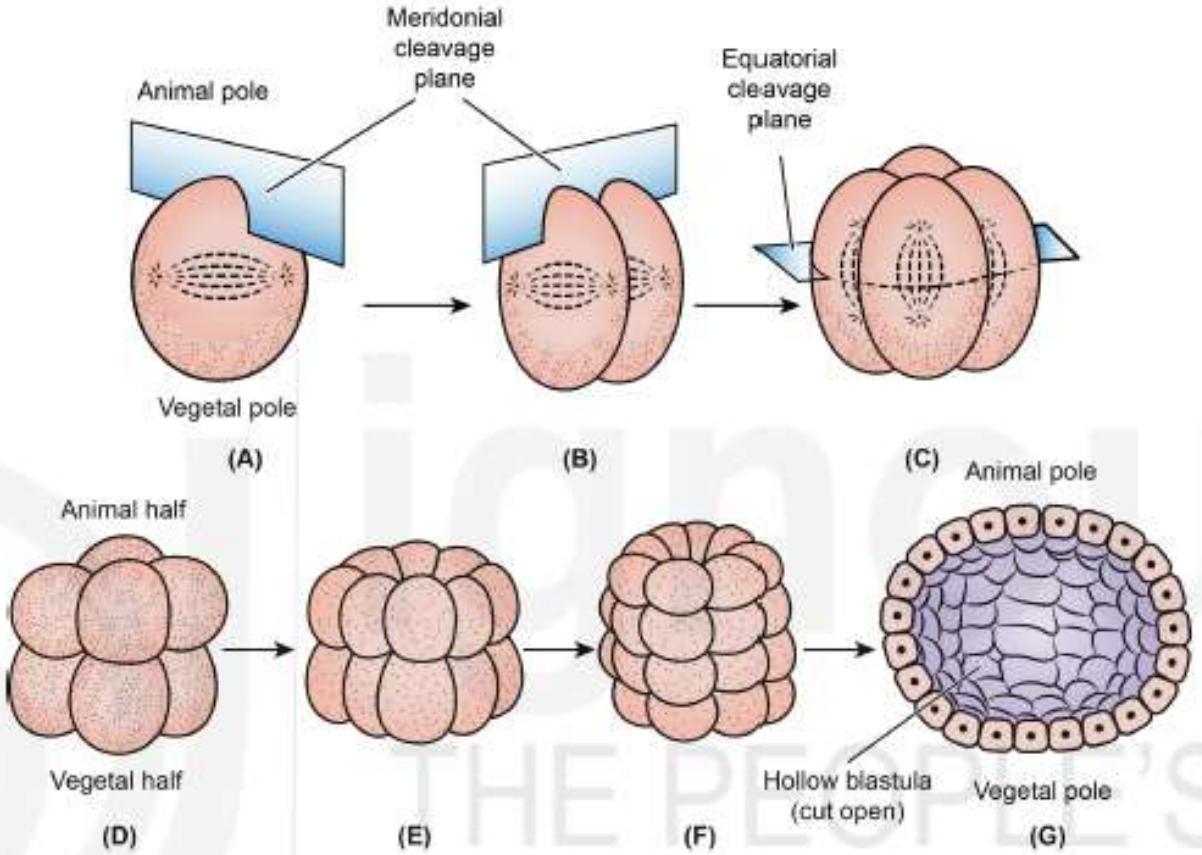

Fig. 13.7: Holoblastic and radial cleavage in the microlecithal egg of *Synapta digita* (Echinoderm) leading to the hollow blastula (G). A-B indicate the meridional planes of 1st and 2nd cleavage; C-equatorial plane (3rd cleavage); D, E, F showing the radial arrangement of blastomeres.

ii) **Unequal holoblastic cleavage:** This takes place in mesolecithal and moderately telolecithal eggs (lower groups of bony fishes and amphibians), in which the yolk is largely concentrated in the vegetal hemisphere. In these eggs the first and second cleavage divisions take place along the meridional planes, producing 4 equal blastomeres. But, because of the yolk being concentrated in the vegetal region, the third cleavage furrow is latitudinal above the equator and closer to the animal pole. The furrow divides each of the 4 blastomeres completely but unequally into small and larger daughter blastomeres. The third cleavage is therefore, an unequal holoblastic cleavage which produces 4 small blastomeres (micromeres) in the animal region and 4 large blastomeres (micromeres) in the vegetal region (Figs.13.8 and refer again in Fig.13.4 E). Subsequently the micromeres containing relatively less yolk divide at a much faster rate than the large, yolky macromeres.

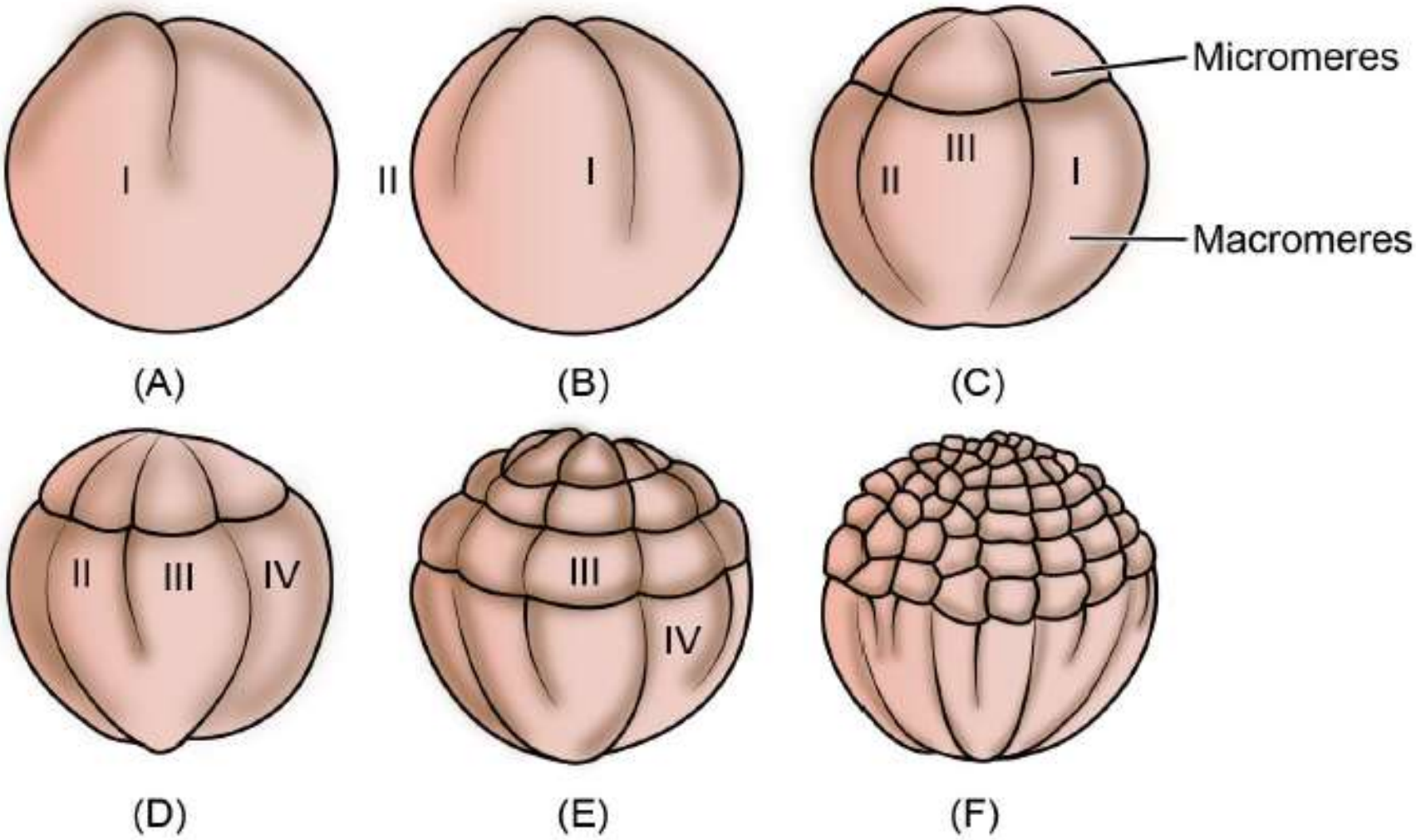

Fig. 13.8: Unequal Holoblastic Cleavage in frog's egg (A-F) cleavage furrows are designated, by Roman numerals indicating the order of appearance.

B) **Meroblastic or partial cleavage:** The fertilized egg does not divide completely because divisions are restricted to only a part of the egg while the rest of the egg remains entirely uncleaved. It is of two types:

i) **Discoidal meroblastic cleavage:** It takes place in the heavily, yolked macrolecithal and highly telolecithal fertilized eggs, as for example in cephalopod molluscs, reptiles, birds (Fig. 13.9) and monotremes (egg laying mammals). The cleavage is restricted to the cytoplamic germinal disc situated at the animal pole. Even the germinal disc divides incompletely while the entire yolk mass remains undivided.

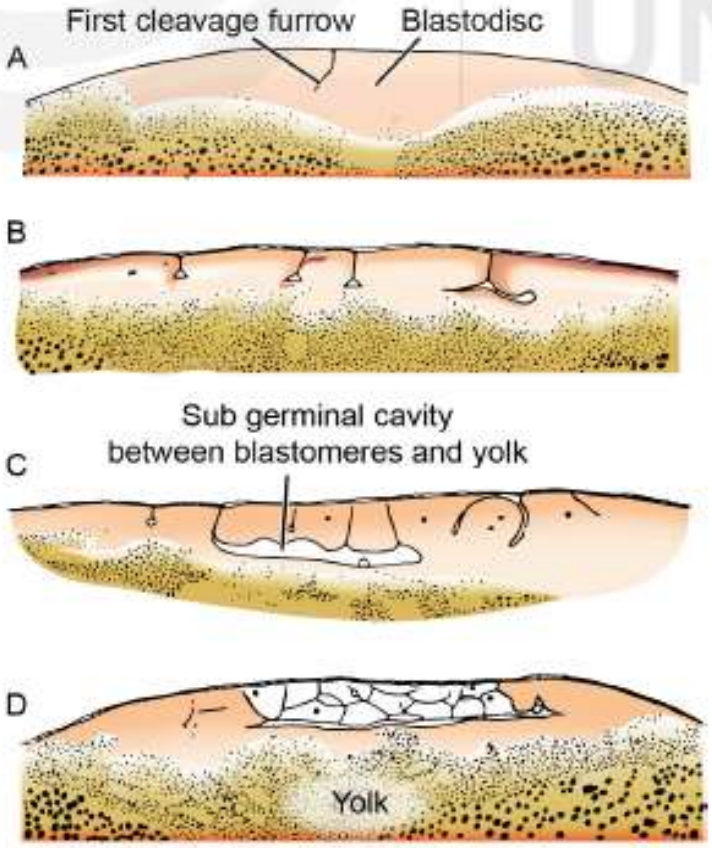

Fig. 13.9: Diagrams of sections of the fertilized chick egg. Discoidal meroblastic cleavage in which the blastodisc lies on top of yolk.Cleavage takes place only in the blastodisc.

ii) **Superficial meroblastic cleavage:** This occurs in the centrolecithal eggs of insects. Cell divisions are restricted to the peripheral cytoplasmic layer while the centrally located yolky is left undivided (Fig.13.10).

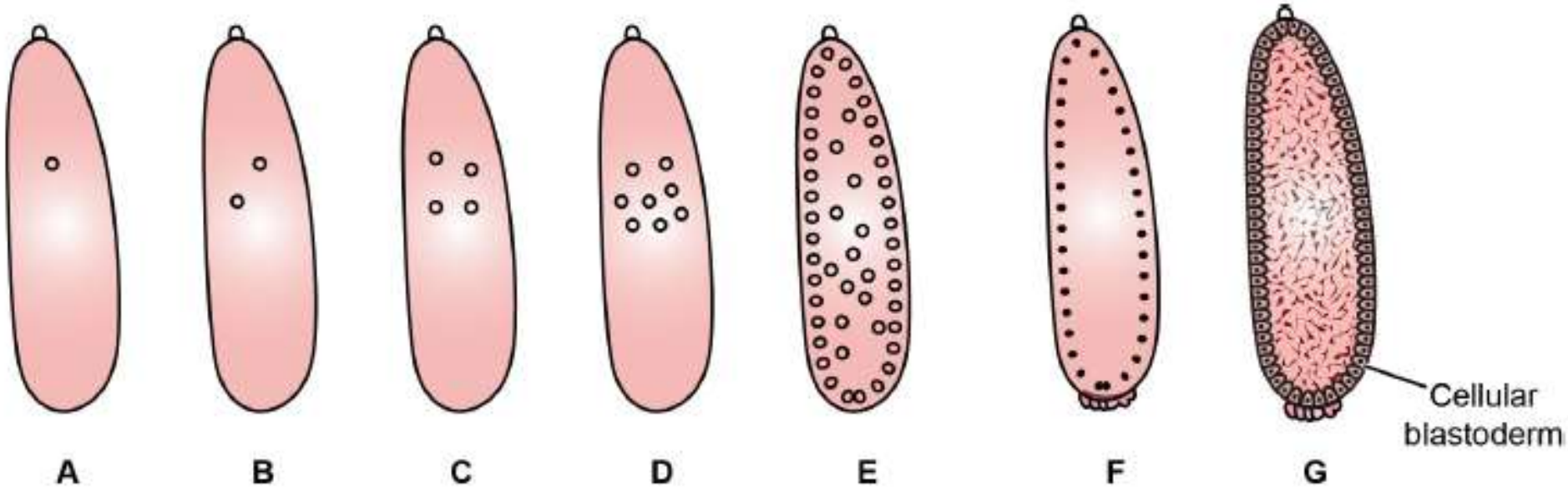

Fig.13.10: Diagramatic representation of superficial cleavage in insect embryo. (A) Undivided zygote nucleus in the yolk. (B) – (E) After 1st, 2nd, 3rd and more divisions of the zygote nucleus. (F) Daughter nuclei have migrated from interior of the egg to peripheral cytoplasm which is still undivided. (G) Peripheral cytoplasm divided into separate cells to form cellular blastoderm around the undivided yolk.

Table 13.1: Summary of Cleavage Types

Cleavage Patterns	Position of Yolk	Cleavage	Representative Animals
HOLOBLASTIC (Complete-cleavage)	Isolecithal (oligolecithal)	Radial /Spiral	Echinoderms, *Amphioxus,* most molluscs, annelids, flatworms, round worms.
	Yolk absent or sparse and evenly distributed	Bilateral/ Rotational	Tunicates eutherian mammals
	Mesolecithal, moderately telolecithal	Radial	Amphibians, lower bony fishes
MEROBLASTIC (Incomplete-cleavage)	Highly Telolecithal (Dense yolk)	Bilateral / Discoidal	Cephalopods molluscs reptiles, bony fishes, birds, egg laying mammals.
	Centrolecithal (Yolk concentrated in the centre of egg)	Superficial	Arthropods especially insects.