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lysis of the chemical patterns with very clear notions about the pattern of cell differentiation. Before we discuss the chemistry of the developing sea urchin embryo we shall therefore devote some attention to this question.

## II. Cell differentiation

WILLMER (1960) has pointed out that all cells may be referred to a few basic cell types, and has emphasized the importance of these cells for ontogenesis and phylogenesis. If WILLMER's views are accepted then it follows that cell differentiation may be resolved into two phases, first a segregation with respect to the basic cell classes, and subsequently differentiation of the cells within each class along separate lines, to give rise to various types of tissue cells. I have recently shown that in the amphibian embryo the first differentiation process, called cell transformation, corresponds to the phase of determination or primary differentiation, whereas the second stage is that of functional or tissue differentiation. It could furthermore be shown that the pattern of cell segregation is a function of the polarities in the egg (1966).

I shall not here enter upon a similar discussion pertaining to the sea urchin embryo, but for the subsequent discussion it will be necessary to outline the cell class concept.

If the properties of a certain cell type, including its potential transformation into other cell types, has formed the basis of phylogenetic evolution, then these same properties must be responsible for ontogenetic development. In other words, the archaic cell type which once gave rise to metazoan evolution, must be represented today by the egg cell. I have previously suggested that the egg is an amoebocyte, supporting this view on recorded observations on eggs and isolated blastomeres (for references cf. 1965b). The mobility of certain oocytes, the separation of the early blastomeres in many cases, and the absence of desmosomes during the first hours of development (WOLPERT and MERCER 1963) are other traits favouring this suggestion. Further support of the view that the amoebocyte represents the basic omnipotent cell type, which through transformations, reversible as well as irreversible, may be changed into various differentiated cell forms, can be found in textbooks of zoology, very well known cases are regeneration in coelenterates and planaria. It should just be mentioned that the typical traits of an amoebocyte is that it is a solitary cell, and that it forms lobopod pseudopodia. The shape is very varying, but it may be postulated that the fundamental cell shape is spherical.

The arguments advanced here pertain only to the egg cell, not to the spermatozoon, which is an epitheliocyte (flagellate form). Although the reversible transformation amoebocyte  $\rightarrow$  epitheliocyte is known to occur in protozoa (cf. WILLMER 1960), there is reason to believe that a similar, but irreversible transformation occurs during ontogenesis. Whether or not the transformation leading to the formation of spermatozoa is reversible remains

to be seen, but it is interesting to note that chemically the spermatozoan seems to represent a higher level of development than the egg cell (cf. below).

The typical epitheliocyte is basically a spherical cell, like the amoebocyte, and is furthermore characterized by at least one of the following properties: high intercellular adhesion, formation of cilia or one to several flagella. Epitheliocytes may exist in three different forms: non-adhesive forms may be solitary ciliated or flagellated cells (e.g. protozoa and spermatozoa), whereas the adhesive cells may either be attached to a basement membrane and form a two-dimensional organization, or exhibit a three-dimensional organization, in which the cells are exposed to other cells on all sides. In the latter case no cilia are formed, in the former cilia formation may occur at the free side opposite to the basement membrane (cf. Fig. 1). It should perhaps be mentioned that these are basic organization forms, which during development may be modified in numerous ways.

The amoebocyte may also transform into a mechanocyte or fibrocyte, a solitary cell characterized by the formation of filiform, contractile pseudopodia, in contrast to the loboform pseudopodia of the amoebocyte. The mechanocyte is often oblong whereas the amoebocyte, as mentioned, may be considered to be basically spherical. The cell shape is not a very distinct criterion, being subject to great variations, thus a mechanocyte may very often be stellate, and an amoebocyte oblong.

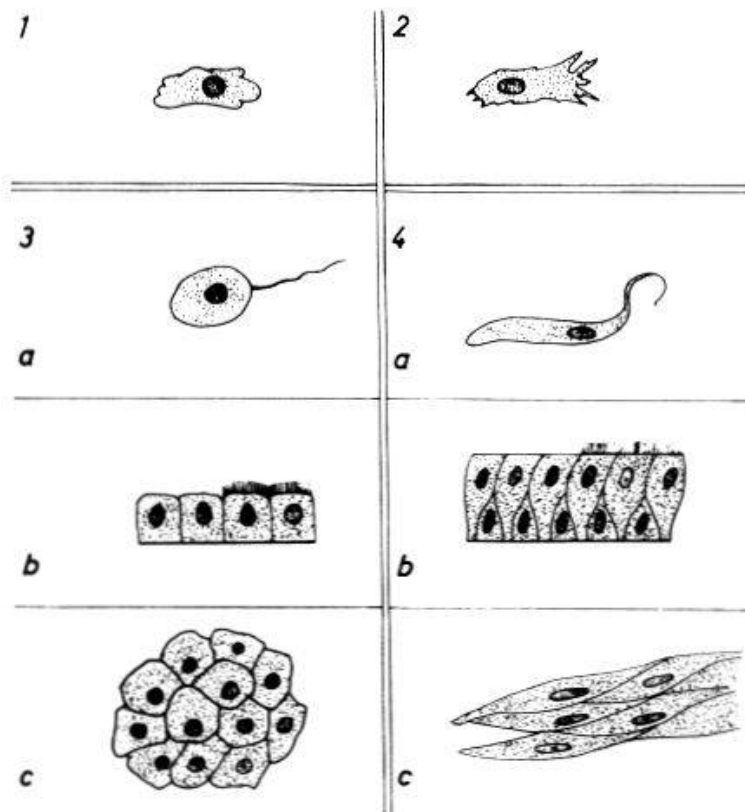


Fig. 1. Schematic illustration of the four cell classes.—1 = amoebocyte (sl-cell), 2 = mechanocyte (sf-cell), 3 = epitheliocytes (cl-cells), 4 = mechano-epitheliocytes (cf-cells); a = flagellate form, b = two-dimensional organization, c = three-dimensional organization. The name "mechanocyte" is used here in a meaning different from the one originally suggested by Willmer (1960).

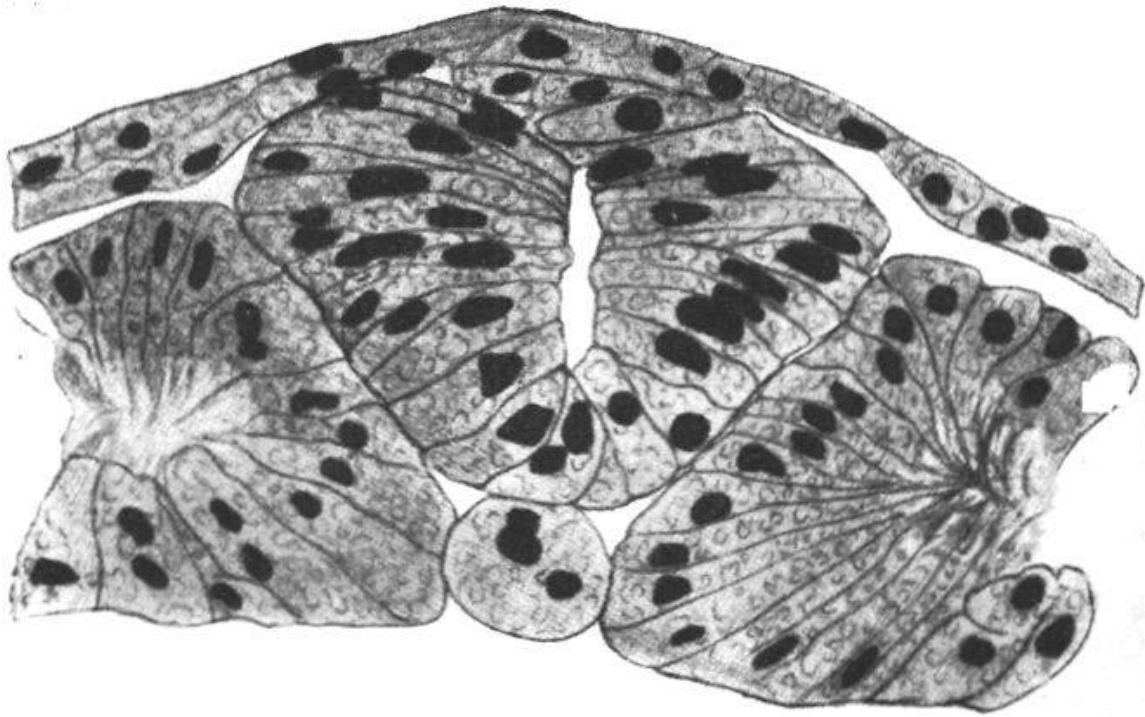


Fig. 2. Transversal section through a tail-bud embryo of *Triton* sp. showing that the myotome cells are flagellated (from LEHMANN: Arch. Entwickl.-mech. Org. 113 [1928]).

If both transformations occur in the same cell we shall get a spindle shaped or at least oblong cells with high intercellular adhesion and (or) forming cilia or a flagellum. The free-living flagellate form is, I believe, found in a certain type of protozoa, viz., the trypanosoma. A flagellated, adhesive form has been observed in the myotomes during amphibian development (LEHMANN 1928; cf. Fig. 2). The two other organization forms are present in many tissues, e.g., in the intestinal wall, and in smooth muscle, respectively (cf. Fig. 1).

This cell type, a mechano-epitheliocyte, has no proper name (cf. LØVTRUP 1966). As a matter of fact one meets with great difficulties to arrive at a nomenclature which is completely unambiguous. In the paper mentioned I have suggested using solo-lobocytes (sl-cells) for the amoebocytes, colligolobocytes (cl-cells) for the epitheliocytes, solo-filocytes (sf-cells) for the mechanocytes, and colligo-filocytes (cf-cells) for the last cell type. This nomenclature is based on the assumption that the four cell types represent the four possible results of the two transformations to which the amoebocyte may be subjected. The first transformation amoebocyte (sl) → epitheliocyte (cl) is concerned with the intercellular adhesion, hence the change of the prefix from solo- to colligo-; the latter is derived from latin *colligere*, to collect or gather. As we have just seen, this name is not quite unambiguous, since solitary cl-cells exist, e.g., the flagellates. I think this difficulty may be circumvented by letting the "c" refer not only to the adhesive properties, but also to the ability to form cilia (or flagella). It might be mentioned that the transformation s → c obviously is concerned not only with adhesion, but also with cortical tension.

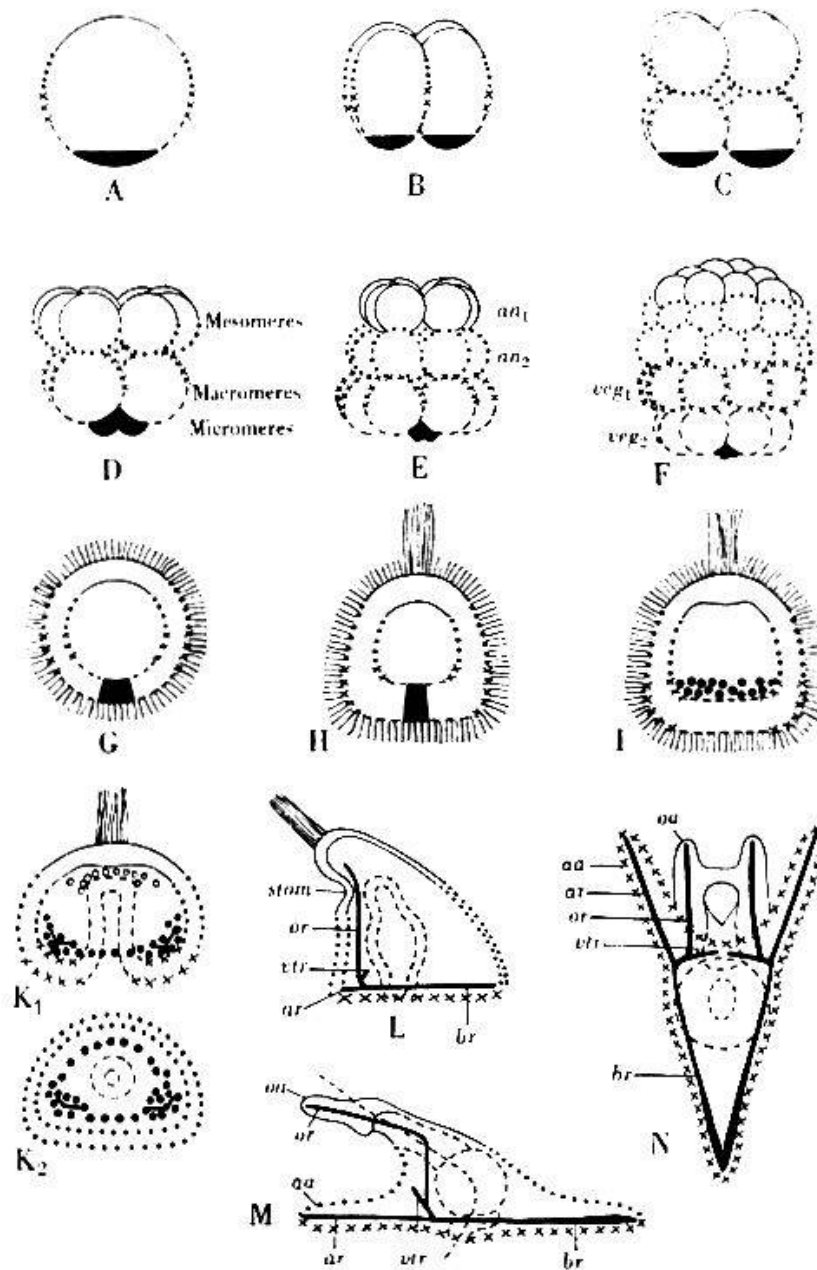


Fig. 3. Morphogenesis in the sea urchin embryo. The strongly ciliated apical cells in figs. H-L indicate that the AV-polarity represents a gradient with respect to the epitheliocyte property. The formation of mesenchyme cells at the vegetal pole shows that the VA-polarity is concerned with mechanocyte formation (from HÖRSTADIUS: *Biol. Rev.* 14 [1939]).

The second transformation amoebocytes (sl) → mechanocytes (sf) refers to the form of the pseudopodia in these solitary forms. The corresponding c-forms do not form pseudopodia, but it is supposed that they have undergone the transformation which in the s-forms influence the form of the pseudopodia.

As mentioned above the pattern of cell class distribution may be referred to the polarities of the egg; it should be emphasized, however, that the polarities of the egg have been discovered on the basis of the cell class distribution. This correlation shows that the direction of the cell transformations

is somehow determined by variations of certain properties along the egg axes. I shall not discuss this problem here but refer to the discussion of the amphibian embryo (1966).

The principal polarities in the sea urchin embryo are the animal-vegetal (AV) and the vegetal-animal (VA) gradients (cf. RUNNSTRÖM 1929; HÖRSTADIUS 1935; LINDAHL 1936). That these polarities are concerned with the cell transformation processes is directly established by the fact that the strongly ciliated apical tuft cells (cl-cells) are formed at the animal cap, whereas mesenchymal sf-cells are formed from the cells around the vegetal pole (cf. Fig. 3 and 4). Between these extremes is found one further region of cl-cells, the presumptive ectoderm, and the endodermal cells, the presumptive intestine. As we shall discuss below there is good reason to presume that the endodermal cells, situated between the two gradients, undergo both transformations and become cf-cells.

### III. Energy metabolism

#### 1. Respiration

I shall in the present discussion make certain assumptions which, although maybe obvious, should be specified at the outset. The first one is that the oxygen consumption is a direct measure of the energy consumption, which implies that there exists a respiratory control mechanism. The energy will

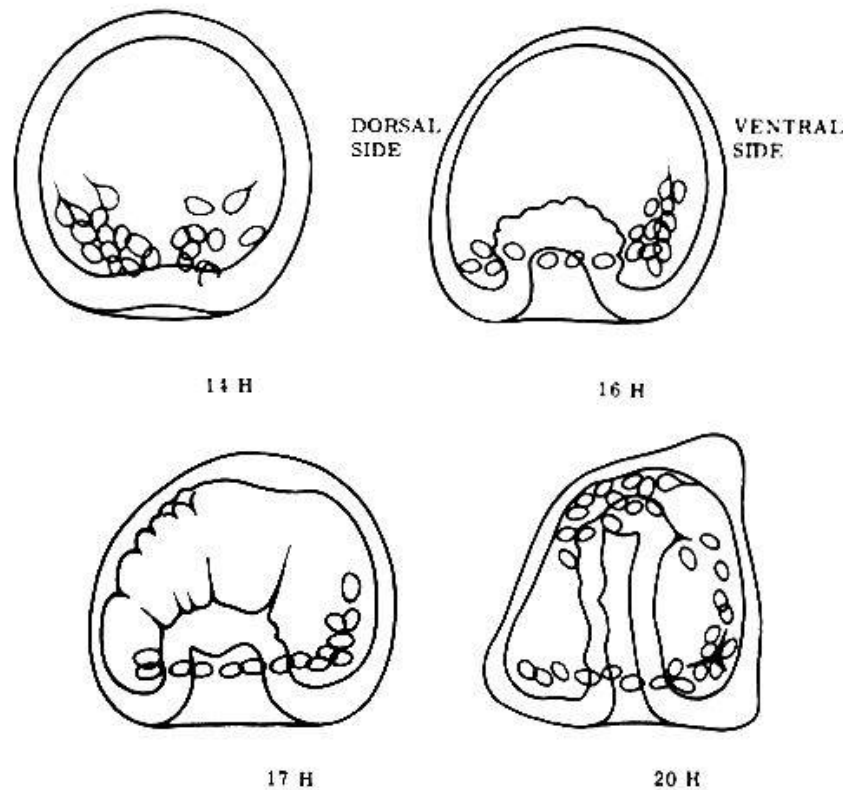


Fig. 4. Gastrulation in the sea urchin embryo. The formation of filiform pseudopodia in primary and secondary mesenchyme mechanocytes is indicated (from GUSTAFSON and WOLPERT: *Int. Rev. Cytol.* 15 [1963]).