CELL AND TISSUE STRUCTURE IN ANIMALS AND PLANTS

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Summary

We discuss the structure of cells and tissues, with special emphasis on vertebrates and flowering plants. These organisms show an evolutionary trend towards the elaboration of tissues - collections of cells specialised for particular functions. Cells contain a nucleus and other membrane-bound organelles, some of them highly specialised. Physical properties of the tissue, such as its rigidity, are influenced by the cell wall or extracellular matrix. Specialised tissue types are very different in animals and plants, and so are some important features of tissue growth. There are similarities, however, such as the existence of reserve populations of cells which can undergo cell division (stem cells, or initials in the meristems). Embryonic development shows similar basic processes in animals and plants (morphogenesis, differentiation, cell division, etc.), although the details differ.

1. Introduction

Since the development of 'cell theory' in the 1830's, it has been realised that organisms are made up of *cells*. Cells are the smallest functional components of an organism that are able to reproduce themselves by division (though they often lose the ability to divide when they become differentiated). During the course of evolution, there is a trend for cells which perform a variety of functions to give way to specialised cell types which perform fewer functions more efficiently.

Another evolutionary trend is the elaboration of *tissues*. These are aggregations of specialised cell types separated by extracellular matrix (ECM), or by a middle lamella in the case of plant cells. At points of contact, the cells are held together by cell adhesion molecules and junctions. A tissue may contain several different cell types. For example, muscle tissue in animals may consist not only of specialised muscle cells, but also of connective tissue cells, blood vessel cells, nerve and other cells. Tissues allow the different functions of an organism to be apportioned to specialised cell assemblages. This does not mean that tissues have only a single function. Thus the vertebrate liver is involved in the manufacture of important blood proteins; the manufacture of compounds which help digest food; energy storage; the detoxification of foreign substances; and many other processes. By definition, tissues are found only in multicellular organisms. Some metazoans (the mesozoa and parazoa) do not form true tissues, sponges being a familiar example.

1.1. Scope of the Article

Our aim in this article is to give examples which illustrate general principles of cell and tissue organisation, with particular emphasis on their structure and development. We will draw illustrative examples in particular from our own areas of interest (vertebrate embryology and higher, flowering plants). We do not aim to give a comprehensive catalogue of species and tissue types, or details of cell function and molecular biology. Among animals, we will refer most commonly to vertebrates, a group of around 45,000 species that includes hagfish and lampreys, cartilaginous and bony fishes, and tetrapods (e.g. amphibians, birds and mammals, including humans). The cells and tissues of several higher vertebrates have been researched in very great detail.

The plants discussed are mainly the economically-important flowering plants (angiosperms). These are classified in the division Anthophyta which has two classes: the Monocotyledons and the Dicotyledons. Examples of monocots are grasses, lilies, orchids and palms. Dicots are herbs, scrubs and trees excluding conifers. Based on their life cycle angiosperms can also be classified as annuals, biennials or perennials. Angiosperms are the most diverse and widest distributed group of plants with 250.000 known species. The mosses, ferns and gymnosperms (to which the conifers belong) comprise 35.000 species.

2. Cell and Tissue Development

Cells and tissues are formed or reorganised in a number of circumstances, namely: during development; as part of the normal maintenance and remodelling of adult tissues; in disease processes; and as a response to mechanical injury.

2.1 Development of Animal Cells and Tissues

In eumetazoan animals (i.e. those which have true tissues), the production of new cells (by cell division), and their subsequent organisation into tissues (through histogenesis) are major features of development. So too is differentiation, a process in which cells synthesise specialised molecules associated with specific functions (e.g. the oxygen-transporting pigment haemoglobin in red blood cells).

The fertilised egg reproduces itself by dividing repeatedly to form a ball or sheet of cells. This process is known as cleavage. A cavity (blastocoel) forms within the cell mass, and in some animals (the pseudocoelomates) persists as the body cavity. Next, histogenesis begins as the cells separate into different embryonic tissue layers or germ layers. In some groups of metazoans (including sea anemones and jelly fish) there are only two true germ layers, but in others (whose members include flatworms, insects and vertebrates) there are three. As a result, animals may be classed as diploblastic and triploblastic respectively. Where three layers are present, the middle layer lies between the other two, like the filling in a sandwich. In the vertebrates, the situation is somewhat complicated by the presence of the neural crest, a tissue which is sometimes thought of as a fourth germ layer. In coelomates, including vertebrates, a cavity (intraembryonic coelom) develops within the mesoderm.

In the vertebrates, the outer (or dorsal) germ layer of the embryo is called the ectoderm, and gives rise to the nervous system and the epidermal layer of the skin. It also contributes, via the neural crest, to many other tissues, including connective tissues in the head and neck. The inner, or ventral, layer of the embryo (endoderm) gives rise to the epithelium of the gut and its glands. The middle layer or mesoderm develops into locomotory and circulatory organs, non-epithelial tissues in the gut, and other structures.

The mesoderm appears during gastrulation, a process which is characteristic of the triploblastic metazoans. In sea urchins for instance, the initially hollow embryo develops an in-pouching which forms the gut. At the same time, cells break away (delaminate) from the epithelial wall of the embryo to form scattered mesoderm cells inside the embryo. The in-pouching is a type of morphogenetic movement which causes cells to take up new positions in the embryo. Cell migration is another morphogenetic movement which redistributes cells, and the migration of neural crest cells is good example of this. Because of cell migration, organs and tissues often have a mixed origin from different germ layers.

Delamination is also seen in the development of neural crest cells from the ectoderm. Like other epithelia, the ectoderm is a layer of cells, tightly packed together, with their basal surfaces resting on a membrane (basal lamina), and their apical surfaces free. Some of these cells lose their epithelial characteristics, including their polarity, and break away from the basal lamina to form the neural crest. As they do so, the cells form a scattered array in which they are separated from each other by extracellular matrix. A tissue with cells arranged in this way is called mesenchyme[To avoid confusion, it should be emphasized that 'mesenchyme' is a tissue type, whereas 'mesoderm' is an embryonic germ layer.]

Because there is a change from an epithelial to a mesenchymal organisation, neural crest development, and gastrulation, are examples of 'epithelial-mesenchymal transformation'. This process is very common and important in metazoan development.

Just as cells can break away from an epithelium to form a mesenchyme, so too can mesenchyme cells move closer together (condense) to form epithelia. This process is known as mesenchymal-epithelial transformation. It is seen, for example, in vertebrate development, when cells in the embryonic kidney bud condense to form epithelia in part of the nephric tubules.

Tissues may be remodelled, and their component cells replenished, throughout life. Even adult tissues that appear to be stable and unchanging, may in fact show a dynamic turnover of cells. Thus the skin and gut lining of vertebrates both show a constant renewal process which serve to replace cells rubbed away at the surface. New cells are formed in the basal layers of the skin or gut epithelium and gradually move towards the surface, becoming differentiated as they do so. The basal cells, which act as a reserve population to provide new cells, are called stem cells.

Remodelling processes involve cell division and differentiation and, at least sometimes, programmed cell death (apoptosis). New tissue can be formed in the adult in response to injury. Wound-healing involves the closure of a wound by cell migration and proliferation, and its filling with new tissue. Some adult animals are able to regenerate entire tissue systems, as in certain amphibians that can regenerate new limbs after amputation. In adult humans, liver tissue shows considerable powers of regeneration, but most other tissue types, including brain, show little or none. Indeed the central nervous system of vertebrates does not generally gain neurons in adult life, except in birds that acquire new central neurons as part of song-learning.

2.2 Developmental Processes in Higher Plants

2.2.1 Tissue Origins in Higher Flowering Plants

Sexual reproduction in flowering plants takes place in the flowers. The female part of the flower is the carpel, and the male parts the stamens. The carpel has, among other structures, a style with a stigma, and a basal ovary with one or more ovules enveloping an embryo sac. The latter contains eight haploid nuclei in seven cells. One of these cells is the egg and a central cell has two haploid nuclei. The stamens have anthers where pollen grains develop each with two haploid sperm cells.

From a pollen grain, after having been deposited on the stigma (at pollination) by wind or insects, a pollen tube grows into the style towards one of the embryo sacs. One sperm cell conjugates with an egg at fertilization, and this diploid cell develops into an embryo. The other sperm cell conjugates with the cell with two haploid nuclei forming a triploid cell. This cell, close to the developing embryo, generates the endosperm a tissue full of nutrients. During this period of embryogenesis, ovules develop into seeds, and the ovary into the surrounding fruit.

The mature embryo, which already shows the body plan of a seedling, often accumulates nutrients from the endosperm in specialized embryonic leaves or cotyledons. The nutrients in the cotyledons, as well as the remaining endosperm after embryogenesis, is used for development of the seedling after seed germination. The stages and processes of development in the embryo are the same as those during plant development.

Usually, after a period of dormancy, the seed germinates: the embryo sheds the surrounding maternal tissue and develops into a plant. Development can be divided in three overlapping stages: growth, morphogenesis and differentiation. In turn, there are four processes underlying those stages are: cell division, cell growth, cell differentiation, and cell maturation. These processes are similar to those described above in animal development, although the details differ. Plant development continues, often with seasonal variation, throughout life of the individual.

A characteristic feature of plant development is the cell proliferation occurring in restricted zones, namely the apical and lateral meristems. Apical meristems are found at the tips of all shoots and roots. In these meristems cells are dividing, thus producing new cells to form respectively, a shoot with leaves, and a root –organs of the so-called primary plant body. In the primary plant body the organs grow mainly in length, although some primary thickening can occur in shoots and roots. In case of primary thickening cells divide periclinally (i.e. the new cell wall lies parallel to the outer surface of the organ) in the outer tissues and the two sister cells grow in radial direction. Most palms (monocots) thicken in this way.

Lateral meristems are not present in all plants, but develop in perennial plants like trees and shrubs (dicots). The shoot and root of these plants increase strongly in thickness (due to secondary thickening) in regions of the organs that are no longer elongating. The lateral meristems, which are tubular in shape, are the vascular cambium and the cork cambium. First the vascular cambium develops rather deep in shoot or root; then, the other lateral meristem, the cork cambium, develops peripherally.

Growth zones are also seen in animals – both during embryonic development (an example being the 'progress zone' at the tip of the growing limb in tetrapod embryos) and in the adult (as in the 'growth plate' of long bones in advanced vertebrates). In those salamanders that can regenerate an amputated limb, an early stage in regeneration is the formation of a cap (blastema) of actively dividing cells. The growth zones of animals are typically transient. Indeed, growth through apical and lateral meristems (containing initials, that remain active throughout life) is regarded as a principle difference between plants and animals. Furthermore, migration of cells, as well as cell replenishment and turnover – prominent in tissue development, remodelling and maintenance in animals – are absent in plants.

2.2.2 Cell Division, Growth and Differentiation

Cell division takes place in the apical and lateral meristems. Derivative sister cells will after more divisions eventually grow and differentiate into mature cells. This implies that adjacent to the meristems zones of dividing derivatives arise. Here growth and differentiation of cells and tissues starts. Next to the apical meristems, three primary meristems (protoderm, procambium and ground meristem) can be distinguished. Differentiation and maturation result in the respective tissue systems and cell types of the primary plant body. This is differentiation in a longitudinal direction. Some cautious parallels can be drawn with the progress zones, growth plates and blastemas of animals, in which cells may fall out of a proliferating zone and undergo differentiation.

In perennials (dicots) the lateral meristems develop in just mature parts of primary shoot and root. First the vascular cambium develops, and later the cork cambium. The vascular cambium develops between primary xylem and primary phloem (vascular tissue) and in connecting ground tissue. Its cells divide periclinally and after cell growth of the sister cells in radial direction the thickness or girth of the plant body increases. The cork cambium originates from a layer of cells immediately below the epidermis. Cells in these tube-like meristems divide periclinally and the derivatives are formed in a radial direction inwards and outwards. After growth and differentiation of the derivatives, shoot and root thicken (secondary thickening growth). Here differentiation is in a radial direction.

Cell division, growth and differentiation and hence the primary development of the plant, therefore, originates from highly restricted zones (some millimeters or centimeters) at the top of shoot and root, in all angiosperms (Figure 1). Secondary growth originates from the whole length of stem and root in scrubs and trees (dicots). In animals growth is a more widely diffusely distributed phenomenon.

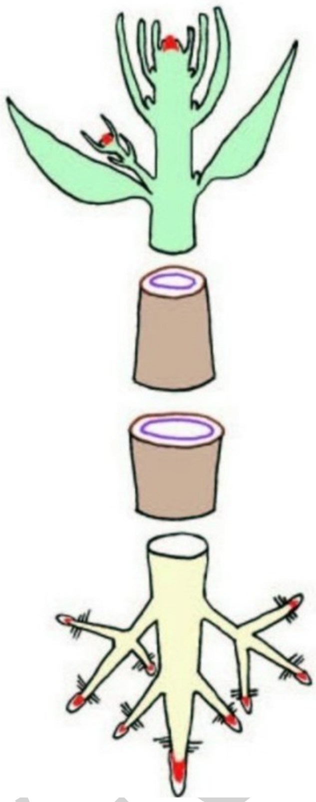

Figure 1. Schematic picture of a perennial dicot showing the location of apical meristems (red: shoot and root meristems) and lateral meristems (violet: vascular cambium, brown: cork cambium). The upper part represents just the primary shoot tip with leaf primordia, young leaves, axillary buds and a lateral shoot, measuring some millimeters or centimeters; the second and third part represent the shoot (stem) and root zone of secondary thickening, measuring in the order of meters; the lower part represents just the primary root tip with root cap, root hairs zone and lateral roots, measuring some millimeters to centimeters. (Goosen-de Roo, L., after Esau, K. 1977).

Where plant apical meristems are damaged, reserve-meristems can take over. The shoot apical meristem has formed buds in the axils of leaves containing new shoot apical meristems. These apical meristems form lateral branches. Deep within roots, in the zone of differentiation or in the zone of maturation, root primordia (young lateral roots) can be formed. When these root primordia develop an apical meristem and primary meristems, the newly formed root pushes its way through the surrounding mature root tissue.

2.2.3 Initials in Meristems

The population of cells in meristems is composed of initials and derivatives. An initial divides in such a way that one of the sister cells remains meristematic (initial) while the other sister cell (derivative) will later become part of a mature organ. Initials are therefore the cells that can continue to divide, and do not grow, differentiate or mature; they remain always in the meristem. The majority of cells in the meristem consists of derivatives which divide a few times before they grow, differentiate and mature. Derivatives from the apical meristems become more remote from the top as the initials continue to divide. Derivatives from the lateral meristems become further away from the meristem in radial direction, to the outside or the inside, in the thickening stem or root.

The development of a plant also depends, in part, on temporary meristems (i.e. meristems without initials). Leaf formation depends on numerous temporarily active meristems (which vary with shape and thickness of the leaf). Elongation of internodes of the shoot occurs by a temporarily active meristem lying between mature regions.

The vascular cambium contains two type of initials: fusiform initials and ray initials. They remain active throughout life in gymnosperm and dicot trees, causing their life long, secondary thickening. The cells differentiating from the fusiform initials are elongated and are arranged in longitudinal rows. From the ray initials shorter cells arranged in radial lines derive.

The initials and derivatives of the lateral meristems are, unlike those in the apical meristems, elongated and highly vacuolated cells.

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Bibliography

Esau, K. (1977) *Anatomy of seed plants*. John Wiley and Sons, NY [Indispensable book about the internal structure of plants for all studies about plants. It presents anatomy of plants during maturity as well as during development. Light microscopical - and electron microscopical data are well matched.]

Raven, P.H. et al. (1999) *Biology of plants*. W.H. Freeman and Company/Worth Publishers, NY [An up-to-date textbook for a first-year university course in biology or botany. The new recombinant DNA techniques are integrated in taxonomic relationships and the model plant Arabidopsis shows its impact on understanding anatomy an physiology]

Ross, M.H. and Romwell, L.J. (1989) *Histology*. Williams and Wilkins [Good introduction to human tissue and cell structure with many excellent illustrations.]

Steeves, T.A. and Sussex, I.M. (1989) *Patterns in plant development*. Prentice Hall, Englewood Cliffs, NJ [This book, meant for students after an introductory course in biology or botany, presents in an accurate, descriptive manner all developmental aspects supplemented with data from experimental morphogenesis research (chimeric plants, microsurgery)]

Various authors: Gray's Anatomy (1995) Churchill Livingstone, London. [Authoritative human anatomy text which includes detailed sections on cytology and histology]

Biographical Sketches

Michael Richardson is the van der Leeuw Professor of evolutionary developmental zoology at the University of Leiden, The Netherlands. He studied basical medical sciences and cell pathology at the University of London. He gained his PhD in avian embryology under Lewis Wolpert at University College London. His research concentrates on analysing phylogenetic patterns in vertebrate embryonic development.

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