Textbook Errors & Misconceptions in Biology: Cell Structure

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The first article in this series suggested numerous textbook errors and misconceptions about photosynthesis (Storey 1989). In this second article I deal with cell structure; in a future one I will focus on cell function and metabolism.

Unlike photosynthesis, textbook problems with cell structure seem to occur more because some of the material in them is not current than because of errors perpetuated down the lineage of textbook editions. I suspect most of the delinquency is linked to the explosion this decade of knowledge about cells. It is extremely difficult for even active researchers to stay current with anything but the most specialized literature on cells. It is the goal of this paper to update high school and introductory level college teachers on selected topics of cell biology as well as identify possible textbook errors and misconceptions. Some recent ideas discussed below may not fit all introductory courses, and it is not anticipated that you will find everything immediately useful beyond reviewing or perhaps updating your working knowledge of cells.

Prokaryotes & Eukaryotes

The differences between prokaryotes and eukaryotes are among the fundamental concepts in biology. These differences are critical to all currently used five-kingdom classification schemes (Curtis & Barnes 1989; Margulis & Schwartz 1988; Audesirk & Audesirk 1989; BSCS Green 1987 & Blue 1989 versions) including those that split the prokaryotes (Monera) into subkingdoms (Starr & Taggart 1989). [Note that splitting prokaryotes into archaebacteria and eubacteria has not been widely accepted, see Carlile 1982.]

In order to understand evolution, even beginning students should know the most important similarities and differences between prokaryotic and eukaryotic cells (see also Margulis & Schwartz 1988; Gould 1989). The basic characteristics are given in most contemporary general biology books, including those listed above. Some even mention the source of the names—prokaryote meaning “before or lacking a nucleus” (no nuclear membrane) and eukaryote meaning “true nucleus” (with a nuclear membrane)—and that prokaryotes lack membrane-bound organelles. However, for a more thorough understanding of the two types of cells, it may be useful to introduce characteristics, both structural and functional, that are not often found in beginning textbooks.

As discussed below, eukaryotes are more structurally diverse than prokaryotes, yet there are similarities. For example, both prokaryotes and some eukaryotes (the plants and fungi) have rigid cell walls but differ in composition (see below on plant cell walls, Alberts, et al. 1989). Although arranged differently, the genetic information is contained in the same four deoxyribonucleotides and proteins are constructed from the same group of amino acids in both cell types. Prokaryotes have sustained much of the central metabolism passed to eukaryotes, but unique pathways have also evolved in the prokaryotes. Processes thought to be exclusive to the bacteria include anoxygenic photosynthesis, energy conversions via oxidation of inorganic compounds and oxidative phosphorylation using electron acceptors other than oxygen (e.g., nitrate, CO₂, sulfate), methane production and nitrogen fixation (Carlile 1982). Eukaryote cells generally have lower metabolic rates, grow slower, divide less often and are larger than prokaryocytes (Carlile 1982; Alberts, et al. 1989). Also, eukaryotes contain actin and tubulin fibers (see cytoskeleton, below), split genes (introns and exons), repetitive sequences of DNA, and RNA splicing that seem to be absent in prokaryocytes (Carlile 1982; Alberts, et al. 1989; Prescott 1988). With all
this in mind you might wish to emphasize an often overlooked but key structural characteristic of eu-
karyotic cells: compartmentation—a sequestering of functional metabolic machinery into discrete packages called organelles. Among other things, compartmentation is an adaption resulting in in-
creased efficiency to “fight two functional battles” that cells constantly encounter—entropy and toxins. With enzymes and cellular metabolites organized and sequestered in various organelles—separated, in many cases, by membranes—counter-productive collisions between these cellular constituents may be minimized or even circumvented. At the same time, within a compartment, optimum concentrations of enzymes and their substrates and effectors (and likely pH) may be achieved. Thus, order can be sus-
tained with less energy expended, while metabolic pathways can operate more efficiently and be more precisely controlled in compartmentalized cells than in prokaryotes. Through compartmentation, toxic by-products of metabolism, such as ammonium re-
leased from the breakdown of amino acids, can be kept away from enzymes and other cellular comp-
ounds that may be sensitive to them. Organelles also help overcome problems of diffusion distance within cells (see Vogel 1987; Carlile 1982; and the next paper in this series) and provide increased sur-
face area for metabolism. For example, the folding of membranes within a chloroplast (thylakoids) or a mi-
tochondrion (crista) allows multiple copies of mem-
brane-bound enzymes to efficiently carry out photo-
phosphorylation or oxidative phosphorylation within a very small, yet highly organized subcellular package.

The traits leading to compartmentation, providing an intracellular division of labor, may have been se-
lected for the maintenance of cellular organization. I tell my students that a key principle for eukaryotic cells is to “stay organized and stay alive” and that organelles are critical in this selective advantage.

Even though compartmentation is not so well de-
veloped in prokaryotes, other selected survival strat-
egies have evolved in them (Alberts, et al. 1989; Mar-
gulis & Schwartz 1988), including complex and di-
verse biochemical adaptations to almost every environment known (see above and Carlile 1982). Moreover, prokaryotes are successful, at least in part, because of their small size and rapid rates of reproduction.

While considering the classification of organisms, the groups known previously as blue-green algae are today called cyanobacteria or blue-green bacteria be-
cause they are prokaryotes. The cyanobacteria are placed in the Kingdom Monera, while the one-celled and multi-celled algae are in the eukaryotic Kingdom Protista (named Protoctista by Margulis & Schwartz 1988).

Cytoplasm

Many textbooks still refer to much of the cell con-
tents as protoplasm and define it as the “living mate-
rial in the cell.” Some even identify cell walls and vacuoles as “the nonliving part of cells,” and there-
fore not as protoplasm. (In high school biology I re-
member labeling the parts of cells with names placed at the end of carefully drawn, parallel lines and iden-
tifying whether the parts were living or dead.) Since cell walls and vacuoles are organized, energy-ex-
changing structures like other organelles of the eu-
karyotic cell, the word protoplasm is a meaningless term, as pointed out years ago by Garrett Hardin (see Vogel 1987). In this sense, all parts of the cell could be considered “alive.” Alternatively, you could ask if any part of a cell is “living” or does life exist only in substantially intact cells in which all the parts work together?

Cytoplasm—all the cellular material outside the nu-
cleus but inside the cell membrane—is an offen-
tused term with value but with some technical draw-
backs: it can be too generic, not describing the various distinctive organelles found in the cyto-
plasm. More recently, the aqueous, proteinaceous material surrounding the organelles of the cytoplasm has been called the cytosol (see Alberts, et al. 1989; Prescott 1988). Thus, when teaching about cells, you might refer to specific functional structures such as mitochondria, chloroplasts, endoplasmic reticulum, ribosomes or lysosomes as organelles and the sur-
rounding material they are bathed in as the cytosol.

Cytoskeleton

For decades cell biologists thought the cytoplasmic material surrounding the organelles (the cytosol) was largely an unorganized aqueous mixture of proteins, lipids, carbohydrates and other cellular constituents, including hundreds of thousands of enzymes. Many biology textbooks still embrace this description. However, our concept of the cytosol and its lack of organization was changed in the 1970s when scient-
ists used a special high-voltage electron microscope to discover a lattice of ultra-fine protein filaments within eukaryotic cells (Porter & Tucker 1981). This complex lattice, resembling an internal scaffolding or skeleton, is called the cytoskeleton (Alberts, et al. 1989; Prescott 1988). The name can be misleading be-
cause it implies a permanent, rigid network when in fact the cytoskeleton appears to undergo rapid, even continuous assembly and disassembly as it is re-
shaped within the cytosol (Prescott 1988).

The cytoskeleton is thought to be responsible for shape and movement in many cells. For example, the biconcave form of human red blood cells is due to the cytoskeleton as is much amoeboid movement in an-
imal and protist cells. The arrangement and transport of membrane-bound organelles within the cytoplasm may depend on the lattice, and it may also provide a framework of organizational attachment for cytosolic enzymes such as those of glycolysis. Some organelles appear to be attached to the cytoskeleton and to move along its "highway-like" network, most notably during cytoplasmic streaming (Alberts, et al. 1989). The cytoskeleton, along with associated cytoplasmic streaming, may also help overcome limitations on cell size imposed by diffusion rates (Carlile 1989). The cytosome, along with the cytoskeleton, may be attached to the inner surface of the cell membrane, providing a highway of chemical communication between the internal organelles, such as the nucleus, and the exterior of the cell as delineated by the cell membrane.

The cytoskeleton is usually composed of varying amounts of three fibrous elements:

1. microtubules, long, hollow rods about 25 to 30 nm in diameter and composed of tubulin protein,
2. microfilaments (recently renamed actin filaments by some workers, see Alberts, et al. 1989), long, rod-like structures only about 9.5 nm in diameter formed by actin protein, and
3. intermediate filaments, long, straight or curved rods of several different proteins and about 7 to 12 nm in diameter (Prescott 1988; Kleinsmith & Kish 1988). Thus, it seems appropriate to think of the cytosol as an ordered gelatinous mass with an organized lattice of protein filaments, the cytoskeleton (Alberts, et al. 1989).

The degree of organization and many specific cellular roles of the cytoskeleton (and cytosol) are currently topics of hot debate among cell biologists. There have been reports recently of a nuclear counterpart to the cytoskeleton—the nuclear matrix—that may have a function in chromosome structure (Prescott 1988). Other new discoveries appear regularly from researchers studying the ultra-fine organizational infrastructure of cells. Readers are referred to Prescott (1988), Alberts, et al. (1989) and Kleinsmith & Kish (1988) and references therein for models and detailed discussions of the cytoskeleton, microtubules and microfilaments. General treatments may be found in introductory biology textbooks such as Curtis & Barnes (1989), Starr & Taggart (1989) and the 6th edition of the BSCS blue version, High School Biology (1989).

Organelle Shape

Highly schematic and artistic diagrams in most textbooks show the chloroplast and the mitochondria as "football shaped" structures three to five times greater in length than diameter. Careful study of original micrographs shows varied shapes for these organelles. Mitochondria, a term meaning filamentous body (Vogel 1987), may assume shapes adapted to the particular cell, as in many animal spermatozoa where they form crescentic rods tightly surrounding the axoneme (Reid & Leech 1980). Chloroplasts may be spherical, discoid, elongated or lobed and often show amoeboid movement (Reid & Leech 1980). Incidentally, in textbook art, entire chloroplasts are often colored green to remind us of the light-reflecting qualities of the chlorophyll pigment found in the organelle. A more accurate sketch would show the green chlorophyll only in the thylakoids inside the chloroplast.

Cell Size

Most introductory biology textbooks ignore the fundamental concepts about the limits on cell size. Prokaryotes are very small: Escherichia coli has a volume of only about 1 um$^3$ while eukaryotes may be 1000 times larger, 1000 um$^3$ (1 mm$^3$). Yet, cells are very small compared to the overall volume of multicellular organisms such as mammals. What are the selective pressures against larger eukaryotic cells? Primarily, it seems to be a matter of efficient movement of materials into and out of the cell related to the changing ratio of surface area to volume (Becker 1986). The volume of the cell dictates the quantity of nutrients that must be imported to the inside and the quantity of wastes that must be exported to the outside of the cell. But, surface area of the cell, defined by the cell membrane, governs the amount and efficiency of import and export.

Maintaining sufficient surface area becomes problematic as cell size expands: as surface area increases by the square ($A = 6w^2$), volume increases by the cube ($V = w^3$) (see Becker 1986; Curtis & Barnes 1989). For example, if a cubiform plant cell is 25 um wide, its volume is 15,625 um$^3$ and its surface area is 3,750 um$^2$; a volume to surface ratio of 4.17 um. If the width of the cell is doubled to 50 um, the volume increases to 125,000 um$^3$ and surface area to 15,000 um$^2$, a volume to surface ratio of 8.33 um. Thus, a doubling in size presents serious problems for efficient export and import, especially given the slowness of diffusion (Vogel 1987) over the increased distance from inside to outside. However, if the same 25 um wide cubical plant cell is divided into 1000 cells of 2.5 um width, the total volume (size) remains constant, but the available surface area of cell membrane increases tenfold. The efficiency of material import and export could increase accordingly. It follows then that the selective pressure is toward numerous smaller cells making up the larger eukaryotic organism. This argument could also hold for organelles

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1 $A = \text{area; } w = \text{width, on an edge; } V = \text{volume.}$

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within the eukaryotic cell. The interesting problems of scaling and overall size encountered during the evolution of multi-cellular organisms have been considered by others (see Vogel 1987; Schmidt-Nelson 1984 and references therein).

Cell Walls

Most introductory textbooks state that plant cell walls are composed of cellulose, erroneously implying that this is the only constituent material. Actually, the primary cell wall of plants contains about 9 to 25 percent cellulose, 10 to 35 percent pectin polysaccharides (mostly rhamnogalacturonans, homogalacturonan, arabinan and galactan), 20 to 50 percent hemicelluloses (xyloglucan and glucuronarabinogalactan) and 10 percent protein, including numerous enzymes (Salisbury & Ross 1985; Darvill, et al. 1980). Long, unbranched cellulose molecules are bundled into cylindrical microfibrils about 3.5 nm thick. The microfibrils are then imbedded in a surrounding matrix of the other three cell wall components. An analogy is that plant cell walls are structurally similar to reinforced concrete, with the cellulose acting as the wire mesh or rebar rods but running in several directions. Thus, to state unequivocally that plant cell walls are made of cellulose is somewhat akin to stating that reinforced concrete is made of steel rebar. (Note that cell walls are functionally unlike concrete in that they offer no substantial resistance to diffusion.)

The secondary wall, which surrounds the primary wall in many older plant cells, contains about 40 to 45 percent cellulose, 30 percent hemicelluloses and 22 to 28 percent lignin, a complex molecule even stronger than cellulose (Salisbury & Ross 1985). Secondary walls form wood, a very strong structure extremely resistant to decomposition in nature. Cellulose microfibrils, when embedded in a matrix of proteins, hemicelluloses and pectins or lignins, form the primary and secondary walls of plant cells. The microfibrils may be among the most important factors in the evolution of terrestrial plants because of the mechanical strength and structural integrity of the wall architecture (Duchesne & Larson 1989). The evolution of plant cell walls and their role as composite hydrostats was recently discussed by Niklas (1989).

Membrane Structure

Cellular membranes, whether forming the surface of the cell or the partitions that delineate the internal compartments, are essentially films of hydrated lipoproteins (see Bretsch 1985). They are remarkably similar in their basic architecture as shown best by the fluid mosaic model of membrane structure proposed in the early 1970s by Singer and Nicholson. This familiar model, which has been widely accepted and is detailed in all general biology textbooks, shows a lipid bilayer with proteins extending through it or attached to its surface.

However, general biology textbooks often fail to emphasize two key concepts about membranes: fluidity and asymmetry. The proteins on the surface of the membrane (periodal or extrinsic) and those extending through it (integral or intrinsic) are in motion, as are the phospholipids of the bilayer. It is a fluid, dynamic system—not static, as some textbooks seem to suggest. Also, it is an asymmetrical structure. The proteins are different on the outer and inner surface of the membrane. Many (perhaps most or even all) of those on the outer surface are glycoproteins (proteins with carbohydrate attached) that are important in chemical communication and recognition between cells and organelles. The phospholipid composition may also be different in each half of the bilayer, adding to asymmetry.

Most textbooks fail to point out that lipids may make up about 50 percent of the mass of many membranes (Alberts, et al. 1989), but also that there can be considerable variability in the lipid/protein content among membranes. For example, myelin is about 80 percent lipid and 20 percent protein, thylakoids are about 50 percent each and cristae are about 25 percent lipid and 75 percent protein, while erythrocyte cell membranes may be 20 to 40 percent lipid and 60 to 80 percent protein (Kleinsmith & Kish 1988). Cholesterol can compose 3 to 23 percent of animal cell membranes, affecting their fluidity and decreasing permeability to small, water-soluble molecules (Alberts, et al. 1989). No cholesterol has been found in plant or prokaryotic cell membranes. Glycolipids (lipid-protein complexes) are also found on the surface of membranes but their specific role is not known (Alberts, et al. 1989). As mentioned above, the cytoplasmic side of the cell membrane may be attached to components of the cytoskeleton (Prescott 1988). The attachment is to peripheral proteins, but also probably to integral proteins, at least in erythrocytes, restricting their mobility in the fluid bilayer (Alberts, et al. 1989; Kleinsmith & Kish 1988).

In some animal cells, there is a layer of polysaccharide material external to the outer membrane surface called the glyocalyx or cell coat (Kleinsmith & Kish 1988; Alberts 1989). The polysaccharides are thought to be secreted from the cells, then adsorbed to the integral proteins of the cell membrane. Some types of glyocalyx appear not to be attached to the membrane. These include the carbohydrate layer around many animal eggs, the outer coat of amoebas and the sarcolemma of muscle fibers (Kleinsmith & Kish 1988).

The functions of membranes are discussed at length in all general biology textbooks and will be
considered in the next paper. However, it is worth stating here that membranes are not for mechanical protection or for shape as some textbooks suggest. (Note that in erythrocytes it is difficult to know what is peripheral protein and what is cytoskeleton, the structure that determines shape in these cells.)

The Extracellular Matrix

Animal cells often secrete materials that accumulate in the extracellular matrix, the spaces between cells (Alberts, et al. 1989; Kleinsmith & Kish 1988). Considerable extracellular matrix is seen around bone, connective tissue, brain and skin cells. The matrix contains fibrous proteins such as collagens embedded in a polysaccharide gel (Alberts, et al. 1989) and may be elastic around tendons or rigid around bone or teeth, viscous around nerves or fluid around the cornea. Between connective tissue and epithelium, and extracellular matrix forms a thin, tough mat that controls cell behavior (Alberts, et al. 1989). Some of the polysaccharides of the glycoalyx may be components of the extracellular matrix (Alberts, et al. 1989). The point is that tissues are not necessarily composed entirely of cells as most textbooks lead students to believe. Depending on the type, a considerable portion of a tissue may be extracellular matrix that can help hold the cells of the tissue together and provide a gel medium where cells can move and communicate within the tissue. Thus, tissues—and therefore organisms—can be composed of cells and the products of cells.

Cell Junctions

Alberts, et al. (1989) recognize three main types of connections between animal cells that are generally called cell junctions:

1. occluding or tight junctions that seal cells of epithelial tissue preventing leakage of fluid
2. anchoring junctions, including desmosomes that rivet cells to contiguous cells or the extracellular matrix and
3. communicating junctions such as gap junctions that are low resistance pathways for the flux of ions and other metabolites.

These junctions should not be confused with the more permanent channels between plant cell walls called plasmodesmata. Many introductory textbooks do not mention cell junctions, an area of very active research among animal cell biologists.

Stomates

Finally, the confusion about stomate structure and opening should be resolved. Textbooks usually tell us that the walls of the guard cells forming stomates are thicker on the inside than the outside. They usually also say that when the guard cells fill with water (turgor pressure) the stomates open because the thinner walls on the outside of the guard cell expand or bow out more than the thicker walls lining the stomatal aperture. Although this explanation is appealing, the classroom models with bicycle tubing thickened on the inside appear to demonstrate stomatal opening, it is probably wrong (Curtis & Barnes 1989). We now know that the two guard cells of a stomate are attached at the ends like sausage and that each guard cell is surrounded by hoops of cellulose microfibrils resembling iron rings around a barrel. This structure, known as radial micellation, accounts for stomatal opening. When water enters the guard cell the cell can expand only lengthwise because microfibrils do not stretch and expansion in diameter is limited. Since the guard cells are attached at the end, linear expansion bends them outward, forming a hole called the stomatal aperture between the two guard cells. Wall thickening has been observed in only a few guard cells and does not appear to play a role in stomatal opening.

There are at least two great frontiers of science still to be explored—cells and the universe. Answers to questions in such diverse areas of study as disease (AIDS, cancer), development (differentiation, aging), behavior (memory, mating, psychosis) and evolution (mechanisms, extinctions) might be found at the cellular level. Bioengineered cells might alleviate hunger (food production, pest resistance) and even pollution (recycling, oil-spill decomposition). Research on cells and on the universe have similar restraints and problems despite the obvious differences in their sizes and the distances from us. Astronomers would like to remove the stars from the sky to examine their structure and analyze their content. Cell biologists, and their scientific offspring, would love to do the same thing with the “distant” molecules of cells and even tiny organelles like the cytoskeleton. At present both of these aspirations remain largely out of the realm of developed technology. Nonetheless, the volume and importance of recent discoveries about cells is staggering. In an upcoming article I will outline some of these exciting advances in cell functions.

Acknowledgment

Shortly before his untimely death, William V. Mayer encouraged me to continue this series for The American Biology Teacher, and we discussed this particular manuscript in depth. It is fondly dedicated to Bill and his memory.

References

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