Eukaryote

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Animals, plants, fungi, and protists are eukaryotes (IPA: [juˈkeːrɑːti]), organisms with a complex cell or cells, in which the genetic material is organized into a membrane-bound nucleus or nuclei. Animals, plants, and fungi are mostly multicellular. Many sorts of protist, however, are unicellular. Unlike eukaryotes, prokaryotes (bacteria and archaea) lack nuclei and other complex cell structures. Eukaryotes share a common ancestor, which identifies them as a superkingdom, empire, or domain. In the domain system, eukaryotes have more in common with archaean prokaryotes than bacterial prokaryotes. The name, also spelled "eucaryote," comes from the Greek καρυόν, κοινός, meaning good/true, and κύλιον, meaning nut, in reference to the cell nucleus.

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Structure

Eukaryotic cells are generally much larger than prokaryocytes. They have a variety of internal membranes and structures, called organelles, and a cytoskeleton composed of microtubules, microfilaments and intermediate filaments, which play an important role in defining the cell's organization and shape. Eukaryotic DNA is divided into several linear bundles called chromosomes, which are separated by a microtubular spindle during nuclear division. In addition to asexual cell division (mitosis), most eukaryotes have some process of sexual reproduction via cell fusion (meiosis), which is not found among prokaryocytes.

Internal membrane

Eukaryotic cells include a variety of membrane-bound structures, collectively referred to as the endomembrane system. Simple compartments, called vesicles or vacuoles, can form by budding off other membranes. Many cells ingest food and other materials through a process of endocytosis, where the outer membrane invaginates and then pinches off to form a vesicle. It is probable that most other membrane-bound organelles are ultimately derived from such vesicles.

The nucleus is surrounded by a double membrane (commonly referred to as a nuclear envelope), with pores that allow material to move in and out. Various tube- and sheet-like extensions of the nuclear membrane form what is called the endoplasmic reticulum or ER, which is involved in protein transport and maturation. It includes the Rough ER where ribosomes are attached, and the proteins they synthesize enter the interior space or lumen. Subsequently, they generally enter vesicles, which bud off from the Smooth ER. In most eukaryotes, this protein-carrying vesicles are released and further modified in stacks of flattened vesicles, called Golgi bodies or dictyosomes.

Vesicles may be specialized for various purposes. For instance, lysosomes contain enzymes that break down the contents of food vacuoles, and peroxisomes are used to break down peroxide which is toxic otherwise. Many protozoa have contractile vacuoles, which collect and expel excess water, and extrusomes, which expel material used to deflect predators or capture prey. In multicellular organisms, hormones are often produced in vesicles. In higher plants, most of a cell's volume is taken up by a central vacuole, which primarily maintains its osmotic pressure.

Mitochondria and plastids

Mitochondria are organelles found in nearly all eukaryocytes. They are surrounded by double membranes, the inner of which is folded into invaginations called cristae, where aerobic respiration takes place. They contain their own DNA and are only formed by the fission of other mitochondria. They are now generally held to have developed from endosymbiotic prokaryocytes, probably proteobacteria. The few protozoa that lack mitochondria have been found to contain mitochondrion-derived organelles, such as hydrogenosomes and mitosomes.

Plants and various groups of algae also have plastids. Again, these have their own DNA and developed from endosymbiotes, in this case cyanobacteria. They usually take the form of chloroplasts, which like cyanobacteria contain chlorophyll and produce energy through photosynthesis. Others are involved in storing food. Although plastids likely had a single origin, not all plastid-containing groups are closely related. Instead, some eukaryotes have obtained them from others through secondary endosymbiosis or ingestion.

Endosymbiotic origins have also been proposed for the nucleus, for which see below, and for eukaryotic flagella, supposed to have developed from spirochetes. This is not generally accepted, both from a lack of cytological evidence and difficulty in reconciling this with cellular reproduction.

Cytoskeletal structures

Many eukaryocytes have long slender motile cytoplasmic projections, called flagella. These are composed mainly of tubulin and shorter cilia, both of which are variously involved in movement, feeding, and sensation. These are entirely distinct from prokaryotic flagella. They are supported by a bundle of microtubules arising from a basal body, also called a kinetosome or centriole, characteristically arranged as nine doublets surrounding two singlets. Flagella also may have hairs, or mastigonemes, and scales connecting membranes and internal rods. Their interior is continuous with the cell's cytoplasm. Microfilament structures composed by actin and actin binding proteins e.g. α-actinin, fimbrin, filamin are present in submembraneous cortical layers and bundles as well. Motor proteins of microtubules e.g. dynein or kinesin and actin e.g. myosins provide dynamic character of the network.

Centrioles are often present even in cells and groups that do not have flagella. They generally occur in groups of one or two, called kinetids, that give rise to various microtubular roots. These form a primary component of the cytoskeletal structure, and are often assembled over the course of several cell divisions, with one flagellum retained from the parent and the other derived from it. Centrioles may also be associated in the formation of a spindle during nuclear division.
Significance of cytoskeletal structures is underlined in determination of shape of the cells as well as they are essential components of migratory responses like chemotaxis and chemokinesis. Some protists have various other microtubule-supported organelles. These include the radiolarians and heliozoa, which produce axopodia used in flotation or to capture prey, and the haptophytes, which have a peculiar flagellum-like organelle called the haptonema.

Reproduction

Nuclear division is often coordinated with cell division. This generally takes place by mitosis, a process which allows each daughter nucleus to receive one copy of each chromosome. In most eukaryotes there is also a process of sexual reproduction, typically involving an alternation between haploid generations, where only one copy of each chromosome is present, and diploid generations, where two are present, occurring through nuclear fusion (syngamy) and meiosis. There is considerable variation in this pattern, however.

Eukaryotes have a smaller surface to volume area ratio than prokaryotes, and thus have lower metabolic rates and longer generation times. In some multicellular organisms, cells specialized for metabolism will have enlarged surface areas, such as intestinal villi.

Origin and evolution

The origin of the eukaryotic cell was a milestone in the evolution of life, since they include all complex cells and multi-cellular organisms. The timing of this series of events is hard to determine; Knoll (1992) suggests they developed approximately 1.6 - 2.1 billion years ago. Fossils that are clearly related to modern groups start appearing around 1200 million years ago, in the form of a red alga.

mRNA trees constructed during the 1980s and 1990s left most eukaryotes in an unresolved “crown” group (not technically a true crown), which was usually divided by the form of the mitochondrial cristae. The few groups that lack mitochondria branched separately and so the absence was believed to be primitive, but this is now considered an artifact of long branch attraction and they are known to have lost them secondarily.

Trees based on actin and other molecules have painted a different and more complete picture. Most eukaryotes are now included in several supergroups:

- Opisthokonts: Animals, fungi, choanoflagellates, etc.
- Amoebozoa: Most lobose amoeboidea and slime moulds.
- Rhizaria: Foraminifera, Radiolarians, and various other amoeboid protozoa
- Excavates: Various flagellate protozoa
- Prionoplagiota (or Archaeplastida): Land plants, green algae, red algae, and glaucophytes
- Chromists: Brown algae, diatoms, water molds, etc.
- Alveolates: Ciliates, Apicomplexa, dinoflagellates, etc.

The chromists and alveolates may be part of a larger group that is ancestrally photosynthetic, called the chromalveolates, but this remains contentious. Otherwise the relationships between the different supergroups are mostly uncertain, and in particular there is dispute about where the root of the evolutionary tree belongs, and as a result what the earliest eukaryotes were like. A few small protist groups have not been related to any of the major supergroups, notably the centrohelids, apusozoans, and ebrids.

Eukaryotes are closely related to archaea, at least in terms of nuclear DNA and genetic machinery. In other respects, such as membrane composition, they are similar to eubacteria. Three main explanations for this have been proposed:

- Eukaryotes resulted from the complete fusion of two or more cells, the cytoplasm forming from a eubacterium and the nucleus from an archaean (alternatively a virus).
- Eukaryotes developed from Archaea, and acquired their eubacterial characteristics from the proto-mitochondrion.
- Eukaryotes and Archaea developed separately from a modified eubacterium.

The origin of the endomembrane system and mitochondria are also disputed. The phagotrophic hypothesis states the membranes originated with the development of endocytosis and later specialized; mitochondria were acquired by ingestion, like plastids. The syntrophic hypothesis states that the proto-eukaryote relied on the proto-mitochondrion for food, and so ultimately grew to surround it; the membranes originate later, in part thanks to mitochondrial genes (the hydrogen hypothesis is one particular version).

A new hypothetical theory thinks of the Eucarya ancestor as the Urkaryote. This ancestor is only the precursor of the Eucarya and is not the ancestor of the Archaea or Bacteria. The common ancestor of all three of these domains is a more primitive organism with a variety of different cell structures (less vs more complex structures, pseudomurein vs peptidoglycan cell wall, rRNA differences, lipid bilayer membrane vs phospholipid bilayer membrane, nucleoid region vs defined nucleus, differences in metabolic processes, Enther Dnodroff Pathway vs Glycolysis Pathway, etc).

See also

- List of sequenced eukaryotic genomes

References

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This page was last modified 17:22, 7 February 2007.