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Cell nucleus

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In [cell biology](https://en.wikipedia.org/wiki/Cell_biology), the **nucleus** (pl. ***nuclei***; from [Latin](https://en.wikipedia.org/wiki/Latin) *nucleus* or *nuculeus*, meaning *kernel* or *seed*) is a [membrane-bound](https://en.wikipedia.org/wiki/Biological_membrane#Function) [organelle](https://en.wikipedia.org/wiki/Organelle) found in [eukaryotic](https://en.wikipedia.org/wiki/Eukaryote) [cells](https://en.wikipedia.org/wiki/Cell_%28biology%29). Eukaryotes usually have a single nucleus, but a few cell types, such as mammalian [red blood cells](https://en.wikipedia.org/wiki/Red_blood_cell), have [no nuclei](https://en.wikipedia.org/wiki/Cell_nucleus#Anucleated_cells), and a few others including [osteoclasts](https://en.wikipedia.org/wiki/Osteoclast) have [many](https://en.wikipedia.org/wiki/Multinucleate). The main structures making up the nucleus are the [nuclear envelope](https://en.wikipedia.org/wiki/Nuclear_envelope), a double membrane that encloses the entire organelle and isolates its contents from the cellular [cytoplasm](https://en.wikipedia.org/wiki/Cytoplasm); and the [nuclear matrix](https://en.wikipedia.org/wiki/Nuclear_matrix) (which includes the [nuclear lamina](https://en.wikipedia.org/wiki/Nuclear_lamina)), a network within the nucleus that adds mechanical support, much like the [cytoskeleton](https://en.wikipedia.org/wiki/Cytoskeleton) supports the cell as a whole.

The cell nucleus contains all of the cell's [genome](https://en.wikipedia.org/wiki/Genome), except for the small amount of [mitochondrial DNA](https://en.wikipedia.org/wiki/Mitochondrial_DNA) and, in plant cells, [plastid](https://en.wikipedia.org/wiki/Plastid) DNA. Nuclear DNA is organized as multiple long linear molecules in a [complex](https://en.wikipedia.org/wiki/Protein_complex) with a large variety of [proteins](https://en.wikipedia.org/wiki/Protein), such as [histones](https://en.wikipedia.org/wiki/Histone), to form [chromosomes](https://en.wikipedia.org/wiki/Chromosome). The [genes](https://en.wikipedia.org/wiki/Gene) within these chromosomes are [structured](https://en.wikipedia.org/wiki/Nuclear_organization) in such a way to promote cell function. The nucleus maintains the integrity of genes and controls the activities of the cell by regulating [gene expression](https://en.wikipedia.org/wiki/Gene_expression)—the nucleus is, therefore, the control center of the cell.

Because the nuclear envelope is impermeable to large molecules, [nuclear pores](https://en.wikipedia.org/wiki/Nuclear_pore) are required to regulate [nuclear transport](https://en.wikipedia.org/wiki/Nuclear_transport) of molecules across the envelope. The pores cross both nuclear membranes, providing a [channel](https://en.wikipedia.org/wiki/Ion_channel) through which larger molecules must be actively transported by carrier proteins while allowing free movement of small molecules and [ions](https://en.wikipedia.org/wiki/Ion). Movement of large molecules such as proteins and [RNA](https://en.wikipedia.org/wiki/RNA) through the pores is required for both gene expression and the maintenance of chromosomes.

Although the interior of the nucleus does not contain any membrane-bound subcompartments, its contents are not uniform, and a number of [nuclear bodies](https://en.wikipedia.org/wiki/Nuclear_bodies) exist, made up of unique proteins, RNA molecules, and particular parts of the chromosomes. The best-known of these is the [nucleolus](https://en.wikipedia.org/wiki/Nucleolus), which is mainly involved in the assembly of [ribosomes](https://en.wikipedia.org/wiki/Ribosome). After being produced in the nucleolus, ribosomes are exported to the cytoplasm where they translate [messenger RNA](https://en.wikipedia.org/wiki/Messenger_RNA).

## **Structures**



Diagram of the nucleus showing the [ribosome](https://en.wikipedia.org/wiki/Ribosome)-studded outer nuclear membrane, nuclear pores, [DNA](https://en.wikipedia.org/wiki/DNA) (complexed as [chromatin](https://en.wikipedia.org/wiki/Chromatin)), and the [nucleolus](https://en.wikipedia.org/wiki/Nucleolus).

The nucleus contains nearly all of the cell's DNA, surrounded by a network of fibrous [intermediate filaments](https://en.wikipedia.org/wiki/Intermediate_filaments) and enveloped in a double membrane called the "[nuclear envelope](https://en.wikipedia.org/wiki/Nuclear_envelope)". The nuclear envelope separates the fluid inside the nucleus, called the [nucleoplasm](https://en.wikipedia.org/wiki/Nucleoplasm), from the rest of the cell. The size of the nucleus depends on the size of the cell it is contained in, with a nucleus typically occupying about 8% of the total cell volume.[[1]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-1) The nucleus is the largest [organelle](https://en.wikipedia.org/wiki/Organelle) in animal cells.[[2]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Lodish_2016-2):12 In [mammalian](https://en.wikipedia.org/wiki/Mammal) cells, the average diameter of the nucleus is approximately 6 [micrometres](https://en.wikipedia.org/wiki/Micrometre) (µm).[[3]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Alberts-3)

### Nuclear envelope and pores

*Main articles:*[*Nuclear envelope*](https://en.wikipedia.org/wiki/Nuclear_envelope)*and*[*Nuclear pores*](https://en.wikipedia.org/wiki/Nuclear_pores)



A cross section of a [nuclear pore](https://en.wikipedia.org/wiki/Nuclear_pore) on the surface of the [nuclear envelope](https://en.wikipedia.org/wiki/Nuclear_envelope) (1). Other diagram labels show (2) the outer ring, (3) spokes, (4) basket, and (5) filaments.

The [nuclear envelope](https://en.wikipedia.org/wiki/Nuclear_envelope) consists of two [membranes](https://en.wikipedia.org/wiki/Cell_membrane), an inner and an outer nuclear membrane.[[4]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Alberts2015-4):649 Together, these membranes serve to separate the cell's genetic material from the rest of the cell contents, and allow the nucleus to maintain an environment distinct from the rest of the cell. Despite their close apposition around much of the nucleus, the two membranes differ substantially in shape and contents. The inner membrane surrounds the nuclear content, providing its defining edge.[[2]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Lodish_2016-2):14 Embedded within the inner membrane, various proteins bind the intermediate filaments that give the nucleus its structure.[[4]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Alberts2015-4):649 The outer membrane encloses the inner membrane, and is continuous with the adjacent [endoplasmic reticulum](https://en.wikipedia.org/wiki/Endoplasmic_reticulum) membrane.[[4]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Alberts2015-4):649 As part of the endoplasmic reticulum membrane, the outer nuclear membrane is studded with [ribosomes](https://en.wikipedia.org/wiki/Ribosome) that are actively translating proteins across membrane.[[4]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Alberts2015-4):649 The space between the two membranes, called the "perinuclear space", is continuous with the endoplasmic reticulum [lumen](https://en.wikipedia.org/wiki/Lumen_%28anatomy%29).[[4]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Alberts2015-4):649

[Nuclear pores](https://en.wikipedia.org/wiki/Nuclear_pores), which provide aqueous channels through the envelope, are composed of multiple proteins, collectively referred to as [nucleoporins](https://en.wikipedia.org/wiki/Nucleoporin). The pores are about 60–80 million [daltons](https://en.wikipedia.org/wiki/Atomic_mass_unit%22%20%5Co%20%22Atomic%20mass%20unit) in [molecular weight](https://en.wikipedia.org/wiki/Molecular_weight) and consist of around 50 (in [yeast](https://en.wikipedia.org/wiki/Yeast)) to several hundred proteins (in [vertebrates](https://en.wikipedia.org/wiki/Vertebrate)).[[2]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Lodish_2016-2):622–4 The pores are 100 nm in total diameter; however, the gap through which molecules freely diffuse is only about 9 nm wide, due to the presence of regulatory systems within the center of the pore. This size selectively allows the passage of small water-soluble molecules while preventing larger molecules, such as [nucleic acids](https://en.wikipedia.org/wiki/Nucleic_acid) and larger proteins, from inappropriately entering or exiting the nucleus. These large molecules must be actively transported into the nucleus instead. The nucleus of a typical mammalian cell will have about 3000 to 4000 pores throughout its envelope,[[5]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Rhoades-5) each of which contains an eightfold-symmetric ring-shaped structure at a position where the inner and outer membranes fuse.[[6]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Shulga-6) Attached to the ring is a structure called the *nuclear basket* that extends into the nucleoplasm, and a series of filamentous extensions that reach into the cytoplasm. Both structures serve to mediate binding to nuclear transport proteins.

### Most proteins, ribosomal subunits, and some RNAs are transported through the pore complexes in a process mediated by a family of transport factors known as [karyopherins](https://en.wikipedia.org/wiki/Karyopherin%22%20%5Co%20%22Karyopherin). Those karyopherins that mediate movement into the nucleus are also called importins, whereas those that mediate movement out of the nucleus are called exportins. Most karyopherins interact directly with their cargo, although some use [adaptor proteins](https://en.wikipedia.org/wiki/Signal_transducing_adaptor_protein).[[8]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Pemberton-8) [Steroid hormones](https://en.wikipedia.org/wiki/Steroid_hormone) such as [cortisol](https://en.wikipedia.org/wiki/Cortisol) and [aldosterone](https://en.wikipedia.org/wiki/Aldosterone), as well as other small lipid-soluble molecules involved in intercellular [signaling](https://en.wikipedia.org/wiki/Cell_signaling%22%20%5Co%20%22Cell%20signaling), can diffuse through the cell membrane and into the cytoplasm, where they bind [nuclear receptor](https://en.wikipedia.org/wiki/Nuclear_receptor) proteins that are trafficked into the nucleus. There they serve as [transcription factors](https://en.wikipedia.org/wiki/Transcription_factor) when bound to their [ligand](https://en.wikipedia.org/wiki/Ligand_%28biochemistry%29); in the absence of a ligand, many such receptors function as [histone deacetylases](https://en.wikipedia.org/wiki/Histone_deacetylase) that repress gene expression

*Main article:*[*Nuclear lamina*](https://en.wikipedia.org/wiki/Nuclear_lamina)

*Nuclear lamina*

In animal cells, two networks of [intermediate filaments](https://en.wikipedia.org/wiki/Intermediate_filaments) provide the nucleus with mechanical support: The [nuclear lamina](https://en.wikipedia.org/wiki/Nuclear_lamina) forms an organized meshwork on the internal face of the envelope, while less organized support is provided on the cytosolic face of the envelope. Both systems provide structural support for the nuclear envelope and anchoring sites for chromosomes and nuclear pores.[[9]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-MBoC-9)

The nuclear lamina is composed mostly of [lamin](https://en.wikipedia.org/wiki/Lamin%22%20%5Co%20%22Lamin) proteins. Like all proteins, lamins are synthesized in the cytoplasm and later transported to the nucleus interior, where they are assembled before being incorporated into the existing network of nuclear lamina.[[10]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Sturrman-10)[[11]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Goldman-11) Lamins found on the cytosolic face of the membrane, such as [emerin](https://en.wikipedia.org/wiki/Emerin%22%20%5Co%20%22Emerin) and [nesprin](https://en.wikipedia.org/wiki/Nesprin%22%20%5Co%20%22Nesprin), bind to the cytoskeleton to provide structural support. Lamins are also found inside the nucleoplasm where they form another regular structure, known as the *nucleoplasmic veil*,[[12]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-RGoldman-12)[[13]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Broers_2004-13) that is visible using [fluorescence microscopy](https://en.wikipedia.org/wiki/Fluorescence_microscopy). The actual function of the veil is not clear, although it is excluded from the nucleolus and is present during [interphase](https://en.wikipedia.org/wiki/Interphase).[[14]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Moir-14) Lamin structures that make up the veil, such as [LEM3](https://en.wikipedia.org/wiki/LEM_domain-containing_protein_3), bind chromatin and disrupting their structure inhibits transcription of protein-coding genes.[[15]](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-Spann-15)

Like the components of other [intermediate filaments](https://en.wikipedia.org/wiki/Intermediate_filament), the lamina [monomer](https://en.wikipedia.org/wiki/Monomer) contains an [alpha-helical](https://en.wikipedia.org/wiki/Alpha-helix) domain used by two monomers to coil around each other, forming a [dimer](https://en.wikipedia.org/wiki/Protein_dimer) structure called a [coiled coil](https://en.wikipedia.org/wiki/Coiled_coil). Two of these dimer structures then join side by side, in an [antiparallel](https://en.wikipedia.org/wiki/Antiparallel_%28biochemistry%29) arrangement, to form a [tetramer](https://en.wikipedia.org/wiki/Tetramer_protein) called a *protofilament*. Eight of these protofilaments form a lateral arrangement that is twisted to form a rope like *filament*. These filaments can be assembled or disassembled in a dynamic manner, meaning that changes in the length of the filament depend on the competing rates of filament addition and removal.[[](https://en.wikipedia.org/wiki/Cell_nucleus#cite_note-MBoC-9)

# Nucleolus



Nucleolus contained within the [cell nucleus](https://en.wikipedia.org/wiki/Cell_nucleus)

The **nucleolus** ([/nuː-, njuːˈkliːələs, -kliˈoʊləs/](https://en.wikipedia.org/wiki/Help%3AIPA/English), plural: **nucleoli** [/-laɪ/](https://en.wikipedia.org/wiki/Help%3AIPA/English)) is the largest structure in the [nucleus](https://en.wikipedia.org/wiki/Cell_nucleus) of [eukaryotic](https://en.wikipedia.org/wiki/Eukaryote) [cells](https://en.wikipedia.org/wiki/Cell_%28biology%29).[[1]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-keystone-1) It is best known as the site of [ribosome biogenesis](https://en.wikipedia.org/wiki/Ribosome_biogenesis#Eukaryotes). Nucleoli also participate in the formation of [signal recognition particles](https://en.wikipedia.org/wiki/Signal_recognition_particle) and play a role in the cell's response to stress.[[2]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-2) Nucleoli are made of [proteins](https://en.wikipedia.org/wiki/Protein), [DNA](https://en.wikipedia.org/wiki/DNA) and [RNA](https://en.wikipedia.org/wiki/RNA) and form around specific chromosomal regions called [nucleolar organizing regions](https://en.wikipedia.org/wiki/Nucleolar_organizing_regions). Malfunction of nucleoli can be the cause of several human conditions called "nucleolopathies"[[3]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-pmid24631655-3) and the nucleolus is being investigated as a target for [cancer](https://en.wikipedia.org/wiki/Cancer) [chemotherapy](https://en.wikipedia.org/wiki/Chemotherapy).[[4]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-pmid24389329-4)[[5]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-pmid25464032-5)

## **Structure[**[**edit**](https://en.wikipedia.org/w/index.php?title=Nucleolus&action=edit&section=2)**]**

Three major components of the nucleolus are recognized: the fibrillar center (FC), the dense fibrillar component (DFC), and the granular component (GC).[[1]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-keystone-1) Transcription of the rDNA occurs in the FC.[[10]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-sirri-10) The DFC contains the protein [fibrillarin](https://en.wikipedia.org/wiki/Fibrillarin),[[10]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-sirri-10) which is important in rRNA processing. The GC contains the protein [nucleophosmin](https://en.wikipedia.org/wiki/NPM1%22%20%5Co%20%22NPM1),[[10]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-sirri-10) (B23 in the external image) which is also involved in [ribosome biogenesis](https://en.wikipedia.org/wiki/Ribosome_biogenesis).

However, it has been proposed that this particular organization is only observed in higher eukaryotes and that it evolved from a bipartite organization with the transition from [anamniotes](https://en.wikipedia.org/wiki/Anamniotes) to [amniotes](https://en.wikipedia.org/wiki/Amniote). Reflecting the substantial increase in the DNA [intergenic region](https://en.wikipedia.org/wiki/Intergenic_region), an original fibrillar component would have separated into the FC and the DFC.[[11]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-11)



Nucleus from a cell line. Fibrillarin in red. Transcription regulatory protein [CTCFL](https://en.wikipedia.org/wiki/CTCFL) in green. Nuclear DNA in blue.

Another structure identified within many nucleoli (particularly in plants) is a clear area in the center of the structure referred to as a nucleolar vacuole.[[12]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-12) Nucleoli of various plant species have been shown to have very high concentrations of iron[[13]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-13) in contrast to human and animal cell nucleoli.

The nucleolus [ultrastructure](https://en.wikipedia.org/wiki/Ultrastructure) can be seen through an [electron microscope](https://en.wikipedia.org/wiki/Electron_microscope), while the organization and dynamics can be studied through [fluorescent protein tagging](https://en.wikipedia.org/wiki/Fluorophore) and fluorescent recovery after [photobleaching](https://en.wikipedia.org/wiki/Photobleaching) ([FRAP](https://en.wikipedia.org/wiki/Fluorescence_recovery_after_photobleaching)). Antibodies against the PAF49 protein can also be used as a marker for the nucleolus in immunofluorescence experiments.[[14]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-14)

Although usually only one or two nucleoli can be seen, a diploid human cell has ten [nucleolus organizer regions](https://en.wikipedia.org/wiki/Nucleolus_organizer_region) (NORs) and could have more nucleoli. Most often multiple NORs participate in each nucleolus.[[15]](https://en.wikipedia.org/wiki/Nucleolus#cite_note-15)

**Nucleolus Function:**The **nucleolus** is a round body located inside the nucleus of a eukaryotic cell. It is not surrounded by a membrane but sits in the nucleus. The nucleolus makes ribosomal subunits from proteins and ribosomal RNA, also known as rRNA. It then sends the subunits out to the rest of the cell where they combine into complete ribosomes. Ribosomes make proteins; therefore, the nucleolus plays a vital role in making proteins in the cell.

* Fibrillar Centers: It is the place where the ribosomal proteins are formed.
* Granular Components: Before ribosomes are formed, these components have rRNA that binds to ribosomal proteins.
* Dense Fibrillar Components: It has a new transcribed RNA that connects to the ribosomal proteins.
* Nucleolar vacuoles: It is present only in plant cells.

The ultrastructure of the nucleolus can be easily visualized through an electron microscope.  The arrangement of the nucleolus within the cell can be clearly studied by the techniques –  fluorescent recovery after photobleaching and fluorescent protein tagging.

The nucleolus of several plant species has very high concentrations of iron in contrast to the human and animal cell nucleolus.