MITOCHONDRIAL DNA GENOME VARIANTS

A species-indexed catalogue of chromosome form, gene content, RNA genes, control regions, genetic codes and exceptional architectures

Scope: eukaryotic mitochondrial and mitochondrion-related organelle genomes

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Executive summary

Mitochondrial genomes are not a single conserved object. They range from the compact, usually circular 16–20 kb bilaterian animal chromosome to gene-rich ~70 kb jakobid genomes, repeat-rich plant genome graphs hundreds of kilobases or megabases long, linear fungal and protist chromosomes, multipartite animal genomes, thousands of diplonemid chromosomes, kinetoplastid maxicircle/minicircle networks, and complete loss of organellar DNA in some anaerobic lineages.

The familiar vertebrate “D-loop” is only one kind of replication/transcription control region. Outside vertebrates it is safer to say control region, major non-coding region, terminal repeat, origin-containing repeat, or recombination-active repeat. A triple-stranded displacement loop has not been demonstrated for most sequences casually labelled “D-loop”.

This catalogue is exhaustive at the level of established genome architectures and major gene-content variants, and extensive at species level. It is not literally one entry for every eukaryotic species: most species lack a complete, experimentally validated mitogenome, and databases contain hundreds of thousands of assemblies of uneven quality. Closely related species also show haplotypes, heteroplasmy and structural polymorphism that make a single “species genome” an approximation.

How to read the catalogue

- Protein genes are given by standard lower-case symbols: cox1–3, cob, nad1–6 and nad4L, atp6/8/9, and lineage-specific ribosomal-protein or other genes.
- rRNAs: animal rrnS/12S and rrnL/16S are homologues of small- and large-subunit mitochondrial rRNAs. Some protists encode multiple fragmented rRNA pieces; plants, fungi and gene-rich protists may encode 5S rRNA (rrn5), whereas animal mtDNA normally does not.
- tRNA count means recognizable mtDNA-encoded tRNA genes, not necessarily the full functional mitochondrial tRNA set. Missing tRNAs are usually imported from the cytosol; highly reduced animal tRNAs may lack D or T arms.
- “Circular” describes a useful assembly representation, not always the predominant physical molecule. Plant mtDNA in vivo commonly forms branched, linear and subgenomic molecules represented best by an assembly graph.
- Gene absence from mtDNA can reflect transfer to the nucleus, functional replacement, genuine pathway loss, or failure of annotation—especially for short/divergent atp8, nad4L and tRNAs.

1. Reference gene repertoires

Archetype	Protein-coding genes	tRNAs	rRNAs	Other defining features

Archetype	Protein-coding genes	tRNAs	rRNAs	Other defining features
Typical vertebrate animal	13: cox1–3, cob, nad1–6, nad4L, atp6, atp8	22	rrnS + rrnL	One major non-coding/control region; compact; no introns
Typical bilaterian animal	Usually the same 13; atp8 may be missing	~22, but 0–25+	Usually 2	Gene order and strand use variable
Fungal core	cox1–3, cob, nad1–6/4L, atp6/8/9; variable losses	~20–30	rrnS, rrnL; sometimes rrn5	Introns and intron ORFs often dominate size
Land plant core	cox1–3, cob, nad1–7, nad9, nad4L, atp1/4/6/8/9, ccmB/C/Fc/Fn, matR, mttB; variable rps/rpl/sdh	~15–35	rrn5, rrn18, rrn26	Large repeats, recombination, RNA editing, trans-splicing
Jakobid/protist gene-rich	Respiratory + ATP synthase + many rps/rpl, secY, tat genes and bacterial-type extras	~20–30	Usually 3	Closest to bacterial breadth; lineage-specific
Apicomplexan reduced	cox1, cox3, cob	0	Highly fragmented SSU/LSU pieces	~6 kb concatemeric linear molecules; no ATP synthase or nad genes
Dinoflagellate core	cox1, cox3, cob	0	Fragmented, sometimes trans-spliced	Multiple recombining/concatemeric molecules; extensive editing
Kinetoplastid maxicircle	~18 protein genes including cryptogenes; products completed by U-insertion/deletion editing	0	2 rRNAs	Maxicircle plus guide-RNA minicircles in a catenated network

2. Species-indexed architecture catalogue

Gene counts refer to the principal mitochondrial chromosome(s) and accepted annotations; “CR” means control region. Sizes are approximate because repeats, strains, haplotypes and assembly conventions differ.

2.1 Animals

Species / group	Physical form	Protein genes	tRNAs	rRNAs	Control-region and other variants
Homo sapiens	16.57 kb circle	13	22	2	One ~1.1 kb CR containing OH, promoters and CSBs; D-loop/7S DNA occurs in a subset of molecules. Canonical vertebrate order.
Mus musculus	16.30 kb circle	13	22	2	Compact vertebrate CR; strong laboratory haplotype literature.
Gallus gallus	16.8 kb circle	13	22	2	Bird-type rearrangement near CR: duplicated/translocated tRNA genes; one CR.
Amazona parrots / several birds	~17–19 kb circle	13	22+	2	Duplicated control regions and adjacent genes in several lineages; concerted evolution possible.
Sphenodon punctatus (tuatara)	Two deeply divergent mt genome forms; ~18 kb	13 with duplicated segments	22+	2+ fragments/copies	Coexisting structural haplotypes; duplications around CR/rRNA region; extreme within-individual organization.
Python/other snakes	~17–19 kb circle	13	22+	2	Duplicate CRs in many taxa; rearranged tRNA clusters; duplicate regions can remain functional.
Notothenioid fishes	~17–20+ kb circles/heteroplasmic forms	13, some duplicated	22+	2	Large duplications and alternative rearranged molecules; extensive structural heteroplasmy reported.
Petromyzon marinus (lamprey)	~16 kb circle	13	22	2	Vertebrate-like but divergent gene order/control features; alternative vertebrate code details.
Drosophila melanogaster	19.5 kb circle	13	22	2	Very large A+T-rich control region with tandem repeats; compact coding block.

Species / group	Physical form	Protein genes	tRNAs	rRNAs	Control-region and other variants
Apis mellifera	16.3 kb circle	13	22	2	Extremely A+T rich; numerous tRNA rearrangements; long non-coding intervals.
Metaseiulus occidentalis (mite)	~24.9 kb circle	13	22	2	Unusually large arthropod mtDNA; duplicated genes/pseudogenes, repeats and rearrangements.
Ixodes ticks	~14.5–15 kb circles	13	22	2	Duplicate control regions in Australasian lineages; rearranged tRNAs.
Pediculus humanus (human louse)	~20 minichromosomes, 3–4 kb each	13 distributed	22 distributed	2 distributed	Each minichromosome has coding region plus conserved non-coding replication/transcription region; extensive fragmentation.
Columbicola/other lice	Variable 1–20+ minichromosomes	13, sometimes duplicates/losses	variable	2/fragments	Rapid transitions between single and multipartite mt genomes; recombination and gene-copy variation.
Caenorhabditis elegans	13.8 kb circle	12 (no atp8)	22	2	All genes on one strand; very short, structurally reduced tRNAs; AT-rich non-coding region.
Strongyloides stercoralis	~13.8 kb circle	12 (no atp8)	22	2	Highly derived nematode gene order; truncated tRNAs.
Schistosoma mansoni	~14.4 kb circle	12 (no atp8)	22	2	Flatworm mitochondrial code; compact; derived gene order.
Gyrodactylus spp.	~14–15 kb circle	12 (no atp8)	22	2	Monogenean gene-order rearrangements; non-coding repeat regions.
Lampsilis/Unionidae mussels	~16–18 kb circles	13	22–24	2	Doubly uniparental inheritance: distinct F and M genomes; male genomes may encode M-ORF and show sex-associated divergence.
Mytilus spp.	~16–18 kb circles	13	22	2	DUI with divergent paternal and maternal lineages; recombination/masculinization events.
Octopus vulgaris / cephalopods	~16 kb circle	13	22–28	2	Duplicated tRNAs and, in some cephalopods, conserved duplicated structural genes; extensive RNA editing occurs mainly in nuclear transcripts, not a general mtDNA feature.
Brachionus plicatilis (rotifer)	Two circles, ~11.2 and ~12.7 kb	12 (no atp8), partitioned	22, partitioned	2, partitioned	Two chromosomes of unequal copy number; sizeable non-coding regions; rearranged relative to bdelloids.
Adineta vaga (bdelloid rotifer)	~14.1 kb circle	12	22	2	Single compact chromosome in published assembly; contrasts with Brachionus multipartition.
Aurelia aurita (moon jelly)	~16.9 kb linear	14 incl. polB	2	2	Terminal inverted repeats; encodes a DNA polymerase; linear cnidarian architecture.
Hydra oligactis / Hydra spp.	Two linear chromosomes (~8 kb each)	13	2–3	2	Genes split between linear molecules; terminal repeats; very few mt-tRNAs, requiring import. Some Hydra species differ in chromosome junctions.
Metridium senile (sea anemone)	~17.4 kb circle	13	2	2	cox1 and/or nad5 group-I introns in anthozoans; intron-encoded homing endonucleases possible; slow sequence evolution.
Oscarella carmela (sponge)	~20 kb circle	14+	~24	2	Expanded ancestral-like animal gene/tRNA complement; unusual gene content and introns relative to bilaterians.
Trichoplax adhaerens	~43 kb circle	12+	24	2	Large animal mtDNA with long intergenic regions, introns and bacterial-like retained features.

2.2 Fungi

Species	Physical form	Protein genes	tRNAs	rRNAs	Distinctive variation
Saccharomyces cerevisiae	~75–86 kb circle/map; strain-variable	8: cox1–3, cob, atp6/8/9, var1	24	rrnS, rrnL, 9S RNA	Very AT-rich; GC clusters; many optional introns; lacks complex-I nad genes; ori sequences and recombination.
Schizosaccharomyces pombe	~19.4 kb circle	11 incl. cob, cox, atp and some nad	25	2	Compact yeast mtDNA; intron content strain-variable.
Candida albicans	~40 kb circle	14 core incl. nad set and atp9	~24	2	Repeat-rich intergenic regions; strain-level rearrangements useful for typing.

Species	Physical form	Protein genes	tRNAs	rRNAs	Distinctive variation
Candida parapsilosis	~30 kb linear	core fungal set	~24	2	Linear chromosome with terminal structures/telomeres; related yeasts vary between linear and circular forms.
Hyaloraphidium curvatum	29.97 kb linear	core fungal set	~25	2	Identical 1.43 kb inverted terminal repeats; monomeric linear molecule.
Neurospora crassa	~64 kb circle	14 core + intron ORFs	~25	2	Classic fungal mtDNA; many group-I/II introns and mobile endonucleases.
Podospora anserina	~100 kb circle/map; senescent rearrangements	14 core + ORFs	~27	2	Ageing associated with amplification/rearrangement of mitochondrial plasmid-like and intronic sequences.
Allomyces macrogynus	~58 kb circle	gene-rich fungal complement	~27	3 incl. 5S	Lower-fungal genome retaining additional ribosomal-protein genes and bacterial-like features.
Rhizophagus irregularis	multiple circular/linear haplotypes reported	core fungal set	variable	2	Recombination, homing endonucleases and within-isolate polymorphism complicate a single consensus.

2.3 Plants and green algae

Species	Physical form	Protein genes	tRNAs	rRNAs	Distinctive variation
Arabidopsis thaliana	~367 kb master-circle reference; graph/branched molecules in vivo	~33 proteins	22	3	Large repeats generate alternative subgenomic arrangements; many introns and trans-spliced nad genes; C-to-U RNA editing; no animal-type D-loop.
Oryza sativa (rice)	~491 kb reference; recombining multipartite forms	~35	~17	3	Large repeats, chloroplast-derived inserts, RNA editing and trans-splicing; cytoplasmic male-sterility-associated ORFs in some lines.
Zea mays (maize)	~570 kb, genotype-dependent	~33 + chimeric ORFs	~20	3	Recombination and substoichiometric shifting; CMS genomes carry chimeric ORFs; plasmid-like linear elements can integrate.
Beta vulgaris (beet)	~369 kb; multiple molecules	core angiosperm set + CMS ORFs	~25	3	Cytoplasmic male sterility and fertility restoration linked to novel mitochondrial ORFs.
Silene conica	Dozens of circular chromosomes; total >11 Mb	~25–30 core, dispersed	variable	3, dispersed	Largest known plant mtDNA systems; extreme multipartition, fast sequence evolution and huge noncoding content.
Silene noctiflora	~6.7 Mb, multiple chromosomes	reduced/typical core	variable	3	Enormous expansion with rapid mutation and extensive intergenic DNA.
Viscum scurruloideum (mistletoe)	~66 kb, fragmented/reduced	Loss of all complex-I nad genes; other respiratory genes retained	few	3	First described multicellular eukaryote mtDNA lacking complex-I genes; extreme respiratory remodeling.
Marchantia polymorpha	~187 kb circle reference	~42 proteins	29	3	Bryophyte gene-rich plant mtDNA; relatively conservative; numerous introns, little RNA editing in this liverwort lineage.
Physcomitrium patens	~105 kb circle	~40	27	3	Compact moss mitogenome, more conserved gene order than angiosperms; RNA editing present but modest.
Cycas taitungensis	~415 kb	~39	~22	3	Gymnosperm genome with introns, repeats and plastid-derived DNA; slower structural evolution than many angiosperms.
Chlamydomonas reinhardtii	15.8 kb linear	7: cob, cox1, nad1/2/4/5/6	3	fragmented LSU + SSU pieces	Terminal repeats; no ATP-synthase genes; highly reduced tRNA set and fragmented rRNAs.
Polytomella spp.	linear, ~13–24 kb	7–8	few	fragmented	Nonphotosynthetic chlorophytes with linear mtDNA; terminal repeats and rapid structural evolution.
Pedinomonas minor	~25 kb circle	13+	~10	2	Compact green-algal mitogenome, intermediate gene retention.

2.4 Protists and mitochondrion-related organelles

Species	Physical form	Protein genes	tRNAs	rRNAs	Distinctive variation
Reclinomonas americana (jakobid)	69 kb circle	67 protein genes, including many rps/rpl, secY and respiratory genes	26	3	Most bacterium-like known mtDNA gene complement; no animal-type CR/D-loop.
Andalucia godoyi (jakobid)	~69 kb circle	highly gene-rich (~66)	~25	3	Retains bacterial-like respiratory/ribosomal genes; independent rearrangements among jakobids.
Acanthamoeba castellanii	41.6 kb circle	~30+	16	3	Gene-rich amoebozoan mtDNA with several ribosomal proteins; compact coding.
Dictyostelium discoideum	55.6 kb circle	~33	18	2	AT-rich, multiple rps genes; group-I introns; conserved social-amoeba core with rearrangements.
Tetrahymena pyriformis	~47 kb linear	~40+	7	fragmented/atypical	Linear chromosome with telomeric repeats; unusual split genes and lineage-specific ORFs.
Paramecium aurelia complex	~40 kb linear	~40	few	2+	Linear telomere-bearing mtDNA; high coding density and ciliate genetic code.
Plasmodium falciparum	~6 kb linear tandem concatemer	3: cox1, cox3, cob	0	~20 fragmented rRNA pieces	Extreme reduction; fragments scattered among protein genes; no CR/D-loop in vertebrate sense.
Toxoplasma gondii	~5.9 kb sequence units in complex concatemeric/recombined molecules	3	0	fragmented	Multiple sequence blocks assemble into heterogeneous molecules; architecture not a simple single circle.
Babesia/Theileria spp.	~6–11 kb linear or circular, lineage-dependent	3	0	fragmented	Terminal inverted repeats in some; rearranged three-gene core and rRNA fragments.
Cryptosporidium parvum	No mitochondrial genome	0	0	0	Mitosome-like organelle has lost mtDNA; mitochondrial proteins are nuclear encoded.
Giardia intestinalis	No mitochondrial genome	0	0	0	Mitosomes lack DNA and organellar translation.
Encephalitozoon cuniculi (microsporidian)	No mitochondrial genome	0	0	0	Mitosome lacks genome; extreme nuclear reduction and imported proteins.
Nyctotherus ovalis	~48 kb hydrogenosomal genome	respiratory/ribosomal subset	tRNAs present	rRNAs present	Hydrogenosome retaining DNA, demonstrating that anaerobic mitochondrion-related organelles need not be genome-free.
Trypanosoma brucei	Kinetoplast network: ~20–30 maxicircles + thousands of minicircles	~18 maxicircle genes/cryptogenes	0	2	Minicircles encode guide RNAs; massive U insertion/deletion RNA editing; catenated kDNA disk.
Leishmania tarentolae	Kinetoplast maxicircle/minicircle network	~18	0	2	Guide-RNA minicircle classes and edited maxicircle transcripts; conserved kinetoplastid principle.
Diplonema papillatum	Thousands of small circular chromosomes	genes split into modules; ~18 proteins after trans-splicing/editing	0	rRNA modules	Each gene fragmented into modules on different chromosomes; trans-splicing, U additions and substitutions reconstruct RNAs.
Hemistasia phaeocysticola	Hundreds–thousands of chromosomes	fragmented modules	0	fragmented	Diplonemid-style multipartite genome with extensive RNA maturation.
Crypthecodinium cohnii (dinoflagellate)	Multiple small/concatemeric recombining molecules	3: cox1, cox3, cob	0	fragmented	Extensive RNA editing, gene fragments and recombination; no single canonical chromosome.
Symbiodinium spp.	Multiple mtDNA molecules	3	0	fragmented	Dinoflagellate core; fragmented rRNAs and complex transcript processing.
Cafeteria roenbergensis (stramenopile)	~43 kb circle	~35	~25	2	Gene-rich heterokont mtDNA with rps genes; conventional circle relative to apicomplexans/dinoflagellates.
Phytophthora infestans (oomycete)	~37.9 kb circle	~35	25	2	Two major mitochondrial haplogroups; gene-rich stramenopile genome and useful population marker.
Naegleria gruberi	~49.8 kb circle	~42	22	2	Gene-rich excavate mtDNA; conventional translation apparatus relative to kinetoplastids.

3. Cross-cutting dimensions of mtDNA variation

Dimension	Observed variants and implications
Chromosome topology	Circular maps; linear chromosomes with terminal inverted repeats or telomeres; branched/recombining molecules; catenated networks; tandem concatemers.
Chromosome number	One chromosome; stable two-part systems (Hydra, Brachionus); tens of louse or plant minichromosomes; thousands of diplonemid chromosomes; maxicircle/minicircle division of labour.
Genome size	~6 kb in apicomplexans to >11 Mb total in Silene; size usually reflects non-coding DNA, introns, repeats and duplicated segments more than protein number.
Protein-gene repertoire	Loss/transfer of nad, atp, rps/rpl, sdh and ccm genes; rare acquisition/retention of polB, secY, tat, matR, mttB, plasmid ORFs, homing endonucleases and lineage-specific ORFs.
tRNA repertoire	Complete or near-complete sets; supernumerary duplicates; extreme reduction (Hydra/green algae); total absence (apicomplexans, dinoflagellates, kinetoplastids); highly truncated nematode tRNAs; import from cytosol.
rRNA organization	Two compact genes; inclusion of 5S; split or fragmented genes; modules on different chromosomes; trans-splicing; extremely divergent pieces detectable mainly by structure/transcriptomics.
Control/replication regions	Single CR; duplicated CRs; A+T-rich repeat regions; conserved minichromosome NCRs; terminal repeats; multiple ori-like elements; recombination-active plant repeats; no homologous D-loop.
Gene order and strand use	Near-invariant vertebrate order versus rampant rearrangement in tunicates, mites, lice, fungi and protists; inversion may change mutational strand bias.
Introns	Rare in bilaterians; common group-I/II introns in fungi, plants, algae, sponges and cnidarians; may encode maturases or homing endonucleases; plant genes may be trans-spliced.
RNA processing/editing	Minimal punctuation processing in animals; C-to-U/U-to-C editing in plants; extensive substitutions/indels in dinoflagellates; guide-RNA-directed U insertion/deletion in kinetoplastids; module trans-splicing in diplonemids.
Genetic code	UGA→Trp common in mitochondria; AUA→Met in many animals; AGR may be stop or Ser/Gly; CUN→Thr in budding yeasts; lineage-specific start/stop codons. Code must be selected before annotation.
Inheritance and heteroplasmy	Usually maternal/uniparental, but paternal leakage, biparental inheritance, bivalve DUI, recombination, structural heteroplasmy, copy-number differences and substoichiometric plant molecules occur.
Plasmids and mobile DNA	Linear/circular mitochondrial plasmids; integrated plasmid polymerases; intron homing endonucleases; horizontally acquired elements and viral-like ORFs.
Nuclear/plastid insertions	NUMTs can confound assemblies and barcoding; plant mtDNA often incorporates plastid and nuclear DNA; mitochondrial segments can move into nuclear genomes.

4. The D-loop and control-region problem

In mammalian mtDNA, the major non-coding region contains the heavy-strand origin (OH), transcription promoters and conserved sequence blocks. Short nascent heavy-strand 7S DNA can remain annealed to the template, displacing the parental heavy strand and producing a three-stranded D-loop. The term therefore has a physical meaning, not merely “the non-coding region”.

Across vertebrates, sequence motifs and the persistence/abundance of 7S DNA vary. Some taxa have duplicated control regions, often with concerted evolution; others split or transpose CR-associated blocks. In arthropods the analogous region is often called the A+T-rich region. In louse minichromosomes, conserved non-coding regions are repeated on every chromosome and likely coordinate replication/transcription. Linear genomes use terminal repeats or telomeric structures. Plant

replication and segregation involve repeats, recombination and multiple origins/priming modes, so assigning a single “D-loop” is misleading.

Recommended terminology in comparative work: reserve D-loop for demonstrated triple-stranded displacement-loop structures; otherwise use control region (when functional evidence exists), putative control region, major non-coding region, A+T-rich region, origin-containing region, conserved minichromosome non-coding region, or terminal repeat.

5. Important annotation and interpretation traps

- A circularized assembly can be an assembler convention. Validate topology with long reads, read pairs, restriction/physical mapping, pulse-field gels or microscopy where feasible.
- Short, rapidly evolving tRNAs and atp8 are often missed; “gene loss” should be checked with covariance models, transcript evidence and synteny.
- NUMTs may be co-assembled as heteroplasmy, especially from short reads. Coverage, molecule-spanning reads and organelle enrichment help discriminate them.
- Plant “master circles” may represent one traversal of a repeat graph rather than a dominant chromosome in vivo.
- RNA editing can make the genomic open reading frame appear defective. Protein inference should incorporate transcript data and the correct mitochondrial genetic code.
- Counts vary by annotation policy: intron ORFs, pseudogenes, duplicated partial genes, unidentified ORFs and rRNA fragments may or may not be counted.
- Species may contain stable, sex-specific, tissue-specific, strain-specific or substoichiometric genome forms; a single accession is not always species-representative.

6. Taxonomic checklist for describing any mitogenome

Item	Minimum information to report
Physical architecture	Molecule count; circular/linear/branched/network; terminal structures; alternative isoforms; evidence method.
Sequence statistics	Total and component sizes; GC%; repeats; coverage/copy number; heteroplasmy; assembly graph.
Protein genes	Full inventory, duplicates, pseudogenes, frameshifts, introns, editing, nuclear transfers and lineage-specific ORFs.
tRNAs	Anticodons and isoacceptors; secondary structures; missing arms; duplicates; import evidence; genetic-code compatibility.
rRNAs	SSU/LSU/5S inventory; fragmentation; order; trans-splicing; structural evidence and transcript boundaries.
Non-coding/control DNA	Origins/promoters; D-loop evidence; repeats; CR duplication; conserved minichromosome NCRs; terminal repeats.
Expression	Promoters, polycistrons, punctuation cleavage, introns, RNA editing, trans-splicing, polyadenylation and ribosome peculiarities.
Inheritance/population	Maternal/paternal/biparental/DUI; recombination; strain/haplotype structure; tissue/sex differences.

Item	Minimum information to report
Validation	Long-read support, junction PCR, Northern/RNA-seq, proteomics, physical mapping, and exclusion of NUMTs/contaminants.

7. Selected primary literature and data resources

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8. Bottom-line classification

Nearly all described mtDNA diversity can be located along five independent axes: (1) molecule topology and number; (2) retained gene repertoire; (3) RNA-gene completeness and import; (4) control/replication architecture; and (5) post-transcriptional reconstruction. Similar-looking compact genomes can therefore function very differently, while extremely different physical genomes can encode broadly comparable respiratory outputs.

The 37-gene animal circle is a useful reference, not an ancestral or universal template. The deepest-branching gene-rich mitogenomes retain far more bacterial functions; plants expand mainly through repeats, foreign inserts and recombination; fungi vary through introns, mobile elements and respiratory-gene transfer; and several protist groups have replaced a conventional chromosome with fragmented, edited or networked information systems.