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Euglena gracilis: Photogenic, flexible and hardy

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Graphical abstract

Images of Euglena morphologies and annotations of major cell structures, some of which are discussed in the text. At left a single cell showing positions of the defining eyespot, flagellum and other structures. At right multiple cells with morphologies typical for free swimming forms, spherical cells and multiple forms likely engaged in crawling or ;euglenoid' movement. The image is an adaptation of an original illustration from CG Ehrenberg published in 1838, and while ostensibly of *E. viridis*, at the level of detail shown, is indistinguishable from *E. gracilis*.

Abstract

Euglena gracilis is a unicellular photosynthetic eukaryotic flagellate, belonging to the Excavata supergroup. The chloroplasts are secondarily acquired, with green algal origins. The nuclear genome is extremely large, containing genes with a broad range of origins, suggesting multiple endosymbiotic events. *E. gracilis* is remarkably robust and capable of growth in environments contaminated with heavy metals and acids and has a broad presence within ecosystems. A mixotrophic lifestyle and extraordinary metabolic plasticity confers an ability to thrive in a range of harsh environments, as well as facilitating production of many novel metabolites, making *Euglena* of considerable biotechnological importance.

Taxonomy

Kingdom: Eukaryota; Supergroup: Excavata; Phylum: Euglenozoa; Class: *Eugelenoidea*; Order: *Euglenales*; Family: *Euglenacea*e; Genus: *Euglena*; Species: *Euglena gracilis.*

Properties

Euglena was first described by van Leeuwenhoek in 1684 (Dobell 1932) and were probably one of the '*animalcules*' in a sample of lake water with motion he described as '*so swift, and so various, upwards, downwards, and round about, that 'twas wonderful to see*'. Over a century later Ehrenberg noted the eyespot, establishing the genus Euglena in 1830. The name *Euglena* (beautiful "eu", eye "glena") refers to this structure formed of orange-red, carotenoid-rich granules. *E. gracilis* has two motile cilia, one emergent and another non-emergent from the flagellar pocket. In addition to flagella-driven motility, euglenids alter their morphology, a feature termed metaboly or euglenoid movement, a mode preferentially employed within confined spaces (Hammond et al., 2021).

Genome

The *E. gracilis* genome remains to be assembled, although a draft is available as are three independently determined transcriptomes that encompass >99% of open reading frames (Ebenezer et al., 2019). The genome is estimated at 500 Mb encoding >36000 proteins, but is likely considerably larger and contains a high level of repeat sequence. There is evidence for alternate splicing, *trans*-splicing and multiple intron types, indicating highly complex mRNA processing (Gumińska et al., 2018). Several families consisting of very large numbers of parlours have been described, some of which are likely involved in signalling pathways and environmental sensing; there is no evidence for clustering of these families within the genome. Protein coding genes can have considerable intronic components, and at least some are present as isolated regions within large stretches of non-coding sequence. The genome is polyploid, with an unknown number of chromosomes. The chloroplast genome has rather conventional coding potential (Hallick et al., 1993), but the mitochondrial genome, encoding only seven proteins, is highly reduced (Dobáková et al., 2015).

Phylogeny

Euglenids are a diverse group of flagellates within the phylum Euglenozoa and Excavata supergroup, a likely early branching lineage following eukaryogenesis. The Euglenozoa includes many prominent parasites within the order Kinetoplastida as well as the mostly free-living diplonemids and symbiontids (Kostygov et al., 2021). The presence

of nuclear genes of red and green algae origin servicing the plastid is consistent with sequential endosymbiosis that has been described as the 'shopping bag model' for plastid origin (Larkum et al., 2007). As a member of the Excavata, *E. gracilis* also possesses the unique microtubule arrangement defining the group and used as evidence for monophyly (which is contested). *E. gracilis* is a model organism amongst over 800 diverse euglenoid species, principally due to ease in culturing. While there are reports of genetic manipulation, this appears technically challenging at present.

Key features and discoveries

The defining eyespot acts as a reflective structure or shading device for the proximal photoreceptor, accommodated within the paraflagellar body, which together control negative and positive phototaxis (Kato et al., 2020). The photoreceptor is a heteromeric 400 kDa photoactivated adenylyl cyclase complex that harvests light energy via bound flavin chromophores, catalysing cAMP production (Iseki et al., 2002).

The cell surface is a unique pellicle, composed of proteinaceous strips beneath the plasma membrane, and intimately linked to the tubulin cytoskeleton; the number of pellicle strips is characteristic for each *Euglena* species. Theses strips are composed of articulins, in a heterooligomeric assembly containing many distinct parlous of this euglenoid specific protein. Articullins are thought to interact with the paracrystalline arrays of the major integral plasma membrane protein of 39 kDa (IP39) (Cavalier-Smith 2017), that polymerizes in trimeric units (Suzuki et al., 2013) and also the tubulin cytoskeleton, potentially being involved in euglenoid movement.

Cell shape is responsive to the dark-light cycle: spherically shaped cells ~20 μm in diameter dominate during the dark period (Lonergan, 1983) and elongated 100 μm forms at maximum photosynthetic capacity. The complex and rapid motility of *E. gracilis* is likely augmented by the presence of a full glycolytic pathway located within the flagellum, providing rapid access to an anaerobic system for ATP generation.

E. gracilis grows mixotrophically with extraordinary metabolic plasticity and accumulates various metabolites, including amino acids, vitamins A, C and E, polyunsaturated fatty acids, biotin and paramylon, the latter an insoluble β-1,3 polymer of glucose. Paramylon is unique to euglenoids and deposited in cytosolic paramylon granules as carbon storage and contributes up to 85% dry weight. Under anaerobic conditions *Euglena* switches to the production of wax esters as main storage compound, making it a potential biofuel producer. Given the possibility of large-scale, high-density cultivation,

Euglena has attracted considerable attention for biotechnology application: biomass can be used as food or feed source and to produce metabolites relevant for nutrition, pharmaceuticals, biomaterials and biofuels.

A large gene repertoire, several gene families of considerable size and evidence for frequent gene acquisition events likely contributes towards the metabolic plasticity and extreme adaptability of *E. gracilis* to various environmental cues. *E. gracilis* has been considered for bioremediation applications, but can also contribute towards algae blooms which are highly detrimental towards ecosystems. Complex splicing increases the flexibility of *E. gracilis* still further, while, in common with many organisms alterations in protein abundance are mainly controlled post-transcriptionally.

Open questions

What is the molecular mechanism of euglenoid movement and structure of the pellicle?

What are the full range of secondary metabolites produced and how can production be optimised?

What mechanisms control gene expression, life cycle progression and responses to changing conditions?

Can a facile and reliable system for genetic manipulation be developed?

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Conflicts of interest

The authors have no conflicts of interest to declare.

Recommended reading

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