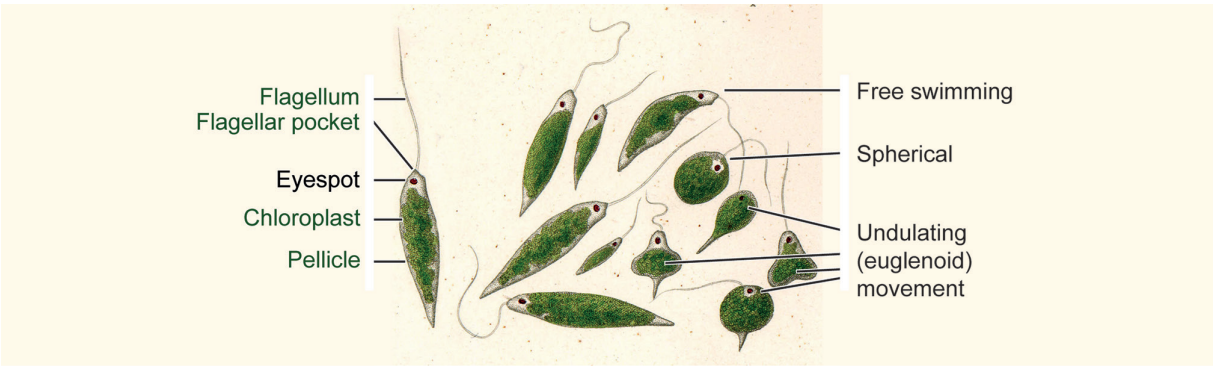
INSIGHT REVIEW
Zoltner and Field, *Microbiology*
DOI 10.1099/mic.0.001241

Euglena gracilis: photogenic, flexible and hardy

Martin Zoltner[1,*] and Mark C. Field[2,3,*]



Graphical abstract

Images of *Euglena* morphologies with annotations of major cell structures, some of which are discussed in the text. At left is a single cell showing positions of the defining eyespot, flagellum and other structures. At right are multiple cells with morphologies typical for free swimming forms, spherical cells and forms probably engaged in crawling or 'euglenoid' movement. The image is an adaptation of an original illustration from C. G. Ehrenberg published in 1838, and while ostensibly of *E. viridis*, at the level of detail shown, is indistinguishable from *E. gracilis*, which in the 19th century were almost certainly impossible to distinguish.

Abstract

Euglena gracilis is a unicellular photosynthetic eukaryotic flagellate of the Discoba supergroup, which also encompasses Kinetoplastida and Diplonema. Plastids have green algal origin and are secondarily acquired. The nuclear genome is extremely large and many genes suggest multiple endosymbiotic/gene transfer events, i.e. derivation from prokaryotes of various lineages. *E. gracilis* is remarkably robust and can proliferate in environments contaminated with heavy metals and acids. Extraordinary metabolic plasticity and a mixotrophic lifestyle confers an ability to thrive in a broad range of environments, as well as facilitating production of many novel metabolites, making *Euglena* of considerable biotechnological importance.

TAXONOMY

Kingdom: Eukaryota; Supergroup: Excavata/Discoba; Phylum: Euglenozoa; Class: *Euglenida*; Order: *Euglenales*; Family: *Euglenaceae*; Genus: *Euglena*; Species: *Euglena gracilis*.

PROPERTIES

Euglena was first described by van Leeuwenhoek in 1684 [3] and these organisms 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

Received 26 May 2022; Accepted 28 July 2022
Author affiliations: [1]Faculty of Science, Department of Parasitology, Charles University, BIOCEV, Vestec, Czechia; [2]Institute of Parasitology, Biology Centre, Czech Academy of Sciences, 37005 Ceske Budejovice, Czechia; [3]School of Life Sciences, University of Dundee, Dundee, DD1 5EH, UK.
***Correspondence:** Mark C. Field, mfield@outlook.com;mfield@mac.com;mcfield@dundee.ac.uk; Martin Zoltner, zoltnerm@natur.cuni.cz
Keywords: *Euglena*; evolution; genome; protists; secondary endosymbiosis.

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. *Euglena gracilis* has two motile cilia, one emergent and another non-emergent from the flagellar pocket. In addition to flagella-driven motility, *Euglena* alter their morphology, a feature termed metaboly or euglenoid movement, a mode preferentially employed within confined spaces [7].

GENOME

The *E. gracilis* genome remains unassembled, although a draft is available as are three independently determined transcriptomes encompassing >99% of ORFs (Ebenezer et al., 2019 *inter alia*). The genome is estimated at 500 Mb, encoding >36000 proteins, AQ3 but is probably considerably larger with a high content of repeat sequences. There is evidence for alternate splicing, *trans*-splicing and multiple intron types, indicating highly complex mRNA processing [4]. Several families consisting of very large numbers of paralogues have been described, some of which are probably 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, albeit with a high frequency of introns [5], but the mitochondrial genome, encoding only seven proteins, is highly reduced and unusually is linear [2].

PHYLOGENY

Euglenids are a diverse group of flagellates within the phylum Euglenozoa and Excavata supergroup, a probable early branching lineage following eukaryogenesis. The Euglenozoa include many prominent parasites within the order Kinetoplastida as well as the mostly free-living diplonemids and symbiontids [10]. 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 [11]. As a member of the Euglenozoa, *E. gracilis* also possesses the unique microtubule arrangement defining the group and used as evidence for monophyly (but which is contested). *E. gracilis* is a model organism amongst over 800 diverse euglenoid species, principally due to ease of culture. While there are reports of genetic manipulation, this remains to be more fully exploited.

Key features and discoveries

The taxon-defining eyespot acts as a shading device for the proximal photoreceptor, accommodated within the paraflagellar body, which together control negative and positive phototaxis [9]. The photoreceptor is a heteromeric 400 kDa photoactivated adenylylcyclase complex (PACα and PACβ) that utilizes light energy via bound flavin chromophores to trigger production of cAMP and downstream signalling [6]. The mechanistic details for phototaxis based on changes to light intensity are probably distinct [6].

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. These strips are composed of articulins, in a heterooligomeric assembly containing many distinct paralogues of this euglenoid-specific protein. Articulins are thought to interact with the paracrystalline arrays of an abundant homotrimeric 39 kDa (IP39) integral plasma membrane protein [1, 13] and also the tubulin cytoskeleton, potentially involved in euglenoid movement.

Cell shape is responsive to the dark–light cycle: spherically shaped cells ~20 μm in diameter dominate during dark periods (Lonergan, 1983) and elongated 100 μm forms dominate at maximum photosynthetic capacity. The complex and rapid motility AQ4 of *E. gracilis* is probably augmented by a full glycolytic pathway located within the flagellum, providing rapid access to anaerobic ATP production.

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 last being an insoluble β-1,3 polymer of glucose. Paramylon is unique to euglenoids and is 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 the main storage compound, making *Euglena* a potential biofuel producer. Given the possibility of large-scale, high-density cultivation, *Euglena* is attracting considerable attention for biotechnology applications; biomass can be used as a food or feed source and for metabolite production relevant for nutrition, pharmaceuticals, biomaterials and biofuels.

A large gene repertoire, several gene families of considerable size and evidence for frequent gene acquisition events probably contribute 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 algal blooms, which are highly detrimental to 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

Can reliable systems for genome-wide genetics be developed?

What is the full range of secondary metabolites produced and can production be optimized?

What mechanisms control gene expression, life cycle progression and responses to environmental changes?

How is metabolism remodelled in the dark to culminate in reversible bleaching, a rather unique ability? A related question is what are the precise signalling mechanisms accompanying photosensing?

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

Funding information
This work was supported by grants from the Wellcome Trust (204697/Z/16/Z to M.C.F.) and the Czech Ministry of Education (project OPVVV/0000759 to M.Z.).

Acknowledgements
Many thanks to Vladimir Hampl (BIOCEV) for comments on the manuscript.

Conflicts of interest
The authors have no conflicts of interest to declare.

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