



## Review

## Flagellar motility in eukaryotic human parasites



Timothy Krüger, Markus Engstler\*

Department of Cell and Developmental Biology, Biocentre, University of Wuerzburg, Am Hubland, 97074 Wuerzburg, Germany

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## ABSTRACT

A huge variety of protists rely on one or more motile flagella to either move themselves or move fluids and substances around them. Many of these flagellates have evolved a symbiotic or parasitic lifestyle. Several of the parasites have adapted to human hosts, and include agents of prevalent and serious diseases. These unicellular parasites have become specialised in colonising a wide range of biological niches within humans. They usually have diverse transmission cycles, and frequently manifest a variety of distinct morphological stages. The motility of the single or multiple flagella plays important but understudied roles in parasite transmission, host invasion, dispersal, survival, proliferation and pathology. In this review we provide an overview of the important human pathogens that possess a motile flagellum for at least part of their life cycle. We highlight recently published studies that aim to elucidate motility mechanisms, and their relevance for human disease. We then bring the physics of swimming at the microscale into context, emphasising the importance of interdisciplinary approaches for a full understanding of flagellate motility – especially in light of the parasites' microenvironments and population dynamics. Finally, we summarise some important technological aspects, describing challenges for the field and possibilities for motility analyses in the future.

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\* Corresponding author.

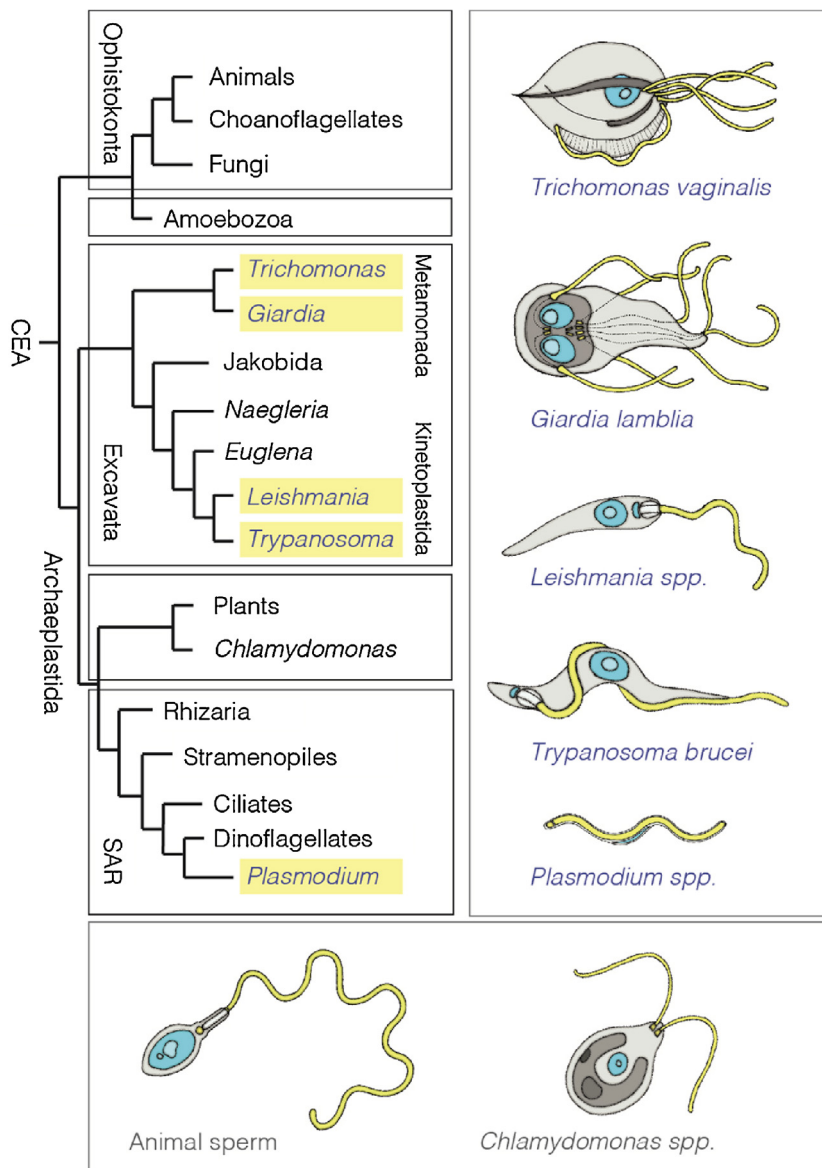
E-mail address: [markus.engstler@biozentrum.uni-wuerzburg.de](mailto:markus.engstler@biozentrum.uni-wuerzburg.de) (M. Engstler).

## 1. Introduction

Flagellar motility is an ancestral eukaryotic concept. It is widely accepted that the last eukaryotic common ancestor featured a motile, microtubule-scaffolded organelle powered by dynein motor proteins [1]. Consequently, flagellates are widespread across eukaryotic supergroups [2,3]. Flagellates, possessing one or several of these snakelike appendages, are free-swimming or sessile protists, and can be either free-living or symbiotic. They are a major constituent of the global planktonic microbiome, whose huge diversity is currently being charted [4]. Flagellates have also been recognised as important parasites of animals and humans since the late nineteenth century [5]. Flagellate parasites of humans belong either to the group Metamonada, which are amitochondriate, tetrakont zooflagellates [6], including *Giardia* and *Trichomonas*, or to the kinetoplastids (Fig. 1). Kinetoplastids are characterised by their eponymous mitochondrial DNA structure. They may be the

earliest-branching group of parasitic protists, and have a very broad distribution of animal and plant hosts [7]. Kinetoplastid parasites of humans belong to the genera *Trypanosoma* and *Leishmania*. In addition, the almost entirely parasitic Apicomplexa rely on flagellate male microgametes during sexual reproduction. The group contains several human- and livestock-infecting genera, amongst them *Plasmodium* and *Toxoplasma*, which form cell-invasive asexual sporozoites during their life cycle [8]. Finally, another human parasite has to be mentioned, *Naegleria fowleri*, a free-living amoeboid flagellate that feeds and divides in an amoeboid life-cycle form. In this trophozoite stage, *Naegleria* infects the central nervous system, albeit rarely but with deadly outcome [9,10]. *Naegleria* trophozoites have the fascinating ability to change from the amoeboid form into a flagellate by developing two flagella de novo, together with a complete microtubule cytoskeleton and basal bodies [11].

Free-living flagellates display a tremendous morphological variety (e.g. [12]), reflecting their vast range of habitats, lifestyles, and



**Fig. 1.** Flagellate morphotypes of human eukaryotic parasites. Left: The evolutionary position of the parasites (coloured boxes) is shown, based on the classification of the five boxed super-groups according to [3] and comparing several other flagellate species and groups. Typical views of flagellate forms are shown in comparison (for dimensions see Table 1). CEA = common eukaryotic ancestor, SAR = Stramenopiles, Alveolates and Rhizaria. Yellow shading highlights the parasitic flagellates that are discussed in this review, while the classical model systems *Chlamydomonas* and sperm are shown in the lower box.

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