

Review

Evolution of parasitism in kinetoplastid flagellates

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ABSTRACT

Kinetoplastid protists offer a unique opportunity for studying the evolution of parasitism. While all their close relatives are either photo- or phagotrophic, a number of kinetoplastid species are facultative or obligatory parasites, supporting a hypothesis that parasitism has emerged within this group of flagellates. In this review we discuss origin and evolution of parasitism in bodonids and trypanosomatids and specific adaptations allowing these protozoa to co-exist with their hosts. We also explore the limits of biodiversity of monoxenous (one host) trypanosomatids and some features distinguishing them from their dioxenous (two hosts) relatives.

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1. Emergence of parasitism: setting (up) the stage

With a certain degree of simplification, when the frequency of eukaryotic parasites encountered in vertebrate and invertebrate hosts is considered, probably only apicomplexans surpass kinetoplastid protists in abundance and diversity, and only parasitic nematodes seem to have a broader host range [1,2]. Kinetoplastids are evolutionarily more ancestral compared to the majority of other groups of parasitic protists, widespread and adaptable, which is an apparent reflection of their extremely successful life style. A recent taxonomy places Kinetoplastea along with its three sister groups

(Euglenida, Symbiontida and Diplonemea) into Euglenozoa that belongs to the Discicristata, a group of protists unified by a striking feature—discoidal mitochondrial cristae [3] (Fig. 1). Euglenida are phototrophic or less frequently phagotrophic, the latter life strategy being characteristic for all known symbiontids and diplomonids [3]. Accordingly, parasitism must have emerged uniquely in the kinetoplastid lineage. It is an exciting challenge to identify genetic changes and/or inventions underlying this dramatic switch to a parasitic life style; however, it has to be postponed until the whole genomes for these sister clades of kinetoplastids are available.

Phylogenetic evidence strongly supports the early-branching of Prokinetoplastina within Kinetoplastea. This tiny group harbors only two known representatives – *Ichthyobodo* and *Perkinsella* (Fig. 2) [4,5]. While *Ichthyobodo* (also called *Costia*) is a bi-flagellar ectoparasite of fish, *Perkinsella* (also known as PLO, parasome and *Perkinsiella*) resides directly in the cytoplasm of certain amoebae parasitizing the gills of fish. This aflagellar kinetoplastid seems

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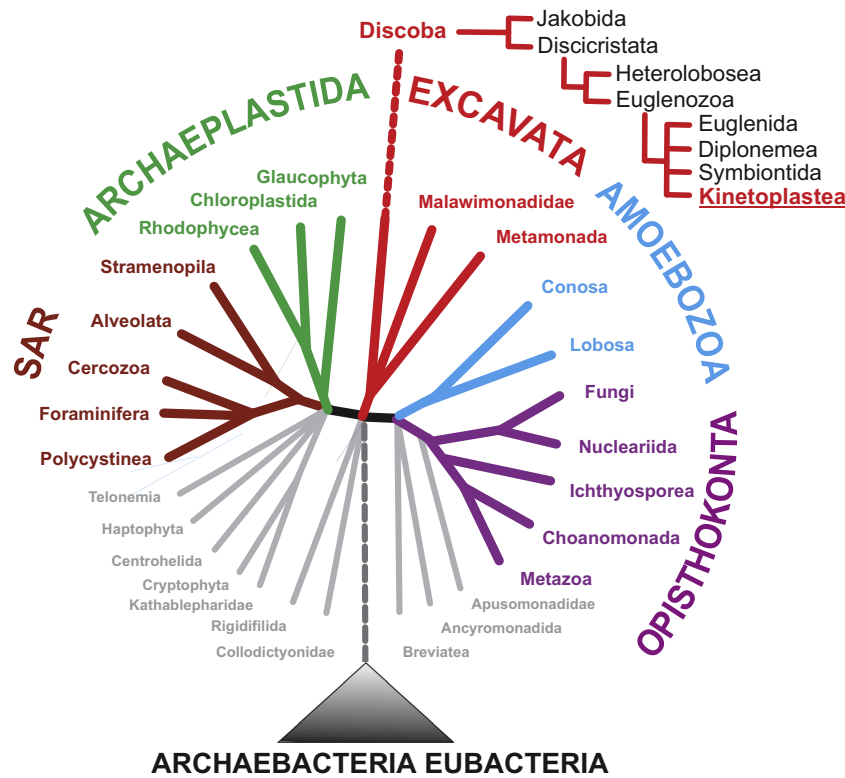


Fig. 1. A view of general eukaryote phylogeny reflecting the recent classification (based on [3]) and highlighting the taxonomic position of Kinetoplastea.

to behave like an organelle, invariably located close to the host nucleus and dividing synchronously with the host cell [6]. Based on DAPI staining, mitochondrial (=kinetoplast [k]) DNA of *Perkinsella* seems to be much more abundant than its nuclear DNA [7]. It will be exciting to investigate whether the extremely tight relationship with the amoeba host is reflected in the kDNA and nuclear genome of *Perkinsella*. Due to its robust branching at the basis of the Kinetoplastea clade, it is tempting to interpret the endosymbiont-like intracellularity of *Perkinsella* as some ancestral form of parasitism via which the kinetoplastid invaded first hosts. However, the absence of flagella, which are otherwise present in all sister clades (euglenids, symbiontids and diplomonids) as well as in all derived lineages, qualifies *Perkinsella* as a unique case of parasitic reductionism.

All the remaining bodonids fall into Metakinetoplastina, a group further subdivided into four clades (Neobodonida, Parabodonida, Eubodonida and Trypanosomatida) (Fig. 2), of which only the latter is obligatory parasitic [3,4]. Mutual relationships within the bodonids are far from being firmly established, yet it is obvious that they acquired parasitic life style independently more than once. Still, only a handful of parasitic bodonids is known, whereas some free-living species are virtually omnipresent and ecologically highly significant [5,8]. Members of the genera *Trypanoplasma* and *Cryptobia* parasitize fish and snails [9,10], respectively. *Azumobodo hoyamushi* causes economically important damage to cultured ascidians [11], while *Jarrellia attramentii* found in the blowhole of whales and dolphins [12] may rather be a commensal than a parasite (Fig. 2). For the purpose of this review, we will focus on flagellates belonging to Trypanosomatida as they embrace an absolute majority of parasitic species (see below).

2. Diversity versus taxonomy: closing the gap

The taxonomy of Trypanosomatida was originally defined by a set of morphotypes, which differ in respect to the mutual positions

of the kDNA, nucleus and flagellar pocket, and the presence or derived loss of a single flagellum [13–16]. Extensive application of electron microscopy in studies of trypanosomatids did not add any important distinguishing features [17,18]. Since the advent of molecular methods it became obvious that neither the individual morphotypes nor their combination within a given life cycle hold any taxonomic value, as they are randomly distributed in the sequence-based phylogenetic trees [19]. Moreover, it seems plausible that there is a continuum of cell forms rather than eight distinct morphotypes.

Due to this dearth of morphological features, one has to resort to DNA sequencing in order to establish taxonomic position of a given trypanosomatid flagellate. There are two categories of genes of choice suitable for this purpose: the small subunit (SSU) rRNA and the glycosomal glyceraldehyde-3-phosphate dehydrogenase (gGAPDH) genes are informative for higher level taxonomy, and are usually sufficient for the genus-level ranking [20–22], while the sequences of the spliced leader (SL) RNA gene and the respective intergenic region allow distinguishing among individual species or even populations [23–27]. The growing number of species and strains, for which sequence data are available, revealed the artificial character of all previously described monoxenous (=one invertebrate host) genera, however, all three dixenous (=vertebrate or plant host and invertebrate vector) genera *Trypanosoma*, *Leishmania* and *Phytomonas* remain monophyletic and well supported (Fig. 3) [19,28].

One approach to close the gap between the outdated morphology-based taxonomy and the molecular-based cladistics that better reflects the relationships among trypanosomatids is to attach taxonomic units to the latter clades. Using this approach, some decades-old taxa rendered paraphyletic by molecular studies and hence invalidated, can be “recycled”, i.e. used just for a single clade containing the type species of a given genus. This solution is taxonomically acceptable, and was successfully used in several instances so far [29–31]. In an alternative approach, novel clades

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