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The Symbiotic Bacterium Fuels the Energy Metabolism of the Host Trypanosomatid *Strigomonas culicis*

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The mutualistic relationship between trypanosomatids and their respective endosymbiotic bacteria represents an excellent model for studying metabolic co-evolution since the symbiont completes essential biosynthetic routes of the host cell. In this work, we investigated the influence of the endosymbiont on the energy metabolism of *Strigomonas culicis* by comparing the wild strain with aposymbiotic protists. The bacterium maintains a frequent and close association with glycosomes, which are distributed around the prokaryote. Furthermore, 3D reconstructions revealed that the shape and distribution of glycosomes are different in symbiont-bearing protists compared to symbiont-free cells. Results of bioenergetic assays showed that the presence of the symbiont enhances the O_2 consumption of the host cell. When the quantity of intracellular or released glycerol was evaluated, the aposymbiotic strain presented higher values when compared to symbiont-containing cells. Furthermore, inhibition of oxidative phosphorylation by potassium cyanide increased the rate of glycerol release and slightly diminished the ATP content in cells without the symbiont, indicating that the host trypanosomatid enhances its fermentative activity when the bacterium is lost.

Key words: Cell evolution; cell ultrastructure; endosymbiosis; glycosome; respiration; trypanosomatid.

Introduction

The compartmentalization of biological activities into organelles is a hallmark of eukaryotic cells and it is widely accepted that endosymbiosis contributed to the optimization of cell metabolism and organization (Archibald 2015; Cavalier-Smith 2002; Gray 2012; Margulis 1993). Although the origin of the eukaryotic cell is still a matter of debate, phylogenetic analyses and the discovery of Lokiarcheota, with seemingly more eukaryotic-like genes, suggest that the mitochondrial host was an archaeon (López-García and Moreira 2015; Martin 2010; Spang et al. 2015). In this sense, the chimeric nature of eukaryotic genomes, which contain many

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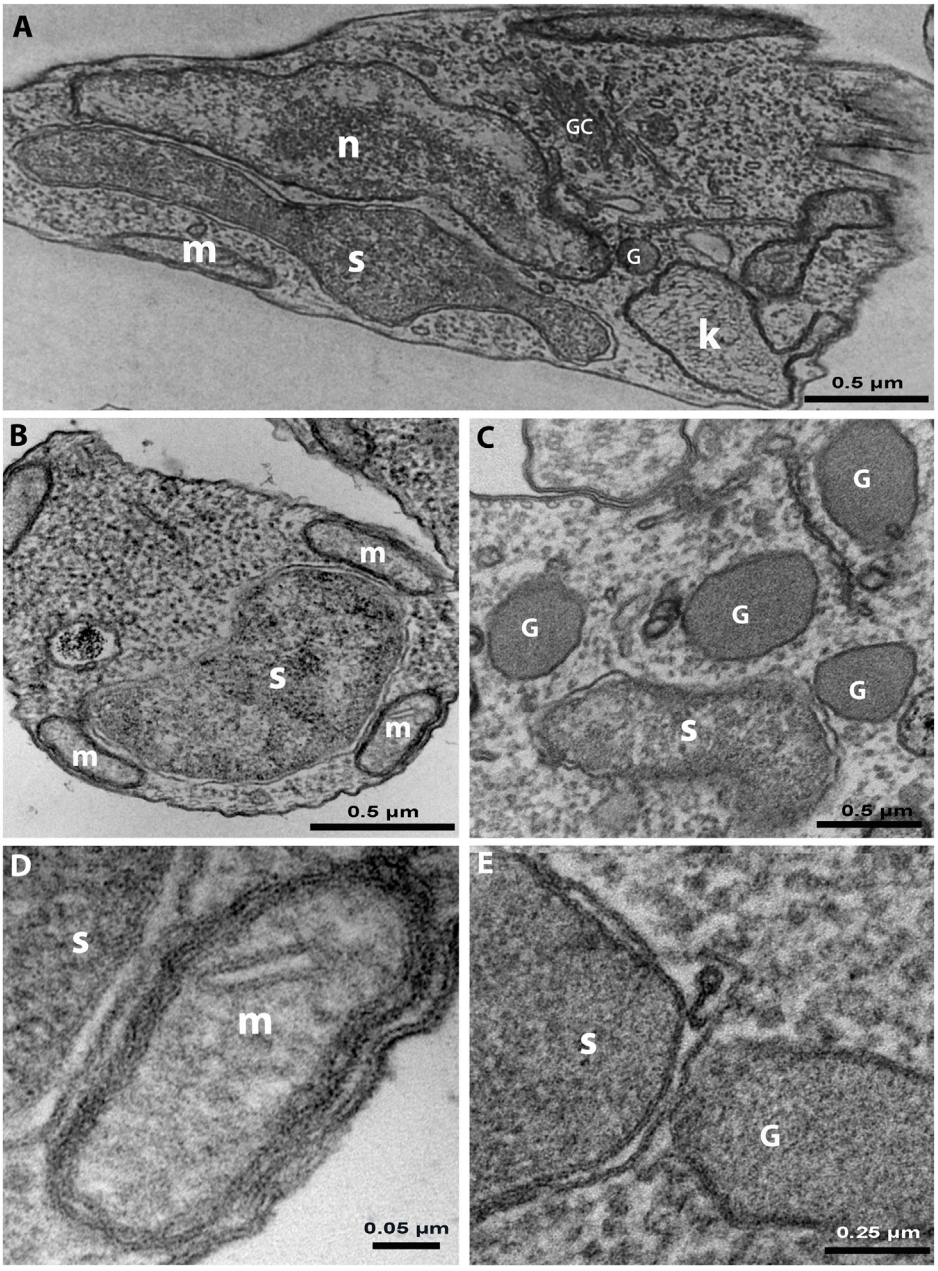

Figure 1. Ultrastructural characteristics of *S. culicis* assessed by transmission electron microscopy. (**A**) A view of *S. culicis* wild-type strain showing organelles and the symbiont close to the host cell nucleus. (**B**) A close proximity is observed between the symbiotic bacterium and mitochondrial branches. (**C**) The bacterium surrounded by glycosomes. (**D**) At higher magnification, it is possible to observe a close association between the symbiont envelope and mitochondrial membrane. (**E**) A close proximity is also observed between the symbiont envelope and the glycosomal membrane. Glycosome (G), Golgi complex (GC), kinetoplast (k), mitochondrial branches (m), nucleus (n) and symbiont (S). The sizes of the scale bars are indicated in each figure.

sequences coding for metabolic enzymes derived from prokaryotes, is a result of multiple gene transfers (Lake 2015; Moya et al. 2008). Some trypanosomatids maintain a mutualistic relationship with endosymbiotic bacteria, such as *Angomonas deanei* and *Strigomonas culicis* (previously named *Crithidia deanei* and *Blastocrithidia culicis*, Teixeira et al. 2011). Such organisms represent an excellent model for studying the evolution of specialized