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Authors: Vittorio Boscaro, Sergei I. Fokin, Giulio Petroni, Franco Verni, Patrick J. Keeling, Claudia Vannini



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## ORIGINAL PAPER

# Symbiont Replacement Between Bacteria of Different Classes Reveals Additional Layers of Complexity in the Evolution of Symbiosis in the Ciliate *Euplotes*

**Running title:** New Symbiotic *Devosia* in *Euplotes*

Vittorio Boscaro<sup>a,b</sup>, Sergei I. Fokin<sup>a,c</sup>, Giulio Petroni<sup>a</sup>, Franco Verni<sup>a</sup>, Patrick J. Keeling<sup>b</sup>, and Claudia Vannini<sup>a,1</sup>

<sup>a</sup>University of Pisa, Department of Biology, Italy

<sup>b</sup>University of British Columbia, Department of Botany, Canada

<sup>c</sup>St.-Petersburg State University, Department of Invertebrate Zoology, Russia

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<sup>1</sup>Corresponding author; fax +39 0502211393

e-mail claudia.vannini@unipi.it (C. Vannini).

Symbiosis is a diverse and complex phenomenon requiring diverse model systems. The obligate relationship between a monophyletic group of *Euplotes* species (“clade B”) and the betaproteobacteria *Polynucleobacter* and “*Candidatus* Protistobacter” is among the best-studied in ciliates, and provides a framework to investigate symbiont replacements. Several other *Euplotes*-bacteria relationships exist but are less understood, such as the co-dependent symbiosis between *Euplotes magnicirratu*s (which belongs to “clade A”) and the alphaproteobacterium “*Candidatus* *Devosia euplotis*”. Here we describe a new *Devosia* inhabiting the cytoplasm of a strain of *Euplotes harpa*, a clade B species that usually depends on *Polynucleobacter* for survival. The novel bacterial species, “*Candidatus* *Devosia symbiotica*”, is closely related to the symbiont of *E. magnicirratu*s, casting a different light on the history of bacteria colonizing ciliates of this genus. The two *Devosia* species may have become symbionts independently or as the result of a symbiont exchange between hosts, in either case replacing a previous essential bacterium in *E. harpa*. Alternatively, both may be remnants of an ancient symbiotic relationship between *Euplotes* and *Devosia*, in which case

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