

Biodiversity and systematics of nematode–bacterium entomopathogens

Byron J. Adams^{a,*}, Andras Fodor^b, Heather S. Koppenhöfer^d,
Erko Stackebrandt^e, S. Patricia Stock^f, Michael G. Klein^c

^a Microbiology and Molecular Biology Department, Evolutionary Ecology Laboratories, Brigham Young University, Provo, UT 84602-5253, USA

^b Department of Genetics, Eötvös University, H-1117 Budapest, Pázmány Peter sétány 11C, Hungary

^c The Ohio State University, USDA-ARS, 1680 Madison Ave., Wooster, OH 44691, USA

^d Entomology and Nematology Department, University of Florida, Gainesville, FL 32611-0620, USA

^e DSMZ-Deutsche Sammlung von Mikroorganismen und Zellkulturen GmbH, Mascheroder Weg 1b, 38124 Braunschweig, Germany

^f Department of Entomology, University of Arizona, 410 Forbes Building, P.O. Box 210036, Tucson, AZ 85721-0036, USA

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Abstract

Nematodes are one of the most abundant animals on earth, and bacteria comprise the most biologically and phylogenetically diverse domains of organisms. On at least two separate occasions a soil dwelling nematode and a bacterium have entered into a mutualistic, insecticidal association. From such origins arose two distinct lineages of nematode–bacterium entomopathogens, *Steinernema–Xenorhabdus* and *Heterorhabditis–Photorhabdus*. Herein, we present a summary and discussion of the known evolutionary diversity and systematics of these two groups relative to other nematodes and bacteria, and their shared evolutionary history.

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1. Introduction

Nematodes are the most abundant animals on earth, and bacteria are the most biologically and phylogenetically diverse (Bongers and Ferris, 1999; Curtis and Sloan, 2004; Curtis et al., 2002; Rappe and Giovannoni, 2003; Torsvik et al., 2002). Cyanobacterial fossils date to 2.9 billion years ago (Noffke et al., 2003), whereas nematodes most likely arose slightly prior to or during the Cambrian explosion (Ayala and Rzhetsky, 1998; Rodriguez-Trelles et al., 2002; Wray et al., 1996). Discovering the full extent of biodiversity of these two clades is one of the greatest challenges facing modern science. Technological and analytical challenges faced by nematode and bacterial systematists are similar, yet the greatest dilemma may be the overwhelming discrepancy between the number of systematists working

on the problem and the estimated number of species needing description (Wheeler et al., 2004). The number of nematode taxonomists has diminished to critical levels, with extinction looming on the horizon (Ferris, 1994). Institutional support for bacterial culture collections is at present incapable of accommodating even a small fraction of the yet to be catalogued specimens, and dollar estimates to see such projects to completion involve multiples of billions. But despite the unknown systematic status for the majority of nematode and bacterial taxa, nematode–bacterium entomopathogens are some of the best-studied members of these tremendously diverse groups of organisms.

It has been speculated that in the mid-Paleozoic (approximately 350 million years ago) ancestors of the Heterorhabditidae and Steinernematidae began to independently explore mutualistic relationships with Gram-negative enteric bacteria (Enterobacteriaceae), the respective lineages of which would evolve to comprise *Photorhabdus* and *Xenorhabdus* (Poinar, 1993). The resulting bacterium–nematode complex comprises

* Corresponding author. Fax: +1 801 422 0519.

E-mail address: bjadams@byu.edu (B.J. Adams).

a formidable biological control weapon against insect pests, which probably best explains the accelerated pace of systematic activity that has focused on these groups over the last 15 years. Our knowledge of bacterial and nematode biodiversity at the present is so poor that even the most sophisticated bootstrapping estimates are at best a modest grope towards reality (Boucher and Lambshhead, 1995; Lambshhead, 1993). In sharp contrast are the entomopathogenic bacterium–nematode complexes, which have been the subject of substantial efforts to reveal their true biological diversity and place them in a meaningful systematic framework. As dynamic processes of discovery, these research programs include sampling efforts that extend to previously unexplored regions of the globe, and evolutionary studies of their historical lineages, from their position within the tree of life, to population genetic structure. Acknowledging that the discovery of each new species renders previous statements of biodiversity obsolete and that there are considerable technological and analytical challenges and gaps that need further scrutiny, the goal of this paper is to summarize entomopathogenic bacterial–nematode biodiversity within an increasingly consistent phylogenetic, systematic framework.

2. Bacterial biodiversity

2.1. Phylogenetic diversity and distribution of major bacterial lineages

The recognition of the major lineages (named “phyla” in the domain Bacteria and “kingdoms” in the domain Archaea; only Bacteria are covered here) is mainly based on the comparative analyses of genes coding for the RNA of the small subunit of ribosomes (16S rDNA of Prokaryotes, 18S rDNA of Eukaryotes). The most comprehensive database of these sequences, ARB (Ludwig et al., 2004), contains about 70,000 aligned sequences from strains, including type material, and from DNA extracted from environmental samples of uncultured organisms. During the past 20 years, about 44 bacterial phyla have been recognized, mostly as a result of gene sequence analyses (Rappe and Giovannoni, 2003). The vast majority of described species are found in only six phyla, Proteobacteria (the majority of Gram-negative organisms), Firmicutes (Gram-positives with low mol% G+C), Actinobacteria (Gram-positives with high mol% G+C), Cyanobacteria, Flavobacteria/Bacteroides, and Spirochaeta [nomenclature according to Garrity et al. (2003)]. These lineages not only contain the most well known organisms of medical, biotechnological, and industrial interest but also the majority of as yet uncultured isolates from terrestrial and marine environments. Ten to hundred species are members of 12 additional phyla. Among these are the lineages containing the deeply rooting Thermotogales and Aquificae, the budding Planctomycetes and Verrucomicrobia, Fusobacteria, and *Deinococcus/Thermus* to name only a few phyla. Another six lineages contain as few as one to six mostly recently described species, whereas the majority of phyla do

not contain cultured species at all. These lineages, worthy of phylum rank, emerged from molecular environmental studies, embracing putative species because of their low degree of relatedness to any described species. As nothing more than the sequence of a single gene is known (sometimes detection of cells by in situ hybridization with fluorescently labeled oligonucleotide probes allow recognition of morphologies), information on cultural and metabolic properties has not yet been elucidated. It can be assumed that the biotechnological potential of the novel strains is high, considering the phylogenetically isolated position and the sometimes-extreme environments the organisms inhabit (hot springs, peat, and alkaliphilic and acidic soils and waters, soda lakes, and anaerobic sediments).

The 16S rRNA gene sequence-based phylogeny is strongly supported by analysis of other genes with similar features which define a valuable phylogenetic marker: ubiquitous distribution, stable function, and conservative primary structure, including a mixture of variable and less variable sequence stretches. Most of these genes, coding for proteins, are named “housekeeping” genes, as they maintain basic functions in anabolic and catabolic cell processes. While some of them are truly ubiquitous and can be used to evaluate the 16S rDNA-based gene tree topology, others are phylum-specific, to be used in the evaluation of lower ranks (classes, families). The advantages of working with rRNA genes rather than genes coding for proteins are given in Table 1.

2.2. Delimitation of bacterial species

The term “species” has two levels of understanding. The first one is the concept, referring to the theoretical framework (evolution, speciation mechanisms), generality, operability, and applicability. The second refers to the provision of practical or applied definitions. At present, a unified species concept is missing in bacteriology. Because the boundaries of bacterial species, should they exist in nature, cannot be recognized between closely related and strain-rich entities, bacteriologists have agreed to work with a definition of the taxonomic unit “species” that is arbitrary, artificial, and pragmatic (Stackebrandt, 1999). Thus, a species is defined as a genomically coherent cluster

Table 1
Comparison of properties of 16S rRNA genes and genes coding for proteins used in phylogenetic studies

Property	16S rRNA gene	Protein-coding genes
Universal	+	Some
Intracellular amplification	Up to 14 copies	one copy
Degeneration of the code	Not applicable	+
(Universal) PCR primers available	+	Rarely
Database	Large	Rare (few are substantial)
Conservative evolution	Orthologous ^a	Orthologous or paralogous ^a

^a Orthology describes genes in different species that derive from a common ancestor, paralogy describes similar phenotype expressed by genes having a different genealogical origin.

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