

A Brief History of Short Bacteria: A Chronicle of *Bdellovibrio* (and Like Organisms) Research

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Abstract Like many good things in science (and in life at large, starting with evolutionary processes), the obligate predatory bacteria *Bdellovibrio* and like organisms (BALOs) were discovered by chance. These fascinating creatures have since been studied by (not too) many great scientists. As the community studying these organisms has never been too large, small changes in its number of scientists have had a large impact on the advancement of this field. A historical perspective of BALO research is presented here.

1 Introduction

Predation is pervasive at all levels of life and maybe as old as life, or cellular life, itself (Maynard Smith and Szathm ry 1995; Bengston 2002). From the tiniest viruses that parasitize and finally lyse their bacterial hosts to the largest of the sharks, it is found in all walks of life, and possibly in all environments.

Predators kill their prey. Predation is a significant cause of mortality, an important evolutionary force, driving the selection of escape strategies in prey and of effectiveness in predators. Predation is such a basic tenet of life that it is strongly embedded in the human psyche; it has been used to describe economic processes (predatory pricing), asocial, criminal behaviors (sexually violent predator), or political developments (predatory democracy).

This central role played by predation in nature is reflected in the great interest it is generating among the scientific community. The scientific literature abounds with articles and books dealing with this matter but a simple search through a few databases reveals that the amount of work performed on predation in the various fields of ecology differ greatly.

Table 1 Numbers of entries in the PubMed and GoogleScholar databases relevant to predation in predator and prey systems of vertebrates, arthropods, and microorganisms

Search engine	Keywords						
	Predation + mammals	Mammals	Predation + arthropods	Arthropods	Predation + Bacteria	Predation + Bacteria (-protozoa, protozoan)	Bacteria
PubMed	1127	11 328 519	952	165 401	207		969 292
Google Scholar	21 100	451 000	7370	59 200	10 500	261	1 170 000

As seen from Table 1, no rule can be formulated as to the relationship of the number of studies centered on predation and the size of the subject organisms, be they predator or prey. However, one thing appears to be clear: a dearth of work on predatory interactions within the prokaryotic realm.

Predation between bacteria has been known for a long time (Beebe 1941, and probably earlier) but the described interactions were of a facultative nature. Mostly, myxobacterial systems have served as “role models” for this type of interaction. However, because of the peculiar and fascinating social behavior exhibited by these bacteria, predation usually took the back seat of research priorities in these systems. Nevertheless, the lytic activities of myxobacteria and other facultative predators have been thoroughly investigated and some data pertaining to the ecological significance of predation by these organisms is available (see chapter by Jurkevitch and Davidov in this volume).

Another class of predatory bacteria are the obligate predators. Although this book is not solely dedicated to these organisms, they form its central theme. I shall therefore present a short history of the discovery and development of the research centered on *Bdellovibrio*, or according to present designation, the *Bdellovibrio* and like organisms (BALOs).

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Historical Perspective

In 1963, Moshe Shilo, from the Hebrew University of Jerusalem was spending a sabbatical in Berkeley at Roger Stanier’s laboratory, working on endotoxic properties of bacterial lipopolysaccharides. During the very same year, Heinz Stolp was also in California as a postdoctoral fellow, staying with Mortimer Starr in UC Davis.

A year earlier, Stolp had described small, fast-swimming gram negative bacteria, obligate predators of other gram negative cells (Stolp and Petzold 1962). At that time, Heinz Stolp (today a professor Emeritus of the Uni-

versity of Bayreuth) was working in Berlin at the Institut für Bakteriologie, developing lyzotyping methods for pseudomonads. In a particular experiment designed to isolate bacteriophages of the phytopathogen *Pseudomonas syringae* pv. *phaseolicola* from a soil suspension, he ran short of filters, and instead used sintered glass filters. The following day, no lytic plaques were apparent in the top agar, so the plates should have been discarded. However, they were not, and when reexamined two days later, plaques had developed (also see Stolp 1973). Then, “just because the belated generation of the plaque spoke against the existence of phage activity, the cause of this lysis was further inspected” (Stolp 1968). What Heinz Stolp saw were rapidly moving, tiny bacteria that attached to the substrate cell, and finally, lyzed them. Hence, they were named *Bdellovibrio bacteriovorus*, the name describing the morphology and the supposed way of life of the bacteria; they were curved and seemed to stick to their prey and to absorb the prey cell content, reminiscent of a leech (“bdella” in Greek). The term was coined by Robert E. Buchanan, a noted taxonomist and Professor at Iowa State College of Agriculture and Mechanic Art. Had the required filters been available, their cut-off size ($0.2\ \mu\text{m}$) would not have enabled the *Bdellovibrio* cells ($0.25 - 0.5 \times 0.75 - 2\ \mu\text{m}$) to pass, but the sintered glass ($1.35\ \mu\text{m}$) allowed their passage. Moreover, had the negative plates been discarded ...*Dans les champs de l'observation le hasard ne favorise que les esprits préparés* (In the fields of observation, chance only favors the prepared mind – Louis Pasteur, lecturing in at the Université de Lille, December 7, 1854).

Back to Davis, 1963. Stolp and Starr thoroughly investigated the newly discovered organism, describing its morphology, providing first insights into the dynamics of predation and isolating saprophytic host-independent mutants. They remarked that isolates vary in prey (always gram negative) range, that prey bacteria surviving predation do not appear to be mutants, and that since *Bdellovibrio* could be recovered in many natural habitats, it probably was an integral component of the microbial flora (Stolp and Starr 1963). These results are as pertinent today as when they were first published. However, *Bdellovibrio* was thought to remain extracellular and was therefore called an ectoparasite. The term ectoparasite rather than exoparasite was used to distinguish it from a parasite that does not require a continuous contact with the prey. Starr and Baigent (1966) later described host penetration and the intraperiplasmic nature of the predator.

Moshe Shilo went on a visit to Davis and “met the bdellovibrios”. From his correspondence, he seems to have been fascinated, and rapidly started to work on the subject along with Barbara Bruff, a student in Stanier’s lab. By the summer of 1963, they had developed an efficient protocol for the recovery of host-independent mutants, which were then used to demonstrate the presence of enzymatic activities able to lyze dead prey cells (Shilo and Bruff 1965). Excited about these new and peculiar bacteria, Shilo wrote from Berkeley to Mazal Varon, who had just terminated her M.Sc., and proposed that she

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