The pedagogical genealogy of Terrance J. Beveridge – A legacy of bonds

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ABSTRACT

Terrance J. Beveridge (TJB) was a professor at the University of Guelph for nearly three decades. He died on September 10, 2007. TJB was a pioneer who pushed the frontier of microbiology and bacteriology. His legacy includes 22 postdoctoral scholars and 24 graduate students. His two dozen graduate student progeny have, in turn, mentored at least 52 additional graduate students. This paper presents TJB's pedagogical tree and touches on many of the topics that he studied during his life including: bacteria cell surfaces, biomineralization, biofilms, and geomicrobiology.

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A countless number of individuals feel a special bond or connection with Terrance J. Beveridge (TJB). He touched our lives. He inspired us. Many of the papers in this special issue will certainly inspire others as they present novel, forward-thinking ideas related to bacteriology and geomicrobiology. TJB would indeed approve. I hope that my paper sparks an interest in some young scientist. But, I must admit that this was not the primary impetus for my paper. I began writing this paper on the day that TJB passed away. I am sure the writing was a way for me to cope with my extreme sadness. Truth be told, I wrote my first version of this paper for an audience of one - Jan Beveridge. In this my final revision, I have tried to broaden the scope of my paper while still maintaining the original, personal intent. As such, this manuscript is a look back into the past, more than a paper that presents forward-thinking ideas. Nonetheless, I think the reader will appreciate many facets of my paper, especially the pedagogical tree that is presented herein. This "family tree" shows the bonds that TJB formed with many of us. For me, inspiration comes through the realization that this tree is only a sapling with endless potential for growth.

I will always remember the first time I met TJB. It was the afternoon of Wednesday, October 27, 1999. I was a graduate student attending the annual meeting of the Geological Society of America in Denver, Colorado (USA). Not only was I to deliver my first oral presentation at a national conference, I was also scheduled to follow Terry in the session. The word intimidation does not even scratch the surface of my feelings

at that time. In fact, I was so nervous that I actually went into the lecture hall the night before my presentation and delivered a mock talk to the cleaning crew.

The time came for my presentation. Nervously, I approached the front of the room with a picture of my wife and three children in my pocket for inspiration and comfort. I gave a 12-min lecture describing a technique called force microscopy that I had used to measure intermolecular forces and bonds between a living bacterium (*Escherichia coli*) and mineral surface (muscovite, goethite, and graphite). I discussed nanoNewton forces that a bacterium could feel over distances of a few nanometers. As I closed my lecture, one hand quickly shot up from a very distinguished looking gentleman in the front row. You guessed it. The hand belonged to Terry. His mouth began to open and my mind began to swirl. What would he ask? How would I respond? Surely my career was over before it had even begun.

But Terry did not ask a question, rather he made a statement. He said, "One word, exciting!" While I doubt that my presentation was that exciting, I will remember those three words forever. Of course, Terry eventually hit me with a deeply probing question. He asked whether I could distinguish force signatures between the poles versus the middle of a rod-shaped bacterium. I don't remember my response, but I doubt that my answer was an adequate one. Nonetheless, Terry did not seem to mind. In fact, after my lecture he asked if I would like to chat with him. We sat down together on some steps outside the conference hall, and we talked one-on-one for about an hour.



Fig. 1 The graduate student pedagogical genealogy of Terrance J. Beveridge (TJB). First generation progeny are shown in large font. The second generation students are shown in smaller, italicized font. The right side of this figure shows roughly the timeframe that each student was working on her/his Master of Science or Doctor of Philosophy degree.

Why would TJB take the time to talk to me? I was, after all, a simple graduate student at that point in my career. By 1999, he had already published 183 peer-reviewed manuscripts, 55 book chapters, and 165 abstracts. He had been the Editor of the *Journal of Bacteriology*. He was a Fellow of the American Academy of Microbiology. He was even a Fellow of the Royal Society of Canada. Surely, TJB had better things to do than talk with a student whom he had never met before. Yet, Terry had two qualities that made him very endearing to the little guy. He was patient and he truly cared.

Of course, I was not the only student to benefit from Terry's mentoring. Terry served as the primary advisor to over 20 graduate students since he became a professor at the University of Guleph in 1978. His reach extends far beyond his primary educational progeny as shown in Fig. 1. The pedagogical genealogy of Fig. 1 had to be limited to only graduate students as it became virtually impossible to manage with the 22 postdoctoral scholars and the 34 visiting scientists who also worked with TJB.

As shown in Fig. 1, there are at least 76 individuals who can trace their educational lineage back to TJB. The scientific

as: ultrastructures on or within a bacterium; biomineralization of carbonates, iron oxides, and silica; stress response and signal transduction in bacteria; electron transfer reactions between metal-reducing bacteria and iron oxides; bacterial oxidation of sulfide minerals; metal sorption to bacteria surfaces; biophysical binding mechanisms within biofilms; and membrane vesicles produced by bacteria. These are by no means the only topics that were studied by TJB and his students. But, they reflect the broad span of Terry's reach. Indeed, TJB directed and defined many of the important concepts related to bacteria surfaces and macromolecules, biofilms, geomicrobiology, transmission electron microscopy and atomic force microscopy.

directions of these students are diverse and include topics such

I have included my name on Terry's pedagogical tree despite the fact that Terry was not my formal advisor during my PhD studies. Michael Hochella, Jr. (Virginia Tech), was my advisor. Mike was the best advisor I could ever have, as I'm sure Terry would agree. I was working with Mike on a PhD in the newly emerging field of geomicrobiology. Mike was an expert on the geo-side of things, but I needed someone to help with the microbiology. Who better to work with than Terry Beveridge?



Fig. 2 Force-signatures of bonds observed between the following pairs: *Shewanella oneidensis*-FeOOH (open circle and cross symbols), MtrC-Fe₂O₃ (dotted curve), and OmcA-Fe₂O₃ (solid curve). Data taken from Lower *et al.* (2001, 2005, and 2007).

For reasons that I will never know, Terry decided to help me earn my dissertation.

During my PhD, I became interested in determining whether bacteria possess a primitive sense of touch. The dogma was, and still is, that prokaryotes, unlike larger organisms, are too small to sense a gradient along their body length (Madigan *et al.*, 2003). To test this idea of touch, one would need to measure the force with which a bacterium feels another surface. Just as importantly, one needed to decide which of the countless species of bacteria to use as a test subject. Mike, Terry, and I certainly did not prove that bacteria have a universal sense of touch, but we took a small step in that direction with the publication of a paper (Lower *et al.*, 2001), which probably launched my career as a professor.

In that paper, we were able to show that *Shewanella oneidensis*, a metal-reducing bacterium, is able to discriminate between two very similar mineral phases (FeOOH vs. AlOOH) but only after a short period of time in contact with each mineral, a period of "recognition time." This observation was not based on some intricate electron micrograph, which was one of Terry's hallmarks. Rather, we collected our data by using an atomic force microscope to literally feel the force of a bond between a living cell of *S. oneidensis* and the surface of either FeOOH or AlOOH. Figure 2 shows some of these force measurements. We hypothesized that the force-signatures shown in Fig. 2 were due to outer membrane cytochromes produced by *S. oneidensis* to form a specific bond with FeOOH as opposed to AlOOH. This hypothesis was corroborated in a

subsequent paper, which showed a correlation between the whole-cell spectra and force-signatures of purified, outer membrane cytochromes from *S. oneidensis* (Lower *et al.*, 2007).

I could go on discussing other ventures with TJB. We had, for example, started to collect force data on 1000 different clinical strains of *Staphylococcus aureus* (see for example, Yongsunthon *et al.*, 2007). We believed that the nanometerscale binding force-signature of an *S. aureus* isolate could be used as a fundamental and practical indicator of pathogenrelated risk for patients with prosthetic implants. Terry was also involved in another project in which we created Braille-like affinity maps that revealed ultrastructural regions defined not by topography or morphology, but the activity of binding proteins on the outer cell wall of *S. aureus*. Shortly before his death, in between surgery and chemotherapy, Terry managed to find time to review the results of our *S. aureus* experiments. Not surprisingly, he sent me a laundry list of questions that we were going to address together.

Before closing, I want to share some of those unresolved, forward-thinking questions that Terry posed to me. Many of these questions can be traced to the original question that Terry and I tested back in 2001. Do bacteria have a sense of touch? How does a bacterium sense or perceive when it has come into contact with another surface? Is this perception due to the biomechanical structure of binding proteins on a bacterium's cell wall? Does the presence of a solid interface cause a signal transduction within a bacterium? Does the presence of a solid interface trigger the expression of specific genes? If so, what is the genetic coding for such a feat? These are just some of the questions that intrigued TJB. I am certainly intrigued by these questions myself. Hopefully, they will inspire other young scientists to become yet another bud on TJB's pedagogical tree.

REFERENCES

- Lower SK, Beveridge TJ, Hochella MF Jr (2001) Bacterial recognition of mineral surfaces: nanoscale interactions between *Shewanella* and α-FeOOH. *Science* **292**, 1360–1363.
- Lower BH, Hochella MF Jr, Lower SK (2005) Putative mineral-specific proteins synthesized by a metal reducing bacterium. *American Journal of Science* **305**, 687–710.
- Lower BH, Shi L, Yongsunthon R, Droubay TC, McCready DE, Lower SK (2007) Specific bonds between an iron oxide surface and outer membrane cytochromes MtrC and OmcA from *Shewanella oneidensis* MR-1. *Journal of Bacteriology* 189, 4944–4952.
- Madigan MT, Martinko JM, Parker J (2003) *Brock Biology of Microorganisms*, 10th edn. Prentice Hall, Upper Saddle River, New Jersey.
- Yongsunthon R, Fowler V, Lower BH, Alexander E, Reller B, Corey R, Vellano FP, Lower SK (2007) Correlation between binding forces and clinical prognosis of *Staphylococcus aureus* biofilms on medical implants. *Langmuir* 23, 2289–2292.