AS IT WAS IN THE BEGINNING, IS NOW, AND EVER SHALL BE

TEAM SCOTT F. GILBERT*

*Chosen by the author, the descriptor "Team Scott F. Gilbert" pays homage to the multitude of more-than-human beings, among them microbes, that collaboratively constitute what we refer to as "I".

Before Jacob von Uexküll defined the Umwelt, his fellow Estonian, Karl Ernst von Baer was using it to ridicule the progressivist notion that animals evolved by successively adding new stages to development. von Baer had a branched-chain view of development, and one form of life was not necessarily superior to another. He wrote (1828, p. 203):

> Let us only imagine that birds had studied their own development, and that it was they in turn who investigated the structure of the adult mammal and of man. Wouldn't their physiological textbooks teach the following? "Those four and two-legged animals bear many resemblances to embryos, for their

> cranial bones are separated, and they have no beak, just as we do in the first five or six days of incubation; their extremities are all very much alike, as ours are for about the same period; there is not a single true feather on their body, rather only thin feather-shafts, so that we, as fledglings in the nest, are more advanced than they shall ever be … And these mammals that cannot find their own food for such a long time after their birth, that can never rise freely from the earth, want to consider themselves more highly organized than we?"

Yet, we persist in our notions of ourselves being the most advanced creature. Stephen J. Gould (1994) pointed out that we call the Cambrian the "Age of Invertebrates," and the Devonian which succeeded it as "The Age of Fishes." Thence came the Carboniferous "Age of Amphibians," which was superseded by the famous Mesozoic "Age of Reptiles." Finally, there was the Cenozoic "Age of Mammals." And now, we have the Anthropocene, "The Age of Humans." It seems the linear Great Chain of Being is still with us. However, as Gould points out, "The most salient feature of life has been the stability of its bacterial mode from the beginning of the fossil record until today and, with little doubt, into all future time so long as the earth endures. This is truly the 'age of bacteria' - as it was in the beginning, is now, and ever shall be."

Half the population of cells in the human body are bacterial. For every cell that you get from the zygote, the fertilized egg, there is a bacterium. Most of the microbes are in our gut, but we have bacterial ecosystems on our eyes, our tongues, on our reproductive orifices, and around and in every pore. The population of bacteria on our right hands differs from the ecosystem on our left hands, as we use them for different functions. Seen from the bacteria's point of view, each of us is a biome—not just an ecosystem, but a collection of ecosystems. We are each a world. The term for such a world/organism is a holobiont, the entire animal including the cells it receives from the zygote and the microbes dwelling in and on it.

So let's look at the world through the perspective of the microbial component of our lives. Let's study the Ur-Umwelt from one of their introductory biology textbooks, where the bacteria discuss the birds and the bees and Big History:

We bacteria are the glory of the world and the crowning achievement of Creation. We can live in hot springs where the temperature is close to boiling, and we can live in Antarctic ice. That yellow ring around the hot springs in Yellowstone Park—that's *Synechoccus*, which can grow at 74°C. The orange ring around that is *Chloroflexus*, a bacteria that grow at 65°C. We microbes live in a thoroughly microbial world that we share with other microbes and with the bigger organisms (plants, animals, and fungi) that we've created to be our niches. These niches have allowed us to diversify into millions of species. In fact, 78% of the life forms of the earth are bacteria, and we've more mass than any other living thing on the planet.

We microbes have been here for about 3.7 billion years, about 2 billion years before multicellular organisms. And we are responsible for all the forms of life present on earth today. One of the big things we did was to set the stage for all subsequent evolution by adding oxygen to the air. And we discovered how to have sex— far more efficiently than other organisms. While the DNA of macrobes is usually passed vertically from generation to generation, we can do that and more. We live in a world of both vertical and horizontal transmission of DNA more baroque and combinatorial than anything that human Deleuze could have imagined. Our DNA is common property that we exchange much more freely than do bigger organisms. If a bacterium dies, other bacteria can ingest its DNA and acquire new properties from it. Indeed, when humans finally figured out that DNA is the basis of such heredity, it was from their observations that DNA from dead *Streptococcus* was capable of giving other Streptococci their virulent traits. We bacteria have also separated sex from reproduction, something humans didn't perfect until very recently.

But it would be boring residing only in the abiotic niches that the world provides us. Life became really exciting when we invented eukaryotic cells. Here, our historical records suggest that we bacteria had help from our microbial cousins, the archaea. Archaea and bacteria probably arose from the same set of microorganisms, who kept exchanging genes.

Eventually two groups got sets of genes that worked together. One group became the bacteria and the other became the archaea. They had some differences in their membranes and metabolism, but they got along well, competing and cooperating with each other, just as we do now. Then, one archaean tried to digest a bacterium, who wouldn't be eaten. That bacterium replicated inside the archaean cell, and this became the first mitochondrion. This gave the archaeal cell energy and permitted it to develop a nucleus and a cytoskeleton. We think the first nucleated single-cell organism was created by this bacterium who refused to be digested; and we have lived, undigested, in digestive tracts ever since.

Indeed, once we microbes invented nucleated cells, there was a whole way of living. Each type of single-celled organism evolved along a different path, creating new niches for bacteria, places where we had never lived before. One remarkable path was for a photosynthetic Cyanobacterium to reside within one of those single-celled "protists" to become the first plant. This holobiont was to have an amazing history that would forever change the world. A second experiment with unicellular protists gave way to the production of multicellular animals. We bacteria had been excellent at multicellularity, sometimes even using it to make two or more different cell types having the same genes. The host-friendly *Bacillus subtilis* and the predatory *Myxococcus xanthus* are particularly adept at this. The cells that became multicellular animals started off as unicellular Choanoflagellates.

Left to their own devices, these cells reproduce monotonously by dividing into two genetically identical Choanoflagellates. But when they divide in the presence of *Algoriphagus* bacteria, they stick together and form colonies. There are cytoplasmic connections between the cells, and there is even an extracellular matrix around the colony.

Not only did we microbes invent the eukaryotic cell and promote eukaryotic multicellularity, we also promoted multicellular sex. Another kind of bacteria secretes a protein that causes those Choanoflagellates to swarm together, undergo meiosis, and have sex, complete with cell fusion and nuclear fusion.

Now eukaryotes can really start evolving. Whereas we microbes can evolve rapidly because we divide so often, are prone to mutation, and can transfer genes laterally, eukaryotes don't have those advantages. But the eukaryotes can undergo meiosis and sexual fusion. This allows them to get recombinations of genes that are the incredibly important creating the variation necessary for evolution. If bacteria were to have new and different living niches to occupy, we had to stimulate meiosis and sex.

The multicellular animals evolved and grew larger. But they are still fragile and need our help. Fish, for instance, can start making their guts, but they need microbes to get their stem cells dividing and get their insulin-secreting pancreas cells up to normal levels. Bacteria also instruct the mammalian gut how to make the capillaries that take food to the rest of its big body. And that's a fascinating story. *Bacteroides*

bacteria live inside the intestine. They tell these intestinal cells to secrete a protein that tells the cells surrounding the intestine to turn into capillaries. That's good for the mammal. Now, that same protein that makes the capillaries form is also one that kills *Listeria* bacteria, the major competitor of *Bacteroides*. We build our niches, helping the mammal as we help ourselves. Bacteria even made it possible for some mammals and insects to become plant-eaters, herbivores. Herbivory came later than carnivory, because animals can't digest plants. Animal genomes make no enzymes that can digest cellulose. We bacteria are great at that, as we eat detritus all the time. So the animal stores us in their guts and feeds us detritus—ground up plants. This is a great niche, as plant cell walls contain the densest concentration of carbon resources on the planet.

In this way, we bacteria invented niche construction. The animal gut helps us, as we help build the animal gut. As soon as the mammalian amnion breaks, we colonize the gut. We bacteria put the colon into colonization. One mammal once wrote, "No man is an island." He was wrong. A man is a perfect island. The first colonizers dock on uninhabited space and expand to make the environment for the next wave, and so forth. Mammalian milk even has special sugars that can't be digested by any mammal or by any bacteria except for those first colonizers, *Bifidobacteria*.

Bacteria control the formation of numerous organs throughout the animal kingdoms, but one of our finest discoveries was how to regulate the animal's immune system. The immune system is not the animal's defensive weaponry against bacteria. It's their passport control office, and we bacteria help make it. Without bacteria, there is no gut-associated immune system, and the levels of immune cells plummet. The immune system is a holobiont activity, that is the activity of the zygote-derived cells and us microbes. Indeed, the resident bacteria help decide which other bacteria are allowed inside each animal.

And last, the humans are starting to theorize that we bacteria may control brain development and social behaviors. Mice that dare to be born free of bacteria are asocial and will not reproduce. This scares humans, because humans believe that they are in control of their destiny. But we want more niches, so we help make them social and facilitate their reproduction. Animals and plants are niches created by bacteria to help multiply and diversify bacteriakind. And if this makes the humans say "Holy shit!", please recall that this phrase resonates with our most profound theology.

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REFERENCES

— Baer, K. E. von. 1828. Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion. Bornträger, Königsberg. P. 203-204. Quoted in Gould, Stephen J. 1977. *Ontogeny and Phylogeny*. Belknap Press, Cambridge. P. 54.

— Gould, S. F. 1994. The evolution of life on earth. Scientific American. <https://www.slideshare.net/DolonPal/sci-am-special-online-issue-2006no28-evolution> or http://brembs.net/gould.html

— Much of the work here is discussed, from a vertebrate perspective, in Gilbert, S. F. and Epel, D. 2015. *Ecological Developmental Biology*. Sinauer Associates. Sunderland, MA.