Growth, Diversity, Chaos… and Death

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Two great personalities in the life sciences did not live to see the new year: Rita Levi-Montalcini (right) and Carl Woese (left).

Rita Levi-Montalcini died on December 30th in Rome as the oldest living Nobel Prize winner (1986, together with Stanley Cohen) at the age of 103. With the discovery and isolation of the nerve growth factor NGF, as well as later the epidermal growth factor EGF, she provided crucial foundations for deciphering the concept of development control by polypeptide growth factors. More about this in the obituaries here , here and here .

On the same day, Carl Woese , the "father of the archaea" and a key pioneer of molecular systematics and evolutionary research through sequence comparisons, died in Urbana, Illinois, at the age of 84. Woese did not receive a Nobel Prize (but did receive the Crafoord Prize, among others), but he was perhaps even more influential on modern biology than Levi-Montalcini. The reason for this is revealed in a conversation that our colleague Karin Hollricher had with Woese almost ten years ago (*Laborjournal* 4/2003: 28-32) — and which we present again here:

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Carl Woese in an interview

"Early evolution was chaotic"

Carl Woese was the first to compare the ribosomal RNAs of microorganisms — and in doing so discovered the *Archaea* as a separate organism domain alongside the *Eubacteria* and the *Eukaryota* . A few weeks ago he received the Crafoord Prize for this. Only shortly before, he had published a new, provocative theory on the early evolution of cells. Karin Hollricher met him for a conversation in Chicago on Thanksgiving.

Carl Woese in front of his car on Thanksgiving 2003.
Note the license plate. (Photo: Karin Hollricher)

LJ: Mr. Woese, people say that you have your best ideas in the evening over a glass of beer.

Woese: (laughs) It's not the only way to produce good ideas. Alcohol lets your thoughts fly. But I only drink light beer; I can't think when I'm drunk.

Last autumn, you published an article in PNAS: "On the evolution of cells" . In it, you write that in your opinion the universal ancestor proclaimed by Darwin did not exist; rather, the origin of all life came from a variety of original cells, of which only a few ultimately prevailed and became the ancestors of bacteria, archaea and eukaryotes. Did this idea also arise over beer?

Woese: The ideas in the article developed as I was writing. And while I was writing, I certainly drank a beer or two... But you know, the 20th century was dominated almost exclusively by molecular biology and genetics. It was an amazing, breathtaking era. Nevertheless, the view of these disciplines is a very reductionist view.

In what way?

Woese: Well, it was a vision of biology to understand the cell. From a molecular biology perspective, you have to take the cell apart. That's what they did. First, they analyzed its genes - very successfully. But even though we now know a lot of genomes, we don't understand the cell. In other words, we have a "Humpty Dumpty" problem.

What is that?

Woese: That's an analogy to a nursery rhyme. It goes something like this:

Humpy Dumpty sat on a wall
Humpty Dumpty had a great fall
all the kings horses and all the kings men
couldn't put Humpty together again.

So even though you've taken the cell apart and examined its individual parts, you still can't understand from the individual pieces of information how the cell works, why it is the way it is. I think you have to look at how cells developed, how their biological form came about. This kind of analysis has been pushed aside for a long time. After Darwin, everything is just about variation and selection. All forms were variants and these were selected. In other words, the biological form had no meaning per se - it is what it is.

What is wrong with this way of looking at things?

Woese: I see the form, the nature of the cell, its organization and its evolution as inseparably linked problems. But any molecular biologist would say that the nature of the cell is one thing, its evolution something else. Let's do a thought experiment: If you were on the moon and found a black box

there, what would you do? Of course you would open the box and look at what was inside, what it was made of. But you would be crazy not to ask yourself where the box came from. And that is precisely the question that molecular biology does not ask.

But you ask this question about where. In your last publication, which I struggled with quite a bit by the way...

Woese: (greatly amused): Really? That 's okay. No molecular biologist understands that. What 's so difficult about it?

You claim that there were many primordial cells from which the precursors of bacteria, archaea and eukaryotes arose independently. What arguments do you use to support your theory?

Woese: Look, there are a lot of scenarios that describe how the eukaryotic cell could have evolved. Eukaryotes have organelles. And we know that the organelles got into the cells through endosymbiosis. Some researchers propagate that eukaryotes have absorbed many endosymbionts and thus many new properties. But I believe that endosymbiosis was a relatively late development in the evolution of the eukaryotic cell, that it only appeared when the eukaryotic cell was essentially developed. Now, many biologists interpret the fact that eukaryotes have bacterial forms of enzymes to mean that these enzymes originate from the endosymbionts . But Charles Kurland and his colleagues Canback and Andersson have shown that all eubacterial versions of enzymes involved in glycolysis form a separate phylogenetic group , the eukaryotic versions form a different group. These groups must have separated long ago, long before they branched into individual lineages. This means that the eukaryotes had these enzymes before the endosymbionts came in. However, this is not true for Krebs cycle enzymes. These really come from the endosymbionts. Until then, the eukaryotes probably lived anaerobically.

And where did the essentially fully developed eukaryotic cell come from?

Woese: You can ask this question for all cells: Where did they come from? How did the cells develop? We don't know. But I have a theory and I want to support it with three arguments. Firstly, translation, secondly, horizontal gene transfer and finally the nature of dynamic systems.

Let's start with translation.

Woese: The translation apparatus is the key "organ" of the cell, because genes are not genes until the cell has the ability to translate them into proteins. However, genes that do not code for proteins are a special case. How did translation come about ? Well, I will not live to see this problem solved. But what do we know about it today ? Translation is a highly complicated process, with many components involved. For this very reason, it is impossible that translation came about from nothing. I believe it developed from an RNA machine. Even today, RNA is an essential part of translation in modern cells. tRNA, for example, brings the amino acids. And the peptidyl transferase, which transfers the growing peptide from one tRNA to the next, is an RNA.

An RNA? Not an enzyme?

Woese: No, that's what people thought for a long time; you can tell from the name. But the crystal structure of the ribosomes shows that the so-called peptidyl transferase center contains no enzyme, in fact no protein at all. Moreover, it was shown decades ago that translation in the cell-free system works without the elongation factor EF2 or EFG **-** also a protein **.** That's why I say that the original translation machine was a small RNA-based machine that worked imprecisely.

Why imprecise?

Woese: Because precision is very complicated. But the original cells had to function simply and be constructed simply. I imagine them as machines that consist of parts that are not yet fully developed. Such systems only work if they tolerate errors. If that was the case, then DNA replication and translation could not have existed in the original cells in their current form.

Now to your second argument, horizontal gene transfer, or HGT for short.

Woese: Horizontal gene transfer was a widespread phenomenon in early evolution, as we know today. In order for a gene transfer to take place, in which a foreign gene replaces the existing one, the donor and recipient must first be in close proximity to each other, living in the same niche. They must also have the same genetic code, speak the same lingua franca , otherwise gene trafficking cannot work.

So what determines whether a gene is transferred frequently or rarely? The key to my theory of what shapes HGT is the translation apparatus. It consists of many different components **-** the RNAs, proteins, elongation factors and tRNA synthetases. If you look at whether and how these components were transferred horizontally, you can see a clear difference. Ribosomal proteins and elongation factors were only minimally exchanged between organisms, which happened very rarely . You never see archaea-type ribosomal proteins in bacteria **-** and not vice versa . But with tRNA synthetases everything is different, they were transferred many times between organisms. For two years I studied the genes for these molecules and often found archaea versions in both bacteria and eukaryotes. So what could be the reason that the tRNA synthetase genes were transferred by HGT, but the genes for the other ribosomal components were not? This is because the ribosomal components interact and work together. In contrast, the tRNA synthetases are independent of the ribosomes. The enzymes only have to bind the right tRNA. They can work in any organism as long as they recognize the tRNAs and bring them to the ribosome. It follows that the organization of the cell defines which genes can be replaced by foreign genes and how different the foreign genes can be. This determines the quality of HGT.

So is HGT an important component for the early evolution of the cell?

Woese: It is the most important force. Variation and selection within a lineage have only a limited influence on evolution compared to the uptake of new genes . I think early evolution was quite chaotic. There must have been a real gene trade back then. This phase of the evolution of the cell must have encompassed the entire world of organisms. It was a community phase before species or lineages developed as Darwin defined them.

How can we categorize these primordial organisms if not as lineages or species? Can we even speak of a genealogy if there were no individual lineages?

Woese: At some point in evolution, 1 to 3 billion years ago, after organisms had been constantly exchanging genes, there was a point at which certain genes remained in a cell, they were literally locked in there. At this point, the genealogy of these cells begins - a lineage is created that eventually branches out into species. I call this critical point, when a lineage is created, the Darwinian threshold.

This brings us to my third argument: cells are self-organizing organisms that can be compared to dynamic systems. A dynamic system is stable for a long time until something suddenly happens that changes it significantly. Then the system crosses a critical point and a phase change occurs. An example of this is the freezing of water into ice. Today I am more convinced than ever - even more than when I wrote the paper - that the Darwinian threshold is such a critical point in the process of evolution. It is the first critical point defined in biology.

So before the Darwinian threshold we have the community phase in which cells happily exchange their genes, and then the Darwin era in which lines only branch out?

Woese: In principle, yes. And the phase transition is sudden. The key to this is the interconnectedness, the integration of the individual parts of the cellular design. At first, the components are largely independent of each other, the hierarchy is flat. Then more and more connections are made - until the individual components can no longer work independently of each other, and can therefore no longer be exchanged through HGT.

So there must be a "point of no return"?

Woese: That's right, and from there there was no turning back . That's what happened with the mitochondrion, for example. Once the endosymbiont was in the cell, it became more and more dependent on it.

What was the reaction in the scientific community to your new theory?

Woese: There were only a few reactions. The majority of biologists are not interested in it. There will probably be some who ask themselves: "What's new about that?" Or those who say: "That's interesting, can he prove it?" To them I say: "So what?" The paper conveys a certain idea: that of the community phase. At that time, no single cell probably even had a complete genome - rather, the complete genome was that of the community of all organisms in a niche that developed as a whole system in and with their ecosystem. It may not have been that way - but I think it was.

How do you imagine the development of the three domains of bacteria, archaea and eukaryotes?

Woese: The three designs started in the RNA world, they evolved from different structures and they were self-organizing systems.

So there was no primordial cell?

Woese: Exactly!

But at least three primordial cells?

Woese: I think much, much more. But only three designs managed to cross the Darwinian threshold independently of each other and probably at different times.

Which means nothing other than that Darwin was wrong with his hypothesis that "all the organic beings which have ever lived on this earth have descended from some one primordial form…." If he were still alive today, what would he be working on and with whom?

Woese: In my lab.

Why?

Woese: (*laughs*) Not because I'm the best. There are many good scientists . But he would work, as he did in his time, at the forefront of science. Now the classical evolutionary biologists have withdrawn from this front and only worked on details. Now molecular evolution is at the forefront. That's where Darwin would work. Because with these methods you can now ask and answer questions that were previously unthinkable in the classical context.

This year you were awarded the prestigious Crafoord Prize for your discovery that archaea are not bacteria, but represent their own third domain of organisms. How do you feel now?

Woese: I feel very good. This award is the formal and ultimate recognition of what I have given to biology - namely, the genetic approach to classifying the microbial world.

In terms of prestige, this award is equivalent to a Nobel Prize. Do you now experience the same hype as a Nobel Prize winner?

Woese: Not at all. There weren't many reactions. Some friends congratulated me, of course. But here in America, only the Nobel Prize counts; Americans don't notice anything else.

Is Ernst Mayr, the "grand old man" of modern evolutionary biology, among those congratulating him? He knows the significance of the Crafoord Prize very well; he received it in 1999 together with John Maynard Smith and George Williams.

Woese: Yes, he congratulated me.

That surprises me, because to this day he doesn't believe in their archaea theory.

Woese: That's true, but he congratulated me anyway. He sees the question: "Are there two or three domains in biology?" from the perspective of taxonomy. He classifies biology according to taxonomic criteria. But I say that biology defines taxonomy. That's why I come to different conclusions.

What will you do with the prize money? It's half a million dollars, after all? Will you retire with it?

Woese: No, definitely not. Of course I want to continue researching. And the money - I have no idea what I'll do with it... But I do know: first I'll pay $290,000 in taxes.

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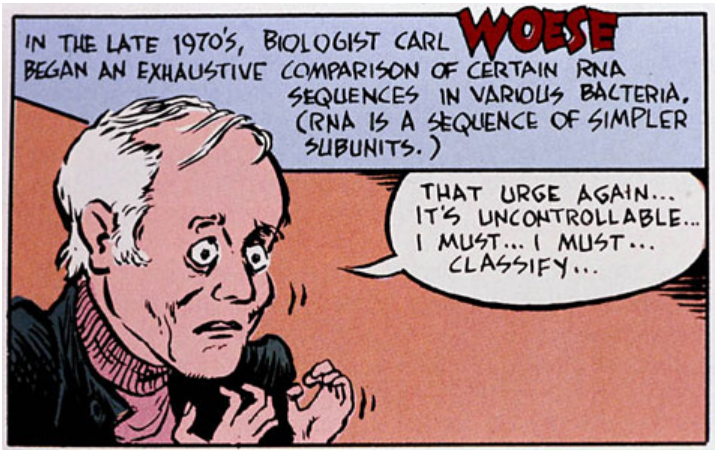

via [O amigo de Wigner]

Carl R. Woese was born on July 15, 1928 in Syracuse (New York) and is a professor of microbiology at the University of Illinois at Urbana-Champaign. He has been teaching and researching there for almost 40 years - in the middle of a US state that stretches endlessly flat south of Chicago.

Shortly after his arrival in the university town that had grown out of the towns of Urbana and Champaign, he began to grapple with a fundamental problem: the taxonomy of bacteria. A major challenge, because the tiny organisms do not have enough morphological or physiological characteristics to classify them. Many famous biologists had failed miserably at this.

Woese, however, did not concern himself with morphology, but focused instead on molecular biology. At the beginning of the 1970s, when DNA-DNA hybridization experiments were still being carried out to determine the similarity of the nucleic acids used, he began to analyze the ribosomal RNAs of bacteria and archaea. The researcher, who had already been studying the evolution of the genetic code in the 1960s, had chosen these molecules because he assumed that, due to their essential function, they must be very old molecules and therefore have changed very little over the course of evolution. This assumption turned out to be completely correct: with his rRNA studies, Woese laid the foundations for modern molecular evolutionary biology.

Due to the differences that Woese found in the 1970s between the 16S rRNAs of bacteria and (then still so-called) archaebacteria, he postulated that the latter should not be counted among the bacteria, but that they form an independent, third domain. This meant that the family tree of life that had been valid up to that point, with its two branches, the origins of bacteria on the one hand and animals and plants on the other, was wrong. Woese postulated a family tree with three branches that symbolized the ancestors of prokaryotes, archaea and eukaryotes.

Although this view is now widely accepted, there is still opposition, even from prominent sources. For example, evolutionary biologist Ernst Mayr (died 2005) does not believe in Woese's theory, as he stated in *PNAS* in 1998. This debate may never end, because it is not about facts, but about which facts are more important: the morphological or the molecular. "The archaea are actually prokaryotes, and to elevate them to a separate domain is simply absurd," Mayr recently lectured in an interview with *Amherst Magazine* . "I think the problem might be that Woese is trained as a physicist — and he applies his biological ignorance to his classification methods."

In fact, Woese studied mathematics and physics at Amherst College before he became fascinated with biology, especially the early phase of evolution. It was not until his dissertation at Yale University (1953) that he approached biology - a subject he has not abandoned to this day. He still sits in his office every day and digs through genomes and sequences, searching for the answer to the question: "Where does the cell, the origin of life, come from?" He has just published a new theory on this topic, which will surely be the subject of much discussion (*PNAS* 99, p. 8742; *see interview*).

Woese is now considered a legend in biology. So it is not surprising that there are rumors that he has been considered for a Nobel Prize several times. But his work simply does not fit into any of the Nobel categories. And so he has so far had to forego the trip to Stockholm and the chance to shake hands with the Swedish king.

But now - and this fills him with great satisfaction - the time has almost come. On September 24, 2003, he will receive the Crafoord Prize, including 500,000 dollars, from the King in the Swedish capital.

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(An extensive list of links to articles about Woese's life and work can be found on Jonathan Eisen's blog "Tree of Life .")

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A thought on “Growth, Diversity, Chaos… and Death”

1. *Ralf Neumann* says:
   January 5, 2013 at 18:42

   Rita Levi-Montalcini published her last paper with 102!

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