EXTREMOPHILES: OVERVIEW OF THE BIOTOPES

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Summary

Environments characterized by extreme physical conditions, including high pressure, high or low temperature, high or low pH, high salinity, and the presence of toxic substances or radiation, can still harbor life as long as liquid water and an energy source are present.

Microbes from the domain of the archaea, and to a limited extent also from the other two domains of life, have evolved specific adaptations enabling the survival in the presence of one or even several of these stress factors.

In colonizing extreme environments, they have extended the biosphere into the abysses of the deep sea and into the Antarctic ice shield, and they may have played important roles in the early evolution of life on our planet.

1. Introduction

Life on Earth is more widespread and more robust than most people think. Since the 1970s, scientists have rapidly made many discoveries of extremophiles living in hostile conditions including high pressure, high or low temperature, high or low pH, high salinity, and the presence of toxic substances or radiation, which had previously been seen as incompatible with life. In the following, I shall give a general overview of the most important extreme biotopes of our planet, followed by an appreciation of the role that extremophiles may have played during the early evolution of life on Earth.

2. Extreme Temperatures

2.1. Terrestrial Hot Springs

When Thomas Brock visited Yellowstone National Park for the first time in 1964, he was particularly interested in the ecology of microorganisms, and hence he was surprised and fascinated to find rich microbial life in the outflow channels of the hot springs, in the form of colorful mats or pale pink gelatinous masses. The next summer he and his wife Louise Brock returned with scientific equipment for a two-week "working vacation." They first studied the algae that lived in the outflow channels at more than 60 °C. But then they found evidence that bacteria flourished even in springwaters as hot as 82 °C. They isolated and described the first extremely thermophilic bacteria. Among the very first isolates was one that Brock baptized *Thermus aquaticus*. More than two decades later, the DNA-synthesizing enzyme of this bacterium (*Taq* polymerase) became a bestselling biochemical thanks to the invention of the polymerase chain reaction.

This discovery encouraged other microbiologists to hunt for microbes in the hot springs and boiling mud holes of other volcanic regions in other continents and on the sea floor. Suitable places are found, for instance, around the Pacific, in Iceland, and in Italy. Many new extremophilic microbes were described by the group of the German microbiologist Karl Otto Stetter, who travels regularly to the geysers of Iceland, the solfatara fields in Italy, or the volcanoes of New Zealand. In all these places, water is heated by volcanic activity, often up to the boiling point. Stetter introduced “hyperthermophilic” as a term to describe the microbes whose optimal growth temperature is above 80 °C.

Most (but not all) hot springs are found near active volcanoes. They heat the water continuously while it flows through. Groundwater sifts through cracks in the ground down to the volcanically heated rocks, from where it rises to the surface through different channels. Geysers, in contrast, heat a large amount of water discontinuously, discharging at regular intervals.

Solfatara occur in areas of fading volcanic activity. They are gas excretions of the volcanic soil, which contain (as the name suggests) sulfuric gases, mainly the malodorous hydrogen sulfide (H_2S). Investigations of the hot, humid soils of solfatara fields in various places has shown that these always contain two distinct layers. The upper 15 to 30 cm are ochre-colored due to the presence of iron oxides and are characterized by the presence of oxygen as well as the high acidity. They often contain boiling hot mud or water pits, with the same chemical conditions. Although they do not look very hospitable, these volcanic soup kettles often turn out to be rich hunting grounds for microbiologists. The deeper layers of the soil, in contrast, are blue to black, oxygen-free and only weakly acidic. Some solfatara fields also contain alkaline, strongly saline, hot springs.

All of these volcanic excretions of gas and water have in common that they bring chemical compounds to the surface, which would otherwise not be found. For instance, they contain many elements in the reduced form, while chemicals in contact with the oxidizing atmosphere tend to assume the more oxidized forms of the elements, as iron does when it turns to rust. This means that the reduced chemicals from volcanic excretions are a potential source of energy for any organisms that can take control of their oxidation reaction. And this rich source of chemical energy makes the hot springs and solfatara fields an attractive biotope for organisms that can stand the heat.

The inhabitants of hot springs and of the upper layer of solfatara fields are therefore aerobic, which means they need oxygen to grow. In addition, most of them need sulfur or reduced sulfur compounds. The archaeon *Sulfolobus acidocaldarius*, for instance, lives in solfatara fields and draws energy from the reaction of sulfides with oxygen, which results in sulfuric acid. In the same way as our metabolism "burns" carbohydrates (to produce biochemical energy, carbon dioxide and water), *Sulfolobus* burns sulfides.

In the open terrestrial geothermal biotopes, temperatures up to 100 °C and the very variable degrees of acidity are the major stress factors, while energy-rich nutrients are normally in ample supply. Additional stress factors are encountered in the hot biotopes on the ocean floors.

2.2. Hot Springs on the Ocean Floor and Black Smokers

Volcanically heated areas of the ocean floor resemble those on the continents in their geological and chemical characteristics, but they are much richer biologically. More than three-quarters of the hyperthermophiles known today come from the deep sea. Their exploration only began after a surprising discovery that, in 1977, opened up new worlds for marine microbiologists.

In 1975, geologists hunting for evidence to confirm the as yet unproven theory of plate tectonics were for the first time able to detect fresh lava at the mid-Atlantic cleavage zone. When they tried to discover further indications of the movement of the continental plates by suspending a camera above the seafloor of the Pacific at a depth of 2500 m in a geologically active region north of the Galapagos Islands, they discovered surprising turbidities in the seawater, as well as unusual white "sediments".

In order to inspect these mysterious apparitions more closely, the geologists John B. Corliss (Oregon State University) and John M. Edmond (Massachusetts Institute of Technology) boarded the research submarine *Alvin* in the spring of 1977. When they reached the slope of the midoceanic ridge, the geologists first noticed that the outside temperature was five degrees higher than the normal 2 °C. They knew that some marine geologists had predicted that the total volume of the oceans must flow through hot volcanic rocks once in eight million years—only this as yet undiscovered process could account for the chemical composition of seawater, which is drastically different from river water boiled down in an evaporation pan. Hence, this very first hint of hot springs on the ocean floor was a sensational discovery.

The researchers took water samples so that they would be able to determine the chemical composition of this unexpectedly warm water in the laboratory. Then, they made *Alvin* mount the slope of the ridge. At the top, a much bigger sensation was waiting for them. Where they had expected to find a basalt rock desert, they found an oasis richly populated with clams, crabs, sea anemones (which are in fact animals in spite of their name and flower-like appearance), and large pink fish. As Edmond later recalled in *Scientific American*, they spent the five remaining hours of their dive in frantic excitement. They measured temperatures, conductivity, pH, and oxygen content of the seawater, took photographs, collected specimens of all the animal species. As it turned out, the researchers had discovered an entire field of warm springs. On an area ~100 m in diameter, relatively warm water of up to 17 °C was sifting through every little crack of the sea floor. And in spring 1979, another dive of the *Alvin* brought new sensations: hot springs that eject thermal fluid at 350 °C into the ocean.

These hydrothermal vents, commonly known as "black smokers," are hot springs in geologically active regions of the ocean floor. There are a few distinctions with respect to their terrestrial cousins. Firstly, the hydrostatic pressure at depths of around 3000 m is 300 atmospheres, which is enough to increase the boiling point of water beyond 400 °C. Hence, "hot water" can be really hot on the ocean floor, where the normal temperature is 2 °C. Secondly, the hot water is not ejected into the air but into cold seawater. The rapid mixing of the overheated volcanic fluid with cold water leads to the instantaneous precipitation of several substances (mostly heavy metal sulfides) in the immediate vicinity of the outflow site. These precipitates form the characteristic chimneys, which can reach heights of up to 5 m. Further precipitation reactions lead to the typical black "smoke," which has given the vents their nickname. Up to now, around 30 regions with such vents have been discovered. Even the death of a black smoker and its rebirth at a nearby site could be observed "live" as it happened.

The chemical composition of the water ejected by a black smoker matches exactly the predictions of marine geologists. Due to reactions of the seawater with hot basalt deep under the sea floor, the thermal fluid is poorer in magnesium and sulfate, but richer in iron, manganese, and sulfide than is ordinary seawater. The discovery of black smokers had instantaneously put the material balance of the oceans right, the apparent imbalance of which had worried geologists for decades. To appreciate the importance of the newly discovered exchange process, one has to realize that the total volume of the oceans circulates through the hot basalt rock every eight million years. For geologists, this timespan is a mere moment, and it means that every drop of water in the oceans has gone through deep sea vents hundreds of times since our planet's surface consolidated.

Surrounding the smoking vents, researchers found wonderful worlds of yet unknown creatures, resembling the biotopes discovered at warm sea floor springs two years earlier. More than 370 new species have been discovered in deep sea thermal biotopes, and more than 90% of these are exclusive to these biotopes. Population densities in these pitch dark oases exceed those of sunny, nutrient-rich, coastal waters. Molluscs, tube worms, sea anemones, snails, and crabs thriving in the lukewarm waters surrounding the vents and sources would not stand a chance of surviving in the dark and cold deep sea if it was not for the presence of the thermal waters.

The question of how species can spread to populate several of these small biotopes, which lie far apart and are unreliable on a longer time scale, is a tricky one. In 1996, Verena Tunicliffe and Mary Fowler of the University of Victoria (Canada) suggested that the animals had learned their lessons in plate tectonics and somehow brought their larvae to migrate preferably alongside the midoceanic ridges. The pattern of species spread over the globe is most easily explained on the basis of the assumption that certain pathways leading through the inhospitable deep sea were taken with lesser probability than those that may have been longer, but followed plate boundaries and were more likely to meet new oases in regular intervals. If confirmed, this finding would suggest the interesting possibility of using the evolutionary relationships between the inhabitants of geothermal habitats to detect ancient plate boundaries, the geological traces of which may have vanished already.
However, the cozy temperatures alone cannot explain the wealth of the fauna in the surroundings of hydrothermal vents. After all, at 3000 m below sea level, photosynthesis is out of the question, and the nutrient supply raining down from the upper layers cannot be called generous. Hence, there would not be enough energy to feed the deep-sea biotopes, if there wasn't another source.

Investigations into the ecology of the hydrothermal vent communities have shown that all of the multicellular organisms found in these biotopes are depending on the thermophilic bacteria, because only they know how to draw energy from the reduced sulfur compounds contained in the thermal waters. This special kind of metabolism was discovered by Russian microbiologists more than a century ago in the bacterium *Beggiatoa*, but was not paid very much attention at the time. In the case of the tube worm, *Riftia pachyptila*, the dependence has developed into an intracellular symbiosis. The worms, which have neither mouth nor gut, live exclusively off the nutrients that the chemosynthetic bacteria produce inside them. In compensation, they provide the bacteria with raw materials, mainly hydrogen sulfide, oxygen, and carbon dioxide, in highly enriched concentrations.

It is obvious that the sparse nutrients raining down from the photosynthesis-dependent food chain in the top layers of the oceans can only contribute a minute fraction of the energy requirements of the abundant black-smoker communities. Instead, there is an independent food chain, which starts from the sulfur-oxidizing bacteria as the primary producers and leads to the crabs, molluscs, and fishes as consumers. Being hyperthermophilic definitely is an advantage for the primary producers of this newly discovered food chain, as it allows them access to a unique broth of energy-rich compounds.

The resistance of microorganisms against temperatures beyond 110 °C is found only in certain branches in the family tree of life (Figure 1). Of the more than 20 genera of hyperthermophilic species, only two (*Thermotoga* and *Aquifex*) belong to the domain of the ordinary bacteria (eubacteria). The first representative of the genus *Thermotoga*, the bacterium *Thermotoga maritima*, was first discovered in the Mediterranean, off the shores of Italy. It has been studied intensively, resulting in the characterization of many of its enzymes, and in the sequencing of its entire genome.

In contrast, the overwhelming majority of hyperthermophiles belongs to the domain of the archaea (the discovery of which will be discussed later on), a third life form distinct from both "normal" bacteria (eubacteria) and the complex cells of higher organisms (eukarya). Among the achaebacteria, we also find the "most extreme" extremists, like the orders of *Pyrococcus*, *Pyrobaculum*, and *Methanopyrus*, whose members all grow at temperatures beyond 100 °C. The current (2001) record is held by *Pyrolobus fumarii*, an archaeon isolated by Stetter and coworkers from the wall of a black smoker in the Atlantic, which grows between 90 and 113 °C. Nobody knows, however, where the upper limit of adaptation is. Most researchers in the field believe that it lies somewhere between 115 and 150 °C.

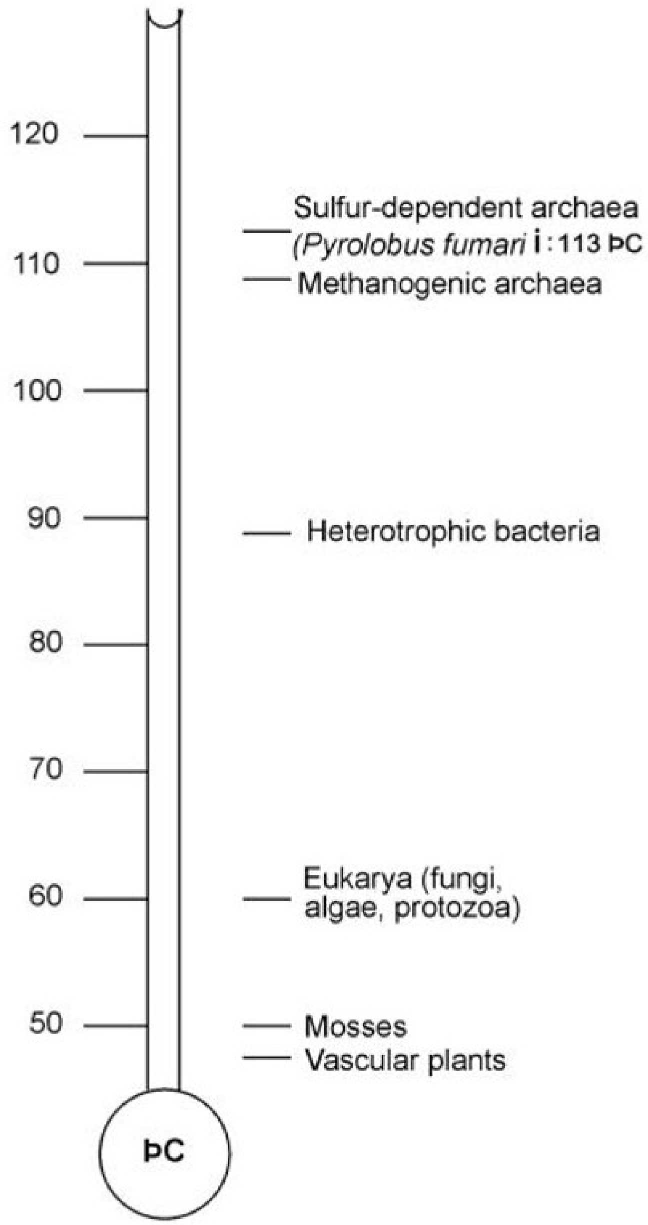

Figure 1. The temperature scale of life with the highest temperatures at which members of the specified groups can survive

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Biographical Sketch

Michael Gross studied chemistry, and (briefly) chemical engineering and obtained his doctorate in physical biochemistry working with Professor Rainer Jaenicke. His doctoral research has focussed on the influence of high pressures on proteins and ribosomes. During his seven years of post-doctoral research at the Oxford Centre for Molecular Sciences, he investigated different aspects of protein folding, often choosing model systems relating to extremophily or stress response.

He is the author of two well-received general science books ("Life on the Edge" and "Travels to the Nanoworld," published by Plenum in 1998 and 1999, respectively, and now available as paperbacks from Perseus Books), each of which he prepared in an English as well as in a German version. Since May 2000, he is writing full time, and he is now a science writer in residence at the School of Crystallography, Birkbeck College, London. He is a regular contributor to Chemistry in Britain, Current Biology, Spektrum der Wissenschaft, and Nachrichten aus der Chemie, and has also published science journalism in a number of other periodicals including The Guardian, The Independent, Nature, New Scientist, Süddeutsche Zeitung, Berliner Zeitung, La Recherche, and others.

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