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2002 J. Phys.: Condens. Matter 14 11489

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High pressure and the origin of life

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Received 18 June 2002

Published 25 October 2002

Online at stacks.iop.org/JPhysCM/14/11489

Abstract

Three lines of experimental research suggest that high pressure may have played a significant role in the origin of life. Discoveries of abundant life in high-pressure environments, including deep oceans, hydrothermal vents, and crustal rocks, point to the adaptation of life to a variety of aqueous habitats. Cultures of microbes at high pressure display both barotolerant and barophilic behaviour. And studies of high-pressure hydrothermal organic synthesis reveal unexpectedly facile reaction mechanisms for the production of a variety of requisite biomolecules.

1. Introduction

Discoveries of life in diverse high-pressure environments, including deep-ocean ecosystems associated with hydrothermal vents and microbial communities that survive in a variety of crustal lithologies, point to the possibility that pressure played an important role in life's origin. This view is bolstered by recent experimental studies of organic synthesis reactions and biological activity at pressure. This review considers both these lines of evidence, from high-pressure ecosystems as well as high-pressure hydrothermal organic synthesis experiments, in addressing that possibility.

2. High-pressure life

The existence of high-pressure life was first documented by the oceanographic surveys of the *HMS Challenger*, during the 1870s [1]. This pioneering expedition for the first time made extensive collections of deep-sea biota, with more than 100 dredgings at depths of more than 1 km. These collections revealed an unexpected abundance of life in the abyssal depths.

Nevertheless, it would be another 100 years before the role of pressure in biology would begin to attract significant attention, and even then the primary focus was on the pressure adaptations of marine animals [2].

The 1977 discovery by Corliss *et al* [3] of a diverse ecosystem associated with hydrothermal activity at a sea-floor spreading centre transformed our view of life and its

diversity. A succession of subsequent finds in similar hydrothermal environments has demonstrated that deep life is common and robust [4–7]. Furthermore, much of the biota at these vents obtains its energy from geochemical sources, thus challenging the paradigm that the Sun is the only source of life's energy [8].

Recent findings suggest that the dramatic hydrothermal vent communities may represent only a small fraction of Earth's high-pressure life. Microbes have been isolated from numerous deep crustal environments, including oil reservoirs [9, 10], deep terrestrial aquifers [11, 12], oceanic sediments [13, 14], terrestrial sedimentary rocks [15–17], granite [18], and basalt [19]. It now appears possible that life is ubiquitous anywhere on Earth that water persists in liquid form [20–22]. By some estimates the biomass of the subsurface may equal or exceed that of the surface [23].

3. High-pressure experiments on microbes

Laboratory studies of microbial cultures at high pressure reinforce the view that life is compatible with extreme conditions. Ground-breaking studies by Holger W Jannasch at the Woods Hole Oceanographic Institute [24–27] documented microbial growth at pressures approaching 100 MPa. He developed isolation chambers for the collection and culturing of microbes, and demonstrated a variety of growth responses. For example, he documented barotolerant microbes that displayed reduced metabolic rates at high pressure, as well as barophilic organisms that display enhanced metabolism and growth rates at high pressure.

Subsequent work by Baross and co-workers [28, 29] revealed that some hydrothermal vent microbes are barotolerant at lower temperatures, but display barophilic behaviour at higher temperatures. These investigations also clearly documented that some microbes thrive at temperatures exceeding 100 °C.

The upper pressure and temperature limits for life are not known, but recent experiments in our laboratory indicate that microbial metabolism may persist at pressures exceeding 10 000 atm [30].

4. Effects of pressure on biomolecules

Although high-pressure studies on biomolecules are relatively few, a number of observations suggest that pressure plays an important role in the stability and conformation of biomolecules and their macromolecular structures [31–33]. Gruner and co-workers [34, 35], for example, have demonstrated a variety of pressure-dependent transitions in lipid bilayers and lyotropic phases. Other recent observations point to systematic effects of pressure on protein folding, as well as on protein interactions with various substrates [36].

One can anticipate that the cumulative impact of pressure on the conformations and functionality of structural and metabolic molecules will, ultimately, have an inhibitory effect on microbial growth rate and cellular division [37]. However, the experimental study of biomolecules at high pressure is in its infancy and this field represents an important area for future research.

5. High-pressure hydrothermal synthesis

Whether or not life arose in a high-pressure environment, pressure may nevertheless have played a significant role in the prebiotic synthesis of key biomolecules. We have, therefore, commenced an experimental programme in high-pressure hydrothermal organic synthesis.

This research focuses on the stability and reaction pathways of key organic molecules under high-pressure, hydrothermal conditions.

The critical point of water is approximately 374 °C and 22.1 MPa. A central question in our research is whether the unique properties of aqueous solutions at supercritical conditions might affect the synthesis and stability of important biomolecules. Our experiments are typically run at $50 \leq P \leq 500$ MPa and $150 \leq T \leq 300$ °C, which are conditions typical of many deep-ocean and crustal environments. At these elevated temperatures the dielectric constant of water is greatly reduced, while the ionic product increases [38, 39]. These changes in the physical properties of water strongly affect its chemical properties, as well. Indeed, at elevated temperature the solubility parameter of water approaches that of polar organic solvents [40]. Other important properties of water in natural systems include variations of aqueous species as a function of temperature and pressure, as well as phase separation and critical phenomena [41].

An extensive literature now documents organic reactions in aqueous media, both subcritical and supercritical [40, 42–44]. Most of this research is directed toward commercial applications related to fossil fuels, as well as implementation of environmentally benign process for chemical synthesis and recycling. Our work employs this approach, but focuses on the hydrothermal synthesis and stability of biologically relevant molecules.

We employ two complementary techniques. In most experiments reactants are sealed into gold tubes, which are subjected to pressure and temperature in an internally heated gas-media apparatus [45]. We also study reaction kinetics with hydrothermal diamond anvil cells [46].

The richness of hydrothermal organic chemistry is exemplified by studies of pyruvic acid from 150 to 300 °C at pressures to 0.5 GPa [47]. Three primary reaction pathways are observed. Up to 50% of the pyruvic acid decarboxylates, yielding acetic acid and carbon dioxide. In competing reactions, pyruvic acid forms dimers and trimers through aldol condensation. A significant fraction of dimers undergo decarboxylation to form methyl succinate. Other pyruvic acid oligomers transform to cyclic aromatic compounds through Diels–Alder cyclo-addition reactions. A significant fraction of these products display surface activity and form vesicles when placed in a phosphate-buffered (pH = 8.5) aqueous solution. We observe that pressure strongly favours formation of cyclic compounds, including the membrane-forming molecules.

In these experiments we find that pressure plays two important roles. First and foremost, as in all high-pressure hydrothermal experiments, pressure greatly expands the temperature stability of the aqueous phase. At these higher temperatures, the physical and chemical properties of water are more amenable to a variety of organic reactions. In addition, pressure appears to favour certain reactions. In the case of pyruvic acid, we observe enhanced yields of the cyclic aromatic compounds at 0.2 and 0.5 GPa, compared with lower pressures.

In other experiments we have studied the stability and reaction pathways of citric acid as a function of temperature (to 300 °C) and pressure (50–500 MPa) [48]. At temperatures ≥ 200 °C citric acid reacts within 2 h to a number of other products. Pressure enhances decarboxylation, lactonization, and hydration reactions (figure 1).

A principal focus of our research has been the effects of minerals on organic stability, catalysis, and synthesis under hydrothermal conditions [49]. Of special interest is the stability of amino acids, which under most conditions decompose rapidly at temperatures above 150 °C [50, 51]. We find, for example, that the half-life of leucine at 200 °C and 50 MPa is <10 min. In the presence of FeS (troilite), however, the half-life of leucine increases to 30 h.

Mineral-mediated catalysis is also observed under high-pressure hydrothermal conditions [52–54]. We find, for example, that N₂ and H₂ in the presence of catalytic ferrous iron minerals react to form ammonia (NH₃), an essential component for further synthesis of amines and other nitrogen-bearing organics [52]. These results lead us to conclude that hydrothermal vents could have been a major source of ammonia on the Archaean earth.

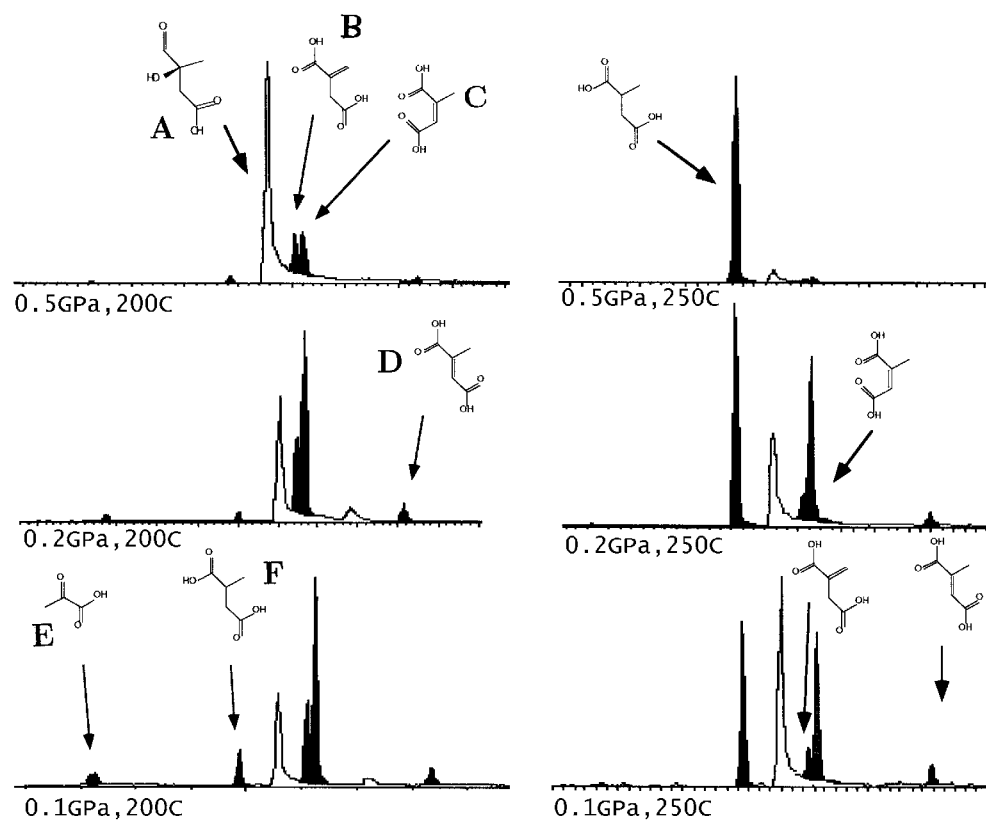


Figure 1. Hydrothermal reaction products of citric acid. (A) Hydroxy isobutyric acid; (B) oxaloacetic acid; (C) citraconic acid; (D) mesaconic acid; (E) pyruvic acid; (F) methylsuccinic acid. Pressure enhances the yields of decarboxylation, lactonization, and hydration reactions.

Other hydrothermal experiments that incorporate iron and nickel sulphides reveal facile carbon-addition reactions, including chain elongation (by Fischer–Tropsch reactions) and carbonylation to form organic acids [53]. In the process sulphide minerals dissolve and react, forming organic sulphides, thiols, and carbonylated organo-metallic clusters that may promote new reaction pathways.

On the basis of these studies, we conclude that hydrothermal organic synthesis may have played a significant role in the evolving organic inventory of the prebiotic earth. Pressure, which stabilizes the aqueous phase to temperatures significantly greater than 100 °C, may thus have played a key role in life’s origin.

6. Conclusions

The origin of life was a local geochemical event—it was a local assemblage of self-replicating organic molecules. A key question regarding that origin remains the nature of the environmental conditions under which the critical biomolecules were synthesized and assembled.

For most of the past century conventional wisdom has pointed to the Earth’s energy-rich surface as the most logical site for life’s origin. However, recent discoveries of abundant deep life, the surprising high-pressure stability of some microbes, and the often facile reaction

pathways of high-pressure hydrothermal organic synthesis suggest a wider range of plausible origin environments. This expanded view of life-sustaining habitats, furthermore, points to the intriguing prospect that life-forming processes might have also occurred in the wet, pressurized interiors of Mars, Europa, and other solar system objects.

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