

Current developments in marine microbiology: high-pressure biotechnology and the genetic engineering of piezophiles

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A key aspect of marine environments is elevated pressure; for example, ~70% of the ocean is at a pressure of at least 38 MPa. Many types of *Bacteria* and *Archaea* reside under these high pressures, which drive oceanic biogeochemical cycles and catalyze reactions among rocks, sediments and fluids. Most marine prokaryotes are classified as piezotolerant or as (obligate)-piezophiles with few cultivated relatives. The biochemistry and physiology of these organisms are largely unknown. Recently, high-pressure cultivation technology has been combined with omics and DNA recombination methodologies to examine the physiology of piezophilic marine microorganisms. We are now beginning to understand the adaptive mechanisms of these organisms, along with their ecological functions and evolutionary processes. This knowledge is leading to the further development of high-pressure-based biotechnology.

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Introduction

Marine ecosystems have always been a fascinating topic for scientists. A heroic era of deep-sea research began the moment the HMS Challenger weighed anchor. From 1872 to 1876, the Challenger Expedition explored the Mariana Trench and many prodigious life forms at great ocean depths [1]. In general, the geological settings of the

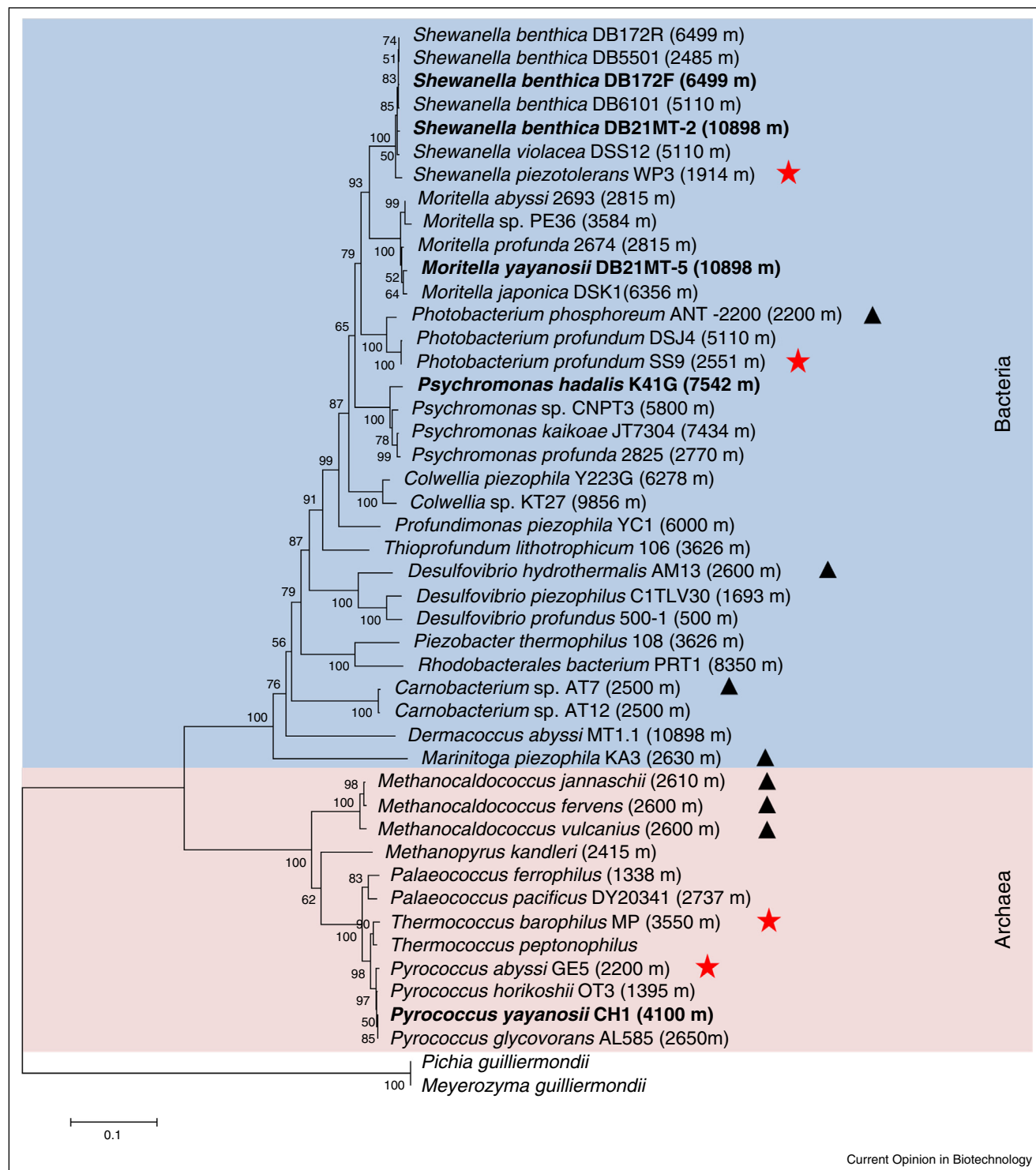
deep ocean cannot be described in terms of their physical and chemical characteristics, except with respect to the high hydrostatic pressure (HHP). ‘Barophilic’ was the first term used to define ‘pressure-loving’ organisms [2] but was subsequently replaced by the term ‘piezophilic’ (from the Greek ‘piezo’, meaning pressure) [3]. The current terminology defines pressure-adapted microorganisms as piezotolerant (with similar growth rates at atmospheric pressure and high pressure), piezophilic (with more rapid growth at high pressure than at atmospheric pressure) or hyperpiezophilic (with growth only at high pressure) [4,5]. The pressure maxima increase in rank order, which reach the peak point for hyperpiezophiles. Organisms that grow best at atmospheric pressure and with little to no growth at increased pressure are termed piezosensitive. As sampling and cultivation techniques have been largely improved, it has become possible to isolate various piezophilic microorganisms from the deep-sea, including certain obligate piezophilic species that cannot grow at atmospheric pressure [6,7]. In this review, we focus on how HHP has profoundly influenced the life strategy of marine microorganisms. We also describe the primary research strategies used by marine microbiologists to study these organisms.

Piezophilic microorganisms and HHP adaptation

Since the first known obligate piezophile, *Colwellia* sp. MT-41, was isolated from the bottom of the Mariana Trench by Yayanos and colleagues [8,9], many other isolates have been obtained from the deep ocean, hydrothermal vents and sub-seafloor (Figure 1). Most of these piezophiles are psychrophilic gram-negative bacterial species that belong to the *Gammaproteobacteria* class, which includes species from the genera *Shewanella*, *Psychromonas*, *Photobacterium*, *Colwellia*, *Thiopfundum* and *Moritella* [5]. Few piezophilic bacteria belong to the *Alphaproteobacteria* and *Deltaproteobacteria* classes. All of the piezophilic archaea that have been isolated thus far are thermophilic and fall within the Euryarchaea and Crenarchaea kingdoms, including the obligate piezophilic anaerobic hyperthermophilic archaeon *Pyrococcus yayanosii* CH1 [10,11].

By obtaining an increasing amount of complete genomic and metagenomic data, we are beginning to better understand the nature of piezophiles. For example, deep ocean microbial assemblages tend to be characterized by larger genome sizes, longer intergenetic regions and

Figure 1



Phylogenetic tree constructed on the basis of 16S rRNA gene sequences, showing the distribution of piezophiles. Tree topography and evolutionary distances were determined using the neighbor-joining method with 1000 replicates of bootstrapping. Bootstrap values providing $\geq 50\%$ support are indicated. The scale bar indicates 0.1 substitutions per nucleotide position. A red star indicates species with constructed genetic systems; a black triangle indicates species containing plasmid(s); obligatory piezophiles are shown in bold; water depths of the original samples are indicated in brackets.

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