

# Extremophiles

Microbiology and Biotechnology

Edited by

Roberto Paul Anitori

Division of Environmental and Biomolecular Systems  
Oregon Health and Science University  
Beaverton, OR  
USA

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# Contents

	List of Contributors	iv
	Foreword	ix
	Preface	xiii
1	<b>Extremophiles and Biotechnology: How Far have we Come?</b> Mark Paul Taylor, Lonnie van Zyl, Marla Tuffin and Don Cowan	1
2	<b>Ionizing Radiation-resistant Microorganisms</b> Kelley R. Gwin and John R. Battista	25
3	<b>Psychrophiles: Life in the Cold</b> Corien Bakermans	53
4	<b>SM1: A Cold-loving Archaeon with Powerful Nano-grappling Hooks</b> Christine Moissl-Eichinger, Ruth Henneberger and Robert Huber	77
5	<b>Enzyme Activities and Biotechnological Applications of Cold-active Microfungi</b> Helena Nevalainen, Ron Bradner, Sania Wadud, Suja Mohammed, Christopher McRae and Junior Te'o	89
6	<b>Metabolic Diversity of Thermophilic Prokaryotes – What's New?</b> Elizaveta Bonch-Osmolovskaya	109
7	<b>Cellulolytic Microorganisms from Thermal Environments</b> Tatiana A. Vishnivetskaya, Babu Raman, Tommy J. Phelps, Mircea Podar and James G. Elkins	131
8	<b>Extreme to the Fourth Power! Oil-, High Temperature-, Salt- and Pressure-tolerant Microorganisms in Oil Reservoirs. What Secrets can they Reveal?</b> Hans Kristian Kotlar	159
9	<b>Hyperthermophiles: Metabolic Diversity and Biotechnological Applications</b> Kazem Kashefi	183
10	<b>Microbiology of Piezophiles in Deep-sea Environments</b> Chiaki Kato	233
11	<b>Physiological Adaptations and Biotechnological Applications of Acidophiles</b> Mark Dopson	265
	Index	295

*This book is dedicated to my late father, Vittorio Anitori,  
who was not a scientist by profession,  
but certainly possessed the mind of one.*

# Foreword

How do we define an extreme environment and its inhabitants, the extremophiles? I first made an attempt to do this over 40 years ago, in the pre-genome days (Brock, 1969). However, I think this definition still is valid today:

It is not appropriate to define [an extreme environment] anthropocentrically, as we should be the first to admit that human life is not everywhere possible. More appropriate is its definition as a condition under which some kinds of organisms can grow, whereas others cannot. If we accept this definition it means that an environmental extreme must be defined *taxonomically*. Instead of looking at single species, or groups of related species, we must examine the whole assemblage of species, microbial and multicellular, living in various environments. When we do this we find that there are environments with high species diversity and others with low species diversity. In some environments with low species diversity we find that whole taxonomic groups are missing. For instance, in saline and thermal lakes there are no vertebrates and no vascular plants, although they may be rich in microorganisms, and very high in the numbers of the species that do live there. In many extreme environments we find conditions approaching pure cultures, with only a single species present.

When I first began to study the biology of Yellowstone hot springs, I was struck by the very visible evidence that there was an upper temperature for photosynthetic life that was *lower* than the upper temperature for microbial life in general. Detailed observations of a large number of hot

springs, and an extensive review of the literature, showed that this was a general phenomenon. My work eventually led to a summary of the relationships between taxonomy and the upper temperature for different groups that is shown in Table 1. As far as I know, the relationships developed in this table are still valid.

This table raises some interesting questions. Why, for instance, is there an upper temperature for eukaryotic life at about 60°C, whereas prokaryotes (even phototrophic ones) can function well at considerably higher temperatures? Why are microorganisms able to live at considerably higher temperatures than multicellular ones?

Interestingly, for another environmental factor, low pH, a completely different set of relationships exist (Table 2). Some animals and plants can live well at fairly low pH values, whereas the prokaryotic phototrophs (cyanobacteria) have a distinct lower pH limit of around 4. Indeed, for low pH, many eukaryotic phototrophs thrive at pH values well below those of the cyanobacteria. (Brock, 1973). Even certain multicellular animals and plants will grow at lower pH values than cyanobacteria.

Why are eukaryotes able to thrive at very low pH values, but not at high temperature? Why can heterotrophic and lithotrophic bacteria and archaea grow well at temperatures of 100°C and higher, whereas phototrophic life does not exceed 70–73°C? These are evolutionary questions that derive from a careful study of the ecology of extreme environments and the extremophiles that inhabit them.

As this book shows, there are other environmental factors that can be considered extreme,

**Table 1** Upper temperature limits for growth of various taxonomic groups

Major group	Group	Approximate upper temperature limit (°C)
Animals	Fish and other aquatic vertebrates	38
	Insects	45–50
	Ostracods (crustaceans)	49–50
Plants	Vascular plants	45
	Mosses	50
Eukaryotic microorganisms	Protozoa	56
	Algae	55–60
	Fungi	60–62
<b>Prokaryotic microorganisms</b>		
<i>Bacteria</i>	<i>Cyanobacteria</i> (Oxygenic)	70–73
	Phototrophic bacteria (anoxygenic)	70–73
	Chemolithotrophic bacteria	>90
	Heterotrophic bacteria	>90
<i>Archaea</i>	Chemolithotrophs	121
	Heterotrophs	110

Modified from Brock (1978, p. 40).

**Table 2** Lower pH limits for various taxonomic groups

Major group	Group	Lower pH limit <sup>1</sup>	Examples
Animals	Fish	4	Carp
	Insects	2	Ephydrid flies
Plants	Cyanobacteria	4	<i>Mastigocladus</i> , <i>Synechococcus</i>
	Vascular plants	2.5–3	<i>Eleocharis</i> , <i>Sellowiana</i> , <i>Carex</i> , Ericacean plants
	Mosses	3	<i>Sphagnum</i>
Eukaryotic microorganisms	Protozoa	2	Amoebae, Heliozoans
	Eukaryotic algae	1–2	<i>Euglena mutabilis</i> , <i>Chlamydomonas acidophila</i> , <i>Chlorella</i>
		0	<i>Cyanidium caldarium</i>
	Fungi	0	<i>Acontium velatum</i>
<b>Prokaryotic microorganisms</b>			
<i>Bacteria</i>		0.8	<i>Thiobacillus thiooxidans</i>
			<i>Sulfolobus acidocaldarius</i>
		2–3	<i>Bacillus</i> , <i>Streptomyces</i>

<sup>1</sup>Lower pH limits are only approximate.

Table based on Brock (1978, p. 392).

and the evolution of organisms capable of thriving (or at least surviving) raises further questions. As Bakermans indicates in Chapter 3, adaptation to low temperatures (psychrophily) is not an uncommon trait, and cold-adapted organisms are

found throughout all three domains of life. In fact, several distinct mechanisms for adaptation to low temperatures have evolved.

On the other hand, high ionizing radiation is not a common natural environmental factor. Only

since the rise of nuclear physics has this factor existed. As Gwin and Battista discuss in Chapter 2, there is no obvious selective advantage to being resistant to ionizing radiation. Yet a significant number of microorganisms (only microbes; no higher organisms) exhibit this interesting characteristic. For this environmental factor, resistance is probably a chance consequence of another evolutionary pathway.

Finally, high hydrostatic pressure is a very common environmental factor, but difficult to study because of the remote regions where piezophiles (barophiles) live, and the complicated equipment needed to maintain this extreme factor (Kato, Chapter 10). Because the deep oceans are also cold, the piezophiles are also psychrophiles. Piezophiles have been identified in many bottom regions of the world's oceans, and significant advances have been made in understanding the mechanisms of piezophily.

I think that the interesting evolutionary questions raised by extremophily are valid, and I would hope that in this genome age that research on these topics will be carried out. Extreme environments and extremophiles are of enormous biological interest, initially for ecological and evolutionary relationships, and now for biotechnological reasons as well.

Many extremophiles have important practical uses, and the biotechnological aspects discussed in this book have not been neglected by the scientific community and private industry. Although the best example is *Taq* polymerase from *Thermus aquaticus*, this enzyme is only one of a large variety of important economic uses for which extremophiles have been harnessed. It has become a watchword that unique microbes are found in

unique environments. It is probable that biotechnology has only scratched the surface in its search for new micro-organisms of practical use.

Thomas D. Brock

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# Preface

Living cells are truly astounding. That is what I like to tell my undergraduate microbiology students. Not just the processes and reactions that occur, but the microscopic scale at which they occur. I therefore think that the term mind boggling would not be inappropriate to describe extremophiles, those microorganisms that conduct these processes and reactions under chemical and physical extremes that are usually lethal to cellular molecules. How can extremophiles possibly cope with, and even thrive, under these conditions? A major part of the 'microbiology' element of this book is devoted to reviewing the latest insights into the mechanisms used for survival by these fascinating organisms, from the ability of acidophiles to maintain a neutral intracellular pH (see Chapter 11 by Dopson), to the way that psychrophiles 'loosen up' their proteins at low temperatures (Bakermans, Chapter 3), to other equally ingenious adaptations in other classes of extremophiles (see Chapter 2 by Gwin and Battista, and Chapter 10 by Kato). Living an extreme lifestyle also imposes metabolic constraints on microbes, and has led to an astounding array of metabolic strategies, as exemplified by those lovers of high temperatures, the (hyper)thermophiles (see Chapter 6 by Bonch-Osmolovskaya, and Chapter 9 by Kashefi).

Tough microbes produce tough molecules. Since their discovery, the practical, biotechnological promise of extremophiles and their molecules has therefore been front and centre for both science and industry. The 'biotechnology' component of this book covers both established and recent, novel applications. Can extremozymes improve on their thus far relatively minor

penetration of the enzyme market (Taylor *et al.*, Chapter 1)? Will extremophiles play a significant role in the production of sustainable energy in our current 'green' era (Vishnivetskaya *et al.*, Chapter 7)? How can the oil industry contribute (Chapter 8, Kotlar)? It will be fascinating to follow these and other biotechnology-related issues in the coming years.

The chapters in this book are self-contained, and hence need not be read in the order in which they appear. Most chapters are general review articles, whilst a few (e.g. those by Moissl-Eichinger *et al.*, Chapter 4, and Nevalainen *et al.*, Chapter 5) provide a more focused discourse on specific examples of extremophilic microbes. It is my hope that, taken as a whole, or as individual chapters, they will serve as helpful, up-to-date reference guides to their subject matter. The 'Future trends' and 'Web resources' sections located at the end of each chapter will help the reader keep up-to-date with new developments.

This editing adventure, my first, has been at times challenging and daunting, yet ultimately rewarding. The challenge has not been mine alone, so I would like to thank Julie and Lilyanne for dealing with my numerous excursions into the world of 'the book'.

I am confident that the audience to which this book is targeted, graduate students and researchers, are not immune to the sense of wonder elicited by extremophiles. My hope is that the information in the chapters herein will not only inform and educate, but also astound.

Roberto Paul Anitori  
Vancouver, Washington, USA



**A**

Acid mine drainage (AMD) 284  
 Acid rock drainage (ARD) 284  
 Acidophiles 12, 265–281  
   arsenic 278  
   autotrophs and heterotrophs 273  
   biofilms 276  
   biomining 281  
   biotechnological applications 281  
   definition 265  
   ecology and metabolism 266  
   growth on sulfide minerals 273  
   growth substrates 266  
   habitats 266  
   hydrogen utilization 275  
   inorganic sulfur compound (ISC)  
     metabolism 271–273  
   iron 279  
   iron metabolism 266–271  
   mesophilic 275  
   metal and metalloid homeostasis and resistance 277  
   methane oxidation 275  
   pH homeostasis 280–281  
   physiological adaptations 12  
   psychrotolerant 275  
   quorum sensing 276  
   thermophilic 275  
   zinc 279  
 Acidophilic biocatalysts, whole cell 13  
 Acidophilic biomolecules 12–13  
 Acidophilic enzymes 12–13  
 Alcohols, 2nd generation (2G) 171  
 Alkaliphiles, physiological adaptations 12  
 Alkaliphilic biocatalysts, whole cell 15  
 Alkaliphilic biomolecules 15  
 Ammonia monooxygenase 112. *See also amoA*  
 Ammonia-oxidizing archaea 112–114  
*amoA* 112  
 Anaerobic ammonia oxidation, thermophilic 112  
 Anaerobic cellulolytic thermophiles from Yellowstone  
 National Park 145–152  
   enrichments 145  
   physiological characteristics of enrichments 146  
   DNA-based community analysis of enrichments 148

  changes in community structure during continuous  
   enrichment 148  
   isolation of 151  
   phylogenetic identification of 151  
 Anaerobic cellulolytic thermophiles 138  
   *Anaerocellum thermophilum* 138  
   *Caldicellulosiruptor saccharolyticus* 138  
   *Clostridium thermocellum* 138  
 Annamox 112  
 Antarctica 90, 91, 95  
   environment 90  
   fungi 91  
   lipases 95  
   microbiota 91  
   yeasts 91  
 Archaea, ammonia-oxidizing 112–114  
 Arrhenius equation 55  
 Asphaltene precipitation, oil well 166  
 Astrobiology, cold environments 68–69

**B**

Barophiles *see* Piezophiles  
   definition 233  
 Bioalcohols 167  
 Biocatalysts, whole cell 13, 15, 16  
   acidophilic 13  
   alkaliphilic 15  
   piezophilic 16  
 Biodiesel 167, 168, 171  
   1st generation (1G) 167  
   European Union regulations and 167  
   from biocatalytic conversion of triglycerides 168  
   from commingling of raw materials 171  
   use of thermophilic microorganisms for production  
     of 171  
 Biofuels 142, 167  
   ethanol 142  
   hydrogen 142  
 Bioleaching 281  
 Biomining 13–15, 281, 283  
   microorganisms involved 283  
 Biomolecules 12–13, 15  
   from acidophiles 12–13  
   from alkaliphiles 15

Bioprospecting, using oil-associated microorganisms 180–181

Bioremediation 284

Bioremediation of crude oil 96, 97  
enzymatic 96  
fungal 97

Bioremediation, petroleum-based pollutants 96

Bioshrouding 15  
degradation by fungi 102, 103  
substrate for fungal growth 102–103

Biotechnology xv, 1–2, 17–18, 164, 220

## C

C1 metabolism, thermophilic 117

Carbohydrate active enzymes 136–142  
complexed systems 137  
modular nature of 137  
non-complexed systems 137

Carbohydrate binding module (CBM) 136

Carbohydrate esterase (CE) 136

Carbon monoxide oxidation, thermophilic 115. *See also*  
Hydrogenogenic carboxydrotrophs

Cellulases 136

Cellulolytic enzymes  
domain composition 138–142  
from anaerobic thermophilic bacteria 138

Cellulolytic fermentations 142–145

Cellulolytic microorganisms 133, 136  
enzyme systems of 136

Cellulose 132, 136

Cellulose decomposition  
in natural environments 133  
microbial 133

Cellulosome 137  
architecture 137  
cohesins 137  
dockerins 137

Challenger Deep, Mariana Trench 234

Chaperones 60, 61

Climate change, effect on low temperature environments 68

Cold heavy oil extraction with sand (CHOPS) 173, 180

Compatible solutes 62

Consolidated bioprocessing (CBP) 132

Contact leaching 282

Cooperative leaching 282

Co-opted adaptation 43

Crude oil degradation 99, 100–102  
growth and analysis of fungal isolates 100  
*n*-alkane and other products 100–102  
screening of Antarctic fungal isolates 99

Cryoprotectants 62

Cultivation, versus metagenomics 3

## D

D<sub>37</sub> dose 28

Deep biosphere 159  
identification of microorganisms in 159  
microorganisms in 159

DEEPBATH system for high-pressure cultivation 244

*Deinococcus radiodurans* 29–30, 35–38, 39–41  
genomic DNA repair 38

global gene expression 35

hypothesized radioresistance mechanisms 39–41

manganese (II) and radioresistance 37–38

mechanisms for avoiding cellular damage 35–38

multiple genomes 36

nucleoid organization 37

protein expression 35–36

recovery of genome post-irradiation 29–30

role of antioxidants 37

*Deinococcus* sp., genomic sequencing 34

Denaturing gradient gel electrophoresis (DGGE) 161

Dihydrofolate reductase, activity under high pressure 254

## E

Efficient growth, survival mechanism at low temperatures 64

Electrogenic thermophiles 124

Enthalpy 54

Enzymes 7–8, 9–10, 12–13, 16, 92, 93  
cold-adapted 92  
commercial psychrophilic 9–10  
commercial thermophilic 7–8  
from acidophiles 12–13  
from piezophiles 16  
industrial applications of cold-adapted 93

Eurypsychrophiles 53. *See also* Psychrotolerant microorganisms

Extreme environments, definition xi

Extremophiles and biotechnology, web resources 18

Extremophiles xi, 3  
cultivation of 3  
definition xi 3

Extremophilic biotechnology, future prospects 17–18

Extremozymes 2, 3, 285

## F

Fatty acid desaturation 62

Formate oxidation 120  
by *Thermococcales* 120  
thermophilic 120

Freezing point depression 54

Fuel cells, microbial 124

Fungi 89, 90, 91, 93, 97, 102–103  
Antarctic 91  
crude oil degradation 97  
hydrolase production 103  
in extreme environments 90  
refined bitumen degradation 102–103  
taxonomy and microstructure 89

## G

Glycoside hydrolase (GH) 136

## H

Halophiles 10, 11–12  
adaptive strategies 10, 11–12  
definition 10  
whole cell applications 11–12

Hami 83–86  
as ‘nano-Velcro’ 83–86

- hook shape 83
  - morphology 83
  - nanobiotechnological potential of 85
  - structure and formation 84
  - Heavy oil 172, 173, 174–180
    - bioconversion of 172, 174
    - bioconversion using reservoir extraction models 174–180
    - traditional extraction of 173
  - Hemicellulose 136
  - High temperatures, survival mechanisms at 6
  - High-pressure cultivation 164
  - High-pressure microscopy 247
  - Hydrate formation, oil well 166
  - Hydrocarbon pockmarks 161
  - Hydrocarbon seeps 162
  - Hydrogenogenic carboxydrotrophs, thermophilic 115–116
  - Hydrogenogenic formate oxidation 120
    - thermophilic (*Thermococcales*) 120
    - thermophilic 120
  - Hydrolases, produced by oil-degrading fungi 103
  - Hydrothermal systems 183
  - Hyperthermophiles 6, 121, 162, 183, 204, 206–211, 213, 215–222, 247
    - applications in biomass conversion 220
    - applications in molecular biology 220
    - archaeal 206
    - arsenate respiration 210
    - bacterial 207
    - biodiversity 204
    - biotechnological applications 220–222
    - definition 183
    - dissimilatory reduction of sulfur-containing compounds 211
    - electron acceptors and modes of respiration 208
    - elemental sulfur respiration 213
    - habitats 183
    - humic acid reduction 217
    - iron (III) for culturing of 219
    - iron (III) respiration 216
    - metabolic diversity 207–208
    - metabolic versatility 204
    - metabolic versatility of iron (III) reducers 218
    - methanogenesis 215
    - nitrate respiration 209
    - organotrophic 121
    - oxygen respiration 208
    - phylogeny 183, 204
    - piezophilic 247
    - reduction of extracellular quinones 217
    - reduction of toxic, radioactive and precious metals 217
    - selenate respiration 210
    - selenite respiration 210
  - Hyperthermophilic archaea, hydrolytic activities of 122
  - Hyperthermophilic enzymes 220
- I**
- Ice-binding proteins 63
  - Increased oil recovery (IOR) 165
    - use of microorganisms for 165
  - Ionizing radiation resistance 30, 41–43, 44–45
    - laboratory evolution of 44–45
    - natural evolution of 41–43
    - phylogenetic distribution 30
  - Ionizing radiation resistant species, habitats of 30
  - Ionizing radiation 25, 27–28, 33
    - damage to carbohydrates 27
    - damage to DNA 27
    - damage to lipids and membranes 28
    - damage to proteins 27
    - effect on cellular macromolecules 25
    - proposed mechanisms of resistance 33
    - sensitivity to 27
  - Iron (III) reduction 215
  - Iron (III) respiration 215
  - Isopropylmalate dehydrogenase, activity under high pressure 256
- L**
- Lipase, from Antarctic isolate *Penicillium expansum* 97
  - Lipases 94–95
    - antarctic 95
    - cold-active 94
  - Lithoautotrophs 112, 116
    - dismutation of sulfur compounds 116
    - novel metabolic groups 112
  - Low temperatures 54, 56, 61
    - adaptations to 56
      - membrane adaptations to 61
      - nucleic acid adaptations to 61
      - physicochemical constraints of 54
      - protein adaptations to 56
- M**
- Macrofungi, definition 89
  - Mariana Trench, Challenger Deep 234
  - Membranes 61, 65
    - adaptations to low temperatures 61
    - low-temperature functional limits 65
  - Metabolism at low temperatures 55, 65–67
  - Metagenomics 3–6
    - versus conventional cultivation 3
  - Methane oxidation, thermophilic 118
  - Methanol oxidation, thermophilic 119
  - Methanotrophs, thermoacidophilic 117
  - Microfungi 89, 97
    - crude oil degradation 97
    - definition 89
  - Mining extreme environments 2
- N**
- Nanobiotechnology, hami 85
  - Natural gas associated microorganisms 160
  - Nitrification, thermophilic 112
  - Non-contact leaching 282
  - Nucleic acids 61, 65
    - adaptations to low temperatures 61
    - low-temperature functional limits 65

**O**

- Oil-reservoir associated microorganisms 160, 162–163, 181–182
  - Metagenomics 181–182
- Ordering effects 54
- Organotrophs 121
  - hyperthermophilic 121
  - thermophilic 121
- Origin of life 233

**P**

- Panspermia 43
- Pectin 136
- Penicillium expansum* lipase 97–99
  - characterization and production 97–98
  - pH and temperature optima 98–99
- Petroleomics 179
- Physicochemical constraints of low temperatures 54–55
  - Piezophiles 16, 164, 233–247, 254. *See also*
    - Barophiles
    - adaptation to high hydrostatic pressures 247
    - Colwellia* 240
    - cultured from the Japan Trench 244
    - definition 233. *See also* Barophiles
    - distribution, taxonomy and diversity 234–241
    - enzymes from 254
    - from Mariana Trench 234
    - high-pressure cultivation of 242
    - hyperthermophilic, 247
    - isolate characterization 243
    - methods for the isolation of 241–247
    - Moritella* 240
    - Photobacterium* 240
    - polyunsaturated fatty acids (UFA) of 240, 241
    - Psychromonas* 241
    - Shewanella* 237
- Piezophilic biocatalysts, whole cell 16
- Piezophilic enzymes 16
- Plant cell walls 136
  - composition 136
  - enzymatic degradation 136
- Polysaccharide lyase (PL) 136
- Pressure-bag method, piezophile isolation 243
- Pressure-regulated gene expression 251
  - FtsZ 251
  - respiratory systems 251
- Proteins 56, 58, 65
  - adaptations to low temperatures 56
  - increased flexibility at low temperatures 58
  - low-temperature functional limits 65
- Psychrophiles 9, 53, 55–56
  - in sea ice 56
  - definition 53
  - diversity and ecology 55
- Psychrophilic piezophiles, cultivation of 245
- Psychrotolerant microorganisms 53. *See also*
  - Eurypsychrophiles
- Psychrotolerant organisms 9
  - commercial enzymes from 9

**R**

- RNA polymerase, high-pressure stability 253

**S**

- Scaling, oil well 166
  - Sediment sampler, deep-sea 243
  - Shewanella violacea* 249–253, 256–257
    - genome analysis 256–257
    - pressure-regulated gene expression in 249–253
  - Simultaneous saccharification and co-fermentation (SSCF) 132
  - Sippenauer Moor, cold sulfidic springs 77
  - SM1 euryarchaeon 78, 80, 82–84
    - ‘archaeal ninjas’ 83
    - anaerobic biofilm lifestyle 82
    - cell surface appendices 83. *See also* Hami
    - from Islinger Mühlbach 80
    - from Sippenauer Moor 78
    - microscopic morphology 83–84
  - Steam assisted gravity drainage (SAGD) for heavy oil extraction 173, 174
  - String-of-pearls prokaryotic community 78–81
    - 16S rRNA analysis 78, 80
    - aerobic lifestyle 78
    - in situ* cultivation 80–81
    - proposed sulfur cycle 79
    - SM1 euryarchaeon 78
    - Thiothrix* 78
  - Sulfide minerals 273
  - Sulfur compounds, dismutation by lithotrophs 116
  - Supercooling 54–55
  - Sustainable energy production, biofuels 142
- T**
- Thermoacidophiles, methanotrophic 117
  - Thermococcales 120, 206
    - hydrogenogenic formate oxidation 120
  - Thermophiles 6, 8–9, 109–110, 112, 115, 117–122, 124, 162, 171
    - anaerobic ammonia oxidation 112. *See also*
      - Annamox
    - anaerobic methane oxidation 118
    - anaerobic oxidation of non-fermentable substrates 122
    - C1 metabolism 117
    - carbon monoxide oxidation 115
    - diversity of 109–110
    - electrogenic 124
    - for biodiesel production 171
    - hydrogenogenic formate oxidation 120
    - methanol oxidation 119
    - nitrification 112
    - organotrophic 121
    - whole cell biocatalysts 8–9
  - Thermophilic lithoautotrophs, novel metabolic groups of 112
  - Thermotolerant organisms 6
  - Thin layer chromatography 176

**V**

Vapour extraction (VAPEX) for heavy oil extraction 173, 180

**W**

Web resources, extremophiles and biotechnology 18  
Whole cell biocatalysts, thermophilic 8–9

**X**

Xylanolytic bacteria 136

**Y**

Yeasts, Antarctic 91  
Yellowstone National Park xi, xiii, 6, 109, 113, 116, 118, 134, 145–152, 206, 219