Contents

Preface xi
Béatrice CLOUET-D'ORVAL, Bruno FRANZETTI and Philippe OGER

Chapter 1. The Discovery of Archaea 1
Patrick FORTERRE

1.1. Introduction. 1
1.2. Prokaryotic–eukaryotic dichotomy 2
1.3. Two domains for prokaryotes: archaebacteria and eubacteria 3
1.3.1. Ribosomal RNA as a molecular marker: a historical choice. . . . 3
1.3.2. Atypical ribosomal RNA of methanogenic "bacteria" 7
1.3.3. The concept of archaeobacteria. 8
1.3.4. The grouping of halophilic and thermo-acidophilic "bacteria" with methanogens within archaeobacteria. 9
1.4. The living trilogy 11
1.4.1. The concept of archaeobacteria confirmed by the uniqueness of their membrane phospholipids 11
1.4.2. German biochemists: champions of the archaeobacteria concept 12
1.4.3. The evolutionary link between archaeobacteria and eukaryotes and the introduction of the term archaea 13
1.5. Archaea and high-temperature living. 14
1.5.1. The discovery of anaerobic hyperthermophilic archaea 14
1.5.2. The race for the thermophilia record. 18
1.5.3. The discovery of viruses in hyperthermophilic archaea 20

1.6. Non-extremophilic archaea discovered by molecular ecology: a new vision of the third domain 22
1.7. Conclusion 23
1.8. References 24

Chapter 2. Evolution of Archaea and Their Taxonomy 29
Patrick FORTERRE

2.1. Introduction. 29
2.2. One domain, three major branches and a few isolated "phyla" 30
2.2.1. One domain, two phyla 30
2.2.2. A first orphaned phylum, the *korarchaeota*. 31
2.2.3. The first phylogenies based on conserved proteins 32
2.2.4. The special case of *Methanopyrus kandleri* 35
2.2.5. The special case of *Nanoarchaeum equitans* 36
2.2.6. Thaumarchaea 37
2.3. From phyla to superphyla 39
2.3.1. Metagenomics and the explosion in the number of archaeal phyla 39
2.3.2. The superphylum TACK. 41
2.3.3. The DPANN 45
2.3.4. The Asgard archaea. 50
2.3.5. *Stygia/Hadarchaeota* 55
2.3.6. *Hydrothermarchaeota* 55
2.4. Euryarchaea. 56
2.4.1. Group I Euryarchaea 57
2.4.2. Group II Euryarchaea. 59
2.5. A new nomenclature for the taxonomy of archaea? 64
2.6. Reconstructing the last common ancestor of archaea: LACA 67
2.6.1. Rooting the archaeal tree. 67
2.6.2. Two opposing visions of LACA: simple or complex 71
2.6.3. The likely hyperthermophilic nature of LACA. 72
2.6.4. The possibility of a methanogenic LACA 74
2.7. Conclusion 76
2.8. References 76

Chapter 3. Archaea and the Tree of Life. 89
Patrick FORTERRE

3.1. Introduction. 89
3.2. The progenote concept 90

3.3. Archaea: prokaryotes related to eukaryotes 91
3.4. Rooting the universal tree 92
3.5. The nature of LUCA 97
3.5.1. A simpler LUCA compared to the organisms of the three current domains 97
3.5.2. An RNA genome for LUCA? 97
3.5.3. A presumably mesophilic LUCA 100
3.5.4. LUCA's proteome 105
3.6. The topology of the universal tree under debate 110
3.6.1. Early challenge to the Woese tree: the eocyte hypothesis 110
3.6.2. Searching for the archean ancestor of eukaryotes 111
3.6.3. Discovery of the Asgard archaea: validation of the 2D hypothesis? 112
3.6.4. Controversies over the position of Asgard archaea 113
3.7. The origin of new eukaryotic-like proteins discovered in Asgard archaea 125
3.8. Asgard archaea and the origin of eukaryotes 130
3.8.1. Asgard archaea at the origin of eukaryotes: a new paradigm . . . 130
3.8.2. The inside-out model based on nanotubes discovered in Asgard archaea 131
3.8.3. The two-bacteria 2D model 132
3.8.4. The origin of eukaryotic cell complexity 132
3.9. The biological issues posed by the 2D model 133
3.10. Viruses and the universal tree of life 136
3.11. Conclusion 141
3.12. References 141

Chapter 4. Archaea: Habitats and Associated Physiologies 153
Karine ALAIN, Marc COZANNET, Maxime ALLIOUX, Sarah THIROUX and Jordan HARTUNIANS

4.1. Introduction 153
4.2. Archaea of extreme habitats: extremophiles 156
4.2.1. Psychrophiles 158
4.2.2. Thermophiles/hyperthermophiles 161
4.2.3. Acidophiles 164
4.2.4. Alkalophiles 166
4.2.5. Halophiles 167
4.2.6. Piezophiles 168
4.2.7. Radiotolerant archaea 169

4.2.8. Poly-extremophilic archaea 170
4.2.9. Record-holding archaea 171
4.3. Archaea populating ordinary, non-extreme environments 172
4.3.1. Phytobiomes, rice paddies and peatlands 174
4.3.2. Aquatic habitats: lakes, oceans and estuaries 178
4.3.3. Environments linked to human activities: example of waste treatment and anaerobic digesters (methanizers) 183
4.3.4. Animal microbiomes 185
4.4. Archaea resistant to cultivation efforts 188
4.5. Challenges and success stories 191
4.6. Conclusion 193
4.7. References 193

Chapter 5. Methanogenic Archaea 205
Tristan WAGNER, Laurent TOFFIN and Guillaume BORREL

5.1. Diversity of methanogens and their environments 205
5.1.1. Methane sources and sinks 205
5.1.2. Taxonomic and metabolic diversity 207
5.1.3. Ecological diversity of methanogens 210
5.2. Interactions of methanogens with their environment 216
5.2.1. Competition for substrates 216
5.2.2. Ecological and syntrophic interactions 217
5.2.3. Human–methanogen association 218
5.3. Bioenergetics and biochemistry of methanogenesis 219
5.3.1. Energy extremophiles 219
5.3.2. Cofactors used in methanogenesis 219
5.3.3. Different types of methanogenesis 222
5.3.4. MCR, the unique enzyme capable of generating biogenic methane 230
5.4. Anaerobic methanotrophs and anaerobic oxidation of multi-carbon alkanes 232
5.5. Evolution of methanogenesis 233
5.5.1. An ancestral metabolism 233
5.5.2. Metabolic adaptations 234
5.6. The impact of methanogens in our modern society 234
5.7. References 236

Chapter 6. Hyperthermophilic Archaeal Viruses 247
Diana BAQUERO, Mart KRUPOVIC, Claire GESLIN and David PRANGISHVILI

6.1. Introduction. 247
6.2. Morphological and structural diversity. 248
6.2.1. Viruses with unique morphologies: families *Ampullaviridae*, *Spiraviridae* and *Guttaviridae* 248
6.2.2. Filamentous viruses: families *Rudiviridae*, *Lipothrixviridae*, *Tristromaviridae* and *Clavaviridae* 249
6.2.3. Spherical and icosahedral viruses: families *Globuloviridae*, *Ovaliviridae*, *Portogloboviridae* and *Turriviridae* 251
6.2.4. Fusiform viruses: families *Fuselloviridae* and *Bicaudoviridae* 253
6.3. Genomic features of hyperthermophilic archaeal viruses. 254
6.3.1. Genome content. 254
6.3.2. Structural genomics. 257
6.4. Virus–host interactions 258
6.4.1. Virus entry 259
6.4.2. Virion egress. 259
6.5. Conclusions. 260
6.6. References 261

List of Authors 269

Index 271