LIFE IN HOT SPRINGS AND HYDROTHERMAL VENTS*

ANDREAS H. SEGERER, SIGFRIED BURGGRAF, GERHARD FIALA, GERTRUD HUBER, ROBERT HUBER, URSULA PLEY, and KARL O. STETTER

Lehrstuhl für Mikrobiologie, Universität Regensburg, Universitätsstr. 31, D-8400 Regensburg, Federal Republic of Germany

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Abstract. Hot springs and hydrothermal systems occurring within volcanic areas are inhabited by hyperthermophilic microorganisms, some of which grow at temperatures up to 110 °C. Hyperthermophiles grow anaerobically or aerobically by diverse metabolic types. Within the high temperature ecocystems, primary production is independent from solar energy.

1. Introduction

Microbiological exploration of extreme biotopes has recently led to the discovery of unusual hyperthermophilic organisms with optimum growth temperatures of at least 80 °C occurring in volcanic habitats. Some hyperthermophiles are able to grow up to 110 °C. In contrast, the upper temperature limit of usual thermophilic and extremely thermophilic prokaryotes, which have been recognized since a long time, is usually in the range of 60–80 °C. This paper will give an overview about the hyperthermophiles. The reader is also referred to other general reviews on hyperthermophiles (Setter, 1989a; Stetter *et al.*, 1990; Segerer *et al.*, 1991a) and reviews focussing on specified hyperthermophilic taxa (R. Huber and Stetter, 1991a; R. Huber and Stetter, 1991b; Segerer and Stetter, 1991a; Segerer and Stetter, 1991b) which have been published recently.

2. Habitats

Hyperthermophiles have almost exclusively been isolated from volcanic habitats, i.e. continental solfatara fields and submarine hydrothermal areas (Corliss *et al.*, 1979; Williams and McBirney, 1979). A few isolates were also obtained from suitable anthropogenic biotopes.

Within solfataras, hyperthermophiles occur in sulfur-rich boiling springs, mudholes, and heated soils. Solfataric springs are either highly acidic and rich in sulfate or almost neutral, sometimes even slightly alkaline, reflecting the chemical composition of the ground (Brock, 1978). Depending on the altitude above sea level,

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the temperatures can be as high as 100 °C. The soils exhibit a bilayered profile which is defined by pH value and redox state (Stetter *et al.*, 1986a; Stetter *et al.*, 1986b): (a) The surface layer is typically about 30 cm thick, highly acidic (pH 0.5–4), and oxidized. Ferric iron compounds cause a rusty appearance. (b) The lower zone is essentially anaerobic due to the permanent stream of volcanic exhalations containing reducing compounds (e.g., H_2S). Characteristically, the pH value is significantly higher than in the oxidized layer (pH 4–8). The color is blackisch-grey due to the presence of heavy metal sulfides. Both zones are rich in molecular sulfur which is generated by the reaction of H_2S with SO_2 or O_2. Solfataric hyperthermophiles are well adapted to their environment. There are both extreme acidophiles and neutrophiles which thrive aerobically, facultatively anaerobically, or strictly anaerobically (see section on physiology below). No hyperhermophiles could be isolated from highly acidic wet fumaroles at Stromboli and Fossa volcano (Southern Italy) and Hawaii, possibly due to their high content of SO_2 and HCl which are toxic to laboratory cultures in higher concentrations (A.H.S. and K.O.S, unpublished results; T.D. Brock, personal communication).

The marine biotopes include anaerobic hot sediments, submarine fumaroles and hydrothermal vents. These habitats usually exhibit pH values close to neutrality (pH 5–8.5). Due to the elevated hydrostatic pressure, the temperatures of the hot waters may exceed 100 °C. Vent systems occurring at ocean floor spreading zones discharge hydrothermal fluids into the surrounding seawater which are rich in sulfides and heavy metals and may exhibit temperatures of up to almost 400 °C (Corliss *et al.*, 1979; Jannasch and Wirsen, 1979; Jannasch, 1989).

Presumably due to their different chemical composition, marine and terrestric high temperature biotopes are each colonized by characteristic, distinct communities of hyperthermophiles. As an exception, some isolates of the solfataric species *Acidianus infernus* and *Thermoplasma volcanium* could be obtained from highly acidic sandy marine sediments off Vulcano Island, Italy (Segerer *et al* 1986, 1988).

Anthropogenic habitats include heated overflow waters from geothermal power plants (Stetter, 1985; R. Huber *et al.*, 1987), acidic hot water drainages and soils self-heated coal refuse piles (Darland *et al.*, 1970; Brock, 1978; Marsh and Norris, 1985) and from a uranium mine containing graphite and pyrite in eastern Germany (A.H.S. and K.O.S., unpublished observation).

3. Taxonomy and Phylogeny

To date, about 45 species of hyperthermophiles and related extreme thermophiles have been described and assigned to a number of different genera and orders (Table I). All hyperthermophiles but the Thermotogales belong to the archaeal domein (Woese *et al.*, 1990) of life which had previously been disignated 'archaebacteria' (Woese *et al.*, 1978). Based on sequence analyses of 16S rRNA genes and paralogous genes that deverged from each other before the domains emerged from their common ancestor, the Archaea were shown to represent a distinct monophyletic lineage of

TABLE I

Taxonomy of hyperthermophiles and related thermophiles

Order	Genus	Species	Reference
Domain Archaea (Kingdom Crenarchaeota)			
Sulfolobales	*Sulfolobus*	*S. acidocaldarius*	Brock *et al.*, (1972)
		S. solfataricus	Zillig *et al.*, 1980
		S, shibatae	Grogan *et al.*, 1991
		S. metallicus	G. Huber and Stetter, 1991
	Metallosphaera	*M. sedula*[b]	G. Huber *et al.*, 1989
	Sulfurococcus	*Sc. mirabilis*[b]	Golovacheva *et al.*, 1987; Zhilina *et al.*, 1989
	Acidianus	*A. infernus*	Segerer *et al.*, 1986
		A. brierley[b]	Zillig *et al.*, 1980, Segerer *et al.*, 1986
	Desulfurolobus	*D. ambivalens*	Zillig *et al.*, 1986
	Stygiolobus	*Stl. azoricus*	Segerer *et al.*, 1991b
Thermoproteales	*Thermoproteus*	*T. tenax*	Zillig *et al.*, 1981
		T. neutrophilus	Stetter, 1986; Zillig, 1989
		T. uzoniensis	Bonch-Osmolovskaya *et al.*, 1990
	Pyrobaculum	*Pb. islandicum*	R. Huber *et al.*, 1987
		Pb. organotrophum	R. Huber *et al.*, 1987
	Thermofilum	*Tf. pendens*	Zillig *et al.*, 1983a
		Tf. librum	Stetter, 1986
	Desulfurococcus	*Dc. mucosus*	Zillig *et al.*, 1982
		Dc. mobilis	Zillig *et al.*, 1982
		Dc. saccharovorans	Stetter, 1986
		Dc. amylolyticus	Bonch-Osmolovskaya *et al.*, 1985
	Staphylothermus	*Stt. maritimus*	Fiala *et al.*, 1986
'Pyrodictiales'	*Pyrodictium*	*Pd. occultum*	Stetter *et al.*, 1983
		Pd. brockii	Stetter *et al.*, 1983
		Pd. abyssi	Pley *et al.*, 1991
	Hyperthermus	*H. butylicus*	Zillig *et al.*, 1990
	Thermodiscus	*Td. maritimus*	Stetter, 1986
Thermococcales	*Thermococcus*	*Tc. celer*	Zillig *et al.*, 1983b
		Tc. litoralis	Neuner *et al.*, 1990
		Tc. stetteri	Miroshnickenko *et al.*, 1989
	Pyrococcus	*Pc. furiosus*	Fiala and Stetter, 1986
		Pc. woesei	Zillig *et al.*, 1987
'Archaeoglobales'	*Archaeoglobus*	*Ag. fulgidus*	Stetter *et al.*, 1987; Stetter, 1988
		Ag. profundus	Burggraf *et al.*, 1990b
'Thermoplasmatales'	*Thermoplasma*	*Tp. acidophilum*[b]	Darland *et al.*, 1970
		Tp. volcanium[b]	Segerer *et al.*, 1988
'Methanopyrales'	*Methanopyrus*	*Mp. kandleri*	R. Huber *et al.*, 1989a
Methanococcales	*Methanococcus*[a]	*Mc. jannaschii*	Jones *et al.*, 1983
		Mc. igneus	Burggraf *et al.*, 1990a
		Mc. thermolithotrophicus	H. Huber *et al.*, 1982
Methanobacteriales[a]	*Methanothermus*	*Mt. fervidus*	Stetter *et al.*, 1981
		Mt. Sociabilis	Lauerer *et al.*, 1986

Table I (continued).

Order	*Genus*	*Species*	*Reference*
Domain Bacteria			
Thermotogales	*Thermotoga*	*Tt. maritima*	*R. Huber et al.*, 1986
		Tt. neapolitana	Jannasch *et al.*, 1988
		Tt. thermarum[b]	Windberger *et al.*, 1989
	Thermosipho	*Ts. africanus*[b]	R. Huber *et al.*, 1989b
	Fervidobacterium	*F. nodosum*[b]	Patel *et al.*, 1985
		F. islandicum[b]	R. Huber *et al.*, 1990b

[a] The order or genus contains further mesophilic organisms which are not listed here.
[b] Thermophilic but not hyperthermophilic organism, mentioned due to relationship to hyperthermophiles.

evolution beside the domeins Bacteria (after recognition of archaebacteria designated as 'eubacteria') and Eucarya (eukaryotes) (Woese and Fox, 1977; Fox *et al.*, 1980; Woese, 1987; Gogarten *et al.*, 1989; Iwabe *et al.*, 1989; Woese *et al.*, 1990).

The archaeal phylogenetic tree consists of two main branches (kingdoms) (Woese *et al.*, 1990): (a) The Crenarchaeota which almost exclusively include hyperthermophiles (Stetter and Zillig, 1985; R. Huber and Stetter, 1991a; Segerer and Stetter, 1991b); and (b) the Euryarchaeota. The first crenarchael organisms discovered in the 70s and early 80s were sulfur metabolizers and either extreme acidophiles (e.g., *Sulfolobus acidocaldarius*) or acid tolerant (e.g., *Thermoproteus tenax*) (Brock *et al.*, 1972; Zillig *et al.*, 1980; 1981). Therefore, the whole group has sometimes been called 'thermoacidophilic' or 'sulfurdependent' archaebacteria (Zillig *et al.*, 1981; Stetter and Zillig, 1985). However, a number of isolates are now known to be either not dependent on sulfur, neutrophilic, or both. Hence, these designations are no longer appropriate. In contrast to the Crenarchaeota, the Euryarchaeota represent a phenotypically highly diverse group of organisms including methanogens, sulfate reducers, extreme halophiles, thermoacidophiles, and fermentative archaea, only some of which are thermophilic or hyperthermophilic (Woese, 1987).

The only hyperthermophilic bacteria recognized to date are included within the order Thermotogales (R. Huber and Stetter, 1991b). By 16S rRNA sequences, this order represents the deepest branch of the bacterial phylogenetic tree (Woese, 1987).

4. Morphology, Physiology and Distribution

The hyperthermophilic archaea and *Thermotoga* usually are of the size of a typical prokaryotic cell ($\varnothing \approx 0.5$–2 μm) e.g., Figures 1–4) and employ a variety of different morphotypes, including rods (*Thermoproteus, Pyrobaculum, Methanopyrus, Methanothermus) (Figure 1), thin filaments* ($\varnothing \approx 0.1$ μm; *Thermofilum*), discs *(Pyrodictium, Thermodiscus)* (Figure 2) and cocci (most hyperthermophiles) (Figures 3, 4). The cocci may be more or less regularly or highly irregularly in shape, depending on the organism (Stetter *et al.*, 1990; Table II). Highly irregular, lobed cells are characteristic of most members of the Sulfolobales (Brock *et al.*, 1972; Stetter,

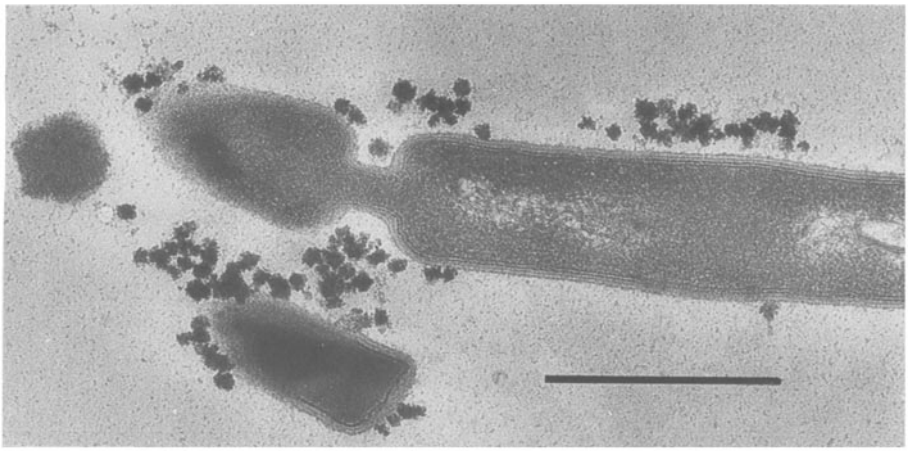

Fig. 1. *Methanopyrus* kandleri isolate Av19. EM micrograph of an ultrathin section. Bar, 0.5 μm.

1989b; Segerer and Stetter, 1991b). There are some exceptional morphological types: (a) *Pyrodictium* cells possess ultraflat areas and are connected by a network of hollow proteinaceous fibres of yet unknown function (Stetter, 1982; König *et al.*, 1988; Pley *et al.*, 1991) (Figure 2); (b) cells of *Thermoproteus, Pyrobaculum* and *Thermofilum* produce spherical terminal protrusions ('golf club forms') with unknown biological function (Zillig *et al.*, 1981, 1983a; R. Huber *et al.*, 1987; R. Huber and Stetter, 1991a); (c) *Thermoproteus* cells may be truely branched (Zillig *et al.*, 1981; R. Huber and Stetter, 1991a); (d) *Staphylothermus*, which normally occurs in huge grape-like aggregats, is able to form giant cells (∅ up to 15 μm) in nutrient-rich medium (Fiala *et al.*, 1986); and (e) *Thermotaga* spp. possess a characteristic

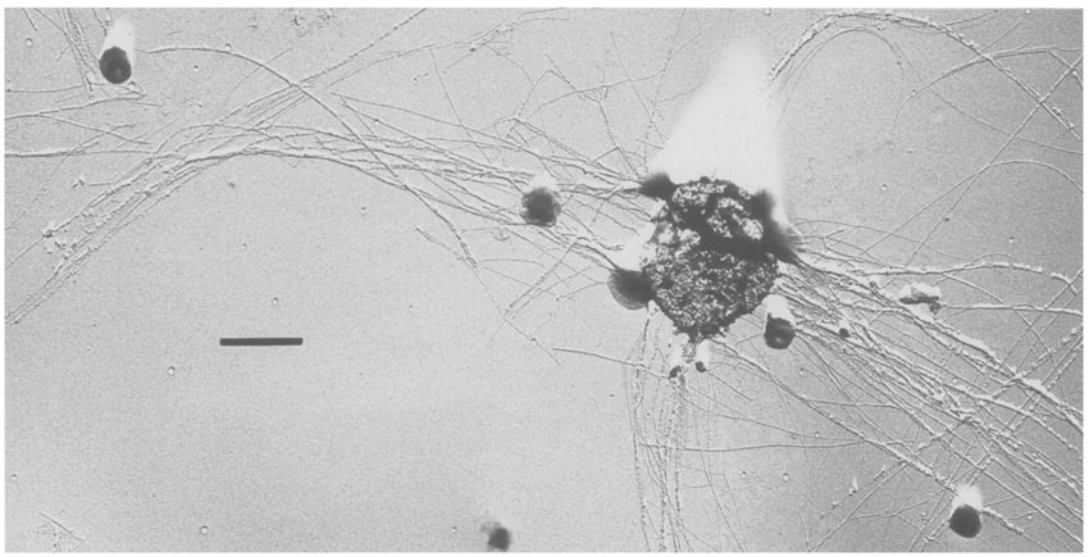

Fig. 2. *Pyrodictium occultum* isolate PL 19. EM mocrograph, Pt shadowing. Bar, 2 μm.

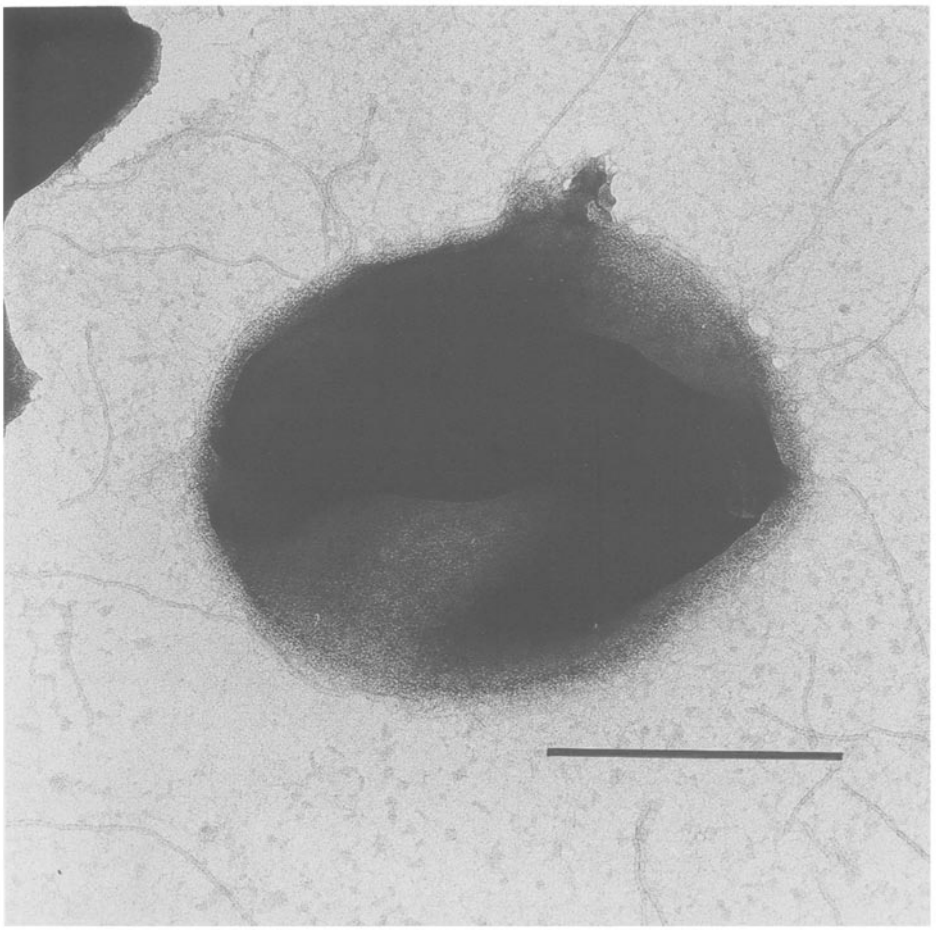

Fig. 3. *Stygiollobus azoricus* isolate FC6. EM micrograph, Pt shadowing. Bar 0.5 μm.

sheath-like outer membrane ballooning over both ends (R. Huber *et al.*, 1986; Jannasch *et al.*, 1988; Rachel *et al.*, 1990).

Most hyperthermophiles are flagellated (e.g., Figure 4), but are usually immotile at room temperature and run only at temperatures of $\geq$ 50 °C (R. Huber *et al.*, 1987; Grogan, 1989; R.H. and K.O.S., unpublished obeservations).

Whereas the majority of hyperthermophiles thrive optimally at pH values around neutrality, the members of the Sulfolobales (and the less extremely thermophilic *Thermoplasma* spp.) are extreme acidophiles that grow optimally around pH 2–3 and lyse at pH $\geq$ 7 (Darland *et al.*, 1970; Brock *et al.*, 1972; Segerer *et al.*, 1988; Segerer and Stetter, 1991b) (Table II). With the exception of *Stygiolobus* (Segerer *et al.*, 1991b), all of these acidophiles are able to grow aerobically (Segerer and Stetter, 1991a, b; Table II). All other hyperthermophiles are extreme anaerobes which are usually killed even by traces of oxygen. Special techniques are required for successful cultivation, therefore (Balch *et al.*, 1979). No dormant stages like

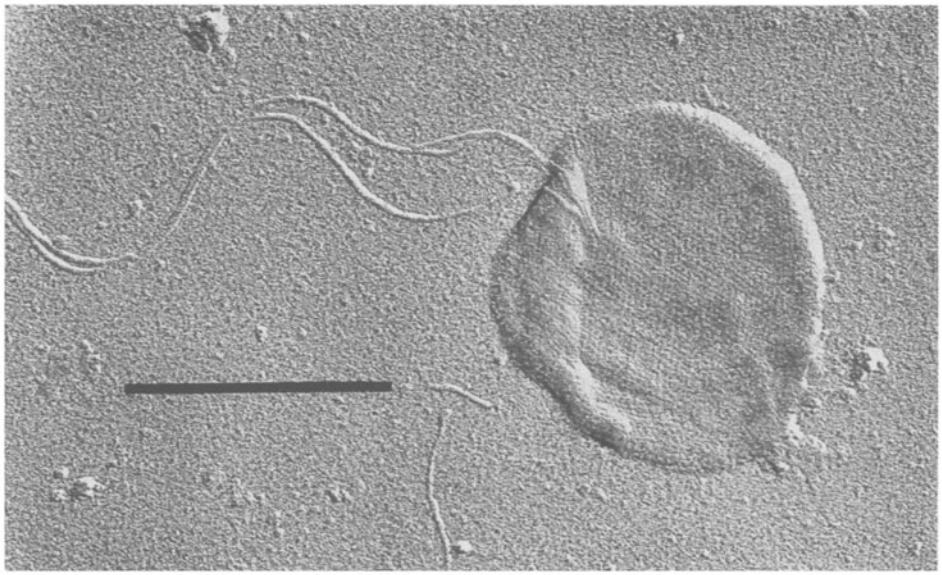

Fig. 4. *Archaeoglobus fulgidus* isolate Vc 16. EM micrograph, Pt shadowing. Bar, 0.5 μm.

endospores are formed by the hyperthermophiles known to date.

As a rule, hyperthermophiles have an optimum growth temperature well above 80 °C and cannot grow below ≈ 60 °C. *Methanopyrus* (Figure 1) and *Pyrodictium* (Figure 2) are the most thermophilic organisms known, growing maximally at 110 °C and being unable to grow below 80 °C (Stetter *et al.*, 1983; Pley *et al.*, 1991; R.

TABLE II

Morphological and physiological properties of some hyperthermophiles

Species	Morphology	Growth temperature (°C)			Growth at pH	anaerobic (an)/ aerobic (ae)
		Min.	Opt.	Max.		
Acidianus infernus	lobed, irregular cocci	60	88	95	0.8–5.5	ae/an
Pyrobaculum islandicum	rods, sometimes with terminal spherical protrusions	74	100	103	5–7	an
Thermofilum pendens	thin filaments, sometimes with a terminal spherical protrusions	70	88	95	4–6.5	an
Pyrodictium occultum	discs with fibres	82	105	110	5–7	an
Pyrococcus furiosus	cocci	70	100	103	5–9	an
Archaeoglobus fulgidus	irregular cocci	60	83	95	5.5–7.5	an
Methanococcus igneus	irregular cocci	45	88	91	5–7.5	an
Methanothermus sociabilis	rods in clusters	65	88	97	5.5–7.5	an
Methanopyrus kandleri	rods	84	98	110	5.5–7	an
Thermotoga maritima	rods with a sheath-like outer membrane ('toga')	55	80	90	5.5–9	an

Huber *et al.*, 1989a; Table II). The temperature optimum of *Pd. occultum* and *Pd. brockii* at 105 °C (under slight overpressure) is the highest one of any organism described so far (Stetter, 1982). Hyperthermophiles cannot grow at low temperatures, but survive in the cold (e.g., at 4 °C) at moderately acidic or neutral pH values at least for years. At least some anaerobic hyperthermophiles are able to tolerate oxygen stress significantly better at low temperatures than at growth temperature (Fiala *et al.*, 1986; R. Huber *et al.*, 1987). This property is most probably essential for their dispersal through cold, oxidized areas. Evidently, volcanic eruptions are a major source of their propagation. In-field studies demonstrated the presence of $> 10^6$ viable anaerobic hyperthermophilic archaea per liter of seawater within the eruption plume of Macdonald seamount (Polynesia, Southern Pacific) at a distance of 1 km from the active crater (R. Huber *et al.*, 1990a).

5. Metabolism

Some hyperthermophiles (e.g., Figures 1–4) grow chemolithoautotrophically on inorganic energy sources and CO_2 as sole carbon source. From an ecological point of view, these organisms can be considered as primary producers of organic matter within the high temperature ecosystems (Figure 5). Some of them are able to grow faculatively heterotrophically and/or to use a variety of electron donors and acceptors, thus being metabolically versatile. Possibly, this property is important for efficient competition within the ecosystem. The hyperthermophilic methanogens (e.g., Figure 1) and *Stygiolobus azoricus* (Figure 3) are probably highly specialized, growing obiligately autotrophically by only one means of energy yielding reaction (methanogenesis and H_2-S^0 lithoautotrophy, respectively; see below). Four types of chemolithoautotrophic metabolism have been recognized (Figure 5): (1) The formation of H_2SO_4 by oxidizing molecular sulfur (S^0) is characteristic of most Sulfolobales (Shivvers and Brock, 1973; Stetter, 1989b; Segerer and Stetter, 1991b). Usually, oxygen serves as terminal acceptor of electrons. However, most if not all S^0-oxidizing species are able to use molybdate and ferric iron as alternative electron sinks and can thus be considered to be facultative anaerobes (Brock and Gustafson, 1976; Brierley and Brierley, 1982). Many species are able to use sulfide (including sulfidic ores), tetrathionate and/or ferric iron as alternative energy sources (Brierley and Murr, 1973; Brierley and Brierley, 1973; Brock *et al.*, 1976; G. Huber *et al.*, 1986; Wood *et al.*, 1987). (2) Some species (Figure 5) of the orders Sulfolobales, Thermoproteales and 'Pyrodictiales' grow by the reduction of S^0 to H_2S by means of H_2 (H_2-S^0 lithoautotrophy; Fischer *et al.*, 1983). *Acidianus* spp. and the closely related *Desulfurolobus ambivalens* are unique in being capable of facultatively growing by oxidation or reduction of S^0, depending on the growth conditions (Segerer *et al.*, 1985; Zillig *et al.*, 1985). (3) The marine sulfate reducing archaeon, *Archaeoglobus fulgidus*(Figure 4), is able to grow facultatively autotrophically by the reduction of thiosulfate with H_2 by means of a not yet elucidated pathway (Stetter, 1988). (4) The hyperthermophilic methanogens produce CH_4 exclusively from CO_2 plus

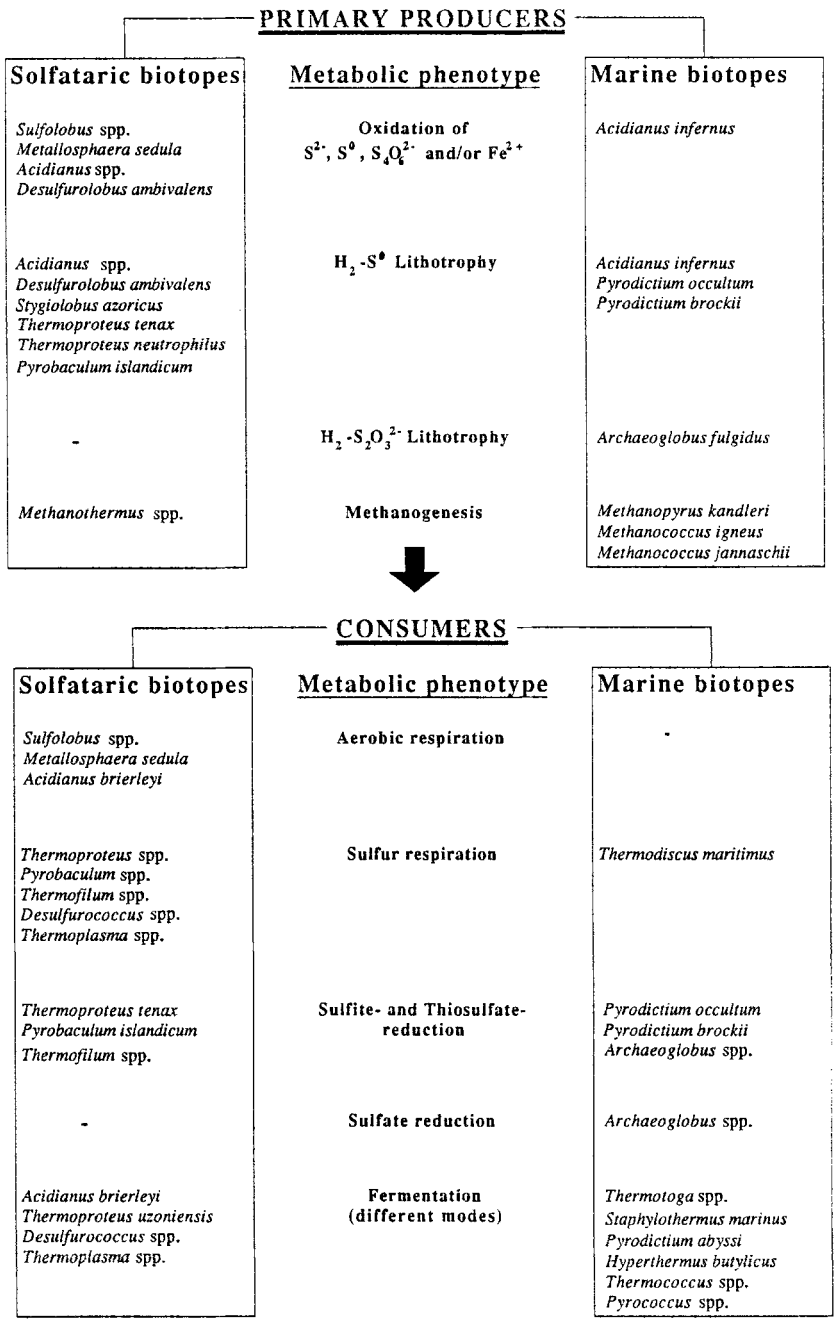

Fig. 5. Metabolism of terrestric and marine hyperthermophiles and food chain within the high temperature ecosystems.

H_2 (Stetter *et al.*, 1981; Jones *et al.*, 1983; Lauerer *et al.*, 1986; R. Huber *et al.*, 1989a; Burggraf *et al.*, 1990a).

The biomass produced by the autotrophs is consumed by heterotrophic hyperthermophiles growing on organic material (Figure 5). There are both chemolitho-heterotrophic (= mixotropic) and chemoorganotrophic organisms. *Pyrodictium occultum* and *Pd. brockii* are able to grow facultatively mixotrophically by reducing thiosulfate (*Pd. occultum*) and sulfite (*Pd. brockii*) with H_2 in the presence of organic substrate (König *et al.*, 1988; Stetter *et al.*, 1990; Pley *et al.*, 1991). *Archaeoglobus profundus* grows obligately mixotrophically by reducing sulfate, sulfite or thiosulfate with H_2 (Burggraf *et al.*, 1990b). The matabolic types of the organotrophs include: (1) aerobic respiration, which is typical for some Sulfolobales (Brock *et al.*, 1972; Lübben *et al.*, 1989; Segerer and Stetter, 1991b); (2) sulfur respiration (Pfennig and Biebl, 1976) which is employed by several members of the Thermoproteales (some of which are also able to reduce sulfite and thiosulfate) (R. Huber and Stetter, 1991a), 'Pyrodictiales' (Stetter, 1986), and the less thermophilic *Thermoplasma*spp. (Segerer *et al.*, 1988); (3) the reduction of sulfate, sulfate and thiosulfate which is a characteristic of *Archaeoglobus fulgidus* (Stetter *et al.*, 1987); and (4) various modes of fermentation. With the exception of *Thermoplasma* (Budgen and Danson, 1986; Danson, 1988) and *Pyrococcus* (Schäfer and Schönheit, 1991), the fermentative pathways have not yet been elucidated in detail. Some of the fermentative organisms possess H_2 evolving hydrogenases (Adams, 1990). In the presence of S^0, however, no H_2 is formed, but electrons are channelled to a sulfur reductase, forming H_2S in a non-energy yielding reaction (Zillig *et al.*, 1983b; Fiala and Stetter, 1986; Adams, 1990; R. Huber and Stetter, 1991b; Schäfer and Schönheit, 1991). This reaction is probably of biological significance, as H_2 is a strong inhibitor of growth of these organisms.

6. The Upper Temperature Limit of Life

At the growth temperature of hyperthermophiles, essential cell components of mesophiles and usual thermophiles like enzymes, nucleic acids and membranes, become rapidly denatured. Hyperthermophiles, however, are highly adapted to high temperatures and cannot even grow below 60–80 °C. Hence, some principles must exist conferring stabilization and/or optimal conformation to essential cell components of hyperthermophiles. Although there are some clues, these principles are still very poorly understood.

Hyperthermophiles contain histone-like proteins and reverse gyrase, the action of which possibly stabilizes the double helix of DNA (Searcy, 1975; Thomm *et al* 1982; Kikuchi and Asai, 1984; Reddy and Suryanarayana, 1988; de la Tour *et al.*, 1990). In addition *Methanopyrus* and *Methanothermus* contain a high intracellular salt concentration (*Methanopyrus*: 3.3 moles L^{-1} potassium *cyclo* 2,3-diphosphoglycerate) (Hensel and König, 1988; R. Huber *et al.*, 1989a) which could also contribute to thermal stabilization of the double helix. Possibly, the numerous

posttranscriptional base modifications occurring in the RNA of all hyperthermophiles studied thus far confer thermostability to these molecules (Edwards *et al.*, 1991).

Purified enzymes and proteins of hyperthermophiles are highly thermophilic and thermostable. For example, anaerobically grown *Acidianus* spp. contain a H_2-oxidizing hydrogenase which exhibits an optimum turnover rate of 117 ^{0}C in vitro and does not loose activity (in the presence of hydrogen) when incubated several hours at 110 ^{0}C (A.H.S. *et al.*, manuscript in preparation). The thermostability of this and many other hyperthermophilic proteins characterized to date is an intrinsic property of the polypeptides (Jaenicke and Zavodszky, 1990). In addition, hyperthermophilic methanogens stabilize some enzymes by potassium *cyclo*-2,3-diphosphoglycerate (Hensel and König, 1988).

Acidophilic hyperthermophiles have to cope with a highly acidic environment in addition to temperature stress. These organisms generally thrive by extruding protons, thus keeping their interior pH close to neutrality (Hsung and Haug, 1975; Searcy, 1976; Lübben and Schäfer, 1989; Matin, 1990). The mechanism of stabilization of their exterior cell structures against is not understood. As the cells lyse at pH $\geq$ 7, protons seem to be specifically required for structural maintenance of cellular stability (Smith *et al.*, 1973).

The upper temperature limit at which life can exist is still unclear. Since the stability of some amino acids and low molecular weight compounds like ATP and NAD rapidly decreases at temperatures above 100 °C (Bernhardt *et al.*, 1984), hyperthermophiles can most probably live only at temperatures allowing resynthesis of thermolabile compounds at a rate sufficiently higher than the rate of their thermal destruction (Stetter *et al.*, 1986a; Fiala *et al.*, 1986). Because of this limitation, the upper temperature border of life may possibly be found between 110 and 150 °C.

7. Conclusions

Thermophilic and hyperthermophilic organisms occur in numerous phylogenetically highly divergent lineages of evolution and could therefore represent an ancient phenotype already existing since billions of years (Achenbach-Richter *et al.*, 1987; Woese, 1987). Recently, a theory of a thermophilic chemolithoautotrophic origin of life has been worked out (Wächtershäuser, 1988; Wächtershäuser, 1990). Within the complex communities of hyperthermophilic organisms existing in volcanic habitats, primary production of organic matter occurs at temperatures of up to 110 °C. The metabolism of anaerobic chemolithoautotrophic hyperthermophiles is based on the consumption of H_2, CO_2 and inorganic sulfur compounds, or, in case of the methanogens, on H_2 and CO_2 alone. These compounds may be formed exclusively within the volcanic habitat. Hence, the organisms are uncoupled from the global life cycle which is dependent on the input of solar energy. Rather, they depend on planetary energy and could in principle also exist outside the terrestrial ecosphere (provided that liquid water and a terrestrial kind of volcanism are present). With respect to the instability of biomolecules at high temperatures, 'black smoker'

conditions (250 °C; 260 bar) are highly unlikely to be compatible with life (Baross and Deming, 1983; Bernhard *et al.*, 1984; Trent *et al.*, 1984; White, 1984).

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