Icarus 225 (2013) 775–780

Contents lists available at SciVerse ScienceDirect

Icarus

journal homepage: www.elsevier.com/locate/icarus

Drastic environmental change and its effects on a planetary biosphere

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ARTICLE INFO

Article history:
Received 8 January 2013
Revised 26 March 2013
Accepted 2 May 2013
Available online 14 May 2013

Keywords:
Earth
Venus
Mars
Exobiology

ABSTRACT

Environmental conditions can change drastically and rapidly during the natural history of a planetary body. These changes affect the biosphere and can spur evolution via the mechanism of directional selection leading to the innovation of new processes and forms of life, or alternatively leading to the extinction of certain life forms. Based on the natural history of Earth, the effect on a planet's biosphere depends on three factors: (1) the nature and time scale of change, (2) the composition of the biosphere prior to change, and (3) the nature of the environment following the change. Though Earth has undergone various periods of drastic environmental change, life has shown an enormous resiliency and became more diverse and complex as a consequence of these events. Mars and Venus have undergone even larger environmental changes, both from habitable conditions under which the origin of life (or transfer of life from Earth) seem plausible, to a dry and cold planet punctuated by wetter conditions, and a hyperthermic greenhouse, respectively. Given its planetary history, life on Mars could have retreated to a psychrophilic lifestyle in the deep subsurface or to environmental near-surface niches, such as hydrothermal regions and caves. Further, strong directional selection could have pushed putative martian life to evolve alternating cycles between active and dormant forms, as well as the innovation of new traits adapted to challenging near-surface conditions. Life in the subsurface or on the surface of Venus seems impossible today, but microorganisms may have adapted to thrive in the lower cloud layer, possibly using a biochemical strategy analogous to Photosystem I and chemoautotrophic sulfur metabolism, and employing cycloocta sulfur for UV protection.

1. Introduction

The planetary environment determines whether a given planet or even a locality on that planet is habitable. Habitability is here defined as the environmental conditions in a planetary setting that are conducive to life, i.e., physical and chemical parameters of that environment that fall within the known constraints of life (Schulze-Makuch and Irwin, 2008). This in general assumes that the planet or at least part of the planet can provide the necessary resources for life. Although the physical and chemical limits of habitability are imprecise, there are certain environmental parameters that clearly favor habitability, including the presence of an atmosphere, a liquid solvent, an energy source, organic chemicals, and a particular thermal range (Schulze-Makuch et al., 2011). Drastic environmental change is not only prevalent on Earth (e.g., Snowball Earth events; *K*/*T* (Cretaceous/Tertiary) boundary and other time-period transitions during the Phanerozoic triggered by environmental alterations due to different causes), but also on our neighboring planets Venus and Mars, and some of the moons of the outer Solar System such as Europa and Titan. The onset of rapid and drastic environmental changes seems often to be triggered by exogenic events such as asteroid impacts or supernova explosions; others are triggered by endogenic processes in the planet or moon itself (e.g., supervolcano eruptions, cessation of inner core dynamos or plate tectonics). The question to be explored here is how these events affect the habitability of the planet and in particular what effects they are expected to have on any existing biosphere.

2. Environmental change and the biosphere: lessons from Earth

Environmental change can be extremely rapid and drastic, especially when triggered by astronomical or geological events. In the extreme case it may even prohibit the origin of life, or be so devastating that existing life would not be able to recover, being all but extinguished from a planet (Ryder, 2003). If the proposed cataclysmic event presumed to have created our Moon (Hartmann et al., 1986) would have occurred later in time, when life was already present on Earth, it would surely have extinguished all life by pushing the planet beyond any reasonable habitability constraints. Fortunately, most catastrophes are not that cataclysmic, but may

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http://dx.doi.org/10.1016/j.icarus.2013.05.001

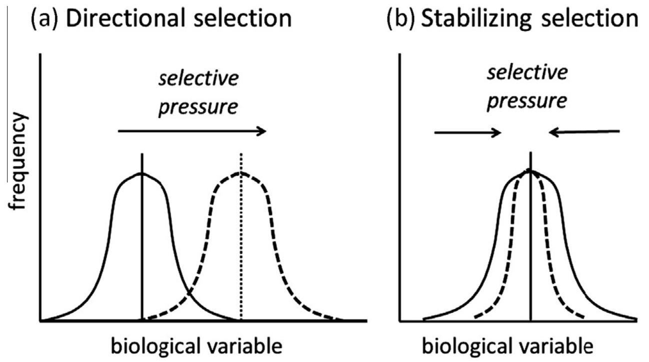

Fig. 1. Effect of selective pressure on biological characteristics, illustrated by changes in the frequency distribution of a quantitative biological trait in response to different forms of selective pressure. (a) In changing environments, natural selection favors change in the direction that better adapts the organism to the new environment. The range for the majority of organisms from the original population and their mean value (solid vertical line) shift toward a different mean (dashed vertical line) without changing the range of the variable in the new population. (b) In stable environments, stabilizing selection promotes elimination of peripheral values in the original population, reducing the range in the descendent population without altering the mean value (solid vertical line). Modified from Irwin and Schulze-Makuch (2011), based on Campbell (1996).

even promote evolutionary advance and biological innovation. For example, mass extinctions that took out a large part of the biosphere., such as the catastrophic events that marked the *P–T* (Permian/Triassic) and *K–T* boundaries created vacant niches that quickly filled with a new mix of organisms characterized by a variety of innovative anatomical and physiological characteristics.

Organisms adapt to environmental changes through evolution driven primarily by natural selection. As the environment changes, traits that fit the organism better for the new environment are favored, hence the mean but not necessarily the variance of the trait shifts in the direction favored by the new environment – a process known as directional selection (Fig. 1a). When the environment is stable, on the other hand, any evolutionary change that occurs tends to optimize existing traits around the mean value favored by environmental constancy, while narrowing the range of deviations from the optimal value – a process known as stabilizing selection.

If the environment is constant and stabilizing selection occurs, most species settle into an evolutionary plateau (Campbell, 1996). This plateau can be stable for millions or even billions of years, as illustrated by turtles and cyanobacteria. Turtles have remained virtually unchanged for the last 200 myr, while cyanobacteria have not significantly changed for at least 1 Ga (Cowen, 1995). When the environment changes, species have to adapt. The more subtle and less rapid the environmental change is, the higher the chance the species has to adapt and develop the necessary new traits via directional selection. However, if the change is both drastic and rapid, for example when caused by a natural disaster, the species will not be able to adapt fast enough, and will go extinct. Examples are the trilobites after the Permian mass extinction event and the dinosaurs after the *K–T* transition. However, occasionally, especially if an organism is pre-adapted to conditions occurring after the environmental change, a particular innovation conveys a marked new advantage, which results in a major transition to a new form (Cowen, 1995; Campbell, 1996). Examples are the innovation of flight in insects and birds, and homeothermy in early mammals and birds.

How the natural history of a planet affects its biosphere depends on three factors: (1) the nature and time scale of change, (2) the composition of the biosphere prior to change, and (3) the nature of the environment following the change. First, in regard to nature and time scale of change, the change may be sudden and catastrophic or it could be gradual, but radical. A suitable example of a sudden and catastrophic change is the *K–T* transition. Mammals and birds, which had traits making them better suited to the new conditions, were able to survive, but not the dinosaurs. An example of a gradual but radical change is the thawing of the latest Snowball Earth at the end of the Proterozoic. A large variety of organisms could fill in the new niches as they became habitable, so directional selection pushed forward the evolution of a whole set of animal phyla (Cowen, 1995; Peterson et al., 2004). Second, the composition of the biosphere prior to the environmental change also plays a critical role. A diverse multicellular Ediacaran fauna was present just before the latest Snowball Earth (Collins et al., 2000; Fedonkin and Waggoner, 1997; Narbonne, 2005). By surviving through the Snowball Earth event in restricted environmental niches, certain innovative forms were able to thrive under the warmer conditions that came about when Snowball Earth started to thaw. No such evolutionary leap, however, was observed after the Snowball Earth event during the Proterozoic (Huronian Glaciation, 2.4–2.1 Ga ago). Though protist diversification and habitat expansion have been suggested for that transition (Vidal and Moczydlowska-Vidal, 1997), unicellular marine microbes were both the dominant type of organism before and after that Snowball Earth event. Finally, the nature of the environment following the environmental change is important. One likely reason that there were no major evolutionary leaps after the Huronian Glaciation is that the atmosphere remained substantially less oxygenated than today, with the oxygen increase leveling off at about 15% of the present level (Holland, 1984; Bekker et al., 2004). The thawing of the Snowball Earth at the end of the Proterozoic, on the other hand, not only provided new land areas but also a highly oxygenated atmosphere, which plants and animals could colonize. Furthermore, animals could expand and increase their size and complexity through oxidative metabolism.

3. Rapid environmental change on Mars and its effects on a possible biosphere

Early Mars and today's Mars are very different. Early Mars was a cold, albeit relatively wet planet with abundant evidence of flowing water and an active hydrosphere (e.g., Clifford and Parker, 2001; Fairén, 2010). Oceans have been suggested to exist at least temporarily on Mars' surface (Baker et al., 1991; Fairén et al., 2003; Perron et al., 2007). Even evidence of rain exists during that time (e.g., Mangold et al., 2004) and it has been suggested that the martian atmosphere had a thickness of at least about 10^5 Pa (1 bar, Brain and Jakosky, 1998; de Niem et al., 2012). At this time liquid water was stable on the surface, and a magnetosphere likely shielded the planet from harsh radiation exposure (Connerney et al., 2001). Compared to the cold and wet Noachian time period of early Mars (Fairén, 2010), the planet today is hyperarid and much colder (McKay and Stoker, 1989). The atmosphere is very thin at a pressure of a few hundred Pa, with no liquid water stably on the surface, except perhaps within some deeper parts of Valles Marineris. Liquid water on the surface is only present temporarily and very constrained in location (Haberle et al., 2001), quickly sublimating if it makes it to the surface (Malin and Edgett, 2000). The magnetosphere collapsed long ago and organics probably exist on the martian surface only in oxidized form (Benner et al., 2000). Mars clearly underwent a major transition during its natural history, which would have had major consequences for any life that was present on early Mars. But there was more. There is clear evidence of major impacts on the surface of Mars (e.g., Hellas, Argyre, Isidis), which surely had global environmental consequences. The Tharsis volcanism created the tallest mountain in the Solar System and must have episodically pumped enormous amounts of carbon dioxide, water, and other greenhouse gases into the atmosphere (Dohm et al., 2001). It is conceivable that Mars held large accumulations of surface water during these time periods (Dohm et al., 2001; Fairén et al., 2003; Perron et al., 2007), before it reverted to a desert planet. Also, the periodic tilting of the martian axis would lead to a re-deposition of water accumulations from the pole to the equator and vice versa (Touma and Wisdom, 1993). This would have been accompanied by a thicker atmosphere and likely habitable conditions. The scenario that thus emerges from martian history is that the planet has been mostly cold and dry, with the possible exception of the first wetter 500 myr, but (1) punctuated with sporadic global flooding triggered by episodic volcanisms and asteroid/cometary bombardment, and (2) localized flow from snowmelt or ground-water eruptions (Schulze-Makuch et al., 2005). There are many surface features on Mars that are consistent with this picture, both catastrophic flooding (Baker and Milton, 1974; Carr, 1979; Williams and Malin, 2004; Harrison and Grimm, 2008) and local sapping or seepage of groundwater (Malin and Edgett, 2000; Luo and Howard, 2008).

What type of life forms would we expect to originate and thrive on such a planet? First, the origin of life seems feasible since Mars is a terrestrial planet like Earth and the environmental conditions on early Earth and Mars were somewhat similar (Fairén et al., 2010). Thus, if life was able to originate on Earth, it could have done so on Mars as well. And even if life did not originate on Mars, a good argument could be made that it could have arrived there from Earth via meteorites (or vice versa), as it has been shown that a fraction of bacteria within any rock fragment could survive ejection, travel through space, and re-enter a planetary atmosphere (Davies, 1996; Mileikowsly et al., 2000; Horneck and Rettberg, 2002; Nicholson et al., 2006). This suggests the possibility that life on Mars and Earth may be related. In any event, whatever life may have existed on Mars might be expected to be somewhat similar to life on Earth, at least in regard to the use of some major molecular building blocks, use of water as liquid solvent, and possibly similar metabolic strategies. Therefore, we can arguably use Earth biota to model what evolutionary changes life would have undergone after early Mars became what it is today.

If life evolved independently on Mars, it would probably have originated as a chemoautotroph. The evolutionary advantages of chemoautotrophic organisms are that they are independent of pre-existing organic nutrients and can operate in the dark, deep subsurface. Subterranean moisture would have provided a stable, protected environment for the proliferation of these types of microbes on Mars (Irwin and Schulze-Makuch, 2011). If organic compounds were abundant on early Mars (and stable on the surface), some of these chemoautotrophic organisms would have had the opportunity to evolve into heterotrophic organisms. However, as Mars became increasingly dry and colder, chemoautotrophy as metabolism would have been clearly favored. Phototrophic organisms may have evolved as well on early Mars, given the more environmentally benign planetary surface conditions on the fourth planet from the Sun at that time. The primary habitat of these phototrophs might have been near wet or icy patches on the martian surface. Further down, in liquid puddles beneath the vast ice sheets, chemoautotrophic psychrophiles could have been quite abundant.

Given that Mars does not, at least currently, have plate tectonics and no other obvious large-scale recycling mechanisms, the potential biomass on Mars might be constrained by the total amount of energy able to construct it. Based on available geochemical sources of energy, Jakosky and Shock (1998) suggested that sufficient energy was available to support an origin of life on Mars, but not a ubiquitous and diverse biosphere. Using a similar approach, Cockell et al. (2012) argued that the lack of readily available redox coupling for energy acquisition by life (e.g., productive photosynthetic biosphere generating organic carbon and oxygen) would have increased the scope and abundance of unoccupied habitats for much of the geological history of the planet.

As the planetary conditions changed to drier and colder (Fairén et al., 2010), any biosphere would have had to adapt accordingly, at least in areas close to the martian surface. As the surface became more oxidizing and the access to organic compounds became restricted, heterotrophs might have become extinct. The same fate might have befallen phototrophs, though endoliths in the Antarctic demonstrate that phototrophs can still survive in very dry and cold conditions, protected from an excess of UV-irradiation by retreating into the pore spaces of rocks (Sun and Friedmann, 1999; Dong et al., 2007). Chemoautotrophic microbes might have simply retreated to remaining favorable environmental niches such as hydrothermally active areas (Schulze-Makuch et al., 2007) and

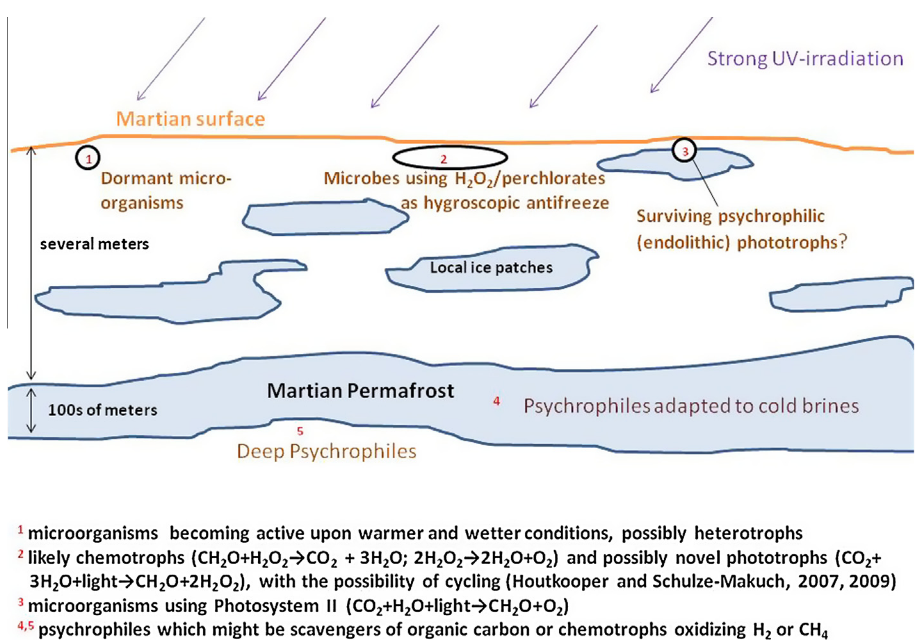

Fig. 2. Subsurface Habitats of present Mars with putative microbial colonization. (See above-mentioned references for further information.)

caves (Boston et al., 2001), while psychrophilic organisms deep beneath the ice sheets and permafrost would just have continued scavenging inorganic nutrients still present in the subsurface (Fig. 2). There they would be subject to stabilizing selection and would probably have not changed much from their ancestral stage during the Noachian time period. If the above scenario is correct, the remaining life on today's Mars would be microbial and mostly chemoautotrophic in nature, constrained to the deep subsurface and to a few environmental niches near the surface (such as hydrothermal areas and caves).

However, there are two intriguing possible ways that near-surface life on Mars could have mastered the challenge and adapted to the changing conditions. The first possibility is by inventing dormant stages of life to persist through the very rough dry and cold conditions on Mars (Schulze-Makuch et al., 2005), while waiting for the time periods of warmer and wetter conditions that are proposed to occur occasionally on Mars, because of volcanic activity (Dohm et al., 2001) or tilting of the axis (Touma and Wisdom, 1993). Martian microbes may now be simply in a cryptobiotic repose awaiting the end of the long "precessional winter" (Sagan, 1971). Many microbes on Earth can form spores, cysts, and other dormant stages and survive for very long periods of time when environmental conditions are not adequate for the proliferative stages to persist. In theory, spores can stay viable for an indefinite time period through which they do not expend any energy. Thus, microbes on Mars could have adapted to survive in this fashion even if the dry and cold spells would have lasted tens or hundreds of millions of years – punctuated only by time periods of a few thousand years during which liquid water was available on the martian surface. The drastically changing martian environmental conditions would certainly have exerted selective pressure to form dormant stages of life; but whether life had enough time to invent some of these very efficient and protective stages such as spores, is unclear. The second possibility for near-surface life (not mutually exclusive with the first) is to adjust to the changing environmental conditions by inventing new adaptations. One suggestion is the use of a hydrogen-peroxide–water mixture rather than water as an intracellular liquid, which could have the advantages of lowering the freezing point of water, providing a source of oxygen and hygroscopicity (Houtkooper and Schulze-Makuch, 2007). Hygroscopicity would be especially advantageous, because it would provide organisms the ability to attract water directly from the atmosphere, analogous to the use of hygroscopic salt crystals in the Atacama desert that are used by microbes in a similar way (Davila et al., 2008). Alternatively to hydrogen peroxide, perchlorates have similar properties and were recently discovered on Mars by the Phoenix lander (Hecht et al., 2009) and confirmed by current explorations by the Curiosity rover (Mahaffy et al., 2013). An adaptation to these highly oxidative compounds would also give putative near-surface microbes on Mars an adaptive edge to counter radiation damage, as the biochemical protection mechanisms against oxidants and radiation (which produces oxidants) are complementary.

4. Rapid environmental change on Venus and its effects on a possible biosphere

Venus is the terrestrial planet in our Solar System that has changed most dramatically with regard to climate and surface temperature during its natural history. It has been proposed that it started out as "Earth's twin" in the so-called Habitable Zone of our Solar System, a zone where liquid surface water is stable. Early Venus probably had an ocean or oceans on its planetary surface, based on (a) similar amounts of CO_2 and N_2 in the near-surface volatile reservoir of Earth and Venus (Matsui and Tajika, 1991), the evolution of H_2O–CO_2 atmospheres (Abe and Matsui, 1988), enhanced D/H ratios (Donahue et al., 1982), and the location of Venus, which should have still received a large amount of water through water–ice rich comets (Abe, 1988). Assuming the presence of liquid water on the surface of Venus during its early history and given its dynamic endogenic-driven activity, it seems reasonable that life could have originated on Venus. Another possibility is that organisms could have been delivered by meteorites from early Earth or Mars (as argued above for transport from Earth to Mars or vice versa), to a suitable habitat on early Venus (Schulze-Makuch and Irwin, 2006). Once life originated on Venus or was transported from Earth, it would have become established in the venusian ocean and spread into environmental niches, which would have increased its survival chances by utilizing directional selection to its advantage. Kasting (1989) shares the view that there was an early ocean on Venus, but also points out that it was likely a hot sea.

Thermophilic chemotrophs and heterotrophs, but possibly also phototrophs which use Photosystem I ($2H_2S + CO_2 + \text{light} \rightarrow CH_2O + H_2O + S_2$) could have become established in this kind of a sea. It is unclear how long this hot sea remained on the surface of Venus. As the Sun increased in brightness, Venus trapped ever more heat within its thickening greenhouse gas atmosphere (Grinspoon, 1997). Directional selection could have coped with increasing temperatures, but only to a certain extent. Microbes on Earth have been isolated from terrestrial hot springs that can tolerate temperatures of up to 113 °C (Stetter, 2002); and Kashefi and Lovley (2003) reported culturing organisms in the laboratory at a temperature of 121 °C. Hyperthermophilic microbes utilize fundamental changes in their macromolecular structure to compensate for the increased mobility and fluidity at high temperature (Charlier and Droogmans, 2005). However, the putative venusian biosphere would not only have had to deal with higher temperatures, but also with a loss of water and eventual desiccation. It is unclear how long Venus could have retained liquid water on its surface. Once all the water was gone from the surface, life on Venus would surely have become extinct. Or, would it?

There is one habitat that microbial life could have retreated to under the given conditions: the lower cloud layer. Even today the lower cloud layer of Venus can be considered borderline habitable. The possibility of life in the venusian atmosphere has been discussed by various authors (Sagan, 1961; Grinspoon, 1997; Cockell, 1999; Schulze-Makuch and Irwin, 2002; Schulze-Makuch et al., 2004; Irwin and Schulze-Makuch, 2011) and the habitability constraints of the lower cloud layer can be summarized as follows: (1) the clouds of Venus are much larger, more continuous, and stable than the clouds on Earth; (2) the atmosphere is in chemical disequilibrium, with H_2 and O_2, and H_2S and SO_2 coexisting; (3) the lower cloud layer contains non-spherical particles comparable in size to microbes on Earth; (4) conditions in the clouds at 50 km in altitude are relatively benign, with temperatures of 300–350 K, pressure of 10^5 Pa, and a pH of about 0; (5) the super-rotation of the atmosphere enhances the potential for photosynthetic reactions; (6) COS is present in the atmosphere, which on Earth is a strong indicator of biological activity; (7) CO is less abundant than expected under venusian atmospheric conditions, and could be oxidized as a reactant in plausible metabolic pathways; (8) the biologically critical elements of carbon, phosphorus, and nitrogen are present; and (9) while water is scarce on Venus, water vapor concentrations reach several hundred ppm in the lower cloud layer (Schulze-Makuch and Irwin, 2006).

It is important to point out that at this time we do not know of any microorganism on Earth that naturally grows under these combined conditions in the aerosol state permanently in clouds (Cockell and Westall, 2004). However, directional selection could have driven venusian microorganisms to move up into the lower cloud layer. A thicker atmosphere would have made this transition easier as transport between the surface and the lower atmosphere would occur more frequently. Also, since particle residence times in the venusian atmosphere are much longer than in Earth's atmosphere, it would have been easier to remain suspended in the atmosphere. Yet, there are major obstacles for life to prevail under such conditions, especially (a) lack of water, (b) low pH, and (c) large amounts of UV irradiation. However, these obstacles can be overcome via directional selection:

In regard to (a), lack of water, microbial organisms could have developed a mechanism with which they assimilate water vapor from hydrated sulfur compounds or from the atmosphere, similar to the assimilation of carbon from CO_2 by microbes in the atmosphere of Earth.

In regard to (b), low pH, some organisms on Earth can live at an even lower pH (Schleper et al., 1996). A low pH is a serious challenge due to the instability of the nucleotides adenosine and cytidine, and most Earth organisms solve this challenge by pumping protons to maintain an intracellular pH well above the pK_a (negative logarithm of the equilibrium coefficient of the neutral and charged forms of a compound) of the protonated nucleobases. However, a more effective adaptation of microbial life on Venus could be to replace cytidine with 5-nitrocytidine, which has a considerably lower pK_a than cytidine (Benner et al., 2004; Schulze-Makuch and Irwin, 2006).

In regard to (c), large amounts of UV irradiation, cycloocta sulfur (S_8) could be used by microbes for protection (Schulze-Makuch et al., 2004). S_8 has the capability of shielding organic macromolecules such as DNA and protein at wavelengths most susceptible to UV damage. S_8 has been shown to be a common component in the cloud layers of Venus, is thermodynamically stable and does not react with sulfuric acid (Schulze-Makuch et al., 2004). In fact, elemental sulfur is used by some microbes on Earth for a similar purpose. For example, purple sulfur bacteria, green sulfur bacteria, and some cyanobacterial species deposit elemental sulfur granules outside the cell (e.g., Pierson et al., 1993; Tortora et al., 2001); and thermophilic microbes in Yellowstone Park, Wyoming, reveal microbial filaments fully covered by a mineral phase that contains significant amounts of elemental sulfur.

Thus, adaptation of microbial life to live in the lower cloud layer of the venusian atmosphere seems to be possible, in principle. Since the venusian surface and subsurface is outside the habitability constraints (at least for life as we know it, and likely for all carbon-based life), the only location where we possibly could find life at Venus is the lower cloud deck. Schulze-Makuch and Irwin (2002) and Schulze-Makuch et al. (2004) went further and suggested the

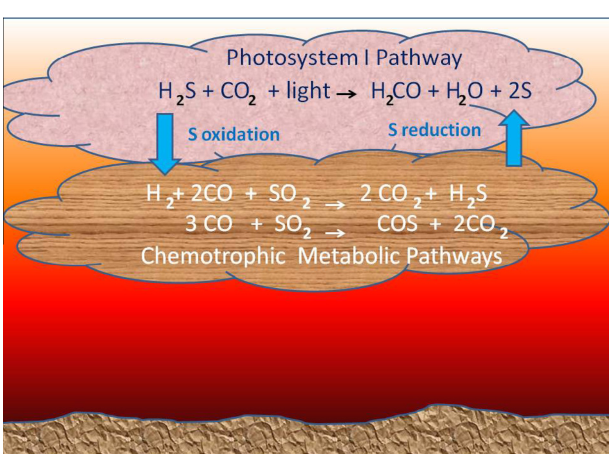

Fig. 3. Putative metabolic ecosystem in the venusian lower cloud layer.

possibility of a basic ecosystem in the lower cloud layer. Phototropic organisms could use the Photosystem I pathway to produce water and reduced carbon, while chemoautotrophic organisms would close the feedback cycle and produce reduced sulfur, needed by the phototrophs (Fig. 3).

What are the chances of such a basic ecosystem in the venusian clouds or that microbial life remains there? This depends much on the timing and force of the environmental changes. Particularly important are (a) how fast the venusian greenhouse effect set in, (b) the extent and force of the volcanic eruptions once plate tectonics ceased (assuming it ever got fully established), and (c) the force and timing of the cataclysm (meteorite impact?) that thrust Venus into a retrograde rotation. Perhaps these (or other changes we do not know about) occurred so rapidly and forcefully, that life had no chance to adapt and was extinguished. However, if changes occurred more gradually, life could have adapted via directional selection to a lifestyle in the venusian clouds.

5. Conclusions

Rapid and drastic environmental change has occurred frequently on our planet, posing a critical challenge to life. However, directional selection has overcome those challenges and driven life on Earth to ever increasing diversity and complexity. Even more drastic changes have occurred on our neighboring planets, Mars and Venus – one becoming a cold and dry planet except for enigmatic episodes associated with flooding and precipitation, and the other becoming a hyperthermic greenhouse with moderate temperatures in its lower cloud layers, respectively. However, life could have survived by adapting to the new planetary conditions. On Mars, life could have persisted most likely in the deep subsurface as psychrophiles, or in restricted environmental niches, perhaps making use of dormant stages to survive challenging environmental periods and employing innovative adaptations (e.g., use of H_2O_2 or perchlorates as antifreeze compounds). On Venus, life could possibly have survived by adapting to perpetual floatation in the lower cloud layer, using Photosystem I and chemoautotrophic sulfur metabolism, and employing cycloocta sulfur for UV protection.

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