Sulfur: Fountainhead of Life in the Universe?

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Sulfur is ubiquitous in the Universe and essentia! to all life forms that we know, it supports the chemoautotrophic way of life and *the photosynthetic. It may inhabit niches we cannot imagine, and the life zone about a star may therefore be wider than now estimated.*

In July 1976, the first of two unmanned spacecraft, the Viking Landers, set down on the surface of Mars. Thus began the most ambitious search for extraterrestrial life to date, on the most Earth-like body in our Solar System. Disappointingly, the chemical tests for metabolic activity in Martian soil proved negative or ambiguous (Klein, 1978). There were no signs of lifelike forms in either lander pictures or the thousands of pictures taken by the dual orbiters. No warm, wet spots (oases) or organic compounds in the soil were found. Much was and is being learned of the geology and climatology of Mars, however, and one surprising finding has been the high sulfate content (—10—15%) of Martian soil (Clark et al., 1976), which has led one investigator to suggest the possibility of an indigenous biology, perhaps now extinct, whose energy metabolism is nonphotosynthetic in nature, but rather based on cycling of sulfur compounds through various redox states by enzymic catalysis of inorganic sulfur with atmospheric photolysis products (Clark, 1979).

Just over six months after the Viking adventure began, two other spacecraft began exploring another hostile (to man), yet unique environment. One craft, named the Angus, took 70,000 reconnaissance photographs of this never-before-explored zone. A second craft, the Alvin, was a manned submersible. The mission was the geological exploration of ocean-bottom thermal springs on the 2.5-km-deep center of the Galápagos rift zone. Hydrothermal vents were indeed found, and although these are of considerable geochemical and geophysical interest, the most important discovery was the existence of previously unknown species of animals whose communal life is dependent on the primary productivity of sulfur-oxidizing bacteria (Corliss et al., 1979; Corliss and Ballard, 1977).

The parallels between these two explorations are striking, though coincidental. Three common threads are special environments, unique life forms, and the element sulfur. It is the purpose of this brief report to reemphasize the importance of sulfur and sulfur-containing compounds in biology as we know it, in planetary evolution, and in the Universe at large. Although it seems most likely that liquid water and organic compounds are essential ingredients for the vast majority of (if not all) biotic systems in the Universe, it will be my theme that sulfur compounds may be of equivalent rank and may well permit the proliferation of life in certain environments not otherwise considered hospitable.

COSMOCHEMISTRY OF SULFUR

The most common isotope of sulfur, ^{32}S, has a nuclear proton-neutron complement equivalent to eight alpha particles or two ^{16}O nuclei. Nucleosynthesis during explosive oxygen burning in the supernova phase of stellar evolution produces sulfur at high yield (Truran, 1973). Indeed, if the relative abundances of the elements in the Sun (Cameron, 1973) are a reasonable guide to element profiles in other main-sequence stars, then iron is the only element above sulfur in the periodic table that is more abundant than sulfur in the Universe.

Even the so-called chemically peculiar (CP) stars contain the “normal” complement of sulfur (Preston, 1974). At the time of the tabulation by Herbst (1978), over 1/6 of all molecular species identified in interstellar space were sulfur-bearing (COS, CH_2S, H_2S, CS, etc.). The omnipresence of sulfur in the Universe is summarized in table 1.

In our own Solar System, sulfur compounds are not only surprisingly common, but often play key roles in planetary processes. Besides the high level of sulfur in the Sun and widespread and diverse occurrences on Earth, the Venusian atmosphere is laden with sulfuric acid aerosol droplets — in spite of original expectations (Lewis, 1 972) that sulfur would not accrete as condensed compounds at or within the orbits of Venus and Mercury. The Martian regolith is surprisingly rich in sulfur, as is almost certainly its core, jupiter and the rings of Saturn contain sulfur, as does at least one comet

TABLE 1.-SULFUR IN THE UNIVERSE

Solar System	
Sun	S/Si ^0.5
Venus	Atmosphere (H_2S0_4, $S0_2$, COS, S^c ,CS_2?)
Earth	Core, mantle, evaporites, ocean, biosphere, ores
Mars	Regolith, core ($S0_4^{-2}$, FeS)
Io	Surface (S°, H_2S,$S0_2$,S_20)
Jupiter	
Saturn	
Comets	
(Asteroids), meteorites	
Interstellar dust clouds	COS, CH_2S, H_2S, CS, SO, $S0_2$, SiS, NS
Main-sequence stars	
CP stars, T-tauri stars	
Supernovae and supernova remnants	
“Hot gas” in galaxy clusters	
Cosmic rays	

(A. Delsemme, private communication, 1979), probably most asteroids, and virtually all meteorites. The latter can contain up to *6%* by weight of sulfur (Moore, 1971). The surface of Io is extremely sulfur-rich and may include several allotropes of native sulfur, and possibly frozen $S0_2$ (Hapke, 1979).

ROLE IN PLANETARY EVOLUTION

The core of Earth is believed to be predominantly iron, with minor alloyed nickel and up to 15% sulfur (Murthy and Hall, 1972). Sulfur is suspected of playing a key role during formation of the core since the Fe-S eutectic melts at a temperature several hundred degrees lower than pure Fe or Fe-Ni. Even though as much as 99% of Earth’s total sulfur inventory may be sequestered in the core, the residual crustal average abundance of about 500 ppm is of extraordinary importance. Volcanic and fumarolic emissions are conspicuously rich in sulfurous gases, notably H_2S and $S0_2$, with much lower levels of S°, COS, and $S0_3$ (table 2). Many ore deposits consist of massive sulfides of several different elements; many evaporite beds are gypsiferous ($CaS0_4$). In sea water, sulfate ion is second only to chlorine as the most common dissolved anion. Total evaporation of the oceans would leave a layer of sulfates over 3 m thick. Earth’s stratosphere is laced with sulfate aerosol particles. Both inorganic and organic forms of sulfur have

TABLE 2.-COMPOSITION OF REACTIVE VOLCANIC GASES (PERCENT)*

	Showa-Shinzan Volcano		Kilauea Volcano
	194°C	750°C	1200°C
H_2	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	[illegible]
[illegible]	[illegible]	[illegible]	.04
SO_2	[illegible]	[illegible]	49.6
[illegible]	[illegible]	[illegible]	1.4
[illegible] + HF)	[illegible]	[illegible]	.03

*H_20- and N_2-free values. Data summarized in Carmichael etal. (1974).

apparently been crucial to the evolution of life on Earth (see below). The 0_2-$C0_2$ balance of our atmosphere is intimately connected with the buffering action by the reduced and oxidized sulfur reservoirs (Garrels et al., 1976).

Planetary evolution need not invariably involve sulfur, even though the examples in table 1 appear to implicate its involvement as a rule. An interesting exception is the Moon, whose surface is low in sulfur as well as most other volatile elements. The Moon is not only sterile today, but is almost completely devoid of the resources required to sustain life as we know it and can conceive it.

SULFUR COMPOUNDS

The versatility of sulfur lies in its ability to take up numerous valence states, including -2, 0, +2, +4, and +6, and to form chain compounds and compounds in which sulfur atoms appear in more than one valence. Table 3 is a brief list of many of the known types of inorganic sulfur compounds. Most occur to one degree or another in nature, although some, such as dithionite (an extremely strong reducing agent) and peroxydisulfate (a powerful oxidant), are much too reactive to persist. The properties of the sulfur atom which render it of great importance in organic chemistry and biochemistry were first summarized by Wald (1962).

TABLE 3.-SULFUR COMPOUNDS

H_2S,CS_2,COS
FeS (pyrrhotite, troilite)
$Fe_3S_20_2$ (sulfomagnetite)
-SH (sulfhydry!)
FeS_2 (pyrite)

S° , S_8

SO
$Na_2S_20_3$ (thiosulfate, “hypo”)
$Na_2S_40_6$ (tetrathionate)
$Na_2S_20_4$ (dithionite)
$Na_2S_30_6$ (trithionate)

SO_2
Na_2S0_3 (sulfite)
$Na_2S_20_5$ (pyrosulfite)
$Na_2S_20_6$ (dithionate)

SO_3
Na_2S0_4 (sulfate)
$Na_2S_20_7$ (pyrosulfate)
$Na_2S_20_8$ (peroxydisulfate)

ROLE IN BIOLOGY

In the chemistry of life, sulfur plays major roles in energy transduction, enzyme action, and as a necessary constituent in certain biochemicals. The latter include important vitamins (biotin, thiamine), cofactors (CoA, CoM, glutathione), and hormones. Table 4 summarizes the biological utilization of sulfur compounds. Prebiotic chemical evolution may also have involved sulfur (Raulin and Toupance, 1977).

TABLE 4.-BIOLOGICAL UTILIZATION OF SULFUR

1. Energy source (sulfate reduction, sulfide oxidation)
2. Photosynthesis (non-0_2-evolving)
3. Amino acids (met, cys)
4. Protein conformation (disulfide bridges)
5. Energy storage (APS, PAPS)
6. Enzyme Prosthetic group, (Fe-S proteins)
7. Unique biochemicals (CoA, CoM, glutathione, biotin, thiamine, thiocyanate, penicillin, vasopressin, insulin)

BIOENERGETICS

Sulfur is continuously cycled through its valence states by the biogeochemical cycle in nature. Figure 1 shows some of the organisms that participate in the biological component of these reactions. All valence states of sulfur are susceptible to biological attack.

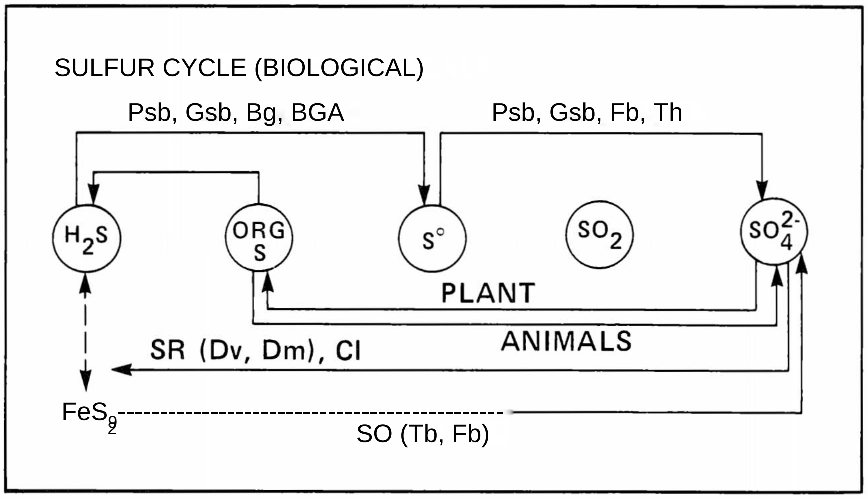

Figure 1. *Sulfur cycle in nature, as mediated by biological activity. Psb, purple sulfur bacteria; Bg, Beggiatoa; Fb, Ferrobacillus; Th, Thiobaciiius; SR, sulfate reducers; SO, sulfate oxidizers; Dv, Desuifovibrio; Dm, Desu/fotomaculum; Cl, Clostridium.*

Autotrophic energy metabolism, that is, the growth of organisms whose sources of chemical energy do not include organic compounds, involves sulfur compounds in a surprising variety of cases. As shown in table 5, chemosynthetic organisms exist for both oxidation and reduction of sulfur compounds: sulfur bacteria, sulfate reducers, and sulfur oxidizers. The sulfate reducers are not strict chemoautotrophs, however, in that not all of their internal organics can be synthesized from inorganic carbon ($C0_2$). A requirement for small levels of either acetate or lactate as a partial carbon source has led to the classification of these organisms as mixotrophs. These organisms are broadly distributed despite their lack of satisfactory defenses against atmospheric 0_2 (they are obligatory anaerobes).

Photosynthesis in the sulfur bacteria proceeds not by splitting H_20, as in green plants and algae, but by splitting H_2S to obtain H atoms. This scheme of photosynthesis is simpler biochemically (involving a single stage, rather than the two-stage process for reduction of water), and it was only the

TABLE 5.-ENERGY METABOLISM INVOLVING SULFUR COMPOUNDS*

Chemoautotrophy (sulfur oxidizers)	
$H_2S + 20_2$ -+H_2S0_4	Thiobacillus
Mixotrophy (sulfate reducers)	
$Na_2S0_4 + 4H_2$ -> $Na_2S + 4H_20$	Desulfovibrio
Photoautotrophy (purple and green sulfur bacteria)	
$H_2S + 2C0_2 + 2H_20$ -*• $2(CH_20) + H_2S0_4$	Chromatium
$2H_2S + C0_2$ -*■ $(CH_20) + 2S + H_20$	Chlorobium

*In sulfur oxidation, H_2S may be replaced by native sulfur, thiosulfate, or tetrathionate. For *T. denitrificans,* 0_2 may be replaced by nitrate. In sulfate reduction, SO|~ is replaceable by sulfite as well as the H_2S alternates listed above. Molecular hydrogen can be substituted by organic hydrogen donors.

abundance of H_20 compared to H_2S that provided the evolutionary pressure for the development of 0_2-evolving photosynthesis.

Indeed, it is widely recognized that photoautotrophy arose with the sulfur bacteria, possibly antedating the blue-green algae by as much as a billion years. The reconstructed evolutionary sequence for microorganisms, as proposed by Schwartz and Dayhoff (1 978) and Hall (1 979), indicates the primitive nature of sulfur bacteria and the somewhat uncertain origin of the sulfate reducers. Enzyme-sequence studies of Desulfovibrio species lead to conflicting interpretations. Rubredoxin sequences place this organism close to one of the primitive heterotrophs, Clostridium, but other molecules (ferrodoxin and flavodoxin) indicate a later development. As shown below, there is a plausible basis for the production of sulfites and sulfates even in the primordial anoxic atmosphere. The presence of these substrates and residual reducing power (H_2 and organics) provides the desired environment for the sulfate reducers at very early times.

ENZYME CATALYSIS

The reactivity of the -SH group of cysteine has long been recognized as important to the catalytic function of many enzymes. Additionally, the -S-S- linkage to form cystine is a strong stabilizing force in establishing the tertiary structure of proteins, which so often exerts a remarkable influence on functional potency.

Sulfur plays yet another role in catalysis — perhaps its most fundamental contribution to living systems. That role is a “collaboration” with the iron atom to form Fe-S moieties that serve as prosthetic groups in the class of enzymes known as the “iron-sulfur proteins” (Lovenberg, 1973).

Iron-sulfur proteins are found in all living systems, including the highly unique methanogenic bacteria. These remarkable proteins are particularly suited to the catalysis of oxidation-reduction reactions, spanning the range +400 to -600 mV (scaled to the hydrogen electrode at -420 mV). Biological reactions catalyzed by Fe-S enzymes include uptake and evolution of molecular hydrogen (all known hydrogenases are Fe-S proteins), nitrogen fixation (nitrogenase), pyruvate metabolism, electron transport in bacterial photosynthesis (ferrodoxin and HiPIP), $C0_2$ fixation, $NADP^+$ reduction (chloroplasts), NADH oxidation (mitochondria), hydroxylation reactions, sulfite reduction, nitrite and nitrate reduction, xanthine oxidation, and probably many others (Hall et al., 1977). Indeed, they are the most numerous and most diversified components of the entire mitochondrial electron-transport system.

A particularly interesting subgroup of Fe-S proteins is the low-molecular-weight proteins, the ferrodoxins (Fd). They, too, apparently occur in all known organisms. The smallest and simplest Fd is found in Clostridium butyricum. It contains only 55 amino acid residues, 91% of which involve only 9 different amino acids (Hall et al., 1975). Ferrodoxins are thus interpreted as among the most primitive proteins available today for analysis. They represent the earliest electron-transport system and may even have formed the basis for the later evolution of heme-group binding in c-type cytochromes. Ferrodoxins are acid-labile and degrade under 0_2. The Fe-S prosthetic group is particularly sensitive, and one purpose of the apoprotein is to protect this group from destruction by environmental reactants.

GALÁPAGOS DISCOVERY

The finding of small, isolated, and more or less complete ecosystems at the mouths of active hydrothermal submarine vents is important since such systems do not depend on photosynthesis for their primary productivity. The low $5^{13}C$ value of about -33 per mil for tissue from filter feeders collected at these vents is consistent with a chemosynthetic food source (Rau and Hedges, 1979). The presence of H_2S and $C0_2$ in the vented water, the abundance of sulfur-oxidizing bacteria, and the scarcity of heterotrophs all point to an energy source other than sunlight (Corliss and Ballard, 1977). However, these extraordinary communities mainly involve oxidizers and hence require dissolved 0_2 from seawater. This 0_2 is *not* generated by the vent, but mainly by photosynthesis in the surface layers.

It is interesting to speculate, however, that submarine volcanic emissions *could* provide all the necessary ingredients for a self-sustained ecosystem. As indicated in table 2, volcanic emissions include a number of reactive gases, including both reduced compounds (H_2, H_2S, CH_4, CO) and oxidized species ($C0_2$, $S0_2$, $S0_3$). Proportions vary considerably, even at the same volcanic area, but almost invariably include most of these species. Note that 0_2 is so small as to be negligible. Quenching of high-temperature equilibrium compositions by rapid cooling provides a supply of gases that can further react with one another at seawater temperatures. For example, H_2 can react with either CO or $C0_2$ (to produce CH_4 and H_20). These reactions are the sole energy source for growth by the methanogens.

Another energy source is the linked reactions shown in table 6. Here the sulfurous acid produced by volcanic $S0_2$ and H_20 ultimately yields sulfates by weathering reactions with igneous minerals such as olivine. These sulfates, which can include Mg, Ca, Na, or Fe salts, are then reduced by sulfate-reducing organisms with the aid of volcanic H_2. Once core formation had approached completion on the primitive Earth, and volcanic gases had settled into a redox balance that permitted formation of $S0_2$ and $C0_2$, the substrates for sulfate reduction and methane production became available.

TABLE 6.-A SULFUR-BASED ENERGY SOURCE FOR SUPPORT OF A BIOLOGICAL SYSTEM*

1. Volcanic:	$so_2 + h_2o - h_2so_3$
2. Weathering:	$2H2SO3 + Fe_2Si0_4\ 2FeS0_3 + 2H2O + Si0_2$
3. Disproportionation:	$4FeS0_3 \text{->} 3FeS0_4 + FeS$
4. Biological:	$FeS0_4 + 4H_2 \text{->} FeS + 4H_20$
Net:	$2S0_2 + 6hi2 + Fe_2Si0_4$ -*■ $2FeS + Si0_2 + 6H_20$

*Step 4, the reduction of sulfate, is an energy-yielding reaction (as are the preceding ones) commonly employed by *Desuifovibrio* and other sulfate reducers as a metabolic energy source. Step 3, the disproportionation of sulfite to sulfate and sulfide, is not necessarily a required part of the reaction sequence since the sulfate reducers can also utilize sulfite as a substrate.

OTHER WORLDS

Hart (1979) presented calculations of climatological evolution for Earth-like planets orbiting other stars. His surprising conclusion is that the continuously habitable zone (CHZ), defined as the orbital distance at which such planets enjoy moderate temperatures (i.e., neither runaway glaciation nor runaway greenhouse heating occur), is narrow about G stars (±3% of the optimum distance for our own Sun) but probably nonexistent about K and M stars. It is wider about F stars, but such stars evolve rapidly into red giants. The likelihood of the terrestrial environment is thus lower than heretofore expected. Certainly none of the 13 other large bodies (Moon-sized or larger) in the Solar System possess atmospheres or climates similar to Earth's. As the space exploration program has clearly shown, the only safe generalization is that planetary bodies cannot be generalized. They are *all* different in very fundamental respects, including bulk and atmospheric composition, thermal history, and climate.

The assumption that only Earth-like environments qualify as CHZs is not a secure one. We have been biased by the idea that photosynthesis is of such fundamental significance that advanced biotic systems can persist only in environments coupled to illumination. However, the existence of niches only very indirectly coupled with the solar photon flux, such as the Galápagos vent communities, other benthic and marine mud ecosystems, and salt-marsh environments, emphasizes that the most fundamental requirement is energy flow to provide recycling of, or a fresh supply of, chemical potential energy.

The basic requirements of life may simply be (1) a flux of energy, (2) a stable temperature regime compatible with the biochemistry of the organisms, (3) a liquid milieu, and, of course, (4) an initial supply of building-block elements, such as C, H, N, O, P, S, and transition metals. These elements need not, in principle, be replenished since they can be recycled. Under these conditions, certain non-Earth-like environments may not only be conducive to life, but may be available in far greater abundance in the Universe.

Consider H_20-rich bodies. In our Solar System, this includes not only Earth, but quite possibly Mars and Triton, and certainly Ganymede, Callisto, and Europa. Liquid water does not exist at the surface of any of these bodies, except Earth, but we should not discount the existence of "buried" liquid water reservoirs. All planet-sized bodies were once hot. Possible sources of this heat include gravitational potential energy, impact heating during accretion, short-lived radioisotopes (^{26}Al), and long-lived radioisotopes (K, U, Th). For most bodies, the loss of this heat by radiation to space is not yet complete, even after 4 billion years. In some cases, especially bodies very rich in H_20, much of this heat may have been lost by transfer to the surface by liquid and solid-state convection (Reynolds and Cassen, 1979), though three-body tidal interactions of the type apparently responsible for continuous heating of Io are also possible (Peale et al., 1979). Regardless of the manner in which they are formed, there is good reason to consider buried liquid water reservoirs as possible life-supporting environments. The probable availability of dissolved salts, including sulfur compounds, and the existence of energy flow, in the form of a planetary heat flux, satisfy the life-support requirements listed above. Coupling to stellar or planetary luminosity may be completely unnecessary. For example, the scheme in table 6, whereby high-temperature reactions deep within the planet release upward-moving gases, which then may undergo additional, biologically catalyzed reactions, is possible. Recycling of the FeS produced by convective consumption into deeper layers could rejuvenate SO_2 and hence continuously support the process until the heat source is finally exhausted. This is not necessarily any more limiting than photosynthesis, since our own Sun will become a red giant in about another 6 billion years, in the process destroying not only terrestrial life, but all traces of its prior existence.

CONCLUSIONS

Sulfur is ubiquitous and probably plays several important roles in any exobiological organization. Although it can participate in photosynthesis, it also permits the chemoautotrophic way of life. Habitable zones include not only the surface ocean environment, but also the much more probable subsurface oceanic regions. Earth-like environments as abodes for life may be the exception rather than the rule. Occupation of the more abundant buried zones is possible, and these should ultimately become an object of exploration. Whether such environments can support life long enough and at a sufficient level of activity to permit the evolution of highly encephalized forms (intelligent life) is conjectural. But the exotic and diversified nature of the mere handful of planetary bodies in our own Solar System substantiates the point of view that life in other parts of the Universe may inhabit environments we are not even capable of conceptualizing today.

Future accomplishments in many research fields will bear on the speculations presented here. These fields include chemical evolution, biological evolution, sulfur chemistry, enzyme mechanisms, chemoautotrophic ecological niches, planet and satellite formation, and the thermal history of planet-sized bodies. Of special interest are the large planetary satellites (e.g., the Galilean satellites of Jupiter) — their thermal history and the longevity of subsurface liquid water (Reynolds and Cassen, 1979). Another key question is the likelihood of totally chemoautotrophic systems surviving at scales and for durations adequate to permit higher evolution. Further elucidation of the evolutionary rise of microorganisms on Earth will shed light on this problem, as will additional study of special environments, such as submarine volcanic vents and their colonization by microorganisms.

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