

Venus, an Astrobiology Target

Sanjay S. Limaye,¹ Rakesh Mogul,² Kevin H. Baines,³ Mark A. Bullock,⁴ Charles Cockell,⁵ James A. Cutts,³ Diana M. Gentry,⁶ David H. Grinspoon,⁷ James W. Head,⁸ Kandis-Lea Jessup,⁹ Vladimir Kompanichenko,¹⁰ Yeon Joo Lee,¹¹ Richard Mathies,¹² Tetyana Milojevic,¹³ Rosalyn A. Pertzborn,¹ Lynn Rothschild,⁶ Satoshi Sasaki,¹⁴ Dirk Schulze-Makuch,^{15–17} David J. Smith,⁶ and Michael J. Way¹⁸

Abstract

We present a case for the exploration of Venus as an astrobiology target—(1) investigations focused on the likelihood that liquid water existed on the surface in the past, leading to the potential for the origin and evolution of life, (2) investigations into the potential for habitable zones within Venus' present-day clouds and Venus-like exo atmospheres, (3) theoretical investigations into how active aerobiology may impact the radiative energy balance of Venus' clouds and Venus-like atmospheres, and (4) application of these investigative approaches toward better understanding the atmospheric dynamics and habitability of exoplanets. The proximity of Venus to Earth, guidance for exoplanet habitability investigations, and access to the potential cloud habitable layer and surface for prolonged *in situ* extended measurements together make the planet a very attractive target for near term astrobiological exploration. Key Words: Venus—Extreme environments—Extremophiles—Life in extreme environments—Search for life (biosignatures). *Astrobiology* 21, 1163–1185.

1. Introduction

THE SCIENTIFIC ARGUMENTS for life beyond Earth have changed in recent decades with new discoveries and pathfinding measurements. As early as the late 19th century, Proctor (1870) argued for life on many of the planets in the Solar System and remarked, “the forms of life on Venus or in Mars must be in their special characteristics from those existing on our own Earth.” Decades later, Vallentyne (1963) presented arguments on empirical grounds for the ubiquity of

life despite extreme environmental conditions. At that time, Venus was considered quite similar to Earth and the possibility of life and vegetation was generally accepted well into the 20th century, based solely on the general similarity to Earth, known and assumed (Arrhenius, 1918). The Mariner and Venera missions in the 1960s shattered this view (Sagan, 1967) when the planet's surface was discovered to be very hot and dry under a thick atmosphere of mostly carbon dioxide.

The discovery that the Venus atmosphere was far more enriched in deuterium relative to hydrogen, compared with

¹Space Science and Engineering Center, University of Wisconsin–Madison, Madison, Wisconsin, USA.

²Chemistry and Biochemistry Department, Cal Poly Pomona, Pomona, California, USA.

³Jet Propulsion Laboratory, California Institute of Technology, Pasadena, California, USA.

⁴Science and Technology Corp., Hampton, Virginia, USA.

⁵School of Physics and Astronomy, University of Edinburgh, Edinburgh, Scotland.

⁶NASA Ames Research Center, Moffett Field, California, USA.

⁷Planetary Science Institute, Washington, District of Columbia, USA.

⁸Department of Earth, Environmental and Planetary Sciences, Brown University, Providence, Rhode Island, USA.

⁹Southwest Research Institute, Boulder, Colorado, USA.

¹⁰Institute for Complex Analysis of Regional Problems, Russian Academy of Sciences, Birobidzhan, Russia.

¹¹Zentrum für Astronomie und Astrophysik, Technical University of Berlin, Berlin, Germany.

¹²Chemistry Department and Space Sciences Lab, University of California, Berkeley, Berkeley, California, USA.

¹³Department of Biophysical Chemistry, University of Vienna, Vienna, Austria.

¹⁴School of Health Sciences, Tokyo University of Technology, Hachioji, Japan.

¹⁵Center for Astronomy and Astrophysics (ZAA), Technische Universität Berlin, Berlin, Germany.

¹⁶German Research Centre for Geosciences (GFZ), Potsdam, Germany.

¹⁷Leibniz-Institute of Freshwater Ecology and Inland Fisheries (IGB), Stechlin, Germany.

¹⁸NASA Goddard Institute for Space Studies, New York, New York, USA.

Earth's atmosphere (Donahue *et al.*, 1982), suggested that Venus once had at least 0.3% (volume) of a terrestrial ocean of water on its surface and possibly much more. Since then, a great deal has been learned, discussed, and debated about possible origins of life (on Earth). Recently the possible existence of liquid water for 2–3 billion years (Ga) on the surface of Venus has been suggested (Way *et al.*, 2016; Way and Del Genio, 2020). This raises the possibility that at some time in the past, Earth and Venus were similarly poised for the origin of life as we presently know it (National Academies of Sciences and Engineering Medicine, 2019).

The interest in the possibility of life on Venus is driven not just by curiosity about life originating in another Earth-like environment, but because of the possibility that life may be playing a critical role in the planet's present, and possibly its past, atmospheric state. The brilliance of Venus in the night sky (as viewed from Earth) is due to its highly reflective cloud cover, about 28 km thick at the equator. Its spectral albedo is about 90% at wavelengths >500 nm, but it drops gradually to about 40% around 370 nm before rising slightly at shorter wavelengths. This albedo drop is due to the presence of several absorbers in the atmosphere and the cloud cover. A very large fraction of the energy absorbed by Venus is at ultraviolet (UV) wavelengths with sulfur dioxide above the clouds contributing to the absorption below 330 nm; however, the identities of the other absorbers remain unknown (Pérez-Hoyos *et al.*, 2018; Titov *et al.*, 2018).

The inability to identify the absorbers that are responsible for determining the radiative energy balance of Venus over the last century is a major impediment to understanding how the planet “works,” a major component of NASA's efforts in planetary exploration. Limaye *et al.* (2018a) presented a hypothesis suggesting that cloud-based microbial life could be contributors to the spectral signatures of Venus' clouds, building upon previous suggestions of the possibility of life in the clouds of Venus (Morowitz and Sagan, 1967; Grinspoon, 1997; Cockell, 1999; Schulze-Makuch and Irwin, 2002).

This possibility relies on the origin of life on Venus occurring when it presumably had liquid water oceans. Alternatively, Venus may have been seeded with life originating elsewhere through panspermia—in-falling materials from impacts on other terrestrial worlds (Melosh and Tonks, 1993)—which then survived and evolved in the oceans. It is likely that the early Venus environment was similar to Earth's at the time life began here and did not present extreme conditions that were hostile to life. McKay *et al.* (2018) discussed the origin of life on Enceladus as being similar to the ideas debated for Earth—local origin and seeding externally (panspermia) from space. We suggest that the same case can be made for Venus.

Diverse life forms may have evolved and led to survival of a few species as the planet's environment evolved from Earth-like clement to hothouse, with some species drifting upward to a sustained niche in the clouds. There are still many unknowns about the clouds and the lower atmosphere (Cockell *et al.*, 2021) including the presence of trace species and state of chemical equilibrium. Venus' cloud cover presumably changed from water/ice clouds to the current acidic composition over some unknown period in the past. Terrestrial microorganisms can respond rapidly to changing environmental conditions (Bell and Gonzalez, 2011), and adaptation from hospitable surface oceans to acidic clouds over time as Venus warmed is possible (Kohli *et al.*, 2020) via membrane and

protein adaptations (Dhakar and Pandey, 2016; Bringer *et al.*, 2018). McKay (2020) presented an approach to search for life on other worlds and suggested a list of prerequisites for the undertaking of a life detection mission. We do not yet know if Venus met some of these prerequisites in the past or if it meets them now until we learn more about the habitability conditions and availability of essential nutrients Carbon, Hydrogen, Nitrogen, Oxygen, Phosphorous and Sulfur (CHNOPS) and other trace species (Cockell *et al.*, 2021). Thus, Venus is not yet a target for life detection, but we present a case for a strategy for astrobiology investigation of Venus to ascertain the habitability of its cloud layer.

This article is based on the ideas about habitability presented and discussed at the first workshop on the habitability of the Venus cloud layer organized by the Roscosmos/IKI-NASA Venera-D Joint Science Definition Team in Moscow in October 2019.

We outline a strategy for the exploration of Venus as an astrobiology target—(1) investigations focused on the likelihood that liquid water existed on the surface in the past leading to the potential for the origin and evolution of life, (2) investigations into the potential for habitable zones within Venus' clouds and Venus-like atmospheres, (3) theoretical investigations into how active aerobiology may impact the radiative energy balance of Venus' clouds and Venus-like atmospheres, and (4) application of these investigative themes toward better understanding the atmospheric dynamics; chemistry and habitability of exoplanets. We discuss these items below, along with proposed Venus Astrobiology Goals and Objectives, followed by suggestions for measurements for future missions, as those developed by the Venus Exploration Analysis Group (VEXAG), which is organized by NASA as a community-based mechanism to plan for the future exploration of Venus independent of the National Academies' Planetary Sciences and Astrobiology Decadal Survey currently underway for 2023–2032.

We address the laboratory work that can begin now and provide a brief discussion of potential mission approaches and instruments and the required technical development. The scientific investigation of Venus has also been discussed in two recent reports—Search for Life across Space and Time (National Academies of Sciences and Engineering Medicine, 2017) and “An Astrobiology Strategy for the Search for Life in the Universe” (National Academies of Sciences and Engineering Medicine, 2019).

We begin with the possibility of appreciable surface water oceans in the past (Section 2), and scenarios for life taking hold on Venus (Section 3), followed by a discussion of habitability and polyextremophiles (Section 4). We then review the status of absorbers in the Venus atmosphere and clouds, which affect the radiative balance of the planet (Section 4). We make the case for Venus as an astrobiology target in Section 5. Finally, Section 6 discusses the experiments, measurements, and modeling for the conceptual astrobiology investigation program for Venus and presents a plausible mission architecture that could be implemented incrementally.

2. Presence of Past Liquid Water on Venus and the Beginnings of Life

Based on our understanding of Earth's biosphere, an essential element for the emergence and survival of life is the

availability of liquid surface and/or groundwater over long geological time periods. For nearly two decades, astrobiology has been partially guided by the principle “follow the water” (Carr and Garvin, 2001; Hubbard *et al.*, 2002) in search of life on other worlds. The presence or history of liquid water, on the surface or beneath it, and in contact with rock on some Solar System bodies, such as Mars, Europa, and Enceladus, and possibly even Ceres, make these worlds attractive targets for astrobiological investigation. Unlike these bodies, direct indications of past water on the Venus surface are few and far between (Khawja *et al.*, 2020) due to the obscuration of the surface by the global cover and the absence of ultra-high-resolution radar and near-infrared (NIR) compositional mapping. However, the presence of past liquid water is strongly suggested by Donahue *et al.* (1982). Ivanov and Head (2011, 2013, 2015) presented an overview of the stratigraphy and geological history of the currently exposed geological features and the volcanic and tectonic processes (Byrne *et al.*, 2020) that occurred during the recent history of Venus. Multispectral NIR spectral imaging of emission from the hot surface of Venus is possible through a few narrow spectral windows, but multiple scattering within the clouds and the deep atmosphere limits the spatial resolution to about 50–100 km from orbit (Moroz, 2002; Knicely and Herrick, 2020). Regional (>50 km spatial scale) discrimination of some diagnostic mineral types based on their infrared surface emissivity is possible (Hashimoto and Sugita, 2003; Dyar *et al.*, 2020; Filiberto *et al.*, 2020).

Surface mineralogy is one possible means to indicate the past presence of liquid water on Venus (Ivanov and Head, 1996; Hashimoto *et al.*, 2008; Mueller *et al.*, 2017). The regional rock composition of tessera terrains on Venus (tessera are the most ancient and heavily deformed terrains preserved in the visible geological record) (Ivanov and Head, 1996, 2011) may attest to the presence of past water (Gilmore *et al.*, 2017, 2019). Granitic tesserae would be a clue to the presence of past water on the basis of the role of water in the fractional crystallization development of such high-silica rocks as outlined in recent articles such as those by Weller and Kiefer (2020) and others.

The first hint that Venus may have had a watery past came in 1978 when its atmospheric composition was measured by the Neutral Mass Spectrometer on the Pioneer Venus Large Probe. The D/H ratio in Venus’ atmosphere below the clouds was found to be 120 times Earth’s (Donahue *et al.*, 1982; de Bergh *et al.*, 1991; Donahue and Hodges, 1992), suggesting that Venus lost a great deal of water to space (Donahue, 1999). We know little about the history of water on Venus or about the possibility of hydrothermal activity on the surface. Head and Wilson (1986) discussed volcanism on Venus during the post-surface ocean period. Kane *et al.* (2019) provided a succinct account of water loss on Venus. The Venus Express mission (Svedhem *et al.*, 2009) found the D/H ratio above the clouds to be 240 ± 25 times higher than Earth’s (Fedorova *et al.*, 2008) possibly implying even greater loss of water to space over time than estimated from the Pioneer Venus subcloud value of the D/H ratio. Fractionation, outgassing, and impacts determine the water loss, although some impacts could also have brought water to Venus (Grinspoon, 1993; Donahue, 1999). Estimates of escaping H^+ (Delva *et al.*, 2008) and O^+ ions can provide some information about how much water has been

lost from the interaction with the solar wind (Persson *et al.*, 2020) over time. Venus Express measurements show water escaping from Venus via H^+ and O^+ ions (Persson *et al.*, 2018). Masunaga *et al.* (2019) reported that a majority of the O^+ escape flux is through the induced magnetotail and the rest through ion pickup processes, but to date, both mechanisms have been insufficiently measured (Futaana *et al.*, 2017). Extrapolating back in time using the current rate of escape of O^+ ions, Persson *et al.* (2020) concluded that the escape rates from its present thick CO_2 dominated atmosphere and their relation to the upstream solar wind conditions indicate that the escape of ions to space cannot fully explain the evolution of the water in the venusian atmosphere.

Recently, Way and Del Genio (2020) explored the climate history of Venus through numerical models and concluded that solar insolation is not the limiting factor for the longevity of an ocean if a carbonate–silicate rock cycle was at work. They concluded that Venus could have had surface water for >3 Ga. Previous studies suggest that Venus would have had liquid water for periods sufficiently long-lasting for the origin and evolution of life. Grinspoon and Bullock (2003) modeled the early atmosphere of Venus with a one-dimensional radiative transfer model and cloud formation. They found that the last drops of a warm ocean may not have evaporated until 1 or 2 Ga and that this event may be linked to the geological upheaval that erased most of its surface by volcanic resurfacing (Stofan *et al.*, 2005) and impact craters (Phillips *et al.*, 1992; Phillips and Izenberg, 1995). Extending the work of Pollack (1971), Kasting (1988), and Grinspoon and Bullock (2003), Way *et al.* (2016) concluded that the clouds and atmospheric dynamics of slowly rotating worlds (such as Venus) would mitigate atmospheric temperatures and water loss, and an ocean could have lasted several billion years. Thus, there is a strong possibility that Venus had oceans over long geological periods—as has been hypothesized for Mars (Carr and Head, 2010). There is already convincing evidence for the presence of life on Earth over 3 Ga (Westall *et al.*, 2006, 2019; Baumgartner *et al.*, 2019) and possibly as early as 4.2 Ga (Bell *et al.*, 2015; Dodd *et al.*, 2017). Over such a long period, diverse life forms could have arisen on Venus, but once the planet began to lose its water and warm up, only those microorganisms that could adapt and find a niche in the clouds would have survived. The Venus clouds would appear to be easier to adapt to because of the more conducive environmental conditions over their vertical extent, ambient moisture, nutrients, and sunlight.

It is not known whether Venus lost its water gradually over time through warming or through episodic impacts (*e.g.*, Ahrens, 1993; Kegerreis *et al.*, 2020). However, it is important to learn the history of water on Venus because it contextualizes the potential timeline of the origin of life, and the divergent evolution of the two most similar planets in our solar system. The Venus community comprising VEXAG has prioritized learning the history of water as a major scientific goal (https://www.lpi.usra.edu/vexag/reports/VEXAG_Venus_GOI_Current.pdf). Following many others who have discussed the possibility of life on Venus, we argue that the study of Venus will also have important impacts on our understanding of the origin of life, and thus, Venus must be considered an important extraterrestrial destination for exploration and the advancement of astrobiology studies.

3. Life on Venus: Origins and Panspermia

It is possible that conditions on early Venus were similar to those on primitive Earth when microbial life originated (Lunine, 2006). The presence of surface oceans is believed to provide one possible medium for the requisite development of simple organic compounds from inorganic precursors, facilitated by energetic inputs (Patel *et al.*, 2015). Marshall (2020) discussed the challenges to origins of life presented by water. That life began in the oceans was proposed independently nearly a century ago by Alexander Oparin and J.B.S. Haldane (Oparin, 1959; Fleischaker, 1990; Tirard, 2017). This idea has evolved into origins in shallow bodies of water, which may go through wet and dry spells to counter the idea that the basic molecules of life breakdown in the presence of water. The “inversion” model proposes the origin of life as the enhanced response of prebiotic microsystems to incessant ambient physiochemical fluctuations (Kompanichenko, 2017). Accordingly, a vast ocean of liquid water is not essential for the origins—life could have evolved on land in the presence of water.

It has been proposed that life evolved near Earth’s hydrothermal vents relatively soon after the formation of Earth’s oceans, potentially enhanced by the delivery of extraterrestrial materials (Chyba and Sagan, 1997; Pasek and Lauretta, 2008; Zahnle *et al.*, 2020). Others have proposed that life may have originated in hydrothermal vents, springs, or pools (Deamer and Georgiou, 2015; Damer, 2016; Damer and Deamer, 2019). Resurfacing by volcanic lava flows and tectonism in recent history have been invoked to explain the small number of recognizable impact craters on the surface of Venus (Schaber *et al.*, 1992). Recently, Weller and Kiefer (2020) suggested that Venus may have had a mobile-lid convection and liquid water on the surface for more than 3 Ga from a consideration of the planet’s thermal evolution. Thus, it would appear Venus would have been even more suitable for the origin of life in the presence of past water conditions (Way *et al.*, 2016; Weller and Kiefer, 2020), assuming that there were several active volcanoes globally or seafloor-like spreading in the past when liquid water was on the surface.

Volcanoes are found ubiquitously on Venus (Ivanov and Head, 2013), and there is evidence that volcanism was vigorous in the past (Bullock *et al.*, 1993). Indications of recent volcanism on Venus (Shalygin *et al.*, 2015) are growing and becoming more convincing as well. From modeling of the shapes of the coronae, Gülcher *et al.* (2020) suggested that Venus is still tectonically active and hence also volcanically active, and evidence has been presented for current (*e.g.*, Shalygin *et al.*, 2015) and recent volcanism (*e.g.*, Bondarenko *et al.*, 2010). It is likely that volcanoes were active in its ancient past (Ivanov and Head, 2013) when it had surface water. With liquid water oceans on the active surface over a few billion years (Way *et al.*, 2016; Way and Del Genio, 2020), hydrothermal vents would have been inevitable. By analogy to Earth, therefore, it appears possible that life could have originated on Venus, at about the same time it originated on Earth as has been speculated previously (Morowitz and Sagan, 1967; Hapke and Nelson, 1975; Shimizu, 1977; Boyer, 1986; Grinspoon, 1997; Cockell, 1999; Schulze-Makuch *et al.*, 2004; Grinspoon and Bullock, 2007; Limaye *et al.*, 2018a).

3.1. Panspermia

It is possible that biogenic material could have been brought to Venus in its early history through impacts (Melosh and Tonks, 1993). There is considerable influx of cosmic dust into Venus every day (Plane *et al.*, 2018), which probably deposited on the land surface before the formation of global cloud cover and possibly into the former hypothesized ocean. From there, it could have been injected into the Venus atmosphere. Frankland *et al.* (2017) estimated the mass influx into the Venus atmosphere from the Jupiter family of comets to be about 32 tons/day. Turco *et al.* (1983) suggested that meteoric dust could also act as condensation nuclei for thin ice haze layers in the Venus atmosphere. Gao *et al.* (2014) considered the condensation of photochemically formed sulfuric acid onto meteoric dust for explaining the observed size distribution of the aerosol particles in the mesosphere from 70 to 90 km. Aerosols formed on meteoric dust cloud condensation nuclei would be suspended indefinitely for particles with diameters $<10\ \mu\text{m}$ (Garvin, 1981), and larger particles would settle over months. Garvin (1990) estimated the thickness of the global sediment of fine dust accumulated in the last 1 Gy from impacts seen in Magellan and Arecibo radar data to be 1–2 mm, comparable to Earth (larger by a factor of 2–4). Together, these analyses provide for an alternate origin of a Venus biosphere, apart from independent surface genesis.

3.2. Chemical disequilibrium

The presence of life is generally associated with chemical disequilibrium (Baum, 2018). Among the primary measures required to assess the habitability of Venus’ clouds is the extent of chemical disequilibria across the aerosol and gas phases, and between the surface and atmosphere. Barge *et al.* (2017) argued that life only emerges when and where particular planetary scale conditions of chemical disequilibria are produced through the interactions of the atmosphere and hydrosphere. Calculations by Krissansen-Totton *et al.* (2016) suggest that the free energy available in Venus’ atmosphere is ~ 2000 -fold lower than that of Mars. On a global scale, therefore, these calculations effectively lower any potential for a habitable zone within Venus’ clouds. However, the available *in situ* measurements from Venus’ atmosphere (Johnson and de Oliveira, 2019) show potential signs of chemical disequilibria.

The recent reports of the potential existence of phosphine near 60 km altitude in the Venus atmosphere from Earth-based observations (Greaves *et al.*, 2020a, 2020b) have led to a reexamination of the Pioneer Venus Large Probe Neutral Mass Spectrometer (PV LNMS) data, which has revealed many examples of disequilibria involving nitrogen species (Mogul *et al.*, 2021). The detection of phosphine has been questioned along with its vertical abundance profile (Cockell *et al.*, 2020; Encrenaz *et al.*, 2020; Villanueva *et al.*, 2020; Lincowski *et al.*, 2021) and defended (Greaves *et al.*, 2020c), and more measurements are needed while other past data do indicate the presence of P-bearing compounds (Andreichikov *et al.*, 1987; Krasnopolsky, 1989, 2006; Mogul *et al.*, 2021). Similarly, NH_3 was detected by the Venera-8 Gas

Chromatograph (Surkov *et al.*, 1973), which is not expected to exist in the Venus atmosphere under chemical equilibrium (Goettel and Lewis, 1974) but can exist under chemical disequilibrium (Florenskii *et al.*, 1978; von Zahn and Moroz, 1985). Together, these suggest a potential for local disequilibria (Zolotov, 1991a, 1991b), rather than global, within the clouds—which could serve as a driver for niche habitats. Additionally, measured abundances of H₂ (Johnson and de Oliveira, 2019) at altitudes of <140 km of 10 ppm are ~4700-fold higher than the equilibrium abundances predicted in the model of Krissansen-Totton *et al.* (2016). In contrast, this model yields abundances for the major atmospheric constituents of Venus (CO₂, N₂, SO₂, and CO; at ~50 km) that are essentially equivalent to measured values, which lends support to H₂ abundances serving as an indicator of disequilibrium. Furthermore, in Venus' atmosphere, measured abundances of O₂ are <50 ppm at altitudes of <60 km, whereas abundances of methane (CH₄) are 980 ppm at altitudes of >50 km (Johnson and de Oliveira, 2019). These diverse chemical signatures reflect the lack of adequate measurements of trace species in the Venus atmosphere. We posit that assessments of disequilibria via remote spectroscopy will not adequately capture the chemical dynamics within the lower and middle cloud layers. Measurements of vertical abundance profiles (cloud tops to surface) of minor and trace species are needed to better understand the range of chemistries at work and sustained within the non-ideal conditions of Venus' cloud layer. In the foreseeable future, the DAVINCI+ mission (Garvin *et al.*, 2020b), currently under consideration for NASA's Discovery Program competition, and the proposed Venera-D mission are expected to carry analytical instruments (*e.g.*, mass spectrometers, tunable laser spectrometers), which can provide such measurements.

4. Microorganisms as Possible Absorbers of Solar Radiation in the Clouds

Because of its high Bond albedo (0.76), Venus absorbs less energy from the Sun than Earth does at present, despite being in a closer orbit. Figure 1 shows the spectrum of Venus between 280 and 4000 nm (Kuiper, 1969). This albedo spectrum indicates increasing absorption below about 500 nm. Weaker absorption occurs over a wider range of wavelengths beyond 500 nm.

The spectral albedo is 0.9 or higher at $\lambda > 550$ nm but is much lower at the UV end, between 0.2 and 0.5 (Fig. 1). The bulk of the energy that is not reflected to space by the planet is absorbed in the thick cloud layer between ~72 and 48 km (0.2–10 atm), with only about 4% reaching the surface at noon (Moroz *et al.*, 1983). It has been suggested that between 57 and 70 km nearly all the radiation at UV wavelengths is absorbed (Crisp, 1986) as little UV downward flux was observed by the nephelometers on the Pioneer Small Probes (Ragent and Blamont, 1979; Ragent *et al.*, 1985). However, later measurements by the Venera 14 filter photometer detected radiation between 320 and 390 nm down to 48 km (Economov *et al.*, 1983, 1984). These measurements also indicated the presence of different UV absorbers above and below 57 km. Subsequently, night-side presence of the UV absorbers in the clouds down to 47 km altitude was confirmed by the Izmeritel' Spektrov Atmosfery Venery (ISAV) instruments on the VeGa 1 and VeGa 2 landers, which entered the atmosphere at local midnight (Bertaux *et al.*, 1996). These instruments measured the atmospheric absorption by continuously drawing it into an internal 1-m long tube, illuminating it between 220 and 400 nm with a Xenon lamp and measuring the absorption spectrum.

Despite many attempts, the search for the identity of the UV absorbers has not been successful (Esposito *et al.*, 1983;

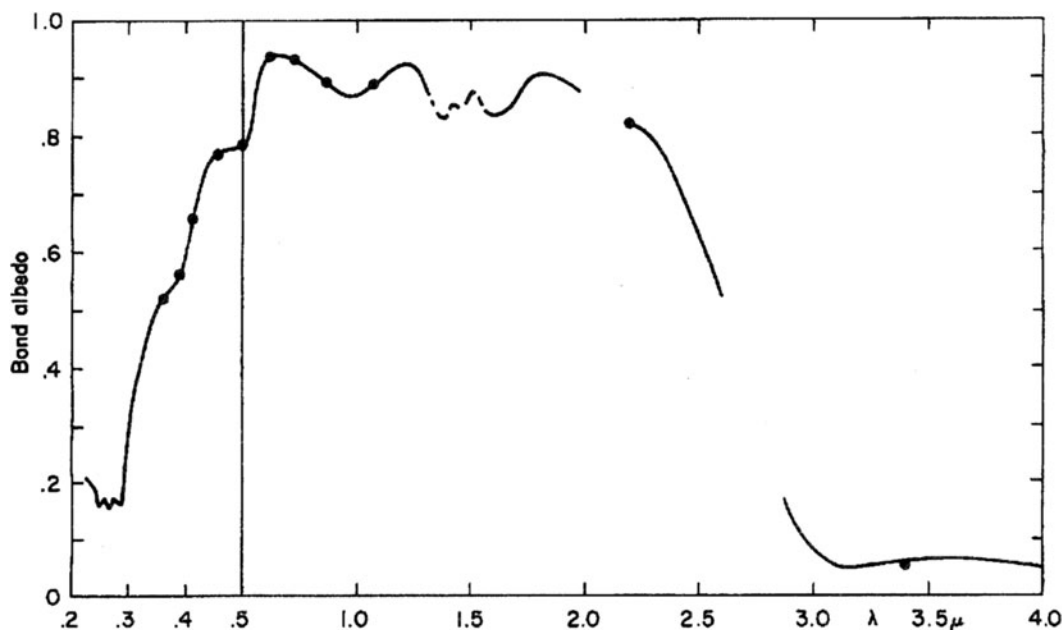


FIG. 1. Full disk albedo of Venus showing the strong absorption below 500 nm (Kuiper, 1969). The disk resolved spectra of the planet show noticeable differences over latitudes and phase angles.

Pérez-Hoyos *et al.*, 2018; Titov *et al.*, 2018). Only SO₂, COS, and CS₂ have been identified as (minor) absorbers in the Venus atmosphere from spectroscopy, and OSSO (Frandsen *et al.*, 2016, 2020; Krasnopolsky, 2018) has been proposed recently. Pérez-Hoyos *et al.* (2018) presented the most recent spectrum-based investigation of candidate absorbers and concluded that no single chemical absorber could fit the observations. In addition to matching the observed spectrum, it is important that the candidate species are plausible within our current understanding of Venus' active chemical and microphysical production and loss cycles. OSSO, the most recent candidate proposed (Frandsen *et al.*, 2016, 2020; Wu *et al.*, 2018), has been rejected as inconsistent with photochemical models (Krasnopolsky, 2018; Pérez-Hoyos *et al.*, 2018; Bierson and Zhang, 2020) on the basis of its vertical distribution. Multiple efforts to determine the likelihood of potential absorber candidates relative to photochemical modeling have been completed over the years (Young, 1973, 1975, 1977; Mills and Allen, 2007; Mills *et al.*, 2007; Krasnopolsky, 2012, 2013, 2016, 2017, 2018). The models are imperfect; while the reaction rates are mostly known, chemical equilibrium coefficients are not exhaustive, and equilibrium conditions are implicit. The S isotope abundances in the cloud layer have not been quantified, and the key roles of S species remain to be evaluated. Furthermore, none of these models have included biological transformations involving sulfur (*i.e.*, sulfur-based metabolism), which could potentially account for the observed spectral absorptions. Identification of candidate biosignatures for the Venus clouds cover is needed.

In this context, Limaye *et al.* (2018a) proposed that the biochemical constituents of hypothetical microorganisms in Venus' clouds could contribute to the absorption of the incident solar radiation. Straightforward comparisons show reasonable overlaps between Venus' spectra and the absorption of ferroproteins (*e.g.*, Fe [heme] and FeS groups between 250 and 500 nm), photosynthetic pigments (*e.g.*, chlorophylls between 250 and 700 nm), biochemicals found in green sulfur bacteria (*e.g.*, absorption of carotenoids and biopterin between 250 and 700 nm), and lipids (*e.g.*, absorption of C-H at $\sim 2.3 \mu\text{m}$).

Although Fig. 1 shows that only weak absorption occurs longward of 400 nm, it is important to know whether chemical species producing the underlying continuum absorption shortward of 300 nm also contribute weakly to absorption properties evident longward of 400 nm to explain the weaker contrasts seen at the longer wavelengths in day side images and in NIR wavelengths in the night side images. This absorption may also combine with the CO₂ and H₂O absorptions identified at visible and NIR wavelengths. The decrease in albedo beyond $\lambda > 2.5 \mu\text{m}$ is not fully understood (Krasnopolsky, 1983) and can only be resolved by identifying the composition and nature of the unknown continuum absorption source at the short wavelengths, and potential absorbers at long wavelengths. It is likely that there is more than one chemical or biochemical species, as has been postulated by multiple researchers over the decades (Travis, 1975; Pollack *et al.*, 1980; Pérez-Hoyos *et al.*, 2018). Spatial and spectral contrast patterns may be used as a key constraint on properties of absorber candidates, whether organic, inorganic, and/or biological, and the limiting conditions that control their evolution.

The temporal evolution of Venus' UV bright and dark cloud top patterns on short (Limaye *et al.*, 2018b) and long

timescales (Lee *et al.*, 2015, 2019) is linked to dynamics (see, *e.g.*, Toon *et al.*, 1982) and may also be related to microphysics and other chemical properties. The zone of large-scale horizontal divergence in the subsolar region is darker in UV images on average and areas of convergence are brighter (Limaye, 1988) from Pioneer Venus data. Analysis of similar data from Akatsuki is underway while Bertaux *et al.* (2016) report from Venus Express UV images that show the UV albedo is correlated with topography. It remains to be confirmed as the longitudinal sampling of UV images is not uniform from the Venus Express data (Lee *et al.*, 2019). Similar investigation on smaller scale with more frequent images (every 2–30 min) at 1–10 km pixel scale and mapping of trace species may reveal more insights into the evolution of the contrasts and thereby provide clues to their origins. Further study of the correlations between gas species distributions and other chemical cycles and atmospheric properties may ultimately help us define the identity of the absorber. Even so, current studies of the cloud optical properties indicate that the aerosol particle sizes within dark and bright regions are equivalent. In light of this result, the question of what specific property of the absorber creates and supports the dramatic level of spectral contrast (Lee *et al.*, 2017; Limaye *et al.*, 2018a, 2018b) observed within the clouds remains a persistent mystery.

Hapke and Nelson (1975) investigated the spectra of several proposed candidate absorbers and found that sulfur-containing models provided reasonable fits to the UV absorption. They also pointed out that many examples of anaerobic, terrestrial microorganisms are known in which the reduction or oxidation of various forms of sulfur are important sources of energy in their metabolisms. If these microorganisms do not find conditions in the clouds totally inimical, their effect on the energy balance of the planet may not be negligible. Their implicit assumption is that similar microorganisms may exist in the clouds of Venus.

Boyer and Guérin (1969) used spectral contrast patterns seen in Earth-based telescopic images of Venus to infer the superrotation of Venus' atmosphere. Such contrasts seen in spacecraft images are still used to track zonal motions (*e.g.*, Limaye and Suomi, 1981; Horinouchi *et al.*, 2018) to infer the global structure of the atmospheric circulation. Boyer (1986) suggested that, if phototrophic organisms contribute to the dark (solar absorbing) regions, then they would influence variations in the zonal wind speeds. The effect of the vertical distribution of the UV absorbers on the radiative balance of Venus was investigated by using parameterized optical properties of the unknown absorbers from the works of Haus *et al.* (2017) and Pérez-Hoyos *et al.* (2018). Optical measurements reveal that submicron particles are present throughout the layered structure of the clouds along with micron-sized (and larger) particles in the lower clouds (Knollenberg *et al.*, 1980; Ekonomov *et al.*, 1983; Knollenberg, 1984; Moshkin *et al.*, 1986). The residence times of any microorganisms in the clouds depend on their size. Submicron-sized particles can reside for an indefinite amount of time while the larger particles will fall out. Seager *et al.* (2020) proposed that the persistence of life can be sustained by a reservoir below the clouds of spores or spore-like bodies formed from desiccating larger organisms as they fall out of the cloud layer and some of them may get lofted to the clouds to sustain the life cycle.

Since the lower size limit for microorganism spores is comparable to the submicron-sized particles found throughout the cloud layer, it is possible that they themselves may also be spores. Puzzling, of course, is the observed trimodal distribution of the particles in the clouds and how biology may explain it. Thus, the vertical distribution of the absorbers may be an important constraint in the investigations of the vertical recycling of particles (abiotic or biotic) within the cloud layer (Limaye *et al.*, 2018a; Bullock and Grinspoon, 2019; Seager *et al.*, 2020).

4.1. Potential for a habitable zone for polyextremophiles in Venus' clouds

The surface conditions on Venus today are hostile not only to organic molecules but also to the preservation of most biosignatures, as they are currently understood. A plausible scenario for a Venus habitable zone is that microorganisms from the hospitable conditions of the past surface ocean were transported to the clouds and adapted to the local extreme conditions, as surface conditions became inhospitable (Limaye *et al.*, 2018a). Such microorganisms would be considered polyextremophiles (Seckbach and Rampelotto, 2015) by terrestrial standards and can be considered in the context of the limits of known life in Earth's extreme environments. Alternately, the existence of subsurface high-pressure water refugia has been discussed (Schulze-Makuch and Irwin, 2002) as have alternative biochemistries compatible with Venus surface conditions, such as those based on supercritical CO₂ as a polar solvent (Budisa and Schulze-Makuch, 2014). The prevailing interest, however, is on the possible transition from ocean-based life to an ecosystem based in the dense persistent clouds (Morowitz and Sagan, 1967; Grinspoon and Bullock, 2007; Limaye *et al.*, 2018a). If, following Morowitz and Sagan (1967), one assumes that the conditions of early Venus were similar to conditions when life on Earth originated, the likelihood of such a transition depends on factors including (A) the duration of the ocean era, (B) the overlap of the ocean era with the formation of a potentially habitable cloud layer, (C) the availability of sufficient energetic and biochemical inputs to the cloud layer after the loss of liquid water bodies on the surface, and (D) the subsequent short- or long-term adaptation processes toward survival in suspended aerosols in the warm acidic clouds.

Venus' current global, layered cloud cover consists mainly of three different-sized particles (Ragent *et al.*, 1985) with mean diameters ranging from $\sim 0.5 \mu\text{m}$ (Mode 1), approximately 2–3 μm (Mode 2 and 2'), to $>3 \mu\text{m}$ (Mode 3). The exact composition of the smallest particles, which are likely spherical, is uncertain but suggested to be sulfuric acid solutions containing various minerals. These are more prevalent at higher altitudes, with the 2–3 μm -sized particles found throughout the cloud layer, and the largest particles found near the bottom of the cloud layer (Titov *et al.*, 2018). The abundance of water in the aerosols peaks near the base of the clouds at 42 km and is about 0.52% mole fraction (Oyama *et al.*, 1980). The temperature range across the lower clouds is well within growth limits for terrestrial microbes (Domagal-Goldman *et al.*, 2016), from $\sim 100^\circ\text{C}$ at 47 km to approximately -20°C (-18°C to -22°C) at 62 km; similarly, pressure (Kato *et al.*, 1998; Nicholson *et al.*, 2010), UV and high-energy radiation flux (Cockell, 1999; Dartnell *et al.*,

2015), and photonic energy (Raven and Cockell, 2006) do not appear to be limiting, and hypothetical redox-based nutrient cycling and phototrophy have been proposed (Schulze-Makuch *et al.*, 2004; Limaye *et al.*, 2018a).

Potential habitability of the current Venus cloud layer was assessed by Cockell (1999) and considered to be favorable for terrestrial microbial-type life. High above the Venus surface with 93 bar pressure and 750 K temperature, the cloud layers between ~ 48 and 70 km present temperatures and pressures comparable to conditions found in terrestrial clouds (Table 1) where microorganisms have been detected or isolated (Amato *et al.*, 2007a; Christner *et al.*, 2008; Joly *et al.*, 2013). The effective pH of the aerosols can be interpreted differently given the extremes of $>80\%$ sulfuric acid solutions (Grinspoon and Bullock, 2007; Seager *et al.*, 2020). Even under the most generous values of -1.5 to 1, the pH range is near the limit where only a few lineages of archaea (Johnson and Hallberg, 2008) and eukaryotic acidophiles such as *Cyanidium* (Rothschild and Mancinelli, 2001) are known to survive under Venus-like CO₂-based conditions (Seckbach and Libby, 1970). Such acidophilic archaea are among the oldest organisms on Earth (Woese, 1998). Similarly, $>75\%$ sulfuric acid corresponds to a very low water activity (a_w) of <0.02 (Gentry and Dahlgren, 2019), substantially below that of even the most saturated brines (Bolhuis *et al.*, 2006) and at best on par with Earth's driest deserts (Kieft, 2003). Sulfuric acid abundances in Venus' aerosols are not based on direct measurements but rather from the index of refraction deduced from polarization data (Hansen and Hovenier, 1974; Rossi *et al.*, 2015), and optical glory feature data (Markiewicz *et al.*, 2014), along with computational simulations (Krasnopolsky, 2015) and compatible with vapor abundances determined from radio occultation profiles (Steffes and Eshleman, 1982). Yet, recent observations indicate higher index of refraction values, thereby suggesting the presence of other chemicals in the presumed sulfuric acid droplets (Markiewicz *et al.*, 2014, 2018). Priorities for future Venus studies, therefore, include direct *in situ* measurements (Limaye *et al.*, 2018a) in the cloud layer of the concentrations of sulfuric acid, water, and hydronium ion in the aerosols, with spectral comparisons to elucidate the potential for contributions from derivatives of sulfate including HSO₄⁻¹, organosulfates, and sulfate diesters.

The measured size and assumed spherical shape of Venus aerosols have been used to calculate an upper limit for the potential density of airborne cells based on the physical constraints of the aerosols, with values of approximately 10^8 – 10^{10} cells/m³ for 2 and 8 μm -sized particles, respectively (Modes 2' and 3) (Knollenberg and Hunten, 1980a; Limaye *et al.*, 2018a). Measurements of aerosol shape, size, and residence time remain key subjects for future investigations. As discussed further below, these studies are especially important in an astrobiological context due to the typically long generation times (weeks to months) for many terrestrial extremophiles under stressed conditions, particularly in low-water environments (Stevenson *et al.*, 2015). A summary of known habitability factors is provided in Table 1.

Earth's atmosphere, as an analogue environment, cannot yet be considered a permanent habitat for life, as reproduction/division have yet to be seen in the aerial environment, although microorganisms are known to be transported over large distances (Smith, 2013; Irwin and Schulze-Makuch,

TABLE 1. TERRESTRIAL HABITABILITY BOUNDS AND NOMINAL VENUS ATMOSPHERIC CONDITIONS

Challenge	Microbial reproduction limits	Microbial activity limits	Venus' conditions (~47–57 km)
Temperature (°C)	–12 to 121 ^{a,b}	Less than –40 to 121 ^b	0 to 100 ^c
Pressure (kPa)	5 to 100,000 ^{d,e}	~2.5 to 130,000 ^{b,d}	~120 to 80 ^c
Acidity/alkalinity (pH)	~0 to 12 ^f	–0.06 to 12 ^{b,f}	Approximately –1.5 to 0.5 ^g
UV flux (315–400 nm; W/m ²)	<30 to 50 ^h	<57 ⁱ	~50 to 53 ^j
Photosynthetic photon flux density: 400–700 nm [μmol/(m ² ·s)]	n/a	~0.01 to 8000 ^k	~2200 to 2500
Water activity (<i>a_w</i>)	0.6 to ~1 ^l	>0.585 to ~1 ^l	~0.02 ^m

An enduring biosphere requires that organisms be able to reproduce; the range of areas in which short-term or transitory biological activity can occur may be larger. Reproductive limits of terrestrial biology can be inferred empirically from the most extreme habitats where organisms are known to undergo a complete life cycle. See Rothschild and Mancinelli (2001) for classification and examples of extremophiles.

^aRummel *et al.* (2014).

^bDomagal-Goldman *et al.* (2016).

^cLimaye, *et al.* (2018a).

^dNicholson *et al.* (2010).

^eKato *et al.* (1998).

^fSchleper *et al.* (1996); Baker and Banfield (2003); Sun *et al.* (2019).

^gAssuming sulfuric acid mixed with water (Grinspoon and Bullock, 2007).

^hThis reproduction value represents a typical terrestrial flux (Liu *et al.*, 2007).

ⁱThis value represents the 37% survival after irradiation at 315–400 nm for *Deinococcus radiodurans* R1 when using unshielded samples (Pogoda de la Vega *et al.*, 2005). Data exist on longer term low-dose effects; most “highly radiation resistant” organisms have been studied in the context of short-term high-dose exposure regimens rather than continuous culture.

^jThis value represents the cumulative irradiance between 315 and 400 nm (using 20 nm intervals) across the middle and lower clouds of Venus at noon, at low latitudes.

^kRaven and Cockell (2006).

^lGrant *et al.* (2004); Bolhuis *et al.* (2006); Connon *et al.* (2007).

^mAssuming 75% w/w sulfuric acid (Deno and Taft, 1954).

a_w = Water activity.

2020). Nevertheless, various suggestions for sustained life in Venus' cloud layer have been proposed (Morowitz and Sagan, 1967; Hapke and Nelson, 1975; Shimizu, 1977; Grinspoon, 1997; Schulze-Makuch *et al.*, 2004; Limaye *et al.*, 2018a; Seager *et al.*, 2020). Unlike in Earth's atmosphere, in which warm tropospheric clouds are generally transient, and higher altitude aerosols with longer residence times are much colder and drier, Venus' lower/middle clouds are warm, whereas the aerosols may remain afloat for longer periods, in part due to global circulation, convection and gravity waves, and definitive measurements from long duration aerial platforms are needed to confirm this. Some of these suggestions have included models of coupled and/or noncoupled iron- and sulfur-centered metabolic pathways (Schulze-Makuch *et al.*, 2004; Limaye *et al.*, 2018a) powered by phototrophic reduction of CO₂ for long-term survival in Venus cloud aerosols, with observable CH₄ in Venus' clouds being a probable product of the global geochemical and/or metabolic cycles.

Fluxes of gases required for metabolic processes could occur through chemicals released in recent times by volcanoes such as sulfur dioxide, as suggested (Esposito *et al.*, 1988; Marcq *et al.*, 2020) to explain the decrease of SO₂ above cloud tops (on a decadal scale); active and recurrent volcanism certainly occurred in the past (Ivanov and Head, 2013; Shalygin *et al.*, 2015). Furthermore, thermomechanical modeling of the coronae on the Venus surface indicates that Venus is tectonically active today with active plumes (Gülcher *et al.*, 2020). Such injections of sulfur dioxide at altitudes of tens of km above the surface are known to occur on Earth (Pyle, 2012) and have been discussed in articles on explosive volcanism on Venus (Wilson and Head, 1983; Head and Wilson, 1986; Glaze, 1999; Airey *et al.*, 2015).

On Earth, microorganisms in clouds are known to be transported over long distances over time, with the aerial environment being generally hospitable, except at high altitudes where UV radiation presents a challenge (Smith *et al.*, 2011, 2013). Airborne metabolic activity has so far only been detected in warm, low-altitude cloud water samples (Amato *et al.*, 2019), but viable bacteria have also been detected as high as the aerosol layer (Smith *et al.*, 2018) within Earth's stratosphere (Junge *et al.*, 1961a, 1961b). The chemistry of this stratospheric aerosol layer is comparable to the sulfuric acid chemistry of Venus' clouds (Prinn and Fegley, 1987), with relative isolation from surface water and nutrient sources, relatively long residence times, and cool temperatures. The stratosphere, which is still relatively unexplored, could therefore serve as a worthwhile terrestrial analogue for researching the potential limits, properties, and survival strategies of cloud-based microorganisms (Gentry and Dahlgren, 2019).

Viable microbes recovered from stratospheric air samples are very sparse and largely limited to metabolically inactive forms that are able to survive extended desiccation and UV exposure. While cell densities in the stratosphere can reach ~10⁵ cells/m³ (Bryan *et al.*, 2019), values in the cloud-forming regions of the lower troposphere can reach ~10¹¹ cells/m³ (Amato *et al.*, 2007b). Interestingly, these tropospheric values are similar to maximum cell density estimates for Venus' lower clouds of 10⁸–10¹⁰ cells/m³, which were calculated by using measured densities of Mode 2 and 3 particles (1 and 4 μm radii, respectively), an average presumed cellular volume of 1 μm³, and a cell density of 1.041 g/cm³. On Earth, cloud water, under optimal conditions, can carry 10³–10⁵ cells/mL, and the total volume of the Mode 2 and 3 particles is

$\sim 2 \times 10^{12} \text{ m}^{-3}$ (back of the envelope calculation from Knollenberg and Hunten), so if the Venus aerosols were capable of sustaining the same level of biomass, the total Venus biomass would be $\sim 2 \times 10^{21}$ to 2×10^{23} cells. That is about one one-millionth of Earth's microbial biomass.

Comparatively, the conditions in Venus' clouds present an extreme state of desiccation and acidity (relative to terrestrial habitats), and the bioavailability of some nutrients is unknown. As inferred from particle sizes and densities, the cloud-based microorganisms hypothesized by Limaye *et al.* (2018a) are recycled between lower and upper extremes of the cloud layer through merging and dividing cloud droplets, which theoretically maintains access to water and nutrients through bulk mixing. However, the acidity within the aerosols is likely much greater than the reported pH range of -1.5 to 0.5 estimated for the clouds between 48 and 65 km (Grinspoon and Bullock, 2007; Seager *et al.*, 2020). Spores may act as active cloud condensation nuclei (Bullock, 2018) and may comprise the small particles in the upper clouds.

Table 1 shows the most biologically limiting individual physical conditions in Venus' cloud layers from available observations (Titov *et al.*, 2018). These numbers should not collectively be considered as a simple sum of individual limits, as temperature, pressure, solute concentration, water activity, freezing, and boiling points all interact; and Venus contains combinations of such multiple physical extremes not found in terrestrial environments. In addition, small-scale effects such as shadowing, turbulence, and phase transitions can create microenvironments dramatically different from the larger-scale locale. Furthermore, polyextremophiles on Earth show tradeoffs in adaptation that indicate further habitability limits: for example, growth at pH 0 has not been observed above 65°C , and growth above 100°C has only been observed at high pressures (Dartnell *et al.*, 2015; Merino *et al.*, 2019). Whether these are intrinsic biological limits, limits particular to known terrestrial biology, a consequence of the distribution of terrestrial extreme environments, or simply the current evolutionary boundaries is unknown (Capece *et al.*, 2013; Harrison *et al.*, 2013).

Bearing these caveats in mind, Table 1 shows that the temperature, pressure, UV, and available photonic energy estimated to be within Venus' major cloud layers are inside the bounds of terrestrial microbial habitability and available trace species and aerosol measurements (which are globally insufficient given spatial/temporal variability). We point the readers to the works of Horikoshi and Bull (2011) and Rothschild and Mancinelli (2001) for further classification and examples of terrestrial extremophiles. Similarly, other frequently considered constraints such as ionizing radiation, cosmic radiation, and periodic solar activity have been previously reviewed and determined to likely not present a survival challenge (Nordheim *et al.*, 2015; Plainaki *et al.*, 2016; Herbst *et al.*, 2020). However, water activity, residence time, and elemental abundances remain significant, and fundamental constraints to extant biology in Venus' clouds and additional definitive measurements are needed.

Water activity might be the most severe constraint to life as we know it in the Venus atmosphere (Gentry and Dahlgren, 2019; Cockell *et al.*, 2021). More representative measurements of D/H ratio from the cloud tops to the surface and water vapor

abundance would be very useful, and the proposed aerosol sampling mass spectrometer (Baines *et al.*, 2021) can provide direct estimates of the water activity. On Venus, most of the atmospheric liquid water is dissolved in sulfuric acid droplets in the clouds. Estimates of the water fraction of these droplets range up to 25%, due to the hygroscopic nature of H_2SO_4 , but this is still only equivalent to a water activity (a_w) of 0.02, on par with the driest terrestrial environments known, for example, the Atacama Desert (Crits-Christoph *et al.*, 2013; Schulze-Makuch *et al.*, 2018). Life in such environments must expend considerable energy to further concentrate water. For example, endoliths commonly use hygroscopic salts such as NaCl (Dávila and Schulze-Makuch, 2016; Jung *et al.*, 2019); and according to Maus *et al.* (2020), some archaea remain active by relying on water obtained through deliquescence (when the relative humidity levels allow this process to occur).

Airborne terrestrial microorganisms have been found to have surface properties that allow them to preferentially nucleate water and ice (Bauer *et al.*, 2003). The presence of enhanced water fractions in Venus aerosols, or the accumulation of additional hygroscopic compounds, could thus be a possible biosignature. If microbial life exists in Venus' clouds today, it likely migrated from the oceans and into the aerosols by the action of surface winds or even raindrops in the hospitable past (Blanchard, 1964; Wilson *et al.*, 2015; Joung *et al.*, 2017). On Earth, the planetary surface provided a rich habitat, whereas on Mars, life may have found refuge in the subsurface and on Venus, environmental adaptations may have driven life into the lower cloud layer as the last possible habitat on a warming planet (Schulze-Makuch *et al.*, 2013). Seeding of the cloud layers could result from present-day volcanic activity (Shalygin *et al.*, 2015; Gülcher *et al.*, 2020). Explosive eruptions (Glaze *et al.*, 2011) and outgassing could introduce both sulfur dioxide and water vapor into the lower atmosphere via topographically induced standing gravity waves (Young *et al.*, 1994; Bertaux *et al.*, 2016; Fukuhara *et al.*, 2017; Kouyama *et al.*, 2017; Kitahara *et al.*, 2019) and global circulation.

When considering a sporadic influx of water and nutrients, a potential Venus biosphere could have adapted to desiccation by undergoing extended periods of inactivity between brief injections of water, as is the typical survival strategy of terrestrial xerophiles. Spore formation as a strategy for survival in this type of environment is an additional possibility, as has been discovered recently on Earth (Morono *et al.*, 2020) and has been suggested for Venus (Seager *et al.*, 2020). As desiccated spores may be much smaller than active cell forms, the submicron haze particles found in the upper clouds and above, although below the typical size range of many microbes, could still possibly carry or consist of such spores.

Residence time in the cloud layer is therefore an important consideration. Earth's atmosphere is not generally considered a habitat in the traditional sense, although microbial life is regularly detected throughout the troposphere and stratosphere (Smith *et al.*, 2018), with some reports of active growth and metabolism in warm low-altitude clouds (Amato *et al.*, 2019). Cloud-borne microbes on Earth are transitory and always return to the surface via wet or dry deposition (Reche *et al.*, 2018). For microorganisms to inhabit the Venus cloud layer, a vertically dynamic life cycle would potentially be required (Limaye *et al.*, 2018a; Seager *et al.*, 2020). In this hypothetical

global cycle, reproduction or division by airborne microbes would likely need to occur faster than the continual loss of larger aerosol droplets over time since larger particles would ultimately fall below the base of the clouds, evaporate, potentially degrade, and re-aerosolize into the cloud layers. In other words, for an airborne biosphere to persist without a surface reservoir habitat, the mean residence time, including vertical cycling, must exceed the mean generation time, including periods of inactivity. Seager *et al.* (2020) proposed that the lower haze layer (below the clouds) may be a reservoir of such aerosolized spores, which may then act to seed the lower clouds. This is especially relevant in light of the typically long generation times (weeks to months) of many terrestrial extremophiles, particularly at low water activities (Stevenson *et al.*, 2015), and the relative favorability of a Venus ecosystem model with long periods of metabolic and reproductive inactivity. Diurnal abundance profiles of the trace species throughout the clouds and below, down to the surface, are very much needed in this context.

The last major unknown likely to constrain the habitability of Venus aerosols is the question of nutrient availability. “CHNOPS” are considered to comprise the basic palette of biological building blocks, which must be present not only in elemental abundance but also in a bioavailable form (*e.g.*, oxidation state and chemical form). This is particularly important for nitrogen, which only specialized microbes on Earth are capable of fixing, and phosphorus, which must generally be taken up in the form of phosphate (Dixon and Kahn, 2004; Hirota *et al.*, 2010; Milojevic *et al.*, 2020). In addition, thermoacidophiles on Earth commonly rely on Fe and other metals for metabolism. Venus aerosol composition is known to include H, O, and S in some abundance (H₂O, H₂SO₄), and the Venus atmosphere contains plentiful C and N (CO₂, N₂). Phosphorus and iron have been inferred by X-ray fluorescence in the sampled cloud particles by the VeGa 1 and 2 landers during their descent (Andreichikov *et al.*, 1987; Krasnopolsky, 2017). The presence of phosphorous compounds has also been recently discovered unambiguously in new interpretations of the PV LNMS data (Mogul *et al.*, 2021). Milojevic *et al.* (2020) proposed that extreme acidification of airborne phases in Venus’ atmosphere ensures a certain amount of soluble P that can be bioavailable for a potential ecosystem in the clouds. Obtaining CHNOPS profiles of abundances, including biologically important transition metals such as Fe and Cu, should be a focus for *in situ* sampling by future aerial platform and descent probe missions to Venus.

5. Venus, an Essential Astrobiology Target for Exploration

Did early Venus have the conditions necessary for life to arise? Looking ahead, this question should be addressed as it has been for other astrobiological targets such as Mars, Europa, and Enceladus, inclusive of exoplanets. Critical issues pertaining to all these targets include assessments of past and current water availability, detection of chemical indicators of past or current life, accurate modeling of abiotic geochemical and geological processes, and *in situ* confirmation of findings obtained from remote spectroscopy. Beyond these solar system targets, Venus also offers some value for exoplanet astrobiology investigations (Kane *et al.*, 2019). Accordingly, the immediate astrobiology objectives

(in alignment with VEXAG goals) and the National Academies’ Strategy for the search for life in the Universe (National Academies of Sciences and Engineering Medicine, 2019) for Venus can be identified as:

- (1) To better understand the geochemical and geological (volcanism) forces that influence radiative energy balance and cloud dynamics.
- (2) To better constrain the timelines framing (i) the formation of potential surface water bodies, (ii) subsequent rates of water loss to the atmosphere, and (iii) formation of stable cloud layers.
- (3) To obtain detailed physical, chemical, and biological characterizations of the cloud aerosols, inclusive of:
 - (a) abundances of biologically relevant elements (CHNOPS and transition metals), phosphorous oxides, and low-molecular-weight chemicals (*e.g.*, H₂O, H₂SO₄, NO_x, CH₄, PH₃, and H₂) within the cloud layers, inclusive of vertical profiles and fluxes,
 - (b) abundances within the cloud layers, inclusive of vertical profiles and fluxes,
 - (c) microscopic imaging and characterization of the aerosols, and
 - (d) biological investigations when and if feasible.
- (4) To validate findings from remote spectroscopy by using terrestrial geological, atmospheric, geochemical, biochemical, and photochemical–biological experimental models.
- (5) To validate the findings on trace species abundances from remote observations and modeling by spatially distributed *in situ* measurements at different local times, from at least 70 km down to the surface.

These goals are holistically consistent with those developed by VEXAG. Table 2 presents a notional traceability matrix for astrobiology goals and investigations relating to those described in the Goals, Objectives, and Investigations (GOI; https://www.lpi.usra.edu/vexag/reports/VEXAG_Venus_GOI_Current.pdf) document (updated most recently in 2019).

The current VEXAG GOI document (2019) articulates habitability as its first goal—“Understand Venus’ early evolution and potential habitability to constrain the evolution of Venus-sized (exo) planets.” As per the VEXAG document, the first objective (I.A), as part of this initial goal, is “Did Venus have temperate surface conditions and liquid water at early times?” The associated investigations aimed at meeting this goal are relevant to Astrobiology Objectives 1 and 2 outlined above, which pertain to the past and present habitability of Venus:

- VEXAG Investigation I.A.HO. Hydrous Origins:
 - For Venus astrobiology, surface rock composition (NIR mapping), and geomorphology (radar mapping) of tessera to reveal geological processes that formed them, and elucidate the presence and perhaps extent of any past water ocean.
- VEXAG Investigation I.A.AL. Atmospheric Losses:
 - For Venus astrobiology, it is important to determine how long liquid water was present on the surface and how and when the water was lost. Some clues can be obtained from the atmospheric loss estimates by sampling of ions from different orbits near and far from Venus.

TABLE 2. VENUS ASTROBIOLOGY GOALS, OBJECTIVES, AND INVESTIGATIONS

<i>Venus astrobiology goal</i>	<i>Venus astrobiology objective (VAO)</i>	<i>Venus astrobiology investigation</i>	<i>Measurements/ modeling/theory</i>	<i>VEXAG investigations</i>	<i>VEXAG objective</i>	<i>VEXAG goal</i>
Did life begin on Venus in the surface ocean in the past?	I. Was Venus habitable in the past?	VAO.I.A. How long did liquid water ocean last?	Characterization of exposed ancient terrains by radar and mineralogy	I.A.HO, III.A.GH, III.A.GA, I.A.RE	I.A. Did Venus have temperate surface conditions and liquid water at early times? III.A. What geologic processes have shaped the surface of Venus?	I. Understand Venus' early evolution and potential habitability to constrain the evolution of Venus-size (exo)planets. III. Understand the geologic history preserved on the surface of Venus and the present-day couplings between the surface and atmosphere.
		VAO.I.B. When did it become inhospitable on the surface by losing its liquid water ocean?	Climate Modeling			
Is the Venus cloud layer habitable today?	II. What are the chemical and physical conditions with respect to life in the present-day Venus atmosphere?	VAO.II.A. How have the theoretical requirements for habitability changed over time?	Isotopic abundance profiles of noble gases and other biologically significant elements, climate models		III.B. How do the atmosphere and surface of Venus interact?	II. Understand atmospheric dynamics and composition on Venus. III. Understand the geologic history preserved on the surface of Venus and the present-day couplings between the surface and atmosphere.
		VAO.II.B. What are the global abundances of the essential bioavailable nutrients (CHNOPS)	Accurate estimates of the atmospheric composition from <i>in situ</i> measurements below 70 km at representative latitudes and local solar times	III.A.GC		
		VAO.II.C. What other elements are bioavailable in the Venus atmosphere (trace species)?		II.B. OG, II.B. AE, II.B. UA, II.B. IN		
		VAO.II.D. What are the physical, spectral, and chemical properties of the cloud particles?	<i>In situ</i> measurements of the cloud particles at different local solar times and representative latitudes			
		VAO.II.E. What chemical disequilibria exist in the Venus atmosphere?	Vertical profiles of trace species in the atmosphere (0–70 km)	III.B. CI, III.B. LW, III.B. GW		
Is there life in clouds of Venus today?	III. Are there signs of biogenic activity?	If there are microorganisms in the cloud layer, are they absorbing solar radiation?	Spectral and optical properties of the microorganisms	II.B. RB	II.B. What processes determine the baseline and variations in Venus atmospheric composition and local radiative balance?	
		What would be the theoretical biomass if the clouds could support life?	Modeling/theory			

AE = Aerosols; GA = Geologic Activity; GC = Geochemistry; GH = Geologic History; HO = Hydrous Origins; OG = Outgassing; RE = Recycling.

The second VEXAG Goal includes Objective II.B., “What processes determine the baseline and variations in Venus atmospheric composition and global and local radiative balance?” This question and the associated investigations are aligned with Venus Astrobiology Objectives. This is an exciting area of investigation with the potential for cloud-based microorganisms to contribute to the planetary radiation budget. Suggested and related VEXAG investigations include:

- VEXAG Investigation II.B.RB. Radiative Balance:
 - These investigations will help measure the downwelling solar spectrum, upwelling visual, NIR and thermal infrared spectrum, and net flux at different altitudes from a floating or flying platform at multiple latitudes from equator to polar.
- VEXAG Investigation II.B.IN. Interactions:
 - These investigations will help characterize the nature of the physical, chemical, and possible biological interactions among the constituents of the Venus atmosphere.
- VEXAG Investigation II.B.AE. Aerosols:
 - These investigations will help physical and chemical properties and microscopic imaging of small and larger aerosols (approximately 1–20 μm radii).
- VEXAG Investigation II.B.UA. Unknown Absorber:
 - These investigations will help physical and chemical characterization of small and larger aerosols (approximately 1–20 μm radii).
- VEXAG Investigation II.B.OG. Outgassing:
 - These investigations will provide estimates of influx of gases into the atmosphere from the surface.

The third VEXAG Science Goal, “Understand the geologic history preserved on the surface of Venus and the present-day couplings between the surface and atmosphere,” includes the following investigations, which are related to Astrobiology Objectives 2 and 3:

- VEXAG Investigation III.A.GH. Geologic History:
 - These investigations will help elucidate the origins of water and possibility of fossilized remnants of habitability.
- VEXAG Investigation III.A.GC. Geochemistry:
 - These investigations will help address the availability of nutrients and other chemicals needed for life.

5.1. Venus—a laboratory for exoplanets

The search for life in the Universe is the primary focus for astrobiology research. Pragmatically that means mostly the search for water, organic compounds, and Earth-like conditions. The physical similarity between Earth and Venus and their divergent evolution from a presumably similar ancient past represents a critical test for habitable exoplanets. Was Venus ever habitable? Is the Venus cloud layer habitable today? When and how long was the Venus surface habitable? What happened to the water? Answers to these questions can guide the studies of exoplanets. Although a planet’s size is important (*e.g.*, Arnscheidt *et al.*, 2019), it is not sufficient to define the habitable zone region around a star where water can exist in a liquid state on the surface of a planet with sufficient atmospheric pressure as evidenced by

Venus and Earth, so a Venus zone has been proposed by Kane *et al.* (2014) with an inner limit defined by runaway greenhouse occurring on the planet. If Venus’ cloud layer should prove to be habitable, it will influence the study of habitable exoplanets. For these reasons, Venus is a relevant planet to understand.

6. Validating the Life in Venus’ Clouds Hypothesis: Experiments, Measurements, and Modeling

To evaluate the plausibility of the present Venus cloud life hypothesis, we need to constrain a number of important factors relative to Venus’ habitability and the manner in which microorganisms might have arisen and survived in the Venus environment. Thus, we should design experiments to search for biogenic signatures in well-defined chemical and physical context (*i.e.*, as in the NASA Astrobiology Roadmap described by des Marais *et al.*, 2008). Some of these are achievable through laboratory and field examinations, some by computational models, and others by measurements from orbiters and *in situ* investigations of the Venus atmosphere. Pertinent example questions include:

- (1) Did early Venus have the conditions necessary for Earth-like life to arise, based on comparable assumptions made about other astrobiological targets such as Mars, Europa, and Enceladus? What is the potential for modern-day Venus to harbor signatures of preserved past life? New analytical measurements including agnostic approaches (Johnson *et al.*, 2019), as per Venus Astrobiology Objective 3 (listed above), from *in situ* sampling and measurements are needed to assist in addressing this question.
- (2) Assuming Venus’ ancient surface waters were habitable, do the timeframes for the putative oceans and the emergence of continuous cloud cover presence with sufficiently long surface water residence times support the potential evolution of life to the present day? To fully understand how these progress over the history of the planet, the relative change in the cloud recycling (microphysics evolution) over time would need to be explored.
 - (a) Can this long-term evolution be computationally modeled? Are there laboratory or field experiments that may address this question? Can *in situ* measurements in the Venus atmosphere help determine the duration of residence times?
 - (b) What adaptations would life have required to survive from clement conditions to present-day desiccated, acidic, warmer and low-nutrient conditions?
- (3) Do the cloud aerosols contain sufficient water to support Earth-like life, when accounting for the residence time constraints imposed on periods of inactivity due to desiccation and the bioenergetic costs of maintaining a water activity gradient? *In situ* measurements at Venus in different parts of the cloud layer over extended observational periods will be required to address this.
- (4) Is there sufficient phosphorus in the cloud layer to support Earth-like life? If so, what is the total biomass that could be supported given its upper limit and

is this sufficient to survive the expected die-offs during periods of low water activity, high radiation, etc.? *In situ* measurements of atmospheric and aerosol composition with modern instruments are needed.

- (a) Are there low- and/or higher-molecular-weight organics present in the atmosphere? A significant and puzzling amount of CH₄ was reported by the Pioneer Venus Large Probe (Donahue and Hodges, 1993). Altitude-resolved *in situ* investigations of gas and aerosol composition with modern instrumentation could provide answers.

6.1. Surface/interior investigations

Knowing the history of water on Venus—the abundance, duration, and pathways by which putative surface waters evolved in a changing climate are critical to assessing the likelihood of the existence of life via panspermia or origins and diversity of life on Venus. Geological climate forcing (*e.g.*, widespread crustal resurfacing from lava flows, large body impacts that create impacts ~200 km size craters) must also be understood. Thus, the past habitability of Venus is critical for assessing the possibility of life in the present potentially habitable layer in the clouds. Changes in the climate may also have affected the lithospheric conditions resulting in altering the style of mantle convection over time (Weller and Kiefer, 2020), leading to changes in the habitability conditions on the planet.

6.2. Compositional indications from surface rocks

The highly tectonically deformed tesserae (complex ridged terrains) are believed to be some of the oldest rocks currently exposed on Venus (*e.g.*, Ivanov and Head, 2011, 2015; Kreslavsky *et al.*, 2015), although their absolute ages are unknown and different tessera subunits may have formed at different times (Gilmore *et al.*, 2015). Their regional lithology (rock composition on scales of tens of km) holds clues for the past presence of water and thus habitability and evolution of life (Gilmore *et al.*, 2017), and perhaps even signs of aqueous erosion (*e.g.*, Khawja *et al.*, 2020).

6.3. Clouds and atmosphere investigations

Whether or not microorganisms play any role in the radiative balance of Venus, the identity and distribution of the dominant absorbers in the venusian atmosphere is a critical factor for understanding Venus. There are many other unknowns about the atmosphere from an astrobiological perspective—abundance profiles with altitude of minor and trace constituents of the atmosphere, meteorological conditions, and concurrent aerosol chemical composition from *in situ* measurements at equatorial, mid, and polar latitudes over day and night are essential. These are critical pieces of information considering the reports of disequilibria in the lower atmosphere (Volkov, 1991); Mogul *et al.* (2021) report that reanalysis of Pioneer Venus Large Probe Neutral Mass Spectrometer (PV LNMS) data reveals several chemicals that are suggestive of redox disequilibria. This includes the detection of nitrogen species across differing oxidation states, such as nitric acid, nitrous acid, nitrogen gas, hydrogen cyanide, and possibly ammonia.

6.4. Spatial/spectral and thermal studies of cloud contrast features

Spatial/spectral contrast patterns may be used as a key constraint on absorber candidate properties. Studies of the temporal evolution of contrasts on different spatial scales across the UV-NIR spectrum (Limaye *et al.*, 2018b), including the spatial and temporal evolution of local spectral albedo patterns (Lee *et al.*, 2015, 2019) at moderate to high resolutions, provide the essential data for constraints on the lifetimes and evolution of the absorbers on the day side. However, concurrent chemical composition data are lacking for an understanding of these changes.

On the night side, cloud opacity maps in the NIR also show the spatial and temporal evolution of the night-side cloud contrast (Limaye *et al.*, 2018b; Peralta *et al.*, 2019, 2020). Comparison with concurrent thermal (brightness temperature) maps (*e.g.*, Akatsuki Longwave InfraRed (LIR) camera data) with higher accuracy (>0.1 K) on the same spatial scale should reveal any patterns between the absorbed (day) and emitted radiation (night) and the contrasts in day- and night-side cloud cover. Long- and short-term 365 nm albedo changes observed on Venus can drive the cloud layer climate on Venus (Bullock *et al.*, 2013) through changes in solar absorption. The desired continuous cloud layer observations over a narrow range of phase angles for obtaining albedo could eventually be obtained from L1 and L2 Lagrange point orbits as recently proposed (Kovalenko *et al.*, 2019; Limaye and Kovalenko, 2019) similar to the DSCOVR mission monitoring of Earth from its Sun-Earth L1 point (Su *et al.*, 2020). However, coordinated observations from orbit and with long-term *in situ* measurements at different altitudes of the cloud layer are needed to understand the nature and influence of the absorbers.

6.5. Physical, chemical, and biological properties of aerosols

It is critical to understand the nature of absorbers responsible for energy deposition in the Venus cloud layer. For example, if the larger aerosols in the lower cloud deck contain S_x as an absorber and those aerosols in fact harbor microorganisms, the S_x coating could provide UV protection and material for energy conversion. This would allow putative microorganisms to photosynthesize in the lower venusian atmosphere to meet their energy needs (Schulze-Makuch *et al.*, 2004). A coupled iron- and sulfur-centered metabolism for life in Venus' clouds has also been proposed (Limaye *et al.*, 2018a); however, there may be other geochemical cycles that could support life. Studies measuring the abundances of alternative redox active nutrients (*e.g.*, H_xS_yO_z, H_xN_yO_z, C_xH_yO_z, and H₂) would help in assessing the potential habitability of the clouds (Limaye *et al.*, 2018a).

While the ~1 μm radius particles apparently dominant in the Venus clouds (Knollenberg and Hunten, 1980b; Ekonomov *et al.*, 1984; Moshkin *et al.*, 1986) are believed to be nearly spherical (Hansen and Hovenier, 1974; Titov *et al.*, 2018), the properties and dimensions of the larger particles found in the lower clouds are unknown. Organic hazes with fractal shapes rather than spherical shaped particles have been suggested for Titan (Rannou *et al.*, 1997; Wolf and

Toon, 2010) and primitive Earth (Arney *et al.*, 2016). Images of the aerosols with a microscope (Yamagishi *et al.*, 2016; Sasaki *et al.*, 2019) would help settle the question of the identity of the large aerosols. To date, aerosol size populations have been inferred from *in situ* backscattering (Ragent and Blamont, 1980), the glory feature at the cloud tops (Markiewicz *et al.*, 2014), polarization data (Kawabata *et al.*, 1980, 1986; Sato *et al.*, 1996; Rossi *et al.*, 2015), and from forward scattering (Wilquet *et al.*, 2012), but no direct measurements have been made.

Sustained measurements to characterize the elemental, chemical, and physical properties of gases and aerosols throughout the depth of the cloud layer and the lower haze layer and over day and night are needed to assess the temporal changes observed in the currently available multispectral images. Instruments to obtain such measurements have been demonstrated on Earth and can be adapted for Venus applications. For example, miniature chemical analysis systems have successfully detected ppb amounts of amino acid biosignatures in dry Atacama desert soils (Skelley *et al.*, 2007), and low-mass Micro-Electro-Mechanical Systems (MEMS) species-specific sensors are being developed (Kremic *et al.*, 2020). Remote Raman detection has been used to detect specific chemical signatures from distances of ~ 1700 m under ambient daylight conditions. Two instruments under development—an aerosol mass spectrometer (Baines *et al.*, 2021) and a fluorescent imaging microscope (Sasaki *et al.*, 2019) could provide critical data from a capable future aerial platform potentially at the end of the decade. Finally, to understand the nature of the absorbers, which may be critical for identifying the absorption source(s), *in situ* observations that trace changes in the absorption relative to the ambient environment will be essential.

The Venus Express finding that the index of refraction of the cloud particles inferred from analysis of the disk resolved observations of the optical glory phenomenon and polarization is somewhat higher (Rossi *et al.*, 2015; Markiewicz *et al.*, 2018) than that inferred by the whole disk observations of Lyot analyzed by Hansen and Hovenier (1974). This suggests that the cloud droplets at least in the upper one scale height contain another substance besides (dilute) sulfuric acid. Thus, droplet chemical composition and their optical properties warrant further investigation. The increase has been suggested to be due to the presence of other high index of refraction material(s) in the cloud droplets such as FeCl_3 . Direct *in situ* measurements of the index of refraction (Zibaii *et al.*, 2010) of the Venus aerosols together with altitude-resolved trace gas chemistry will place much better constraints on their composition, including microorganisms should they reside in the Venus aerosols.

6.6. Noble gas abundances to determine water history

Accurate isotopic ratios of abundances of argon, krypton, and xenon can provide information on the role of planetesimals in the accumulation and loss of water on Venus compared with that of comets. This should lead to a better understanding of the history of liquid water that may have existed on Venus (Baines *et al.*, 2013; Garvin *et al.*, 2020a), especially if established within the cloud layer.

6.7. Global mapping of elemental and chemical abundances (P, S, Fe, CH_4 , and phosphine)

Among the many potential molecular biogenic signatures relevant for exoplanets (Seager *et al.*, 2012), phosphine has been promoted by Sousa-Silva *et al.* (2020). The possible existence of phosphine in the cloud layer of Venus (Encrenaz *et al.*, 2020; Greaves *et al.*, 2020a, 2020b; Mogul *et al.*, 2021) has been strongly debated in the literature—with each measurement/observation being susceptible to observation technique limitations. A stable presence of phosphine in the clouds of Venus is unexpected from a chemistry perspective (rapid degradation by hydroxyl radicals, reactivity with sulfuric acid, decomposition at high temperatures leading to short atmospheric life). Clarity about the existence of phosphine (or any other gas that has both abiotic and biotic pathways) and its associated fractionation gases will be significant for both Venus and exoplanets in the Venus zone for considering chemical disequilibrium and continuous production (Schulze-Makuch, 2021). Unambiguous detection of phosphorus or phosphine over different local times within the cloud layers would also be highly significant as disequilibrium processes may show diurnal dependence (Florenskii *et al.*, 1978). Likewise, the confirmation of atmospheric CH_4 and ammonia and an understanding of their diurnal variations would significantly influence our comprehension of disequilibria in Venus' atmosphere. For these reasons, measurements of phosphorous-bearing compounds as well as ammonia and CH_4 at other local times and altitudes are needed. Both CH_4 and phosphine have observable spectral features in the NIR or thermal infrared spectrum; however, instrumentation with high spectral resolution is needed to distinguish between these species and other gas species known to be prominent in Venus' atmosphere through remote sensing techniques. The evidence for the presence or absence of phosphine in the cloud layer of Venus may be best ascertained by *in situ* study using high-resolution mass or tunable laser spectroscopy instrumentation, ideally at <1 ppm concentration level.

6.8. Solar wind interaction

Water has been lost over the history of Venus as detected from loss of OH radicals (Lammer *et al.*, 2006; Delva *et al.*, 2008) and loss of H^+ and O^+ from spacecraft measurements (Persson *et al.*, 2018, 2020). Improved estimates of present-day atmospheric escape will produce better estimates of the total loss of water from Venus leading to a more robust estimate for the total inventory of water on Venus over geological time. Most of the atmospheric loss from Venus is due to charge exchange and sputtering and has been estimated from spacecraft measurements from polar orbits around Venus. Measurements from Lagrange orbiters around L1 and L2 points of the Sun-Venus system can provide continuous sampling of the incoming solar wind and the outgoing flux from Venus' magnetotail (Limaye and Kovalenko, 2019) since the Venus magnetotail has been detected even from the Sun-Earth Lagrange point (Grünwaldt *et al.*, 1997), much farther than the separation of L2 from Venus (~ 1 million km).

6.9. Laboratory studies

It would be useful to obtain laboratory data on optical and chemical properties of candidate biogenic materials under

the currently known Venus cloud-like conditions. This includes spectral studies of aerosolized biochemicals and microorganisms, and measurements of the chemical half-lives of biopolymers under the acidic conditions of the cloud aerosols. Moreover, fundamental studies regarding the survival of terrestrial extremophiles in aerosols, including suggested Venus analogue environments such as Earth's stratospheric sulfate aerosols, and the potential for metabolism and division while suspended in aerosols, are also of significant interest.

An alternate hypothesis proposed for the origin of life is based on the effects of environmental stresses through varying environmental conditions (Herkovits, 2006; Kompanichenko, 2017). To test this hypothesis, Kompanichenko (2019) proposed some experiments on prebiotic chemistry to be carried out under oscillating rather than stable conditions. A goal of such experiments is to check the hypothesis that primary forms of life on Earth or other planets originate through the intensified response in prebiotic microsystems to their "pumping" by external oscillations (*i.e.*, just a continuous chemical complex of organic compounds is insufficient for launching life). If this point of view is confirmed, the extreme conditions in the atmosphere of Venus (large range of conditions and variations) can be considered as a factor supporting possible life in the atmosphere, as well as on Venus-like exoplanets.

The limit of sulfuric acid concentration that microbial life on Earth can adapt to has not been fully investigated. Also, whether Earth life can thrive without (or with very little) metals is not known or investigated. Thus, experiments to determine the limits of low pH survival of terrestrial microorganisms and availability of metals will also be informative.

6.10. Modeling

The photochemical models developed to understand the chemical abundances in the Venus atmosphere (Mills and Allen, 2007; Mills *et al.*, 2007; Krasnopolsky, 2012) include hundreds of chemical reactions involving sulfur and other major and minor species detected in the atmosphere. For many of the photochemical reactions, the rates are not well known. We propose that the lack of biological pathways included in these models may be a major drawback. For example, the iron and sulfur reactions similar to those involving microorganisms on Earth may occur on Venus and contribute to the atmospheric chemical cycles. If so, these reactions may be linked to a number of open questions about Venus including those involving the mechanisms that maintain photochemical stability of CO₂ at Venus (Marcq *et al.*, 2018), and the mechanisms responsible for efficient SO₂ loss within the clouds (Vandaele *et al.*, 2017a, 2017b; Marcq *et al.*, 2018). Incorporation of such photobiological reactions could be valuable in solving the mystery of the unknown absorbers and other Venus chemistry cycle puzzles.

7. Future Exploration of Venus

The Venus cloud layer has been sampled by Venera, VeGa, and Pioneer Venus entry probes and *in situ* by two VeGa balloons in 1985 with measurements over 48-hour long flights (Sagdeev and Moroz, 1986; Sagdeev *et al.*, 1986). Therefore, *in situ* observation of Venus' cloud habitable zone is a very achievable and worthy endeavor for astrobiology investigations. Furthermore, advances in aerial platform

technology and descent probe technology (*e.g.*, Kosenkova, 2019) show that longer duration flights in the cloud layer are possible (Polidan *et al.*, 2015; Cutts *et al.*, 2018); continued technology development investment is required to make such flights an achievable reality. The VERITAS radar and NIR mapping mission, DAVINCI+ probe/fly-by/orbiter mission, and EnVision radar and NIR mapping missions are currently in Phase A study and if selected will be launched in next 10 years. ISRO is planning on an orbiter with a radar and other atmospheric instruments for launch in late 2024 or later. JAXA is also considering a Lagrange Point orbiter mission. None of these have habitability of the cloud layer as a science goal, but the observations should be useful. It is quite apparent, however, that a single mission will not address all the VEXAG goals for Venus and key astrobiological priorities. Helbert *et al.* (2020) suggested a conceptual Venus Program to implement the multiple missions needed. Gilmore *et al.* (2020) presented a multiplatform concept for a NASA Venus flagship mission, which includes the assessment of habitability as a goal, while a systems approach to future exploration has been described by Limaye *et al.* (2020a) with Lagrange Point orbiters around Venus-Sun L1 and L2 points, a pair of short period polar and equatorial orbiters, aerial platforms, and long-lived surface stations. To implement the many missions needed will be challenging for any single agency, and international collaborations and cooperation that have proved useful for Venus in the past, will continue to be productive. Limaye *et al.* (2020b) advocated for expanded efforts in internationally coordinated future missions.

8. Summary

We presented four lines of reasoning for considering Venus an astrobiology target: (1) the possibility of long-standing oceans (2–3 Ga), erupting volcanoes, and/or mobile lid tectonics with water would have provided opportunity for the origin of life similar to what is suggested to have occurred on early Earth, or life could have evolved if seeded via large impactors, (2) the potential for survival of microbial life until the present day in the current extreme environment of the clouds, (3) the possibility for microbial life in the cloud layer, and (4) Venus as proxy for habitability of exoplanets. Together, these provide a basis for exploring the possibility of past and present life on Venus. Addressing the VEXAG goals for exploration with an astrobiology perspective will provide guidance for a step-by-step approach for identifying or prioritizing potential biosignatures and their potential preservation as outlined in this article.

Venus is our nearest neighbor and an important resource for exploring the diversity, evolution, and potential habitability of terrestrial exoplanets (Kane *et al.*, 2019). It may guide us on how a planet transitioned from being habitable to a greenhouse planet with a seemingly uninhabitable planetary surface environment. Although much has been learned from space exploration about short-term survival of microorganisms in space and the upper atmosphere of Earth (Horneck *et al.*, 2010), much more remains to be discovered about the potential for sustained habitability of the Venus cloud layer and the implications for terrestrial exoplanets (*e.g.*, DasSarma and Schwieterman, 2018). Clearly, Venus should be of astrobiological interest scientifically for better understanding the origins of life everywhere.

New insights into the atmospheric chemistry and clouds are still needed to understand the various disequilibria and their implications for habitability. Therefore, Venus is uniquely suited for the exploration of its past and current habitability, consistent with high priority VEXAG goals and objectives, and those described by the National Academies Planetary Sciences and Astrobiology Decadal Survey now underway for 2023–2032.

Acknowledgments

This contribution benefited from the Venus Cloud Layer Habitability and Landing Site Selection workshop organized by the Roscosmos-IKI/NASA Venera-D Joint Science Definition Team. We gratefully acknowledge (Late) Leonid Ksanfomality for his long-term research contributions and interests in Venus science and exploration. We acknowledge the contributions of Jaime A. Cordova during revision of the article. We are grateful for critical reviews from Drs. C.P. McKay, E. Stofan, and J. Garvin. Extensive review comments by Dr. Garvin led to substantial improvements in the article.

Author Disclosure Statement

No competing financial interests exist.

Funding Information

The workshop was supported by NASA HQ Planetary Science (A. Ocampo, Lead Venus Scientist) and Astrobiology programs (Mary Voytek) and Russian Academy of Sciences, Space Research Institute. This research was supported by NASA Grants NNX16AC79G (S.S.L.), NNX16AK82G (K.-L.J.), and NNX16AC81G (M.A.B.). Y.J.L. receives funding from EU Horizon 2020 MSCA-IF No. 841432.

References

- Ahrens TJ (1993) Impact erosion of terrestrial planetary atmospheres. *Annu Rev Earth Planet Sci* 21:525–555.
- Airey MW, Mather TA, Pyle DM, *et al.* (2015) Explosive volcanic activity on Venus: the roles of volatile contribution, degassing, and external environment. *Planet Space Sci* 113–114:33–48.
- Amato P, Besaury L, Joly M, *et al.* (2019) Metatranscriptomic exploration of microbial functioning in clouds. *Sci Rep* 9: 4383.
- Amato P, Parazols M, Sancelme M, *et al.* (2007a) Microorganisms isolated from the water phase of tropospheric clouds at the Puy de Dôme: major groups and growth abilities at low temperatures. *FEMS Microbiol Ecol* 59:242–254.
- Amato P, Parazols M, Sancelme M, *et al.* (2007b) An important oceanic source of micro-organisms for cloud water at the Puy de Dôme (France). *Atmos Environ* 41:8253–8263.
- Andreichikov B, Akhmetshin I, Korchuganov B, *et al.* (1987) VEGA 1 and 2 X-ray radiometer analysis of the Venus cloud aerosol. *Kosmicheskie Issledovaniia* 25:737–743.
- Arney G, Domagal-Goldman SD, Meadows VS, *et al.* (2016) The pale orange dot: the spectrum and habitability of hazy Archean Earth. *Astrobiology* 16:873.
- Arnscheidt CW, Wordsworth RD, and Ding F (2019) Atmospheric evolution on low-gravity waterworlds. *Astrophys J* 881:60.
- Arrhenius S (1918) *The Destinies of Stars*. G.P. Putnam and Sons, The Knickerbocker Press, New York and London, p 256.
- Baines KH, Atreya SK, Bullock MA, *et al.* (2013) The atmospheres of the terrestrial planets: clues to the origins and early evolution of Venus, Earth, and Mars. In *Comparative Climatology of Terrestrial Planets*, Vol. 1, edited by SJ Mackwell, AA Simon-Miller, JW Harder, and MA Bullock, University of Arizona Press, Tucson, pp 137–160.
- Baines K, Nikolic Dragan, Cutts J, *et al.* (2021) Investigation of Venus cloud aerosol and gas composition including potential biogenic materials via an aerosol-sampling instrument package. *Astrobiology* 21:1316–1323.
- Bains W, Petkowski JJ, Seager S, *et al.* (2020) Phosphine on Venus cannot be explained by conventional processes. *Astrobiology* 21:1277–1304.
- Baker BJ and Banfield JF (2003) Microbial communities in acid mine drainage. *FEMS Microbiol Ecol* 44:139–152.
- Barge LM, Branscomb E, Brucato JR, *et al.* (2017) Thermodynamics, disequilibrium, evolution: far-from-equilibrium geological and chemical considerations for origin-of-life research. *Orig Life Evol Biosph* 47:39–56.
- Bauer H, Giebl H, Hitzemberger R, *et al.* (2003) Airborne bacteria as cloud condensation nuclei. *J Geophys Res Atmos* 108(D21):AAC 2-1–AAC 2-5. <https://doi.org/10.1029/2003JD003545>
- Baum DA (2018) The origin and early evolution of life in chemical composition space. *J Theor Biol* 456:295–304.
- Baumgartner RJ, Van Kranendonk MJ, Wacey D, *et al.* (2019) Nano-porous pyrite and organic matter in 3.5-billion-year-old stromatolites record primordial life. *Geology* 47:1039–1043.
- Bell EA, Boehnke P, Harrison TM, *et al.* (2015) Potentially biogenic carbon preserved in a 4.1 billion-year-old zircon. *Proc Natl Acad Sci U S A* 112:14518–14521.
- Bell G and Gonzalez A (2011) Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. *Science* 332:1327–1330.
- Bertaux J-L, Widemann T, Hauchecorne A, *et al.* (1996) VEGA 1 and VEGA 2 entry probes: an investigation of local UV absorption (220–400 nm) in the atmosphere of Venus (SO₂ aerosols, cloud structure). *J Geophys Res Planets* 101:12709–12745.
- Bertaux J-L, Khatuntsev IV, Hauchecorne A, *et al.* (2016) Influence of Venus topography on the zonal wind and UV albedo at cloud top level: the role of stationary gravity waves. *J Geophys Res Planets* 121:1087–1101.
- Bierson CJ and Zhang X (2020) Chemical cycling in the Venusian atmosphere: a full photochemical model from the surface to 110 km. *J Geophys Res Planets* 125:e2019JE006159.
- Blanchard DC (1964) Sea-to-air transport of surface active material. *Science* 146:396.
- Bolhuis H, Palm P, Wende A, *et al.* (2006) The genome of the square archaeon *Haloquadratum walsbyi*: life at the limits of water activity. *BMC Genomics* 7:169.
- Bondarenko NV, Head JW, and Ivanov MA (2010) Present-day volcanism on Venus: evidence from microwave radiometry. *Geophys Res Lett* 37:L23202.
- Boyer C (1986) The upper atmosphere of Venus. Attempt to explain its rotation (La haute atmosphère de Vénus. Tentative d'explication de sa rotation). *L'Astronomie* 100:77.
- Boyer C and Guérin P (1969) 4-Day Retrograde Rotation Study of the Outer Cloud Layer of Venus (Étude de la Rotation Rétrograde, en 4 Jours, de la Couche Extérieure Nuageuse de Vénus). *Icarus* 11:338.
- Bringer C, Spradlin S, Cobani L, *et al.* (2018) The more adaptive to change, the more likely you are to survive: protein

- adaptation in extremophiles. *Semin Cell Dev Biol* 84:158–169.
- Bryan NC, Christner BC, Guzik TG, *et al.* (2019) Abundance and survival of microbial aerosols in the troposphere and stratosphere. *ISME J* 13:2789–2799.
- Budisa N and Schulze-Makuch D (2014) Supercritical carbon dioxide and its potential as a life-sustaining solvent in a planetary environment. *Life (Basel)* 4:331–340.
- Bullock M (2018) The total possible biomass of Venus' clouds. American Astronomical Society, DPS meeting #50, id.102.04.
- Bullock M and Grinspoon DH (2019) Venus atmospheric chemistry and possible metabolic pathways for microbial organisms. Venus Cloud Layer Habitability Workshop, Space Research Institute, Moscow, http://venera-d.cosmos.ru/uploads/media/11_-_Bullock_Moscow_10-5-19.pdf.
- Bullock MA, Grinspoon DH, and Head JW, III (1993) Correction to “Venus resurfacing rates: constraints provided by 3-D Monte Carlo simulations.” *Geophys Res Lett* 20:2783.
- Bullock MA, Grinspoon DH, Simon-Miller AA, *et al.* (2013) The atmosphere and climate of Venus. In *Comparative Climatology of Terrestrial Planets*, edited by SJ Mackwells, AA Simon-Miller, JW Harder, and MA Bullock, University of Arizona Press, Tucson, pp 19–54.
- Capece MC, Clark E, Saleh JK, *et al.* (2013) Polyextremophiles and the constraints for terrestrial habitability. In *Polyextremophiles*, Vol. 27, edited by J Seckbach, A Oren, and H Stan-Lotter, Springer, pp 3–59.
- Carr MH and Garvin J (2001) Mars exploration. *Nature* 412:250–253.
- Carr MH and Head JW (2010) Geologic history of Mars. *Earth Planet Sci Lett* 294:185–203.
- Christner BC, Morris CE, Foreman CM, *et al.* (2008) Ubiquity of biological ice nucleators in snowfall. *Science* 319:1214.
- Chyba CF and Sagan C (1997) Comets as a source of prebiotic organic molecules for the early Earth. In *Comets and the Origin and Evolution of Life*, edited by PJ Thomas, CF Chyba, and CP McKay, Springer, New York, pp 147–173.
- Cockell CS (1999) Life on Venus. *Planet Space Sci* 47:1487–1501.
- Cockell CS, McMahon S, and Biddle JF (2020) When is life a viable hypothesis? The case of venusian phosphine. *Astrobiology* 21:261–264.
- Cockell CS, Higgins PM, and Johnstone AA (2021) Biologically available chemical energy in the temperate but uninhabitable venusian cloud layer: what do we want to know? *Astrobiology* 21:1224–1236.
- Connon SSA, Lester EDE, Shafaat HHS, Obenhube, DC, and Ponce A (2007) Bacterial diversity in hyperarid Atacama Desert soils. *J Geophys Res Biogeosci* 112, G04S17. doi: 10.1029/2006JG00031
- Crisp D (1986) Radiative forcing of the Venus mesosphere: I. Solar fluxes and heating rates. *Icarus* 67:484–514.
- Crits-Christoph A, Robinson CK, Barnum T, *et al.* (2013) Colonization patterns of soil microbial communities in the Atacama Desert. *Microbiome* 1:28.
- Cutts JA, Thompson TW, Baines K, *et al.* (2018) Aerial platforms for scientific investigation of Venus. Jet Propulsion Laboratory, Pasadena, California, p 25.
- Damer B and Deamer D (2019) The hot spring hypothesis for an origin of life. *Astrobiology* 20:429–452.
- Dartnell LR, Nordheim TA, Patel MR, *et al.* (2015) Constraints on a potential aerial biosphere on Venus: I. Cosmic rays. *Icarus* 257:396–405.
- DasSarma S and Schwieterman EW (2018) Early evolution of purple retinal pigments on Earth and implications for exoplanet biosignatures. *Int J Astrobiol* 1–10. doi: 10.1017/S1473550418000423
- Davila AF and Schulze-Makuch D (2016) The last possible outposts for life on Mars. *Astrobiology* 16:159–168.
- de Bergh C, Bezard B, Owen T, *et al.* (1991) Deuterium on Venus: observations From Earth. *Science* 251:547–549.
- Damer B (2016) A field trip to the Archaean in search of Darwin's warm little pond. *Life* 6:21.
- Damer B and Deamer D (2019) The hot spring hypothesis for an origin of life. *Astrobiology* 20:429–452.
- Deamer DW and Georgiou CD (2015) Hydrothermal conditions and the origin of cellular life. *Astrobiology* 15:1091–1095.
- Deamer D, Damer B, and Kompanichenko V (2019) Hydrothermal chemistry and the origin of cellular life. *Astrobiology* 19:1523–1537.
- Delva M, Zhang TL, Volwerk M, *et al.* (2008) First upstream proton cyclotron wave observations at Venus. *Geophys Res Lett* 35:L03105.
- Deno NC and Taft RW (1954) Concentrated sulfuric acid-water. *J Am Chem Soc* 76:244–248.
- Des Marais DJ, Nuth JA, Allamandola LJ, *et al.* (2008) The NASA Astrobiology Roadmap. *Astrobiology* 8: 715–730.
- Dhakar K and Pandey A (2016) Wide pH range tolerance in extremophiles: toward understanding an important phenomenon for future biotechnology. *Appl Microbiol Biotechnol* 100:2499–2510.
- Dixon R and Kahn D (2004) Genetic regulation of biological nitrogen fixation. *Nat Rev Microbiol* 2:621–631.
- Dodd MS, Papineau D, Grenne T, *et al.* (2017) Evidence for early life in Earth's oldest hydrothermal vent precipitates. *Nature* 543:60–64.
- Domagal-Goldman SD, Wright KE, Adamala K, *et al.* (2016) The astrobiology primer v2. 0. *Astrobiology* 16:561–653.
- Donahue TM (1999) New analysis of hydrogen and deuterium escape from Venus. *Icarus* 141:226–235.
- Donahue TM and Hodges RR (1993) Venus methane and water. *Geophys Res Lett* 20:591–594.
- Donahue TM and Hodges RR, Jr. (1992) Past and present water budget of Venus. *J Geophys Res* 97:6083–6091.
- Donahue TM, Hoffman JH, Hodges RR, *et al.* (1982) Venus was wet—a measurement of the ratio of deuterium to hydrogen. *Science* 216:630–633.
- Ekonomov AP, Moshkin BE, Moroz VI, *et al.* (1983) Experiment on UV-photometry aboard Venera 13 and Venera 14. *Kosmicheskie Issledovaniia* 21:254–268.
- Ekonomov AP, Moroz VI, Moshkin BE, *et al.* (1984) Scattered UV solar radiation within the clouds of Venus. *Nature* 307:345–347.
- Encrenaz T, Greathouse TK, Marcq E, *et al.* (2020) A stringent upper limit of the PH₃ abundance at the cloud top of Venus. *Astron Astrophys* 643:L5.
- Esposito LW, Copley M, Eckert R, *et al.* (1988) Sulfur dioxide at the Venus cloud tops, 1978–1986. *J Geophys Res* 93:5267–5276.
- Esposito LW, Knollenberg RG, Marov MI, *et al.* (1983) The clouds and hazes of Venus. In *Venus*, edited by DM Huntens, University of Arizona Press, Tucson, pp 484–564.
- Fedorova A, Korablev O, Vandaele A-C, *et al.* (2008) HDO and H₂O vertical distributions and isotopic ratio in the Venus mesosphere by Solar Occultation at Infrared spectrometer on board Venus Express. *J Geophys Res Planets* 113:E00B22.
- Filiberto J, Trang D, Treiman AH, and Gilmore MS (2020) Present-day volcanism on Venus as evidenced from weathering rates of olivine. *Sci Adv* 6: eaax7445.10.1126/sciadv.aax7445

- Fleischaker GR (1990) Origins of life: an operational definition. *Orig Life Evol Biosph* 20:127–137.
- Florenskii CP, Volkov VP, and Nikolaeva OV (1978) A geochemical model of the Venus troposphere. *Icarus* 33:537–553.
- Frandsen BN, Wennberg PO, and Kjaergaard HG (2016) Identification of OSSO as a near-UV absorber in the Venusian atmosphere. *Geophys Res Lett* 43:11,146–11,155. doi: 10.1002/2016GL070916.
- Frandsen BN, Farahani S, Vogt E, *et al.* (2020) Spectroscopy of OSSO and other sulfur compounds thought to be present in the Venus atmosphere. *J Phys Chem A* 124:7047–7059.
- Frankland VL, James AD, Carrillo-Sánchez JD, *et al.* (2017) CO oxidation and O₂ removal on meteoric material in Venus' atmosphere. *Icarus* 296:150–162.
- Fukuhara T, Futaguchi M, Hashimoto George L, *et al.* (2017) Large stationary gravity wave in the atmosphere of Venus. *Nat Geosci* 10. DOI: 10.1038/ngeo2873.
- Futaana Y, Stenberg Wieser G, Barabash S, *et al.* (2017) Solar wind interaction and impact on the Venus atmosphere. *Space Sci Rev* 212:1453–1509.
- Gao P, Zhang X, Crisp D, *et al.* (2014) Bimodal distribution of sulfuric acid aerosols in the upper haze of Venus. *Icarus* 231: 83–98.
- Garvin JB (1981) Dust cloud observed in Venera 10 panorama of Venusian surface: inferred surface processes. <https://ui.adsabs.harvard.edu/abs/1981LP...12..324G> (accessed March 18, 2021).
- Garvin JB (1990) The global budget of impact-derived sediments on Venus. *Earth Moon Planets* 50-51:175–190.
- Garvin JB, Arney GN, Atreya S, *et al.* (2020a) Deep atmosphere of Venus probe as a mission priority for the upcoming decade. A White Paper for the Planetary Science and Astrobiology Decadal Survey 2023–2032, The National Academies of Science Engineering and Medicine, <https://arxiv.org/ftp/arxiv/papers/2008/2008.12821.pdf>
- Garvin JB, Arney G, Getty S, *et al.* (2020b) DAVINCI+: deep atmosphere of Venus investigation of noble gases, chemistry, and imaging plus. Available online at <https://ui.adsabs.harvard.edu/abs/2020LPI...51.2599G> (accessed March 18, 2021).
- Gentry D and Dahlgren RP (2019) Venus aerosol sampling considerations for in site biological analysis. In *Venera-D Landing Sites and Cloud Layer Habitability Workshop*, Space Research Institute, Moscow. http://venera-d.cosmos.ru/uploads/media/6_-_VDW2019_presentation_Gentry.pdf
- Gilmore MS, Mueller N, and Helbert J (2015) VIRTIS emissivity of Alpha Regio, Venus, with implications for tessera composition. *Icarus* 254:350–361.
- Gilmore M, Treiman A, Helbert J, *et al.* (2017) Venus surface composition constrained by observation and experiment. *Space Sci Rev* 212:1511–1540.
- Gilmore M, Whitten J, Perkins R, and Brossier JF (2019) The ancient environments of Venus as recorded by tessera terrain. American Geophysical Union Fall Meeting. <https://ui.adsabs.harvard.edu/abs/2019AGUFM.P51G3445G/> (accessed March 18, 2021).
- Gilmore MS, Beauchamp PM, Kane SR, *et al.* (2020) Venus Flagship Mission Planetary Decadal Study, a mission to the closest exoplanet. <https://ui.adsabs.harvard.edu/abs/2020LPICo2195.3045G> (accessed March 18, 2021).
- Glaze LS (1999) Transport of SO₂ by explosive volcanism on Venus. *J Geophys Res* 104:18899–18906.
- Glaze LS, Baloga SM, and Wimert J (2011) Explosive volcanic eruptions from linear vents on Earth, Venus, and Mars: comparisons with circular vent eruptions. *J Geophys Res Planets* 116. 10.1029/2010je003577.
- Goettel KA and Lewis JS (1974) Ammonia in the atmosphere of Venus. *J Atmos Sci* 31:828–830.
- Grant WD (2004) Life at low water activity. *Phil Trans Biol Sci* 359:1249–1267.
- Greaves JS, Richards AMS, Bains W, *et al.* (2020a) Phosphine gas in the cloud decks of Venus. *Nat Astron* doi: 10.1038/s41550-020-1174-4.
- Greaves JS, Richards AMS, Bains W, *et al.* (2020b) Re-analysis of phosphine in Venus' clouds. arXiv:2011.08176.
- Greaves JS, Bains W, Petkowski JJ, (2020c) On the robustness of phosphine signatures in Venus' clouds. arXiv:2012.05844.
- Grinspoon DH (1993) Implications of the high D/H ratio for the sources of water in Venus' atmosphere. *Nature* 363:428–431.
- Grinspoon DH (1997) *Venus Revealed: A New Look Below the Clouds of Our Mysterious Twin Planet*. Cambridge, Perseus Publishing; 351 pp.
- Grinspoon DH and Bullock MA (2003) Did Venus experience one great transition or two? [abstract 35]. AAS/Division for Planetary Sciences Meeting Abstracts. Available online at <https://ui.adsabs.harvard.edu/abs/2003DPS....35.4403G> (accessed March 18, 2021).
- Grinspoon D and Bullock M (2007) Astrobiology and Venus exploration. In *Exploring Venus as a Terrestrial Planet*, edited by LW Esposito, ER Stofan, and TE Cravenspp, American Geophysical Union Monograph, pp 191–206.
- Grünwaldt H, Neugebauer M, Hilchenbach M, *et al.* (1997) Venus tail ray observation near Earth. *Geophys Res Lett* 24: 1163–1166.
- Gülcher AJP, Gerya TV, Montési LGJ, *et al.* (2020) Corona structures driven by plume–lithosphere interactions and evidence for ongoing plume activity on Venus. *Nat Geosci*. DOI: 10.1038/s41561-020-0606-1.
- Hansen JE and Hovenier J (1974) Interpretation of the polarization of Venus. *J Atmos Sci* 31:1137–1160.
- Hapke B and Nelson R (1975) Evidence for an elemental sulfur component of the clouds from Venus spectrophotometry. *J Atmos Sci* 32:1212.
- Harrison JP, Gheeraert N, Tsigelnitskiy D, *et al.* (2013) The limits for life under multiple extremes. *Trends Microbiol* 21: 204–212.
- Hashimoto GL and Sugita S (2003) On observing the compositional variability of the surface of Venus using nightside near-infrared thermal radiation. *J Geophys Res Planets* 108(E9): 5109, doi: 10.1029/2003JE002082, E9.
- Hashimoto GL, Roos-Serote M, Sugita S, *et al.* (2008) Felsic highland crust on Venus suggested by Galileo Near-Infrared Mapping Spectrometer data. *J Geophys Res Planets* 113. doi: 10.1029/2008je003134.
- Haus R, Kappel D, and Arnold G (2017) Radiative energy balance of Venus: an approach to parameterize thermal cooling and solar heating rates. *Icarus* 284:216–232.
- Head JW, III and Wilson L (1986) Volcanic processes and landforms on Venus: theory, predictions, and observations. *J Geophys Res* 91:9407–9446.
- Helbert J, Dyar MD, Izenberg NR, *et al.* (2020) Why we need a long-term sustainable Venus program. In *Lunar and Planetary Science Conference*. <https://ui.adsabs.harvard.edu/abs/2020LPI...51.1427H> (accessed March 18, 2021).
- Herbst K, Banjac S, Atri D, *et al.* (2020) Revisiting the cosmic-ray induced Venusian radiation dose in the context of habitability. *Astron Astrophys* 633:A15.

- Herkovits J (2006) Evoecotoxicology: environmental changes and life features development during the evolutionary process—the record of the past at developmental stages of living organisms. *Environ Health Perspect* 114:1139–1142.
- Hirota R, Kuroda A, Kato J, *et al.* (2010) Bacterial phosphate metabolism and its application to phosphorus recovery and industrial bioprocesses. *J Biosci Bioeng* 109:423–432.
- Horikoshi K and Bull AT (2011) Prologue: definition, categories, distribution, origin and evolution, pioneering studies, and emerging fields of extremophiles. In: *Extremophiles Handbook*, edited by K Horikoshis. Springer Japan, Tokyo, pp 3–15.
- Horinouchi T, Kouyama T, Lee YJ, *et al.* (2018) Mean winds at the cloud top of Venus obtained from two-wavelength UV imaging by Akatsuki. *Earth Planets Space* 70(1):ID10; 19 pp.
- Horneck G, Klaus DM, and Mancinelli RL (2010) Space Microbiology. *Microbiol Mol Biol Rev*, 74:121.
- Hubbard GS, Naderi FM, and Garvin JB (2002) Following the water, the new program for Mars exploration. *Acta Astron* 51: 337–350.
- Irwin LN and Schulze-Makuch D (2020) The astrobiology of alien worlds: known and unknown forms of life. *Universe* 6: 130. <https://doi.org/10.3390/universe6090130>
- Ivanov MA and Head JW (1996) Tessera terrain on Venus: a survey of the global distribution, characteristics, and relation to surrounding units from Magellan data. *J Geophys Res* 101:14861.
- Ivanov MA and Head JW (2011) Global geological map of Venus. *Planet Space Sci* 59:1559–1600.
- Ivanov MA and Head JW (2013) The history of volcanism on Venus. *Planet Space Sci* 84:66–92.
- Ivanov MA and Head JW (2015) The history of tectonism on Venus: a stratigraphic analysis. *Planet Space Sci* 113–114: 10–32.
- Johnson DB and Hallberg KB (2008) Carbon, iron and sulfur metabolism in acidophilic micro-organisms. *Adv Microb Physiol* 54:201–255.
- Johnson NM and de Oliveira MR (2019) Venus atmospheric composition in situ data: a compilation. *Earth Space Sci* 6: 1299–1318.
- Johnson SS, Graham H, Anslyn E, *et al.* (2019) Agnostic approaches to extant life detection. In: Mars Extant Life: What's Next? 5-8 November, 2019; Carlsbad, New Mexico. LPI Contribution No. 2108, 2019, id.5026.
- Joly M, Attard E, Sancelme M, *et al.* (2013) Ice nucleation activity of bacteria isolated from cloud water. *Atmos Environ* 70:392–400.
- Joung YS, Ge Z, and Buie CR (2017) Bioaerosol generation by raindrops on soil. *Nat Commun* 8:14668.
- Jung P, Schermer M, Briegel-Williams L, *et al.* (2019) Water availability shapes edaphic and lithic cyanobacterial communities in the Atacama Desert. *J Phycol* 55:1306–1318.
- Junge CE, Chagnon CW, and Manson JE (1961a) A world-wide stratospheric aerosol layer. *Science* 133:1478–1479.
- Junge CE, Chagnon CW, and Manson JE (1961b) Stratospheric aerosols. *J Atmos Sci* 18:81–108.
- Kane SR, Kopparapu RK, and Domagal-Goldman SD (2014) On the frequency of potential Venus analogs from Kepler data. *Astrophys J* 794:L5.
- Kane SR, Arney G, Crisp D, *et al.* (2019) Venus as a laboratory for exoplanetary science. *J Geophys Res Planets* 124:2015–2028.
- Kasting JF (1988) Runaway and moist greenhouse atmospheres and the evolution of Earth and Venus. *Icarus* 74:472–494.
- Kato C, Li L, Nogi Y, *et al.* (1998) Extremely barophilic bacteria isolated from the Mariana Trench, Challenger Deep, at a depth of 11,000 meters. *Appl Environ Microbiol* 64:1510–1513.
- Kawabata K, Coffeen DL, Hansen JE, *et al.* (1980) Cloud and haze properties from Pioneer Venus polarimetry. *J Geophys Res* 85:8129–8140.
- Kawabata K, Lane W, Sato M, *et al.* (1986) Local variation of haze thickness on the equatorial region of Venus. In *15th International Symposium on Space Technology and Science*. Proceedings. Vol. 2. Tokyo, AGNE Publishing, Inc., pp 1829–1834.
- Kegerreis JA, Eke VR, Massey RJ, *et al.* (2020) Atmospheric erosion by giant impacts onto terrestrial planets. *Astrophys J* 897:161.
- Khawja S, Ernst RE, Samson C, *et al.* (2020) Tesserae on Venus may preserve evidence of fluvial erosion. *Nat Commun* 11:5789.
- Kieft TL (2003) Desert environments: soil microbial communities in hot deserts. In: *Encyclopedia of Environmental Microbiology*, edited by G Bittons. John Wiley & Sons, Inc., Hoboken, NJ, pp 1–25.
- Kitahara T, Imamura T, Sato TM, *et al.* (2019) Stationary features at the cloud top of Venus observed by ultraviolet imager onboard Akatsuki. *J Geophys Res Planets* 124:1266–1281.
- Knicely J and Herrick RR (2020) Evaluation of the bandwidths and spatial resolutions achievable with near-infrared observations of Venus below the cloud deck. *Planet Space Sci* 181:104787.
- Knollenberg R and Hunten D (1980a) The microphysics of the clouds of Venus: results of the Pioneer Venus particle size spectrometer experiment. *J Geophys Res Space Phys* 85: 8039–8058.
- Knollenberg RG and Hunten DM (1980b) The microphysics of the clouds of Venus—results of the Pioneer Venus particle size spectrometer experiment. *J Geophys Res* 85:8039–8058.
- Knollenberg R, Travis L, Tomasko M, *et al.* (1980) The clouds of Venus—a synthesis report. *J Geophys Res* 85:8059–8081.
- Knollenberg RG (1984) A reexamination of the evidence for large, solid particles in the clouds of Venus. *Icarus* 57:161–183.
- Kohli I, Joshi NC, Mohapatra S, *et al.* (2020) Extremophile—an adaptive strategy for extreme conditions and applications. *Curr Genomics* 21:96–110.
- Kompanichenko V (2017) *Thermodynamic Inversion*. Springer, p 294.
- Kompanichenko V (2019) The rise of a habitable planet: four required conditions for the origin of life in the Universe. *Geosciences* 9. doi: 10.3390/geosciences9020092.
- Kosenkova AV (2019) Investigation of the possibilities of aerodynamic forms of a lander capable of maneuverable descent in the venus atmosphere. AIP Conference Proceedings, Vol. 2171, 160005 <https://doi.org/10.1063/1.5133309>
- Kouyama T, Imamura T, Taguchi M, *et al.* (2017) Topographical and local time dependence of large stationary gravity waves observed at the cloud top of Venus. *Geophys Res Lett* 44: 12098–12105.
- Kovalenko I, Eismont N, Limaye S, *et al.* (2019) Micro-spacecraft in Sun-Venus Lagrange point orbit for the Venera-D mission. *Adv Space Res* 66:21.
- Krasnopolsky VA (1983) Spectroscopy of the 3000–8000 Å region. In *Venus*, edited by DM Hunten, L Colin, TM Donahue, VI Moroz. The University of Arizona Press, Tucson, AZ, pp 459–483.
- Krasnopolsky VA (2012) A photochemical model for the Venus atmosphere at 47–112km. *Icarus* 218:230–246.
- Krasnopolsky VA (2013) S3 and S4 abundances and improved chemical kinetic model for the lower atmosphere of Venus. *Icarus* 225:570.
- Krasnopolsky VA (2015) Vertical profiles of H₂O, H₂SO₄, and sulfuric acid concentration at 45–75 km on Venus. *Icarus* 252:327–333.

- Krasnopolsky VA (2016) Sulfur aerosol in the clouds of Venus. *Icarus* 274:33-36.
- Krasnopolsky VA (2017) On the iron chloride aerosol in the clouds of Venus. *Icarus* 286:134-137.
- Krasnopolsky VA (2018) Disulfur dioxide and its near-UV absorption in the photochemical model of Venus atmosphere. *Icarus* 299:294-299.
- Kremic T, Ghail R, Gilmore M, *et al.* (2020) Long-duration Venus lander for seismic and atmospheric science. *Planet Space Sci* 190:104961.
- Kreslavsky MA, Ivanov MA, and Head JW (2015) The resurfacing history of Venus: Constraints from buffered crater densities. *Icarus* 250:438. [10.1016/j.icarus.2014.12.024](https://doi.org/10.1016/j.icarus.2014.12.024).
- Krissansen-Totton J, Bergsman DS, and Catling DC (2016) On detecting biospheres from chemical thermodynamic disequilibrium in planetary atmospheres. *Astrobiology* 16:39-67.
- Kuiper GP (1969) Identification of the Venus cloud layers. *Commun Lunar Planet Lab* 6:229.
- Lammer H, Lichtenegger H, Biernat HK, *et al.* (2006) Loss of hydrogen and oxygen from the upper atmosphere of Venus. *Planet Space Sci* 54:1445-1456.
- Lee Y, Yamazaki A, Imamura T, *et al.* (2017) Scattering properties of the Venusian clouds observed by the UV imager on board Akatsuki. *Astron J* 154:44.
- Lee YJ, Imamura T, Schröder SE, *et al.* (2015) Long-term variations of the UV contrast on Venus observed by the Venus Monitoring Camera on board Venus Express. *Icarus* 253:1-15.
- Lee YJ, Jessup K-L, Perez-Hoyos S, *et al.* (2019) Long-term variations of Venus's 365 nm Albedo observed by Venus Express, Akatsuki, MESSENGER, and the Hubble Space Telescope. *Astron J* 158:126. <https://iopscience.iop.org/article/10.3847/1538-3881/ab3120>
- Limaye SS (1988) Venus: cloud level circulation during 1982 as determined from Pioneer cloud photopolarimeter images. II—solar longitude dependent circulation. *Icarus* 73:212-226.
- Limaye SS, Abedin NM, Ao CO, *et al.* (2020a) Venus observing system. National Academies of Science, Engineering and Medicine, Planetary Science and Astrobiology Decadal Survey, p 8.
- Limaye SS, Bullock MA, Zasova L, *et al.* (2020b) Future exploration of Venus: international coordination and collaborations. National Academies of Science Engineering and Medicine, p 8.
- Limaye SS and Kovalenko ID (2019) Monitoring Venus and communications relay from Lagrange Points. *Planet Space Sci* 179:104710.
- Limaye SS, Mogul R, Smith DJ, *et al.* (2018a) Venus' spectral signatures and the potential for life in the clouds. *Astrobiology* 18:1181-1198.
- Limaye SS and Suomi VE (1981) Cloud motions on Venus: global structure and organization. *J Atmos Sci* 38:1220-1235.
- Limaye SS, Watanabe S, Yamazaki A, *et al.* (2018b) Venus looks different from day to night across wavelengths: morphology from Akatsuki multispectral images. *Earth Planets Space* 70:24.
- Lincowski AP, Meadows VS, Crisp D, *et al.* (2021) Claimed detection of PH₃ in the clouds of Venus is consistent with mesospheric SO₂. pp arXiv:2101.09837, <https://ui.adsabs.harvard.edu/abs/2021arXiv210109837L>
- Liu Y, Yao T, Kang S, *et al.* (2007) Microbial community structure in major habitats above 6000 m on Mount Everest. *Chinese Sci Bull* 52:2350-2357.
- Lunine JI (2006) Physical conditions on the early Earth. *Philos Trans R Soc B Biol Sci* 361:1721-1731.
- Marcq E, Jessup KL, Baggio L, *et al.* (2020) Climatology of SO₂ and UV absorber at Venus' cloud top from SPICAV-UV nadir dataset. *Icarus* 335:113368.
- Marcq E, Mills FP, Parkinson CD, *et al.* (2018) Composition and chemistry of the neutral atmosphere of Venus. *Space Sci Rev* 214:10.
- Markiewicz WJ, Petrova E, Shalygina O, *et al.* (2014) Glory on Venus cloud tops and the unknown UV absorber. *Icarus* 234:200-203.
- Markiewicz WJ, Petrova EV, and Shalygina OS (2018) Aerosol properties in the upper clouds of Venus from glory observations by the Venus Monitoring Camera (Venus Express mission). *Icarus* 299:272-293.
- Marshall M (2020) Life's big bang. *New Scientist* 247:34-38.
- Masunaga K, Futaana Y, Persson M, *et al.* (2019) Effects of the solar wind and the solar EUV flux on O⁺ escape rates from Venus. *Icarus* 321:379-387.
- Maus D, Heinz J, Schirmack J, *et al.* (2020) Methanogenic Archaea Can Produce Methane in Deliquescence-Driven Mars Analog Environments. *Sci Rep* 10:6. <https://doi.org/10.1038/s41598-019-56267-4>
- McKay CP (2020) What is life—and when do we search for it on other worlds. *Astrobiology* 20:163-166.
- McKay CP, Davila A, Glein CR, *et al.* (2018) Enceladus astrobiology, habitability, and the origin of life. In *Enceladus and the Icy Moons of Saturn*, edited by P Schenk, RN Clark, CJA Howett, AJ Verbiscer, and JH Waite, University of Arizona Press, Tucson, pp 437-452.
- Melosh HJ and Tonks WB (1993) Swapping rocks: ejection and exchange of surface material among the terrestrial planets. *Meteoritics* 28:398.
- Merino N, Aronson HS, Bojanova DP, *et al.* (2019) Living at the extremes: extremophiles and the limits of life in a planetary context. *Front Microbiol* 10. doi: 10.3389/fmicb.2019.00780.
- Mills FP and Allen M (2007) A review of selected issues concerning the chemistry in Venus' middle atmosphere. *Planet Space Sci* 55:1729.
- Mills FP, Esposito LW, and Yung YL (2007) Atmospheric composition, chemistry, and clouds. *Washington DC Am Geophys Union Geophys Monogr Ser* 176:73-100.
- Milojevic T, Limaye SS, and Treiman A (2020) Phosphorus in Venus clouds: potential for bioavailability. *Astrobiology* 21:1250-1263.
- Mogul R, Limaye SS, Way MJ, and Cordova JA (2021) Venus' mass spectra show signs of disequilibria in the middle clouds. *Geophys Res Lett* 48:e2020GL091327. <https://doi.org/10.1029/2020GL091327>
- Morono Y, Ito M, Hoshino T, *et al.* (2020) Aerobic microbial life persists in oxic marine sediment as old as 101.5 million years. *Nat Commun* 11:3626.
- Morowitz H and Sagan C (1967) Life in the clouds of Venus? *Nature* 215:1259-1260.
- Moroz VI (2002) Estimates of visibility of the surface of Venus from descent probes and balloons. *Planet Space Sci* 50:287-297.
- Moroz VI, Ekonomov AP, Golovin YM, *et al.* (1983) Solar radiation scattered in the Venus atmosphere: the Venera 11,12 data. *Icarus* 53:509-537.
- Moshkin BE, Moroz VI, Gnedykh VI, *et al.* (1986) VEGA-1 and VEGA-2 optical spectrometry of Venus atmospheric aerosols at the 60-30-km levels—preliminary results. *Soviet Astron Lett* 12:36-39.
- Mueller NT, Tsang C, Nunes DC, *et al.* (2017) Near infrared multispectral mapping of Venus supports the hypothesis that Tessera plateau material was formed in the presence of surface water. <https://ui.adsabs.harvard.edu/abs/2017AGUFM.P53A2645M> (accessed March 18, 2021).

- National Academies of Sciences Engineering Medicine (2017) Searching for life across space and time. In *Proceedings of a Workshop*. The National Academies Press, Washington, DC. DOI: <https://doi.org/10.17226/24860>.
- National Academies of Sciences Engineering Medicine (2019) An astrobiology strategy for the search for life in the Universe. The National Academies Press, Washington, DC. DOI: 10.17226/25252.
- Nicholson WL, Fajardo-Cavazos P, Fedenko J, *et al.* (2010) Exploring the low-pressure growth limit: evolution of *Bacillus subtilis* in the laboratory to enhanced growth at 5 kilopascals. *Appl Environ Microbiol* 76:7559–7565.
- Nordheim TA, Dartnell LR, Desorgher L, *et al.* (2015) Ionization of the Venusian atmosphere from solar and galactic cosmic rays. *Icarus* 245:80–86.
- Oparin AI (1959) Introductory address. In *The Origin of Life on the Earth*, edited by AI Oparin, AE Braunshtein, AG Parynskii, and TE Pavlovskayas. Pergamon, pp 1–3.
- Oyama VI, Carle GC, Woeller F, *et al.* (1980) Pioneer Venus gas chromatography of the lower atmosphere of Venus. *J Geophys Res* 85:7891.
- Pasek M and Lauretta D (2008) Extraterrestrial flux of potentially prebiotic C, N, and P to the early Earth. *Orig Life Evol Biosph* 38:5–21.
- Patel BH, Percivalle C, Ritson DJ, *et al.* (2015) Common origins of RNA, protein and lipid precursors in a cyanosulfidic protometabolism. *Nat Chem* 7:301–307.
- Peralta J, Navarro T, Vun CW, *et al.* (2020) A long-lived sharp disruption on the lower clouds of Venus. *Geophys Res Lett* 47:e87221.
- Peralta J, Sánchez-Lavega A, Horinouchi T, *et al.* (2019) New cloud morphologies discovered on the Venus's night during Akatsuki. *Icarus* 333:177–182.
- Pérez-Hoyos S, Sánchez-Lavega A, García-Muñoz A, *et al.* (2018) Venus upper clouds and the UV absorber from MESSENGER/MASCS observations. *J Geophys Res Planets* 123:145–162.
- Persson M, Futaana Y, Fedorov A, *et al.* (2018) H⁺/O⁺ escape rate ratio in the Venus magnetotail and its dependence on the solar cycle. *Geophys Res Lett* 45:10805.
- Persson M, Futaana Y, Ramstad R, *et al.* (2020) The Venusian atmospheric oxygen ion escape: extrapolation to the early solar system. *J Geophys Res Planets* 125:e2019JE006336.
- Phillips RJ and Izenberg NR (1995) Ejecta correlations with spatial crater density and Venus resurfacing history. *Geophys Res Lett* 22:1517–1520.
- Phillips RJ, Raubertas RF, Arvidson RE, *et al.* (1992) Impact craters and Venus resurfacing history. *J Geophys Res Planets* 97:15923–15948.
- Plainaki C, Paschalis P, Grassi D, *et al.* (2016) Solar energetic particle interactions with the Venusian atmosphere. *Ann Geophys* 34:595–608.
- Plane JMC, Flynn GJ, Määttänen A, *et al.* (2018) Impacts of cosmic dust on planetary atmospheres and surfaces. *Space Sci Rev* 214:23.
- Pogoda de la Vega U, Rettberg P, Douki T, Cadet J, and Horneck G (2005) Sensitivity to polychromatic UV-radiation of strains of *Deinococcus radiodurans* differing in their DNA repair capacity. *Int J Radiat Biol* 81: 601–611.
- Polidan RS, Lee G, Ross F, *et al.* (2015) Venus atmospheric maneuverable platform science mission. *AAS/Division for Planetary Sciences Meeting Abstracts*. <http://adsabs.harvard.edu/abs/2015DPS...4721703P> (accessed March 18, 2021).
- Pollack JB (1971) A nongrey calculation of the runaway greenhouse: implications for Venus' past and present. *Icarus* 14:295–306.
- Pollack JB, Toon OB, Whitten RC, *et al.* (1980) Distribution and source of the UV absorption in Venus' atmosphere. *J Geophys Res Space Phys* 85:8141–8150.
- Prinn RG and Fegley B (1987) The atmospheres of Venus, Earth, and Mars: a critical comparison. *Annu Rev Earth Planet Sci* 15:171–212.
- Pyle DM (2012) Small volcanic eruptions and the stratospheric sulfate aerosol burden. *Environ Res Lett* 7:031001.
- Ragent B and Blamont J (1979) Preliminary results of the Pioneer Venus nephelometer experiment. *Science* 203:790–792.
- Ragent B and Blamont J (1980) The structure of the clouds of Venus—results of the Pioneer Venus nephelometer experiment. *J Geophys Res* 85:8089–8105.
- Ragent B, Esposito LW, Tomasko MG, *et al.* (1985) Particulate matter in the Venus atmosphere. *Adv Space Res* 5:85–115.
- Rannou P, Cabane M, Botet R, *et al.* (1997) A new interpretation of scattered light measurements at Titan's limb. *J Geophys Res* 102:10997–11013.
- Raven J and Cockell C (2006) Influence on photosynthesis of starlight, moonlight, planetlight, and light pollution (reflections on photosynthetically active radiation in the Universe). *Astrobiology* 6:668–675.
- Reche I, D'Orta G, Mladenov N, *et al.* (2018) Deposition rates of viruses and bacteria above the atmospheric boundary layer. *ISME J* 12:1154–1162.
- Rossi L, Marcq E, Montmessin F, *et al.* (2015) Preliminary study of Venus cloud layers with polarimetric data from SPICAV/VEX. *Planet Space Sci* 113:159–168.
- Rothschild LJ and Mancinelli RL (2001) Life in extreme environments. *Nature* 409:1092–1101.
- Rummel JD, Beaty DW, Jones MA, *et al.* (2014) A new analysis of Mars "Special Regions": Findings of the Second MEPAG Special Regions Science Analysis Group (SR-SAG2). *Astrobiology* 14:887–968.
- Sagan C (1967) Life on the surface of Venus? *Nature* 216: 1198–1199.
- Sagdeev RZ and Moroz VI (1986) Project VEGA first stage—missions to Venus. *Pisma Astron Zhurnal* 12:5–9.
- Sagdeev RZ, Linkin VM, Blamont JE, *et al.* (1986) The Vega Venus balloon experiment. *Science* 231:1407–1408.
- Sasaki S, Yamagishi A, Yoshimura Y, *et al.* (2019) In situ bio/chemical characterization of Venus cloud particle using Life-signature Detection Microscope for Venus, Venera-D Landing Sites selection and Cloud Layer Habitability Workshop. Institut Kosmicheskii Issledovaniy (Space Research Institute), Moscow, Russia, http://venera-d.cosmos.ru/uploads/media/7_-_20191004_VeneraD_Moskva-sasaki_onthego.pdf
- Sato M, Travis LD, and Kawabata K (1996) Photopolarimetry analysis of the Venus atmosphere in Polar regions. *Icarus* 124:569–585.
- Schleper C, Puhler G, Klenk H-P *et al.* (1996) *Picrophilus oshimae* and *Picrophilus torridus* fam. nov., gen. nov., sp. nov., Two Species of Hyperacidophilic, Thermophilic, Heterotrophic, Aerobic Archaea. *Int J Syst Evol Microbiol* 46:814–816.
- Schulze-Makuch D (2021) The case (or not) for life in the Venusian clouds. *Life* 11, 3:255. <https://doi.org/10.3390/life11030255>
- Schulze-Makuch D, Grinspoon DH, Abbas O, *et al.* (2004) A sulfur-based survival strategy for putative phototrophic life in the Venusian atmosphere. *Astrobiology* 4:11–18.
- Schulze-Makuch D and Irwin LN (2002) Reassessing the possibility of life on Venus: proposal for an astrobiology mission. *Astrobiology* 2:197–202.

- Schulze-Makuch D, Irwin LN, and Fairén AG (2013) Drastic environmental change and its effects on a planetary biosphere. *Icarus* 225:775–780.
- Schulze-Makuch D, Wagner D, Kounaves SP, *et al.* (2018) Transitory microbial habitat in the hyperarid Atacama Desert. *Proc Natl Acad Sci U S A* 115:2670–2675.
- Seager S, Petkowski JJ, Gao P, *et al.* (2020) The venusian lower atmosphere haze as a depot for desiccated microbial life: a proposed life cycle for persistence of the venusian aerial biosphere. *Astrobiology* 21:1206–1223.
- Seager S, Schrenk M, and Bains W (2012) An astrophysical view of earth-based metabolic biosignature gases. *Astrobiology* 12:61–82.
- Seckbach J and Libby WF (1970) Vegetative life on Venus? Or investigations with algae which grow under pure CO₂ in hot acid media at elevated pressures. *Space Life Sci* 2:121–143.
- Seckbach J and Rampelotto P (2015) Polyextremophiles. In *Microbial Evolution under Extreme Conditions*, edited by C Bakermans, De Gruyter, Berlin, Germany, pp 153–170.
- Shalygin EV, Markiewicz WJ, Basilevsky AT, *et al.* (2015) Active volcanism on Venus in the Ganiki Chasma rift zone. *Geophys Res Lett* 42:4762–4769.
- Shimizu M (1977) Ultraviolet absorbers in the Venus clouds. *Astrophys Space Sci* 51:497.
- Skelley AM, Aubrey AD, Willis PA, *et al.* (2007) Organic amine biomarker detection in the Yungay region of the Atacama Desert with the Urey instrument. *J Geophys Res Biogeosci* 112: G04S11.
- Smith DJ (2013) Microbes in the upper atmosphere and unique opportunities for astrobiology research. *Astrobiology* 13:981–990.
- Smith DJ, Griffin DW, McPeters RD, *et al.* (2011) Microbial survival in the stratosphere and implications for global dispersal. *Aerobiologia* 27:319–332.
- Smith DJ, Ravichandar JD, Jain S, *et al.* (2018) Airborne bacteria in Earth's lower stratosphere resemble taxa detected in the troposphere: results from a new NASA Aircraft Bioaerosol Collector (ABC). *Front Microbiol* 9. doi: 10.3389/fmicb.2018.01752.
- Smith DJ, Timonen HJ, Jaffe DA, *et al.* (2013) Intercontinental dispersal of bacteria and archaea by transpacific winds. *Appl Environ Microbiol* 79:1134–1139.
- Sousa-Silva C, Seager S, Ranjan S, *et al.* (2020) Phosphine as a biosignature gas in exoplanet atmospheres. *Astrobiology* 20: 235–268.
- Steffes PG and Eshleman VR (1982) Sulfuric acid vapor and other cloud-related gases in the Venus atmosphere: abundances inferred from observed radio opacity. *Icarus* 51:322–333.
- Stevenson A, Burkhardt J, Cockell CS, *et al.* (2015) Multiplication of microbes below 0.690 water activity: implications for terrestrial and extraterrestrial life. *Environ Microbiol* 17:257–277.
- Stofan ER, Brian AW, and Guest JE (2005) Resurfacing styles and rates on Venus: assessment of 18 Venusian quadrangles. *Icarus* 173:312.
- Su W, Minnis P, Liang L, *et al.* (2020) Determining the daytime Earth radiative flux from National Institute of Standards and Technology Advanced Radiometer (NISTAR) measurements. *Atmos Meas Tech* 13:429–443.
- Sun W, Xiao E, Krumins V, *et al.* (2019) Comparative analyses of the microbial communities inhabiting coal mining waste dump and an adjacent acid mine drainage creek. *Microbial Ecol* 78:651–664.
- Surkov YA, Andrejchikov BM, and Kalinkina OM (1973) On the content of ammonia in the Venus atmosphere based on data obtained from Venera 8 automatic station. *Akademiia Nauk SSSR Doklady* 213:296–298.
- Svedhem H, Titov D, Taylor F, and Witasse O (2009) Venus Express mission. *J Geophys Res Planets* 114: <http://adsabs.harvard.edu/abs/2009JGRE.114.0B33S>
- Tirard S (2017) J.B.S. Haldane and the origin of life. *J Genet* 96:735–739.
- Titov DV, Ignatiev NI, McGouldrick K, *et al.* (2018) Clouds and hazes of Venus. *Space Sci Rev* 214:126.
- Toon OB, Turco RP, and Pollack JB (1982) The ultraviolet absorber on Venus: amorphous sulfur. *Icarus* 51:358–373.
- Travis LD (1975) On the origin of ultraviolet constraints on Venus. *J Atmos Sci* 32:1190–1200.
- Turco RP, Toon OB, Whitten RC, *et al.* (1983) Venus: mesospheric hazes of ice, dust, and acid aerosols. *Icarus* 53:18–25.
- Vallentyne JR (1963) Environmental biophysics and microbial ubiquity. *Ann N Y Acad Sci* 108:342–352.
- Vandaele AC, Korablev O, Belyaev D, *et al.* (2017a) Sulfur dioxide in the Venus atmosphere: I. Vertical distribution and variability. *Icarus* 295:16–33.
- Vandaele AC, Korablev O, Belyaev D, *et al.* (2017b) Sulfur dioxide in the Venus Atmosphere: II. Spatial and temporal variability. *Icarus* 295:1–15.
- Villanueva G, Cordiner M, Irwin P, *et al.* (2020) No phosphine in the atmosphere of Venus. pp arXiv:2010.14305.
- Volkov VP (1991) Lithospheric and atmospheric interaction on the planet Venus. In: *NAS-NRC, Planetary Sciences: American and Soviet Research*, pp 218–233. <https://ui.adsabs.harvard.edu/abs/1991plsa.rept.218V>
- von Zahn U and Moroz VI (1985) Composition of the Venus atmosphere below 100 km altitude. *Adv Space Res* 5: 173.
- Way MJ and Del Genio AD (2020) Venusian habitable climate scenarios: modeling Venus through time and applications to slowly rotating Venus-like exoplanets. *J Geophys Res Planets* 125:e2019JE006276.
- Way MJ, Del Genio AD, Kiang NY, *et al.* (2016) Was Venus the first habitable world of our Solar System? *Geophys Res Lett* 43:8376–8383.
- Weller MB and Kiefer WS (2020) The physics of changing tectonic regimes: implications for the temporal evolution of mantle convection and the thermal history of Venus. *J Geophys Res Planets* 125:e05960.
- Westall F, de Vries ST, Nijman W, *et al.* (2006) The 3.466 Ga “Kitty’s Gap Chert,” an early Archean microbial ecosystem. In *Processes on the Early Earth. Special Paper of the Geological Society of America*, Vol. 405, Boulder, Colorado, pp 105–132.
- Westall F, Hickman-Lewis K, and Cavalazzi B (2019) Biosignatures in deep time. In: *Biosignatures for Astrobiology*, edited by B Cavalazzi and F Westall. Advances in Astrobiology and Biogeophysics. Springer, Cham, pp 145–164.
- Wilquet V, Drummond R, Mahieux A, *et al.* (2012) Optical extinction due to aerosols in the upper haze of Venus: four years of SOIR/VEX observations from 2006 to 2010. *Icarus* 217:875–881.
- Wilson L and Head JW (1983) A comparison of volcanic eruption processes on Earth, Moon, Mars, Io and Venus. *Nature* 302:663–669.

- Wilson TW, Ladino LA, Alpert PA, *et al.* (2015) A marine biogenic source of atmospheric ice-nucleating particles. *Nature* 525:234.
- Woese C (1998) The universal ancestor. *Proc Natl Acad Sci U S A* 95:6854–6859.
- Wolf ET and Toon OB (2010) Fractal organic hazes provided an ultraviolet shield for early Earth. *Science* 328:1266–1268.
- Wu Z, Wan H, Xu J, *et al.* (2018) The near-UV absorber OSSO and its isomers. *Chem Commun* 54:4517–4520.
- Yamagishi A, Satoh T, Enya K, *et al.* (2016) LDM (life detection microscope): in situ imaging of living cells on surface of Mars. *Trans Jpn Soc for Aeronaut Space Sci Aerospace Technol Jpn* 14:Pk_117–Pk_124.
- Young AT (1973) Are the clouds of Venus sulfuric acid? *Icarus* 18:564–582.
- Young AT (1975) The clouds of Venus. *J Atmos Sci* 32:1125.
- Young AT (1977) An improved Venus cloud model. *Icarus* 32: 1–26.
- Young RE, Walterscheid RL, Schubert G, *et al.* (1994) Characteristics of finite amplitude stationary gravity waves in the atmosphere of Venus. *J Atmos Sci* 51:1857–1875.
- Zahnle KJ, Lupu R, Catling DC, *et al.* (2020) Creation and evolution of impact-generated reduced atmospheres of early Earth. *Planet Sci J* 1:11 (21pp).
- Zibaii MI, Kazemi A, Latifi H, *et al.* (2010) Measuring bacterial growth by refractive index tapered fiber optic biosensor. *J Photochem Photobiol B Biol* 101:313–320.
- Zolotov MY (1991a) Redox conditions of the nearsurface atmosphere of Venus I. Some reevaluations. <https://ui.adsabs.harvard.edu/abs/1991LPI...22.1571Z> (accessed March 18, 2021).
- Zolotov MY (1991b) Redox conditions of the nearsurface atmosphere of Venus. II. Equilibrium and disequilibrium

models. *Abstracts of the Lunar and Planetary Science Conference*, 22:1573. <https://ui.adsabs.harvard.edu/abs/1991LPI...22.1573Z> (accessed March 18, 2021).

Address correspondence to:
 Sanjay S. Limaye
 Space Science and Engineering Center
 University of Wisconsin–Madison
 1225 West Dayton Street
 Madison, WI 53706
 USA

E-mail: sslimaye@wisc.edu

Submitted 24 March 2020

Accepted 1 February 2021

Abbreviations Used

AE	= Aerosols
a_w	= water activity
CH ₄	= methane
GC	= Geochemistry
GH	= <i>Geologic History</i>
GOI	= Goals, Objectives, and Investigations
HO	= Hydrous Origins
IN	= Interactions
ISAV	= Izmeritel' Spektrov Atmosfery Venery
OG	= Outgassing
PV LNMS	= Pioneer Venus Large Probe Neutral Mass Spectrometer
UA	= Unknown Absorber
UV	= ultraviolet
VEXAG	= Venus Exploration Analysis Group