Venus’ Spectral Signatures and the Potential for Life in the Clouds

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Abstract

The lower cloud layer of Venus (47.5–50.5 km) is an exceptional target for exploration due to the favorable conditions for microbial life, including moderate temperatures and pressures (~60°C and 1 atm), and the presence of micron-sized sulfuric acid aerosols. Nearly a century after the ultraviolet (UV) contrasts of Venus’ cloud layer were discovered with Earth-based photographs, the substances and mechanisms responsible for the changes in Venus’ contrasts and albedo are still unknown. While current models include sulfur dioxide and iron chloride as the UV absorbers, the temporal and spatial changes in contrasts, and albedo, between 330 and 500 nm, remain to be fully explained. Within this context, we present a discussion regarding the potential for microorganisms to survive in Venus’ lower clouds and contribute to the observed bulk spectra. In this article, we provide an overview of relevant Venus observations, compare the spectral and physical properties of Venus’ clouds to terrestrial biological materials, review the potential for an iron- and sulfur-centered metabolism in the clouds, and identify spectral and biological experiments that could measure the habitability of Venus’ clouds. Together, our lines of reasoning suggest that particles in Venus’ lower clouds contain sufficient mass balance to harbor microorganisms, water, and solutes, and potentially sufficient biomass to be detected by optical methods. As such, the comparisons presented in this article warrant further investigations into the prospect of biosignatures in Venus’ clouds. Key Words: Venus—Clouds—Life—Habitability—Microorganism—Albedo—Spectroscopy—Biosignatures—Aerosol—Sulfuric Acid. Astrobiology 18, xxx–xxx.

1. Introduction

The habitability of Venus’ clouds has been a subject of discussion for several decades (Morowitz and Sagan, 1967; Grinspoon, 1997) yet has gained limited traction as a popular target in astrobiology research. Initially stirring excitement, Cockell (1999) concluded that the conditions between the lower and middle atmosphere were conducive to (terrestrial) biology, and that conditions at higher altitudes would freeze but not necessarily kill microorganisms. Since then, subsequent studies, such as those by Schulze-Makuch et al. (2004), have highlighted the potential for life in Venus’ cloud layers due to favorable chemical and physical conditions, including the presence of sulfur compounds, carbon dioxide (CO2), and water, and moderate temperatures (0–60°C) and pressures (~0.4–2 atm).

In this hypothesis article, we further consider these conditions and examine the potential for terrestrial microorganisms to both survive within and contribute to the bulk spectral properties of Venus’ clouds. Herein, we provide a short review of relevant Venus observations, compare the properties of Venus’ clouds to terrestrial biological materials, and present conceivable mechanisms...
of transport from the surface to the clouds. Finally, we identify spectral and biological experiments, including instruments, which can address the habitability of Venus’ clouds through use of ground-based terrestrial analogues and \textit{in situ} measurements at Venus.

2. Overview of Venus’ Spectral Observations

Comparisons of spectral measurements (Fig. 1) obtained from the Akatsuki and MESSENGER missions show several differences in albedo across the spectrum in the ultraviolet

![Images of clouds on Venus (A–H) and Earth (I–N) demonstrating the relationships of contrast with wavelength. The images were obtained at (A) 283 nm, (B) 365 nm, (C) 430 nm, (D) 830 nm, (E) 900 nm, (F) 2.02 μm, (G) 1.74, 2.26, and 2.32 μm, and (H) 8–12 μm. Images A, B, E, and F were taken by the Akatsuki orbiter using filters with central wavelengths equal to the aforementioned wavelengths on May 6, 2016. Images C and D were taken by the MDIS camera on the MESSENGER spacecraft (Hawkins et al., 2009) on June 6, 2007. Images G (March 25, 2016) and H (May 6, 2016) show the nightside of Venus and were, respectively, taken from the Akatsuki orbiter with the IR2 and LIR cameras; the bandwidth of the Akatsuki dayside filter was much wider (14 nm) than that of the MESSENGER MDIS filters (5 nm), and the orientation of the MESSENGER images is somewhat more tilted, compared with the Akatsuki images (rotation axis ∼45°). For Earth’s clouds, images were obtained between (I) 0.5–0.75 μm, (J) 1.55–1.75 μm, (K) 3.5–4.0 μm, (L) 6.5–7.5 μm, (M) 10.5–11.5 μm, and (N) 11.5–12.5 μm. Akatsuki data are available at: https://www.darts.isas.jaxa.jp/planet/project/akatsuki; Earth images were obtained by the INSAT-3D weather satellite (Katti et al., 2006) operated by ISRO/Space Applications Center.}
Venus is globally covered in clouds and devoid (or nearly devoid) of contrasts in the visible and IR wavelengths in dayside images (images C–F). Rather, contrasts in the cloud cover are observed only at wavelengths shorter than blue in reflected sunlight (images A and B), and at near-IR wavelengths (1.7–2.4 μm) on the nightside (image G). Despite spacecraft investigations from orbit and entry probes, the chemical and physical properties of these contrasts are still unknown, including the identities of the contrasting substances, the sources of these substances, the lack of mixing, and any potential sinks.

Thermal IR images (8–12 μm) show small-scale (~50 km) contrasts of <2 K in brightness temperature on the day and night hemispheres at all latitudes (image H), except poleward of ~65° latitude in both hemispheres. At these latitudes, Hadley circulation is presumed to lower the cloud tops, due to downwelling in the polar regions, as observed near the top and bottom of the Venus images (images F and H). In contrast, clouds on Earth are often observed in satellite images as discrete features, with clear air in between, at visible and (short to thermal) IR wavelengths (images I–N). Unlike on Earth, where the contrasts are independent of wavelength, the observed contrasts in Venus’ global clouds vary in morphology and magnitude at wavelengths from visible to IR (Limaye et al., 2018), as seen from images A–H in Figure 1.

The Venus UV contrasts were first observed in Earth-based photographs (Ross, 1928) and subsequently characterized by ground-based polarimetry (Hansen and Hovenier, 1974), spectroscopy (Barker, 1978), remote spacecraft observations (Kawabata et al., 1980; Titov et al., 2008), and entry probes (Knollenberg and Hunten, 1980; Knollenberg et al., 1980; Esposito et al., 1983; Knollenberg, 1984). Together, these studies indicate that the global cloud cover is composed of sulfuric acid droplets (~1.1 μm equivalent radius) in a mixture consisting mostly of small particles (~0.2–0.3 μm equivalent radius), with larger particles (~2–8 μm diameter) present at lower altitudes (Knollenberg and Hunten, 1979). In addition, slight differences in cloud particle properties at the polar regions have been inferred from the Venus Express data (Wilson et al., 2008).

Provided in Figure 2 is a collective summary of Venus’ spectra between 200 and 1000 nm, including global geometric or spherical albedo estimates (Irvine, 1968; Travis, 1975; Moroz et al., 1985) and measurements from ground-based telescopes (Barker et al., 1975) and the MESSENGER spacecraft during the second Venus fly-by (Perez-Hoyos et al., 2013; Pérez-Hoyos et al., 2017). Also shown is the calculated difference between the VIRA cloud model and the MESSENGER spectra as reported by Perez-Hoyos et al. (2013), which gives an indication of the spectral absorption by the unknown materials in the clouds of Venus.

We note here that the original identification of the sulfuric acid composition of Venus’ cloud particles was derived by matching the index of refraction, required for matching the phase dependence of disk-integrated polarization at different optical wavelengths (Hansen and Hovenier, 1974), and not by spectral identification. Interpretation of Venus’ UV and IR spectra, along with questions about the cloud composition and UV absorbers, are summarized by Krasnopolsky (2006) and in chapters within the review books on Venus (Hunten et al., 1983) and Venus II (Bougher et al., 1989).

Herein, we briefly summarize the pertinent cloud properties, which must play a part in the absorption of incident sunlight and the observed contrasts. Travis (1975) pointed out the differences in spectral dependence of albedo and cloud contrasts, thus indicating at least two different absorbers. Pollack et al. (1980) identified gaseous sulfur dioxide (SO₂) as a potential absorber and ruled out many other suggested

FIG. 2. Venus’ spectra as measured by Moroz et al. (1985), Irvine (1968), Travis (1975), Wallace et al. (1972) (scaled geometric albedo), MESSENGER (Perez-Hoyos et al., 2013; Pérez-Hoyos et al., 2017), and Barker et al. (1975), including the unexplained absorption, as calculated from the difference between the VIRA cloud model and the MESSENGER spectra. The real Venus spectrum varies with location and time, so the residual curve is illustrative and not definitive.
candidates due to insufficient spectral overlap. Esposito and Travis (1982) suggested from analysis of the polarization data obtained from the Pioneer Venus orbiter that the differential polarization between bright and dark UV features could not be explained by haze abundance variations, which favored a chemical model where water vapor and molecular oxygen are depleted at the cloud tops.

Zasova et al. (1981) pursued a suggestion by Kuiper (1969) to propose the presence of incompletely hydrated iron chloride in the clouds, and offered that SO$_2$ (<330 nm) along with ferric chloride (FeCl$_3$) (>330 nm) could explain the observed lowered albedo <500 nm. Partial contribution of SO$_2$ to the UV absorption of incident solar radiation has been inferred through observations by Venus Express (Lee et al., 2015b), as well as those from the Hubble Space Telescope (Jessup et al., 2015), and can also be discerned from differences in the 283 and 365 nm appearance of Venus (images A and B of Fig. 1) taken by Akatsuki at 283 nm (where there is some absorption by SO$_2$) and 365 nm (where the contrast peaks, and SO$_2$ does not absorb).

Based on Venus Express measurements, however, analysis of the glory feature, as observed in unpolarized (Markiewicz et al., 2014) and polarized light (Rossi et al., 2015), yielded values for the index of refraction that were larger than those inferred by Hansen and Hovenier (1974). In fact, Markiewicz et al. (2014) found that their measured indices of refraction exceeded the values expected from sulfuric acid cloud particles, thereby suggesting the presence of FeCl$_3$ attached to the sulfuric acid droplets, or within the droplets to serve as cloud condensation nuclei. Furthermore, Krasnopolsky (2017) concluded that sulfur aerosols cannot be the UV absorber since the required abundance and vertical profile were incompatible with Venera 14 observations; however, the presence of FeCl$_3$ was compatible with contributions toward the higher indices of refraction inferred by Markiewicz et al. (2014). Nevertheless, some doubt remains as to whether the analysis of glory features can provide accurate inferences of the index of refraction between 1.07 and 1.7 (Laven, 2008), which encompasses the range of values for Venus.

3. Spatial Contrasts in the UV Spectrum

From ground-based and spacecraft observations, it is widely accepted that Venus’ clouds contain micron-sized particles (Hansen and Hovenier, 1974; Knollenberg et al., 1980) consisting of sulfuric acid solutions (75–98%). In fact, all UV and blue images of Venus (Belton et al., 1992) show small-scale (10–100 km) contrasts at 270 nm (Pioneer Venus OCPP, polarimetry mode; Limaye, 1984), 283 nm (Akatsuki), 365 nm (Mariner 10, Venus Monitoring Camera [VMC] on Venus Express), 410 nm (Galileo), and 430 nm (MESSENGER MDIS; Peralta et al., 2017). These contrast features have been observed to evolve over time scales ranging from minutes (Limaye et al., 2018), on small scales (~5 km), to days and weeks (del Genio and Ros sow, 1982) on larger spatial scales (~100 km). Temporal changes in cloud contrasts have additionally been noted by Ross (1928) and in spacecraft images (Murray et al., 1974; Rossow et al., 1980; Titov et al., 2012).

Figure 3 provides exemplar images of the equatorial region of Venus, which illustrate the variability of the UV contrasts, over a variety of scales as captured by the VMC on the Venus Express orbiter (Titov et al., 2012). Similarly, Figure 4 provides two mapped UV images from the VMC on Venus Express taken only 12 min apart. The short-term evolution (growth and decay in terms of areal extent and contrast) of these features has been challenging to explain in terms of cloud structure, cloud top altitude differences (Ignatiev et al., 2009), and/or purely dynamical processes. Nevertheless, absorption <330 nm has been attributed to SO$_2$ and sulfur monoxide (SO) as a result of ground-based observations (Barker, 1979), and spacecraft (Conway et al., 1979; Stewart et al., 1979; Pérez-Hoyos et al., 2017) and entry probe measurements (Sukrov et al., 1978; Oyama et al., 1980).

Between 200 and 500 nm, other proposed absorbing candidates (besides SO$_2$) include fine graphite grains (Shimizu, 1977), elementary sulfur polymers (Young, 1973; Hapke and Nelson, 1975; Toon et al., 1982), octasulfur (Schulze-Makuch and Irwin, 2006), nitric oxide (Shaya and Caldwell, 1976), croconic acid (Hartley et al., 1989), hydrated FeCl$_3$ (Kuiper, 1969), hydrobromic acid (Sill, 1975), and chloride (Pollack et al., 1980). Besides SO$_2$ and SO, other compounds absorbing <330 nm, but not between 330 and 600 nm (Mills et al., 2007), include carbon sulfide (Barker, 1978; Young, 1978) and carbonyl sulfide (Bezard et al., 1990). Esposito et al. (1983) and Krasnopolsky (2006) have also published discussions regarding the unknown “ultraviolet absorber.” Furthermore, Zasova et al. (2007) point out that the spectrally active compound/s may absorb in both the visible and near IR regions.

Sulfur aerosols have also been postulated as the UV absorbers (Krasnopolsky, 2016, 2017), where analysis of the (limited) data from in situ measurements has suggested a role for FeCl$_3$. In addition, a sulfur oxide isomer (OSSO) has been recently proposed as an alternative UV absorber (between 320 and 400 nm) and a potential sulfur reservoir. However, the lifetimes of the two isomers of OSSO are very short (a few seconds), and the estimates of opacity are uncertain (Frandsen et al., 2016). Nevertheless, recent studies (Pérez-Hoyos et al., 2017) have concluded that the identity of the UV absorber in the clouds is still unresolved, even after considering the newly proposed isomers of disulfur dioxide (as inferred from analysis of spectroscopic observations from the MESSENGER spacecraft made during the Venus fly-by).

On the dayside, the UV component of the incident sunlight is progressively absorbed, as the radiation penetrates the cloud tops and travels downward, and is almost immeasurable at an altitude of 57 km (Tomasko et al., 1980), thereby preventing detection of the absorber by using sunlight. However, the absorber is present below this altitude, as inferred from spectroscopic measurements by the VeGa 1 and VeGa 2 landers. Using a xenon lamp, these probes descended on the nightside and established that the UV absorbers are present at the highest altitudes measurable (64 km), down to the base of the clouds at 47 km (Bertaux et al., 1996). In terms of spatial and temporal variability of the absorbers, studies of the cloud tops support such fluctuations for SO$_2$ (Encrenaz et al., 2016); however, the reasons or causes remain unknown, as detailed investigations of spatial and temporal variability of contrast features are yet to be conducted. Similarly, near-simultaneous Akatsuki observations of Venus at 283 and 365 nm also indicate (Lee
et al., 2017) that SO₂ variations can partly explain the differences in contrasts; however, as noted earlier, there are a number of other trace species that may contribute to the observed variations.

Based on observations of the glory feature in Venus’ images, FeCl₃ has also been re-proposed as a candidate (Markiewicz et al., 2014) and remains the most likely contender as a UV contrasting agent (Krasnopolsky, 2017), as FeCl₃ in the clouds has also been detected by X-ray fluorescence data (Krasnopolsky, 1985; Andreychikov et al., 1987). However, Zasova et al. (1981) note that FeCl₃ is not stable in the presence of sulfuric acid, presumably due to

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**FIG. 3.** Views of the equatorial region of Venus from the Venus Monitoring Camera obtained using a 365 nm filter; numbers below each view indicate the orbit number of Venus Express (nominal period of 24 h), while the white bar in the lower right of each image indicates a 200 km scale. Figure adapted from Titov et al. (2012).

**FIG. 4.** Rapid changes in the shape, size, and magnitude of the UV contrasts, as observed through distribution and intensity of the white thread-like lines, with specific examples highlighted by the black ovals. Images show Venus’ clouds at low latitudes (where the absorption of incident solar radiation is greater) and were obtained 12 min apart, on a scale of 5 m/pixel, on September 27, 2016, at 04:45:58 (A) and at 04:57:53 UT (B). Mapped views include grid lines 5° apart in latitude and longitude. These images were obtained by the Akatsuki mission from the UVI camera (Yamazaki et al., 2017) and used the 365 nm filter. They were processed to bring out subtle contrasts by using ratios of local brightness deviations and average brightness. UV, ultraviolet; UVI, Ultraviolet Imager.
formation of Fe$_2$(SO$_4$)$_3$. As such, a continuous resupply of FeCl$_3$ would be required to support the observed contrasts. The most logical source for resupply of FeCl$_3$ would be the Venus’ surface, since on Earth, FeCl$_3$ is commonly found in volcanic regions as the mineral molysite (which is brownish or reddish in color, and soluble in water). This assessment, however, introduces several questions as to how FeCl$_3$ particles are transported, on the timescales of the contrasts, to ~50 km above the Venus’ surface, and whether FeCl$_3$ particles act as cloud condensation nuclei.

In summary, the identities of the absorber(s) in the 330–600 nm region remain uncertain. In addition, current cloud models (and observations) do not adequately explain the origin of the contrasts and the spatial and temporal changes in opacity (i.e., lack of mixing of the absorbers and spatial variations in abundances over time). Therefore, in the absence of cohesive physical and chemical explanations, we present a discussion of Venus’ clouds serving as a favorable habitat for life, where biological sources may contribute to the observed spectral contrasts.

4. Can Biology Contribute to Venus’ Spectral Signatures?

The possibility of Venus life in the clouds was initially discussed by Morowitz and Sagan (1967), Grinspoon (1997) and followed up by Cockell (1999), Schulze-Makuch and Irwin (2002), Schulze-Makuch et al. (2004), and considered by Grinspoon and Bullock (2007). These reports introduced the premise that acid-resistant terrestrial bacteria could potentially tolerate the Venus’ cloud environment, and metabolize through phototrophic and chemotrophic means. In his book “Venus Revealed,” Grinspoon (1997) proposed that a photosynthetic pigment may serve as the “unknown ultraviolet absorber.” In fact, Grinspoon posited that the “unknown ultraviolet absorber” may represent one of four possible signs of life, with the remaining signs, including absorption of solar energy by (micro)organisms as a driving force for superrotation, the presence of larger and irregularly shaped cloud particles (mode 3) that may be “creatures,” and the presence of bright radar signatures on the mountain tops, which may be covered with life. Grinspoon and Bullock (2007) also explored life in the clouds and discuss Venus life in the context of comparative planetary astrobiology. In fact, numerous studies have contributed to the current understanding of Venus’ clouds, including analysis of data collected by the Galileo orbiter, during its fly-by of Venus (Carlson et al., 1991; Grinspoon et al., 1993), and by the Venus Express mission (Ignatiev et al., 2009; Tsang et al., 2010; Barstow et al., 2012; Cottini et al., 2012; Parkinson et al., 2013a, 2013b, 2015).

As is the case for any discussion of extremotolerant biology, parameters such as temperatures, radiation levels, and the presence of available water serve as major limitations for habitability. However, in the context of Venus’ clouds, these specific issues are likely nonlimiting. As displayed in Figure 5, the bottom cloud layer of Venus at ~48–50 km possesses rather favorable conditions, with temperatures of ~60°C and pressures of ~1000 mbar (~1 atm). Furthermore, as described by Cockell (1999), UV radiation in Venus’ clouds is likely not prohibitive to life, as UV flux in the upper levels of the atmosphere of Venus is comparable with the surface flux of Archean Earth, when photosynthetic life was considered to be present (Olson, 2006), and substantially attenuated within the Venus’ cloud layer due to atmospheric CO$_2$ and the aforementioned UV absorbers.

In terms of water availability, water vapor values (mixing ratios) at altitudes of 40 km and higher are thought to vary widely from 20 to 50 ppm at latitudes of 60°, to >500 ppm near the equator, with global averages suggesting mixing ratios of 40–200 ppm (Donahue and Hodges, 1992; Barstow et al., 2012). However, desiccation in the Venus’ atmosphere may be avoidable, despite these low water abundances, due to the hygroscopic nature of sulfuric acid [which would likely yield droplets or aerosols containing liquid water (Carleton et al., 1997; McGouldrick et al., 2011), even at high altitudes due to the freezing point depression]. Nonetheless, any inferences regarding the cloud particles, either near the cloud tops or at high altitudes, are the result of remotely sensed observations and not conclusive with respect to particle states as liquid or solid. However, if the Venus’ cloud particles are spherical, then the prevailing theory is that the droplets must be liquid (Hansen and Hovenier, 1974).

Across the cloud layers, the sulfuric acid aerosols are described in roughly three size modes ranging in diameter between ~0.4–0.6 μm (mode 1), ~2–2.8 μm (modes 2 and 2’), and ~7.3–8 μm (mode 3), with a small number of particles as large as ~35 μm in diameter, as measured by the Venera missions and inferred from Galileo data (Knollenberg et al., 1980; Grinspoon et al., 1993). For the total cloud layer (lower, middle, and upper clouds), ~70% of the columnar mass loading (~32 mg cm$^{-3}$, assuming a total 12.5 km column) arises from particles in the lower clouds (~21 mg cm$^{-3}$), where ~94% of this mass is associated with mode 3 particles (~20 mg cm$^{-3}$), ranging in diameter of 8.0±2.5 μm. Assuming that these particles are indeed suspensions (or possibly heterogeneous mixtures similar to terrestrial aerosols), then the majority of the observed UV contrasting materials and/or the major biomass are likely to be found in the lower clouds. In comparison, the middle cloud layer comprises only 24% of the total cloud columnar mass loading (assuming a 6 km column), despite the potential habitability of this region, where temperatures and pressures range from 10–50°C and 400–800 mbar.

For the lower cloud layer (47.5–50.5 km), particle densities are reported (Knollenberg and Hunten, 1980; Ragent et al., 1985) to be ~50 particles cm$^{-3}$ for the larger sizes (~2–8 μm diameter) and 600 particles cm$^{-3}$ for the smallest sizes (~0.4 μm diameter). In the middle and upper cloud region (~50–70 km), the respective particle densities are 10–50 particles cm$^{-3}$ (~2–8 μm diameter) and 300–800 particles cm$^{-3}$ (~0.3–0.4 μm diameter), with the largest particle densities of ~800 particles cm$^{-3}$ (~0.4 μm diameter) being detected at the highest altitudes. Among these particle distributions, the largest masses are associated with the ~5–15 μm-sized particles in the lower clouds, and ~2–15 μm-sized particles in the middle clouds; with mass loading estimates ranging ~0.1–100 and ~0.01–10 mg m$^{-2}$ for the lower and middle cloud regions (50.5–56.5 km), respectively, as reported by Knollenberg et al. (1980).

In comparison, the primary biological aerosols in Earth’s atmosphere range in particle size from nanometer to submillimeter, and are composed of differing biological materials, including bacteria, fungal spores, fungal hyphens fragments,
pollen, plant spores, plant debris, algae, and viral particles (Morris et al., 2011; Fröhlich-Nowoisky et al., 2016). A majority of these materials are associated with dust particles and black carbon, while a minority is suspended in water vapor or sea spray (Smith et al., 2013). Global estimates of the total primary biological aerosols indicate \( \sim 10^6 \) particles m\(^{-3}\), where the median diameters of particles containing cultivable bacteria are reported to be \( \sim 4 \) \( \mu \)m at continental sites, and \( \sim 2 \) \( \mu \)m at coastal sites (Després et al., 2012). Global measurements show that primary biological aerosols are dominated by bacteria at \( \sim 10^5 \) cells m\(^{-3}\) (Fröhlich-Nowoisky et al., 2016), thus amounting to a biomass of \( \sim 5 \) ng m\(^{-3}\) when assuming a buoyant cell density of 1,041 g cm\(^{-3}\) (Bakken and Olsen, 1983). However, localized measurements in the cloud-forming regions of the lower troposphere reveal much higher abundances of \( 8.1 \times 10^4 \) cells mL\(^{-1}\), or \( \sim 10^{11} \) cells m\(^{-3}\) (Amato et al., 2007), amounting to a theoretical cloud biomass of \( \sim 44 \) mg m\(^{-3}\).

Thus, for Venus’ lower clouds, the mass loading estimates (0.1–100 mg m\(^{-3}\)) are comparable to the upper biomass value for terrestrial biological aerosols (\( \sim 44 \) mg m\(^{-3}\)), while the particle size regime (\( \leq 8 \) \( \mu \)m) opens the possibility that the clouds may similarly harbor suspensions of single cells or aggregated microbial communities. In theory, the 2- and 8-\( \mu \)m-sized particles (modes 2 and 3) could harbor a maximum of \( \sim 10^9 \) and \( 10^{10} \) cells m\(^{-3}\), respectively; these estimates assume spherical cloud particles, spherical microorganisms with a mean diameter of 1 \( \mu \)m, and particle densities of 50 particles cm\(^{-3}\) (5 \times 10^9 \) particles m\(^{-3}\)). Using these assumptions (including buoyant cell density), the theoretical and maximum biomass loadings for these particles amount to 0.2 and 14 mg m\(^{-3}\), respectively. Again, these values are comparable to the upper biomass levels of bacterial aerosols on Earth (\( \sim 44 \) mg m\(^{-3}\)). Moreover, when compared with Venus, these values are respectively \( \sim 6 \) and \( \sim 1.5 \)-fold lower than the columnar mass loadings for the mode 2 and 3 particles (1.3 and 20 mg m\(^{-3}\)) from the lower cloud region (when assuming a 3 km column depth), and well within the aforementioned range of total mass loading estimates. These calculations and comparisons suggest that the mode 2 and 3 particles, from Venus’ lower cloud layer, possess sufficient mass balance to harbor microorganisms, solutes, and water.

To date, there are no in-depth studies focusing on the spectroscopy of aerosolized microorganisms or biomolecules under Venus conditions. Under terrestrial conditions, there are limited reports on the passive detection of aerosolized Bacillus spores using IR spectroscopy (FT-IR), with measurements on \( \sim 10^4 \) to \( 10^7 \) cells m\(^{-3}\) providing (mass) extinction coefficients (at \( \sim 1100 \) cm\(^{-1}\)) in the range of \( \sim 720–1400 \) cm\(^{-1}\) g\(^{-1}\) (Gurton et al., 2001; Ben-David, 2003; Ben-David and Ren, 2003; Blecka et al., 2012). Furthermore, turbidity (or optical density) measurements (at 540 nm) on concentrated aqueous suspensions of bacteria (\( \sim 10^{15} \) cells m\(^{-3}\)) provide extinction coefficients of \( \sim 4000 \) cm\(^{-1}\) g\(^{-1}\) (Spaun, 1962). In addition, there are multiple reports on the remote sensing of microbial blooms in fresh and ocean waters, where the intense absorption and/or fluorescence properties of photosynthetic pigments (e.g., chlorophyll \( a \) and phycocyanin) yield very large extinction coefficients, with \( \sim 2 \times 10^3 \) cm\(^{-1}\) g\(^{-1}\) (at \( \sim 640 \) nm) representing the terrestrial global average of chlorophyll \( a \) in the oceans (Bidigare et al., 1990; Schalles, 2006; Hunter et al., 2010).

The lower clouds of Venus exhibit comparable extinction coefficients ranging from \( \sim 500 \) to \( 5000 \) cm\(^{-1}\) g\(^{-1}\), as estimated from size particle spectrometer (LCPS) measurements at 600 nm, and calculated using a density of 2 mg cm\(^{-3}\), as indicated by Knollenberg and Hunten (1980). These total values suggest that Venus’ lower cloud region could harbor sufficient biomass to be characterizable and quantifiable through optical techniques. Moreover, comparison of Venus and Earth extinction coefficients supports the plausibility of the presence of high cell densities and/or appreciable concentrations of chromogenic pigments in Venus’ lower clouds (as inferred from measurements at 600 nm).

If Venus’ clouds indeed harbor biology, then these biotic materials could potentially exhibit spectral signatures that overlap with those of Venus’ clouds. For example, the observed contrasts at 270, 283, 365, 410, and 430 nm (Pioneer, Akatsuki, Galileo, and MESSENGER) are tantalizingly similar to the absorption properties of terrestrial biological molecules, which have peak absorptions at wavelengths across the UV and visible regions of the electromagnetic spectrum. Examples include nucleic acids and proteins,
which have respective $\lambda_{\text{max}}$ values of 260 and 280 nm, where absorbances from the molecules often overlap, as is shown in Figure 6A for cellular extracts of *Escherichia coli*. *Acidithiobacillus ferrooxidans* has a UV spectrum that is very similar to that of Venus (Wieckowski et al., 1999). Typical absorbances of iron-containing proteins (which would presumably be high in abundance in an Fe-rich environment) are also shown in Figure 6A, with Fe–heme and iron–sulfur (Fe–S) cluster proteins displaying $\lambda_{\text{max}}$ values between 350 and 450 nm (for the coordinated iron complex within the protein) and at $\sim$280 nm (for the aromatic amino acids within the protein). Across the visible spectrum, many organic cofactors (or biochemicals) such as pterins, carotenoids, and chlorophylls also strongly absorb between 300 and 500 nm (Fig. 6B), with the photosynthetic pigments additionally absorbing in the far visible and near IR regions (Fig. 6B).

As described in the preceding section, however, there are several abiotic candidates that show reasonable spectral overlap with Venus, including aerosolized elemental sulfur and FeCl₃. Comparisons of the transmission spectra for these compounds, along with the dayside Venus albedo, are displayed in Figure 7A and collectively show similar transmission properties between 300 and 500 nm (Knapmalsky, 2017). Similarly, as also shown in Figure 7A, the transmission spectra for the Iro protein (which contains an Fe–S cofactor) additionally show reasonable overlap with the Venus albedo. In the context of Venus’ survival, these spectral similarities are perhaps important, as the Fe–S-containing Iro protein is believed to be involved in iron respiration in the acidophilic and sulfur-metabolizing bacterium, *Acidithiobacillus ferrooxidans* (Zeng et al., 2007). As shown in Figure 7B, comparisons of both the Venus scaled geometric albedo (Wallace) and absorption residuals (MESSENGER) to differing Fe–S- and Fe–heme-containing proteins (Iro, HdrC, and catalase) also reveal several similarities between $\sim$215–290 and $\sim$300–480 nm, while whole cells of *E. coli* showed limited overlap. Although speculative, these spectral comparisons are consistent with the potential presence of cloud-based microorganisms containing high abundances of iron-based cofactors (relative to *E. coli*).

In Figure 7C and D, the Venus scaled geometric albedo (Wallace) and absorption residuals (MESSENGER) are additionally compared to the organic cofactors of biopterin, carotenoids, and chlorophylls a, b, and f. As shown in Figure 7C, especially when considering the impacts of relative abundance, the Venus absorption shares several overlapping regions with biopterin ($\sim$255 nm) and proteins ($\sim$280 nm, catalase). Again, in terms of speculation, this is interesting, as bacterial pterin cofactors are involved in the metabolism of sulfur compounds such as sulfite and dimethyl sulfoxide. Finally, as displayed in Figure 7D, the Venus absorption residuals (MESSENGER) share significant overlaps with the aforementioned organic cofactors between $\sim$300 and 480 nm. Together, these preliminary spectral comparisons demonstrate that overlaps may be obtained from abiotic and biotic sources, thereby illuminating the need for in-depth ground-based studies focusing on the spectroscopy of chromogenic microorganisms (unlike *E. coli*) under Venus’ cloud conditions.

Of course, these discussions must also consider the nightside opacity contrasts, which are observed vividly at 2.3 μm (Fig. 1G, H) and revealed in spectacular detail by the Akatsuki orbiter (Limaye et al., 2018). Similar to the UV contrasts, the 2.3 μm contrasts are not well understood, with potential causes including the presence of CO and the effects of differential opacities in the upper clouds, which may impede the transmission of radiation emitted by the surface of Venus or lower atmosphere (Carlson, 1993; Grinspoon, 1993; Pollack et al., 1993). Interestingly, IR studies on

**FIG. 6.** Absorbance spectra for (A) whole cells of *Escherichia coli* and purified iron-containing proteins of Iro and HdrC, which are Fe–S proteins from *Acidithiobacillus ferrooxidans*, and catalase, an Fe–heme protein from *Acinetobacter gyllenbergii* 2P01AA; and (B) various cofactors and biochemicals, including biopterin, carotenoids, and chlorophylls a, b, and f; plots are adapted from (A) Derecho et al. (2014), Ossa et al. (2011), and Zeng et al. (2007); and (B) Airs et al. (2014) and http://hyperphysics.phy-astr.gsu.edu/hbase/Biology/ligabs.html.
biological and organic molecules show that reflectance and absorption at \( \sim 2.3 \mu m \) are clearly associated with C–H groups (C–H stretch) (Dalton et al., 2003; Clark et al., 2009), found in high abundance in lipid molecules (the primary constituent of cellular membranes). While the cloud layer of Venus has zonal flows, which circle the planet in 4–6 days in the cloud layer (\( \sim 50–65 \) km), the atmosphere is very stably stratified, within and above the cloud layer, and should be well mixed. However, this expectation is inconsistent with the vertical gradients in nitrogen abundance, as detected between 22 and 60 km (Peplowski and Lawrence, 2016). Hence, in the context of Venus’ global contrasts, the
planetary winds may potentially carry indigenous microorganisms around the planet, where these biological sources may additionally contribute to the nightside contrasts.

5. Survival in Venus’ Clouds

Several terrestrial microorganisms could serve as relevant analogues for life in Venus’ clouds, which are sulfuric acid-enriched, anaerobic (CO₂ dominated), and iron-containing environments. On Earth, airborne and cultivable microorganisms have been found with specialized aircraft and balloons at altitudes ranging from 15 to 42 km (Narlikar et al., 2003; Smith et al., 2013). As mentioned, cell counts of terrestrial primary biological aerosols range from 10⁶ to 10¹⁰ cells·m⁻², with active spectral techniques, such as laser-induced fluorescence, providing measures of 10⁴ to 10⁵ particles·m⁻³ (fluorescent biological particle aerosols of >1 μm) (Després et al., 2012; Huffman et al., 2012).

For Venus’ clouds, however, any potential biomass would clearly depend on available water, carbon, and other biogenic nutrients (e.g., sulfur, nitrogen, phosphorous, boron, and transition metals). The phototropic reduction of atmospheric CO₂ would likely be a major source for carbon acquisition, with an attenuated UV flux within the cloud layer providing the driving energy source. Furthermore, both phosphorus and sulfur (along with iron) have been detected by the X-ray fluorescent radiometer on VeGa 1 and VeGa 2 landers (Andreychikov et al., 1987), with the most abundant phosphorus compound in the lower cloud layer possibly being partially hydrated phosphoric anhydride P₂O₅·H₂PO₄ (Krasnopol’sky, 2006). For water availability, the low vapor pressure in the clouds is likely offset by the aerosols composed of aqueous sulfuric acid (75–98% and pH of ~1.5 to 0.5 between 48 and 65 km; Grinspoon and Bullock, 2007), where the aforementioned 2 and 8 μm spherical particles (modes 2’ and 3) equate to suspension volumes of ~4 and 260 pL, respectively.

In terms of survival in sulfur-rich and low pH environments, A. ferrooxidans serves as an exemplar terrestrial analogue for life in Venus’ clouds, as this bacterium thrives at extremely low pH values (pH 1 to 2), fixes both CO₂ and nitrogen gas from the atmosphere (Valdes et al., 2008), and obtains its energy for growth from the oxidation of hydrogen, ferrous iron, elemental sulfur, or partially oxidized sulfur compounds (Vera et al., 2008). This chemolithoautotrophic and acidophilic γ-proteobacterium also thrives at temperatures of 50–60°C, similar to those found in the lower clouds of Venus (Fig. 3). Moreover, under low pH and anaerobic conditions, this bacterium produces sulfuric acid, and possibly other oxidized forms of sulfur by metabolically oxidizing elemental sulfur and using Fe³⁺ as a terminal electron acceptor (Prönk et al., 1992).

Members of the archaeal Stygiolobus genus of the order Sulfolobales also anaerobically oxidize elemental sulfur to yield sulfuric acid under acidic conditions, and optimal growth temperatures of ~80°C, and also utilize Fe³⁺ as a terminal electron acceptor (Segerer et al., 1991). Additional terrestrial analogues include green sulfur bacteria, which couple the oxidation of elemental sulfur to the anoxygenic phototrophic reduction of CO₂ (Frigaard and Dahl, 2009), and the sulfate-reducing bacteria, which couple the oxidation of low-molecular-weight organics and hydrogen gas to the reduction of sulfuric acid (and other oxidized forms of sulfur) to form compounds, including sulfite and hydrogen sulfide (Muyzer and Stams, 2008).

Together, these terrestrial analogues assist in framing the biochemical potential for an iron- and sulfur-centered metabolism in Venus’ clouds, where oxidation of Fe³⁺ and sulfur compounds would be intrinsically coupled to the anoxic photosynthetic reduction of CO₂. As summarized in Figure 8, these respective iron and sulfur redox cycles could also be sustained by coupling to the redox-reactive constituents within Venus’ clouds and atmosphere. For instance, Fe²⁺ oxidation could additionally be coupled to the reduction of nitrate, while completion of the Fe⁷⁺/Fe²⁺ redox cycle could be afforded by coupling the reduction of Fe³⁺ to the oxidation of hydrogen, methane, and/or differing low oxidation state sulfur compounds (e.g., S₀, HS⁻, SO₄²⁻, H₂R₂S, and H₂R₃SO₄). In parallel, redox cycling between the differing sulfur oxidation states could be afforded by coupling the reduction of polyatomic sulfur compounds to the oxidation of hydrogen and/or low-molecular-weight organics.

6. Transport from the Surface to the Clouds

Numerical simulations have suggested that Venus had a habitable climate for at least 750 million years, with liquid water on its surface for perhaps as long as 2 billion years (Grinspoon and Bullock, 2007; Way et al., 2016). The presence of past liquid water is supported by comparisons of atmospheric deuterium/hydrogen ratios between Venus and Earth (Donahue et al., 1982; Donahue and Hodges, 1992). In context, this suggests a geological time frame that is sufficient for life to have evolved in the Venus’ environment, especially when the time estimates required for the evolution of life on Earth are considered (Lazcano and Miller, 1994; Des Marais, 1998; Nisbet and Sleep, 2001). As conditions on Venus’ surface warmed and became increasingly inhospitable, life could have migrated to the clouds (Grinspoon and Bullock, 2007) as the surface water evaporated, with multiple possible mechanisms transporting microorganisms from the surface to the clouds. Ultimately, these microorganisms could have adapted to the cloud environments due to selective pressures (in the biological sense) arising from surface transport, aerosolization, limited water availability, and low pH environments (Cockell, 1999; Schulze-Makuch et al., 2004; Grinspoon and Bullock, 2007).

Within the context of terrestrial biology, surface-to-atmosphere transport of microorganisms is reasonably well accepted, as is the atmospheric transport of biologically relevant elements and low-molecular-weight metabolites (Burrows et al., 2009; Morris et al., 2011; Fröhlich-Nowoisky et al., 2016). The movement of water, organics, and other life-essential nutrients in the upper atmosphere on Venus is likely similarly regulated by surface topography, diurnal cycles, strong storms, and a variety of other conceivable physical weathering forces. On Earth, all evidence to date indicates that airborne microbes do not remain perpetually aloft. Instead, biological aerosols are continuously swept into the atmosphere through strong convections that emanate from diverse marine and surface sources, and eventually fall out of the atmosphere through gravitational settling or precipitation.

On Venus therefore, any cloud-based microbial population would need to remain aloft for long periods and replenished...
on relatively fast timescales. Plausible atmospheric nutrient transport mechanisms can be inferred from the experience of VeGa 1 and VeGa 2 balloons, which occasionally experienced very strong updrafts and downdrafts (some triggered by underlying topography) at their nominal float level (∼54 km). Blamont et al. (1986) reported that the typical vertical motions (up and down) encountered by the two balloons were 1 to 2 m s$^{-1}$. Furthermore, residence times of the cloud particles on Venus are quite long, and are comparable to the Hadley circulation times of 2 to 3 months, which are several orders of magnitude greater than the division time of bacteria (Grinspoon and Bullock, 2007).

The recent discovery, from Akatsuki measurements (Fukuhara et al., 2017), of stationary gravity waves at the cloud tops, which are considered to be the result of surface topography, indicates that vertical motions are possible even within the very stable cloud layer. These measurements suggest that ambient winds blowing over mountains and hills on the surface appear to trigger vertical motions, which can reach the bottom of the clouds without any impediment and extend up to the middle cloud layer. The very stable lapse rates in the Venus’ clouds could also maintain airborne particles of essential nutrient-rich minerals aloft for long periods. (Grinspoon and Bullock, 2007).

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material at the higher altitudes would then likely be partly or fully degraded through photochemical means, where the resulting organic products could be recycled through the cloud layer, potentially serving as carbon sources for any cloud-based biology. Such a scenario would be consistent with the conclusions of Knollenberg and Hunten (1980) that there is a source for the smaller particles in the upper cloud layer. Alternatively, Venus’ clouds could have been seeded by interplanetary exchange of rocks (harboring terrestrial bacteria or the building blocks of life) resulting from large impacts on Earth (Melosh, 1988; Grinspoon and Bullock, 2007; Gao et al., 2014).

7. Conclusions and Future Studies

Our comparative analyses support the blended hypotheses that terrestrial-type biology can survive within and contribute to the spectral signatures of Venus’ clouds (Fig. 9). To

FIG. 9. A schematic representation summarizing the ideas presented in this hypothesis paper regarding the potential for microorganisms to survive in Venus’ lower clouds and contribute to the observed bulk spectra. In this scheme, the approximate altitude and temperatures are shown on the left axis, the approximate pressure on the right axis, while the surface topography represents an exaggerated perspective view of Venus. The cloud layer is depicted by a yellow-tinted hazy region between an altitude of ~47 and 72 km, where the varying opacities and thicknesses represent differences in mass loading. The black dots within the cloud layer depict the sulfuric acid aerosols with diameters ranging from 0.2 μm (which are found as high as 90 km) to 2.5 μm and to as large as 36 μm (in smaller quantities) near the bottom of the cloud layer (Knollenberg and Hunten, 1980); aerosols below the cloud base have also been reported by the Venera probes. The hypothetical microbial contents of particles from the lower cloud layer are depicted in a magnified view using the dashed-line callout bubble, which shows differing possible microbial morphologies. These microorganisms may potentially survive by fixation of carbon dioxide (CO₂) through the phototrophic or chemolithotrophic oxidation of iron and sulfur compounds, and by a coupled iron-sulfur metabolism (depicted by the blue reaction scheme). The cloud-based microbial communities may remain afloat through gravity waves (red wavy line), which propagate up, and are triggered by westward ambient flows over the elevated topographies; gravity waves have been detected at the cloud tops in thermal infrared in the Akatsuki data (Fukuhara et al., 2017). Additionally, the convective activity of the lower cloud region may persist on the night side, thereby leading to opacity variations and differing thermal emissions through the cloud layer, as is observed in the near infrared in the Akatsuki and Venus Express data. Consequently, the spectra of Venus may include contributions from the cloud-based microorganisms, as is depicted by the dashed-line callout originating from the magnified view of the particles; the inset spectral plot shows the albedo of Venus compiled from differing observations (red) and the sunlight absorption estimated by a singular measurement on the dayside (at one location), as calculated from the difference between the VIRA cloud model and the MESSENGER spectra (Perez-Hoyos et al., 2017). The absorption of sunlight may actually extend to much longer wavelengths based on muted contrasts observed by the Akatsuki orbiter (Limaye et al., 2018), which is consistent with the albedo variation with wavelength.
test the ideas presented here, we propose the need for an integrated chemical, biochemical, and microbiological study focusing on the survival and spectroscopy of terrestrial microorganisms under Venus’ cloud conditions. To accomplish this task, specialized chambers, such as the Glenn Extreme Environment Rig at the NASA Glenn Research Center (https://geer.grc.nasa.gov), would be required to simulate the atmospheric and physical conditions of the clouds, while simultaneously allowing for spectral analysis of aerosolized chemical, biochemical, and microbial samples (via IR, visible, and other means). These studies would also need to address the multiple sources of variation associated with the spectroscopy of bioaerosols, including cell morphology (coccii, bacilli, or spirilla), cell state (vegetative or sporulated), presence of abiotic materials (e.g., dust, salts, and polymer matrices), states of hydration, and emission source/type and location. Crucially, the persistence of terrestrial microorganisms and the potential for metabolism, under these conditions, would serve as positive indicators for habitability. Potential biology-related experiments therefore include measurement of viable plate counts, adenosine triphosphate abundances, and intracellular enzyme activities of sulfur-metabolizing, acid-tolerant, and/or radiation-tolerant microorganisms and the potential for metabolism, under these conditions, would serve as positive indicators for habitability. These studies would also need to address the multiple sources of variation associated with the spectroscopy of bioaerosols, including cell morphology (coccii, bacilli, or spirilla), cell state (vegetative or sporulated), presence of abiotic materials (e.g., dust, salts, and polymer matrices), states of hydration, and emission source/type and location. Crucially, the persistence of terrestrial microorganisms and the potential for metabolism, under these conditions, would serve as positive indicators for habitability.

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No competing financial interests exist for any of the authors.

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