

To What Extent Does Terrestrial Life “Follow The Water”?

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Abstract

Terrestrial life is known to require liquid water, but not all terrestrial water is inhabited. Thus, liquid water is a necessary, but not sufficient, condition for life. To quantify the terrestrial limits on the habitability of water and help identify the factors that make some terrestrial water uninhabited, we present empirical pressure-temperature (P - T) phase diagrams of water, Earth, and terrestrial life. Eighty-eight percent of the volume of Earth where liquid water exists is not known to host life. This potentially uninhabited terrestrial liquid water includes (i) hot and deep regions of Earth where some combination of high temperature ($T > 122^\circ\text{C}$) and restrictions on pore space, nutrients, and energy is the limiting factor and (ii) cold and near-surface regions of Earth, such as brine inclusions and thin films in ice and permafrost (depths less than ~ 1 km), where low temperatures ($T < -40^\circ\text{C}$), low water activity ($a_w < 0.6$), or both are the limiting factors. If the known limits of terrestrial life do not change significantly, these limits represent important constraints on our biosphere and, potentially, on others, since ~ 4 billion years of evolution have not allowed life to adapt to a large fraction of the volume of Earth where liquid water exists. Key Words: Biosphere—Limits of life—Extremophiles—Water. *Astrobiology* 10, 349–361.

1. Introduction

NASA's “FOLLOW THE WATER” strategy for Mars exploration (*e.g.*, Hubbard *et al.*, 2002) is based on the observation that all terrestrial life requires liquid water during some phase of its life cycle (Rothschild and Mancinelli, 2001). This strategy can be refined by including other fundamental requirements of life. Energy, for example—Hoehler (2004), Hoehler *et al.* (2007), and Shock and Holland (2007) described how “follow the water” can be complemented by a “follow the energy” approach. Here, we refine the “follow the water” approach by empirically quantifying the boundaries between the habitable and uninhabitable water on Earth. Research on extremophiles has revealed apparent limits of temperature, water activity, nutrient, pore space, and free energy availability (Baross *et al.*, 2007; Jakosky *et al.*, 2007). These factors are implicated in making some water uninhabitable. However, no empirical study has comprehensively quantified the fraction of uninhabited terrestrial water or comprehensively described where these wet uninhabitable environments are. To this end, we have developed a model for presenting Earth and Mars on a pressure-temperature (P - T) diagram (see Jones and Lineweaver, 2008). See Table 1 for the surface P - T conditions of Solar System bodies.

Figure 1 is a sketch of our main goal: to identify the boundaries between “Life” and “No Life” in the regions of Earth where water is liquid. To this end, Fig. 2 presents water in several ways. The bulk of terrestrial ocean water is in the

narrow vertical wedge. The dotted curves mark the phase space boundaries of “ocean salinity water.” Similarly, the solid curves mark our estimate of the “maximum liquid range,” that is, the largest range of phase space that would be occupied by liquid water (fresh water, salt water, concentrated brines, thin films, and super-heated water) on Earth, if Earth had environments at the full range of temperatures and pressures shown. It does not; see Fig. 3. The melting curve of this “maximum” water has a freezing point depression of -89°C at the triple point, probably due to a combination of thin film effects and high solute (*e.g.*, dissolved salt) concentrations (Clark and Van Hart, 1981). Thin films of unfrozen water can exist at the contact between ice-ice or ice-soil grains at very low temperatures (Price 2000; Davis, 2001; Möhlmann, 2008).

The most soluble common inorganic compounds in water have saturated aqueous molarities less than $\sim 11M$ (Lide and Haynes, 2009). The magnitude of boiling point elevation due to the molality m of the solute is given by Raoult's equation: $\Delta T_b = K_b m$, where K_b is the ebullioscopic constant for water, $0.512^\circ\text{C}/m$ (Silberberg and Duran, 2002), and $m = 11$, giving a boiling point elevation of 5.6°C , which we use to make the thick vapor curve in Fig. 2.

2. The Pressure-Temperature Phase Diagram of Earth

Figure 3 is a P - T phase diagram of all terrestrial environments superimposed on the phase diagram of water from

TABLE 1. AVERAGE PRESSURES AND TEMPERATURES ON SOME SOLAR SYSTEM BODIES

Environment	Pressure (bar)	Temperature (°C)	Reference
Earth surface	1	15	Dziewonski and Anderson, 1981
Mars surface	0.06	-50	Barlow, 2008
Venus surface	93	480	Petculescu and Lueptow, 2007
Titan surface	1.5	-180	Griffith <i>et al.</i> , 2000
Top of Europa's ocean	100	-3.9	Reynolds <i>et al.</i> , 1983; Melosh <i>et al.</i> , 2004

Fig. 2. Conceptually, it is the same as the intersection of the blue and orange circles of Fig. 1; it shows the regions of phase space where there is both Earth and water. It also shows the regions where there is Earth but no liquid water and where there could be liquid water but there is no Earth. The details of our Earth model, including estimates of uncertainties, are described in Table 2 and Appendix A Table A1. The subsurface pressure and temperature gradients of Earth are proportional to each other and are related through density, conductivity, and heat production. This limits the P - T space occupied by Earth. Although the phase diagram labeled "Maximum liquid range" is appropriate for the concentrated briny inclusions and thin liquid films in ice and permafrost on Earth's surface, the maximum freezing point depression for water on, and in, aerosols and organic particles in Earth's atmosphere will be intermediate between the "Ocean salinity water" and "Maximum liquid range."

The phase models in Figs. 3 and 5 include short-term environments that are temporarily at typical mantle temperatures but are at crustal pressures. We have labeled these environments as "Transient" in Fig. 3. They include magma chambers in the crust, surface lava, and subsurface lava lakes (Jonsson and Matthiasson, 1974; Helz and Thornber, 1987). Over timescales of decades, the majority of these environments (Oppenheimer and Francis, 1998) will cool along a constant pressure line to lie within the crustal region. The size of the area occupied by Earth in the P - T space of Fig. 5 is determined by a combination of uncertainty in geothermal

gradients and variations (both spatial and temporal) in geotherms. Thus, we have attempted to include the dynamic nature of Earth in the model by making the shaded Earth region wide enough to include cycling of pressures and temperatures. For example, in Fig. 3 the temperature at the summit of Mount Everest varies between the maximum (point C) and minimum (point D), and atmospheric pressures and temperatures vary within the pink shaded region around the average atmospheric geotherm. Also in Fig. 3 the transient permeation of liquid water to depths of at least 6 km in the crust through permeable rock-cracking (Sleep and Zoback, 2007) is included, as the average crustal geotherm (the solid black line) allows liquid water in the crust to a depth of ~ 30 km. The shallowest crustal geotherm allows liquid water in the crust to a depth of ~ 75 km (green asterisk in Fig. 3). In Fig. 4, the maximum depth of the biosphere is currently determined by the depth of the 122°C isotherm. By "currently" we are referring to the temperature of 122°C as a tentative high limit for life, based on the highest temperature environment in which present-day active life has been found to date (Takai *et al.*, 2008). We acknowledge that this present-day limit may be transient, as environments such as deep sea thermal vents are searched for examples of life at higher temperatures. The depth of 122°C in the crust varies with crustal characteristics such as heat flow and thermal conductivity. From Fig. 3, the 122°C isotherm varies between the surface and a maximum depth of ~ 20 km (along a cool geotherm) in crust.

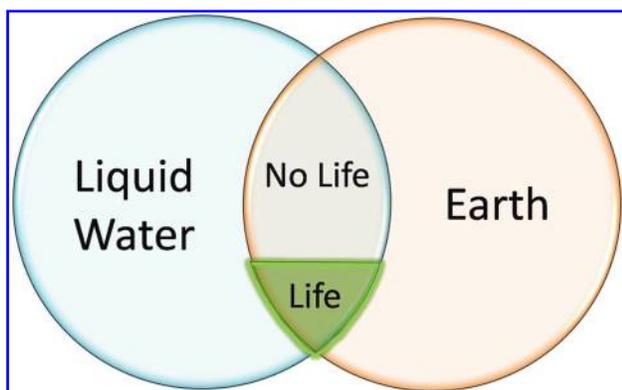


FIG. 1. Water, Earth and Life. In the context of P - T phase diagrams, we plot liquid water (blue circle, *cf.* Fig. 2), all terrestrial environments (orange circle, *cf.* Fig. 3), and all inhabited terrestrial environments (green wedge, *cf.* Fig. 4). From these plots we are able to identify where there is both Earth and liquid water (*i.e.*, the intersection of the blue and orange circles) but where "No Life" has been discovered (Fig. 5). Color images available online at www.liebertonline.com/ast.

3. The Pressure-Temperature Phase Diagram of Terrestrial Life

Figure 4 presents the phase space of life on Earth. We make a provisional distinction between active (green) and dormant (pale green) life. Although spores and other dormant life-forms have evolved to withstand extreme environmental conditions, they could not complete their life cycles in those conditions. Examples of the extreme pressures (P) and temperatures (T) for active and dormant life are given in Tables 3 and 4, respectively (see also Appendix B). These environments include: (i) high P , high T , (*e.g.*, hydrothermal vents on the ocean floor); (ii) high P , low T , (*e.g.*, interstitial environments beneath thick ice sheets); (iii) low P , low T , (*e.g.*, Mt. Everest); and (iv) low P , high T , (*e.g.*, warmest layers of the upper atmosphere).

In constructing these inhabited regions of phase space, we assumed that the $T < 122^\circ\text{C}$ upper limit to life (Takai *et al.*, 2008) and the $T > -20^\circ\text{C}$ lower limit to active life (Junge *et al.*, 2004) are both valid over a broader range of pressures than has been fully explored by microbiologists. The pressure/pore-space relation and the link between barophilic and thermophilic adaptation is still unclear (Horikoshi, 1998;

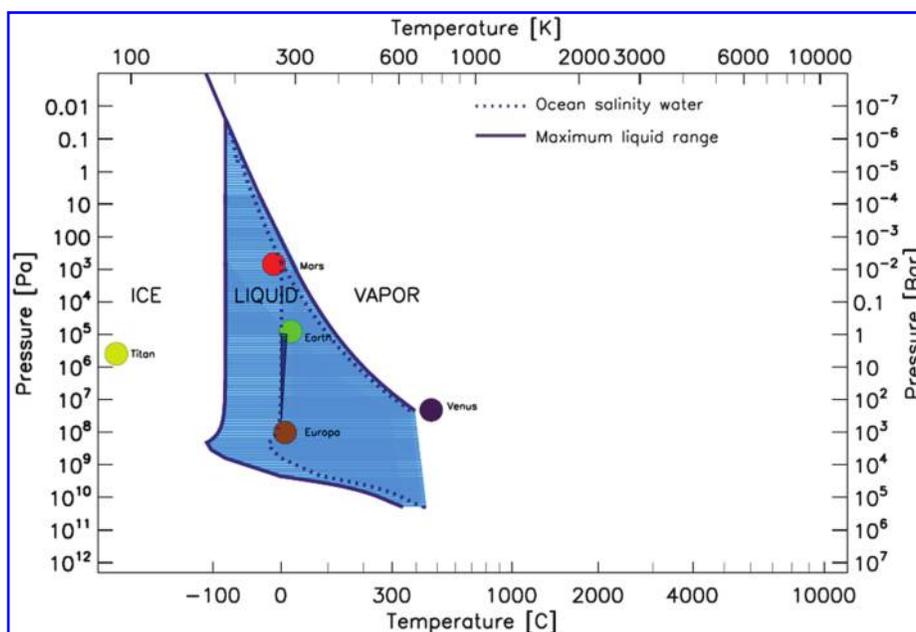


FIG. 2. Pressure-temperature phase diagram for two types of water. The familiar vapor, sublimation, and melting curves for ocean salinity water (3.5% salt by mass, dotted curves) are indistinguishable on this scale from pure water (Lide and Frederikse, 1996). The dark vertical wedge represents the vast majority of Earth’s oceans. We are concerned with the broadest range of pressures and temperatures under which water can remain liquid. This is labeled “Maximum liquid range” (solid curves). Due to increasing concentrations of solute and thin film effects at low temperatures, the coldest liquid water on Earth is -89°C and has a triple point pressure of 3.2×10^{-7} bar (see Table 2, label E). For reference, the average global surface temperatures and pressures for Earth, Mars, Titan, Venus, and the top of Europa’s potential ocean are shown (see Table 1). Color images available online at www.liebertonline.com/ast.

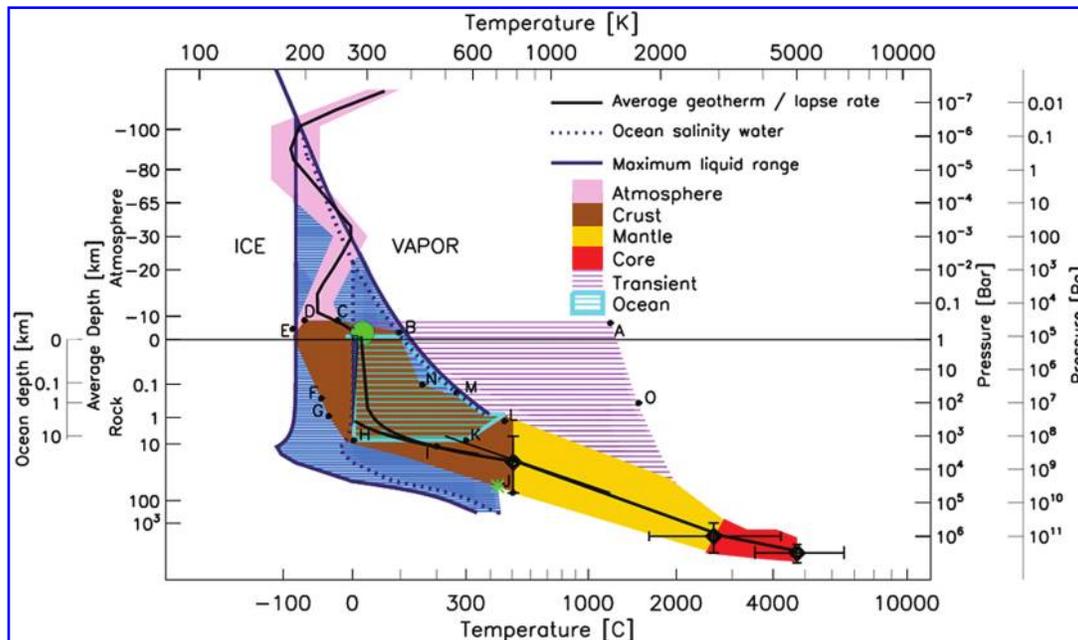


FIG. 3. Superposition of terrestrial environments on the P - T diagram of water from Fig. 2. Earth’s core, mantle, crust, and atmosphere are colored separately and centered on the average geotherm (subsurface) and lapse rate (atmosphere). The ocean and crust geotherms meet at point “I.” A “Transient” region shows mantle that has intruded upwards (e.g., volcanism, geothermal vents). The horizontal thin line at 1 bar is the average sea-level atmospheric pressure of Earth. The parameters of our Earth model (e.g., core, mantle, continental crust, oceanic crust, geotherms, and atmospheric lapse rates) are given in Appendix A. Extreme environments are listed and assigned a letter in Table 2, and they are plotted here. For example, “C” and “D” represent the hottest and coldest days on the summit of Mt. Everest. As in Fig. 2, the dark vertical wedge identifies the majority of ocean water. The green asterisk represents our estimate of the hottest and deepest water on Earth at $T = 431^{\circ}\text{C}$ and $P = 3 \times 10^4$ bar, corresponding to a depth of ~ 75 km. Color images available online at www.liebertonline.com/ast.

Garzón, 2004). Thus, our interpolations of the current high- and low-temperature limits for life in environments at pressures between ~ 1 and $\sim 10^{2-3}$ bar should be viewed with caution. As a further indicator of caution, the current upper temperature limits of life (Kashefi and Lovley, 2003; Takai *et al.*, 2008) are the results of a limited exploration of high T environments in hydrothermal vents. In the future, these limits will undoubtedly be higher and closer to the real limits of terrestrial life (Horsfeld *et al.*, 2006; Kelley *et al.*, 2007; Holden, 2008). In Fig. 4, the question mark and vertical dashed line at $T = 250^\circ\text{C}$ emphasize this uncertainty. Furthermore, in the atmosphere in Figs. 3 and 5, the existence of liquid-water environments are transient. Due to the movement of air currents and the relationship between atmosphere and surface, there are no continual liquid-water environments at low pressures. For example, at the triple point of “ocean salinity water” in Fig. 3 at ~ 25 km altitude, the conditions may be dry even though liquid water is stable.

4. Results

Figure 5 can be used to quantify the potential limits of the terrestrial biosphere. For example, we can compute what fraction of the volume of Earth is inhabited. The radius of Earth $r_E = 6378$ km. The biosphere extends ~ 10 km above this (*e.g.*, throughout the troposphere, on top of mountains) and extends ~ 10 km down in the oceans and about 5 km down into continental crust (see Table 3, “6” and “7”). Assuming oceans occupy 70% of the surface and continents occupy 30%, the biosphere occupies $\sim 1\%$ of the volume of Earth (the 10 km thick troposphere is included in the volume of Earth). Thus, after 4 billion years of evolution, the terrestrial biosphere seems to have been unable to extend into $\sim 99\%$ of the volume of Earth.

Also of interest is what fraction of the volume of Earth where liquid water exists is known to host life. The computation is analogous to that above except, instead of the denominator in the ratio being the volume of the entire Earth, it is the volume of the shell of Earth that contains liquid water. The thickness of such a shell extends to a depth of ~ 75 km and is marked by the green asterisk in Fig. 5. Here, we ignore the atmosphere and obtain the result that $\sim 12\%$ of the volume of Earth where liquid water exists is known to host life. Thus, according to our current state of exploration, 88% of the volume of Earth where liquid water exists is not known to harbor life.

We can obtain analogous results for the area in phase space $[\log P \log T]$ in Fig. 5 by asking: what fraction of the phase space area of Earth where liquid water exists is known to host life? In terms of Fig. 5, this question becomes, what fraction of the yellow area that overlies the blue area is occupied by green (active or dormant life)? Here, for simplicity, we exclude the atmosphere since it is not clear that liquid-water droplets and films on aerosols extend over the full “maximum liquid range.” The computation of the relevant areas yields the result that $\sim 36\%$ of the phase area occupied by terrestrial water has been found to host life. Approximately 30% is occupied by active life, and the remaining $\sim 6\%$ by dormant life. Thus, 64% of the phase space of terrestrial water and 88% of the volume of Earth containing water are not known to harbor life. There are many liquid-water environments on Earth that, as far as we know, do not

host life. If the known limits of life do not require large modifications, these limits represent a significant constraint on the biosphere, since ~ 4 billion years of evolution have not allowed life to adapt to the 64% of P - T phase space and 88% of the volume of Earth where liquid water exists.

5. Summary and Discussion

We have made an empirical description of the phase space and volumetric limits of terrestrial life. Plausible reasons for these limits are combinations of temperature, water activity, energy, and nutrient availability and pore space. However, determining how these factors combine to prevent life will be a challenging part of future extremophilic research.

Our analysis can be summarized as follows:

- (i) *High-pressure limit to life.* Figure 5 suggests that the apparent high-pressure limit of life is a selection effect since life has been found at the maximum depths for which it has been searched. This conclusion is supported by experimental studies in which barophiles were taken to those pressures encountered deep within the crust, and it was found that the organisms remained alive and viable (Sharma *et al.*, 2002 for pressures at ~ 35 km depth; Margosch *et al.*, 2006 for pressures consistent with ~ 50 km crustal depth).
- (ii) *High-temperature limit to life.* The current high-temperature limit for life is 122°C . This limit cannot be verified, as there is a substantial amount of liquid water ($\sim 1\%$ of the total terrestrial liquid volume) at higher temperatures that has not been fully searched for life. If 122°C is a real limit, this indicates a severe restriction of the terrestrial biosphere, where only $\sim 12\%$ of the volume of Earth that has liquid water supports life. If the high-temperature limit for life is increased to 250°C , the thickness of the biosphere would approximately triple to include $\sim 38\%$ of the volume of Earth that has liquid water. However, see Wiersberg and Erzinger (2008) and Ellsworth *et al.* (2005) for indications that hyperthermophiles—specifically methanogens—are limited to $T < 135^\circ\text{C}$.
- (iii) *Low-temperature limit to life.* The current low-temperature limit for life is -20°C . There are thin films of liquid water and potentially briny liquid water that can remain liquid at lower temperatures with a water activity above the proposed limit of 0.6 for life (Grant, 2004). If low water activity is a fundamental limit, rather than low temperature, then active life may occur in water temperatures down to at least -30°C due to the presence of brines. A substantial volume of terrestrial liquid water ($> 1.5 \times 10^7 \text{ km}^3$) exists in permafrost, and a large fraction of this would persist through temperatures below -20°C . It would be significant if life were found to be excluded from these liquid-water sources.
- (iv) *Low-pressure limit to life.* All examples of life found at pressures less than 0.3 bar have been classified as dormant. A low-pressure limit for life may be due to temperature, water activity, or nutrient limits at these altitudes. Liquid water would most likely exist as a thin film on aerosols or organic particles in the atmosphere; however, its existence in low-pressure environments is transient.

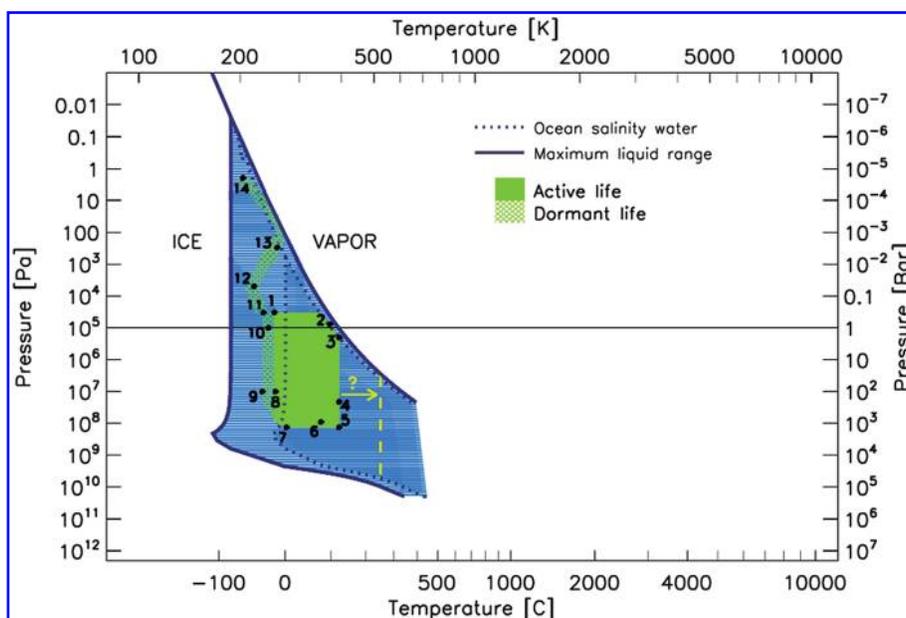


FIG. 4. Inhabited terrestrial environments superimposed on the P - T diagram of water from Fig. 2. Numbers 1–8 circumscribe our estimate of the region occupied by active terrestrial life (green) and are described in Table 3. Numbers 9–14 and the light green area represent our estimate of the region occupied by dormant terrestrial life and are described in Table 4. Atmospheric life is classified as dormant, as most examples are spores and atmospheric non-spore-forming organisms that have extremely low metabolic rates (Appendix B). The question mark and the yellow arrow pointing from the current upper temperature limit of life ($T_{\text{life}} < 122^{\circ}\text{C}$) to the vertical dashed yellow line at $T = 250^{\circ}\text{C}$ represents the change that would occur in this diagram if life were found at $T = 250^{\circ}\text{C}$.

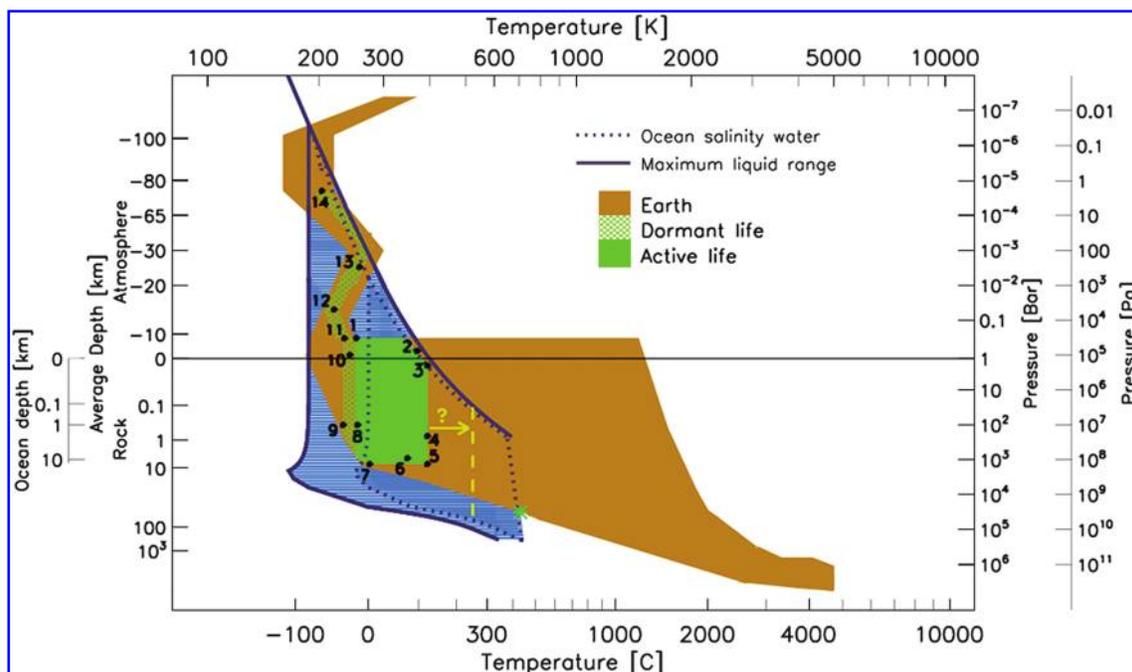


FIG. 5. Superposition of inhabited environments from Fig. 4 and the terrestrial environments from Fig. 3 on the P - T diagram of water from Fig. 2. Life does not seem to inhabit the full range of terrestrial environments where liquid water is available. The upper temperature limit for life, currently 122°C , excludes life from the hottest and deepest water. Color images available online at www.liebertonline.com/ast.

TABLE 2. EXTREME TEMPERATURES AND PRESSURES IN EARTH'S OCEANS AND CRUST

Key	Environment	Pressure (bar) Depth (km)	Temperature (°C)	Reference
A	Surface lava, <i>e.g.</i> , Pahoehoe, rhyolite melt, and basalt—hottest surface temperatures (Cotopaxi, Equador)	0.4 –5.897	1200	Harris <i>et al.</i> , 1998; Fagents and Greeley, 2001; Stein and Spera, 2002; Decker and Decker, 1992
B	Thermal spring/vent (Pork Chop Geyser, Yellowstone, USA)	0.77 –2.293	97	Guidry and Chafetz, 2003
C, D	Mt. Everest summit	0.33 ± 0.01 –8.848	–74 to –26	Team Everest (2003) website; West <i>et al.</i> , 1983
E	Minimum land temperature (Vostok, Antarctica)	0.6 –3.488	–89	National Oceanic and Atmospheric Administration (2007) website
F	Deep ice (South Pole, Antarctica)	72 0.8	–51	Price <i>et al.</i> , 2002
G	Deep ice (Vostok, Antarctica)	2.5 × 10 ² 2.75	–40	Abyzov <i>et al.</i> , 1998
H, K	Marianas trench (Challenger Deep)	1.32 × 10 ³ 10.896	2–300	Todo <i>et al.</i> , 2005; The Mariana trench (2003) website
I	Mean base of oceanic crust	2.0 × 10 ³ 10	200	Lodders and Fegley, 1998; Huppert and Sparks, 1988
J	Crust mantle boundary—lowest temperature at thickest point (Himalaya, southern Tibet)	5 × 10 ⁴ 80	500	Priestley <i>et al.</i> , 2008
L	Seafloor hydrothermal vents—hottest (Mid-Atlantic Ridge)	3.5 × 10 ² 3	464	Koschinsky <i>et al.</i> , 2008
M	Seafloor hydrothermal vents—hottest shallow vents (Tonga arc)	49 0.54	265	Stoffers <i>et al.</i> , 2006
N	Geothermal waters in the crust	28 0.1	157	Ellis and Mahon, 1977
O	Lava lakes (Kilauea Iki, Hawaii; Eldfell volcano, Iceland)	10 ² 0.3	1500	Helz and Thornber, 1987; Jonsson and Matthiasson, 1974

Conversions between depth and pressure for atmosphere; land and water used the density values in Table A1 (Appendix A) and the formula $P(z) = P_0 + \rho gz$, where $P(z)$ = pressure at depth z , P_0 = normalizing pressure, ρ = density, g = gravitation acceleration. Gravitational acceleration values were taken from Dziewonski and Anderson (1981).

Our phase diagrams can be used to refine and focus searches for life on Earth and elsewhere. Our analysis highlights the need to look for environments that have conditions at the extreme limits known for life so as to quantify the extent to which terrestrial life follows the water. Current limits indicate that the terrestrial biosphere inhabits only a small subset of the full range of liquid-water environments on Earth. More work needs to be done to determine how much of the apparently uninhabited water appears that way due to the difficulty and incompleteness of the observations.

A. Appendix A: Details of the Earth Model Shown in Figure 3

A.1. Crust and surface

The thickness of the crust varies widely—between 5 to around 80 km (Pavlenkova and Zverev, 1981; Holbig and Grove, 2008) beneath continental crust (averaging 35 km), and only from 2 to 10 km under oceanic crust (averaging 5–7 km). The global average depth is 19 km (Dziewonski and Anderson, 1981). As the Moho marks a density transition, it does not have a fixed pressure or temperature. Shallow Moho (beneath thin crust) is typically quite cool due to its

lower heat flow. A large fraction of the crust is <40 km thick (Mooney *et al.*, 1998) and lies above mantle cooler than 800 K (Blackwell, 1971). With increasing depth the temperature of the crust and Moho typically increases due to increasing heat flow. Deep Moho beneath thick crust can be cool, however, with the current range of deep Moho temperatures being ~800 K (Hyndman *et al.*, 2005) to 1400 K (Jiménez-Munt *et al.*, 2008). Taking a typical average continental crustal density, the 80 km deep Moho (Sokolova *et al.*, 1978) lies at a pressure of around 20 kPa—roughly an order of magnitude greater than the pressure at shallow Moho. Due to these large variations in pressure and temperature at the base of the crust, there is difficulty in representing this boundary simply on a P - T diagram. We have chosen to mark the average conditions at the base of average thickness continental and oceanic crust and to use error bars to encompass the range of crustal thickness (pressures) and the variation in temperature at different Moho depths. A sloped error bar is due to the general trend of deeper Moho being at higher temperature.

A more fundamental consideration is Earth's heat flow, which is not explicitly represented in our model. Earth's surface heat flow varies predominantly between 40 and

TABLE 3. ACTIVE LIFE ENVIRONMENTS

Key	Description	Pressure (bar) Depth (km)	Temperature (°C)	Reference
1	Mt. Everest summit	0.33 ± 0.01 –8.848	–20	Active microbial life has not been searched for at this location. We set 1 at the same minimum temperature at which active life has been found (see 8). Gangwar <i>et al.</i> (2009) report life at –20°C at 5.6 km.
2	Thermal spring/vent (Pork Chop Geyser, Yellowstone National Park, USA)	0.77 –2.293	97	Guidry and Chafetz (2003) (Lilypad stromatolites)
3	Shallow hydrothermal vents	2 0.01	122	Thermophilic life has been found in shallow vents at temperatures between 40 and 100°C (Amend <i>et al.</i> , 2003; Prol-Ledesma, 2003; Stetter, 2006). Life has not been found at the maximum temperature of 122°C (see 4); however, temperatures of vents at this depth can exceed 122°C (Prol-Ledesma, 2003). We have therefore placed this marker at a temperature of 122°C.
4	Ocean hydrothermal vent where highest-temperature life found (Finn Vent, Mothra Field, Pacific Ocean)	2.1 × 10 ² 2.27	122	Takai <i>et al.</i> (2008) and Kashefi and Lovley (2003) (Archaea, closely related to <i>Pyrodicticum occultum</i> , <i>Pyrobaculum aerophilum</i>) Schrenk <i>et al.</i> (2003)
5	Marianas trench, deepest part of ocean (Challenger Deep, Pacific Ocean)	1.32 × 10 ³ 10.924	122	Thermophilic life has not been searched for at this location. Life could exist in this environment, as the maximum temperature for life found thus far is 122°C (see 4). Vents at this depth can exceed 122°C (The Mariana Trench, 2003 website), and life has been found at 2–3°C temperatures in this environment (Todo <i>et al.</i> , 2005). We have therefore placed this marker at a temperature of 122°C.
6	Deepest active life in crust from borehole (Gravberg, Sweden)	1.55 × 10 ³ 5.278	75	Szewzyk and Szewzyk (1994) (<i>Thermoanaerobacter</i> , <i>Thermoanaerobium</i> , <i>Clostridium</i> , close relationship to <i>Clostridium thermohydrosulfuricum</i>)
7	Marianas trench (Challenger Deep, Pacific Ocean)	1.32 × 10 ³ 10.896	2	Todo <i>et al.</i> (2005), Takami <i>et al.</i> (1997) (Foraminifera: <i>Lagenammina</i> , <i>Nodellum</i> , <i>Resigella</i>)
8	Arctic Ice core, lowest-temperature active life	10 ² 2.75	–20	Junge <i>et al.</i> (2004) [Bacteria (EUB338), Cytophaga-Flavobacteria (CF319a), Archaea (ARCH915)]

85 mW m⁻² (Pollack and Chapman, 1977) with an average of ~ 55 mW m⁻². The heat flow from the Moho beneath the continents is fairly fixed at around 25 mW m⁻² (Čermák *et al.*, 1989) with the discrepancy made up from radiogenic heat production from elements within the crust. There is less radiogenic heat production in the oceanic crust itself (Smith, 1973); thus its heat flow shows much less variation and has an average of 100 mW m⁻² (Sclater and Francheteau, 1970; Davies, 1999). The crustal heat flow and the thermal conductivity of crustal materials together determine the subsurface geotherm, through the relation

$$\frac{\partial T}{\partial z} = \frac{Q}{k}$$

where $\frac{\partial T}{\partial z}$ is the geotherm (K km⁻¹); Q = heat flow (mW m⁻²) and k = thermal conductivity (W m⁻¹ K⁻¹). Hence, this heterogeneity in heat flow (and of course crustal materials) has the consequence that temperatures can still show large regional variation many kilometers beneath the subsurface (Artemieva, 2006), which can continue even into the asthenosphere (Smith, 1973). Thus, oceanic and continental geotherms

TABLE 4. DORMANT LIFE ENVIRONMENTS

Key	Description	Pressure (bar) Depth (km)	Temperature (°C)	Reference	Metabolic activity
9	Vostok ice core life	10 ² 2.757	-40	Abyzov <i>et al.</i> , 1998; Price and Sowers, 2004	Cell activity after incubation; cells interpreted as <i>in situ</i> were able to maintain vital functions but not reproduce
10	Greenland open mine life	1	-30	Langdahl and Ingvorsen, 1997	Sampled at warmer temperatures so metabolic activity at low-temperature limit is unknown (<i>Thiobacillus ferrooxidans</i> , <i>Thiobacillus thiooxidans</i> , and <i>Leptospirillum ferrooxidans</i>)
11	Mt. Everest summit	0.33 ± 0.01 -8.848	-40		Marker 11 is at the minimum temperature at which dormant microbial life has been found in the crust in the presence of liquid water (see 9); the pressure is given by 1.
12	Bacterial spores (atmosphere)	0.0553* -20	-20*	Wainwright <i>et al.</i> , 2002	Dormant (spore) in atmosphere but cultured in laboratory (<i>Bacillus simplex</i> , <i>Staphylococcus asteuri</i> , <i>Engyodontium album</i>)
13	Non-spore-forming eubacteria (atmosphere)	0.0025* -41	-56*	Griffin, 2008	Growth after extended incubation (<i>Micrococcaceae</i> , <i>Microbacteriaceae</i> , <i>Brevibacterium luteolum</i> , <i>Staphylococcus</i>)
14	Bacterial spores (atmosphere)	0.00002* -77	-69*	Imshenetsky <i>et al.</i> , 1978	Dormant (spore) in atmosphere (<i>Circinella muscae</i> , <i>Aspergillus niger</i> , <i>Papulaspora anomala</i> , <i>Penicillium notatum</i> , <i>Mycobacterium luteum</i> , <i>Micrococcus albus</i>)

*Temperature and pressure from Hewitt and Jackson (2003).

cannot be guaranteed convergence until below ~ 200 km in the asthenosphere where convective heat transfer dominates (Andersen, 1979; Chapman, 1986). In our model, the oceanic and continental geotherms converge at ~ 10 km into the continental crust. A typical geothermal gradient in the oceanic crust is ~ 35 K km⁻¹ (100 mW m⁻² heat flow; thermal conductivity for basalt of 3 W m⁻¹ K⁻¹ from Clauser and Huenges, 1995). The mean continental geotherm is 25 K km⁻¹ (Scheidegger, 1976); however, it ranges greatly due to variations in heat flow (10–130 mW m⁻² at the surface) and thermal conductivity of rock (0.5–7 W m⁻¹ K⁻¹ range: Clauser and Huenges, 1995), and is predominantly between 5 and 70 K km⁻¹ (Chapman and Pollack, 1975).

The extreme environments of Earth are given in Table 2. All known environments in the crust, oceans, and surface lie within the *P-T* polygon and within the range of the error bars on the average geotherm. The mean continental crustal geotherm shown, averaged over 35 km of crust, is 15 K km⁻¹. The brown shaded region accommodates much steeper geotherms (up to ~ 80 K km⁻¹) and so is consistent with the range of true geothermal gradients on Earth.

A.2. Core

Earth's core extends from a depth of 2890 to 6378 km. At the center, the pressure is modeled as 3.6×10^6 bar (Dziewonski and Anderson, 1981; Davies, 1999). As the core density is not well constrained from seismic models, there is a range of estimates

for the central core pressure between 2.8×10^6 and 3.8×10^6 bar (Fowler, 1990; Lodders and Fegley, 1998). Similarly, we have chosen a representative pressure value for the core-mantle boundary (CMB) of 1.4×10^6 bar (Davies, 1999) within the range of 0.6 – 3.2×10^6 bar (Fowler, 1990; Lodders and Fegley, 1998; Davies, 1999). The pressure value for the CMB is not essential for our model, as the transition from core to mantle occurs within a layer ~ 40 km thick (Doornbos, 1983; Williams and Garnero, 1996). At its central depth, the core temperature is taken in our model to be 5700 K (Fowler, 1990). Temperature models for the core are dependent on core composition, and estimates for the central temperature range widely from 3800 to 6800 K (Jeanloz, 1990; Davies, 1999). Similarly, with the CMB we have chosen a representative temperature of 2700 K (Davies, 1999) within the range of estimates 1700–4500 K (Jeanloz, 1990; Decker and Decker, 1992; Stein and Wysession, 2003). As stated above, the CMB is thought to be a ~ 40 km thermal boundary layer, with an estimated radial temperature increase of 800 K (Stacey and Loper, 1984) across it. Melting temperatures for the assumed core composition are pressure dependent (Andersen *et al.*, 2002); however, our chosen boundary values and geotherm of 0.85 K km⁻¹ leads to a liquid outer region of the core and a solid inner region (from the solidus of Jeanloz, 1990). This is consistent with recent models (Stein and Wysession, 2003). The central core may be liquid if its temperature exceeds 5120 K (Nakagawa and Tackley, 2004).

The range of estimates of pressure and temperature conditions in the inner core are represented through vertical and

TABLE A1. MODEL PARAMETERS FOR EARTH'S CORE, MANTLE, CRUST AND ATMOSPHERE

	Range	Reference
Core		
Temperature (K)	2700^{+1800}_{-1000} (outer) to 5700^{+1100}_{-1900} (inner)	Fowler, 1990; Jeanloz, 1990; Lodders and Fegley, 1998; Davies, 1999
Pressure (bar)	$1.39^{+1.81}_{-0.76} \times 10^6$ (outer) to $3.57^{+0.23}_{-0.77} \times 10^{-6}$ (inner)	Fowler, 1990; Lodders and Fegley, 1998; Davies, 1999; Dziewonski and Anderson, 1981
Depth (km)	2890–6378	Dziewonski and Anderson, 1981; Lodders and Fegley, 1998
Density (kg m^{-3})	1.3×10^4 (averaged over inner and outer core)	Dziewonski and Anderson, 1981; Lodders and Fegley, 1998
Mean pressure gradient (Pa km^{-1})	1.27×10^5	Lodders and Fegley, 1998; Dziewonski and Anderson, 1981
Geothermal gradient (K km^{-1})	0.6–0.9; our model 0.85	Ernst, 1990; Saxena <i>et al.</i> , 1994; Karato, 2003
Mantle		
Temperature (K)	800^{+1380}_{-570} (outer) to 2700^{+1800}_{-1000} (CMB)	Fowler, 1990; Lodders and Fegley, 1998; Davies, 1999; Decker and Decker, 1992
Pressure (bar)	$3.3^{+26.7}_{-2.1} \times 10^3$ (outer) to $1.39^{+1.81}_{-0.76} \times 10^6$ (inner)	Fowler, 1990; Lodders and Fegley, 1998; Davies, 1999; Decker and Decker, 1992
Depth (km)	5–2890 (average 33 under continents, 7 under oceans)	Scheidegger, 1976; Dziewonski and Anderson, 1981; Lodders and Fegley, 1998
Density (kg m^{-3})	4.5×10^3	Lodders and Fegley, 1998
Mean pressure gradient (Pa km^{-1})	4.41×10^4	Lodders and Fegley, 1998; Dziewonski and Anderson, 1981
Geothermal gradient (K km^{-1})	0.3–1; our model 0.7	Mason, 1958; Schiano <i>et al.</i> (2006)
Continental crust		
Temperature (K)	184–331 (surface) \sim 800 (average base temperature; magma)	Lodders and Fegley, 1998; Huppert and Sparks, 1988
Pressure (bar)	1 (surface) to $1.3^{+0.9}_{-1.03} \times 10^4$ (base)	Lodders and Fegley, 1998
Thickness (km)	35 (mean)	Dziewonski and Anderson, 1981; Scheidegger, 1976; Burtman and Molnar, 1993
Density (kg m^{-3})	10–80 range	Lodders and Fegley, 1998
Mean pressure gradient (Pa km^{-1})	2.8×10^5	Lodders and Fegley, 1998
Geothermal gradient (K km^{-1})	2.74×10^4	Lodders and Fegley, 1998; Dziewonski and Anderson, 1981
Oceanic crust		
Temperature (K)	271–737 (ocean floor)	Scheidegger, 1982
Pressure (bar)	4×10^2 (base ocean) to $1.9^{+4.38}_{-0.33} \times 10^3$ (Moho)	National Oceanic and Atmospheric Administration website, 2007; Koschinsky <i>et al.</i> , 2008
Thickness (km)	5 (mean oceanic)	Lodders and Fegley, 1998
Mean pressure gradient (Pa km^{-1})	4–20 (range)	Dziewonski and Anderson, 1981; Muller <i>et al.</i> , 1997; Mooney <i>et al.</i> , 1998
Density (kg m^{-3})	4 (mean depth under ocean)	
Geothermal gradient (K km^{-1})	2.94×10^4	Lodders and Fegley, 1998; Dziewonski and Anderson, 1981
Atmosphere		
Mean lapse rate temperature (K km^{-1})*	3×10^3	Lodders and Fegley, 1998
Mean lapse rate temperature (K km^{-1})*	40	Scheidegger, 1982
Lapse rate pressure (Pa km^{-1})†	6.5 troposphere	Hewitt and Jackson, 2003; West, 1996; Choi <i>et al.</i> , 1998
below 86 km	–2.0 stratosphere	
	2.6 mesosphere	
	–5.8 thermosphere	
	$-0.0012(1 - \frac{z}{44307.69})^{4.26}$	National Oceanic and Atmospheric Administration website, 2007; Pearson and Ruggie, 1976

*Temperature lapse rate Γ_T is the rate of decrease of temperature with height: $\Gamma_T(z) = -dT/dz$.

†Pressure lapse rate Γ_P is the rate of decrease of pressure with height: $\Gamma_P(z) = dP/dz$ using the equation $z = [1 - (P/10.13)^{0.119}] \times 44307.69$ where z = altitude (km) and P = static pressure (Pa) (Pearson and Ruggie, 1976).

horizontal error bars that encompass the range of estimates in the literature. The same holds for estimates of conditions across the core-to-mantle transition.

A.3. Mantle

Earth's mantle extends from a depth of 2890 km at the core-mantle boundary to a range of 4–80 km beneath oceanic and continental crust. Our chosen average of the Mohorovičić discontinuity (Mohorovičić, 1909) is 3.3×10^3 bar and 800 K, which is consistent with the average continental crustal depth of 35 km (Lodders and Fegley, 1998). The variation in the Moho will be discussed in more detail below. Our CMB values lead to a modeled mantle geotherm of 0.66 K km^{-1} . This temperature profile lies below the assumed mantle solidus (Zerr, 1998; Nakagawa and Tackley, 2004), resulting in the expected solid mantle (Stein and Wysession, 2003). For example, the solidus temperature at the CMB pressure is estimated as 4300 K (Nakagawa and Tackley, 2004).

B. Appendix B: Explanatory Details for Tables 3 and 4

Life has been found throughout Earth's atmosphere, to an altitude of 77 km above the surface (Imshenetsky *et al.*, 1978). These organisms can be classified into two types—spore or spore-forming bacteria (*e.g.*, *Bacillus simplex*; Wainwright *et al.*, 2002) and bacteria that do not form spores (*e.g.*, *Micrococcus*; Griffin, 2008). This classification is made here, as it allows for a distinction to be made between active and potentially dormant life in the atmosphere. Spore structures allow bacteria to survive for extended periods of time in unfavorable conditions. This means that spores collected from the atmosphere can be dormant and yet viable, so they may be able to be cultivated in the laboratory. It is unclear, however, whether such spores were actively metabolizing, be it at a very slow rate, in atmospheric conditions (personal correspondence, Dr. Yogesh Shouche, April 3, 2009). Non-spore-forming bacteria that are retrieved from the atmosphere, however, are thought to have been active in that environment if they are able to be grown in the laboratory. Using this distinction, some have concluded that active life has been isolated from an altitude of 20 km in Earth's atmosphere (Griffin, 2008) at an ambient pressure and temperature of 0.055 bar and -56°C , respectively. This appears to extend the lower temperature limit of life; however, the result should be viewed with caution, as no measurements of metabolism were made. Other species of non-spore-forming bacteria have been isolated from the atmosphere at higher altitudes and warmer temperatures (between 20 and 70 km altitude) but have been found to be viable yet nonculturable (Wainwright *et al.*, 2004), and are examples of dormant life. The current upper boundary of the biosphere (most likely at the tropopause at ~ 10 km altitude, which is a boundary to the vertical movement of particles; Wainwright *et al.*, 2006) lies at 77 m (ambient pressure and temperature of $\sim 10^{-5}$ bar, -70°C respectively) where spores (*e.g.*, *Circinella muscae*) were isolated (Imshenetsky *et al.*, 1978) and were most likely dormant at *in situ* conditions. Examples of the potentially lowest temperature, active life, and the highest altitude (dormant) life are included in our life regime in Fig. 4.

A serious limitation on atmospheric life's capacity to remain active may be the transient nature of low-pressure liquid-water environments. The presence of life in clouds is strongly linked to the availability of liquid water. Studies of low-altitude atmospheric life (samples from <4 km above sea level, Sattler *et al.*, 2001; Bauer *et al.*, 2002; Amato *et al.*, 2005, 2007) have found that the majority of microbes in the clouds are dormant, but viable and remain alive by utilizing cloud water. This suggests that surface life can persist at altitudes up to the triple point of ocean salinity water at ~ 25 km altitude (Fig. 3); however, this life will be largely, or entirely, dormant. Samples isolated at higher altitudes (*e.g.*, ~ 41 km, Wainwright *et al.*, 2002) have a much lower percentage of viable microorganisms, which may be due to the additional stress of almost no cloud water. Cloud water could persist to higher altitudes (lower atmospheric pressures) if it is briny; however, models of liquid-water clouds indicate that water content reaches a minimum at <20 km altitude (Fig. 7 of http://meteora.ucsd.edu/~iacob/scm_recent/arm3/poster.html; Iacobellis *et al.*, 2003).

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Abbreviations

CMB, core-mantle boundary; *P-T*, pressure-temperature.

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