



# Corrigendum: Living at the Extremes: Extremophiles and the Limits of Life in a Planetary Context

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**Keywords:** polyextremophiles, limits of life, astrobiology, habitability and astrobiology, extremophiles/extremophily, search for life

## A Corrigendum on

### Living at the Extremes: Extremophiles and the Limits of Life in a Planetary Context

by Merino, N., Aronson, H. S., Bojanova, D. P., Feyhl-Buska, J., Wong, M. L., Zhang, S., et al. (2019) *Front. Microbiol.* 10:780. doi: 10.3389/fmicb.2019.00780

In the original article, there was a mistake in the legend for **Table 4** as published. The legend in **Table 4** is missing two parentheses around “Poly.” The correct legend appears below.

#### “Table 4. Examples of notable (Poly)extremophiles and their physiological requirements.”

Additionally, there was a mistake in **Table 3** and **Table 5** as published. In **Table 3**, the lowest temperature listed for *Planococcus halocryophilus* Or1 is “–18°C.” It should be “–15°C” instead. In addition, the pH range is “nr” but should be “6–11” instead. In the temperature column, 37 is bold type, but this should be regular type.

In **Table 5**, the atmosphere entry for Earth > Atmosphere > Geochemistry is listed as “8.1% N<sub>2</sub>,” but the actual composition of Earth’s atmosphere is “78% N<sub>2</sub>.”

The corrected **Table 3** and **Table 5** appear below.

Lastly, there is a grammatical error in the original article.

A correction has therefore been made to the section *Can Life Originate, Evolve, or Survive on Other Planetary Bodies?*, paragraph five:

“Solar and galactic cosmic rays (high-energy particles with energies from 10 MeV to >10 GeV) present challenges to life on the surface and near-surface of Mars and other planetary bodies. However, any subsurface aquifer deeper than a few meters would be protected from damaging radiation. Dartnell et al. (2007) calculated the galactic cosmic ray dosage rates and the corresponding survival times (which they defined as a million-fold decrease in cell number) of characteristic microbes at different depths in Mars’s subsurface. At the surface, *E. coli* has a survival time of 1,200 years, while at 20-m depth, that survival time jumps to  $1.5 \times 10^8$  years. Compared to *E. coli*, *D. radiodurans* has survival times an order of magnitude longer. These survival times are, in fact, lower limits in light of recent measurements by the Radiation Assessment Detector onboard the Mars Science Laboratory (Hassler et al., 2014), which found that the actual dose rate at Gale Crater (76 mGy year<sup>−1</sup>) is a factor of 2 lower than that modeled by Dartnell et al. (2007).”

The authors apologize for these errors and state that they do not change the scientific conclusions of the article in any way. The original article has been updated.

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### Edited and reviewed by:

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University of Bologna, Italy

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### Specialty section:

This article was submitted to  
Extreme Microbiology,  
a section of the journal  
*Frontiers in Microbiology*

Received: 02 July 2019

Accepted: 18 July 2019

Published: 13 August 2019

### Citation:

Merino N, Aronson HS, Bojanova DP, Feyhl-Buska J, Wong ML, Zhang S and Giovannelli D (2019)

Corrigendum: Living at the Extremes: Extremophiles and the Limits of Life in a Planetary Context.

*Front. Microbiol.* 10:1785.  
doi: 10.3389/fmicb.2019.01785

**TABLE 3 |** Limits of life as identified by (poly)extremophilic organisms in pure cultures.

Strain	Domain	Extremophile Type	Isolation ecosystem	Temperature (°C)	pH	Pressure (Mpa)	Salinity (%)	Water activity ( $a_w$ )	References
<i>Picrophilus oshimae</i> KAW 2/2	Archaea	Hyperacidophile	Hot springs, Solfataras	47–65 (60) <sup>a</sup>	<b>—0.06–1.8</b> (0.7)	nr	0–20	nr	Schleper et al., 1995, 1996
<i>Serpentinimonas</i> sp. B1	Bacteria	Alkaliphile	Serpentinizing system (water)	18–37 (30)	<b>9–12.5</b> (11)	nr	0–0.5 (0)	nr	Suzuki et al., 2014
<i>Methanopyrus kandleri</i> 116	Archaea	Hyperthermophile	Deep-sea hydrothermal vent	90– <b>122</b> (105)	(6.3–6.6)	0.4–40	0.5–4.5 (3.0)	nr	Takai et al., 2008
<i>Planococcus halocryophilus</i> Or1	Bacteria	Halopsychrophile	Sea ice core	<b>—15</b> –37 (25)	6–11 (7–8)	nr	0–19 (2)	nr	Mykytczuk et al., 2012, 2013
<i>Halarsenatibacter silvermanii</i> SLAS-1	Bacteria	Haloalkaliphile	Soda lake	28–55 (44)	8.7–9.8 (9.4)	nr	20–35 ( <b>35</b> )	nr	Oremland et al., 2005
<i>Thermococcus piezophilus</i> CDGS	Archaea	Piezothermophile	Deep-sea hydrothermal vent	60–95 (75)	5.5–9 (6)	<b>0.1–125</b> (50)	2–6 (3)	nr	Dalmasso et al., 2016
Haloarchaeal strains GN-2 and GN-5	Archaea	Xerophile	Solar salterns (brine)	nr	nr	nr	nr	<b>0.635</b>	Javor, 1984

<sup>a</sup>Data presented as range (optimum) for each parameter. nr, not reported in the original publication. Current limits are highlighted in bold.

**TABLE 5 |** Boundary conditions for different planetary bodies of astrobiological interest (compared to Earth), split into atmosphere, surface, and subsurface layers.

<b>Planetary body</b>	<b>Type</b>	<b>Layer</b>	<b>Temperature (°C)</b>	<b>pH</b>	<b>Pressure (MPa)</b>	<b>Salinity (% NaCl)</b>	<b>Geochemistry</b>	<b>References</b>
Earth	Planet	Atmosphere	-100–40	Neutral, local acidic conditions possible due to volcanism and human activities	0.0001–0.1	0	78% N <sub>2</sub> , 21% O <sub>2</sub> , 9340 ppm Ar, 400 ppm CO <sub>2</sub> , 18.2 ppm Ne, 5.2 ppm He, 1.7 ppm CH <sub>4</sub> , 1.1 ppm Kr, 0.6 ppm H <sub>2</sub> , variable H <sub>2</sub>	Hans Wedepohl, 1995; McDonough and Sun, 1995; Wayne, 2000
		Surface	-98.6–464	-3.6–13.3	0.003–112	0–saturation	Soils and sediments of varying lithologies, siliceous crust, ranging from mafic to felsic composition. Extensive ocean (70% planet surface), with 4,000 m average depth, 4°C and 3.5% average temperature and salinity respectively	
		Subsurface	3.25–<400	~1–12.8	<800	0.05–saturation	Soils and sediments of varying lithologies, siliceous crust, ranging from mafic to felsic composition, ultramafic mantle	
Venus	Planet	Atmosphere	-40–482 <sup>a</sup>	0 <sup>b</sup>	0.1–9.3 <sup>c</sup>	nr	96.5% CO <sub>2</sub> , 3.5% N <sub>2</sub> ; small quantities of CO, SO <sub>2</sub> , HCl, HF, HDO, and H <sub>2</sub> O; H <sub>2</sub> SO <sub>4</sub> condensates	Cockell, 1999; Basilevsky and Head, 2003; Schulze-Makuch et al., 2004; Lang and Hansen, 2006; Bertaux et al., 2007; Airey et al., 2017
		Surface	377–482	nr	4.5–9.3 <sup>c</sup>	nr	Rocks are similar to tholeiitic and alkaline basalts; no liquid water	
		Subsurface	nr	nr	nr	nr	Fluid channels; volcanism	
Mars	Planet	Atmosphere	-138–35 <sup>d</sup>	nr	0.0001–0.0009	nr	95.3% CO <sub>2</sub> , 2.7% N <sub>2</sub> , 1.6% Ar, 0.13% O <sub>2</sub> , 0.08% CO; trace amounts of H <sub>2</sub> O, NO, Ne, Kr, Xe	Varnes et al., 2003; Fairén et al., 2004; Nicholson and Schuerger, 2005; Hecht et al., 2009; Smith et al., 2009; Johnson et al., 2011; Jones et al., 2011; Michalski et al., 2013; Longstaff, 2014; Wordsworth, 2016; Sinha et al., 2017; NASA, 2018
		Surface	-138–30	7.7 <sup>e</sup>	0.0004–0.0009	5.2–5.8	Basaltic, Fe-/Mg-rich phyllosilicates, perchlorate salts, Al-rich clays, sulfates, chlorides, calcite, and silicas; potential cryosphere	
		Subsurface	55 <sup>g</sup>	4.96–9.13 <sup>h</sup>	10–303 <sup>g</sup>	Cl-rich brines	Potential groundwater; basalt crust; possible serpentinization	

(Continued)

**TABLE 5 |** Continued

<b>Planetary body</b>	<b>Type</b>	<b>Layer</b>	<b>Temperature (°C)</b>	<b>pH</b>	<b>Pressure (MPa)</b>	<b>Salinity (% NaCl)</b>	<b>Geochemistry</b>	<b>References</b>
Enceladus	Icy moon	Plume jets	0	~8.5–9	High velocity jets	> 0.5	90–99% H <sub>2</sub> O, ≤0.61–4.27% N <sub>2</sub> , 0.3–5.3% CO <sub>2</sub> , 0.1–1.68% CH <sub>4</sub> , 0.4–0.9% NH <sub>3</sub> , 0.4–39% H <sub>2</sub> , trace amounts of hydrocarbons; high mass organic cations, silicates, sodium, potassium, carbonates	Gioia et al., 2007; Postberg et al., 2009, 2018; Waite et al., 2009; Zolotov et al., 2011; Glein et al., 2015; Holm et al., 2015; Hsu et al., 2015; Taubner et al., 2018
		Icy shell (~10 km thick)	-233 – -23	nr	nr	May have ammonia brine pockets	May have tectonics	
		Subsurface global ocean (~0–170 km depth)	<90	8.5 – 12.2 <sup>k</sup>	1 – 8	0.45 – < 4	Possible serpentinization	
Titan	Icy moon	Atmosphere	-183 – -73 <sup>j</sup>	nr	> 0.01 – 0.15	nr	98.4% N <sub>2</sub> , 1.4% CH <sub>4</sub> , 0.2% H <sub>2</sub> , trace hydrocarbons and organics; 95% N <sub>2</sub> , 5% CH <sub>4</sub> , 0.1% H <sub>2</sub> ; ~50 ppmv CO and ~15 ppbv CO <sub>2</sub> ; C <sub>2</sub> H <sub>3</sub> CN; clouds	Fulchignoni et al., 2005; de Kok et al., 2007; Norman, 2011; Baland et al., 2014; Mastrogiuseppe et al., 2014; Mitri et al., 2014; Sohl et al., 2014; Jennings et al., 2016; McKay, 2016; Mitchell and Lora, 2016; Brassé et al., 2017; Cordier et al., 2017
		Surface	-183 – -179	nr	0.15–0.35 <sup>i</sup>	nr	Lakes and sea have CH <sub>4</sub> , C <sub>2</sub> H <sub>4</sub> , and dissolved nitrogen; dunes of solid organic material; low-latitude deserts and high-latitude moist climates	
		Subsurface	-18	11.8 <sup>l</sup>	50–300 <sup>m</sup>	Likely dense subsurface ocean ( $\leq 1,350 \text{ kg m}^{-3}$ ) suggesting high salinity	CH <sub>4</sub> and C <sub>2</sub> H <sub>6</sub>	
Ceres	Dwarf planet	Atmosphere	nr	nr	nr	nr	Transient atmosphere with possible water vapo	Fanale and Salvail, 1989; Zolotov, 2009, 2017; Küppers et al., 2014; Hayne and Aharonson, 2015; Neveu and Desch, 2015; Hendrix et al., 2016; Villarreal et al., 2017; Vu et al., 2017; Castillo-Rogez et al., 2018; McCord and Castillo-Rogez, 2018; McCord and Zambon, 2019

(Continued)

**TABLE 5 |** Continued

Planetary body	Type	Layer	Temperature (°C)	pH	Pressure (MPa)	Salinity (% NaCl)	Geochemistry	References
Europa	Icy moon	Surface	(−157–−30) <sup>n</sup>	9.7–11.3 <sup>n</sup>	nr	<10 <sup>n</sup>	Surface clays; (Mg, Ca)-carbonates; (Mg, NH <sub>4</sub> )-phylosilicates; Fe-rich clays; salt deposits; chloride salts; water-rock interactions; brucite and magnetite; sulfur species and graphitized carbon; localized Na-carbonates (e.g., Na <sub>2</sub> CO <sub>3</sub> ), NH <sub>4</sub> Cl, NH <sub>4</sub> HCO <sub>3</sub>	
		Subsurface	−143–−93 <sup>o</sup>	Likely alkaline	<140–200 <sup>p</sup>	Potentially has briny or NH <sub>3</sub> -rich subsurface liquid	Active water/ice-driven subsurface processes	
		Atmosphere (tenuous)	nr	nr	0.1 <sup>−12</sup> –1 <sup>−12</sup>	nr	Ion sputtering of the surface; potential water plumes; O <sub>2</sub> ; trace amounts of sodium and potassium	Spencer et al., 1999; Chyba and Phillips, 2001; Marion et al., 2005; McGrath et al., 2009; Zolotov and Kargel, 2009; Travis et al., 2012; Cassidy et al., 2013; Muñoz-Iglesias et al., 2013; Kattenhorn and Prockter, 2014; Soderlund et al., 2014; Hand and Carlson, 2015; Kimura and Kitadai, 2015; Noell et al., 2015; Vance et al., 2016; Teolis et al., 2017; Zhu et al., 2017; Jones et al., 2018; Martin and McMinn, 2018; Pavlov et al., 2018
		Surface (icy shell)	−187–−141	nr	0.1 <sup>−12</sup>	May be saline, as delivered to the surface from a salty ocean, may have brine or salt inclusions	H <sub>2</sub> O <sub>2</sub> , H <sub>2</sub> SO <sub>4</sub> , CO <sub>2</sub> ; salts concentrated in cracks; oxidants and simple organics; potentially MgSO <sub>4</sub> , Na <sub>2</sub> SO <sub>4</sub> , Na <sub>2</sub> CO <sub>3</sub> , may have gas inclusions; may have tectonics	
		Subsurface ocean	Daily inundation of seawater at T=−4–0	Potential for wide range <sup>q</sup>	0.1–30 <sup>r</sup>	<3.5	Likely contains Mg <sup>2+</sup> , SO <sub>4</sub> <sup>2−</sup> , Na <sup>+</sup> , Cl <sup>−</sup> ; oxidants and simple organics	

The observed or putative geochemistry as well as other potential influences are also listed. <sup>a</sup>Thermosphere can be as cold as −173°C (Bertaux et al., 2007); the upper-to-middle cloud layers are between −40 and 60°C (Cockell, 1999).

<sup>b</sup>Acid concentration in upper cloud layer is 81%, in lower layers up to 98% (Cockell, 1999). <sup>c</sup>Up to 11 MPa in a deep depression (Basilevsky and Head, 2003). <sup>d</sup>Summer air temperatures on Mars near the equator can reach a maximum of 35°C (Longstaff, 2014). <sup>e</sup>Measured by the Phoenix Mars Lander Wet Chemistry Laboratory at the northern plains of the Vastitas Borealis (Hecht et al., 2009). <sup>f</sup>Liquid water may have had water activity > 0.95 (Fairen et al., 2009).

<sup>g</sup>Calculated temperature at a depth of 1–30 km (Jones et al., 2011; Sinha et al., 2017); at a depth ~310 km, the calculated temperature is <427°C (Jones et al., 2011); the Martian core has temperature 1527°C (Longstaff, 2014).

<sup>h</sup>Calculated groundwater pH (Varnes et al., 2003). <sup>i</sup>Calculated pressure at Titan's large sea, Ligeia Mare, is 0.20–0.35 MPa (Cordier et al., 2017). <sup>j</sup>Tropospheric temperature can be −193°C; 80% of incident sunlight is absorbed by

Titan's atmosphere, suggesting that there are greenhouse and antigreenhouse effects (Mitchell and Lora, 2016). <sup>k</sup>The subsurface ocean on Enceladus could also have pH range 10.8–13.5 (Glein et al., 2015). <sup>l</sup>Calculated ocean pH with 5 wt% NH<sub>3</sub> (Brassé et al., 2017). <sup>m</sup>Calculated pressure for the subsurface ocean with thickness 100 km and outer shell thickness 40–170 km (Baland et al., 2014); 800 MPa at the mantle ice shell-core boundary (Sohl et al., 2014).

<sup>n</sup>Calculated surface temperatures, illuminated surfaces can have temperature <−173°C (Hayne and Aharonson, 2015); calculated pH and salinity for bright deposits in Occator crater (Zolotov, 2017); temperature for bright deposits in Occator crater might reach <−0.2°C (Zolotov, 2017). <sup>o</sup>Internal temperature might reach 77°C (McCord and Sotin, 2005). <sup>p</sup>Ceres' center pressure (Zolotov, 2009). <sup>q</sup>Acid brine may result from hydrothermal systems and be enriched with sulfuric acid (Kargel et al., 2000); neutral brine may occur as leachate from chondritic material and be enriched with magnesium sulfate (Kargel et al., 2000; Pasek and Greenberg, 2012); alkaline brine may occur in areas with natron (Na<sub>2</sub>CO<sub>3</sub>·10H<sub>2</sub>O), produced from the venting of CO<sub>2</sub> from aqueous reservoirs (Langmuir, 1971; Millero and Rabindra, 1997). <sup>r</sup>At the base of a 100 km Europan ocean, the pressure is calculated to be 146 MPa (Marion et al., 2005).

## REFERENCES

- Airey, M. W., Mather, T. A., Pyle, D. M., and Ghail, R. C. (2017). The distribution of volcanism in the Beta-Atla-Themis region of Venus: its relationship to rifting and implications for global tectonic regimes. *J. Geophys. Res. Planets* 122, 1626–1649. doi: 10.1002/2016JE005205
- Baland, R. M., Tobie, G., Lefèvre, A., and Van Hoolst, T. (2014). Titan's internal structure inferred from its gravity field, shape, and rotation state. *Icarus* 237, 29–41. doi: 10.1016/j.icarus.2014.04.007
- Basilevsky, A. T., and Head, J. W. (2003). The surface of Venus. *Rep. Prog. Phys.* 66, 1699–1734. doi: 10.1088/0034-4885/66/10/R04
- Bertiaux, J.-L., Vandaele, A.-C., Koralev, O., Villard, E., Fedorova, A., Fussen, D., et al. (2007). A warm layer in Venus' cryosphere and high-altitude measurements of HF, HCl, H<sub>2</sub>O and HDO. *Nature* 450, 646–649. doi: 10.1038/nature05974
- Brassé, C., Buch, A., Coll, P., and Raulin, F. (2017). Low-temperature alkaline pH hydrolysis of oxygen-free Titan Tholins: carbonates' Impact. *Astrobiology* 17, 8–26. doi: 10.1089/ast.2016.1524
- Cassidy, T. A., Paranicas, C. P., Shirley, J. H., Dalton, J. B., Teolis, B. D., Johnson, R. E., et al. (2013). Magnetospheric ion sputtering and water ice grain size at Europa. *Planet. Space Sci.* 77, 64–73. doi: 10.1016/j.pss.2012.07.008
- Castillo-Rogez, J., Neveu, M., McSween, H. Y., Fu, R. R., Toplis, M. J., and Prettyman, T. (2018). Insights into Ceres's evolution from surface composition. *Meteorit. Planet. Sci.* 53, 1820–1843. doi: 10.1111/maps.13181
- Chyba, C., and Phillips, C. (2001). Possible ecosystems and the search for life on Europa. *Proc. Natl. Acad. Sci. U.S.A.* 98, 801–804. doi: 10.1073/pnas.98.3.801
- Cockell, C. S. (1999). Life on Venus. *Planet. Space Sci.* 47, 1487–1501. doi: 10.1016/S0032-0633(99)00036-7
- Cordier, D., Garcíá-Sánchez, F., Justo-Garcíá, D. N., and Liger-Belair, G. (2017). Bubble streams in Titan's seas as a product of liquid N<sub>2</sub> + CH<sub>4</sub> + C<sub>2</sub>H<sub>6</sub> cryogenic mixture. *Nat. Astron.* 1:0102. doi: 10.1038/s41550-017-0102
- Dalmasso, C., Oger, P., Selva, G., Courtine, D., L'Haridon, S., Garlaschelli, A., et al. (2016). *Thermococcus piezophilus* sp. nov., a novel hyperthermophilic and piezophilic archaeon with a broad pressure range for growth, isolated from a deepest hydrothermal vent at the Mid-Cayman Rise. *Syst. Appl. Microbiol.* 39, 440–444. doi: 10.1016/j.sympm.2016.08.003
- Dartnell, L. R., Desorgher, L., Ward, J. M., and Coates, A. J. (2007). Modelling the surface and subsurface Martian radiation environment: implications for astrobiology. *Geophys. Res. Lett.* 34, 4–9. doi: 10.1029/2006GL027494
- de Kok, R., Irwin, P. G. J., Teanby, N. A., Lellouch, E., Bézard, B., Vinatier, S., et al. (2007). Oxygen compounds in Titan's stratosphere as observed by Cassini CIRS. *Icarus* 186, 354–363. doi: 10.1016/j.ICARUS.2006.09.016
- Fairén, A. G., Davila, A. F., Gago-Dupont, L., Amils, R., and McKay, C. P. (2009). Stability against freezing of aqueous solutions on early Mars. *Nature* 459, 401–404. doi: 10.1038/nature07978
- Fairén, A. G., Fernández-Remolar, D., Dohm, J. M., Baker, V. R., and Amils, R. (2004). Inhibition of carbonate synthesis in acidic oceans on early Mars. *Nature* 431, 423–426. doi: 10.1038/nature02911
- Fanale, F. P., and Salvail, J. R. (1989). The water regime of asteroid (1) Ceres. *Icarus* 82, 97–110. doi: 10.1016/0019-1035(89)90026-2
- Fulchignoni, M., Ferri, F., Angrilli, F., Ball, A. J., Bar-Nun, A., Barucci, M. A., et al. (2005). In situ measurements of the physical characteristics of Titan's environment. *Nature* 438, 785–791. doi: 10.1038/nature04314
- Gioia, G., Chakraborty, P., Marshak, S., and Kieffer, S. W. (2007). Unified model of tectonics and heat transport in a frigid Enceladus. *Proc. Natl. Acad. Sci. U.S.A.* 104, 13578–13581. doi: 10.1073/pnas.0706018104
- Glein, C. R., Baross, J. A., and Waite, J. H. (2015). The pH of Enceladus' ocean. *Geochim. Cosmochim. Acta* 162, 202–219. doi: 10.1016/j.gca.2015.04.017
- Hand, K. P., and Carlson, R. W. (2015). Europa's surface color suggests an ocean rich with sodium chloride. *Geophys. Res. Lett.* 42, 3174–3178. doi: 10.1002/2015GL063559
- Hans Wedepohl, K. (1995). The composition of the continental crust. *Geochim. Cosmochim. Acta* 59, 1217–1232. doi: 10.1016/0016-7037(95)00038-2
- Hassler, D. M., Zeitlin, C., Wimmer-schweingruber, R. F., Ehresmann, B., Rafkin, S., Eigenbrode, J. L., et al. (2014). Mars' surface radiation environment. *Science* 343:1244797. doi: 10.1126/science.1244797
- Hayne, P. O., and Aharonson, O. (2015). Thermal stability of ice on Ceres with rough topography. *J. Geophys. Res. E Planets* 120, 1567–1584. doi: 10.1002/2015JE004887
- Hecht, M. H., Kounaves, S. P., Quinn, R. C., West, S. J., Young, S. M. M., Ming, D. W., et al. (2009). Detection of perchlorate and the soluble chemistry of Martian soil at the phoenix lander site. *Science* 325, 64–67. doi: 10.1126/science.1172466
- Hendrix, A. R., Vilas, F., and Li, J. Y. (2016). Ceres: sulfur deposits and graphitized carbon. *Geophys. Res. Lett.* 43, 8920–8927. doi: 10.1002/2016GL070240
- Holm, N. G., Oze, C., Mousis, O., Waite, J. H., and Guillet-Lepoutre, A. (2015). Serpentization and the Formation of H<sub>2</sub> and CH<sub>4</sub> on Celestial Bodies (Planets, Moons, Comets). *Astrobiology* 15, 587–600. doi: 10.1089/ast.2014.1188
- Hsu, H. W., Postberg, F., Sekine, Y., Shibuya, T., Kempf, S., Horányi, M., et al. (2015). Ongoing hydrothermal activities within Enceladus. *Nature* 519, 207–210. doi: 10.1038/nature14262
- Javor, B. (1984). Growth potential of halophilic bacteria isolated from solar salt environments: carbon sources and salt requirements. *Appl. Environ. Microbiol.* 48, 352–360.
- Jennings, D. E., Cottini, V., Nixon, C. A., Achterberg, R. K., Flasar, F. M., Kunde, V. G., et al. (2016). Surface temperatures on Titan during northern winter and spring. *Astrophys. J.* 816:L17. doi: 10.3847/2041-8205/816/1/L17
- Johnson, A. P., Pratt, L. M., Vishnivetskaya, T., Pfiffner, S., Bryan, R. A., Dadachova, E., et al. (2011). Extended survival of several organisms and amino acids under simulated martian surface conditions. *Icarus* 211, 1162–1178. doi: 10.1016/j.icarus.2010.11.011
- Jones, E. G., Lineweaver, C. H., and Clarke, J. D. (2011). An extensive phase space for the potential martian biosphere. *Astrobiology* 11, 1017–1033. doi: 10.1089/ast.2011.0660
- Jones, R. M., Goordial, J. M., and Orcutt, B. N. (2018). Low energy subsurface environments as extraterrestrial analogs. *Front. Microbiol.* 9:1605. doi: 10.3389/fmicb.2018.01605
- Kargel, J. S., Kaye, J. Z., Head, J. W., Marion, G. M., Sassen, R., Crowley, J. K., et al. (2000). Europa's crust and ocean: origin, composition, and the prospects for life. *Icarus* 148, 226–265. doi: 10.1006/ICAR.2000.6471
- Kattenhorn, S. A., and Prockter, L. M. (2014). Evidence for subduction in the ice shell of Europa. *Nat. Geosci.* 7, 762–767. doi: 10.1038/ngeo2245
- Kimura, J., and Kitadai, N. (2015). Polymerization of building blocks of life on Europa and other icy moons. *Astrobiology* 15, 430–441. doi: 10.1089/ast.2015.1306
- Küppers, M., O'Rourke, L., Bockelée-Morvan, D., Zakharov, V., Lee, S., Von Allmen, P., et al. (2014). Localized sources of water vapour on the dwarf planet (1) Ceres. *Nature* 505, 525–527. doi: 10.1038/nature12918
- Lang, N. P., and Hansen, V. L. (2006). Venusian channel formation as a subsurface process. *J. Geophys. Res. E Planets* 111:E04001. doi: 10.1029/2005JE002629
- Langmuir, D. (1971). The geochemistry of some carbonate ground waters in central Pennsylvania. *Geochim. Cosmochim. Acta* 35, 1023–1045. doi: 10.1016/0016-7037(71)90019-6
- Longstaff, A. (2014). *Astrobiology: An Introduction*. Boca Raton, FL: CRC Press. doi: 10.1201/b17880
- Marion, G. M., Kargel, J. S., Catling, D. C., and Jakubowski, S. D. (2005). Effects of pressure on aqueous chemical equilibria at subzero temperatures with applications to Europa. *Geochim. Cosmochim. Acta* 69, 259–274. doi: 10.1016/j.gca.2004.06.024
- Martin, A., and McMinn, A. (2018). Sea ice, extremophiles and life on extra-terrestrial ocean worlds. *Int. J. Astrobiol.* 17, 1–16. doi: 10.1017/S1473550416000483
- Mastrogiovanni, M., Poggiali, V., Hayes, A., Lorenz, R., Lunine, J., Picardi, G., et al. (2014). The bathymetry of a Titan sea. *Geophys. Res. Lett.* 41, 1432–1437. doi: 10.1002/2013GL058618
- McCord, T. B., and Castillo-Rogez, J. C. (2018). Ceres's internal evolution: The view after Dawn. *Meteorit. Planet. Sci.* 53, 1778–1792. doi: 10.1111/maps.13135
- McCord, T. B., and Sotin, C. (2005). Ceres: evolution and current state. *J. Geophys. Res. E Planets* 110:E5. doi: 10.1029/2004JE002244
- McCord, T. B., and Zambon, F. (2019). The surface composition of Ceres from the Dawn mission. *Icarus* 318, 2–13. doi: 10.1016/j.icarus.2018.03.004
- McDonough, W. F., and Sun, S. S. (1995). The composition of the Earth. *Chem. Geol.* 120, 223–253. doi: 10.1016/0009-2541(94)00140-4

- McGrath, M. A., Hansen, C. J., and Hendrix, A. R. (2009). "Observations of Europa's Tenuous Atmosphere," in *Europa*, R. T. Pappalardo, W. B. McKinnon, and K. K. Khurana (Tucson, AZ: University of Arizona Press), 485–506.
- McKay, C. P. (2016). Titan as the Abode of Life. *Life* 6:8. doi: 10.3390/life6010008
- Michalski, J. R., Cuadros, J., Niles, P. B., Parnell, J., Deanne Rogers, A., and Wright, S. P. (2013). Groundwater activity on Mars and implications for a deep biosphere. *Nat. Geosci.* 6, 133–138. doi: 10.1038/ngeo1706
- Millero, F. J., and Rabindra, N. R. (1997). A chemical equilibrium model for the carbonate system in natural waters. *Croat. Chem. Acta* 70, 1–38.
- Mitchell, J. L., and Lora, J. M. (2016). The climate of titan. *Annu. Rev. Earth Planet. Sci.* 44, 353–380. doi: 10.1146/annurev-earth-060115-012428
- Mitri, G., Merigliola, R., Hayes, A., Lefevre, A., Tobie, G., Genova, A., et al. (2014). Shape, topography, gravity anomalies and tidal deformation of Titan. *Icarus* 236, 169–177. doi: 10.1016/j.icarus.2014.03.018
- Muñoz-Iglesias, V., Bonales, L. J., and Prieto-Ballesteros, O. (2013). pH and Salinity Evolution of Europa's Brines: Raman Spectroscopy Study of Fractional Precipitation at 1 and 300 Bar. *Astrobiology* 13, 693–702. doi: 10.1089/ast.2012.0900
- Mykytczuk, N. C. S., Foote, S. J., Omelon, C. R., Southam, G., Greer, C. W., and Whyte, L. G. (2013). Bacterial growth at  $-15^{\circ}\text{C}$ ; molecular insights from the permafrost bacterium *Planococcus halocryophilus* Or1. *ISME J.* 7, 1211–1226. doi: 10.1038/ismej.2013.8
- Mykytczuk, N. C. S., Wilhelm, R. C., and Whyte, L. G. (2012). *Planococcus halocryophilus* sp. nov., an extreme sub-zero species from high arctic permafrost. *Int. J. Syst. Evol. Microbiol.* 62, 1937–1944. doi: 10.1099/ijsm.0.035782-0
- NASA (2018). *Mars Fact Sheet*. Greenbelt, MD: NASA. Available at: <https://nssdc.gsfc.nasa.gov/planetary/factsheet/marsfact.html> (accessed September 27, 2018).
- Neveu, M., and Desch, S. J. (2015). Geochemistry, thermal evolution, and cryovolcanism on Ceres with a muddy ice mantle. *Geophys. Res. Lett.* 42, 10197–10206. doi: 10.1002/2015GL066375
- Nicholson, W. L., and Schuerger, A. C. (2005). *Bacillus subtilis* spore survival and expression of germination-induced bioluminescence after prolonged incubation under simulated mars atmospheric pressure and composition: implications for planetary protection and Lithopanspermia. *Astrobiology* 5, 536–544. doi: 10.1089/ast.2005.5.536
- Noell, A. C., Ely, T., Bolser, D. K., Darrach, H., Hodys, R., Johnson, P. V., et al. (2015). Spectroscopy and Viability of *Bacillus subtilis* Spores after Ultraviolet Irradiation: Implications for the Detection of Potential Bacterial Life on Europa. *Astrobiology* 15, 20–31. doi: 10.1089/ast.2014.1169
- Norman, L. H. (2011). Is there life on ... Titan? *Astron. Geophys.* 52, 39–31. doi: 10.1111/j.1468-4004.2011.52139.x
- Oremland, R., Kulp, T., Blum, J., Hoeft, S., Baesman, S., Miller, L., et al. (2005). A microbial arsenic cycle in a salt-saturated, extreme environment. *Science* 308, 1305–1308. doi: 10.1126/science.1110832
- Pasek, M. A., and Greenberg, R. (2012). Acidification of Europa's Subsurface Ocean as a Consequence of Oxidant Delivery. *Astrobiology* 12, 151–159. doi: 10.1089/ast.2011.0666
- Pavlov, A., Cheptsov, V., Tsurkov, D., Lomasov, V., Frolov, D., Vasiliev, G., et al. (2018). Survival of Radioresistant Bacteria on Europa's Surface after Pulse Ejection of Subsurface Ocean Water. *Geosciences* 9:9. doi: 10.3390/geosciences9010009
- Postberg, F., Kempf, S., Schmidt, J., Brilliantov, N., Beinsen, A., Abel, B., et al. (2009). Sodium salts in E-ring ice grains from an ocean below the surface of Enceladus. *Nature* 459, 1098–1101. doi: 10.1038/nature08046
- Postberg, F., Khawaja, N., Abel, B., Choblet, G., Glein, C. R., Gudipati, M. S., et al. (2018). Macromolecular organic compounds from the depths of Enceladus. *Nature* 558, 564–568. doi: 10.1038/s41586-018-0246-4
- Schleper, C., Puehler, G., Holz, I., Gambacorta, A., Janekovic, D., Santarius, U., et al. (1995). *Picrophilus* gen. nov., fam. nov.: a novel aerobic, heterotrophic, thermoacidophilic genus and family comprising archaea capable of growth around pH 0. *J. Bacteriol.* 177, 7050–7059. doi: 10.1128/jb.177.24.7050-7059.1995
- Schleper, C., Puhler, G., Klenk, H.-P., and Zillig, W. (1996). *Picrophilus oshimae* and *Picrophilus torridus* fam. nov., gen. nov., sp. nov., two species of hyperacidophilic, thermophilic, heterotrophic, aerobic archaea. *Int. J.* 46, 814–816. doi: 10.1099/00207713-46-3-814
- Schulze-Makuch, D., Grinspoon, D. H., Abbas, O., Irwin, L. N., and Bullock, M. A. (2004). A sulfur-based survival strategy for putative phototrophic life in the venusian atmosphere. *Astrobiology* 4, 11–18. doi: 10.1089/153110704773600203
- Sinha, N., Nepal, S., Kral, T., and Kumar, P. (2017). Survivability and growth kinetics of methanogenic archaea at various pHs and pressures: implications for deep subsurface life on Mars. *Planet. Space Sci.* 136, 15–24. doi: 10.1016/j.pss.2016.11.012
- Smith, D. J., Schuerger, A. C., Davidson, M. M., Pacala, S. W., Bakermans, C., and Onstott, T. C. (2009). Survivability of *Psychrobacter cryohalolentis* K5 under simulated martian surface conditions. *Astrobiology* 9, 221–228. doi: 10.1089/ast.2007.0231
- Soderlund, K. M., Schmidt, B. E., Wicht, J., and Blankenship, D. D. (2014). Ocean-driven heating of Europa's icy shell at low latitudes. *Nat. Geosci.* 7, 16–19. doi: 10.1038/ngeo2021
- Sohl, F., Solomonidou, A., Wagner, F. W., Coustenis, A., Hussmann, H., and Schulze-Makuch, D. (2014). Structural and tidal models of Titan and inferences on cryovolcanism. *J. Geophys. Res. Planets* 119, 1013–1036. doi: 10.1002/2013JE004512
- Spencer, J. R., Tamppari, L. K., Martin, T. Z., and Travis, L. D. (1999). Temperatures on Europa from Galileo photopolarimeter-radiometer: nighttime thermal anomalies. *Science* 284, 1514–1514. doi: 10.1126/science.284.5419.1514
- Suzuki, S., Kuenen, J. G., Schipper, K., Van Der Velde, S., Ishii, S., Wu, A., et al. (2014). Physiological and genomic features of highly alkaliphilic hydrogen-utilizing Betaproteobacteria from a continental serpentinizing site. *Nat. Commun.* 5:3900. doi: 10.1038/ncomms4900
- Takai, K., Nakamura, K., Toki, T., Tsunogai, U., Miyazaki, M., Miyazaki, J., et al. (2008). Cell proliferation at 122 C and isotopically heavy CH<sub>4</sub> production by a hyperthermophilic methanogen under high-pressure cultivation. *Proc. Natl. Acad. Sci. U.S.A.* 105, 10949–10954. doi: 10.1073/pnas.0712334105
- Taubner, R. S., Pappenreiter, P., Zwicker, J., Smrzka, D., Pruckner, C., Kolar, P., et al. (2018). Biological methane production under putative Enceladus-like conditions. *Nat. Commun.* 9:748. doi: 10.1038/s41467-018-02876-y
- Teolis, B. D., Wyrick, D. Y., Bouquet, A., Magee, B. A., and Waite, J. H. (2017). Plume and surface feature structure and compositional effects on Europa's global exosphere: preliminary Europa mission predictions. *Icarus* 284, 18–29. doi: 10.1016/j.icarus.2016.10.027
- Travis, B. J., Palguta, J., and Schubert, G. (2012). A whole-moon thermal history model of Europa: impact of hydrothermal circulation and salt transport. *Icarus* 218, 1006–1019. doi: 10.1016/j.icarus.2012.02.008
- Vance, S. D., Hand, K. P., and Pappalardo, R. T. (2016). Geophysical controls of chemical disequilibria in Europa. *Geophys. Res. Lett.* 43, 4871–4879. doi: 10.1002/2016GL068547.Received
- Varnes, E. S., Jakosky, B. M., and McCollom, T. M. (2003). Biological potential of Martian hydrothermal systems. *Astrobiology* 3, 407–414. doi: 10.1089/153110703769016479
- Villarreal, M. N., Russell, C. T., Luhmann, J. G., Thompson, W. T., Prettyman, T. H., A'Hearn, M. F., et al. (2017). The dependence of the cerean exosphere on solar energetic particle events. *Astrophys. J.* 838:L8. doi: 10.3847/2041-8213/aa66cd
- Vu, T. H., Hodys, R., Johnson, P. V., and Choukroun, M. (2017). Preferential formation of sodium salts from frozen sodium-ammonium-chloride-carbonate brines – Implications for Ceres' bright spots. *Planet. Space Sci.* 141, 73–77. doi: 10.1016/j.pss.2017.04.014
- Waite, J. H., Lewis, W. S., Magee, B. A., Lunine, J. I., McKinnon, W. B., Glein, C. R., et al. (2009). Liquid water on Enceladus from observations of ammonia and  $\text{Ar}$  in the plume. *Nature* 460, 487–490. doi: 10.1038/nature08153
- Wayne, R. P. (2000). *Chemistry of Atmospheres*, 3rd Edn. Oxford: Clarendon Press.
- Wordsworth, R. (2016). The climate of early mars. *Annu. Rev. Earth Planet. Sci.* 44, 381–408. doi: 10.1146/annurev-earth-060115-012355
- Zhu, P., Manucharyan, G. E., Thompson, A. F., Goodman, J. C., and Vance, S. D. (2017). The influence of meridional ice transport on Europa's ocean stratification and heat content. *Geophys. Res. Lett.* 44, 5969–5977. doi: 10.1002/2017GL072996
- Zolotov, M. Y. (2009). On the composition and differentiation of Ceres. *Icarus* 204, 183–193. doi: 10.1016/j.icarus.2009.06.011

- Zolotov, M. Y. (2017). Aqueous origins of bright salt deposits on Ceres. *Icarus* 296, 289–304. doi: 10.1016/j.icarus.2017.06.018
- Zolotov, M. Y., and Kargel, J. S. (2009). “On the chemical composition of Europa’s icy shell, ocean, and underlying rocks,” in *Europa*, eds R. T. Pappalardo, W. B. McKinnon, and K. Khurana (Tucson, AZ: University of Arizona Press), 431.
- Zolotov, M. Y., Tobie, G., Postberg, F., Magee, B., Waite, J. H., and Esposito, L. (2011). Chemical and phase composition of Enceladus: insights from Cassini data. *EPSC Abstracts* 6:EPSC-DPS2011-1330. doi: 10.1029/2011GL047415

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