

# [Editorial: microbial hydrogen metabolism](https://assignbuster.com/editorial-microbial-hydrogen-metabolism/)

[Health & Medicine](https://assignbuster.com/essay-subjects/health-n-medicine/)

Editorial on the Research Topic
Microbial Hydrogen Metabolism

Among the most ancient and widespread metabolic traits of microbial life is the ability to interconvert molecular hydrogen (H 2 ; [Lane et al., 2010](#B27) ; [Schwartz et al., 2013](#B45) ; [Peters et al., 2015](#B37) ). Two classes of metalloenzymes, [FeFe]-hydrogenase and [NiFe]-hydrogenase, catalyze the reversible oxidation of H 2 to electrons and protons ( [Volbeda et al., 1995](#B52) ; [Peters et al., 1998](#B36) ); a third class of hydrogenase, termed [Fe]-hydrogenase or Hmd, catalyzes the reduction of the substrate methenyltetrahydromethanopterin with H 2 ( [Shima et al., 2008](#B46) ). The three classes of enzyme differ structurally and are phylogenetically unrelated. As such, they represent profound examples of convergent evolution ( [Wu and Mandrand, 1993](#B55) ; [Vignais and Billoud, 2007](#B51) ; [Greening et al., 2016](#B14) ).

Approximately a third of sequenced microorganisms, spanning at least 70 microbial phyla, encode hydrogenases and are thus predicted to be capable of interconverting H 2 ( [Peters et al., 2015](#B37) ; [Greening et al., 2016](#B14) ). The earliest evolving hydrogenase enzymes harbor a [NiFe] co-factor and these are thought to have functioned oxidatively ( [Boyd et al., 2014](#B2) ; [Weiss et al., 2016](#B53) ), with [FeFe]-hydrogenases thought to have emerged more recently ( [Mulder et al., 2010](#B34) ). Both [NiFe] and [FeFe]-hydrogenases have since diversified to function in aerobic and anaerobic, heterotrophic, and autotrophic, and chemotrophic and phototrophic metabolic backgrounds ( [Kovács et al., 2005](#B25) ; [Tamagnini et al., 2007](#B48) ; [Thauer et al., 2010](#B50) ; [Schwartz et al., 2013](#B45) ; [Koch et al., 2014](#B24) ; [Schuchmann and Muller, 2014](#B43) ; [Pinske and Sawers, 2016](#B39) ). Many bacteria and archaea oxidize H 2 as a low potential electron donor, an activity typically (albeit not exclusively) attributed to various lineages of [NiFe]-hydrogenase enzymes. Various bacteria, archaea, and microbial eukaryotes also evolve H 2 as a diffusible end product during fermentative metabolism through the activity of [FeFe]- or [NiFe]-hydrogenases ( [Horner et al., 2000](#B19) ; [Kim and Kim, 2011](#B23) ; [Marreiros et al., 2013](#B31) ; [Schwartz et al., 2013](#B45) ; [Pinske and Sawers, 2016](#B39) ). In many organisms, the ability to metabolize H 2 is a facultative trait that is regulated through the expression and maturation of hydrogenases ( [Schwartz et al., 2013](#B45) ; [Greening and Cook, 2014](#B15) ). In such taxa, H 2 represents a substrate that organisms utilize to supplement their energy metabolism, thereby allowing for an expansion of their niche space in ecosystems where other sources of reductant are low or variable in supply (e. g., [Amenabar et al., 2018](#B1) ).

The implications of H 2 in ecosystem level processes is increasingly being realized in both environmental and biomedical settings. A wide range of ecosystems have now been described where H 2 cycling supports the bulk of primary production and where it forms the basis by which species interact, leading to ecologically structured communities. Much of the research on H 2 metabolism to date has focused on ecosystems where H 2 is present at elevated concentrations due to biological activity (e. g., anoxic sediments, gastrointestinal tracts; [Sørensen et al., 1981](#B47) ; [Wolf et al., 2016](#B54) ; [Greening et al., 2019](#B16) ; [Kessler et al., 2019](#B22) ) or geological activity (e. g., hydrothermal vents, subsurface systems; [Petersen et al., 2011](#B38) ; [Brazelton et al., 2012](#B3) ; [Telling et al., 2015](#B49) ; [Dong et al., 2019](#B11) ; [Lindsay et al., 2019](#B28) ). More recently, it has been recognized that atmospheric H 2 can serve as source of reductant for aerobic soil microorganisms and that this can influence the composition of the atmosphere ( [Conrad, 1996](#B8) ; [Constant et al., 2010](#B9) ; [Ji et al., 2017](#B20) ; [Cordero et al., 2019](#B10) ). In parallel, medical microbiologists have shown that H 2 metabolism is critical for the virulence of numerous pathogens, including *Helicobacter* , Clostridia, and Enterobacteriaceae ( [Kaji et al., 1999](#B21) ; [Olson and Maier, 2002](#B35) ; [Maier et al., 2004](#B30) , [2013](#B29) ).

This special issue, featuring 10 articles from 46 different authors, explores microbial H 2 metabolism from the molecular to the ecosystem scale. In the area of anaerobic metabolism, there are articles exploring the metabolism of H 2 -metabolizing bacteria capable of sulfate reduction, acetogenesis, halorespiration, and fermentation. Two articles investigate H 2 oxidation in sulfate-reducing bacteria using the model system *Desulfovibrio vulgaris* ( [Fauque et al., 1988](#B12) ; [Caffrey et al., 2007](#B5) ). Smith et al. present a mathematical model of the growth and metabolism of this bacterium, whereas Löffler et al. investigate the kinetic isotope fractionation associated with its H 2 oxidation activity. A comprehensive review led by Schuchmann et al. covers recent advances in understanding clostridial H 2 metabolism; it details the discovery and characterization of multimeric electron-bifurcating [FeFe]-hydrogenases, including those associated with formate dehydrogenases ( [Schut and Adams, 2009](#B44) ; [Schuchmann and Müller, 2012](#B41) , [2013](#B42) ; [Buckel and Thauer, 2018](#B4) ). Another article led by Dragomirova et al. focuses on heterologous expression of a [NiFe]-hydrogenase from dehalogenating Chloroflexi ( [Kublik et al., 2016](#B26) ; [Hartwig et al., 2017](#B17) ), reporting another unexpected association with formate dehydrogenase activity. Pinske explores a third type of formate dehydrogenase-linked hydrogenase, namely the classical formate hydrogenlyase complex of Enterobacteriaceae ( [McDowall et al., 2014](#B32) ), and its association with two novel iron-sulfur proteins.

Several articles also investigate aerobic H 2 metabolism. Islam et al. report two other novel iron-sulfur proteins in mycobacteria, demonstrating that they are essential for the activity of the two high-affinity hydrogenases described in this lineage ( [Greening et al., 2014](#B13) ). Carere et al. meanwhile, build on the recent discovery that verrucomicrobial methanotrophs are facultative mixotrophs ( [Carere et al., 2017](#B6) ; [Mohammadi et al., 2017](#B33) ) by showing resource allocation of *Methylacidiphilum* varies depending on H 2 availability. Three articles also explore H 2 metabolism at the ecosystem level. Adam and Perner explore the diversity of aerobic and anaerobic H 2 metabolism in deep-sea hydrothermal vent systems, whereas Meyer-Dombard et al. investigate the influence of H 2 on biogeochemical cycling in serpentinizing springs in the Philippines. Teng et al. review the previously underexplored area of H 2 metabolism in bioremediation, including in the reduction of organohalides, nitroaromatic compounds, and heavy metals ( [Chardin et al., 2003](#B7) ; [Hong et al., 2008](#B18) ; [Schubert et al., 2018](#B40) ).

In summary, this special Research Topic sheds light on the diverse role of H 2 in microbial metabolism and uncovers novel enzymes and pathways that mediate this process. This body of work highlights the intricate linkages between H 2 cycling and the cycling of various other compounds, including methane, formate, carbon dioxide, sulfate, and organohalides, among others. In turn, these findings pave way for future studies on the biochemistry, physiology, ecology, and industrial applications of microbial H 2 metabolism.

## Author Contributions

CG and EB drafted this editorial together and approve its submission.

## Funding

This work was supported by the U. S. Department of Energy, Office of Science, Basic Energy Sciences under Award DE-SC0020246 (EB).

## Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Acknowledgments

We would like to acknowledge all authors, peer reviewers, guest editors, and the Frontiers team for their support in developing this Research Topic. The salary of CG is covered by an Australian Research Council DECRA Fellowship (DE170100310) and a National Health & Medical Research Council EL2 Fellowship (APP1178715).

## References

Amenabar, M. J., Colman, D. R., Poudel, S., Roden, E. E., and Boyd, E. S. (2018). Electron acceptor availability alters carbon and energy metabolism in a thermoacidophile. *Environ. Microbiol.* 20, 2523–2537. doi: 10. 1111/1462-2920. 14270

Boyd, E. S., Schut, G., Adams, M. W. W., and Peters, J. W. (2014). Hydrogen metabolism and the evolution of respiration. *Microbe* 9, 361–367. doi: 10. 1128/microbe. 9. 361. 1

Brazelton, W. J., Nelson, B., and Schrenk, M. O. (2012). Metagenomic evidence for H 2 oxidation and H 2 production by serpentinite-hosted subsurface microbial communities. *Front. Microbiol.* 2: 268. doi: 10. 3389/fmicb. 2011. 00268

Buckel, W., and Thauer, R. K. (2018). Flavin-based electron bifurcation, a new mechanism of biological energy coupling. *Chem. Rev.* 118, 3862–3886. doi: 10. 1021/acs. chemrev. 7b00707

Caffrey, S. M., Park, H.-S., Voordouw, J. K., He, Z., Zhou, J., and Voordouw, G. (2007). Function of periplasmic hydrogenases in the sulfate-reducing bacterium *Desulfovibrio vulgaris* Hildenborough. *J. Bacteriol.* 189, 6159–6167. doi: 10. 1128/JB. 00747-07

Carere, C. R., Hards, K., Houghton, K. M., Power, J. F., McDonald, B., Collet, C., et al. (2017). Mixotrophy drives niche expansion of verrucomicrobial methanotrophs. *ISME J* 11, 2599–2610. doi: 10. 1038/ismej. 2017. 112

Chardin, B., Giudici-Orticoni, M.-T., De Luca, G., Guigliarelli, B., and Bruschi, M. (2003). Hydrogenases in sulfate-reducing bacteria function as chromium reductase. *Appl. Microbiol. Biotechnol.* 63, 315–321. doi: 10. 1007/s00253-003-1390-8

Conrad, R. (1996). Soil microorganisms as controllers of atmospheric trace gases (H 2 , CO, CH 4 , OCS, N 2 O, and NO). *Microbiol. Mol. Biol. Rev.* 60, 609–640. doi: 10. 1128/MMBR. 60. 4. 609-640. 1996

Constant, P., Chowdhury, S. P., Pratscher, J., and Conrad, R. (2010). Streptomycetes contributing to atmospheric molecular hydrogen soil uptake are widespread and encode a putative high-affinity [NiFe]-hydrogenase. *Environ. Microbiol.* 12, 821–829. doi: 10. 1111/j. 1462-2920. 2009. 02130. x

Cordero, P. R. F., Grinter, R., Hards, K., Cryle, M. J., Warr, C. G., Cook, G. M., et al. (2019). Two uptake hydrogenases differentially interact with the aerobic respiratory chain during mycobacterial growth and persistence. *J. Biol. Chem.* 294, 18980–18991. doi: 10. 1074/jbc. RA119. 011076

Dong, X., Greening, C., Rattray, J. E., Chakraborty, A., Chuvochina, M., Mayumi, D., et al. (2019). Metabolic potential of uncultured bacteria and archaea associated with petroleum seepage in deep-sea sediments. *Nat. Commun.* 10: 1816. doi: 10. 1038/s41467-019-09747-0

Fauque, G., Peck, H. D., Moura, J. J. G., Huynh, B. H., Berlier, Y., DerVartanian, D. V, et al. (1988). The three classes of hydrogenases from sulfate-reducing bacteria of the genus *Desulfovibrio* . *FEMS Microbiol. Lett.* 54, 299–344. doi: 10. 1111/j. 1574-6968. 1988. tb02748. x

Greening, C., Berney, M., Hards, K., Cook, G. M., and Conrad, R. (2014). A soil actinobacterium scavenges atmospheric H 2 using two membrane-associated, oxygen-dependent [NiFe] hydrogenases. *Proc. Natl. Acad. Sci. U. S. A.* 111, 4257–4261. doi: 10. 1073/pnas. 1320586111

Greening, C., Biswas, A., Carere, C. R., Jackson, C. J., Taylor, M. C., Stott, M. B., et al. (2016). Genomic and metagenomic surveys of hydrogenase distribution indicate H 2 is a widely utilised energy source for microbial growth and survival. *ISME J.* 10, 761–777. doi: 10. 1038/ismej. 2015. 153

Greening, C., and Cook, G. M. (2014). Integration of hydrogenase expression and hydrogen sensing in bacterial cell physiology. *Curr. Opin. Microbiol.* 18, 30–38. doi: 10. 1016/j. mib. 2014. 02. 001

Greening, C., Geier, R., Wang, C., Woods, L. C., Morales, S. E., McDonald, M. J., et al. (2019). Diverse hydrogen production and consumption pathways influence methane production in ruminants. *ISME J.* 13, 2617–2632. doi: 10. 1038/s41396-019-0464-2

Hartwig, S., Dragomirova, N., Kublik, A., Türkowsky, D., von Bergen, M., Lechner, U., et al. (2017). A H 2 -oxidizing, 1, 2, 3-trichlorobenzene-reducing multienzyme complex isolated from the obligately organohalide-respiring bacterium *Dehalococcoides mccartyi* strain CBDB1. *Environ. Microbiol. Rep.* 9, 618–625. doi: 10. 1111/1758-2229. 12560

Hong, Y.-G., Guo, J., and Sun, G.-P. (2008). Identification of an uptake hydrogenase for hydrogen-dependent dissimilatory azoreduction by *Shewanella decolorationis* S12. *Appl. Microbiol. Biotechnol.* 80: 517. doi: 10. 1007/s00253-008-1597-9

Horner, D. S., Foster, P. G., and Embley, T. M. (2000). Iron hydrogenases and the evolution of anaerobic eukaryotes. *Mol. Biol. Evol.* 17, 1695–1709. doi: 10. 1093/oxfordjournals. molbev. a026268

Ji, M., Greening, C., Vanwonterghem, I., Carere, C. R., Bay, S. K., Steen, J. A., et al. (2017). Atmospheric trace gases support primary production in Antarctic desert surface soil. *Nature* 552, 400–403. doi: 10. 1038/nature25014

Kaji, M., Taniguchi, Y., Matsushita, O., Katayama, S., Miyata, S., Morita, S., et al. (1999). The *hydA* gene encoding the H 2 -evolving hydrogenase of *Clostridium perfringens* : molecular characterization and expression of the gene. *FEMS Microbiol. Lett.* 181, 329–336. doi: 10. 1111/j. 1574-6968. 1999. tb08863. x

Kessler, A. J., Chen, Y.-J., Waite, D. W., Hutchinson, T., Koh, S., Popa, M. E., et al. (2019). Bacterial fermentation and respiration processes are uncoupled in permeable sediments. *Nat. Microbiol.* 4, 1014–1023. doi: 10. 1038/s41564-019-0391-z

Kim, D.-H., and Kim, M.-S. (2011). Hydrogenases for biological hydrogen production. *Bioresour. Technol.* 102, 8423–8431. doi: 10. 1016/j. biortech. 2011. 02. 113

Koch, H., Galushko, A., Albertsen, M., Schintlmeister, A., Gruber-Dorninger, C., Lucker, S., et al. (2014). Growth of nitrite-oxidizing bacteria by aerobic hydrogen oxidation. *Science* 345, 1052–1054. doi: 10. 1126/science. 1256985

Kovács, K. L., Kovács, Á. T., Maróti, G., Meszaros, L. S., Balogh, J., Latinovics, D., et al. (2005). The hydrogenases of *Thiocapsa roseopersicina* . *Biochem. Soc. Trans.* 33, 61–63. doi: 10. 1042/BST0330061

Kublik, A., Deobald, D., Hartwig, S., Schiffmann, C. L., Andrades, A., von Bergen, M., et al. (2016). Identification of a multi-protein reductive dehalogenase complex in *Dehalococcoides mccartyi* strain CBDB 1 suggests a protein-dependent respiratory electron transport chain obviating quinone involvement. *Environ. Microbiol.* 18, 3044–3056. doi: 10. 1111/1462-2920. 13200

Lane, N., Allen, J. F., and Martin, W. (2010). How did LUCA make a living? Chemiosmosis in the origin of life. *BioEssays* 32, 271–280. doi: 10. 1002/bies. 200900131

Lindsay, M. R., Colman, D. R., Amenabar, M. J., Fristad, K. E., Fecteau, K. M., Debes, R. V, et al. (2019). Probing the geological source and biological fate of hydrogen in Yellowstone hot springs. *Environ. Microbiol.* 21, 3816–3830. doi: 10. 1111/1462-2920. 14730

Maier, L., Vyas, R., Cordova, C. D., Lindsay, H., Sebastian, T., Schmidt, B., et al. (2013). Microbiota-derived hydrogen fuels *Salmonella typhimurium* invasion of the gut ecosystem. *Cell Host Microbe* 14, 641–651. doi: 10. 1016/j. chom. 2013. 11. 002

Maier, R. J., Olczak, A., Maier, S., Soni, S., and Gunn, J. (2004). Respiratory hydrogen use by *Salmonella enterica* serovar Typhimurium is essential for virulence. *Infect. Immun.* 72, 6294–6299. doi: 10. 1128/IAI. 72. 11. 6294-6299. 2004

Marreiros, B. C., Batista, A. P., Duarte, A. M. S., and Pereira, M. M. (2013). A missing link between complex I and group 4 membrane-bound [NiFe] hydrogenases. *Biochim. Biophys. Acta* 1827, 198–209. doi: 10. 1016/j. bbabio. 2012. 09. 012

McDowall, J. S., Murphy, B. J., Haumann, M., Palmer, T., Armstrong, F. A., and Sargent, F. (2014). Bacterial formate hydrogenlyase complex. *Proc. Natl. Acad. Sci. U. S. A.* 111, E3948–E3956. doi: 10. 1073/pnas. 1407927111

Mohammadi, S., Pol, A., van Alen, T. A., Jetten, M. S. M., and Op den Camp, H. J. M. (2017). *Methylacidiphilum fumariolicum* SolV, a thermoacidophilic “ Knallgas” methanotroph with both an oxygen-sensitive and -insensitive hydrogenase. *ISME J.* 11, 945–958. doi: 10. 1038/ismej. 2016. 171

Mulder, D. M., Boyd, E. S., Sarma, R., Endrizzi, J. A., Lange, R., Broderick, J. B., et al. (2010). Stepwise [FeFe]-hydrogenase H-cluster assembly revealed in the structure of HydA Δ *EFG* . *Nature* 465, 248–252. doi: 10. 1038/nature08993

Olson, J. W., and Maier, R. J. (2002). Molecular hydrogen as an energy source for *Helicobacter pylori* . *Science* 298, 1788–1790. doi: 10. 1126/science. 1077123

Peters, J. W., Lanzilotta, W. N., Lemon, B. J., and Seefeldt, L. C. (1998). X-ray crystal structure of the Fe-only hydrogenase (CpI) from *Clostridium pasteurianum* to 1. 8 Angstrom resolution. *Science* 282, 1853–1858. doi: 10. 1126/science. 282. 5395. 1853

Peters, J. W., Schut, G. J., Boyd, E. S., Mulder, D. W., Shepard, E. M., Broderick, J. B., et al. (2015). [FeFe]- and [NiFe]-hydrogenase diversity, mechanism, and maturation. *Biochim. Biophys. Acta* 1853, 1350–1369. doi: 10. 1016/j. bbamcr. 2014. 11. 021

Petersen, J. M., Zielinski, F. U., Pape, T., Seifert, R., Moraru, C., Amann, R., et al. (2011). Hydrogen is an energy source for hydrothermal vent symbioses. *Nature* 476: 176. doi: 10. 1038/nature10325

Pinske, C., and Sawers, R. G. (2016). Anaerobic formate and hydrogen metabolism. *EcoSal Plus* 7. doi: 10. 1128/ecosalplus. ESP-0011-2016

Schubert, T., Adrian, L., Sawers, R. G., and Diekert, G. (2018). Organohalide respiratory chains: composition, topology and key enzymes. *FEMS Microbiol. Ecol.* 94: fiy035. doi: 10. 1093/femsec/fiy035

Schuchmann, K., and Müller, V. (2012). A bacterial electron-bifurcating hydrogenase. *J. Biol. Chem.* 287, 31165–31171. doi: 10. 1074/jbc. M112. 395038

Schuchmann, K., and Müller, V. (2013). Direct and reversible hydrogenation of CO 2 to formate by a bacterial carbon dioxide reductase. *Science* 342, 1382–1385. doi: 10. 1126/science. 1244758

Schuchmann, K., and Muller, V. (2014). Autotrophy at the thermodynamic limit of life: a model for energy conservation in acetogenic bacteria. *Nat. Rev. Microbiol.* 12, 809–821. doi: 10. 1038/nrmicro3365

Schut, G. J., and Adams, M. W. W. (2009). The iron-hydrogenase of *Thermotoga maritima* utilizes ferredoxin and NADH synergistically: a new perspective on anaerobic hydrogen production. *J. Bacteriol.* 191, 4451–4457. doi: 10. 1128/JB. 01582-08

Schwartz, E., Fritsch, J., and Friedrich, B. (2013). *H2-Metabolizing Prokaryotes* . eds E. Rosenberg, E. F. DeLong, S. Lory, E. Stackebrandt, and F. Thompson Berlin; Heidelberg: Springer Berlin Heidelberg.

Shima, S., Pilak, O., Vogt, S., Schick, M., Stagni, M. S., Meyer-Klaucke, W., et al. (2008). The crystal structure of [Fe]-Hydrogenase reveals the geometry of the active site. *Science* 321, 572–575. doi: 10. 1126/science. 1158978

Sørensen, J., Christensen, D., and Jørgensen, B. B. (1981). Volatile fatty acids and hydrogen as substrates for sulfate-reducing bacteria in anaerobic marine sediment. *Appl. Environ. Microbiol.* 42, 5–11. doi: 10. 1128/AEM. 42. 1. 5-11. 1981

Tamagnini, P., Leitão, E., Oliveira, P., Ferreira, D., Pinto, F., Harris, D. J., et al. (2007). Cyanobacterial hydrogenases: diversity, regulation and applications. *FEMS Microbiol. Rev.* 31, 692–720. doi: 10. 1111/j. 1574-6976. 2007. 00085. x

Telling, J., Boyd, E. S., Bone, N., Jones, E. L., Tranter, M., MacFarlane, J. W., et al. (2015). Rock comminution as a source of hydrogen for subglacial ecosystems. *Nat. Geosci* . 8, 851–857. doi: 10. 1038/ngeo2533

Thauer, R. K., Kaster, A.-K., Goenrich, M., Schick, M., Hiromoto, T., and Shima, S. (2010). Hydrogenases from methanogenic archaea, nickel, a novel cofactor, and H 2 storage. *Annu. Rev. Biochem.* 79, 507–536. doi: 10. 1146/annurev. biochem. 030508. 152103

Vignais, P. M., and Billoud, B. (2007). Occurrence, classification, and biological function of hydrogenases: an overview. *Chem. Rev.* 107, 4206–4272. doi: 10. 1021/cr050196r

Volbeda, A., Charon, M. H., Piras, C., Hatchikian, E. C., Frey, M., and Fontecilla-Camps, J. C. (1995). Crystal structure of the nickel-iron hydrogenase from *Desulfovibrio gigas* . *Nature* 373, 580–587. doi: 10. 1038/373580a0

Weiss, M. C., Sousa, F. L., Mrnjavac, N., Neukirchen, S., Roettger, M., Nelson-Sathi, S., et al. (2016). The physiology and habitat of the last universal common ancestor. *Nat. Microbiol* . 1: 16116. doi: 10. 1038/nmicrobiol. 2016. 116

Wolf, P. G., Biswas, A., Morales, S. E., Greening, C., and Gaskins, H. R. (2016). H 2 metabolism is widespread and diverse among human colonic microbes. *Gut Microbes* 7, 235–245. doi: 10. 1080/19490976. 2016. 1182288

Wu, L. F., and Mandrand, M. A. (1993). Microbial hydrogenases: primary structure, classification, signatures and phylogeny. *FEMS Microbiol. Rev.* 10, 243–269. doi: 10. 1111/j. 1574-6968. 1993. tb05870. x