Mineralogical Magazine (2021), **85**, 68–75
doi:10.1180/mgm.2021.17

Letter – Frank Reith memorial issue

Gold particles from Kamchatka: A brief look at gold biogeochemical cycling in a distinct environment

Maria Angelica D. Rea[1,2], Joël Brugger[3], Barbara Etschmann[3], Victor Okrugin[4] and Jeremiah Shuster[1,2]*

[1]The University of Adelaide, School of Biological Sciences, North Terrace, Adelaide, South Australia 5005, Australia; [2]Commonwealth Scientific and Industrial Research Organization: Land and Water, Environmental Protection and Technologies Team, Waite Road PMB2, Urrbrae, South Australia 5064, Australia; [3]Monash University, School of Earth, Atmosphere and the Environment, Clayton Victoria 3800, Australia; and [4]Institute of Volcanology and Seismology, Russian Academy of Science, Petropavlovsk-Kamchatsky, 683 006, Russia

Abstract

Kamchatka is a peninsula located on the far eastern side of Russia and is a geologically active region within the Pacific Ring of Fire. Placer gold particles were obtained from a stream located in the Yelizovsky District and were compared to particles from regions at similar latitudes. Russian gold particle surface textures and morphologies were characterised optically and using electron microscopy, and bacteria occurring on the surface of particles were inferred from detected amplicon sequence variants (ASVs). The gold particles contained remarkably variable gold surface textures with an average 70% of surface area containing clay-filled concavities. Particle morphologies, interpreted from axis ratios, suggested that these particles were transported from primary sources. *Proteobacteria* constituted 60% of all the detected ASVs from the particles. Within this phylum, *Gammaproteobacteria* was the most dominant class. This study contributes to the understanding of gold biogeochemical cycling in a distinct bioclimatic environment.

Keywords: gold biogeochemistry, geomicrobiology, gold particles, Kamchatka, gold biogeochemical cycling

(Received 24 January 2021; accepted 17 February 2021; Accepted Manuscript published online: 22 February 2021; Guest Associate Editor: Janice Kenney)

Introduction

Over the past two decades, gold geomicrobiology research has focused primarily on bacterial microcosm experiments or on the characterisation of gold particles sourced from tropical to sub-Arctic environments (see Shuster and Reith, 2018 and references there in). Characterisation-based studies have included the (semi)quantitative assessment of particle structure/chemistry, detection of amplified DNA to infer bacterial presence, and more recently the enrichment of bacteria directly from particles (Reith *et al.*, 2019; Sanyal *et al.*, 2019; 2020a). These studies have demonstrated that the occurrence of pure (>99%) secondary gold on particles can be attributed, in part, to microbial activity (Sanyal *et al.*, 2020b). These bacterial-gold interactions are thought to occur on the surface of particles within concavities containing clays, residual organics and secondary gold structures; collectively, these materials have been called 'polymorphic layers' (Shuster *et al.*, 2017). Therefore, bacteria contribute to gold biogeochemical cycling—the sum of gold dissolution and reprecipitation processes —leading to gold particle transformation (Fairbrother *et al.* 2013; Reith *et al.*, 2013; Rea *et al.*, 2016; Sanyal *et al.*, 2018; Shuster *et al.*, 2017; Shuster and Reith, 2018). The biogeochemical cycling of gold is controlled by a number of complex interactions between climate, landscape, and sediment chemistry (e.g. Melchiorre *et al.*, 2018; Roy *et al.*, 2018; Craw 2018; Rea *et al.*, 2019a,b). In light of this, there is value in continuing gold geomicrobiology research by studying particles from environments with different climatic and ecological conditions, such as the Kamchatka Krai peninsula located on the far eastern side of Russia (Okrugin *et al.*, 2014; Zinkevich and Tsukanov, 2010). This work builds upon the most recent gold geomicrobiology studies by focusing on the characterisation of gold particles obtained from Kamchatka (Fig. 1). In doing so, these particles are compared to previously characterised particles from similar latitudes, e.g. Germany, Switzerland and the United Kingdom. More importantly, this study further highlights the benefit of interdisciplinary research to gain a holistic perspective of biogeochemical processes that contribute to particle transformation within natural environments.

Materials and methods

Thirty four gold particles were obtained by panning within a minor tributary (stream) that flows into the Bystraya River in the Yelizovsky District, Kamchatka, Russia (Fig. 1). The nearest city is Petropavlovsk-Kamchatskiy, located ∼100 km south east of the sampling site. The gold particle sampling procedures are described in Reith *et al.* (2010). The sampling site (53.439667N, 157.613917E) is located within a stream that drains a shallow (∼5 m depth) placer buried under glacial deposits. The region was worked industrially in the 1960–70s, producing ∼543 kg of placer gold with an average grade of 0.745 g/m^3. Gold occurred as small to medium particles (0.25–3.0 mm) with rare individual quartz-rich nuggets weighing up to 1252 g (393 g contained Au).

*Author for correspondence: Jeremiah Shuster, Email: jeremiah.shuster@adelaide.edu.au
This paper is part of a thematic set in memory of Frank Reith

Cite this article: Rea M.A.D., Brugger J., Etschmann B., Okrugin V. and Shuster J. (2021) Gold particles from Kamchatka: A brief look at gold biogeochemical cycling in a distinct environment. *Mineralogical Magazine* **85**, 68–75. https://doi.org/10.1180/mgm.2021.17

Fig. 1. The sampling area is situated between the Sredinny and Vostocny Ranges where the Central Kamchatka Depression meets the Eastern Volcanic Plateau. Placer particle transformation involves both physical reshaping and gold biogeochemical cycling. The former is primarily attributed to sedimentation within hydrological regimes (i.e. rivers and streams). The latter is attributed, in part, to the presence of microbes occurring on the surface of particles (see Reith *et al.*, 2010).

The climate at the site is continental (Dsd; altitude ~400 m) and polar/alpine (ET) at higher altitudes, based on the Köppen–Geiger classification (Kottek *et al.*, 2006). The average monthly precipitation is 108 ± 25 mm; the months of October to December generally receiving more precipitation compared to other months. The average daily temperature in January (winter) and August (summer) is –10.8°C and 13.8°C, respectively (Petropavlovsk-Kamchatskiy, Climate Data, 2021). Permafrost does not exist and water in the stream is sourced from both surface runoff and meltwater from the range (Jones and Solomina, 2015). High humidity, relatively low temperatures, short growing seasons and extremely heavy snowfall during the winter season creates distinct environmental conditions that support Ermann's birch (*Betula ermanii*) forests, more commonly known as 'snow forests' (Krestov *et al.*, 2008). The particles were collected in September 2015 near the peak of summer biological activity.

Ten gold particles were prepared for structural/chemical characterisation following a method adapted from Shuster *et al.* (2019). Briefly, gold particles were placed in 2% glutaraldehyde aqueous solution and incubated at 5°C for 48 hours to fix any bacterial cells. After incubation, the particles were sequentially transferred and incubated for 10 to 15 min in ethanol solution (70 and 90%, 3×100%). Reagent grade hexamethyldisilazane (HMDS) was diluted to 50% using pure 200 proof ethyl alcohol. The particles were transferred to this solution and incubated at 23°C for 30 mins; this step was repeated using 100% HMDS. After the final incubation, the particles were removed from the solution and airdried for 12 hours before being placed onto aluminium stubs with carbon adhesive tabs and coated with a 10 nm thick layer of carbon or iridium. All particles were imaged in secondary electron (SE) and back-scatter electron (BSE) modes using a FEI DualBeam Scanning Electron Microscope (SEM) or a JEOL JSM-7100 SEM operating at 2 or 20 kV. Both microscopes were equipped with an energy dispersive spectrometer (EDS) for semi-quantitative micro-chemical analyses; data were collected in spot mode. The long axis and perpendicular short axis of each particle were measured on the basis of SEM imaging, and the surface area of particles that occurred as clay-filled concavities (polymorphic layers) was estimated by analysing BSE micrographs with *ImageJ* software (NIMH, 2018).

Twenty-four gold particles were used to detect (remnant) bacterial DNA by polymerase chain reaction (PCR) amplification of the 16S rRNA genes combined with next generation sequencing using the Illumina MiSeq platform (Bissett *et al.*, 2016). Two-step nested PCR was performed using the universal primers 27F and 1492R in the first round, then further amplification using 27F and 519R (Lane *et al.*, 1985; Lane 1991; and Osborn *et al.*, 2000). Samples were submitted for sequencing at the Australian Genome Research Facility (AGRF) in Melbourne, Australia. The 16S amplicons were sequenced using 300 bp paired end

https://doi.org/10.1180/mgm.2021.17 Published online by Cambridge University Press

sequencing. Sequences were merged using *FLASH* (Magoc and Salzberg, 2011) and homopolymer runs of >8 bp or reads containing Ns were removed using *MOTHUR v1.34.1* (Schloss *et al.*, 2009). Abundance profiles were built by mapping data to identified amplicon sequence variants (ASV) (see Bissett *et al.* (2016) for detailed method). ASVs that were observed fewer than two times were removed and ASVs with one single read were discarded. ASVs were analysed statistically to identify different bacterial phyla. A maximum-likelihood phylogenetic tree with 1000 bootstrap replicates was constructed using *GENEIOUS 2021.0.3*. Sequences were deposited in GenBank with accession numbers MW563744–MW563751.

The measurements of gold particles and the detected bacterial phyla were compared to particles from Germany (60; Rea *et al.* 2019a), Switzerland (46; Rea *et al.*, 2019b), and the United Kingdom (50, Rea *et al.*, 2018). These comparative samples were selected because they are located at broadly similar latitudes (46° to 56°30′) and both physical and biogeochemical factors are known to influence particle structure, chemistry, and microbial communities on gold particles.

Results

The gold particles from Kamchatka were 100s of micrometres in size and demonstrated a range of morphologies. Nine of the particles had rounded perimeters which gave them a ‘nugget-like’ appearance. One particle occurred as a semi-octahedral platelet with distinct edges. The particles also demonstrated a broad range of surface textures attributed to mechanical re-shaping (smooth surfaces) as well as biogeochemical processes (dissolution features and secondary gold nanoparticles). One nugget-like particle had a ‘cracked’ texture and also contained mercury, based on EDS analysis (Fig. 2). All particle surfaces had concavities of different sizes that contain varying amounts of clay and secondary gold nanoparticles. These concavities covered an average 73% of the surface area. When compared to other particles from similar latitudes, the particles from Russia contained 5 to 7 times more clay-filled concavities on the surface (Switzerland 15%, Germany 19%, and United Kingdom 22%). In terms of particle morphology, all particles from each location had an average long:short axis ratio of 1:0.7 (Fig. 3).

A total of 902 ASV counts were detected from the Russian gold particles. The most abundant phyla included *Proteobacteria* (545 ASVs; 80.5% of total sequencing reads), *Acidobacteria* (81 ASVs; 4.2% of total sequencing reads), and *Bacteroidetes* (69 ASVs; 4.0% of total sequencing reads). Collectively, these phyla constituted more than 75% of all detected ASV counts (Table 1). Within *Proteobacteria*, *Gammaproteobacteria* was the dominant class that constituted more than half of the counted ASVs (290; 54.8% of total sequencing reads). From this class, ASVs representing *Pseudomonas* sp. and *Rahnella* sp. were consistently detected with greater frequency than other ASVs; additionally, *Serratia proteamaculans* was also detected (Fig. 4). When comparing bacterial compositions between sites, *Proteobacteria* from Russian particles were 13, 15 and 20% higher than what was detected on particles from Germany, Switzerland and the United Kingdom, respectively. Similarly, *Acidobacteria* and *Bacteroidetes* were the second and third most abundant phyla of the other locations when taken as an average (Fig. 5).

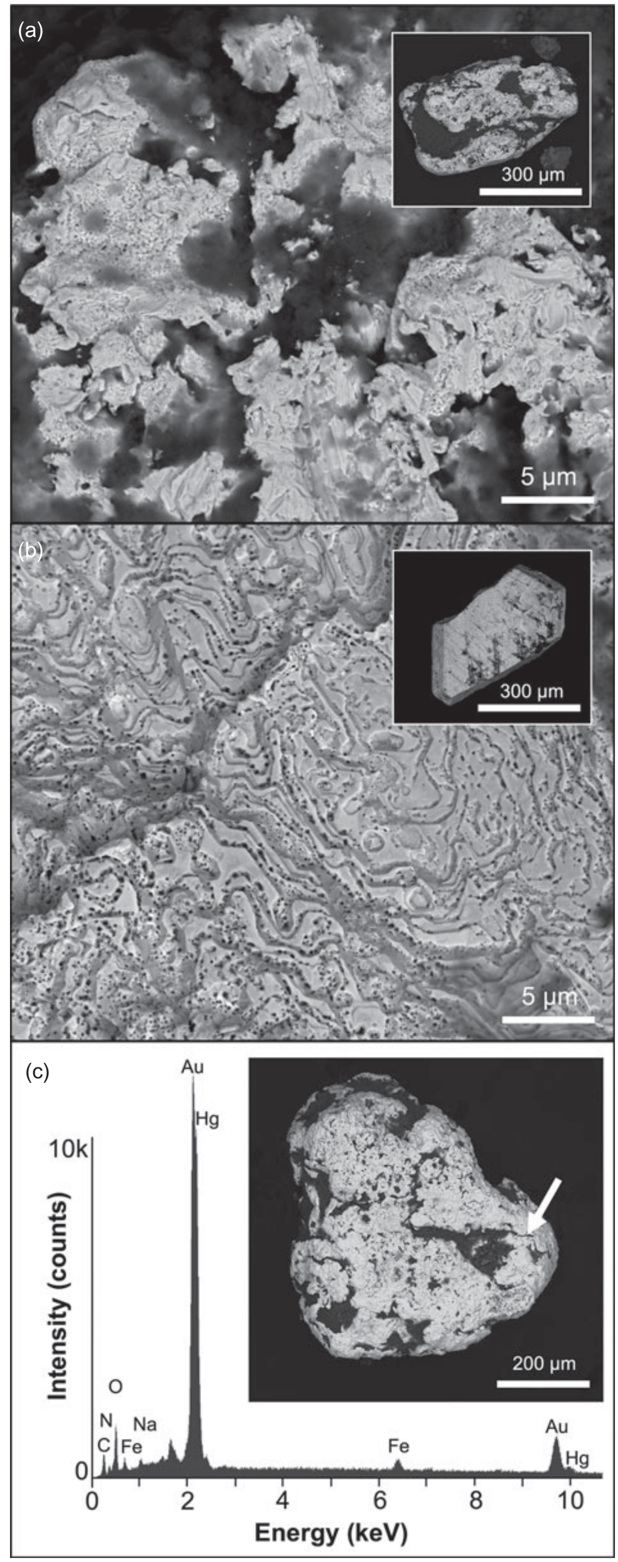

Fig. 2. Back-scatter electron micrographs of gold particles and their respective surface textures. While the majority of particles appeared nugget-like and contained smooth and rounded surfaces attributed to mechanical reshaping (a), one particle appeared more euhedral in morphology but contained a weathered surface texture (b). One nugget-like particle contained a surface texture that appeared cracked (inset, arrow). Mercury was detected, based on EDS analysis (c).

https://doi.org/10.1180/mgm.2021.17 Published online by Cambridge University Press

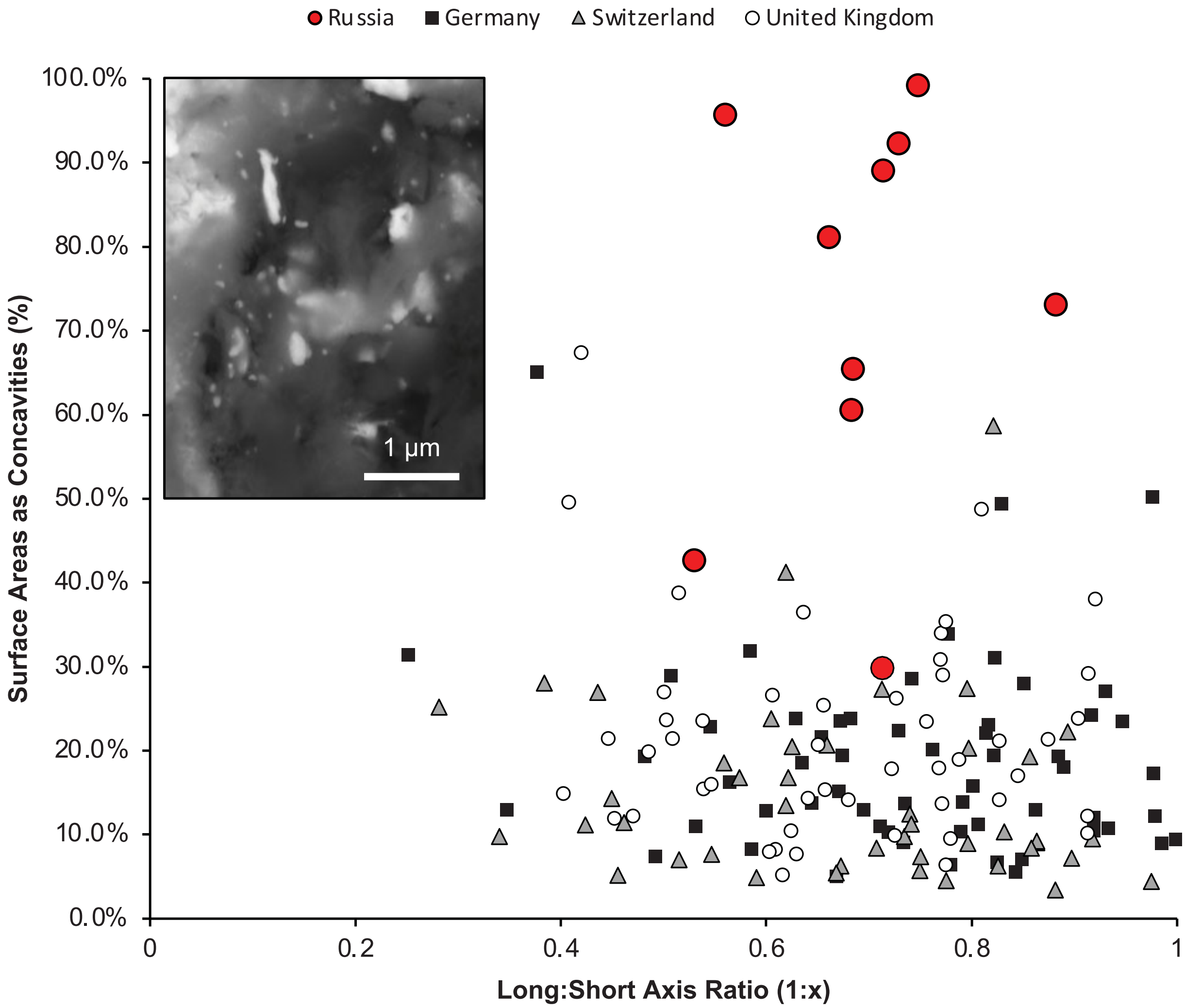

Fig. 3. A comparison of placer gold particles. Russian particles contained more clay-filled concavities relative to particles from Germany (Rea *et al.*, 2019a), Switzerland (Rea *et al.*, 2019b) and the United Kingdom (Rea *et al.*, 2018). The average long:short axis ratio of all particles was 1:0.7. Secondary gold occurred as nanoparticles of varying shape and size. The amount of nanoparticles within clay-filled concavities (polymorphic layers) was also variable (insert).

Table 1. The number of Amplicon Sequence Variants (ASVs) detected from all gold particles.

Phylum	Russia	Germany	Switzerland	United Kingdom
Proteobacteria (Alpha)	97	193	153	156
Proteobacteria (Beta)	133	272	254	318
Proteobacteria (Delta)	15	126	99	194
Proteobacteria (Epsilon)	1	15	14	15
Proteobacteria (Gamma)	290	136	136	133
Proteobacteria (TA18)	0	6	5	7
Proteobacteria (unclassified)	9	15	8	8
Bacilli	7	10	12	11
Clostridia	3	15	22	30
Erysipelotrichi	2	0	4	2
Acidobacteria	81	230	172	307
Actinobacteria	38	51	30	33
Bacteroidetes	69	198	222	309
Chlorobi	1	17	12	29
Chloroflexi	1	30	18	40
Cyanobacteria	1	15	26	23
Gemmatimonadetes	41	22	24	32
Nitrospirae	11	21	22	32
Planctomycetes	45	116	125	170
Verrucomicrobia	20	52	42	83
Other	37	76	63	114
TOTAL	902	1616	1463	2046

Discussion

With active geology and a diverse geography, Kamchatka is a 'natural laboratory' to study the dynamics of gold biogeochemical cycling from particles. Based on field observations and the use of dynamically created maps (Google Maps, Google, 2021), the sampling site is located downstream from eight circular clearings 20–25 m in diameter within the stream. A similar group of circular clearings occurred ca. 600 m and 900 m upstream. These circular clearings were probably shallow pits attributed to placer mining activity during the 1960–70s, which were gradually reclaimed by vegetation over time. Despite this historically recent mining activity, gold was still recoverable from the stream (Figs 1, 6).

It is reasonable to suggest that the majority of gold particles, obtained from the sampling site, were probably derived from the same primary source as all particles had a nugget-like morphology. The particle that occurred as an octahedral platelet presumably came from a different source or represents gold that was unrecovered from the upstream mining pits. In general, smooth surface textures on particles are indicative of mechanical reshaping within sediment, which is consistent with early geological studies highlighting particle movement within a fluvial

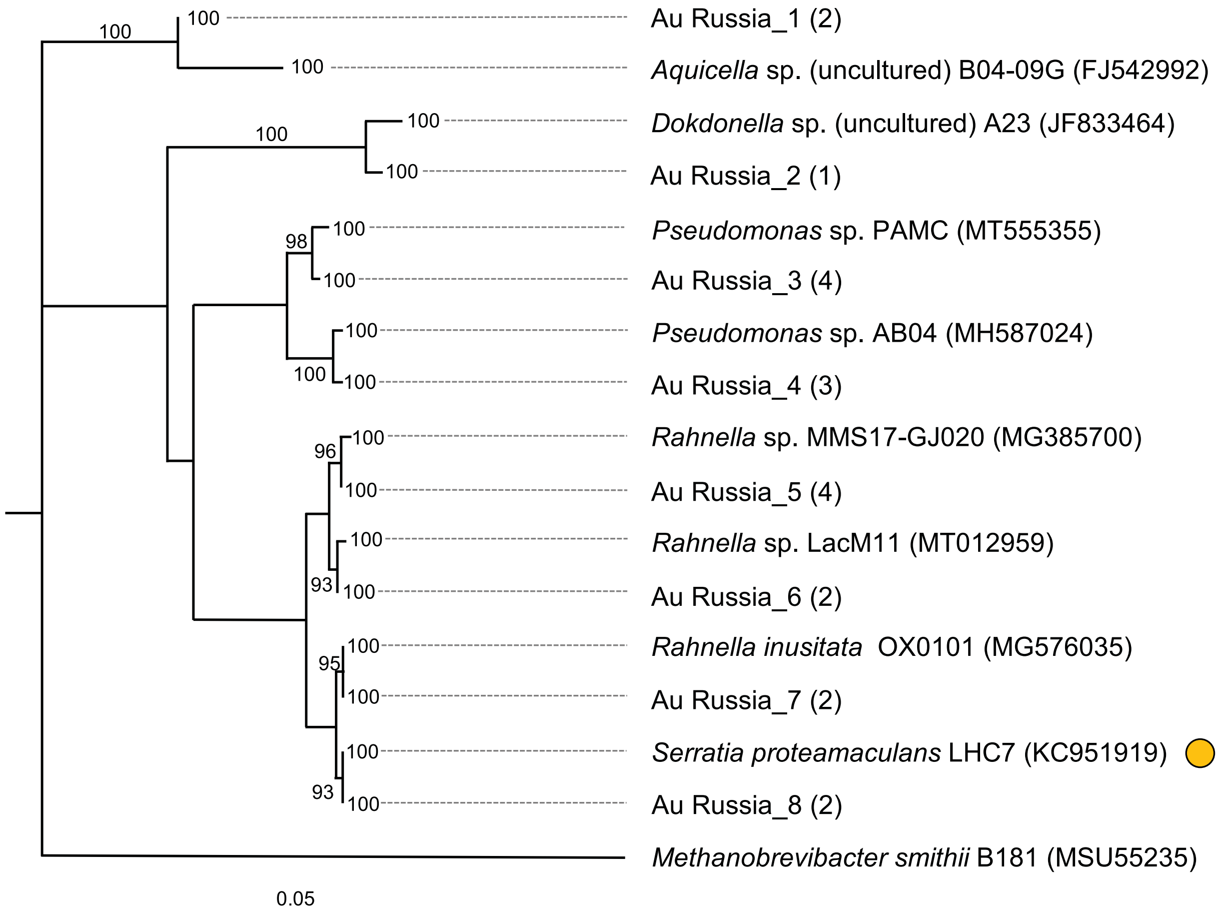

Fig. 4. A maximum likelihood phylogenetic tree of representative 16S rRNA sequence data of *Gammaproteobacteria* on at least 50% of sequenced Russian gold particles. Shown are percentages of 1000 bootstrap values and *Methanobrevibacter smithii* used as the outgroup. A strain of *Serratia proteamaculans* has been isolated from Australian gold particles (yellow circle) and is known to contain heavy-metal resistant genes and to withstand up to 50 µM Au (see Sanyal *et al.*, 2020a).

environment (e.g. Townley *et al.*, 2003) (Figs 2a,b, 6). Some placer gold particles can contain trace levels of mercury, which is indicative of their primary origin (Reith *et al.*, 2010). Additionally, aurihydrargyrumite (Au_6Hg_5) has been detected on the surface of some placer gold particles (Nishio-Hamane *et al.*, 2018). It has been suggested that, in natural environments, the formation of this gold–mercury phase is analogous to how gold-enriched rims develop on particles. Briefly, gold and mercury are dissolved from the particle surface but are immediately re-precipitated back onto the surface via self-electrorefining and forming aurihydrargyrumite (Nishio-Hamane *et al.*, 2018). Therefore, it is possible that some mercury-bearing placer particles from Kamchatka could contain coatings of aurihydrargyrumite. In this study, however, the mercury-bearing particle exhibited a smooth but cracked surface texture (Fig. 2c). This texture has been described as being indicative of environmental contamination as mercury has an affinity for gold and can alter particle surface texture and chemistry. It has been suggested that extensive mercury contamination completely alters gold particle morphology forming near-perfect round spheres, an uncommon morphology for placer gold particles (Sanyal *et al.*, 2020b). Anthropogenic activity such as small-scale artisanal mining has contributed to mercury contamination in a number of natural environments around the globe with devastating impacts (Veiga and Hinton, 2002; Telmer and Veiga, 2009). Mining activity occurred upstream of the sampling site during the 1960–70s; however, there are no known records indicating that mercury was used for amalgamation to concentrate the recovered gold. It has been suggested that the accumulation of mercury in lacustrine sediments from remote regions of Kamchatka is attributed mostly to global fossil fuel combustion (Jones *et al.*, 2015). Therefore, it is reasonable to suggest that fossil fuel combustion used to operate machinery, upstream of the sampling site, probably contaminated the stream with mercury, thereby being dispersed downstream and interacting with gold to form an amalgam on the surface of some particles (Figs 6).

In terms of morphology, placer particles with near-equant axes tend to appear more nugget-like, which correlates with their deposition from the primary source (Townley *et al.*, 2003; Shuster *et al.*, 2017). The average axis ratio of Russian particles was consistent with the particles from Germany, Switzerland and the United Kingdom, suggesting that transport from their respective primary sources were potentially comparable. The most striking difference between the Russian gold particles was that they contained more clay-filled concavities (Figs 3, 6). Recent studies have shown that changes in climate, e.g. wetter winters and increased air temperatures, have contributed to increased weathering and thus more sediment movement and accumulation in rivers and lakes throughout Kamchatka (Jones *et al.*, 2015; Jones and Solomina, 2015; Kuksina, 2019). Therefore, greater sedimentation could explain the 'dirtier' appearance of these particles.

https://doi.org/10.1180/mgm.2021.17 Published online by Cambridge University Press

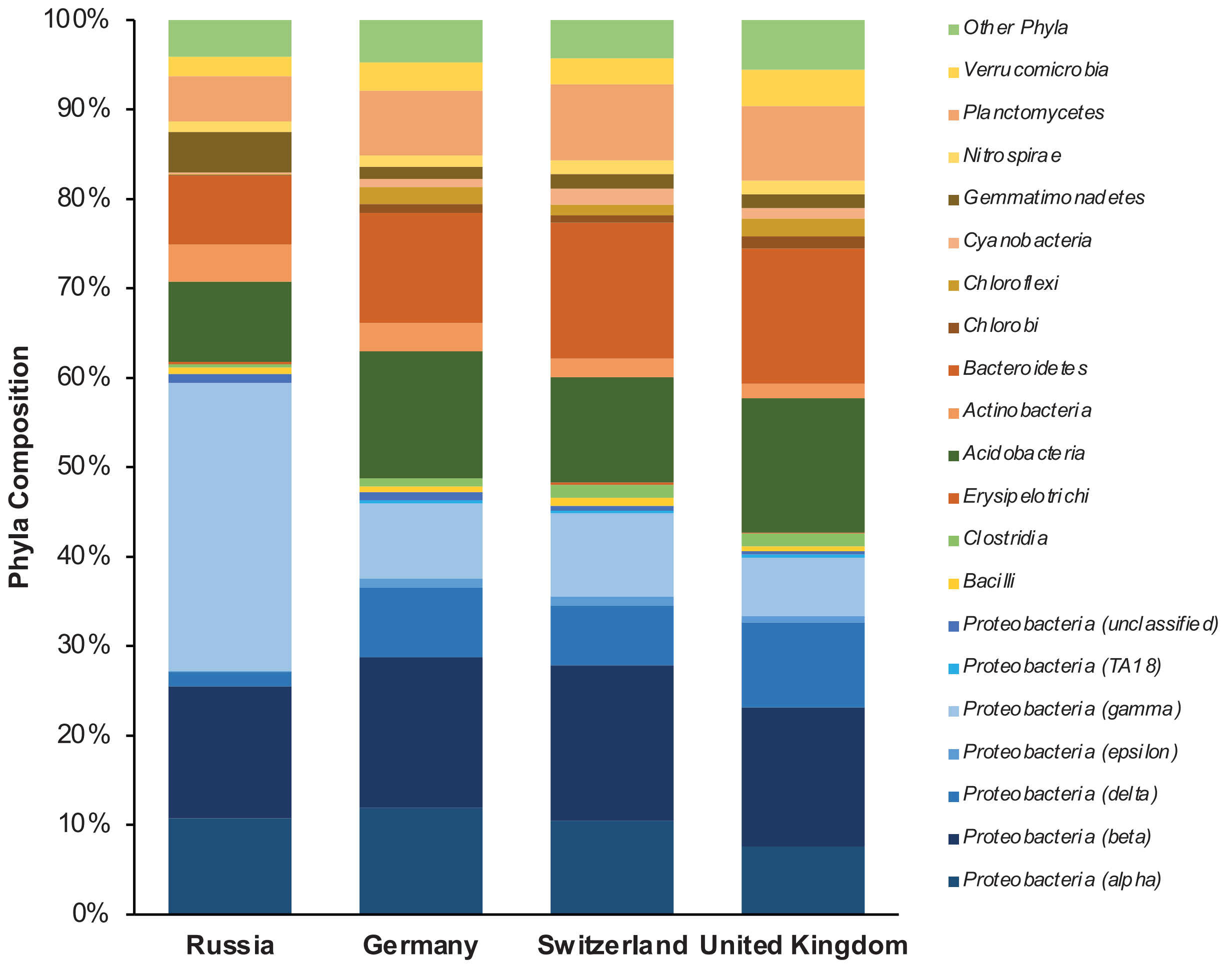

Fig. 5. A comparison of bacterial phyla detected on Russian particles with those that have been detected on particles from Germany, Switzerland and the United Kingdom. On Russian particles, *Proteobacteria* was the dominant bacterial phylum (60% of ASV counts); of this phylum, *Gammaproteobacteria* was the dominant class. Overall, bacteria detected on all particles were diverse.

Overall, *Proteobacteria* and *Gammaproteobacteria* were the most dominant phylum and class, respectively, occurring on the surface of Russian particles (Table 1, Figs 4), which is consistent with previous studies (Reith *et al.*, 2019 and references therein related to bacteria associated with particles). Interestingly, all particles, regardless of locality, contained a diverse range of bacteria and the relative phyla proportions were similar (Fig. 5). Rea *et al.* (2016) proposed that soluble gold, from particles experiencing dissolution, can act as a selective pressure for metal-resistant bacteria occurring on the surface of particles (Fig. 6). This was demonstrated by microcosm experiments involving bacteria grown from particles (Sanyal *et al.*, 2019, 2020a). Additionally, *Proteobacteria* sp. has been detected and cultured from gold particles obtained from an environment impacted by anthropogenic heavy metals in South Africa (Sanyal *et al.*, 2020b). Furthermore, *Serratia proteamaculans* has been cultured from particles obtained from a historic and abandoned gold mine in Australia (Sanyal *et al.*, 2020a). Comparative genome analysis of the *Serratia* sp. isolate contained a number of heavy-metal resistance and stress-response genes that were identical to those detected in *Cupriavidus metallidurans* CH34 – a Au-tolerant microbe (Reith *et al.* 2009; Wiesemann *et al.* 2017). The presence of these genes highlights this microbe's genomic capacity to withstand high concentrations of heavy metals including gold (Sanyal *et al.*, 2020a). Therefore, it is possible that the microbes detected on the surface of Russian particles reflect changes in environmental geochemistry including the impact of past anthropogenic activity within and along the stream. Indeed, other factors such as bioavailability of carbon and nitrogen, attributed to weathering rates, can also result in a shift in bacterial diversity (Lin *et al.*, 2017; Reith *et al.*, 2012). In terms of particle transformation, the detection of ASVs directly from Russian particles highlights the types of bacteria that could contribute to gold biogeochemical cycling in the environment.

Conclusion

This investigation compared gold particles obtained from a distinct ecological environment (Snow Forest, Kamchatka, Russia) to particles obtained from regions at similar latitudes (Germany, Switzerland and the United Kingdom). While Russian particles had more variability in gold surface textures, overall morphologies of all particles were consistent, suggesting that transport was probably comparable. The accumulation of clays within concavities and detection of ASVs representing *Gammaproteobacteria* on particles could reflect localised changes in the environment attributed to anthropogenic activity. Further studies are needed

https://doi.org/10.1180/mgm.2021.17 Published online by Cambridge University Press

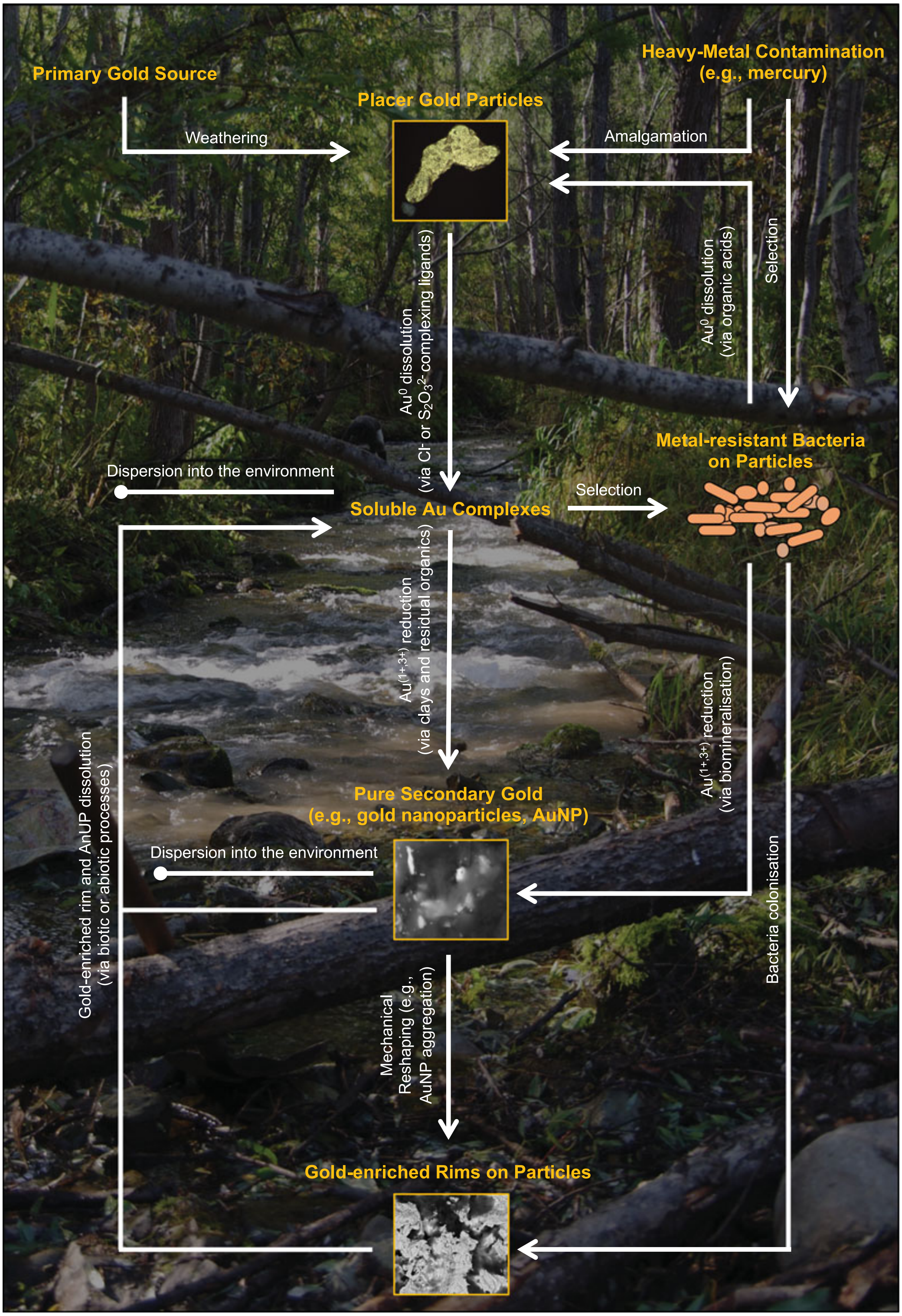

Fig. 6. A schematic of the physical and biogeochemical processes contributing to the transformation of placer gold particles and the dispersion of gold within the stream at Kamchatka, Russia.

to better understand how trace-element composition of particles could relate to changing bacterial compositions over time.

Acknowledgements. This publication is dedicated to Associate Professor Frank Reith. This research was supported by the Australian Research Council (ARC) Future Fellowship (FT100150200) awarded to F. Reith (c/o J. Shuster). Scanning electron microscopy analysis was performed at Adelaide Microscopy, The University of Adelaide (Adelaide, SA 5005, Australia) and the Centre for Microscopy and Microanalysis, The University of Queensland (St. Lucia, QLD 4072, Australia). Molecular analysis was performed at CSIRO Land and Water, Environmental Toxicology and Chemistry in association with the Australian Genome Research Facility (Urrbrae, SA 5064, Australia). We thank A. Bissett and C. Zammit for bioinformatics analysis and Stefan Ansermet (Lausanne) for assistance with the sampling in Kamchatka.

https://doi.org/10.1180/mgm.2021.17 Published online by Cambridge University Press

References

Bissett A., Fitzgerald A., Meintjes T., Mele P.M., Reith F., Dennis P.G. and Brugger J. (2016) Introducing BASE: the biomes of Australian soil environments soil microbial diversity database. *GigaScience*, **5**, 1.

Climate Data (2021) [Petropavlovsk-Kamchatsky]. Retrieved February 16, 2021, from https://en.climate-data.org/asia/russian-federation/kamchatka-krai/petropavlovsk-kamchatsky-1810/

Craw D. (2018) Gold mobility and biology during tectonic evolution of southern New Zealand. *Journal of the Royal Society of New Zealand*, **48**, 111–126.

Google (2021) [53.439667, 157.613917; Yelizovsky District, Kamchatka Krai, Russia]. Retrieved January 21, 2021, from https://www.google.com.au/maps/place/53°26′22.8%22N+157°36′50.1%22E/@53.4396822,157.6117099

Fairbrother L., Etschmann B., Brugger J., Shapter J., Southam G. and Reith F. (2013) Biomineralization of Gold in Biofilms of Cupriavidus metallidurans. *Environmental Science & Technology*, **47**, 2628–2635.

Jones V. and Solomina O. (2015) The geography of Kamchatka. *Global and Planetary Change*, **134**, 3–9.

Jones V., Rose N.L., Self A.E., Solovieva N. and Yang H. (2015) Evidence of global pollution and recent environmental change in Kamchatka, Russia. *Global and Planetary Change*, **134**, 82–90.

Kottek M., Grieser J., Beck C., Rudolf B. and Rubel F. (2006) World Map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, **15**, 259–263.

Krestov P.V., Omelko A.M. and Nakamura Y. (2008) Vegetation and natural habitats of Kamchatka. *Berichte der Reinhold-Tüxen-Gesellschaft*, **20**, 195–218.

Kuksina L.V. (2019) Suspended sediment yield and climate change in Kamchatka, Far East of Russia. *Proceedings of the International Association of Hydrological Science*, **381**, 55–64.

Lane D.J. (1991) 16S/23S rRNA sequencing. *Nucleic Acid Techniques in Bacterial Systematics*, 115–175.

Lane D.J., Pace B., Olsen G.J., Stahl D.A., Sogin M.L. and Pace N.R. (1985) Rapid determination of 16S ribosomal RNA sequences for phylogenetic analyses. *Proceedings of the National Academy of Sciences*, **82**, 6955–6959.

Lin Y.T., Jia Z., Wang D. and Chiu C.Y. (2017) Effects of temperature on the composition and diversity of bacterial communities in bamboo soils at different elevations. *Biogeosciences*, **14**, 4879–4889.

Magoč T. and Salzberg S.L. (2011) FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics*, **27**, 2957–2963.

Melchiorre E.B., Orwin P.M., Reith F., Rea M.A.D., Yahn J. and Allison R. (2018) Biological and geochemical development of placer gold at Rich Hill, Arizona, USA. *Minerals*, **8**, 56.

NIMH (National Institute of Mental Health) (2018) ImageJ. https://imagej.nih.gov/ij/

Nishio-Hamane D., Tanaka T. and Minakawa T. (2018) Aurihydrargyrumite, a natural Au_6Hg_5 phase from Japan. *Minerals*, **8**, 415.

Okrugin V.M., Andreeva, E., Etschmann B., Pring A., Li K., Zhao J., Griffiths G., Lumpkin G.R., Triani G. and Brugger J. (2014) Microporous gold: Comparison of textures from Nature and experiments. *American Mineralogist*, **99**, 1171–1174.

Osborn, A.M., Moore, E.R and Timmis, K.N. (2000) An evaluation of terminal-restriction fragment length polymorphism (T-RFLP) analysis for the study of microbial community structure and dynamics. *Environmental microbiology*, **2**, 39–50.

Rea M.A., Zammit C. and Reith F. (2016) Bacterial biofilms on gold grains: Implications for geomicrobial transformations of gold. *FEMS Microbiological Ecology*, **92**, 1–12.

Rea M.A., Standish C.D., Shuster J., Bissett A. and Reith F. (2018) Progressive biogeochemical transformation of placer gold particles drives compositional changes in associated biofilm communities. *FEMS Microbiology Ecology*, **94**, fiy080.

Rea M.A., Shuster J., Hoffmann V.E., Schade M., Bissett A. and Reith F. (2019a) Does the primary deposit affect the biogeochemical transformation of placer gold and associated biofilms? *Gondwana Research*, **73**, 77–95.

Rea M.A.D., Wulser P.A., Brugger J., Etschmann B., Bissett A., Shuster J. and Reith F. (2019b) Effect of physical and biogeochemical factors on placer gold transformation in mountainous landscapes of Switzerland. *Gondwana Research*, **66**, 77–92.

Reith F., Etschmann B., Grosse C., Moors H., Benotmane M., Monsieurs P., Grass G., Doonan C., Vogt S., Lai B., Martinez-Criado G., George G., Nies D., Mergeay M., Pring A., Southam G. and Brugger J. (2009) Mechanisms of gold biomineralization in the bacterium Cupriavidus metallidurans. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 17757–17762.

Reith F., Fairbrother L., Nolze G. *et al.* (2010) Nanoparticle factories: biofilms hold the key to gold dispersion and nugget formation. *Geology*, **38**, 843–846.

Reith F., Brugger J., Zammit C.M., Gregg A.L., Goldfarb K.C., Andersen G.L., DeSantis T.Z., Piceno Y.M., Brodie E.L., Lu Z., He Z., Zhou J. and Wakelin S.A. (2012) Influence of geogenic factors on microbial communities in metallogenic Australian soils. *ISME Journal*, **6**, 2107–2118.

Reith F., Brugger J., Zammit C., Nies D. and Southam G. (2013) Geobiological cycling of gold: From fundamental process understanding to exploration solutions. *Minerals*, **3**, 367–394.

Reith F., Falconer D.M., Van Nostrand J., Craw D., Shuster J. and Wakelin S. (2019) Functional capabilities of bacterial biofilms on gold particles. *FEMS Microbiology Ecology*, **96**, fiz196.

Roy S., Upton P. and Craw D. (2018) Gold in the hills: Patterns of placer gold accumulation under dynamic tectonic and climatic conditions. *Mineralium Deposita*, **53**, 981–995.

Sanyal S.K., Shuster J. and Reith F. (2018) Cycling of biogenic elements drives biogeochemical gold cycling. *Earth-Science Reviews*, **190**, 131–147.

Sanyal S.K., Shuster J. and Reith F. (2019) Biogeochemical gold cycling selects metal-resistant bacteria that promote gold particle transformation. *FEMS Microbiology Ecology*, **95**, fiz078.

Sanyal S.K., Reith F. and Shuster J. (2020a) A genomic perspective of metal-resistant bacteria from gold particles: Possible survival mechanisms during gold biogeochemical cycling. *FEMS Microbiology Ecology*, **96**, fiaa111.

Sanyal S.K., Brugger J, Etschmann B., Pederson S.M., Delport P.W.J., Dixon R., Tearle R., Ludington A., Reith F. and Shuster J. (2020b) Metal resistant bacteria on gold particles: Implications of how anthropogenic contaminants could affect natural gold biogeochemical cycling. *Science of the Total Environment*, **727**, 138698.

Schloss P.D., Westcott S.L., Ryabin T., Hall J.R., Hartmann M., Hollister E.B., Lesniewski R.A., Oakley B.B., Parks D.H., Robinson C.J. and Sahl J.W. (2009) Introducing mothur: open-source, platform-independent, community-supported software for describing and comparing microbial communities. *Applied and Environmental Microbiology*, **75**, 7537–7541.

Shuster J., Reith F., Cornelis G., Parsons J.E., Parsons J.M. and Southam G. (2017) Secondary gold structures: Relics of past biogeochemical transformations and implications for colloidal gold dispersion in subtropical environments. *Chemical Geology*, **450**, 154–164.

Shuster J. and Reith F. (2018) Reflecting on gold geomicrobiology research: Thoughts and considerations for future endeavours, *Minerals*, **8**, 401.

Shuster J., Southam G. and Reith F. (2019) Application of scanning electron microscopy in geomicrobiology. Pp. 148–165 in: *Analytical Geomicrobiology: A Handbook of Instrumental Techniques* (J.P.L. Kenney, H. Veeramani and D. Alessi, editors). Cambridge University Press, Cambridge, UK.

Telmer K.H. and Veiga M.M. (2009) World emissions of mercury from artisanal and small-scale gold mining. Pp. 131–172 in: *Mercury Fate and Transport in the Global Atmosphere*. Springer.

Townley B.K., Hérail G., Maksaev V., Palacios C., de Parseval P., Sepulveda F., Orellana R., Rivas P. and Ulloa C. (2003) Gold grain morphology and composition as an exploration tool: Application to gold exploration in covered areas. *Geochemistry: Exploration, Environment, Analysis*, **3**, 29–38.

Veiga M.M. and Hinton J.J. (2002) Abandoned artisanal gold mines in the Brazilian Amazon: A legacy of mercury pollution. Pp. 15–26 in: *Natural Resources Forum*, **26**. Wiley Online Library.

Wiesemann N., Bütof L., Herzberg M., Hause G., Berthold L., Etschmann B., Brugger J., Martinez-Criado G., Dobritzsch D., Baginsky S., Reith F. and Nies D. (2017) Synergistic toxicity of copper and gold compounds in *Cupriavidus metallidurans*. *Applied and Environmental Microbiology*, **83**, e01679–17.

Zinkevich V.P. and Tsukanov N.V. (2010) Accretionary tectonics of Kamchatka. *International Geology Review*, **35**, 953–973.

https://doi.org/10.1180/mgm.2021.17 Published online by Cambridge University Press