Biological materials formed by *Acidithiobacillus ferrooxidans* and their potential applications

Mengran Yang^{1,2} · Yue Zhan¹ · Shuang Zhang¹ · Weidong Wang¹ · Lei Yan¹

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Abstract

A variety of biological materials including schwertmannite, jarosite, iron–sulfur cluster (ISC) and magnetosomes can be produced by *Acidithiobacillus ferrooxidans* (*A. ferrooxidans*). Their possible formation mechanisms involved in iron transformation, iron transport, and electron transfer were proposed. The schwertmannite formation usually occurs under the pH of 2.0–3.51, and a lower or higher pH will promote jarosite to be produced. Available Fe^{2+} in the environment and the carrier proteins that can transport Fe^{2+} to the intracellular membranes of *A. ferrooxidans* play a critical role in the synthesis of magnetosomes and ISC. The potential applications of these biological materials were reviewed, including removal of heavy metal by schwertmannite, detoxification of toxic species by jarosite, the transference of electron and ripening the iron sulfur protein by ISC, and biomedical application of magnetosomes. Additionally, some perspectives for the molecular mechanisms of synthesis and regulation of these biomaterials were briefly described.

Keywords *Acidithiobacillus ferrooxidans* · Biological materials · Formation mechanism · Potential application · Iron cycling

Introduction

Acidithiobacillus ferrooxidans (*A. ferrooxidans*) is a chemolithotrophic autotroph able to obtain energy from the oxidation of ferrous iron and also can utilize elemental sulfur (S^0) to grow (Ceskova et al. 2010). Its cellular morphology is related to the energy source, which displays club or rod shapes in the medium with Fe^{2+} or S as the substrate (Chen et al. 2012). The survival, colonization, growth and development of *A. ferrooxidans* are closely related to the environment (Yang et al. 2019a, b and c). It can accelerate the oxidative dissolution of sulfide minerals, which can cause the generation of acidic metal-rich drainage but also promote

the recovery of metals in different species from mineral leachates. *A. ferrooxidans* can catalyze the dissimilatory oxidation of iron, sulfur, and hydrogen, and the reduction of iron and sulfur (Tuovinen et al. 1973). Additionally, it has a significant impact on nutrient and metal biogeochemical cycling in low-pH environments (Harneit et al. 2006). Thus, *A. ferrooxidans* has been regarded as an essential model organism in an extreme acid environment.

Schwertmannite distributes widely and its production has been proved to be closely related to *A. ferrooxidans* in the acidic environment (Wang et al. 2019). It is considered as a sensational adsorbent and can remove some heavy metals such as antimony and arsenic from polluted water (Dou et al. 2013). It has also been documented that *A. ferrooxidans* plays a vital role in jarosite synthesis and the biological oxidation of ferrous is 10^5 – 10^6 times higher than that of chemical oxidation (Bigham et al. 2010; Wang et al. 2013). Jarosite was found to have a strong ability to treat toxic metals in wastewater. Magnetosome, an ideal biomaterial formed by *A. ferrooxidans*, has several specific properties such as superior crystalline, excellent biocompatibility and special magnetic characteristics (Lei et al. 2012; Yan et al. 2016; Zhang et al. 2012). The magnetosomes have potential applications in biomedical areas such as magnetic

✉ Lei Yan
hekouyanlei@gmail.com

¹ Heilongjiang Provincial Key Laboratory of Environmental Microbiology and Recycling of Argo-Waste in Cold Region, College of Life Science and Biotechnology, Heilongjiang Bayi Agricultural University (HBAU), 5 Xinfeng Road, Daqing High-Tech Industrial Development Zone, Daqing, Heilongjiang Province 163319, People's Republic of China

² School of Life Science, Lanzhou University, Tianshui Road No. 222, Lanzhou 730000, People's Republic of China

separation and carriers for labeling and immobilization of various biomolecules (Raguraman et al. 2020). It has been confirmed that ISC is one of the most ancient and universal redox centers in all organisms (Zeng et al. 2007). ISC was found to involve in respiration, photosynthesis and nitrogen fixation in *A. ferrooxidans* and play an essential role in metal bioleaching by *A. ferrooxidans* (under the optimal pH of the bacterium growth) (Arshadi et al. 2020; WUAn-na et al. 2008). Although a large amount of literature on *A. ferrooxidans* is available, the review about the comprehensive and systematic summary of the formation mechanism and potential application of biomaterials produced by *A. ferrooxidans* is very sparse.

Here, the general features of biological materials including schwertmannite, jarosite, iron–sulfur cluster (ISC) and magnetosomes formed by *A. ferrooxidans* have been elaborated. We proposed the possible synthesis pathway to describe the electron transfer and the mechanisms involved in the formation of these biomaterials. Additionally, we summarized the potential application of the materials mentioned above. Finally, some perspectives and possible directions for the synthetic mechanism and application of biomaterials produced by *A. ferrooxidans* are presented in brief.

Biomaterials formed by *A. ferrooxidans*

Schwertmannite

Schwertmannite, an Fe(III) oxyhydroxy sulfate with the general formula $\text{Fe}_8\text{O}_8(\text{OH})_x\text{SO}_y\cdot n\text{H}_2\text{O}$ ($8-x=y$ and $1.0\leq y\leq 1.75$) (Liu et al. 2013a, b, c), is generally regarded as a secondary iron mineral in mining environments. It has been found in nature especially in acid mine drainage (AMD) since it was first described as a pure mineral phase (Kim et al. 2015; Fan et al. 2019). It can adsorb heavy metal ions and microbial cells in liquid environment due to its specific characteristics such as small size, large surface area and high surface absorbability (Dey et al. 2014; Wang et al. 2006). The homogeneity, dispersibility and specific surface area of schwertmannite synthesized by *A. ferrooxidans* were much higher than that by chemical methods (Li et al. 2011). The formation of schwertmannite by *A. ferrooxidans* included two steps (Fig. 1). Firstly, the Fe(II) is oxidized to Fe(III) and the electrons are transferred by the action of cytochrome to generate ATP. Then the Fe(III) combines with H_2O and sulfate ion to produce schwertmannite with the continuous oxidation of Fe(II) and without cell proliferation in this process (Gui-Zhen et al. 2009; Egal et al. 2009; Zhu

Fig. 1 Putative model for the synthesis of schwertmannite and jarosite by *A. ferrooxidans*. Fe^{2+} is oxidized by *A. ferrooxidans* Cyc2 protein, which is located in the outer membrane, to Fe^{3+} (the figure also shows two electronic pathways through which Cyc2 acquires electrons in the oxidation process in *A. ferrooxidans*. Downhill

pathway: $\text{Fe} \rightarrow \text{Cyc2} \rightarrow \text{Rus} \rightarrow \text{Cyc1} \rightarrow \text{Cyt} \rightarrow \text{O}_2$. Uphill pathway: $\text{Fe}^{2+} \rightarrow \text{Cyc2} \rightarrow \text{Rus} \rightarrow \text{CycA1} \rightarrow \text{bc1} \rightarrow \text{ubiquinol pool} \rightarrow \text{NADH}$. Rus: rusticyanin, aa3: aa3 cytochrome oxidase, CycA1: a di-heme cytochrome c4, SdrA1: a short-chain dehydrogenase, QH_2 : quinol pool, bc1: cytochrome bc 1 complex)

et al. 2013). The production of schwertmannite (the Fe(III) combined with H₂O and sulfate ion) was carried out. It has been reported that the purity of biosynthetic schwertmannite is high, because there are no disturbing ions except for iron and organic nutrient ions (Chai et al. 2016). Schwertmannite formation commonly occurs in acidic environment with the pH range of 2.0–3.51, and lower or higher pH will promote jarosite production (Liao et al. 2009).

Jarosite

Jarosite, a secondary mineral, is distributed widely in sulfide mineral deposits and is closely associated with the microbial oxidation of Fe(II) in nature (Gunneriusson et al. 2016). Several features of jarosite such as strong hiding power, good weather resistance, non-toxicity and acid resistance had been characterized (Gupta et al. 2018). Jarosite is able to synthesize in the presence of some ions including Cr(III), Hg(II), Pb(II) under certain temperature and pH in solution, since it is insoluble in a dilute acid environment and easy to precipitate (Daoud et al. 2006). The synthesis rate of jarosite catalyzed by *A. ferrooxidans* (increase in the oxidation rate of Fe(II)) was found to be faster than that by chemical synthesis (Wang et al. 2019; Guay et al. 1977). It has been documented that the biosynthesized jarosite has some specific traits such as uniform dispersive crystal structure and smooth profile (Henao et al. 2010). Jarosite is usually synthesized by *A. ferrooxidans* in the FeSO₄–K₂SO₄–H₂O system, and the possible formation pathway is described in Fig. 1. The synthetic procedure of jarosite mediated by *A. ferrooxidans* is similar to that of schwertmannite, while the formation of the former only occurred at specific pH values (Fig. 1) (Yang et al. 2019a, b, c). A large number of H⁺ were produced due to the desorption of OH[−] from H₂O during Fe(II) oxidation, which can lead to a drop in pH (Yang et al. 2019a, b, c; Yongwei 2018 and Song et al. 2018).

The consumption of H⁺ in the oxidation of Fe²⁺ accompanies the release of OH[−]. Thus, Fe³⁺ combines with OH[−] during hydrolysis to produce [Fe(OH)₃] and [Fe₂(OH)₂⁴⁺], which meets with a monovalent cation K⁺, SO₄^{2−} and H₂O to form jarosite in the pH range 2.0–3.51 and schwertmannite in the favorable pH values of 2.5–4.5 (Egal et al. 2009). The formed iron compounds may precipitate the surface of the bacterial cells and can prevent direct bacterial action and/or Fe³⁺ attack. It has been confirmed that schwertmannite from the bio-oxidation of Fe³⁺ can be spontaneously converted to jarosite under the pH of 1.9–2.1 (Egal et al. 2009).

Iron-sulfur cluster

Iron–sulfur cluster, one of the oldest living substances, usually exists in living organisms (Liu et al. 2007). As an

auxiliary group of electron transport protein, it participates in energy transfer (Li et al. 2020). Additionally, it plays an important role in DNA synthesis and modification, gene expression regulation, and regulation of enzyme activity (Qian et al. 2013). The ISC system contains three core proteins which are assembled by IscS, IscU and IscA (Liu et al. 2013ab, c). *A. ferrooxidans* produce the ISC through a complex biosynthetic process. Previous studies have shown that IscS supplies the sulfur element in ISC, but the provider of the iron element in ISC is unknown. Iron–sulfur protein was found to contain a kind of metal enzyme that has an important biological function (Zhan et al. 2019). It usually exists in the form of [2Fe–2S], [3Fe–4S] and [4Fe–4S] in different environments, and the different forms of ISC are connected by a disulfide bond (Lin et al. 2020). The simplest ISC only contains one iron atom bonded to four cysteine sulfur atoms to form tetrahedrons and the general ISC comprises two, three or four iron atoms that connect with a polypeptide chain (Chen et al. 2011).

The sulfur donors, iron donors, and scaffold proteins were proved to be important and necessary components for ISC biosynthesis (Lill et al. 2020). It was found that cysteine is desulfurized to form L-alanine and elemental sulfur, which can provide sulfur to ISC synthesis. One of the most common biological models of ISC is the USA model including IscU, IscS, and IscA (Nathalie et al. 2020). IscA is a sulfur donor protein, IscS is an iron donor protein, and IscU is a stent protein. The iron ions absorbed by IscA are transferred through L-cysteine to form the L-cysteine–Fe complex, which forms intermediates IscS–S–Fe with cysteine desulfurization enzyme IscS (Liu et al. 2012; Ouyang et al. 2013). Then, S–Fe on IscS is transferred to IscU for assembling ISC through the specific interaction between proteins and proteins (Fig. 2) (Liu et al. 2014).

Magnetosome

Magnetosomes, intracellular structures produced by magnetosome-producing bacteria including magnetotactic bacteria (MTB) and non-MTB (Zhang et al. 2018), are magnetic nanoparticles surrounded by a lipid bilayer membrane (Schüler et al. 1999). They exhibit a narrow size distribution and uniform morphology with high biological compatibility, hypotoxicity, high chemical purity, dispersal ability, ferromagnetism, nanoscale size, and membrane-bound structure (Jacob et al. 2016). *A. ferrooxidans* can also form magnetosomes via the biomineralization of iron (Lohße et al. 2016). Magnetosomes synthesized by *A. ferrooxidans* have been extracted and purified through ultrasonic and lysozyme treatment combined with magnetic separation (Jacob et al. 2016). Magnetosomes disperse in the *A. ferrooxidans*, which is inconsistent with most of the magnetosomes arranged in single or multiple chains in MTB (Yazdi et al. 2018). The

Fig. 2 Putative model for the synthesis of iron–sulfur cluster in *A. ferrooxidans* [Interplay of IscA and IscU in the Biogenesis of Iron–Sulfur Clusters]. IscS: a cysteine desulfurase is a sulfur donor protein in this model. IscU is a protein with a molecular weight of 14 kD, and is a scaffold protein in this model. IscA is a protein in the form of dimers or tetramers with molecular weight of 11 kD and is an iron donor protein in this model. First, IscA absorbs intracellular iron

and produces IscA-Fe^{2+} , then L-cysteine (L-Cys) transfers the iron in IscA to form transient state L-cysteine–S–Fe complex. This complex removal S in the action of IscS to form intermediates IscS-[2Fe-2S] , and $[2\text{Fe-2S}]$ will be transferred to IscU through protein interaction and form IscU-[2Fe-2S] . Eventually, $[2\text{Fe-2S}]$ will be transferred to the target protein and make it mature

magnetosome formation is affected by environmental parameters including iron source, nitrogen source, temperature oxygen concentration and pH (Firlar et al. 2019). Among them, FeSO_4 and $(\text{NH}_4)_2\text{SO}_4$ were found to significantly influence the synthesis of magnetosomes in *A. ferrooxidans* (Dieudonné et al. 2019).

Previous studies have shown that FecA1, FeoAB and MntH are responsible for Fe(II) uptake, and some genes including *tonB*, *exbB* and *exbD* (moreover PorA protein family) involve in Fe(III) transfer in *A. ferrooxidans* (He et al. 2020). The uptake of Fe(II) and Fe(III) is the most crucial stage for magnetosome synthesis because of the requirement of a large amount of iron to biomineralize magnetosomes in *A. ferrooxidans*. Several open reading frames in *A. ferrooxidans* are similar to the genes which encode the proteins related to the magnetosome synthesis in MTB including *magA*, *mamB*, *mamE* and *mamM*. *A. ferrooxidans* uptake Fe^{2+} via FeoAB and MntH systems and/or ingest Fe^{3+} by the FecA1 system. Additionally, PorA, which is a protein similar to porin and ABC (ATP-binding complex), helps these systems to complete the transport of Fe^{2+} or Fe^{3+} . Magnetosomes are made from scratch and gradually grow larger in *A. ferrooxidans*. MamE is hypothesized to be a protein that plays a guiding role in the localization of membrane proteins of magnetosomes. MamM, MamA and other proteins play an important role for magnetosome maturation. Magnetosomes are made from scratch and gradually grow larger in *A. ferrooxidans*. MamE is hypothesized to be a protein that plays a guiding role in the localization of membrane proteins

of magnetosomes. MamM, MamA and other proteins are involved in the maturity of magnetosomes. Though only a few genes related to magnetosome formation have been reported, we proposed a hypothetical model to display the mechanism for magnetosome synthesis in *A. ferrooxidans* (Fig. 3) (Jing et al. 2011; Maoyuan et al. 2012).

Potential applications of biominerals produced by *A. ferrooxidans*

Application of schwertmannite

The schwertmannite synthesized by *A. ferrooxidans* can be used as adsorbent and catalyst (Meng et al. 2017). Schwertmannite has a good adsorption potential for repairing arsenic pollution due to its large specific surface area and hydroxyl groups (Li et al. 2017). The sulfate radical anions can adsorb and co-precipitate with arsenic. Studies have shown that the biosynthesized and chemosynthetic schwertmannite can remove 92% and 85% of As(III) , respectively. This indicated that the As(III) adsorption capacity of biosynthesized schwertmannite is better than that of chemosynthetic schwertmannite (Paikaray et al. 2014). The optimal pH range for As(III) removal using biosynthesized schwertmannite is 6.0–10.0, which is similar to underground water. Therefore, biosynthesized schwertmannite is suitable to remove arsenic from groundwater (Duan et al. 2016). It has been reported that the biosynthesized schwertmannite can remove chrome

Fig. 3 Putative model for synthesis of magnetosomes in *A. ferrooxidans*. Fe^{2+} and Fe^{3+} enter the *A. ferrooxidans* by different processes and are used to synthesize the magnetosomes. Two intake systems (FeoAB and MntH) provide *A. ferrooxidans* with Fe^{2+} , and Fe^{3+} is ingested through the FecA1 system. FecA1, FeoAB and MntH are composed of a variety of transport-related proteins encoded by different genes. PorA (a protein similar to porin) and ABC (ATP-binding

complex) help different systems complete the transport of Fe^{2+} or Fe^{3+} . Magnetosomes are made from scratch and gradually grow larger in *A. ferrooxidans*. MamE is hypothesized to be a protein that plays a guiding role in the localization of membrane proteins of magnetosomes. MamM, MamA and other proteins play an important role for magnetosomes to mature

from the solution (Wang et al. 2015). The methods for Cr(VI) removal include chemical precipitation, adsorption, ion exchange and reverse osmosis (Yu et al. 2014). It has been documented that schwertmannite has a strong selective adsorption for Cr(VI) and the adsorption process conforms to Langmuir equation (Gan et al. 2015). The removal rate of Cr(VI) using biosynthesized schwertmannite is over 90% under certain conditions with a pH ranged from 6.0 to 7.0 (Gan et al. 2015). The adsorption was less affected by other anions and temperature in the range of 20–50 °C (Xianyou et al. 2019).

Additionally, schwertmannite can be used as Fenton-like reaction catalyst (Song et al. 2018). It has been reported that schwertmannite synthesized by *A. ferrooxidans* can degrade methyl orange (Zhang et al. 2018). The biosynthetic schwertmannite can exhibit a high catalytic efficiency at a neutral environment with a pH of 7.5, which can overcome the disadvantage of a narrow pH range for a homogeneous fenton reaction (Wang et al. 2019). The catalytic degradation of methyl orange by biosynthetic schwertmannite can still be carried out under a high concentration of nitrate, sulfuric acid and chloride ions (Xiang Li et al. 2018). The reaction mechanism is the degradation of methyl orange by hydroxyl radicals. Additionally, the biosynthetic schwertmannite can efficiently degrade nitrobenzene which is an organic pollutant. This will provide a good solution for the treatment of wastewater containing organic contaminants.

Application of jarosite

Jarosite can fix and remove metals such as As(III) and Cr(VI) to reduce water pollution (Dan et al. 2019). It has been documented that the biogenic jarosite exhibits good adsorption potential for As(III) at pH 3.0 and the adsorption is found to be spontaneous. The adsorption capacity increases with the increase of temperature from 15 to 35 °C. Previous studies have indicated that the adsorption capacity of As(III) by biogenic jarosite is higher than that by chemical synthesis jarosite in the extreme acid environment (Julia et al. 2018). The adsorption process of As(III) to jarosite can be divided into three consecutive stages based on the analysis of adsorption kinetics including adsorbent diffusion, adsorption and internal diffusion. Studies have shown that adsorption of As(III) by jarosite fits the quasi-second-order kinetics, and the correlation coefficient and the adsorption rate constant K are 0.977 and 0.020 $\text{g mg}^{-1} \text{min}^{-1}$, respectively. The adsorption isotherm of As (III) fitted well with the Langmuir equation and the Freundlich equation (Gao et al. 2020).

It has been proved that Cr(VI) can lead to different sorts of inflammation and cause cancer. Therefore, the treatment of chromium-containing wastewater is necessary and urgent (Reyes et al. 2016). Jarosite also has a strong adsorption capacity to remove Cr(VI) and the removal efficiency is found to be more than 70%. The pH significantly affects

the removal efficiency of Cr(VI), and the adsorption quantity increases with the rise of pH in the range of 2.5–3.2 (Hosokawa et al. 2013). Jarosite can absorb a large amount of heavy metal ions including Cr, Hg and Pb, due to the presence of many crystalline chemical locations (Xiao et al. 2015). The toxic heavy metal ions can absorb into jarosite and the harmless ions are replaced (Fig. 4).

Application of iron-sulfur cluster (ISC)

The ISC plays an important role in many metabolic reactions, cellular energy metabolism and gene expression regulation (Shibue et al. 1991). There are two different states of iron atoms, i.e., oxidation state Fe(III) and reduced state Fe(II) in the ISC (Liu et al. 2013a, b, c). The ISC changes from oxidation to reduced state on receiving electrons and then reverts to its original oxidation state when passing the electrons to other receptor proteins. This process is repeated if more electrons transferred successively (Ryota et al. 2014).

Additionally, the ISC plays an important role in the storage of iron and sulfur to maintain the dynamic balance of iron ions in cells. It also can participate in transcription and translation regulation. It has been reported that SoxR protein can stimulate the transcription of SoxR through oxidative stimulation of [2Fe-2S] under oxidative stress (Mao et al. 2018). Additionally, the ISC can activate the translation of many enzymes under oxidative stress.

Application of magnetosome

Magnetosomes synthesized by MTB have potential applications in various fields including drug development, molecular biology research, diagnostic assessments of products and foods, and environmental monitoring (Yan et al. 2012). However, the information about the application of magnetosomes synthesized by *A. ferrooxidans* is sparse. Magnetosomes have great potential in the diagnosis due to their superiority on the magnetic separation of amyotrophic molecules (Alphand et al. 2014). They are also applied in the detection

of pathogens because the magnetosome outer membrane contains number of of ammo and hydroxyl groups which are easy to be modified. Magnetosome–antibody complex and immunofluorescence technique were used to detect the pathogenic bacteria. In addition, the magnetosomes also have good targeted transport capability (Aihua et al. 2010). Magnetosomes can be used as the ideal drug carrier which can be controlled by an external magnetic field due to their good biocompatibility and low toxicity. Targeted drug delivery can bring the drug to a fixed point through local or systemic blood circulation and reduce drug toxicity and improve drug efficiency by using magnetosomes (Fan et al. 2019a, b). Moreover, the magnetosomes can also be utilized in nucleic acid transfer and gene therapy. We can use a magnetic force to attach nucleic acids to the surface of magnetosomes and guide them into the target cells (Kuzajewska et al. 2020). It has been reported that magnetosome viral vectors are much better than viral vectors for gene therapy. The small dose of virus and the short exposure time can reduce the possibility of adverse effects using magnetosome–virus carriers.

Perspective

A. ferrooxidans can synthesize a variety of biological materials under the natural environment. Although there has been some progress in the wide investigation of the synthetic mechanism and condition, there are still some issues that need to be studied further.

1. The crystal purity of schwertmannite and jarosite synthesized by *A. ferrooxidans* is higher than that by chemical synthesis (Li et al. 2011). However, the yield of schwertmannite and jarosite using *A. ferrooxidans* is very low. Therefore, the biosynthetic mechanism should be further studied at the molecular level (Kim et al. 2015; Fan et al. 2019). All the genes and proteins that control the biosynthesis of schwertmannite and jarosite would be revealed, which can promote their faster and better synthesis (Yang et al. 2019a, b, c).

Fig. 4 Putative model for absorption of metal elements on jarosite. Jarosite can absorb a large amount of heavy metal ions including Cr, Hg and Pb due to the presence of many crystalline chemical locations. The toxic heavy metal ions can absorb into jarosite and the harmless ions (K^+ , Fe^{2+} and SO_4^{2-}) are replaced

2. Although ISC plays an important role in cell metabolism, there are still some deficiencies in the research. The synthesized and regulated mechanism of ISC production in *A. ferrooxidans* under various conditions is not completely known (Li et al. 2020). In addition, the genes and proteins regulated by ISC in the electronic transmission pathway are yet to be studied (Zhan et al. 2019).
3. Great progress has been made in the study of the magnetosomes in *A. ferrooxidans*, but there are still many issues need to be clarified. For example, although the recent genetic and biochemical factors that influence the magnetosome formation have been widely recognized (Fan et al. 2019a, b), their exact function in biomineralization and control of magnetosome composition, shape, size and arrangement remains to be elucidated (Anissa et al. 2019). Therefore, it is urgent to systematically study the effects of various magnetosome genes and proteins on magnetosome formation in the bacterium (Kuzajewska et al. 2020). This will help us to use modern gene engineering methods to produce biogenic functional magnetic nanoparticles using *A. ferrooxidans* massively.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest. This article does not contain any studies with human participants or animals performed by any of the authors. Informed consent was obtained from all individual participants included in the study. We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the position presented in, or the review of, the manuscript.

Ethical statement I certify that this manuscript is original and has not been published and will not be submitted elsewhere for publication while being considered by 3Biotechnology. The study is not split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time. No data have been fabricated or manipulated (including images) to support our conclusions. No data, text, or theories by others are presented as if they were our own.

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