Microbacterium sulfonylureivorans sp. nov., isolated from sulfonylurea herbicides degrading consortium

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Abstract
A novel Gram-stain positive, aerobic, motile, rod-shaped bacterium, designated strain LAM7116T was isolated from a sulfonlurea herbicides degrading consortium enriched with birch forest soil from Xinjiang. Phylogenetic analysis based on the 16S rRNA gene sequences indicated that strain LAM7116T was closely related to the members of the genus Microbacterium, with the highest similarity to Microbacterium flavescens DSM 20643T (98.48%) and Microbacterium kitamiense Kitami C2T (98.48%). Strain LAM7116T formed a distinct subclade with M. flavescens DSM 20643T within the genus Microbacterium in the 16S rRNA gene phylogenetic trees. The genomic DNA G+C content of LAM7116T was 69.9 mol%. The digital DNA–DNA hybridization (dDDH) value between strain LAM7116T and M. flavescens DSM 20643T was 27.20%. The average nucleotide identity (ANI) value was 83.96% by comparing the draft genome sequences of strain LAM7116T and M. flavescens DSM 20643T. The major fatty acids were anteiso-C15:0, anteiso-C17:0, iso-C17:0, and iso-C16:0. The respiratory menaquinones of strain LAM7116T were MK-13 and MK-14. The main polar lipids were diphosphatidylglycerol, phosphatidylglycerol, an unidentified lipid, and an unidentified glycolipid. The peptidoglycan contained the amino acids glycine, lysine, alanine, and glutamic acid. Based on the phenotypic characteristics and genotypic analyses, we consider that strain LAM7116T represents a novel species, for which the name Microbacterium sulfonylureivorans sp. nov. was proposed. The type strain is LAM7116T (=CGMCC 1.16620T =JCM 32823T). Strain LAM7116T secreted auxin IAA and grew well in Ashby nitrogen-free culture medium. Genomic results showed that strain LAM7116T carried the nitrogenase iron protein (nifU and nifR3) gene, which indicated that strain LAM7116T has the potential to fix nitrogen and promote plant growth. At the same time, strain LAM7116T can degrade nicosulfuron (a kind of sulfonylurea herbicides) using glucose as carbon source. Microbacterium sulfonylureivorans sp. nov. LAM7116T is a potential candidate for the biofertilizers of organic agriculture areas, and may possess potential to be used in bioremediation of nicosulfuron-contaminated environments.

Keywords Microbacterium sulfonylureivorans · Polyphasic taxonomy · Herbicide degradation · Plant growth promoting

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Introduction

The genus *Microbacterium*, belonging to the family *Microbacteriaceae*, phylum *Actinobacteria*, was first described by Orla-Jensen (1919) and emended by Collins et al. (1983), and then, Takeuchi and Hatano (1998) revised the description of the genus and transferred *Aureobacterium* into *Microbacterium*. Members of genus *Microbacterium* are typically Gram-positive, non-spore-forming and rod-shaped (Collins et al. 1983, Takeuchi and Hatano 1998). The genus *Microbacterium* includes a very large number of species (over 100) that have been isolated from a wide diversity of environments. At the time of writing, the genus *Microbacterium* consists of 124 species with validly published and correct names in the genus *Microbacterium* recorded on LPSN (http://www.bacterio.net/microbacterium.html). Members of the genus *Microbacterium* play an important role in the environment such as *β*-aminoacylase-producing (Liu et al. 2005), plant-growth-promoting (Matsuyama et al. 1999), xylanolytic (Park et al. 2006), crude-oil-degrading (Schippers et al. 2005) and can be isolated from various habitats, including soil (Kageyama et al. 2006), seawater (Kim et al. 2000), marine environments (Kageyama et al. 2007), biofilms (Kim et al. 2005), sediment (Mawlankar et al. 2015), and other environments, such as human blood (Clermont et al. 2009).

In this study, a novel strain LAM7116^T was isolated from the birch forest soil in Xinjiang, and it was classified as a novel species of the genus *Microbacterium* according to the results of phylogenetic, chemotaxonomic, and biochemical analysis.

Materials and methods

Bacterial strains, growth conditions, and cultivation

Strain LAM7116^T was isolated from a soil sediment sample taken from Haba river birch forest, located in Kulebai township, Haba river county, Altay region, Xinjiang Province, China (coordinates 48° 04’ N, 86° 20’ E), the largest naturally growing birch forest belt in northwest China. Five grams of soil sediment was added to 250 mL Erlenmeyer flasks containing 100 mL of modified mineral salts medium (MSM) supplemented with 100 mg/L nicosulfuron as a sole carbon source, and enrichment cultures were incubated on a rotary shaker (160 rpm) at 30 °C in the dark. After incubation for 2 months, the cultures were called “the degrading consortium”. 2 mL degrading consortium was suspended in 18 mL sterile water and mixed, the liquid phase was diluted 10^-5, and 100 mL samples were spread onto the surface of each cultivation plate. Aliquots (0.2 mL) of the suspension were plated on Luria–Bertani (LB; BD) agar adjusted to pH 7.0, and the isolation plates were incubated at 35 °C for 5 days; one light yellow-colored strain, designated as LAM7116^T, was isolated and purified by transferring onto new plates. Pure cultures of strains LAM7116^T for further characterization are based on their low 16S rRNA gene sequence similarities with known members of the genus *Microbacterium*. The strain was maintained on LB agar and preserved as glycerol suspensions (20%, v/v) at −80 °C. The basal growth condition of the strains for all experiments was maintained at pH 7.0 and 35 °C, unless otherwise stated.

Phenotypic characterization tests of LAM7116^T

Strain LAM7116^T morphological characteristics of the isolates were examined after cells were grown on LB medium at 35 °C for the initial stationary phase. To standardize the physiological age, growth curve for each strain was tested, respectively. The optimum temperature for growth was determined by growing the isolate on LB medium at eight different temperatures (10, 15, 20, 25, 30, 35, 40 °C). Growth at various NaCl concentrations was tested over the range 0–10% (w/v) NaCl (at 1% intervals) by incubating at 35 °C. The optimal pH for growth was tested and pH values 4–13 (at 0.5 intervals pH unit) using LB as the basal medium. For the pH tests, using buffers systems were described by Xu et al. (2005). The pH values of <6, 6–9 and >9 were adjusted using sodium acetate/acetate acid, Tris/HCl and Na_2CO_3 buffers, respectively (Moraine et al. 2010). Anaerobic growth was examined in serum bottles with cysteine (0.001 g) added to nutrient broth (0.5% tryptone, 0.1% yeast extract, and 3.4% sodium chloride) and the upper air layer was replaced with nitrogen. The Gram-staining test was performed using a Gram-stain kit (bioMérieux) according to the manufacturer’s instructions. Cell motility was examined on motility agar (Chen et al. 2007). Catalase activity was determined by observing bubble production in 3% (v/v) hydrogen peroxide solution and oxidase activity was determined using 1% (v/v) tetramethyl-p-phenylenediamine. Cell morphology was observed under a Nikon phase-contrast microscope at ×1000 magnification using cells grown for 48 h at 35 °C on LB plates. Endospores were examined according to the Schaeffer–Fulton staining method (Murray et al. 1994). Biochemical characteristics, sugar fermentation tests, enzyme activities, oxidase activity, and utilization of carbon and nitrogen sources were performed using the API 20NE, ZYM, and 50CH, according to the manufacturer’s instructions (bioMérieux). Hydrolysis of cellulose, gelatin, starch, casein, tyrosine, and Tweens 20, 40, 60 and 80, milk coagulation and peptonization, and utilization of urea and
nitrates were performed as described by Smibert and Krieg (1994). The type strain of *M. flavescens* JCM 3877\(^T\) (= DSM 20643\(^T\)) was used as reference strain.

### Chemotaxonomic characterization

Biomass for chemotaxonomic studies was prepared by growing the strain in LB broth in shake flasks at 35 °C for 7 days. Cells were harvested by centrifugation, washed with distilled water twice, and then freeze-dried. *M. flavescens* JCM 3877\(^T\) was used as a reference strain and was processed under the same conditions. Fatty acid methyl esters were prepared and analyzed using the standard method of the Microbial Identification System but by a Hewlett Packard HP 6890 and Microbial Identification software (Sasser et al. 1990). Strains were cultured in LB at 35 °C for 48 h, and isoprenoid quinones were extracted and analyzed through HPLC (Collins et al. 1977). The whole-cell sugars were tested according to the procedures developed by Lechevalier and Lechevalier (1980). Cell wall amino acids were identified by TLC (Hasegawa et al. 1983) and High-Speed Amino Acid Analyzer (Hitachi LA8080). The preparation of cell wall peptidoglycan in the cell wall was performed in accordance with the work by Komagata and Suzuki (1987). Polar lipids were extracted, separated by two-dimensional TLC, and identified according to Minnikin et al. (1977). TLC plates were sprayed with various specific reagents for the detection of sugars (a-naphthol/sulfuric acid), phosphates (Zinzadze reagent, Schiff reagent), amino groups (ninhydrin/n-butyl alcohol, Dragendorff’s reagent), and total lipids (molybdatophosphoric acid), respectively.

### Phylogenetic 16S rRNA gene analysis

Genomic DNA was extracted from a single colony of the strain grown on LB plates at 35 °C for 48 h. The 16S rRNA gene PCR amplification and sequencing were performed as described by Cai et al. (2011). The 16S rRNA gene was amplified by PCR using the universal primers 27F (5′-AGA GTTTGATCCTGCTCAG-3′) and 1492R (5′-GGTTAC CTGTTAGACTT-3′) (Lane et al. 1991). The amplification reaction and purification of the product were performed according to Pandey et al. (2002). The identification of phylogenetic neighbors was done by searching against the EzTaxon database (http://www.ezbiocloud.net/eztaxon) (Kim et al. 2012). The CLUSTAL_W algorithm was used for sequence alignments using the neighbor-joining (Saitou et al. 1987) and maximum-likelihood (Felsenstein 1981) and maximum-parsimony (Miya et al. 2000) methods that were implemented with Molecular Evolutionary Genetic Analysis (MEGA) software version MEGA 7.0 for analysis evolutionary status of strains (Kumar et al. 2016). Evolutionary distance was computed using the Kimura two-parameter model. The robustness of the tree branches was estimated by bootstrap analysis with 1000 replications (Felsenstein 1985).

### Genome sequencing analysis

The draft genome sequence of strain LAM7116\(^T\) was used to detect genes’ sequence similarity analysis and genomic information. The genome was sequenced by Magigene Bioinformatics Technology Co., Ltd. (Guang dong, PR China). Genomes of the most closely related species chosen above were retrieved from the GenBank database in NCBI. Reads of each data set were filtered using AdapterRemoval SOAPdenovo v1.05 (Mikkelsen et al. 2016; Li et al. 2010) with default parameters which was used to assemble the trimmed reads. The size of the genome was estimated by k-mer analysis (Liu et al. 2013) and genome completeness was determined with CheckM.v1.0.3 (Parks et al. 2015). The digital DNA–DNA hybridization (dDDH) and average nucleotide identity (ANI) values of the strains were employed to further genomically distinguish strain LAM7116\(^T\) and *M. flavescens* JCM 3877\(^T\) using the ortho-ANiU algorithm from Ezbiocloud (Yoon et al. 2017) conducted genome differentiation. The genome-to-genome distance calculator GGDC 2.0 (http://ggdc.dsmz.de) and Formula 2 was used as recommended for the calculation of dDDH values. Average nucleotide identity (ANI) values (https://ani.jgi.doe.gov/html/calc.php?) of the total genomic sequences shared between the genomic sequences of strain LAM7116\(^T\) with closely related genomic sequences from GenBank were determined according to Goris et al. (2007). Functional annotation of the genome was performed with an RAST sever (Aziz et al. 2008). Analysis process is based on RAST default settings (Overbeek et al. 2014).

### Degradation ability of nicosulfuron by strain LAM7116\(^T\)

Strain LAM7116\(^T\) was incubated in liquid LB medium at 35 °C for 48 h in the dark. Cells in the late exponential growth phase were harvested by centrifugation at 8000 rpm for 5 min. The pellet was washed three times with 0.13 M phosphate-buffered saline (PBS) solution (pH 7.2) prior to subsequent studies. The ability of strain LAM7116\(^T\) degrade nicosulfuron in liquid GSM medium (MSM supplemented with 5 g/L glucose) containing 50 mg/L nicosulfuron was analyzed by HPLC, as described by Li et al. (2020). Uninoculated GSM medium served as a control, and the inoculation volume was 3.0% (v/v) unless stated otherwise. All experiments were conducted in triplicate.

### Plant growth-promoting function of LAM7116\(^T\)

The performance of secreting plant growth hormone indoleacetic acid (IAA) of strain LAM7116\(^T\) was measured.
by the PC Salkowski colorimetric method described by Glickmann and Dessaux (1995). The qualitative and quantitative analyses of siderophore production were conducted by the method described by Machuca and Milagres (2003). Through the rate of color change of CAS medium (in millimeters) function of time (in days) when microorganisms were grown in CAS agar plates, quantitatively measure the siderophore production. The utilization of phosphorus by the strain was determined by organic phosphorus and inorganic phosphorus plates (Robert et al. 1999). All experimental analyses were performed in triplicate to ensure reproducibility. The results were expressed as the mean value of these determinations.

### Results and discussion

**Phenotypic characterization**

Morphological observation of LAM7116 T strain cultured on LB medium revealed that the strain has typical characteristics of members of the genus Microbacterium. Strain LAM7116 T showed visible colonies (2 mm in diameter) on LB after 48 h of incubation at 35 °C. The size of the cells was observed by light microscopy (Figure S1a). Strain LAM7116 T was aerobic, Gram-positive, catalase positive, non-motile, and non-spore-forming rods. Colonies were creamish yellow, circular, and opaque with entire edges (Figure S1b). Detailed physiological and biochemical properties, enzyme activity (API 20NE, API ZYM), and the production of acid (API 50CH) are presented in the species description, and the differential characteristics of strain LAM7116 T and the closely related species of the genus Microbacterium are summarized in Table 1. For example, the reactions of salicin, D-rhamnose, D-glucose, β-glucosidase, starch, and glycogen were positive, while the closely related strain was negative. Other phenotypic differences include the hydrolysis of starch and Tweens (20, 40, and 80). The negative characteristics of the enzyme activities (API 20 NE, API ZYM) and the production of acid (API 50CH) for LAM7116 T are summarized in Table S3.

### Isoprenoid quinones, polar lipids, and cellular fatty acid

The main isoprenoid quinone of strain LAM7116 T was identified as MK-13 (98.7%) and MK-14 (1.3%). The major polar lipids of strain LAM7116 T detected were diphosphatidylglycerol (DPG), phosphatidylglycerol (PG), and an unidentified glycolipid (GL) and one unidentified lipid (Fig. S2). The major cellular fatty acids of strain LAM7116 T were anteiso-C_{15:0} (47.8%), anteiso-C_{17:0} (13.4%), and iso-C_{17:0} (12.1%), which were consistent with the related species in Microbacterium flavescens JCM 3877 T. All strains were cultivated with the same medium and growth conditions. In the Biolog system, both strains were symbols: +, positive; −, negative; w, weakly reaction. All are positive for catalase and negative for oxidase, alkaline phosphatase, esterase (C4), esterase lipase (C8), lipase (C14), valine arylamidase, cystine arylamidase, trypsin, chymotrypsin, acid phosphatase and β-galactosidase, β-glucuronidase, β-glucosidase, β-glucosidase, N-acetyl-β-glucosaminidase, α-mannosidase, α-fucosidase, inulin, xylitol, and α-gentiobiose are positive. Nitrates reduce, indole production, urease, arginine dihydrolase, sorbitol, methyl-α-D-mannopyranoside, N-acetyl-β-glucosamine, d-ribose, d-ribose, d-lactose, d-lyxose, d-tagatose, d-fucose, L-fucose, L-arabinose, L-arabinose, potassium gluconate, 2-ketogluconate and 5-ketogluconate are all negative. Capric acid, adipic acid phenylacetic acid, and glycerol, erythritol, d-arabinose L-xylose, d-adenositol, methyl-β-D-xlyopyranoside, dulcitol, and inositol are negative. d-Fructose, d-mannose, L-sorbose, mannitol, d-cellobiose, and

| Table 1 Differential characteristics of strain LAM7116 T and its relative reference strain in the genus Microbacterium |
|---------------------------------------------------------------|
| Characteristic                                      | 1          | 2          |
| Temperature range for growth (°C)                     | 15–40      | 20–35      |
| Optimal growth (°C)                                   | 35         | 28         |
| pH range for growth                                    | 5.5–11.5   | 5.0–12.0   |
| Optimal                                             | 7          | 7          |
| Growth in NaCl                                       | 0–4        | 0–4        |
| Optimal                                             | 2          | 1          |
| Hydrolysis of                                       |            |            |
| Starch                                              | –          | +          |
| Gelatin                                             | +          | –          |
| Casein                                              | –          | –          |
| Tween 20                                            | +          | –          |
| Tween 40                                            | –          | –          |
| Tween 60                                            | –          | –          |
| Tween 80                                            | –          | –          |
| API 20NE                                             |            |            |
| d-Glucose fermentation                               | +          | −          |
| β-glucosidase                                       | +          | −          |
| Gelatinase                                          | w          | +          |
| Mannose                                             | w          | +          |
| N-acetyl-glucosamine                                 | +          | w          |
| Maltose                                             | –          | +          |
| Malic acid                                          | –          | +          |
| Citrate                                             | –          | w          |
| API 50CH                                             |            |            |
| d-Xylose                                            | w          | –          |
| d-Glucose                                           | w          | –          |
| L-Rhamnose                                          | w          | –          |
| Amygdalin                                           | w          | –          |
| Aesculin                                            | +          | w          |
| Salicin                                             | +          | –          |
| d-Melibiose                                         | w          | –          |
| d-Sucrose                                           | w          | –          |
| d-Trehalose                                         | w          | –          |
| d-Raffinose                                         | +          | –          |
| Starch                                              | –          | –          |
| Glycogen                                            | –          | +          |
| L-Arabinose                                         | w          | –          |
| DNA G+C content (mol%)                                | 69.9       | 66.9*      |

Strains: 1, LAM7116 T; 2, Microbacterium flavescens JCM 3877 T. All strains were cultivated with the same medium and growth conditions.
genus *Microbacterium*, but the presence of anteiso-C₁₇:₁ (1.0%) in the two isolates distinguished them from others.

Identification using the EzBioCloud server revealed that strain LAM7116ᵀ belongs to the genus *Microbacterium* and shared high sequence similarities with *M. flavescens* JCM 3877ᵀ (98.48%), *M. kitamiense* Kitami C2ᵀ (98.48%), and *M. binotti* CIP 101303ᵀ (98.35%). It is generally considered that the sequence similarity of 16S rRNA gene is less than 98.60%, which can be defined as the classification of new species (Stackebrandt et al. 2006). Strain LAM7116ᵀ was located within the genus *Microbacterium* as a separated lineage in the neighbor-joining tree (Fig. 1), indicating that LAM7116ᵀ represents a novel species of genus *Microbacterium*. Phylogenetic trees also were reconstructed using the maximum-likelihood algorithms (Supplementary Fig. S4) and maximum-parsimony (Supplementary Fig. S3).

### Phylogenetic analysis

The qualitative determination indicated that strain LAM7116ᵀ secreted auxin IAA, and the color reaction was pink, at a concentration of 4.97 mg/L (Fig. S5). Strain LAM7116ᵀ could grow well in nitrogen-free medium (Ashby), indicating that the strain has the ability of nitrogen fixation (Fig. S6). Strain LAM7116ᵀ generated a color ring on the CAS flat plate (Fig. S9), but no a clear zone was observed around each of the colonies of strain LAM7116ᵀ in the genus *Microbacterium*. 235 of the genes were associated with carbohydrate metabolism, 190 genes with metabolism of amino acids, and 122 genes, with metabolism of cofactors and vitamins, 91 genes, with metabolism energy.

Based on the topology of the phylogenomic tree, strain LAM7116ᵀ formed the branch with *M. flavescens* DSM 20643ᵀ. The ANI and dDDH values for both strains were 83.96% and 27.20%, to the genome of the closest species *M. flavescens* DSM 20643ᵀ was below the species cutoff (95% for ANI and 70% for dDDH). Therefore, draft genome analysis combined with 16S rRNA phylogenetic, physiological, and biochemical properties supported the conclusion that strain LAM7116ᵀ should be considered a novel species in the genus *Microbacterium*.

### Biodegradation of nicosulfuron by strain LAM7116ᵀ

When nicosulfuron was provided in the GSM medium at an initial concentration of 50 mg/L, strain LAM7116ᵀ could degrade 69.56% within 7 days (Fig. S10). At the same time, the pH declined from 7.0 to 4.24 during nicosulfuron degradation by LAM7116ᵀ in the GSM medium. Therefore, the degradation efficiency of nicosulfuron by strain LAM7116ᵀ may be caused by hydrolysis. The results suggested that strain LAM7116ᵀ with the excellent degradation ability of nicosulfuron in GSM system. According to the genome function annotation database Kyoto Encyclopedia of Genes and Genomes (KEGG) annotation analysis, it can be predicted that strain LAM7116ᵀ contains seven esterase-related genes that catalyze the degradation of nicosulfuron.

### Growth promoting characteristics

The draft genome of strain LAM7116ᵀ was 379,171,8 bp. And, the N₅₀ value was 214,759,8 bp (Table S2). The genome was predicted to contain a total of 3591 genes in the plasmid, with a gene average length of 973 bp. The genomic DNA G+C content of strain LAM7116ᵀ was 69.9 mol%, a value that within the range described for the genus *Microbacterium*. 235 of the genes were associated with carbohydrate metabolism, 190 genes with metabolism of amino acids, and 122 genes, with metabolism of cofactors and vitamins, 91 genes, with metabolism energy.

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### Conclusions

Based on the present polyphasic analysis, strain LAM7116ᵀ is considered to represent a novel species within the genus *Microbacterium*, for which we propose the name...
Microbacterium sulfonylureivorans sp. nov. It is predicted that strain LAM7116\textsuperscript{T} had multiple ecological functions, including the secretion of auxin IAA, and produces iron carrier and nitrogen fixation, which can promote plant growth and antagonize pathogens. At the same time, the strain LAM7116\textsuperscript{T} has a certain degradation ability of nicosulfuron, which can be used for remediation of nicosulfuron pollution of environment.
Description of Microbacterium sulfonylureivorans sp. nov

Microbacterium sulfonylureivorans (sul.foen.yl.u.re.i.vo’rans.
N.L. fem. n. sulfonylurea, sulfonylurea; L. v. voro, to eat; N.L. part. adj. sulfonylureivorans, eating sulfonylurea herbicides).

Cells are Gram-reaction-positive; catalase positive but oxidase negative, respectively, aerobic short rods, non-spore-forming and rod-shaped colonies on LB. Cells grow on LB are circular, smooth, and yellowish after 3 day incubation at 35 °C. The temperature range for growth is from 15 to 40 °C (optimum 35 °C). The pH range for growth is from 5.5 to 11.5 (optimum 7.0). The NaCl concentration range for growth is from 0 to 4.0% (optimum 2.0%). In hydrolysis test, strain LAM7116 T is positive for gelatin and Tween20. In API 20NE test strips, positive for hydrolysis adipic acid d-glucose fermentation, β-glucosidase, β-galactosidase, gluconate, mannitol, N-acetyl-glucosamine, gluconate. In the API 50CH test system, strain LAM7116 T is found to be positive for d-glucose, d-fructose, d-mannitol, ascorbic, salicin, d-cellulbiose, d-maltose, d-sucrose, d-raffinose, starch, and glycogen. The predominant respiratory quinones were MK-13 and MK-14. The peptidoglycan hydrolysates of starch, and glycogen. The predominant respiratory quinones is 69.9 mol %.

The type strain is LAM7116 T (= JCM 32823 T), which was isolated from a sulfonylurea herbicides degrading consortium enriched with the birch forest soil, and the soil collected from Xinjiang County, Xinjiang Province, China.

The GenBank/EMBL/DDJB accession number for the 16S rRNA gene sequence of strain LAM7116 T is MG009458. The GenBank accession number for the draft genome sequence of strain LAM7116 T is RJAD00000000.

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Author contributions QYM and DLK: study design; QZ and MML: conceived and supervised the study; DLK: analyzed the data; XYH: prepared the figures; QYM and YQZ: wrote the manuscript; ZYR and WZ: edited the manuscript and reviewed the literature; JC: manuscript revision. All authors have read and agreed to the published version of the manuscript.

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Declarations

Conflict of interest The authors declare that there are no conflicts of interest.

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