**Chryseobacterium paridis** sp. nov., an endophytic bacterial species isolated from the root of **Paris polyphylla** Smith var. *yunnanensis*

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Received: 14 May 2021 / Revised: 9 July 2021 / Accepted: 26 July 2021 / Published online: 3 August 2021

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**Abstract**

A Gram-negative, yellow-pigmented, rod-shaped bacterial strain YIM B02567T was isolated from the root of **Paris polyphylla** Smith var. *yunnanensis* in China. Strain YIM B02567T grew optimally at 25–30 °C and at pH 7.0 in the absence of NaCl on nutrient agar. Phylogenetic analyses based on 16S rRNA gene sequences revealed that strain YIM B02567T belong to the genus *Chryseobacterium*, and was closely related to *Chryseobacterium piperi* CTMT and *Chryseobacterium soli* DSM 19298T. Whole genome sequencing indicated that the genome size was 4,774,612 bp and with a G+C content of 34.5 mol%. Values of the ANI and the dDDH between strain YIM B02567T and its closely related *Chryseobacterium* species were below 81.72% and 24.7%. Strain YIM B02567T contained menaquinone-6 as the sole isoprenoid quinone, anteiso-C15:0, iso-C17:1ω9c and iso-C17:0 3-OH as major fatty acids and phosphatidylethanolamine as major polar lipid. Based on the polyphasic analyses, strain YIM B02567T could be differentiated genotypically and phenotypically from recognized species of the genus *Chryseobacterium*. The isolate, therefore, represents a novel species, for which the name *Chryseobacterium paridis* sp. nov. is proposed. The type strain is YIM B02567T (= CGMCC 1.18657T).

**Keywords** *Chryseobacterium paridis* sp. nov. · Novel species · Polyphasic taxonomy · The root of **Paris polyphylla** Smith var. *yunnanensis*

**Abbreviations**

| GCM | The Global Catalogue of Microorganisms |
|-----|--------------------------------------|
| MK  | Menaquinone                           |
| NJ  | Neighbor-joining                      |
| ML  | Maximum-likelihood                    |
| AAI | Average amino acid identity           |
| ANI | Average nucleotide identity           |
| dDDH| Digital DNA–DNA hybridization         |
| PE  | Phosphatidylethanolamine              |
| AL  | Unidentified aminolipid               |
| GL  | Unidentified glycolipid               |
| L   | Unidentified lipid                    |

**Introduction**

The genus *Chryseobacterium* is a member of the family *Flavobacteriaceae* in the phylum *Bacteroidetes*. It was proposed by Vandamme et al. (1994) to separate six species of the genus *Flavobacterium*, based on the genotypic, biochemical and phenotypic characteristics of the organisms. At the time of writing, more than 100 valid published species of the genus *Chryseobacterium* have been reported (https://lpsn.dsmz.de/genus/chryseobacterium); many of these are abundant in diverse environments, including soil (Benmalek et al. 2010), water (Montero-Calasanz et al. 2013), plants (Du et al. 2015), rhizospheres (Park et al. 2006), raw milk (Hantsis-Zacharov and Halpern 2007), chicken (Kämpfer et al. 2014) and fish (Ilardi et al. 2009). Interestingly, several species of the genus *Chryseobacterium*, were isolated from plants or rhizospheres, hence this genus contains several rhizospheric species. Such as, *Chryseobacterium cucumeris* isolated from cucumber (*Cucumis sativus* L.) root (Jeong et al. 2017), *Chryseobacterium ginsengisoli* isolated from the rhizosphere of ginseng (Nguyen et al. 2013), and *Chryseobacterium ginsenosidimutans* isolated from soil of a *Rhus vernicifera*-cultivated field (Im et al. 2011). In this
study, we described a new species of the genus Chryseobacterium, designated YIM B02567\textsuperscript{T}, isolated from the root of Paris polyphylla var. yunnanensis.

Materials and methods

Bacterial isolation and maintenance

Healthy root samples of *P. polyphylla* var. *yunnanensis* were collected from Shilin in Yunnan province, southwest PR China. Samples were sterilized and pulverized before distribution on nutrient agar (NA) medium as described by Yang et al. (2016). After incubation at 28 °C for 2 weeks, different colonies were randomly selected and their 16S rRNA genes were PCR-amplified. Strain YIM B02567\textsuperscript{T} was selected as a putative novel species of the genus *Chryseobacterium* for further taxonomic characterizations. The purified strain was preserved both on NA slants at 4 °C and in 20% (v/v) glycercol at −80 °C for further use.

16S rRNA gene sequencing and phylogenetic analysis

Genomic DNA of strain YIM B02567\textsuperscript{T} was extracted using a genomic DNA extraction kit (Tiangen, China). The 16S rRNA gene was amplified by PCR using forward primer 27F (5′-AGA GTT TGA TCC TGG CT-3′) and reverse primer 1492R (5′-GTT TAC CTT GTT ACG ACT T-3′). Amplified products were purified and cloned into vector pClone007 (TsingKe, China). The 16S rRNA gene sequence (1536 bp) of strain YIM B02567\textsuperscript{T} was checked manually and submitted to the GenBank database. The similarities of 16S rRNA gene sequences between strain YIM B02567\textsuperscript{T} and closely related type strains were calculated using the EZBioCloud server (https://www.ezbiocloud.net/) (Yoon et al. 2017). The 16S rRNA gene sequences were aligned by using Clustal Omega (Sievers et al. 2011) and concatenating all alignments. Gblocks (Castresana 2000) was used to select the conserved blocks from the concatenation. The reconstruction of a ML tree was using IQ tree (Nguyen et al. 2015).

Morphology and physiology and biochemical analysis

Cell morphology was observed by scanning electron microscope after growth for 2 days in Reasoner’s 2A (R2A) medium at 30 °C. The Gram reaction was performed using 3% (w/v) KOH for cell lysis. The growth of the strain was assessed by incubating inoculated R2A plates in a bacteria culture box at 30 °C for 7 days. Growth was examined at different temperatures (low to 20 °C, up to 50 °C, at intervals of 5 °C) and NaCl concentrations (up to 5.0%, at intervals of 0.5%, w/v) for 7 days. The pH range for growth was tested between 4.0 and 10.0, at intervals of 1.0 pH unit in R2A broths prepared using the buffer system described by Nie et al. (2012). Catalase activity was determined from the production of gas bubbles on the addition of a drop of 3% (v/v) H\textsubscript{2}O\textsubscript{2}. Oxidase activity was detected using API oxidase reagent (bioMérieux) according to the manufacturer’s instructions. Carbon source utilization was calculated using the API 20NE and API ZYM kits (bioMérieux) according to the instructions provided by the manufacturers.

Chemotaxonomic characterization

The fatty acid profile, polar lipids and respiratory quinones of strain YIM B02567\textsuperscript{T} were analyzed in this study. To assess the fatty acids, strain YIM B02567\textsuperscript{T} were cultured on R2A agar plates at 30 °C for 2 days. After saponification
and methylation, fatty acids were extracted using a standard protocol and the Sherlock Microbial Identification (Sherlock version 6.1; MIDI database: TSBA6) according to the manufacturer’s instructions (Sasser 2001) and analyzed on Agilent 7890A gas chromatography apparatus. Respiratory quinones and polar lipids were extracted from freeze-dried cells using the method described by Collins et al. (1977). Subsequently, quinones were analyzed by a reversed-phase HPLC system (Agilent Technologies 1260 Infinity) with a C18 column (25 cm × 4.6 mm, 5 μm). Extracted total lipids from strain YIM B02567T were examined by a two-dimensional TLC procedure on silica gel G60 plates (Minnikin et al. 1984). For the presence of all lipids, TLC plates were sprayed with 5% molybdophosphoric acid. Besides, 0.2% ninhydrin was used to detect aminolipids, molybdenum blue spray reagent was used to detect phospholipids and α-naphthol reagent was used to detect glycolipids.

## Results and discussion

### Phylogenetic and whole-genome analysis

The 16S rRNA gene sequence analysis based on EzTaxon server revealed that strain YIM B02567T belonged to the genus *Chryseobacterium* and had highest gene sequence similarities to *C. soli* DSM 19298T (97.8%), *C. ginsenosidimutans* THG 15T (97.7%), *Chryseobacterium soldanellicola* DSM 17072T (97.5%) and *C. piperi* CTMT (97.4%). The NJ phylogenetic tree based on 16S rRNA gene sequences showed that strain YIM B02567T, *C. soli* and *C. piperi* formed a monophyletic clade (Fig. 1), but did not clustered with *C. ginsenosidimutans* and *C. soldanellicola*. This topology relationship was supported by the ML tree. (Fig. S3). Furthermore, a ML phylogenomic tree reconstructed using 1164 orthologous genes confirm that strain YIM B02567T is most closely with *C. piperi* CTMT (Fig. 2).

The draft genome of strain YIM B02567T contained 12 scaffolds, with a total length of 4,774,612 bp and the N50 length of 2,588,358 bp. The DNA G+C content of strain YIM B02567T was determined from the genome to be 34.5 mol%. The annotated result of YIM B02567T

![Diagram](image_url)
Genome contains 4236 genes, included 4153 protein-coding genes, 3 rRNA genes, 63 tRNA genes and 3 other RNA genes. The ANI values between strain YIM B02567T and its closely related strains C. piperi CTMT and C. soli DSM 19298T were 81.72% and 78.94%, respectively. ANI values between YIM B02567T and other species of Chryseobacterium are shown in Table S1. Strain YIM B02567T has AAI values ranging from 78.77% to 86.67% with the all reference genomes (Table S1). The ANI and AAI values were significantly lower than the widely accepted threshold for describing prokaryote species (95–96%; Kim et al. 2014; Konstantinidis and Tiedje 2005). The dDDH values of strain YIM B02567T to C. piperi CTMT and C. soli DSM 19298T were 24.7% and 22.2%, which were significantly lower than 70% similarity of the species defined threshold (Wayne et al. 1987). Therefore, according to the results of OGRIs (overall genome relatedness indices), strain YIM B02567T can represent a novel species of the genus Chryseobacterium.

Morphology, physiology and biochemical analysis

Cells of strain YIM B02567T were Gram-reaction-negative, aerobic, oxidase- and catalase-positive and rod-shaped (Fig. S1). Colonies on R2A agar were deep orange and smooth after incubation at 30 °C for 2 days. Strains were able to grow at temperatures ranging between 10 and 45 °C, pH 5.0–8.0 and in the presence of up to 2.0% (w/v) NaCl on R2A. Detail physiological and biochemical characteristics of the novel strain were summarized in the species description and compared to those of closely related strains in Table 1.

Chemotaxonomic characterization

The major cellular fatty acids of strain YIM B02567T were iso-C_{15:0} (41.8%), iso-C_{17:0} 3-OH (16.9%), iso-C_{17:1} ω9c (14.0%), Summed Feature 3 (C_{16:1} ω5c and/or C_{16:1} ω6c, 13.9%). Strain YIM B02567T showed a similar major fatty acid composition to the related type strains of Chryseobacterium species. However, some qualitative and quantitative differences in the fatty acid compositions were observed between the novel strain and the other closely related Chryseobacterium species (Table 2). The major polar lipids of strain YIM B02567T was phosphatidylethanolamine (PE). Three unidentified aminolipids (AL), five unidentified glycolipids (GL) and three unidentified lipids (L) were also detected (Fig. S2). The predominant sole respiratory ubiquinone was found to be MK-6, which is the typical ubiquinone of the genus Chryseobacterium.
**Taxonomic conclusion**

Based on morphological, physiological, and chemotaxonomic properties, and phylogenetic analysis, strain YIM B02567T could be considered a representative of a novel species belonging in the genus *Chryseobacterium*, for which the name *Chryseobacterium paridis* sp. nov. is proposed.

**Description of Chryseobacterium paridis** sp. nov.

*Chryseobacterium paridis* (pa’ri.dis. L. gen. n. *paridis of Paris*, a plant genus, from which the type strain was isolated).

Cells are Gram-reaction-negative, short rods. Colonies are deep orange, slimy and smooth on R2A after 2 days of incubation at 30 °C. Growth occurs at 10–45 °C (optimum, 30 °C), at pH 5.0–8.0 (optimum, pH 7.0) and in the presence of 0–2% NaCl (optimum, 0%). Catalase and oxidase activities are positive. Positive for hydrolysis of esculin and gelatin, but negative for reduction of nitrate to nitrite, indole production, fermentation of glucose, arginine dihydrolase, hydrolysis of urea and 4-nitrophenyl-β-d-galactopyranoside.

In Biolog GENIII microplates, positive for utilization of dextrin, d-maltose, d-trehalose, l-fucose, d-fructose, d-mannitol, glycerol, Tween 40, d-glucose-6-phosphate, d-fructose-6-phosphate, gelatin, glycyl-l-proline, l-alanine, l-arginine, l-aspartic acid, l-glutamic acid, l-serine, glucuronamidase, α-keto-glutaric acid, acetoacetic acid and propionic acid. In the API ZYM system, positive for alkaline phosphatase, esterase (C4), esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase; weakly positive for cystine arylamidase.

All strains were Gram-negative rods, catalase and oxidase positive. In API 20 NE and API ZYM kits, all strains were positive for the following characteristics: hydrolysis of esculin and gelatin; alkaline phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase. All strains were negative for the following characteristics: reduction of nitrate to nitrite, fermentation of glucose, lipase (C14), α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-mannosidase and α-fucosidase

+ positive, − negative; w weakly positive

**Table 1** Differential characteristics of YIM B02567T and related species of the genus Chryseobacterium

| Characteristics                                      | 1  | 2  | 3  | 4  | 5  |
|------------------------------------------------------|----|----|----|----|----|
| Optimum temperature (°C)                             | 28–30 | 20–30 | 28–30 | 25–30 | 25–30 |
| Range of temperature (°C)                            | 10–40 | 5–37 | 5–30 | 5–42 | 10–37 |
| Optimum pH                                           | 7.0 | 6.5–8.0 | 6.0–7.0 | 5.0 | 7.0 |
| Range of pH                                          | 6.0–9.0 | 6.0–10.0 | 5.0–9.0 | 5.0–7.0 | 5.5–10.0 |
| NaCl tolerance (%)                                    | 2 | 2 | 3 | 4 | 1 |
| Indole production                                    | − | + | − | − | − |
| Arginine dihydrolase                                 | − | − | − | − | + |
| Hydrolysis of urea                                    | − | + | + | − | + |
| 4-Nitrophenyl-β-d-galactopyranoside                   | − | + | − | − | − |
| Enzyme activity of:                                  |    |    |    |    |    |
| Esterase (C4)                                        | + | w | + | + | − |
| Cystine arylamidase                                  | w | w | + | − | − |
| Trypsin                                              | − | − | + | − | − |
| Naphthol-AS-BI-phosphohydrolase                      | − | + | + | + | + |
| α-glucosidase                                        | − | + | + | + | + |
| β-glucosidase                                        | − | − | − | − | + |
| N-acetyl-β-glucosaminidase                           | − | + | + | − | + |
| Utilization of:                                      |    |    |    |    |    |
| d-Glucose                                            | − | w | + | w | + |
| L-Arabinose                                           | − | − | − | w | + |
| d-Mannose                                            | − | w | + | w | + |
| d-Mannitol                                           | + | w | − | − | − |
| DNA G+C content (mol%)                                | 34.5 | 35.2 | 36.4 | 35.4 | 35.7 |

All strains were Gram-negative rods, catalase and oxidase positive. In API 20 NE and API ZYM kits, all strains were positive for the following characteristics: hydrolysis of esculin and gelatin; alkaline phosphatase, esterase lipase (C8), leucine arylamidase, valine arylamidase, acid phosphatase. All strains were negative for the following characteristics: reduction of nitrate to nitrite, fermentation of glucose, lipase (C14), α-chymotrypsin, α-galactosidase, β-galactosidase, β-glucuronidase, α-mannosidase and α-fucosidase

+ positive, − negative; w weakly positive

**Taxa:** 1 YIM B02567T; 2 *C. piperi* CTMT (Strahan et al. 2011); 3 *C. solii* DSM 19298T (Weon et al. 2008); 4 *C. soldanellicola* PSD1-4T (Park et al. 2006); 5 *C. ginsenosidimutans* THG 15T (Im et al. 2011)

*The DNA G+C contents were calculated based on their genome sequences in this study, except C. ginsenosidimutans THG 15T*
B02567T is MW911623. The whole-genome sequences accession number for the 16S rRNA gene of strain YIM Yunnan Province, southwest PR China. The GenBank of 

G + C content of the type strain is 34.5 mol% (genome). dylethanolamine is detected as major polar lipid. The DNA

Table 2  Cellular fatty acid composition of strains YIM B02567T and the type strains of related Chryseobacterium species

| Fatty acid | 1  | 2  | 3  | 4  | 5  |
|-----------|----|----|----|----|----|
| Saturated |    |    |    |    |    |
| C16:0     | 2.0| 1.1| 1.6| 1.4| –  |
| C16:0 3-OH| 1.7| 1.8| 1.3| 1.6| –  |
| Branched-chain |    |    |    |    |    |
| iso-C13:0 | Tr | 1.1| 1.0| 1.8| –  |
| iso-C15:0 | 41.8| 36.6| 36.5| 40.4| 50.3|
| anteiso-C15:0 | Tr | Tr | 2.6| 2.7| 3.8|
| iso-C17:1ω9c | 14.0| 22.0| 16.9| 12.2| 9.3|
| iso-C17:0 | Tr | Tr | 1.3| Tr | –  |
| Hydroxy  |    |    |    |    |    |
| iso-C15:0 3-OH | 3.5| 4.2| 2.8| 3.6| 5.2|
| iso-C16:0 3-OH | Tr | 1.8| 1.3| 1.6| –  |
| iso-C17:0 3-OH | 16.9| 17.9| 20.7| 19.8| 21.9|
| C17:0 2-OH | Tr | Tr | 1.1| Tr | –  |
| Summed feature 3 | 13.9| 12.6| 11.9| 11.8| 9.5|

Tr trace amount (< 1.0%), – not detected

Taxa: 1, YIM B02567T; 2, C. piperi CTM7; 3, C. soli JS6-6T; 4, C. soldanellicola PSD1-4T; 5, C. ginsenosidimutans THG 15T (Im et al. 2011). Data for columns 2–4 were taken from Strahan et al. (2011). Summed features represent groups of two or three fatty acids that cannot be separated using MIDI system. Summed feature 3, C16:1ω7c and/or C16:1ω6c

remaining tests in Biolog GENIII microplates and in the API ZYM system are negative. Only MK-6 is detected as the isoprenoid quinone. Major cellular fatty acids are anteiso-C15:0, iso-C17:1ω9c and iso-C17:0 3-OH. Phosphatidylethanolamine is detected as major polar lipid. The DNA G + C content of the type strain is 34.5 mol% (genome).

The type strain is YIM B02567T, isolated from a root of P. polyphylla var. yunnanensis collected from Shilin, Yunnan Province, southwest PR China. The GenBank accession number for the 16S rRNA gene of strain YIM B02567T is MW911623. The whole-genome sequences have been deposited at GenBank and GCM under accession JAENHK0000000000 and GCM60020044, respectively.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00203-021-02504-2.

Author contributions ZZ, C-JL, and X-WJ performed the experiments; ZZ and L-LY analyzed the data and wrote the manuscript; X-YZ guided the experiments and revised the manuscript.

Funding This research was supported by the National Natural Science Foundation of China (Grant Number: 32060003); Program for Excellent Young Talents, Yunnan University; as well as grants from the Major Science and Technology Projects of Yunnan Province (Digitalization, development and application of biotic resource, 202002AA100007).

Code availability Not applicable.

Declarations

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

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

Consent for publication The manuscript is submitted with the consent of all authors.

References

Benmalek Y, Cayol J-L, Bouanane NA, Hacene H, Fauque G, Fardeau M-L (2010) Chryseobacterium solincola sp. nov, isolated from soil. Int J Syst Evol Microbiol 60(8):1876–1880. https://doi.org/10.1099/ijs.0.008631-0

Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. Mol Biol Evol 17(4):540–552. https://doi.org/10.1093/oxfordjournals.molbev.a026334

Chun J, Oren A, Ventosa A, Christensen H, Arahal DR, da Costa MS, Rooney AP, Yi H, Xu X-W, Meyer SD, Trujillo ME (2018) Proposed minimal standards for the use of genome data for the taxonomy of prokaryotes. Int J Syst Evol Microbiol 68(1):461–466. https://doi.org/10.1099/ijsem.0.002516

Collins MD, Pirouz T, Goodfellow M, Minnikin DE (1977) Distribution of menaquinones in actinomycetes and corynebacteria. J Gen Microbiol 100(2):221–230. https://doi.org/10.1099/00221-287-100-2-221

Du J, Ngo HTT, Won K, Kim K-Y, Jin F-X, Yi T-H (2015) Chryseobacterium solani sp nov., isolated from field-grown eggplant rhizosphere soil. Int J Syst Evol Microbiol 65(8):2372–2377. https://doi.org/10.1099/ijsem.0.002566

Emms DM, Kelly S (2015) OrthoFinder: solving fundamental biases in whole genome comparisons dramatically improves orthogroup inference accuracy. Genome Biol 16(1):157. https://doi.org/10.1186/s13059-015-0721-2

Felsenstein J (1981) Evolutionary trees from DNA sequences: a maximum likelihood approach. J Mol Evol 17:368–376. https://doi.org/10.1007/BF01734359

Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791. https://doi.org/10.1111/j.1558-5646.1985.tb00420.x

Hanttsis-Zacharov E, Halpern M (2007) Chryseobacterium haifense sp nov., a psychrotolerant bacterium isolated from raw milk. Int J Syst Evol Microbiol 57(10):2344–2348

Ilardi P, Fernández J, Avendaño-Herrera R (2009) Chryseobacterium nosidimutans sp nov., isolated from diseased salmonid fish. J Syst Appl Microbiol 32(5):487–496. https://doi.org/10.1016/j.syapm.2008.12.007

Jain C, Rodriguez-R LM, Phillippy AM, Konstantinidis KT, Aluru S (2018) High throughput ANI analysis of 90K prokaryotic genomes reveals clear species boundaries. Nat Commun 9(1):5114. https://doi.org/10.1038/s41467-018-07641-9
Jeong J-J, Lee DW, Park B, Sang MK, Choi I-G, Kim KD (2017) *Chryseobacterium cucumeris* sp nov., an endophyte isolated from cucumber (*Cucumis sativus* L.), root, and emended description of *Chryseobacterium arthropaeae*. Int J Syst Evol Microbiol 67(3):610–616. https://doi.org/10.1099/ijsem.0.001670

Kämpfer P, Poppel MT, Wilharm G, Busse H-J, McIntyre JA, Gläser SP (2014) *Chryseobacterium gallinarum* sp nov., isolated from a chicken, and *Chryseobacterium contaminans* sp nov., isolated as a contaminant from a rhizosphere sample. Int J Syst Evol Microbiol 64(4):1419–1427. https://doi.org/10.1099/ijsem.0.058933-0

Kim M, Oh H-S, Park S-C, Chun J (2014) Towards a taxonomic coherence between average nucleotide identity and 16S rRNA gene sequence similarity for species demarcation of prokaryotes. Int J Syst Evol Microbiol 64(2):346–351. https://doi.org/10.1099/ijsem.0.059774-0

Kimura M (1980) A simple method for estimating evolutionary rates. Mol Biol Evol 32(1):268–274. https://doi.org/10.1093/molbev/32.1.268

Konstantinidis KT, Tiedje JM (2005) Towards a genome-based taxonomy for prokaryotes. J Bacteriol 187(18):6258–6264. https://doi.org/10.1128/JB.187.18.6258-6264.2005

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. Mol Biol Evol 35:1547–1549. https://doi.org/10.1093/molbev/msy096

Luo R, Liu B, Xie Y, Li Z, Huang W et al (2012) SOAPdenovo2: an empirically improved memory-efficient short-read de novo assembler. Gigascience 1(1):18. https://doi.org/10.1186/2047-217X-1-18

Meier-Kolthoff JP, Auch AF, Klenk H-P, Göker M (2013) Genome extraction of bacterial isoprenoid quinones and polar lipids. J Microbiol Methods 98(2):244–248. https://doi.org/10.1016/j.mimet.2013.06.004

Minnikin DE, O’Donnell AG, Goodfellow M, Alderson G, Athalye M, Schaal A, Parlett JH (1984) An integrated procedure for the extraction of bacterial isoprenoid quinones and polar lipids. J Microbiol Methods 2(5):233–241. https://doi.org/10.1016/0167-7012(84)90018-6

Montoro-Calasanz MDC, Göker M, Rohde M, Spröer C, Schumann P, Busse H-J, Schmid M, Tindall BJ, Klenk H-P, Camacho M (2013) *Chryseobacterium hispalense* sp nov., a plant-growth-promoting bacterium isolated from a rainwater pond in an olive plant nursery, and emended descriptions of *Chryseobacterium defloris*, *Chryseobacterium indolo* genes, *Chryseobacterium waujenue* and *Chryseobacterium gregarium*. Int J Syst Evol Microbiol 63:4386–4395. https://doi.org/10.1099/ijsem.0.052456-0

Nguyen N-L, Kim Y-J, Hoang VA, Yang D-C (2013) *Chryseobacte-rium ginsengisoli* sp nov., isolated from the rhizosphere of ginseng and emended description of *Chryseobacterium gleum*. Int J Syst Evol Microbiol 63(8):2975–2980. https://doi.org/10.1099/ijsem.0.045427-0

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Mol Biol Evol 32(1):268–274. https://doi.org/10.1093/molbev/msu300

Nie G-X, Ming H, Li S, Zhou E-M, Cheng J, Tang X, Feng H-G, Tang S-K, Li W-J (2012) *Amycolatopsis dongchuanensis* sp nov., an actinobacterium isolated from soil. Int J Syst Evol Microbiol 62(11):2650–2656. https://doi.org/10.1099/ijsem.0.038125-0

Park MS, Jung SR, Lee KH, Lee M-S, Do JO, Kim SB, Bae KS (2006) *Chryseobacterium soldanelllicola* sp nov. and *Chryseobacterium taenense* sp nov., isolated from roots of sand-dune plants. Int J Syst Evol Microbiol 56(2):433–438. https://doi.org/10.1099/ijsem.0.063825-0

Saitou N, Nei M (1987) The neighbor-joining method: a new method for reconstructing phylogenetic trees. Mol Biol Evol 4:406–425. https://doi.org/10.1093/oxfordjournals.molbev.a040454

Sasser M (2001) Identification of bacteria by gas chromatography of cellular fatty acids. Technical note 101. Microbial Inc, Newark

Seemann T (2014) Prokka: rapid prokaryotic genome annotation. Bioinformatics 30(14):2068–2069. https://doi.org/10.1093/bioinf/btu153

Shi W, Sun Q, Fan G, Hideaki S, Moriya O, Itoh T et al (2021) gcType: a high-quality type strain genome database for microbial phylogenetic and functional research. Nucleic Acids Res 49(D1):D694–D705. https://doi.org/10.1093/nar/gkaa957

Sievers F, Wilm A, Dineen D, Gibson TJ, Karplus K et al (2011) Fast, scalable generation of high-quality protein multiple sequence alignments using Clustal Omega. Mol Syst Biol 7:539. https://doi.org/10.1038/msb.2011.75

Strahman BL, Tailor KC, Batties AM, Hayes PS, Cicconi KM, Mason CT, Newman JD (2011) *Chryseobacterium piperi* sp nov., isolated from a freshwater creek. Int J Syst Evol Microbiol 61(9):2162–2166. https://doi.org/10.1099/ijsem.0.027805-0

Vandamme P, Bernardet JF, Segers P, Kerstens K, Holmes B (1994) New perspectives in the classification of the Flavobacteria: description of *Chryseobacterium gen. nov.*, *Bergeyella gen. nov.*, and *Emepobacter* nom. rev. Int J Syst Bacteriol 44:827–831. https://doi.org/10.1099/00270713-44-4-827

Wayne L, Brenner DJ, Colwell RR, Grimont PAD, Kandler O et al (1987) Report of the ad hoc committee on reconciliation of approaches to bacterial systematics. Int J Syst Bacteriol 37:463–464. https://doi.org/10.1099/00207713-37-4-463

Yang L-L, Chu X, Jiang Z, Xu L-H, Zhi X-Y (2016) *Oceanobacillus endoradicus* sp nov., an endophytic bacterial species isolated from the root of *Paris polyphylla Smith var. yun- nanensis*. Antonie van Leeuwenhoek 109(7):957–964. https://doi.org/10.1007/s10482-016-0695-4

Yoon S-H, Ha S-M, Kwon S, Lim J, Kim Y, Seo H, Chun J (2017) Introducing EzBioCloud: a taxonomically united database of 16S rRNA gene sequences and whole-genome assemblies. Int J Syst Evol Microbiol 67:1613–1617. https://doi.org/10.1099/ijsem.0.01755

Weon HY, Kim BY, Yoo SH, Kwon SW, Stackebrandt E, Go SJ (2008) *Chryseobacterium soli* sp nov. and *Chryseobacterium jejuense* sp nov. isolated from soil samples from Jeju Korea. Int J Syst Evol Microbiol 58(2):470–473. https://doi.org/10.1099/ijsem.0.05295-0

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