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# *Caballeronia mineralivorans* sp. nov., isolated from oak-*Scleroderma citrinum* mycorrhizosphere

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### ABSTRACT

Six bacterial strains were isolated from the oak-*Scleroderma citrinum* ectomycorrhizosphere in acidic and nutrient-poor forest soil for their high efficacy to weather minerals. Four of the six isolates, PML1(12)<sup>T</sup> and PML1(4), PML1(14) and PML1(16), were further characterized extensively. They were Gram negative, obligate aerobic, motile, non spore forming and rod-shaped. The major fatty acids of strain PML1(12)<sup>T</sup> were cyclo-C<sub>17:0</sub>, cyclo-C<sub>19:0-ω8c</sub>, C<sub>16:0</sub> and C<sub>18:1-ω7c</sub>. The GC content of the DNA was 60.8%. The 16S rRNA and GyrB analyses showed that the four PML strains formed a distinct phylogenetic lineage within the genus *Caballeronia*, most closely related to *Caballeronia udeis*. This result was confirmed by whole-genome phylogeny analyses done on strain PML1(12)<sup>T</sup>. The results of digital DNA–DNA relatedness further supported the separation of the new isolates from closely related species. Morphological, chemotaxonomic properties were also consistent with the description of the genus *Caballeronia*. It is therefore proposed that strains PML1(12)<sup>T</sup> and PML1(4), PML1(14) and PML1(16) be recognized as a novel species, for which the name *Caballeronia mineralivorans* sp. nov. is proposed. The type strain is PML1(12)<sup>T</sup> (= DSM 104028 and LMG 2991).

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*Scleroderma citrinum* is a widely distributed symbiotic fungal species in temperate forests associated with a broad range of tree species such as oak, beech or Norway spruce [4]. This fungal species has the ability to inhabit acidic and nutrient-poor soils, conditions that are commonly found in temperate forest ecosystems. *S. citrinum* belongs to the ectomycorrhizal fungal group, which is characterized by fungi having the ability to colonize the tree root system and to form mixed organs named ectomycorrhiza. Through this interface, mycorrhizal fungi improve the nutrition of the trees by providing them nutrients and water, in exchange of carbohydrates provided by the trees. Such association was demonstrated to modify the rhizosphere conditions leading to the definition of the mycorrhizosphere [19,21].

A wide range of bacterial taxa has been described as inhabitant of the mycorrhizosphere [5,9,15,20,28], but *Betaproteobacteria* have been shown to be dominant in acidic and nutrient-poor soils [27,28]. Cultivation-dependent and -independent analyses highlighted that among these *Betaproteobacteria*, most 16S rRNA gene sequences and isolates were assigned to the genus *Burkholderia sensu lato* (including *Burkholderia*, *Paraburkholderia*, *Caballeronia*

[25,27]. *Burkholderia sensu lato* is a common group of metabolically versatile Gram-negative bacteria. It is composed of species found both in environmental and clinical environments [7]. Multi-locus sequence typing identified that this group was clearly polyphyletic, leading to its proposed scission in two, and then three genera: i) the first one corresponding to the *Burkholderia cepacia* group, mainly composed of animal, human and plant pathogens [3]; ii) the second one regrouping environmental *Burkholderia* species known for their plant-growth promoting (PGPR) effect which has been named *Paraburkholderia* [11,22] and iii) the third one, *Caballeronia* was recently proposed to regroup species such as *Burkholderia glathei*, *Burkholderia grimmiae*, *Burkholderia megalochromosomata*, *Burkholderia jiangsuensis*, *Burkholderia sordicola*, *Burkholderia teluridis*, *Burkholderia terrestris*, *Burkholderia udeis* and *Burkholderia zhejiangensis* [10,14,34]. Environmental members of these three genera (*Burkholderia*, *Paraburkholderia* and *Caballeronia*) have been found in various natural or contaminated ecosystems, but recent small- to medium-scale biogeography analyses revealed that species from these genera were more represented in acidic soils than in neutral or alkaline soils [16,23,31]. This was especially true for *Caballeronia glathei*, *Caballeronia phenazinium*, *Caballeronia fungorum* and *Caballeronia terrae* [23].

In the frame of a study comparing the ability of bacterial strains isolated from *S. citrinum*-oak mycorrhizosphere and from

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**Table 1**  
Differential biochemical characteristics of all examined strains of species of the genus *Caballeronia*. 1: PML group (1a, PML1(4); 1b, PML1(12); 1c, PML1(14) and 1d, PML1(16)); 2: *Caballeronia udeis*; 3: *Caballeronia sordidicola*; 4: *Caballeronia choica*; 5: *Caballeronia telluris*; 6: *Caballeronia terrestris*; 7: *Caballeronia humi*; 8: *Caballeronia glathei*; 9: *Caballeronia zhejiangensis* [32]. The different symbols mean: +, positive; –, negative and w, positive with a weak signal. The data presented for the reference bacterial strains come from the literature. The absence of symbol (+, –, or w) means that the substrate was not tested.

Characteristic	1a	1b	1c	1d	2	3	4	5	6	7	8	9
Growth at												
37 °C	–	–	–	–	–	–	w	–	w	–	+	–
40 °C	–	–	–	–	–	–	–	–	–	–	–	–
pH=8	–	–	–	–	–	+	w	w	–	w	–	+
Nitrate reduction	–	–	–	–	–	–	+	+	+	–	–	+
β-galactosidase activity	+	–	+	+	–	–	–	+	–	–	–	w
Assimilation of												
Arabinose	+	+	+	+	–	–	w	+	+	–	w	+
Mannose	+	+	+	–	+	+	–	+	+	+	+	+
Mannitol	+	+	+	+	+	+	+	+	+	+	+	+
N-acetylglucosamine	+	+	+	–	+	+	+	+	+	+	+	+
Glucuronate	+	+	+	+	+	+	+	+	+	+	+	w
Citrate	+	+	+	+	+	+	–	–	+	+	+	+
Oxidation of												
Trehalose	+	–	–	–	+	+	–	–	–	+	–	–
N-Acetyl-D-glucosamine	+	+	+	–	+	+	+	+	–	+	w	+
α-D-Glucose	+	+	+	–	+	+	–	+	+	+	+	+
D-Mannose	+	+	+	–	+	+	–	+	+	+	+	+
D-Fructose	+	+	+	–	+	+	–	–	+	+	+	+
D-Galactose	+	+	+	–	+	+	–	+	+	+	+	+
L-Fucose	+	–	–	–	+	+	–	+	+	+	+	w
L-Rhamnose	+	+	+	–	+	+	–	+	+	+	+	w
D-Sorbitol	+	+	+	–	+	+	–	–	–	+	w	+
D-Mannitol	+	+	+	+	+	+	–	–	w	+	w	+
D-Arabitol	+	+	+	–	–	+	–	–	–	+	–	w
myo-Inositol	+	+	+	+	+	+	–	–	w	+	+	–
Glycerol	+	+	+	+	–	w	–	–	–	w	–	–
Adonitol	+	+	+	–	–	–	–	–	–	–	–	–
Xylitol	+	+	+	–	–	–	–	–	–	–	–	–
2,3 butanediol	–	–	–	+	+	+	–	–	–	–	+	–
D-Glucose 6 phosphate	+	+	+	+	+	+	–	w	–	+	–	–
Glycyl L-proline	–	–	–	–	+	+	–	–	–	+	+	–
L-Alanine	–	–	–	–	–	w	–	–	–	w	–	–
L-Aspartic acid	+	+	+	+	+	+	–	+	w	+	+	–
L-Glutamic acid	+	+	+	+	+	+	+	+	w	+	–	+
L-Histidine	–	–	–	+	w	+	–	w	w	+	+	–
L-Pyroglutamic acid	–	–	–	+	w	+	w	w	–	+	–	–
L-Phenylalanine	+	+	+	+	–	–	–	–	–	–	–	–
L-Serine	–	–	–	+	–	+	–	–	–	w	–	–
D-Galacturonic acid	+	+	+	+	+	+	–	–	+	+	+	+
L-Galactonic acid lactone	–	+	–	+	+	+	–	+	–	+	+	–
D-Gluconic acid	+	+	+	+	+	+	+	+	+	+	+	–
D-Glucuronic acid	+	+	+	+	+	+	–	+	+	+	+	+
Glucuronamide	–	–	–	+	–	–	–	–	+	w	+	–
Quinic acid	+	+	+	+	–	+	–	–	+	+	+	+
D-Saccharic acid	+	+	+	–	+	+	–	–	+	+	+	–
p-Hydroxyphenylacetyl acid	+	+	–	–	–	+	–	–	+	w	+	–
Methyl pyruvate	+	+	+	+	–	–	+	–	+	w	–	–
L-Lactic acid	+	+	+	–	+	+	+	+	–	+	+	–
Citric acid	+	+	+	+	–	+	–	–	–	+	+	–
α-Ketoglutaric acid	–	–	–	+	–	+	–	–	–	+	–	–
D Glucosaminic acid	+	+	+	+	–	–	–	–	–	–	–	–
Succinic acid	+	+	+	+	–	–	–	–	–	–	–	–
Bromosuccinic acid	+	+	+	+	–	–	–	–	+	w	–	–
Tween 40	+	+	+	+	–	–	–	–	–	w	–	–
γ-Aminobutyric acid	+	+	+	+	–	+	–	–	–	+	–	–
α-Hydroxybutyric acid	+	+	+	+	+	–	–	–	–	–	–	–
α-Ketobutyric acid	–	+	–	–	+	–	+	+	–	–	–	–
Propionic acid	–	–	–	–	+	+	–	–	–	+	–	–
Acetic acid	–	+	–	+	–	+	–	–	–	w	–	–
Formic acid	–	+	–	+	–	+	–	–	–	+	–	–

the surrounding bulk soil to weather minerals, effective mineral weathering bacterial strains were mainly encountered in the mycorrhizosphere [18,25]. Phylogenetic analyses based on the partial 16S rRNA gene sequences revealed that mineral weathering strains from the mycorrhizosphere or the bulk soil belonged to the newly proposed genus *Caballeronia* and presented the strongest homologies with members of the species *C. glathei*, *Caballeronia sordidicola*

and *Caballeronia udeis*. However, a complete sequencing of the 16S rRNA gene and of the *gyrB* gene revealed that the strain PML1(12)<sup>T</sup> was distinct from any known species of this genus. Among the effective mineral weathering isolates obtained by Uroz et al. [25], four were phenotypically and genotypically characterized and are presented in detail in this study.

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