Transfer of eleven species of the genus *Burkholderia* to the genus *Paraburkholderia* and proposal of *Caballeronia* gen. nov. to accommodate twelve species of the genera *Burkholderia* and *Paraburkholderia*

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It has been proposed to split the genus *Burkholderia* into two genera according to phylogenetic clustering: (1) a genus retaining this name and consisting mainly of animal and plant pathogens and (2) the genus *Paraburkholderia* including so-called environmental bacteria. The latter genus name has been validly published recently. During the period between the effective and valid publications of the genus name *Paraburkholderia*, 16 novel species of the genus *Burkholderia* were described, but only two of them can be classified as members of this genus based on the emended genus description. Analysis of traits and phylogenetic positions of the other 11 species shows that they belong to the genus *Paraburkholderia*, and we propose to transfer them to this genus. The reclassified species names are proposed as *Paraburkholderia dipogonis* comb. nov., *Paraburkholderia ginsengiterrae* comb. nov., *Paraburkholderia humisilvae* comb. nov., *Paraburkholderia insulsa* comb. nov., *Paraburkholderia kirstenboschensis* comb. nov., *Paraburkholderia metalliresistens* comb. nov., *Paraburkholderia monticola* comb. nov., *Paraburkholderia panaciterrae* comb. nov., *Paraburkholderia rhizosphaerae* comb. nov., *Paraburkholderia solisilvae* comb. nov. and *Paraburkholderia susongensis* comb. nov. The remaining three species are transferred to the new genus *Caballeronia* gen. nov. proposed to accommodate twelve species of the genera *Burkholderia* and *Paraburkholderia* forming a distinctive clade in phylogenetic trees. The new genus members are *Caballeronia choica* comb. nov., *Caballeronia cordobensis* comb. nov., *Caballeronia giathei* comb. nov., *Caballeronia grimmiae* comb. nov., *Caballeronia humi* comb. nov., *Caballeronia megalochromeosomatula* comb. nov., *Caballeronia jiangsuensis* comb. nov., *Caballeronia sordidicola* comb. nov., *Caballeronia telluris* comb. nov., *Caballeronia terrestris* comb. nov., *Caballeronia udeis* comb. nov., and *Caballeronia zhejiangensis* comb. nov.

The genus *Burkholderia* was proposed by Yabuuchi *et al.* (1992) to accommodate seven species of the genus *Pseudomonas* homology group II (Palleroni *et al*., 1973). *Burkholderia cepacia* comb. nov. was designated as the type species of the genus. The description of the genus *Burkholderia* was later emended to include three additional species, while *Burkholderia pickettii* and *Burkholderia solanacearum* were proposed to be removed from the genus (Gillis *et al*., 1995). The latter two species were transferred to a new genus, *Ralstonia*, with *Ralstonia pickettii* comb. nov. as the type species (Yabuuchi *et al*., 1995). More than 80 other species were described as belonging to the genus *Burkholderia* after its description had been emended, making the genus one of the most populous of the bacterial genera. However, the genus appeared to be polyphyletic and contained at least two phylogenetic clusters. One mainly consisted of animal and plant pathogenic bacteria, and the other included environmental bacteria isolated from soil and water, as well as plant-associated microorganisms, endophytes and legume nodulators. Based on the results of a phylogenetic study using 16S rRNA, recA, gyrB, rpoB and acdS gene sequences of different species of the genus *Burkholderia*, as well as comparing genome sequences of some of them, it was...
planned to describe the second group as a new genus, and even the genus name, Caballeronia, was proposed (Gyaneshwar et al., 2011). But eventually the authors of this multilocus sequence analysis study only declared in their publication that these two large groups might represent different genera and indicated that there were two other distinct lineages within the genus tree, consisting of one (Burkholderia andropogonis) and two (Burkholderia rhizoxinica and Burkholderia endofungorum) species, respectively, which might be considered as separate genera as well (Estrada-de los Santos et al., 2013). The main reason why the new genus or genera were not formally described appears to be the absence of distinctive phenotypic features among the different phylogenetic clades. The authors also mentioned the limited phylogenetic support for the description of a new genus at that time.

Therefore, it was suggested to use conserved sequence indels (CSIs) as molecular markers for the demarcation of the Burkholderia groups revealed by phylogenetic analysis (Sawana et al., 2014). Specific CSIs distinguishing the first group from other bacteria were found in the amino acid sequences of 4-hydroxybenzoate 3-monooxygenase, 6-phosphogluconate dehydrogenase, sarcosine oxidase alpha subunit, a putative lipoprotein, a periplasmic amino acid-binding protein and a putative lyase during a search for such molecular signatures among 45 species of the genus Burkholderia whose genomes had been sequenced. These markers are absent in the genomes of the species from the second (environmental) group, and this group is distinguished by CSIs in the amino acid sequences of an unnamed dehydrogenase and a LysR-family transcriptional regulator. On the basis of these results, as well as the data of phylogenetic analyses using concatenated sequences of 21 conserved proteins and 16S rRNA gene sequences of members of the genus Burkholderia, an emended description of this genus, limited to the species from the first group, was published (Sawana et al., 2014). The other 54 species, mainly environmental bacteria but also the phytopathogens B. andropogonis, B. rhizoxinica, and B. endofungorum, were proposed to be transferred to a new genus, Paraburkholderia (Sawana et al., 2014). Paraburkholderia graminis was proposed as the type species of the new genus (Sawana et al., 2014).

The suggestions to split the genus Burkholderia were criticized by some scientists who stated that the main purpose of the proposed changes was the separation of the pathogen group from that containing plant beneficial bacteria and bacteria that can be used in biocontrol and bioremediation, so that the latter group could be exploited without dealing with safety issues regarding human infections caused by members of this genus (Vandamme & Peeters, 2014). To address the safety concerns, a study of the pathogenic potential of plant-associated symbiotic species of the genus Burkholderia was conducted, resulting in the conclusion that it is highly unlikely that they can infect mammals (Angus et al., 2014), but the study results did not seem to be sufficiently convincing (Vandamme & Peeters, 2014). It was argued that strains of some species from the second group, such as strains of Burkholderia fungorum isolated from various human and veterinary clinical samples, might be opportunistic pathogens.

Nevertheless, the names of the genus Paraburkholderia and its species, at least 46 of them, have recently been validly published by including them on IJSEM validation lists nos. 164 and 165 (Oren & Garrity, 2015a, b). In the period between the effective and valid publications of these species names, 16 novel species of the genus Burkholderia were described. The 16S rRNA gene sequences of two of them, Burkholderia stagnalis and Burkholderia territorii, are most similar to the 16S rRNA gene sequence of Burkholderia glumae, and the nearest neighbours of these novel species in a phylogenetic tree based on concatenated sequences of seven housekeeping gene fragments are Burkholderia ubonensis and Burkholderia latens (De Smet et al., 2015). However, analysis of the taxonomic positions of the other 14 species shows that they need to be reconsidered in accordance with the reclassification of species of the genus Burkholderia proposed by Sawana et al. (2014).

Burkholderia cordobensis is closest to Paraburkholderia zhejiangensis in phylogenetic trees based on 16S rRNA gene sequences and sequences of the gyrB gene (Draghi et al., 2014). Strains of Burkholderia dipogonis have the highest level of 16S rRNA gene similarity to the type strain of Paraburkholderia phytofirmans, and the latter is also their nearest neighbour in a phylogenetic tree based on the alignment of the recA gene sequences (Sheu et al., 2015). The 16S rRNA gene sequences of Burkholderia ginsengiterrae, Burkholderia panaciterrae and Burkholderia insulsa are most similar to those of Paraburkholderia fungorum (Farh et al., 2015a; Rusch et al., 2015). Comparison of the 16S rRNA, recA and gyrB gene sequences showed that the closest relative of Burkholderia humisilvae, Burkholderia rhizospherae, and Burkholderia solisilvae is Paraburkholderia duizotrophica (Lee & Whang, 2015). Burkholderia jiangsuensis is placed in the same clade with Paraburkholderia grimmiae and Paraburkholderia zhejiangensis in phylogenetic trees based on the 16S rRNA, recA and gyrB gene sequences (Liu et al., 2014). The levels of similarity of the Burkholderia kurstenboschensis 16S rRNA gene sequence with the sequences of Paraburkholderia phytofirmans, Paraburkholderia fungorum, Paraburkholderia caledonica, Paraburkholderia bryophila, Paraburkholderia megapolitana and Paraburkholderia díworthii were shown to be ≥98.5% (Steenkamp et al., 2015). The nearest neighbour of this species in a phylogenetic tree reconstructed using concatenated 16S rRNA, atpD, recA and rpoB gene sequences was Paraburkholderia díworthii (Steenkamp et al., 2015). Phylogenetic analysis using 16S rRNA gene sequences showed that the closest relative of Burkholderia megalochromosomata is B. jiangsuensis, and both species were placed in a clade located near Paraburkholderia grimmiae and Paraburkholderia zhejiangensis (Baek et al., 2015a). The highest level of similarity of the Burkholderia metallirezistens 16S rRNA gene sequence was with that of Paraburkholderia tropica (Guo et al., 2015a).
Burkholderia monticola was placed near the Paraburkholderia sprentai/Paraburkholderia tuberum clade in a phylogenetic tree based on 16S rRNA gene sequences and in a dendrogram reconstructed using the average nucleotide identity data of whole-genome sequence comparisons (Baek et al., 2015b). In neighbour-joining and maximum likelihood phylogenetic trees, Burkholderia susongensis is positioned in the same clade with Burkholderia acidiphilus, which was transferred by Sawana et al. (2014) to the genus Paraburkholderia but the new name has not yet been validly published, and the clade is located near Paraburkholderia sprentai and Paraburkholderia tuberum (Gu et al., 2015).

The necessity of taxonomic repositioning of these 14 species described in 2014/2015 as species of the genus Burkholderia is confirmed by our results of the reconstruction of neighbour-joining and maximum likelihood phylogenetic trees based on the 16S rRNA gene sequences of species of the genera Burkholderia and Paraburkholderia (Figs 1 and S1, available in the online Supplementary Material). These species and the eight species of the genus Paraburkholderia with names effectively, but not validly, published, are located in the neighbourhood of the members of the genus Paraburkholderia in our trees. Multiple alignment of the sequences selected for inclusion into the tree’s dataset was conducted using ClustalW (Thompson et al., 1994) in the program BioEdit 7.1.3.0 (Hall, 1999) with manual editing of the alignment results. The phylogenetic trees were generated by the neighbour-joining method (Saitou & Nei, 1987) and the maximum-likelihood method (Felsenstein, 1981) using the software package MEGA 6.0 (Tamura et al., 2013). Evolutionary distances were calculated according to Kimura’s two-parameter model (Kimura, 1980), and the determination of the robustness of the tree by bootstrap analysis was based on 1000 random replicates (Felsenstein, 1985).

Gyaneshwar et al. (2011) mentioned an essential difference in the DNA G+C contents between species from the first and second Burkholderia groups. Expanded analysis of the DNA G+C values of species of the genus Burkholderia confirmed that the DNA G+C content of the first group (67.1 ±1.0 mol%) is higher than that of the second group (62.9 ±1.3 mol%), and the independent lineages of B. andropogonis (59.0 mol%) and B. rhizoxinica/B. endofungorum/ (60.7 mol%) (Estrada-de los Santos et al., 2013). Therefore, the DNA G+C content was included as a differentiating feature in the description of the genus Paraburkholderia and the emended description of the genus Burkholderia. According to the descriptions, the DNA G+C content of members of the genus Paraburkholderia ranges from 61.4 to 65.0 mol %, while the DNA G+C content of species of the genus Burkholderia is in the range from 65.7 to 68.5 mol% (Sawana et al., 2014). It should be mentioned that because B. andropogonis, B. rhizoxinica and B. endofungorum were transferred to the genus Paraburkholderia, the lowest level of the DNA G+C content for members of this genus appears to be less than 61.4 mol%. The G+C content of DNA of the P. andropogonis type strain is 58.9 mol% (Lopes-Santos et al., 2015).

The DNA G+C content values of all the species of the genus Burkholderia whose taxonomic positions we propose to be reconsidered, except B. panaxiterrae and B. ginsengiterrae, are in the range from 61.8 to 64.4 mol% (Table 1), corresponding to the description of the genus Paraburkholderia. The DNA G+C contents of B. panaxiterrae and B. ginsengiterrae are outside of the genus description range (59.4 and 66.0 mol%, respectively). However, Farh et al. (2015a), who described these species, considered their DNA G+C data ‘inconsistent’, possibly because the 16S rRNA, recA and gyrb gene sequences of B. panaxiterrae and B. ginsengiterrae are highly similar (99.4, 100 and 100% similarity, respectively), and the DNA–DNA hybridization values (about 58–59 % in both directions) also demonstrate a high degree of relatedness between these species. It is rather unusual that so closely related species have a more than 6 mol% difference in their DNA G+C contents.

Another distinguishing characteristic of the genus Paraburkholderia indicated in the genus description is that its members ‘are not associated with humans’ (Sawana et al., 2014). All 14 species under consideration were isolated from samples other than of human or other mammalian origin. Strains of 10 species were isolated from soils of different types, two species are legume-nodulating bacteria, one species was isolated from a marine sediment collected in an arsenic-rich hydrothermal area, and another one is a mineral-weathering bacterium isolated from a rock surface (Table 1). The diversity of the isolation sources once again demonstrates the versatility of these bacteria allowing them to occupy various ecological niches.

When considering all of the characteristics and phylogenetic positions of the 14 species of the genus Burkholderia whose descriptions were published or submitted for publication in the period between the effective publication of the description of the genus Paraburkholderia and the valid publication of this genus name, it would be reasonable to transfer all these species to the latter genus. However, the genus Burkholderia has two clearly separated clusters in both phylogenetic trees (Figs 1 and S1). One cluster (A) contains Paraburkholderia graminis, the type species of the genus, and 11 of the 14 species are placed in this clade, while three species are associated with the other cluster (B) flanked by Paraburkholderia sordidicola and Paraburkholderia zhejiangensis branches. Cluster B in particular includes Paraburkholderia glathei (basonym: Burkholderia glathei) and so-called B. glathei-like species which were considered to be a group forming a unique lineage in the genus Burkholderia (Lemair et al., 2012; Vandamme et al., 2013). This conclusion is also confirmed by the results of UPGMA clustering of whole-genome-sequenced species of the genus Burkholderia based on their average nucleotide identity similarities (Baek et al., 2015a). The polyphyletic nature of the genus Paraburkholderia was also mentioned by Sawana et al. (2014). Their analysis revealed two groups within Clade II (Paraburkholderia), Clade Ila and Clade IIb. Clade IIb included Paraburkholderia graminis and other species from the cluster A. Six CSIs in amino acid sequences of
New Paraburkholderia species combinations and Caballeronia gen. nov.

Fig. 1. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences, showing the positions of the type strains of the species of the genus *Burkholderia* whose descriptions were published or submitted for publication in the period between the effective and valid publication of the descriptions of the genus *Paraburkholderia* (names in bold type), the species of the genus *Burkholderia* whose new name combinations as species of the genus *Paraburkholderia* were effectively, but not validly, published (the validly published names are underlined), their close relatives and some other species of the genera...
We propose the name the group of bacteria forming this cluster as a new genus. Protein (group 1 glycosyl transferase, undecaprenyl-phosphate glucose phosphotransferase, putative flavin-binding monoxygenase-like protein and 4-hydroxyacetophenone monoxygenase (two in the latter) were shown to support the differentiation of this clade. Clade IIa consisted mainly of unclassified members of the genus *Burkholderia* due to a lack of genome sequencing data for many species of this genus at that time. There were 16 CSIs proposed as molecular markers specific to this clade (Sawana et al., 2014). Clade IIa in particular contained *Candidatus Burkilliocladius kirkii* clustered in a maximum-likelihood tree based on 16S rRNA gene sequences (Sawana et al., 2014) with the species present in cluster B as well. The genomes of strains of all species from this cluster have now been sequenced. Therefore, the specificity of the Clade IIa CSIs for cluster B was analysed using the approaches described by Sawana et al. (2014). It was found that CSIs in amino acid sequences of prepilin peptidase, 16S rRNA processing protein RimM and hypothetical proteins BYI23_A015260, BUI23_A002220 (cytochrome oxidase subunit I) and BYI23_A006130 (a gramicidin biosynthesis protein) can be used as molecular signatures to distinguish subunit I) and BYI23_A006130 (a gramicidin biosynthesis protein) can be used as molecular signatures to distinguish

We would like to mention that type strains of all the species of the genera *Paraburkholderia* and *Caballeronia* gen. nov. were isolated from environmental sources. In spite of this, retaining the statement 'The species are not associated with humans.' (Sawana et al., 2014) in the description of the genus *Paraburkholderia* would not be correct; several strains of *Paraburkholderia fungorum* were isolated from human clinical samples (Coenye et al., 2001; Gerrits et al., 2005). Such a statement should not be included into the description of the genus *Caballeronia* gen. nov. either; strains of the species *Paraburkholderia zhejiangensis* proposed to be transferred to this genus were also isolated from human clinical samples (Vandamme et al., 2013).

### Emended description of the genus *Paraburkholderia* Sawana et al. 2015

*Paraburkholderia* (Par.ta:burk.hol.de'ri.a. Gr. prep. para beside; N.L. fem. n. *Burkholderia* a genus name; N.L. fem. n. *Paraburkholderia* resembling the genus *Burkholderia*).

<table>
<thead>
<tr>
<th>Species</th>
<th>DNA G+C content (mol%)</th>
<th>Source of isolation</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>B. cordobensis</em></td>
<td>63.6</td>
<td>Agricultural soil</td>
<td>Dragh et al. (2014)</td>
</tr>
<tr>
<td><em>B. dipogonis</em></td>
<td>63.2</td>
<td>Nodules of <em>Dipogon lignosus</em></td>
<td>Sheu et al. (2015)</td>
</tr>
<tr>
<td><em>B. ginsengiterrae</em></td>
<td>66.0</td>
<td>Ginseng soil</td>
<td>Farh et al. (2015a)</td>
</tr>
<tr>
<td><em>B. humisilvae</em></td>
<td>62.8</td>
<td>Forest soil</td>
<td>Lee &amp; Whang (2015)</td>
</tr>
<tr>
<td><em>B. insulsa</em></td>
<td>62.0</td>
<td>Arsenic-rich marine sediment</td>
<td>Rusch et al. (2015)</td>
</tr>
<tr>
<td><em>B. jiangsuensis</em></td>
<td>62.6</td>
<td>Methyl parathion-contaminated soil</td>
<td>Liu et al. (2014)</td>
</tr>
<tr>
<td><em>B. kirstenboschensis</em></td>
<td>61.8</td>
<td>Nodules of <em>Virgilia oroboides</em></td>
<td>Steenkamp et al. (2015)</td>
</tr>
<tr>
<td><em>B. megalochromosomata</em></td>
<td>62.7</td>
<td>Grassland soil</td>
<td>Baek et al. (2015a)</td>
</tr>
<tr>
<td><em>B. mettalliresisintens</em></td>
<td>62.3±0.5</td>
<td>Metal-polluted soil</td>
<td>Guo et al. (2015a)</td>
</tr>
<tr>
<td><em>B. monticola</em></td>
<td>63.8</td>
<td>Mountain soil</td>
<td>Baek et al. (2015b)</td>
</tr>
<tr>
<td><em>B. panaciterrae</em></td>
<td>59.4</td>
<td>Ginseng soil</td>
<td>Farh et al. (2015a)</td>
</tr>
<tr>
<td><em>B. rhizosphaerae</em></td>
<td>64.4</td>
<td>Rhizosphere soil</td>
<td>Lee &amp; Whang (2015)</td>
</tr>
<tr>
<td><em>B. solstitial</em></td>
<td>61.6</td>
<td>Forest soil</td>
<td>Lee &amp; Whang (2015)</td>
</tr>
<tr>
<td><em>B. susongensis</em></td>
<td>63.5</td>
<td>Weathered surface of rock</td>
<td>Gu et al. (2015)</td>
</tr>
</tbody>
</table>

*Paraburkholderia* and *Burkholderia*. The sequence of *Ralstonia pickettii* ATCC 27511<sup>T</sup> was used as the outgroup. The GenBank accession numbers are shown in parentheses. Bootstrap values (>50 %) are given at branch points. Bar, 0.01 substitutions per nucleotide position.
Cells are Gram-stain-negative, straight or slightly curved, in some cases coccoid rods, with one or more polar flagella, occurring singly, in pairs or in clusters. The cell size varies from 0.4 to 1.2 µm in width and from 1.2 to 3.0 µm in length. The morphological and metabolic characteristics are similar in general to those of the genus *Burkholderia*. The DNA G+C content values range from 58.9 to 65 mol%.


The description is as provided by Lee & Whang (2015) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is Y-12T (=KACC 17601T=NBRC 109933T).

**Description of Paraburkholderia insula comb. nov.**

*Paraburkholderia insula* (in.sul’sa. L. fem. adj. *insula* unsalted, bland, boring; in reference to the unsurprising characteristics of the type strain).

Basonym: *Burkholderia insula* Rusch et al. 2015, 193.

The description is as provided by Rusch et al. (2015) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is PNG-AprilT (=DSM 28142T=LMG 28183T).

**Description of Paraburkholderia kirstenboschensis comb. nov.**

*Paraburkholderia kirstenboschensis* (kir.sten.bosch.en’sis. N. L. fem. adj. *kirstenboschensis* of Kirstenbosch, a botanical garden in South Africa, from where the type strain was isolated).


The description is as provided by Steenkamp et al. (2015) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is Kb15T (=LMG 28727T=SARC 695T).

**Description of Paraburkholderia metalliresistens comb. nov.**

*Paraburkholderia metalliresistens* (me.tel.li.re.sis’tens. L. n. *metallum* metal; L. part. adj. *resistens* resisting; N. L. part. adj. *metalliresistens* metal-resistant, referring to the ability of the bacterium to resist heavy metals).
Basonym: Burkholderia metallire sistens Guo et al. 2015b, 2777.

The description is as provided by Guo et al. (2015a) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is D414T (=CICC 10561T=DSM 26823T).

Description of Paraburkholderia monticola comb. nov.

Paraburkholderia monticola (mon.ti.co.la. L. n. mons, montis mountain; -cola from L. n. incola an inhabitant; N.L. fem. n. monticola mountain-dwelling).

Basonym: Burkholderia monticola Baek et al. 2015b, 508.

The description is as provided by Baek et al. (2015b) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is JC2948T (=JCM 19904T=KACC 17924T).

Description of Paraburkholderia panaciterrae comb. nov.

Paraburkholderia panaciterrae (pa.na.ci.ter’rae. N.L. n. Panax the name of the genus accommodating ginseng; L. n. terra soil; N.L. gen. n. panaciterrae of soil from a ginseng field).

Basonym: Burkholderia panaciterrae Farh et al. 2015b, 3764.

The description is as provided by Farh et al. (2015a) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is DCY85-1T (=KCTC 42055T=JCM 19889T).

Description of Paraburkholderia rhizosphaerae comb. nov.

Paraburkholderia rhizosphaerae (rhi.zo.sphae’rae. Gr. n. rhiza root; L. n. sphaera a ball, sphere; N.L. n. rhizosphaera rhizosphere; N.L. gen. n. rhizosphaerae of the rhizosphere).

Basonym: Burkholderia rhizosphaerae Lee & Whang 2015, 2991.

The description is as provided by Lee & Whang (2015) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is Y-47T (=KACC 17602T=NBRC 109934T).

Description of Paraburkholderia solisilvae comb. nov.

Paraburkholderia solisilvae (so.li.si’vae. L. n. solum soil; L. n. silva forest; N.L. gen. n. solisilvae of forest soil).

Basonym: Burkholderia solisilvae Lee & Whang 2015, 2991.

The description is as provided by Lee & Whang (2015) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is L226T (=KCTC 17603T=NBRC 109935T).

Description of Paraburkholderia susongensis comb. nov.

Paraburkholderia susongensis (su.song.en’sis. N.L. fem. adj. susongensis referring to Susong county, Anhui Province, PR China, where the organism was isolated).

Basonym: Burkholderia susongensis Gu et al. 2015, 1035.

The description is as provided by Gu et al. (2015) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the emended genus description.

The type strain is L226T (=CCTCC AB 2014142T=JCM 30231T).

Description of Caballeronia gen. nov.

Caballeronia (Ca.bal.le.ro’ni.a. N.L. fem. n. Caballeronia of Caballero, named after J. Caballero-Mellado, a Mexican microbiologist who pioneered many of the studies on the plant-associated bacteria).

Cells are Gram-stain-negative, ovoid or rod-shaped, non-spor-forming, occurring singly, in pairs or in chains. Some genus members are motile. The cell size varies from 0.2 to 1.5 µm in width and from 1.0 to 2.5 µm in length. Chemoorganotrophic; capable of utilizing a broad range of organic compounds as growth substrates. Grow on tryptone soy agar. Some species can grow on MacConkey agar. All members of the genus are mesophilic. Growth of some species is inhibited at 37 or 42°C. The growth pH range varies from 4.0 to 10.0. The predominant ubiquinone is Q-8. The major fatty acids are C18:1ω7c, summed feature 3 (C16:1ω7c and/or C16:1ω6c) and C16:0. The DNA G+C content values range from 59 to 65 mol%. The species form a distinctive clade between clades containing species of the genera...
Burkholderia and Paraburkholderia, respectively, in phylogenetic trees based on 16S rRNA gene sequences, and they lack the molecular signatures, conserved sequence indels (CSI), which are specific for the latter genera. The CSIs in amino acid sequences of prepilin peptidase, 16S rRNA processing protein RimM and hypothetical proteins BYI23_A015260, BU123_A002220 (cytochrome oxidase subunit I) and BYI23_A006130 (a gramicidin biosynthesis protein) described by Sawana et al. (2014) can be used as molecular markers for distinguishing members of the genus from other bacteria. The genus members were isolated from different types of soil, a wastewater-treatment system, a fungus and a moss. The type species is Caballeronia glathei.

**Description of Caballeronia glathei comb. nov.**

Caballeronia glathei (gla’the.i. N.L. gen. masc. n. glathei of Glathe, named after H. Glathe of Giessen, Germany).


The description is as provided by Zolg & Ottow (1975) and emended by Vandamme et al. (1997) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is N15$^T$ (=ATCC 29195$^T$=DSM 50014$^T$=LMG 14190$^T$).

**Description of Caballeronia choica comb. nov.**

Caballeronia choica (choi’ca. L. fem. adj. choica of earth).

Basonym: Burkholderia choica Vandamme et al. 2013, 4713.

The description is as provided by Vandamme et al. (2013) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is LMG 22940$^T$ (=CCUG 63063$^T$).

**Description of Caballeronia cordobensis comb. nov.**

Caballeronia cordobensis (cor.do.ben’sis. N.L. fem. adj. cordobensis pertaining to the Argentinian province of Córdoba, where the first strains were isolated).


The description is as provided by Draghi et al. (2014) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is MMP81$^T$ (=LMG 27620$^T$=CCUG 64368$^T$).

**Description of Caballeronia grimmiae comb. nov.**

Caballeronia grimmiae (grimm’i.ae. N.L. gen. n. Grimmia the scientific name of a genus of moss; N.L. gen. n. grimmiae of Grimmia, referring to the isolation of the type strain from the moss Grimmia montana).

Basonym: Burkholderia grimmiae Tian et al. 2013, 2111.


The description is as provided by Tian et al. (2013) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is R27$^T$ (=LMG 27580$^T$=DSM 25160$^T$).

**Description of Caballeronia humi comb. nov.**

Caballeronia humi (hu’mi. L. gen. n. humi from soil).

Basonym: Burkholderia humi Vandamme et al. 2013, 4712.


The description is as provided by Vandamme et al. (2013) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is LMG 22934$^T$ (=CCUG 63059$^T$).

**Description of Caballeronia jiangsuensis comb. nov.**

Caballeronia jiangsuensis (jiang.su.en’sis. N.L. fem. adj. jiangsuensis of Jiangsu, a province of PR China, where the type strain was isolated).


The description is as provided by Liu et al. (2014) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.
The type strain is MP-1<sup>T</sup> (=LMG 27927<sup>T</sup>=MCCC 1K00250<sup>T</sup>).

**Description of Caballeronia megalochromosomata** comb. nov.

*Caballeronia megalochromosomata* (me.ga.lo.chro.mo.so.ma.ta. Gr. adj. megas, megal large; N.L. neut. n. chromosoma chromosome; N.L. fem. adj. megalochromosomata having a large chromosome).

Basonym: *Burkholderia megalochromosomata* Baek et al. 2015a, 963.

The description is as provided by Baek et al. (2015a) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is JC2949<sup>T</sup> (=KACC 17925<sup>T</sup>=JCM 19905<sup>T</sup>).

**Description of Caballeronia sordidicola** comb. nov.

*Caballeronia sordidicola* (sor.di.di.co.la. N.L. n. sordida from *Phanerochaete sordida*, a species of white-rot fungus; L. suff. n. -cola inhabitant; N.L. masc. n. sordidicola inhabitant of *Phanerochaete sordida*).

Basonym: *Burkholderia sordidicola* Lim et al. 2003, 1635

Synonym: *Paraburkholderia sordidicola* (Lim et al. 2003)

Sawana et al. 2015a, 2020.

The description is as provided by Lim et al. (2003) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is KCTC 12081<sup>T</sup> (=JCM 11778<sup>T</sup>).

**Description of Caballeronia udeis** comb. nov.

*Caballeronia udeis* [u’d.e.is. N.L. gen. n. udeis (from Gr. gen. n. oudeos) from ground].


The description is as provided by Vandamme et al. (2013) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is LMG 27134<sup>T</sup> (=CCUG 63061<sup>T</sup>).

**Description of Caballeronia terrestris** comb. nov.

*Caballeronia terrestris* (ter.res’tris. L. fem. adj. terrestris of the earth).


The description is as provided by Vandamme et al. (2013) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is LMG 22937<sup>T</sup> (=CCUG 63062<sup>T</sup>).

**Description of Caballeronia zhejiangensis** comb. nov.

*Caballeronia zhejiangensis* (zhe.jiang.en’sis. N.L. fem. adj. zhejiangensis pertaining to Zhejiang, the province where the type strain was isolated).


Synonym: *Paraburkholderia zhejiangensis* (Lu et al. 2012)

Sawana et al. 2015b, 2779.

The description is as provided by Lu et al. (2012) with the following additional properties. The position in phylogenetic trees based on 16S rRNA gene sequences and the specificities of conserved sequence indels are in accordance with the genus description.

The type strain is OP-1<sup>T</sup> (=CCTCC AB 2010354<sup>T</sup>=DSM 28073<sup>T</sup>=LMG 27258<sup>T</sup>).

**References**


