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Strains from the *Burkholderia cepacia* Complex: Relationship to Opportunistic Pathogens[1]

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Abstract: Burkholderia cepacia-like organisms attract much interest from the agricultural industry as natural promoters of plant growth and biological control agents, and for bioremediation. Some of these organisms, however, cause life-threatening infections, particularly in cystic fibrosis patients for whom this multi-resistant bacterium is a major pathogen. The biodiversity of this group of bacteria is severely underestimated, and current identification procedures are inadequate. Presumed *B. cepacia* isolates belong to at least nine distinct genomic species (genomovars), referred to collectively as the *B. cepacia* complex. All these *B. cepacia* complex genomovars have been isolated from clinical and environmental sources. There are no phenotypic, genomic, or taxonomic grounds to differentiate environmental and clinical strains of the *B. cepacia* complex or to use the source of isolation to assess the safety of biopesticides containing members of the *B. cepacia* complex.

Key words: Burkholderia cepacia complex, cystic fibrosis, epidemiology, genomovar, strain typing.

Burkholderia cepacia is an extremely versatile organism that is truly considered both a friend and foe to humans (Govan et al., 2000). It is a genuinely ubiquitous organism with soil, water (including antiseptic and pharmaceutical solutions, and seawater), animals, plants, and humans as niches. Although originally known as a plant pathogen, it is now also recognized as a most useful organism with a range of biotechnological applications that include biocontrol, bioremediation, and plant-growth promotion. However, it simultaneously has become notorious as a naturally multi-resistant and life-threatening pathogen in immune-suppressed hosts such as cystic fibrosis patients and patients with chronic granulomatous disease (LiPuma, 1998; Speert, 2001).

Infections in humans and animals: The genus *Burkholderia* comprises several established human pathogens. Before the early 1980s, reports of human infections caused by *B. cepacia* were sporadic and generally restricted to hospitalized patients exposed to contaminated disinfectant and anesthetic solutions in which this highly adaptable saprophyte survives for long periods (LiPuma, 1998). A rising incidence, particularly in patients with cystic fibrosis, was noted during the early 1980s. Cystic fibrosis is the most common lethal inherited disease of Caucasian populations, with pulmonary infections as the major cause of morbidity and mortality. Infection or colonization by *B. cepacia* leads to different outcomes in different patients (Mahenthiralingam et al., 2001). However, a prime cause for concern is that pulmonary colonization reduces survival by 50% and that about one-third to one-half of the patients succumb to "cepacia syndrome," a rapidly fatal necrotizing pneumonia, sometimes accompanied by bacteremia (Govan and Deretic, 1996). During the 1980s and 1990s, several major outbreaks of *B. cepacia* infections caused numerous deaths in cystic fibrosis populations worldwide and new guidelines were issued to reduce the risk of *B. cepacia* acquisition (Govan and Deretic, 1996). More recently, serious outbreaks with fatalities have occurred in non-cystic fibrosis patients treated in intensive care units in Europe and North America (Holmes et al., 1999; Ledson et al., 1998).

There have been few reports of *B. cepacia* infection in veterinary medicine. *Burkholderia cepacia* has been reported in mixed culture in clinical specimens from horses with pneumonia and in specific-pathogen-free piglets, as the sole organism involved in a case of vegetative endocarditis in a horse, and as the causative agent of an epidemic outbreak of subclinical mastitis associated with infection in a large flock of milking sheep (Berriatua et al., 2001).

Biotechnological applications: Care and concern for the environment urge scientists, private firms, and legal authorities to develop biological alternatives to the present chemical controls in the agro-industry, thereby reducing environmental chemical pollution (Parke and Gurian-Sherman, 2001). The major reasons for the interest in bacterial biopesticides or bioremediation are to provide environmentally benign means of controlling pests, remove toxic and other dangerous chemicals from the environment, or use environment-friendly fertilizers. Control of plant diseases, insects, and nematodes by bacteria and fungi has been proposed as an alternative or supplement to chemical pesticides such as captan, thiram, and thiobendazole. Roots and rhizospheres of various economically important crops including corn, maize, rice, pea, sunflower, and radish can be colonized by *B. cepacia*-like organisms, some of which produce a variety of antimicrobial compounds that are active against soil pathogens (Govan and Vandamme, 1998; Parke and Gurian-Sherman, 2001). Using these *B. cepacia*-like organisms as seed inoculants or root dips for biological control of pathogens that cause rot of seeds or seedlings can increase crop yields significantly. In addition, in absence of soil pathogens, a significant growth-promoting effect has been reported.

The exceptional nutritional potential of some *B. ce-*

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pacia strains is also used in the bioremediation of hazardous waste sites and effluents. Carcinogenic or toxic products such as ethers present in gasoline, polycyclic aromatic compounds, and other constituents of crude oils and coal cause serious concerns whenever accidental spillage, improper disposal, transportation, or improper commercial usage occurs. Herbicides such as 2,4-dichlorophenoxyacetic acid or 2,4,5-trichlorophenoxyacetic acid (the principal component of Agent Orange) can efficiently be degraded by certain *B. cepacia* strains (Govan and Vandamme, 1998; Holmes et al., 1998).

Taxonomic history: Burkholderia cepacia was first described as *Pseudomonas cepacia* by Walter Burkholder in 1950 as the phytopathogen responsible for bacterial rot of onions (Burkholder, 1950). In their seminal taxonomic study published in the 1960s, Stanier and colleagues (Stanier et al., 1966) noted the extraordinary metabolic versatility of another novel pseudomonad, *P. multivorans*. This novel species was mainly isolated from soil and water samples. A few years later Ballard et al. (1970) reported on the synonymy between *P. cepacia* and *P. multivorans*. Nomenclatural priority was given to the former, as this was the oldest validly described species. The same year, Jonsson (1970) proposed the name *Pseudomonas kingii* for CDC group EO-1 (eugonic oxidizer group 1), an opportunistic human pathogen. Subsequent taxonomic analysis by Snell et al. (1972) and Samuels et al. (1973) again revealed that the novel organism was the same as *P. cepacia*.

The taxonomic heterogeneity of the genus *Pseudomonas* was revealed by the work of Palleroni et al. (1973) and led to the gradual dissection of the genus over the following decades (Kersterts et al., 1996). In 1992, *P. cepacia* and several other species of rRNA group II sensu Palleroni et al. were transferred to the new genus *Burkholderia* (Yabuuchi et al., 1992). During the past 10 years, the clinical and biotechnological interest in *B. cepacia*-like organisms led to the discovery and description of a multitude of novel species. The genus now contains 26 species: *Burkholderia andropogonis, B. ambifaria, B. anthina, B. caledonica, B. caribensis, B. caryophylli, B. cepacia* (genomovars I, III, and VI), *B. fungorum, B. gladioli, B. glathei, B. glumae, B. graminis, B. kururiensis, B. mallei, B. multivorans, B. phenazinium, B. plantarii, B. pseudomallei, B. pyrrocinia, B. sacchari, B. stabilis, B. thailandensis, B. ubonensis,* and *B. vietnamiensis*. In addition, several other named species, such as *B. vandii* and *B. cocovenenans,* were shown to represent existing species (Coenye et al., 1999, 2001d) (Table 1). Table 1 gives an overview of the currently known *Burkholderia* species and their typical isolation sources.

In the early 1990s the lack of sensitivity and specificity of various identification approaches for *B. cepacia* was reported (Kiska et al., 1996). Other studies described the presence of hybrid strains with characteristics intermediate between those of typical *B. cepacia* and *B. gladioli,* another well-known plant pathogen (Simpson et al., 1994). These data, together with the striking differences in clinical outcome, transmissibility, plant pathogenic or biocontrol properties, might all have concerned strain-specific differences but could also have pointed to an underlying taxonomic problem. A polyphasic taxonomic study was initiated in 1992 and included comparative 16S rDNA and *rec*A sequence analysis, DNA-DNA hybridization experiments, whole-cell protein and fatty acid analyses, various DNA fingerprinting methods including AFLP analysis, DNA base-ratio determination, and biochemical characterization. Polyphasic taxonomy arose in the early 1970s and aimed at the integration of different kinds of data and information on microorganisms. It comprises three major elements (Vandamme et al., 1996). First, species demarcation is based on DNA-DNA hybridization experiments as described by Wayne et al. (1987). Second, bacterial phylogeny can be deduced from comparative sequence analysis of conserved macromolecules such as 16S rDNA and *rec*A. Third, it recognizes and uses the value of these and various other methods for distinguishing and describing bacteria at different taxonomic levels (Vandamme et al., 1996).

TABLE 1. Current *Burkholderia* species and their sources.

Species	Sources
B. ambifaria (*B. cepacia* genomovar VII)	Soil, humans
B. anthina (*B. cepacia* genomovar VIII)	Soil, rhizosphere, humans, animals
B. andropogonis[a]	Plants
B. caledonica	Rhizosphere
B. caribensis	Soil
B. caryophylli	Plants
B. cepacia (genomovar I)	Plants, soil, water, humans
B. cepacia (genomovar III)	Plants, soil, humans, animals
B. cepacia (genomovar VI)	Humans, soil
B. fungorum	Fungi, root nodules, animals, humans
B. gladioli[b]	Plants, soil, humans
B. glathei	Soil
B. glumae	Plants
B. graminis	Soil, rhizosphere
B. kururiensis	Water
B. mallei	Animals
B. multivorans (*B. cepacia* genomovar II)	Plants, soil, humans
B. phenazinium	Soil
B. plantarii[c]	Plants
B. pseudomallei	Soil, humans
B. pyrrocinia (*B. cepacia* genomovar IX)	Soil, humans
B. sacchari	Soil
B. stabilis (*B. cepacia* genomovar IV)	Soil, humans
B. thailandensis	Soil, humans
B. ubonensis	Soil, humans
B. vietnamiensis (*B. cepacia* genomovar V)	Plants, soil, humans

[a] Including *Pseudomonas woodsii.*
[b] Including *B. cocovenenans* and *Pseudomonas antimicrobica.*
[c] Including *B. vandii.*

The initial polyphasic taxonomy study, published in 1997, dealt with some 80 *B. cepacia*-like organisms and revealed that *B. cepacia* isolates, cultured from clinical or environmental sites, belong to at least five distinct genomic species (genomovars), referred to collectively as the *B. cepacia* complex (Vandamme et al., 1997). Following identification of distinguishing phenotypic characteristics, the names *B. multivorans* and *B. stabilis* have been proposed for genomovars II and IV, respectively (Vandamme et al., 1997, 2000). Genomovar V was identified as *B. vietnamiensis,* an organism originally isolated from the rice rhizosphere. In the absence of differential biochemical tests to separate genomovar III from genomovar I (*B. cepacia*), the former genomic species remained unnamed.

In the same period, the cystic fibrosis community felt the need to coordinate its efforts to study this organism and the "International *B. cepacia* Working Group" was established in 1996 as ". . . a forum for clinicians and scientists interested in advancing knowledge of *B. cepacia* infection/colonization in persons with cystic fibrosis through the collegial exchange of information and promotion of coordinated approaches to research" (http://go.to/cepacia). The collaborative studies between members of this informal working group revealed an even more complex picture of the underestimated biodiversity of these bacteria. By now, up to 3,000 isolates tentatively classified as *B. cepacia* have been examined and new identification tools have been developed (Coenye et al., 2001d; LiPuma et al., 1999; Mahenthiralingam et al., 2000). These collaborative studies revealed the presence of various bacterial species that are regularly misidentified as *B. cepacia* (Coenye et al., 2000, 2002; McMenamin et al., 2000; Shelly et al., 2000). These misidentified organisms included well-known species such as *Pseudomonas aeruginosa, Stenotrophomonas maltophilia, Alcaligenes xylosoxidans,* and *Ralstonia pickettii* and more rare organisms like *Acinetobacter* species, *Bordetella hinzii, Comamonas testosteroni, Chryseobacterium* species, *Herbaspirillum* species, *Moraxella osloensis, Ralstonia gilardii, Ralstonia mannitolilytica, Rhizobium radiobacter, Xanthomonas* species, and several members of the family *Enterobacteriaceae.* In addition, several novel bacteria were identified and described among these isolates, including *Pandoraea sputorum, P. pnomenusa, P. pulmonicola,* unnamed *Pandoraea* species, *B. fungorum,* and *Inquilinus limosus* (Coenye et al., 2000, 2001b, 2002).

This polyphasic study also demonstrated additional heterogeneity within the *B. cepacia* complex, and four novel genomovars were delineated: *B. cepacia* genomovars VI through IX (Coenye et al., 2001a, 2001c; Vandamme et al., 2002). Again, a binomial name was assigned to those genomovars that could be differentiated phenotypically, namely *B. ambifaria* (genomovar VII) (Coenye et al., 2001a) and *B. anthina* (genomovar VIII) (Vandamme et al., 2002). Genomovar IX was recognized as the previously established *B. pyrrocinia* (Vandamme et al., 2002). *Burkholderia cepacia* genomovar VI could not be differentiated biochemically from *B. multivorans* (Coenye et al., 2001c).

All of these *B. cepacia* complex genomovars have been isolated from clinical and environmental sources. Taken together, these data confirmed that there are no phenotypic, genomic, or taxonomic grounds to differentiate environmental and clinical strains of the *B. cepacia* complex and that the source of isolation cannot be used to assess the safety of biopesticides containing members of the *B. cepacia* complex. However, the first reports on the human and plant pathogenic role and the biotechnological potential of these different genomovars suggested marked differences (Mahenthiralingam et al., 2000, 2001; Speert, 2001; Vandamme et al., 1997). It also became evident that it is necessary to establish the precise species status of *B. cepacia*-like organisms with biotechnological interest relative to *B. cepacia*-like organisms with life-threatening properties to provide regulatory bodies with usable criteria when confronted with the authorization of biotechnological application of strains (Jones et al., 2001; LiPuma et al., 2001). At present, if the principle of precaution prevails, strains with useful properties, which superficially resemble *B. cepacia* complex bacteria, can inappropriately be excluded from industrial or agricultural use.

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