

The history and distribution of nodulating *Paraburkholderia*, a potential inoculum for Fynbos forage species

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Abstract

Legumes in the Fynbos vegetation of the Western Cape of South Africa have emerged as candidates for domestication, particularly for their adaptation to acidic and infertile soils. However, South African rhizobia have been shown to be very diverse and unique, and a detailed understanding of them is essential to success in forage breeding programs that seek to exploit these “new” legumes. Symbionts of legumes in South Africa that belong to traditional rhizobial genera have been shown to have a unique origin for their symbiotic loci in comparison to members sampled from other regions of the world. Some of the legume tribes in the Fynbos have also been shown to associate predominantly with unique species in the Betaproteobacterial genus *Paraburkholderia*. The rhizobial members of this genus have two main centres of diversity, of which South Africa is one. In this centre, the legume hosts are principally from the Papilionoideae subfamily while hosts from the mimosoid clade (now in the Caesalpinioideae) are abundant in the South American centre. Not only do these rhizobia differ in terms of host, but their symbiotic loci also show separate origins. The dominance and uniqueness of the *Paraburkholderia* symbionts, in the context of indigenous South African legumes, makes understanding the history and factors that affect the distribution of this genus essential if successful adaptation and effective nodulation of these legumes in Agriculture are to be achieved globally.

KEYWORDS

Aspalathus, *Burkholderia*, *Mimosa*, *Paraburkholderia*, South Africa

1 | INTRODUCTION

Fynbos vegetation is adapted to growth in the sandy, low-nutrient (particularly, nitrogen and phosphorous) and acidic soils, characteristic of the Core Cape subregion (CCR) of South Africa (Howieson et al., 2013; MacAlister et al., 2018; Sprent et al., 2010). Plants in the CCR experience a mild or semi-Mediterranean climate with annual rainfall of 150 to 600 mm (Howieson et al., 2008). In this region, Leguminosae contributes about 10% to the total number of endemic species (Goldblatt & Manning, 2002). In fact, this region represents a notable area of legume endemism or leguminochorion sensu Trytsman et al. (2016) where the dominant taxa are the tribes

Crotalariaeae, Podalyrieae, Indigoferae and Psoraleae (subfamily Papilionoideae; Dlodlu et al., 2018), with several genera restricted to the region (Sprent et al., 2010).

Because of their role in nitrogen fixation, legumes are thought to be an important component of CCR ecosystems (Lemaire et al., 2015; Sprent et al., 2013). Nitrogen fixation is a consequence of the symbiotic relationship between legumes and particular soil bacteria (referred to as rhizobia) (Poole et al., 2018). This symbiosis ultimately results in the formation of root or stem nodules within which the bacterium converts atmospheric nitrogen into ammonia, and that the legume can then use for synthesizing amino acids (Poole et al., 2018). The rhizobium–legume symbiosis is widely regarded to

have positive effects on soil fertility by improving access to essential nutrients such as nitrogen (Raklami et al., 2019; Vessey, 2003). Sprent (2009) reported only one record of a legume (*Schotia afra*) from this region that does not nodulate or engage in the nitrogen-fixing symbiosis.

Previous studies showed that legumes indigenous to the CCR can interact with diverse rhizobial genera, although strains from the bacterial genera *Paraburkholderia* and *Mesorhizobium* are most frequently encountered across studies (Dludlu et al., 2018; Gerding et al., 2013; Hassen et al., 2012; Kanu & Dakora, 2012; Lemaire et al., 2015; Sprent et al., 2010; Yates et al., 2007). The same pattern generally also holds true for those CCR legumes that are increasingly receiving attention in agriculture (Dludlu et al., 2018; Lemaire et al., 2015). These include *Aspalathus linearis* (tribe Crotalariaeae) used for the production of Rooibos tea (van Wyk, 2005) and other species used as forage legumes (e.g., *Rhynchosia* in the tribe Phaseoleae, and *Lessertia* in the tribe Galegeae) (Garau et al., 2009; Sprent et al., 2010). However, certain tribes appear to have more specific associations, e.g., Podalyrieae, containing the Honeybush tea genus *Cyclopia*, has a specific affinity for *Paraburkholderia* symbionts and Psoraleeae for *Mesorhizobium* (Dludlu et al., 2018; Elliott, Chen, Bontemps, et al., 2007; Sprent et al., 2010).

Closely related CCR legumes may differ widely with respect to their rhizobial affinities. For example, in the economically important tribe Crotalariaeae, the so-called “Cape” clade genera *Aspalathus* and *Lebeckia* (Boatwright et al., 2008; Le Roux & van Wyk, 2012) can associate with *Paraburkholderia* and alpha-rhizobia (Ardley et al., 2013; De Meyer, Cnockaert, Ardley, Maker, et al., 2013; De Meyer et al., 2014; Howieson et al., 2013), the genus *Crotalaria* (in the correspondingly named clade) can associate with *Methylobacterium nodulans* (Jourand et al., 2004; Sy et al., 2001), and the “*Lotononis*” clade genus, *Listia* (Boatwright et al., 2011), can associate with rhizobia from unique lineages of *Methylobacterium* sensu lato (Green & Ardley, 2018; Jaftha et al., 2002; Yates et al., 2007). The latter lineages include rhizobia that were initially described as species of *Methylobacterium* (Jaftha et al., 2002; Yates et al., 2007) and *Microvirga* (Ardley et al., 2013), but their taxonomy is currently being revised (Green & Ardley, 2018).

In this study, we aim to provide relevant information on the genus *Paraburkholderia* as it has been proven to contain unique rhizobial members that have a dominant association with legumes from the CCR in South Africa. Successful establishment of this plant-bacterium interaction could prove necessary when trying to establish CCR endemic legumes in Australia and other Mediterranean regions for use as forage crops. To that end, we discuss aspects of the taxonomy of *Paraburkholderia* (as the taxon has recently undergone major taxonomic revision), and its interaction with hosts from the subfamilies Papilionoideae and Caesalpinioideae, specifically those in the latter as there is much more information available for this interaction as opposed to what is known for the papilionoid association. We also discuss the specificity between *Paraburkholderia* and their hosts and what is known regarding the factors potentially affecting the distribution of these rhizobia, as such information could be important

for initiatives involving the establishment of particular legumes in non-native locations.

2 | The Genus *Paraburkholderia*

Soon after the turn of the century, the first rhizobia belonging to the class Betaproteobacteria were reported by two research groups (Chen et al., 2001; Moulin et al., 2001) and confirmation of the nodulation efficacy of these bacteria was provided in several subsequent studies (Chen, de Faria, et al., 2005; Chen, James, et al., 2005; Chen et al., 2001; Elliott, Chen, Bontemps, et al., 2007; Elliott, Chen, Chou, et al., 2007). Until the discovery of these bacteria, all rhizobia were thought to reside in the Alphaproteobacteria (Barrett & Parker, 2006). As a result, the informal terms ‘alpha- and beta-rhizobia’ were introduced to refer to the root-nodulating bacteria from the two classes (Moulin et al., 2001; Sprent et al., 2010). Also, the taxonomy of these first members of the beta-rhizobia have since been resolved. The *Ralstonia taiwanensis* isolates reported by Chen et al. (2001) were moved to the genus *Cupriavidus* (Vandamme & Coenye, 2004), while the *Burkholderia* species isolated by Moulin et al. (2001) now reside in *Paraburkholderia* (Sawana et al., 2014). Additionally, with the move of *Paraburkholderia symbiotica* to the novel genus *Trinickia* (Estrada-de los Santos et al., 2018), a total of three genera from the Betaproteobacteria are now known to contain rhizobia (Paulitsch et al., 2019).

The genus *Paraburkholderia* is part of the larger *Burkholderia* sensu lato, which is a phylogenetically diverse assemblage that includes human, animal and plant pathogens (Beukes et al., 2017; Estrada-de los Santos et al., 2016, 2018). However, the majority of species in this wider taxon have no apparent pathogenic abilities and many possess beneficial properties while being associated with plants and certain environmental niches (Paulitsch et al., 2019; Table 1). The latter bacterial species were referred to as the PBE [“plant-beneficial-environmental”] (Suárez-Moreno et al., 2012) group, which also included the beta-rhizobial species *B. tuberum* and *B. phymatum*. Given this PBE group’s phylogenetic support (Estrada-de los Santos et al., 2016; Suárez-Moreno et al., 2012), it was formally recognized as a distinct taxon, separate from *Burkholderia* sensu stricto, and moved to a new genus. This transfer initially caused some confusion (Estrada-de los Santos et al., 2016), as Gyaneshwar et al. (2011) proposed the name ‘*Caballeronia*’ for this group, while Sawana et al. (2014) proposed ‘*Paraburkholderia*’. Nevertheless, most PBE species are now accommodated in *Paraburkholderia* (Table 1). It should also be noted that, due to their former taxonomic affiliation with pathogens, application of *Paraburkholderia* in agriculture remains somewhat controversial (Angus et al., 2014; Estrada-de los Santos et al., 2016; Mannaa et al., 2019), although various studies have highlighted the improbability of these bacteria in causing opportunistic infections in mammals (Angus et al., 2014; Estrada-de los Santos et al., 2016).

Four other phylogenetic lineages within the broader *Burkholderia* sensu lato were proposed to represent distinct genera (Beukes et al., 2017; de Castro Pires et al., 2018; Dobritsa & Samadpour, 2016;

TABLE 1 The diversity of *Paraburkholderia* species

Species ^a	Type strain	Source, geographic origin of type strain	Host ^{c,d}	Notable properties ^e	Reference
<i>P. acidipaludis</i>	SA33 ^T	Endophyte, Vietnam	<i>Eleocharis dulcis</i>	Possible diazotroph, aluminium tolerant	Aizawa et al., 2010
<i>P. aromaticivorans</i>	BN5 ^T	Gasoline-contaminated soil, South Korea	N/A	Degradation of aromatic hydrocarbon, diazotroph	Lee & Jeon, 2018; Estrada-de los Santos et al., 2018
<i>P. aspalathi</i>	VG1C ^T	Endophyte, South Africa	<i>Aspalathus abietina</i>	Root nodule endophyte (no <i>nod</i> or <i>fix</i> loci)	Mavengere et al., 2014; Estrada-de los Santos et al., 2018
<i>P. azotifigens</i>	NF2-5-3 ^T	Paddy soil, South Korea	N/A	Diazotroph	Choi & Im, 2018
<i>P. bannensis</i>	E25 ^T	Endophyte, Thailand	<i>Panicum repens</i>	Acid-neutralizing, possible diazotroph	Aizawa et al., 2011
<i>P. bryophila</i>	1S18 ^T	Moss gametophytes, Germany	<i>Sphagnum rubellum</i>	Antifungal and plant growth-promoting abilities	Vandamme et al., 2007
<i>P. caballeronis</i> ⁱ	TNe-841 ^T	Tomato rhizosphere, Mexico	<i>Lycopersicon esculentum</i>	Diazotroph, degradation of benzene, plant growth promoter	Caballero-Mellado et al., 2007; Martínez-Aguilar et al., 2013; Rojas-Rojas et al., 2017
<i>P. caffeinilytica</i>	CF1 ^T	Tea plantation soil, China	N/A	Growth on caffeine	Gao, Yuan, et al., 2016
' <i>P. caffeinitolerans</i> '	CF3 ^T	Tea plantation soil, China	N/A	Growth on caffeine	Gao, Zhao, et al., 2016
<i>P. caledonica</i>	W50D ^T	Rhizosphere, UK	N/A	Plant growth promoter	Coenye et al., 2001; Onofre-Lemus et al., 2009
<i>P. caribensis</i>	MWAP64 ^T	Vertisol, Martinique	N/A	Nodulator, plant growth promoter	Achouak et al., 1999; Chen et al., 2003; Onofre-Lemus et al., 2009
<i>P. caseinilytica</i>	HM451 ^T	Forest soil, China	N/A	Cassein dissolving	Gao et al., 2018
<i>P. denitrificans</i>	KIS30-44 ^T	Forest soil, Korea	N/A	Reduces nitrate to nitrogen gas	Lee et al., 2012
<i>P. diazotrophica</i>	JPY461 ^T	Root nodules, Brazil	<i>Mimosa candollei</i>	Nodulator	Sheu et al., 2013
<i>P. dilworthii</i>	WSM3556 ^T	Root nodules, South Africa	<i>Lebeckia ambigua</i>	Nodulator	De Meyer et al., 2014
<i>P. dinghuensis</i>	DHOA04 ^T	Forest soil, China	N/A	N	Fu et al., 2019
<i>P. dipogonis</i>	ICMP 19430 ^T	Root nodules, New Zealand and Australia	<i>Dipogon lignosus</i>	Nodulator	Sheu et al., 2015
' <i>P. dokdonella</i> '	DCR-13 ^T	Plant roots, South Korea	<i>Campunula takesimana</i>	Possible endophyte	Jung et al., 2019
<i>P. eburnea</i>	RR11 ^T	Peat soil, Russia	N/A	Plant growth promoter and can solubilize silica	Kang et al., 2014; Kang et al., 2017
<i>P. ferrariae</i>	FeGI01 ^T	Iron ore, Brazil	N/A	Solubilization of phosphatic minerals, possible diazotroph	Valverde et al., 2006; Martínez-Aguilar et al., 2008
<i>P. flava</i>	LD6 ^T	Forest soil, South Korea	N/A	N	Trinh & Kim, 2020
<i>P. fungorum</i>	Croize P763-2 ^T	Endophyte, France	<i>Phanerochaete chrysosporium</i>	Diazotroph, nodulator, plant growth promoter	Coenye et al., 2001; Ferreira et al., 2012; Onofre-Lemus et al., 2009; da Silva et al., 2012
<i>P. fynbosensis</i>	WSM4178 ^T	Root nodules, South Africa	<i>Lebeckia ambigua</i>	Nodule endophyte	De Meyer et al., 2018

(Continues)

TABLE 1 (Continued)

Species ^a	Type strain	Source, geographic origin of type strain	Host ^{c,d}	Notable properties ^e	Reference
<i>P. ginsengisoli</i>	KMY03 ^T	Ginseng field, South Korea	N/A	Production of β-glucosidase	Kim et al., 2006
<i>P. ginsengiterrae</i>	DCY85 ^T	Ginseng field, South Korea	N/A	Antagonist of <i>Cylindrocarpon destructans</i>	Farh et al., 2015
<i>P. graminis</i>	C4D1M ^T	Maize root system, France	N/A	Plant growth promoter	Viallard et al., 1998; Onofre-Lemus et al., 2009
' <i>P. guartelaensis</i> '	CNPS0 3008 ^T	Root nodules, Brazil	<i>Mimosa gymnas</i>	Nodulator	Paulitsch et al., 2019
<i>P. heleia</i>	SA41 ^T	Endophyte, Vietnam	<i>Eleocharis dulcis</i>	Diazotroph	Aizawa et al., 2010
<i>P. hiiakae</i>	I2 ^T	Volcanic soils, Hawai'i	N/A	Oxidization of carbon monoxide	Weber & King, 2017
<i>P. hospita</i>	LMG 20598 ^T	Agricultural soil, Belgium	N/A	Degradation of 2,4-dichloro-phenoxyacetic acid	Goris et al., 2002
<i>P. humisilvae</i>	Y-12 ^T	Forest soil, South Korea	N/A	N	Lee & Whang, 2015
<i>P. insulsa</i>	PNG-April ^T	Sediment, Papua New Guinea	N/A	Arsenic tolerance, diazotroph	Rusch et al., 2015
<i>P. jirisanensis</i>	JRM2-1 ^T	Forest soil, South Korea	N/A	N	Kim et al., 2016
<i>P. kirstenboschensis</i>	Kb15 ^T	Root nodules, South Africa	Several papilionoids native to South Africa	Nodulator	Steenkamp et al., 2015
<i>P. kururiensis</i>	KP23 ^T	TCE polluted aquifer, Japan	N/A	Degradation of trichloroethylene, diazotroph, plant growth promoter	Zhang et al., 2000; Estrada-de Los Santos et al., 2001; Onofre-Lemus et al., 2009
' <i>P. lacunae</i> '	S27 ^T	Soil near a pond, South Korea	N/A	N	Feng et al., 2019
<i>P. madseniana</i>	RP11 ^T	Forest soil, USA	N/A	Can degrade phenolic acid	Wilhelm et al., 2020
<i>P. megapolitana</i>	A3 ^T	Moss gametophytes, Germany	<i>Aulacomnium palustre</i>	Antifungal and plant growth-promoting abilities	Vandamme et al., 2007
<i>P. metalliresistens</i>	D414 ^T	Heavy metal polluted soil, China	N/A	Resistant to heavy metals, plant growth promoter	Guo et al., 2015
<i>P. metrosideri</i>	DNBP6-1 ^T	Volcanic soil, Hawai'i	N/A	Oxidization of carbon monoxide	Weber & King, 2017
<i>P. mimosarum</i>	PAS44 ^T	Root nodules, Taiwan	<i>Mimosa pigra</i>	Nodulator	Chen et al., 2006
<i>P. monticola</i>	JC2948 ^T	Mountain soil, South Korea	N/A	Can potentially oxidize carbon monoxide	Baek et al., 2015; Sokolova et al., 2017
<i>P. nodosa</i>	Br3437 ^T	Root nodules, Brazil	<i>Mimosa scabrella</i>	Nodulator	Chen et al., 2007
<i>P. oxyphila</i>	OX-01 ^T	Forest soil, Japan	N/A	Conversion of (+)-catechin into taxifolin	Otsuka et al., 2011
<i>P. pallida</i>	7MH5 ^T	Forest soil, China	N/A	N	Xiao et al., 2019
<i>P. pallidirosea</i>	DHOK13 ^T	Forest soil, China	N/A	N	Lv et al., 2016

(Continues)

TABLE 1 (Continued)

Estrada-de los Santos et al., 2016, 2018; Lopes-Santos et al., 2017).

Species ^a	Type strain	Source, geographic origin of type strain	Host ^{c,d}	Notable properties ^e	Reference
' <i>P. panacihumi</i> '	DCY115 ^T	Ginseng field, South Korea	N/A	Plant growth promotion, antagonistic activity against ginseng root rot fungi	Huo et al., 2018
<i>P. paradisi</i>	WA ^T	Volcanic soils, Hawai'i	N/A	Oxidization of carbon monoxide	Weber & King, 2017
<i>P. peleae</i>	PP52-1 ^T	Volcanic soils, Hawai'i	N/A	Oxidization of carbon monoxide	Weber & King, 2017
<i>P. phenazinium</i>	ATCC33666 ^T	Threonine enriched soil	N/A	Production of phenazine and iodinin	Viallard et al., 1998; Mavrodi et al., 2001
<i>P. phenoliruptrix</i> ^g	AC1100 ^T	Contaminated chemostat, USA	N/A	Degradation of xenobiotics, plant growth promoter, nodulator	Coenye et al., 2004; Chen, de Faria, et al., 2005; Onofre-Lemus et al., 2009; Zuleta et al., 2014
<i>P. phosphatilytica</i>	7QSK02 ^T	Forest soil, China	N/A	Plant growth promoter	Gao et al., 2019
<i>P. phymatum</i> ^f	STM815 ^T	Root nodules, French Guiana	<i>Mimosa</i> spp.	Nodulator, diazotroph, plant growth promoter	Vandamme et al., 2002; Elliott, Chen, Chou, et al., 2007; Onofre-Lemus et al., 2009; Mishra et al., 2012; Moulin et al., 2014
<i>P. phytofirmans</i>	PsJN ^T	Root endophyte, Canada	<i>Allium cepa</i>	Plant growth promoter	Sessitsch et al., 2005; Onofre-Lemus et al., 2009
<i>P. piptadeniae</i>	STM7183 ^T	Root nodules, Brazil	<i>Piptadenia gonoacantha</i>	Nodulator	Bournaud et al., 2017
<i>P. rhizosphaerae</i>	WR43 ^T	Rhizosphere soil, South Korea	N/A	N	Lee & Whang, 2015
<i>P. rhynchosiae</i>	WSM3937 ^T	Root nodules, South Africa	<i>Rhynchosia ferulifolia</i>	Nodulator	De Meyer, Cnockaert, Ardley, Trengove, et al., 2013
<i>P. ribeironis</i>	STM7296 ^T	Root nodules, Brazil	<i>Piptadenia gonoacantha</i>	Nodulator	Bournaud et al., 2017
<i>P. sabiae</i>	Br3407 ^T	Root nodules, Brazil	<i>Mimosa caesalpiniiifolia</i>	Nodulator	Chen et al., 2008
<i>P. sacchari</i>	IPT101 ^T	Sugar cane plantation soil, Brazil	N/A	Production of polyhydroxyalkanoic acids	Brämer et al., 2001
<i>P. sartisoli</i>	RP007 ^T	PAH-contaminated soil, New Zealand	N/A	Degradation of polycyclic aromatic hydrocarbon (PAH)	Vanlaere et al., 2008
<i>P. sediminicola</i>	HU2-65W ^T	Freshwater sediment, South Korea	N/A	Can negatively affect the growth of pine mushroom	Lim et al., 2008; Oh & Lim, 2018
<i>P. silvatlanitca</i>	SRMrh-20 ^T	Maize rhizosphere, Brazil	<i>Zea mays</i> , <i>Saccharum</i> sp.	Diazotroph, plant growth promoter	Perin et al., 2006; Onofre-Lemus et al., 2009
<i>P. silviterrae</i>	4 M-K11 ^T	Forest soil, China	N/A	N	Xiao, Gao, Lin, et al., 2019
<i>P. solisilvae</i>	Y-47 ^T	Forest soil, South Korea	N/A	N	Lee & Whang, 2015
<i>P. sprentiae</i>	WSM5005 ^T	Root nodules, South Africa	<i>Lebeckia ambigua</i>	Nodulator	De Meyer, Cnockaert, Ardley, Maker, et al., 2013
<i>P. steynii</i>	HC1.1ba ^T	Root nodules, South Africa	<i>Hypocalyptus sophoroides</i>	Nodulator	Beukes, Steenkamp, et al., 2019
<i>P. strydomiana</i>	WK1.1f ^T	Root nodules, South Africa	<i>Hypocalyptus sophoroides</i>	Nodulator	Beukes, Steenkamp, et al., 2019

(Continues)

TABLE 1 (Continued)

Species ^a	Type strain	Source, geographic origin of type strain	Host ^{c,d}	Notable properties ^e	Reference
<i>P. susongensis</i>	L226 ^T	Rock surface, China	N/A	Weathering of biotite to release Si, K and Al	Gu et al., 2015
<i>P. telluris</i>	DHOC27 ^T	Forest soil, China	N/A	N	Xiao et al., 2019
<i>P. terrae</i>	KMY02 ^T	Forest soil, South Korea	N/A	Diazotroph	Yang et al., 2006
<i>P. terricola</i>	LMG 20594 ^T	Agricultural soil, Belgium	N/A	Degradation of 2,4-dichloro-phenoxyacetic acid	Goris et al., 2002
<i>P. tropica</i>	Ppe8 ^T	Endophyte, Brazil	<i>Saccharum</i> sp.	Diazotroph, plant growth promoter	Reis et al., 2004; Caballero-Mellado et al., 2007
<i>P. tuberum</i> ^h	STM678 ^T	Root nodules, South Africa	<i>Aspalathus carnosa</i>	Nodulator, plant growth promoter	Vandamme et al., 2002; Elliott, Chen, Bontemps, et al., 2007; Lemaire, Chimphango, et al., 2016
' <i>P. ultramafica</i> ' ^b	STM10279 ^T	Root endophyte, New Caledonia	<i>Costularia arundinacea</i>	Growth in ultramafic soils, growth at low pH, heavy metal tolerance, plant growth promoter	Guentas et al., 2016
<i>P. unamae</i>	MTI-641 ^T	Rhizosphere, Mexico	<i>Zea mays</i>	Diazotroph, endophyte, degradation of aromatic compounds, plant growth promoter	Caballero-Mellado et al., 2004; Caballero-Mellado et al., 2007
<i>P. xenovorans</i>	LB400 ^T	Polychlorinated biphenyl (PCB) contaminated soil, USA	N/A	Degradation of PCB, diazotroph, oxidation of carbon monoxide	Goris et al., 2004; Weber & King, 2017

^a Species names listed in inverted commas ('...') are not yet validated and is therefore not on the List of Prokaryotic Names with Standing in Nomenclature (LPSN) as viewed 31 January 2020 (www.bacterio.net; Euzéby, 1997; Parte, 2013, 2018)

^b As yet, no request has been put forward to officially move the species *Burkholderia ultramafica* to the genus *Paraburkholderia*, however, based on its closest phylogenetic relatives (per Guentas et al., 2016) this species should form part of the latter genus

^c N/A = not applicable, none of these species have thus far been found in association with a particular host

^d For more information regarding, for instance, a wider range of legume hosts, etc., please refer to Supplementary Table 1 of Estrada-de los Santos et al., 2016

^e These are characteristics other than those typically included in bacterial species descriptions. N = Not known, indicating those instances where extensive biological information is not yet available for a particular species

^f Although *P. phymatum* was originally thought to be a symbiont of *Machaerium lunatum* (Vandamme et al., 2002), subsequent investigation has shown that it is a *Mimosa*-associated nodulator (Mishra et al., 2012; Moulin et al., 2014)

^g The nodulating *P. phenoliruptrix* strain Br3459a which is a symbiont of *Mimosa flocculosa* (Zuleta et al., 2014) is in actual fact a spontaneous mutant of strain Br3462 (Zuleta et al., 2014) first mentioned as a nodulator in the Chen, de Faria, et al., 2005 paper

^h *Paraburkholderia tuberum* although originally isolated from *Aspalathus carnosa* (Vandamme et al., 2002) first proved capable of nodulation on *Cyclopia* spp. (Elliott, Chen, Bontemps, et al., 2007) where after effective nodulation on *Aspalathus carnosa* has been proven by Lemaire, Chimphango, et al., 2016

ⁱ Although *P. caballeronis* TNe-841^T was initially described (and proven) to nodulate *Phaseolus vulgaris* (Martínez-Aguilar et al., 2013), sequencing of the genome of this strain as well as subsequent nodulation tests (in two independent laboratories) show that this strain no longer possess the ability to form nodules, although it still has the potential to fix nitrogen (Rojas-Rojas et al., 2017)

These were subsequently described as *Robbsia* (Lopes-Santos et al., 2017), *Caballeronia* (Dobritsa & Samadpour, 2016), *Trinickia* and *Mycetohabitans* (Estrada-de los Santos et al., 2018). Of the seven genera currently comprising *Burkholderia* sensu lato, rhizobial species are only found in *Paraburkholderia* and *Trinickia* (Estrada-de los Santos et al., 2018).

Paraburkholderia includes 77 species with 71 of them having validated names, and 20 representing rhizobial symbionts of legumes (Table 1). The species in this genus have been isolated

from a variety of habitats, some have been found in contaminated environments (e.g., *P. aromaticivorans*, *P. sartisoli*, *P. kururiensis*, *P. metalliresistans*, *P. phenoliruptrix* and *P. xenovorans*; Table 1), some are from agricultural settings such as ginseng fields (*P. ginsengisoli*, *P. ginsengiterrae* and '*P. panacihumi*'; Table 1) or tea plantations (*P. caffeinilytica* and '*P. caffeinitolerans*'; Table 1), yet others have been isolated from diverse bulk soil samples such as volcanic (*P. hiikae* and another three species; Table 1) and forest soil in Korea (e.g., *P. denitrificans*, *P. jirisanensis* and several other species; Table 1),

China (e.g. *P. caseinilytica* and *P. dinghuensis*; Table 1), Japan (*P. oxyphila*) and the USA (*P. madseni*). A number of species also associate with plants as endophytes (e.g., *P. aspalathi*, *P. bannensis*, *P. heleia*, *P. tropica* and *P. phytofirmans*; Table 1), while some also associate with moss (*P. megapolitana* and *P. bryophila*) or fungi (*P. fungorum*). Members of this genus therefore possess several notable properties (Table 1) that could have biotechnological potential in several areas, e.g., bioremediation (Suárez-Moreno et al., 2012), due to the ability of these bacteria to degrade recalcitrant pollutants (Lee et al., 2019; Sun et al., 2020), and agriculture where they could serve as probiotics or biofertilizers due to their nitrogen-fixing and plant growth-promoting abilities (Rahman et al., 2018; Suárez-Moreno et al., 2012).

3 | *Paraburkholderia* and Papilionoid Legumes

The symbiotic associations between *Paraburkholderia* rhizobial species and papilionoid legumes have only been reported from South Africa, except in instances where these associations were introduced into other regions (Liu et al., 2014). Also, all of these associations occur in the CCR as Papilionoideae is the dominant legume subfamily in the Fynbos vegetation, with no endemic mimosoids occurring in the region (Sprent et al., 2013). Therefore, studies on the rhizobial associates of endemic Fynbos legumes invariably focus on papilionoids, with *Paraburkholderia* species frequently identified as the predominant symbionts (Tables 1 and 2). Of the 20 known rhizobial *Paraburkholderia* species, eight were found in the CCR. These include the first beta-rhizobial species to be recognized, *P. tuberum* (Moulin et al., 2001; Vandamme et al., 2002) as well as *P. kirstenboschensis*, *P. strydomiana*, *P. steynii*, *P. dilworthii*, *P. sprentiae*, *P. dipogonis* and *P. rhynchosiae* (Beukes, Steenkamp, et al., 2019; De Meyer, Cnockaert, Ardley, Maker, et al., 2013; De Meyer, Cnockaert, Ardley, Trengove, et al., 2013; De Meyer et al., 2014; Sheu et al., 2015; Steenkamp et al., 2015).

Apart from *P. dipogonis* and *P. tuberum*, the distribution range of all South African *Paraburkholderia* root-nodulating species seems to be limited to the CCR. *Paraburkholderia dipogonis* has been described from New Zealand and Australia in association with the South African invasive legume *Dipogon lignosus* (Liu et al., 2014; Sheu et al., 2015), but its nodulation and nitrogen-fixation loci have South African origins (Liu et al., 2014). This bacterium was also encountered in South Africa from several other papilionoid genera (Lemaire, Chimphango, et al., 2016). It is thus likely that *P. dipogonis* is a South African species that was co-introduced into New Zealand and Australia with its plant partner (Liu et al., 2014). In terms of *P. tuberum*, however, reports from hosts and regions outside South Africa (i.e., from *Mimosa* in Brazil, Panama, Costa Rica and French Guiana (Barrett & Parker, 2005; Barrett & Parker, 2006; Bontemps et al., 2010; Mishra et al., 2012) likely reflect instances where the wrong name was applied to the symbiont (Mishra et al., 2012). Indeed, recent genome-based studies are now showing that these

isolates outside of South Africa are not conspecific to the original *P. tuberum* STM678^T (data not shown), and their taxonomic revision is currently underway.

Associations between papilionoids and their *Paraburkholderia* symbionts do not appear to be highly specific. Most of the rhizobial species occurring in the CCR can establish nitrogen-fixing symbioses with multiple papilionoid species (Table 2). Future exploration of the legume-rhizobium symbiosis in the region will likely show that this is also true for bacteria that have been reported from single host species (e.g., *P. steynii* and *P. strydomiana* that nodulate *Hypocalyptus sophoroides* and *P. rhynchosiae* that nodulates *Rhynchosia ferulifolia*) (Beukes, Steenkamp, et al., 2019; De Meyer, Cnockaert, Ardley, Trengove, et al., 2013; Table 2). Likewise, many CCR papilionoids are promiscuous in terms of nodulating partner as several species are capable of nodulating with multiple *Paraburkholderia* species. For example, *Hypocalyptus sophoroides* can form nodules in association with at least five *Paraburkholderia* species (i.e., *P. dipogonis*, *P. kirstenboschensis*, *P. steynii*, *P. strydomiana* and *P. tuberum*) (Beukes, Steenkamp, et al., 2019; Lemaire, Chimphango, et al., 2016; Sheu et al., 2015; Steenkamp et al., 2015; Table 2), while *Virgilia oroboides* nodulates with *P. dipogonis*, *P. kirstenboschensis*, *P. tuberum* and *P. phymatum* (Lemaire, Chimphango, et al., 2016; Sheu et al., 2015; Steenkamp et al., 2015; Table 2). Although some papilionoids have been reported to associate with one or only a few rhizobial species, this is likely due to limited sampling intensity.

Certain South African *Paraburkholderia* species probably represent root nodule endophytes. *Paraburkholderia aspalathi* and *P. fynbosensis* were originally isolated from the nodules of *Aspalathus abietina* and *Lebeckia ambigua*, respectively, but neither are capable of inducing nodules on these or other legumes (De Meyer et al., 2018; Estrada-de los Santos et al., 2018; Mavengere et al., 2014). The genomes of both *Paraburkholderia* species also lack detectable nodulation and nitrogen fixation genes (De Meyer et al., 2018; Estrada-de los Santos et al., 2018). These species may thus impart biologically relevant traits to the plant (e.g., plant growth promotion) as has been postulated for the *Paraburkholderia* isolates occurring as endophytes in the root nodules of *Acacia pycnantha* (Ndlovu et al., 2013). Therefore, although not rhizobial symbionts, the possibility that these species have potentially important agricultural functions cannot be excluded.

A recent study has found numerous nodulating *Paraburkholderia* isolates in the indigenous southern African mimosoid *Vachellia karroo* (formerly, *Acacia karroo*) that was collected in the Fynbos biome (Beukes, Boshoff, et al., 2019). However, this legume does not naturally occur in the region (Sprent et al., 2013) and its presence there can likely be ascribed to its invasive tendencies (Beukes, Boshoff, et al., 2019; Taylor & Barker, 2012). In its native range, this mimosoid plant predominantly nodulates with species of alpha-rhizobia from the genera *Rhizobium*, *Mesorhizobium* and *Ensifer* (Beukes, Boshoff, et al., 2019). Similarly, when papilionoid legumes endemic to the CCR or species closely related to them occur outside the CCR, they are not nodulated by *Paraburkholderia*. For example, the rhizobial symbionts of legumes in the tribe Crotalariaeae from other vegetation

TABLE 2 Legume hosts and the specific *Paraburkholderia* species with which they have been proven to successfully interact^a

Legume species	Species	References
Papilionoid legumes		
<i>Virgilia oroboides</i>	<i>P. dipogonis</i>	Sheu et al., 2015
	<i>P. kirstenboschensis</i>	Steenkamp et al., 2015
	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
	<i>P. phymatum</i>	Lemaire, Chimphango, et al., 2016
<i>Aspalathus carnosa</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Amphithalea ericifolia</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Dipogon lignosus</i>	<i>P. dipogonis</i>	Liu et al., 2014; Sheu et al., 2015
	<i>P. tuberum</i>	Liu et al., 2014
	<i>P. phymatum</i>	Liu et al., 2014
<i>Hypocalyptus sophoroides</i>	<i>P. dipogonis</i>	Sheu et al., 2015
	<i>P. kirstenboschensis</i>	Steenkamp et al., 2015
	<i>P. steynii</i>	Beukes, Steenkamp, et al., 2019
	<i>P. strydomiana</i>	Beukes, Steenkamp, et al., 2019
	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Hypocalyptus oxalidifolius</i>	<i>P. kirstenboschensis</i>	Steenkamp et al., 2015
<i>Hypocalyptus coluteoides</i>	<i>P. kirstenboschensis</i>	Steenkamp et al., 2015
	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Cyclopia subternata</i>	<i>P. dipogonis</i>	Sheu et al., 2015
	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
	<i>P. phymatum</i>	Lemaire, Chimphango, et al., 2016
<i>Podalyria calyptrata</i>	<i>P. dipogonis</i>	Sheu et al., 2015
	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Podalyria canescens</i>	<i>P. tuberum</i>	Suárez-Moreno et al., 2012; Lemaire, Chimphango, et al., 2016
<i>Podalyria burchellii</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Podalyria leipoldtii</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Podalyria myrtifillifolia</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Podalyria rotundifolia</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Podalyria sericea</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Rhynchosia ferulifolia</i>	<i>P. rhynchosiae</i>	De Meyer, Cnockaert, Ardley, Trengove, et al., 2013
<i>Lebeckia ambigua</i>	<i>P. sprentiae</i>	De Meyer, Cnockaert, Ardley, Maker, et al., 2013
	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
	<i>P. dilworthii</i>	De Meyer et al., 2014
<i>Cyclopia falcata</i>	<i>P. tuberum</i>	Elliott, Chen, Bontemps, et al., 2007
<i>Cyclopia galioides</i>	<i>P. tuberum</i>	Elliott, Chen, Bontemps, et al., 2007
<i>Cyclopia genistoides</i>	<i>P. tuberum</i>	Elliott, Chen, Bontemps, et al., 2007
	<i>P. phymatum</i>	Lemaire, Chimphango, et al., 2016
<i>Cyclopia intermedia</i>	<i>P. tuberum</i>	Elliott, Chen, Bontemps, et al., 2007
	<i>P. phymatum</i>	Lemaire, Chimphango, et al., 2016
<i>Cyclopia pubescens</i>	<i>P. tuberum</i>	Elliott, Chen, Bontemps, et al., 2007
<i>Lebeckia sepiaria</i>	<i>P. sprentiae</i>	De Meyer, Cnockaert, Ardley, Maker, et al., 2013
<i>Liparia laevigata</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Liparia splendens</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Indigofera filifolia</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016

(Continues)

TABLE 2 (Continued)

Legume species	Species	References
<i>Stirtonanthus taylorianus</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Xiphotheca fruticosa</i>	<i>P. tuberum</i>	Lemaire, Chimphango, et al., 2016
<i>Phaseolus vulgaris</i>	<i>P. dipogonis</i>	Sheu et al., 2015
	<i>P. caballeronis</i>	Martínez-Aguilar et al., 2013
	<i>P. fungorum</i>	Ferreira et al., 2012
	<i>P. phymatum</i>	Talbi et al., 2010; Lardi et al., 2017
	<i>P. diazotrophica</i>	Lardi et al., 2017
	<i>P. mimosarum</i>	Lardi et al., 2017
	<i>P. tuberum</i>	Lardi et al., 2017
<i>Macroptilium atropurpureum</i>	<i>P. tuberum</i>	Angus et al., 2013; Lardi et al., 2017
	<i>P. kirstenboschensis</i>	Beukes et al., 2013
	<i>P. diazotrophica</i>	Lardi et al., 2017
	<i>P. mimosarum</i>	Lardi et al., 2017
	<i>P. phymatum</i>	Lardi et al., 2017
	<i>P. steynii</i>	Beukes et al., 2013
	<i>P. strydomiana</i>	Beukes et al., 2013
	<i>P. sabiae</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
<i>Vigna unguiculata</i>	<i>P. kirstenboschensis</i>	Beukes et al., 2013
	<i>P. diazotrophica</i>	Lardi et al., 2017
	<i>P. mimosarum</i>	Lardi et al., 2017
	<i>P. phymatum</i>	Lardi et al., 2017
	<i>P. steynii</i>	Beukes et al., 2013
	<i>P. strydomiana</i>	Beukes et al., 2013
Mimosoid legumes		
<i>Vachellia karroo</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Vachellia cochliacantha</i>	<i>P. phymatum</i>	Talbi et al., 2010
<i>Vachellia farnesiana</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Vachellia nilotica</i> subsp. <i>leicocarpa</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Vachellia nilotica</i> subsp. <i>kraussiana</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Vachellia pennatula</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Vachellia seyal</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Vachellia tortilis</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Acacia nilotica</i>	<i>P. phymatum</i>	Moulin et al., 2014
	<i>P. piptadeniae</i>	Bournaud et al., 2017
<i>Acaciella glauca</i>	<i>P. phymatum</i>	Talbi et al., 2010
<i>Mimosa acutistipula</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
	<i>P. sabiae</i>	Chen, de Faria, et al., 2005
	<i>P. nodosa</i>	Chen, de Faria, et al., 2005
	<i>P. mimosarum</i>	Chen, de Faria, et al., 2005
<i>Mimosa adenocarpa</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa affinis</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa albida</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007

(Continues)

TABLE 2 (Continued)

Legume species	Species	References
<i>Mimosa albolanata</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa artemisiana</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa camporum</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa cordistipula</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa debilis</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa dysocarpa</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa foliolosa</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa hexandra</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa himalayana</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa invisa</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa latispinosa</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa menabeensis</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa ophthalmocentra</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa polydactyla</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa somnians</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa tenuiflora</i>	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007
<i>Mimosa pudica</i>	<i>P. caribensis</i>	Chen et al., 2003
	<i>P. diazotrophica</i>	Sheu et al., 2013; Lardi et al., 2017
	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007; Moulin et al., 2014; Lardi et al., 2017
	<i>P. sabiae</i>	Chen et al., 2008; Bournaud et al., 2013
	<i>P. guartelaensis</i>	Paulitsch et al., 2019
	<i>P. mimosarum</i>	Lardi et al., 2017
	<i>P. nodosa</i>	Chen et al., 2007; Bournaud et al., 2013
	<i>P. piptadeniae</i>	Bournaud et al., 2017
	<i>P. ribeironis</i>	Bournaud et al., 2017
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
<i>Mimosa diplotricha</i>	<i>P. caribensis</i>	Chen et al., 2003
	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007 ^b
	<i>P. nodosa</i>	Chen et al., 2007
	<i>P. mimosarum</i>	Chen et al., 2007
	<i>P. sabiae</i>	Chen, de Faria, et al., 2005
<i>Mimosa candollei</i>	<i>P. diazotrophica</i>	Sheu et al., 2013
<i>Mimosa pigra</i>	<i>P. mimosarum</i>	Chen et al., 2006
	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007; Moulin et al., 2014
	<i>P. nodosa</i>	Chen et al., 2007
	<i>P. sabiae</i>	Chen, de Faria, et al., 2005
<i>Mimosa scabrella</i>	<i>P. mimosarum</i>	Chen et al., 2006
	<i>P. nodosa</i>	Chen et al., 2007
	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007 ^b
	<i>P. piptadeniae</i>	Bournaud et al., 2017
<i>Mimosa setosa</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa velloziana</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa flocculosa</i>	<i>P. phenoliruptrix</i>	Zuleta et al., 2014
	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007

(Continues)

TABLE 2 (Continued)

Legume species	Species	References
<i>Mimosa bimucronata</i>	<i>P. nodosa</i>	Chen et al., 2007
	<i>P. phymatum</i>	Elliott, Chen, Chou, et al., 2007 ^b
<i>Mimosa caesalpiniiifolia</i>	<i>P. sabiae</i>	Chen et al., 2008
	<i>P. phymatum</i>	Moulin et al., 2014
<i>Mimosa gymnas</i>	<i>P. guartelaensis</i>	Paulitsch et al., 2019
<i>Mimosa ursina</i>	<i>P. phymatum</i>	Suárez-Moreno et al., 2012
<i>Mimosa xanthocentra</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Calliandra houstiana</i> var. <i>acapulcens</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Calliandra houstiana</i> var. <i>anomala</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Calliandra houstiana</i> var. <i>calothyrsus</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Calliandra juzepczukii</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Calliandra trinervia</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Pithecellobium dulce</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Prosopis juliflora</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Prosopis laevigata</i>	<i>P. phymatum</i>	Talbi et al., 2010
<i>Anadenanthera colubrina</i>	<i>P. phymatum</i>	Moulin et al., 2014
	<i>P. sabiae</i>	Bournaud et al., 2013
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013
<i>Anadenanthera pavonina</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Anadenanthera peregrina</i>	<i>P. sabiae</i>	Bournaud et al., 2013
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013
	<i>P. diazotrophica</i>	Bournaud et al., 2013
<i>Leucaena leucocephala</i>	<i>P. phymatum</i>	Moulin et al., 2014
	<i>P. ribeironis</i>	Bournaud et al., 2017
<i>Leucaena multicapitula</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Microlobius foetidus</i>	<i>P. nodosa</i>	Bournaud et al., 2013
	<i>P. sabiae</i>	Bournaud et al., 2013
<i>Piptadenia stipulacea</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Piptadenia viridiflora</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Piptadenia gonoacantha</i>	<i>P. piptadeniae</i>	Bournaud et al., 2017
	<i>P. ribeironis</i>	Bournaud et al., 2017
	<i>P. sabiae</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
	<i>P. diazotrophica</i>	Bournaud et al., 2013
<i>Parapiptadenia rigida</i>	<i>P. sabiae</i>	Bournaud et al., 2013
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013
	<i>P. caribensis</i>	Bournaud et al., 2013
<i>Parapiptadenia pterosperma</i>	<i>P. phymatum</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013

(Continues)

TABLE 2 (Continued)

Legume species	Species	References
<i>Pityrocarpa moniliformis</i>	<i>P. phymatum</i>	Moulin et al., 2014
	<i>P. sabiae</i>	Bournaud et al., 2013
	<i>P. phenoliruptrix</i>	Bournaud et al., 2013
	<i>P. nodosa</i>	Bournaud et al., 2013
<i>Pityrocarpa obliqua</i>	<i>P. phymatum</i>	Moulin et al., 2014
<i>Pseudopiptadenia contorta</i>	<i>P. nodosa</i>	Bournaud et al., 2013

^aIn this table we only include rhizobial isolates which have been delineated to the species level and when their interaction with the host results in effective nitrogen-fixing nodules

^bNodulation on these hosts by *P. phymatum* STM815^T did not prove successful in the tests conducted by Moulin et al. (2014)

types or biomes in South Africa associate with alpha-rhizobia from genera such as *Bradyrhizobium* and *Ensifer* (Ardley et al., 2013; Beukes et al., 2016).

In situations where endemic South African fynbos papilionoids have been introduced into new areas, their successful establishment have varied greatly. For example, the introduction of several *Lessertia* species (and their *Mesorhizobium* symbionts) into Australia, with the aim of establishment and potential use as forage legumes, was not successful. This was because the symbiosis was interrupted by a more competitive resident alpha-rhizobial species (i.e., *Rhizobium leguminosarum*), which led to inefficient nitrogen fixation (Gerding et al., 2013). Another introduction, albeit unintentional, was that of *Dipogon lignosus* into New Zealand and Australia, which has proven to be quite successful. In part, this has been attributed to the promiscuity of the legume symbiont, which can associate with isolates of *Rhizobium*, *Bradyrhizobium* and *Paraburkholderia*, depending predominantly on soil pH (Liu et al., 2014). This species has even been used as a routine 'trapping' plant for isolating bacteria capable of nodulation from different soils (Lemaire, Chimphango, et al., 2016) because of its ability to interact with diverse rhizobia.

4 | *Paraburkholderia* and *Mimosa* Species

One of the main outputs of the recent, phylogeny-based revision of the family Leguminosae (Legume Phylogeny Working Group (LPWG), 2017) has been the incorporation of the traditional Mimosoideae (now referred to as the "mimosoid clade") in the recircumscribed Caesalpinioideae subfamily (Legume Phylogeny Working Group (LPWG), 2017). The mimosoid clade contains well-known and economically important legumes such as *Mimosa* and *Acacia*. The latter are native to Australia and their preferred rhizobial symbionts belong to the alpha-rhizobial genus *Bradyrhizobium* (Warrington et al., 2019). By contrast, *Mimosa* species associate with either alpha- or beta-rhizobia, depending on their geographic distribution (see below).

The genus *Mimosa* forms part of the "Piptadenia group" (together with genera such as *Piptadenia*, *Pseudopiptadenia* and *Parapiptadenia*) of which most members are native to Brazil (Bournaud et al., 2013,

2017). The "Piptadenia Group" appears to interact predominantly with beta-rhizobia in the genus *Paraburkholderia* (Bournaud et al., 2013, 2017; Paulitsch et al., 2019). For example, species of *Calliandra* (tribe Ingeae) are nodulated by *Paraburkholderia*, many of which are closely related to symbionts of *Mimosa* species (Silva et al., 2018). However, because of the invasiveness of many *Mimosa* species (e.g., *M. pigra*, *M. pudica* and *M. diplotricha*), their association with *Paraburkholderia* has received much attention (Chen, James, et al., 2005; Gehlot et al., 2013). Compared to the *Paraburkholderia*-papilionoid association, considerably more is known about the *Paraburkholderia*-*Mimosa* interaction. A detailed understanding of the latter interaction might thus inform future studies on Fynbos papilionoids, as well as the development of strategies and applications of CCR legumes as forage species.

Mimosa has four major centres of diversity, i.e., two in the New World (Brazil with 350 species and Mexico with 100 species) and two in the Old World (Madagascar with 30 species and India with six species) (Bontemps et al., 2016; Gehlot et al., 2013). Most New World *Mimosa* species are endemic to highlands and have restricted ranges (Simon et al., 2011). Two studies focussing on the rhizobial symbionts of endemic species in Brazil found that plants growing in the Cerrado and Caatinga biomes were all nodulated by *Paraburkholderia* (Bontemps et al., 2010; dos Reis Junior et al., 2010). These bacteria were genetically similar to those nodulating more widespread *Mimosa* species (*M. debilis* and *M. xanthocentra*; dos Reis Junior et al., 2010). Although these more widespread species can also associate with *Cupriavidus taiwanensis* (dos Reis Junior et al., 2010), *Mimosa* species native to Brazil do not seem capable of nodulation with rhizobia from this genus (Klonowska et al., 2012; Liu et al., 2012). Nevertheless, *Paraburkholderia* was also reported as the main rhizobial symbiont of *Mimosa* elsewhere in Brazil, Venezuela, Panama and Costa Rica (Barrett & Parker, 2005, 2006; Chen, de Faria, et al., 2005). In Costa Rica, *Paraburkholderia* is also the dominant symbiont of *M. pigra*, but here *M. pudica* is apparently nodulated equally well by strains of *Rhizobium*, *Cupriavidus* and *Paraburkholderia* (Barrett & Parker, 2006).

Based on the existing literature, *Mimosa* species endemic to Mexico are nodulated mainly by alpha-rhizobia in the genera *Ensifer* and *Rhizobium* (Bontemps et al., 2016; Wang et al., 1999). However,

some species (e.g., *M. skinneri*) associate with both *Rhizobium* and *Paraburkholderia* isolates (Bontemps et al., 2016), while a few apparently prefer *Paraburkholderia*. Two examples of the latter are the widespread species *M. somnians* and *M. occidentalis* (Bontemps et al., 2016; De Meyer et al., 2016; Ormeño-Orrillo et al., 2012). In Uruguay, which is the southern limit of *Mimosa* in the New World, the highly promiscuous *Paraburkholderia phymatum* associates with *M. uragüensis* (Elliott, Chen, Chou, et al., 2007), although other *Mimosa* species endemic to the region predominantly associate with *Cupriavidus* (Platero et al., 2016). These Uruguayan *Cupriavidus* strains are also capable of effectively nodulating the widespread species *M. pudica* (Platero et al., 2016). *Cupriavidus* is also frequently found in association with native *Mimosa* species in other regions of the New World (Andam et al., 2007; Barrett & Parker, 2006; Klonowska et al., 2012; Mishra et al., 2012) and is the main symbiont of other “Piptadenia Group” legumes such as *Parapiptadenia rigida* (Bournaud et al., 2013; Taulé et al., 2012).

Not much is known about the rhizobial symbionts of Old World *Mimosa* species. The limited information currently available suggests that *Mimosa* species in this region would likely also associate with alpha-rhizobia and not *Paraburkholderia*. Gehlot et al. (2013) showed that *M. hamata* and *M. himalayana*, both endemic to India, are nodulated by *Ensifer* isolates that could not nodulate *M. pudica*, which is an invasive species in the region. Also, *Ensifer* isolates from *M. hamata* could nodulate *M. himalayana*, but not the other way around (Gehlot et al., 2013). This is consistent with the idea that *M. himalayana* is more promiscuous as it has also been shown to form nodules in association with *P. phymatum* (Elliott, Chen, Chou, et al., 2007; Gehlot et al., 2013). By contrast, *M. hamata* potentially lost the ability to nodulate with other rhizobia when it became adapted to growth and nodulation in the alkaline and low fertility soils of the Thar Desert (Gehlot et al., 2012, 2013).

From these studies on the rhizobial symbionts of *Mimosa* species in their centres of diversity, a clear biogeographic pattern has emerged (Baraúna et al., 2016; Silva et al., 2018; Sprent et al., 2017). *Paraburkholderia* appears to be the dominant genus found in *Mimosa* nodules in central and southern Brazil (Bontemps et al., 2010), while *Cupriavidus* is the dominant symbiont of *Mimosa* species in southern Uruguay (Platero et al., 2016). In central Mexico, the predominant *Mimosa* symbionts belong to the alpha-rhizobial genera *Rhizobium* or *Ensifer* (Andrews et al., 2018; Bontemps et al., 2016; de Castro Pires et al., 2018), with *Ensifer* also being found in the Indian Old World centre of diversity (Gehlot et al., 2012, 2013). Additionally, beta-rhizobial isolates are most frequently found in association with *Mimosa* species in non-native settings where they are invasive. Notable examples are from India (Gehlot et al., 2013), China (Liu et al., 2011, 2012), Taiwan (Chen, James, et al., 2005) and Australia (Parker et al., 2007).

From studies that have focussed on the *Mimosa*–rhizobium association in non-native or introduced locations, the available data suggest that particular *Mimosa* species may be co-introduced into new locations together with their beta-rhizobial symbionts (i.e., both symbiotic partners are non-native to the new location). An example

of this is *M. pigra* that was co-introduced with its *Paraburkholderia* symbionts into Taiwan (Chen, James, et al., 2005). Evidence has also been documented of cases where the non-native and/or invasive *Mimosa* species associate with apparently indigenous rhizobia. A good example of this is the occurrence of *M. pigra* as a non-native in Australia where it is predominantly nodulated by resident Australian *Paraburkholderia* isolates (Parker et al., 2007).

These studies on the *Paraburkholderia*–*Mimosa* interaction illustrated that the specificity of the symbiotic interaction is not necessarily easy to predict as the plant may or may not have different rhizobial partners in different geographic locations. This would likely also be true for the *Paraburkholderia*–papilionoid interaction, which could significantly influence attempts to relocate and establish a particular *Paraburkholderia*–papilionoid association in a new area. However, it is expected that legumes that can grow well in various sites and within a range of edaphic factors (i.e., invasive legumes such as *M. pudica*) would be more promiscuous (Klonowska et al., 2012). By contrast, legumes that are adapted to growth in specific sites and conditions would probably be more specific with regards to their rhizobial partners, which have to be adapted for the same set of conditions (Andrews & Andrews, 2017; de Castro Pires et al., 2018; Klock et al., 2015). An example of the latter is *M. hamata* versus *M. himalayana* where *M. hamata* adapted to a specific habitat and has become more specific in its interaction, thereby rendering it unable to nodulate with *M. himalayana* symbionts (Andrews & Andrews, 2017; Gehlot et al., 2012, 2013).

5 | Different Centres of Diversity for Symbiotic Loci

A suitable match between legume and rhizobial genotype is essential for establishing an effective nitrogen-fixing symbiosis (Sprent et al., 2010). In the rhizobial symbiont, this “match” with the plant partner is encoded by genes that form part of the symbiotic loci (e.g., *nod* or nodulation genes and *nif* or nitrogen fixation genes) (Wang et al., 2018). When the plant experiences nitrogen shortage, it releases molecules that are recognized by the rhizobial symbiont, which then activates transcription of the rhizobial *nod* loci to produce the Nod Factor (Wang et al., 2012, 2018). Recognition of this signalling molecule by the plant leads to morphological changes that ultimately results in nodule formation (Wang et al., 2012, 2018). However, when signalling between the interacting partners are non-functional, root nodules are either not induced or are ineffective. For example, the root-nodule bacteria of *Aspalathus hispida* can form functional nodules on *Aspalathus linearis*, but those that nodulate *Lebeckia* species are not capable of inducing functional nodules on *A. linearis* (Deschodt & Strijdom, 1976), which is most probably due to the inability for successful signalling or “molecular crosstalk” between the various partners.

Current data suggest that papilionoid-associated *Paraburkholderia* isolates cannot effectively nodulate *Mimosa* hosts (de Castro

Pires et al., 2018; De Meyer et al., 2016; Elliott, Chen, Bontemps, et al., 2007; Elliott et al., 2009; Estrada-de los Santos et al., 2016; Lemaire, Van Cauwenberghe, et al., 2016; Mishra et al., 2012). This is not surprising as the symbiotic loci of the rhizobial species interacting with papilionoid and *Mimosa* hosts have been shown to differ substantially at the DNA sequence level (Mishra et al., 2012). The inability of these bacteria to cross-nodulate papilionoid and *Mimosa* species could thus be due to their markedly different symbiotic loci, which would make signal recognition between the plant and respective bacteria difficult if not impossible (Sprent et al., 2017; Wang et al., 2018).

Phylogenetic analyses of the symbiotic loci of *Paraburkholderia* have shown that the papilionoid- and *Mimosa*-nodulating species do not share the same evolutionary origins (Beukes et al., 2013; Chen, de Faria, et al., 2005; Chen, James, et al., 2005; Chen et al., 2003; De Meyer et al., 2016; Dlodlu et al., 2018; Elliott, Chen, Bontemps, et al., 2007; Estrada-de los Santos et al., 2018; Garau et al., 2009; Gyaneshwar et al., 2011; Silva et al., 2018). *Paraburkholderia* originating from papilionoid hosts share a closer evolutionary relationship with *Bradyrhizobium* and *Methylobacterium nodulans* in the alpha-rhizobia (Beukes et al., 2013; Chen, de Faria, et al., 2005; Chen, James, et al., 2005; Chen et al., 2003; De Meyer et al., 2016; Dlodlu et al., 2018; Elliott, Chen, Bontemps, et al., 2007; Estrada-de los Santos et al., 2018; Sy et al., 2001). In contrast, those from *Mimosa* form a unique and highly supported clade that also contains *Cupriavidus taiwanensis* (Beukes et al., 2013; De Meyer et al., 2016; Estrada-de los Santos et al., 2018; Garau et al., 2009; Mishra et al., 2012). Accordingly, South America and South Africa are viewed as centres of diversity for rhizobial *Paraburkholderia* species (Bontemps et al., 2010; Gyaneshwar et al., 2011; Paulitsch et al., 2019; dos Reis Junior et al., 2010; Sprent et al., 2017; Taulé et al., 2012). In fact, this pattern likely holds for the alpha-rhizobia in these regions because the evolutionary origins of the symbiotic loci of *Mesorhizobium* and *Rhizobium* associating with CCR papilionoids are also highly distinct and unique (Dlodlu et al., 2018).

6 | Possible factors influencing *Paraburkholderia* distribution

Several site-linked environmental factors have been proposed to explain the geographic pattern observed for the association between *Paraburkholderia* and either *Mimosa* or papilionoid hosts (Bontemps et al., 2010; de Castro Pires et al., 2018; Lemaire et al., 2015). Characteristics inherent to the soil at the sampling site have been proposed to influence the dominance of a specific rhizobial genus (Bontemps et al., 2016; de Castro Pires et al., 2018; Lemaire, Chiphango, et al., 2016; Lemaire et al., 2015; Mishra et al., 2012; Silva et al., 2018). These include pH, nitrogen and other nutrient levels (e.g., phosphate and CaCO_3), salinity, granulometry and even the presence of heavy metals.

Paraburkholderia appear to be dominant in soils with a low pH, low nutrient levels (especially available N) and which experience periodic

drought (Elliott et al., 2009; Liu et al., 2014; Mishra et al., 2012; dos Reis Junior et al., 2010; Suárez-Moreno et al., 2012). This could be why these species are so prevalent in central Brazil where the soil is known to be very acidic (Bontemps et al., 2010; dos Reis Junior et al., 2010). A study on *M. pudica* symbionts in French Guiana (north-east coast of South America) also found *Paraburkholderia* in areas with a neutral or acidic pH (Mishra et al., 2012), while *Cupriavidus* was encountered when the soil pH was neutral to around 8.9 (Mishra et al., 2012). A study by Dakora (2012) showed that rhizobial isolates of four *Aspalathus* species (including *A. hispida*) appear to be tolerant to a pH as low as 3. It thus appears that *Paraburkholderia* have developed a tolerance to acidic pH and are accordingly better adapted to outcompete other soil bacteria under these conditions (de Castro Pires et al., 2018; Stopnisek et al., 2014).

Phosphate (P) is essential for the metabolic energy processes responsible for fixing atmospheric nitrogen (Valentine et al., 2017; Vardien et al., 2014) and it also plays a role in nodule development and function (Vardien et al., 2014). However, acidic soil (such as in the CCR) generally has less available P than alkaline soil due to decreased solubility of the complexes it forms with cations such as aluminium (Magadlela et al., 2017; Valentine et al., 2017; Vardien et al., 2014). However, a study on the South African endemic *Virgilia divaricata* has shown that treatments of high and low P availability did not change the bacterial composition within the resulting nodules (Magadlela et al., 2017). Although the host was provided with natural inoculum in the form of soil collected from two sites, the rhizobial isolates from the root nodules under both P regimes belonged to the genus *Paraburkholderia* (Magadlela et al., 2017). It would therefore appear as if these isolates can maintain the symbiotic nitrogen-fixing interaction even under limiting P levels (Magadlela et al., 2017).

In situations where the concentration of available mineral N in the soil is low, *Paraburkholderia* species such as *P. mimosarum* and *P. phymatum* can outcompete *C. taiwanensis* isolates (Elliott et al., 2009). The glasshouse trial of de Castro Pires et al. (2018), using soil from three locations in Brazil and seeds of six *Mimosa* hosts, showed that when the soil had a low N concentration *Paraburkholderia* were dominant, while the soils where *Rhizobium* appeared to dominate had a six-fold higher concentration of mineral N. The less fertile soils were also more acidic, while those higher in mineral N had a pH value closer to neutral, which might also have favoured the dominance of *Rhizobium* (de Castro Pires et al., 2018).

Overall, abilities integral to a bacterial isolate determine its dominance in soils and/or involvement in legume–rhizobium symbiosis. For example, Melkonian et al. (2014) found that competitiveness of the bacterium might be an important factor, which they defined as the ability to influence the biogeographic patterns of nodule occupancy in a particular legume. They showed that *P. phymatum* had a high degree of competitiveness as it outcompeted all other isolates tested on *M. pudica*. Also, in a study of *Dipogon lignosus* in an invasive setting, *Paraburkholderia* isolates were able to solubilize phosphate and produce siderophores, while the resident *Rhizobium* and *Bradyrhizobium* recovered could not (Liu et al., 2014). Therefore, these *Paraburkholderia* isolates and their hosts would have a

competitive advantage in soils where levels of phosphorous and iron are low (Liu et al., 2014).

Thus, when trying to make an informed decision regarding which South African fynbos legume(s) to use for forage purposes in comparable locations abroad, the identity of the preferred rhizobial symbiont/s should be known and information on the environmental and edaphic factors in which the interaction would need to occur should be gathered. Furthermore, the degree of specificity of the interaction between the symbiotic partners should be investigated. For example, more promiscuous legumes could also interact with competitive yet ineffective resident rhizobia (Gerding et al., 2014; Pastor-Bueis et al., 2019), which might make stricter associations more productive under field conditions. Therefore, information on the loci forming the basis of the signal exchange between the symbiotic partners is also essential as are factors intrinsic to each partner (especially, competitiveness and saprophytic competence of the rhizobial symbiont).

7 | Future Perspective

It is apparent that indigenous South African legumes can interact with diverse and 'non-traditional' rhizobia, which in many cases have not yet been fully studied. For the vast majority of indigenous legumes, we do not even know the identity of their rhizobial symbionts. It is becoming clear that *Paraburkholderia* is a potentially dominant rhizobial genus associating with papilionoids in the Cape Fynbos vegetation, an observation supported by the study of Dlodlu et al. (2018) which determined that *Paraburkholderia* is most probably the ancestral symbiont of fynbos legumes (using current nodulation data). Studies aiming to systematically characterize the diversity and biology of rhizobia associating with legumes in the CCR are thus crucial for unlocking the potential of using fynbos legumes as forage species in regions with a Mediterranean type climate outside the CCR.

Based on current information, factors linked to the planting site of the legume host could be instrumental in determining the identity of the rhizobial symbiont. Therefore, conditions at the site where the potential forage legumes will be grown could be quite important to the success of the accompanying rhizobial symbiont, which in turn will most probably affect legume establishment. The commercial development of *Lebeckia ambigua* in Western Australia was predicated upon selecting *Paraburkholderia* capable of surviving in the acid, infertile soils therein (Edwards et al., 2019; Howieson et al., 2013). This is the first (and currently only) instance of the development of a *Paraburkholderia* inoculum that the authors are aware of. The approach taken by the researchers in that program was to seek soils in the CCR with very similar chemical features and select rhizobia from these regions to evaluate in Western Australia. Successful establishment of such "new" legume–rhizobium associations is thus fundamentally dependent on a detailed understanding of the climatic and edaphic conditions needed for sustaining both symbiotic partners in the target region (Drew et al., 2012; Howieson et al., 2016).

Another issue to consider is that the loci responsible for nodulation and nitrogen fixation are carried on mobile genetic elements that can be transferred horizontally among species (Andrews et al., 2018). This means that different species may harbour the same complement of symbiotic loci (Rogel et al., 2011): e.g., strain BR3459a of *P. phenoliruptrix* that is known for its xenobiotic properties has acquired symbiotic loci similar to that of *P. phymatum*, and can accordingly nodulate *Mimosa flocculosa* (Zuleta et al., 2014). Similarly, symbiotic loci can be transferred between inoculant strains and resident soil bacteria, thereby potentially impacting negatively on the success of establishing "new" legume–rhizobium associations in a particular region (Nandasena et al., 2006). Routine monitoring of these associations applied in the field is therefore essential for informing agricultural practices aimed at stable maintenance of productive symbioses (e.g., through application of the rhizobial inoculant in increasing numbers to ensure that it outcompetes ineffective resident rhizobia) (Drew et al., 2012).

As forage legume breeding programs expand to evaluate wild legumes for domestication, particularly those seeking to use legumes from the CCR, an understanding of their microsymbionts will be crucial to successful outcomes. Where these involve fynbos legumes associating with *Paraburkholderia* symbionts, a major issue that requires urgent attention arise from the taxonomic history of the rhizobial partner. This genus of plant-associated and environmental bacteria was previously grouped with predominantly pathogenic species in the genus *Burkholderia* (Angus et al., 2014; Mannaa et al., 2019; Santos et al., 2019). The latter genus includes both animal and human pathogens, including the well-known *Burkholderia cepacia* complex that is prevalent in clinical settings (Mannaa et al., 2019). However, recent phylogenomic and pathogenic studies have demonstrated that the use of *Paraburkholderia* in agricultural applications is safe (Angus et al., 2014; Estrada-de los Santos et al., 2018; Mannaa et al., 2019). Their deployment in agriculture as rhizobial inoculants should therefore be founded on a detailed taxonomic understanding of the target bacteria. In the case of *Paraburkholderia*, this would be crucial as strains from this genus would likely be invaluable as inoculants of legumes adapted to Mediterranean-type climates and soils that are acidic and nutrient poor.

CONFLICT OF INTEREST

The authors wish to declare that there is no conflict of interest.

AUTHOR CONTRIBUTION

Chrizzelle Beukes: Conceptualization (equal); Data curation (equal); Investigation (equal); Writing-original draft (equal); Writing-review & editing (equal). **Stephanus Venter:** Conceptualization (equal); Writing-review & editing (equal). **Emma Steenkamp:** Conceptualization (equal); Funding acquisition (equal); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

All references included in this review have been duly cited and are listed in the Reference List.

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