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Are pathogenic isolates of *Stemphylium* host specific and cosmopolitan?

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Abstract

Stemphylium is a genus of filamentous ascomycetes comprising plant pathogens and saprobes in the family Pleosporaceae (Pleosporales, Dothideomycetes). Species of *Stemphylium* are known from a broad range of plant hosts including a variety of agricultural crops. This paper briefly discusses the occurrence of pathogenic isolates of *Stemphylium* on different host species, pathogenicity, disease severity, distribution and molecular phylogenetic affinities of pathogenic isolates of *Stemphylium*.

Background

Stemphylium Wallr. is a genus of filamentous ascomycetes comprising plant pathogens and saprobes in the family Pleosporaceae (Pleosporales, Dothideomycetes, Ascomycetes). The genus *Stemphylium* was proposed by Wallroth (1833) with *S. botryosum* Wallr. as the type species. About 200 published names currently represent recognizable taxa of *Stemphylium* (Woudenberg et al. 2017, Index Fungorum 2018). *Stemphylium* is a monophyletic genus, which comprises both saprophytic and plant pathogenic species with worldwide distribution (Köhl et al. 2009, Crous et al. 2016, Woudenberg et al. 2017). The genus can be distinguished from other dematiaceous hyphomycetes by its phaeodictyospores produced by the percurrent proliferation of its conidiophores, and by apically swollen conidiogenous cells (Crous et al. 2016, Woudenberg et al. 2017). The sexual morph of *Stemphylium*, is *Pleospora* which is a polyphyletic genus (Woudenberg et al. 2017). The type species of *Pleospora*, *Pleospora herbarum*, has *Stemphylium herbarum* as asexual morph (Simmons 1985), but several other *Pleospora* spp. have been linked to different asexual genera such as *Alternaria*, *Coniothyrium* and *Bipolaris* (Inderbitzin et al. 2009, De Gruyter et al. 2009, Ariyawansa et al. 2015, Crous & Groenewald 2017). The use of *Stemphylium* over *Pleospora* has been recommended by the Working Group on Dothideomycetes of the International Committee on the Taxonomy of Fungi (Rossman et al. 2015). *Stemphylium* species are successful colonisers of decaying plant tissues (Hudson 1971, Köhl et al. 2009) and well known as plant pathogens (Falloon et al. 1987, Prados-Ligero et al. 1998, Basallote et al. 1993, Leuprecht 1990, Koike et al. 2001, Crous et al. 2016, Woudenberg et al. 2017).

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Occurrence of pathogenic isolates of *Stemphylium*

Stemphyium species have been reported from various agricultural crops such as, alfalfa, red clover, tomato and potato (Ellis & Gibson 1975, Irwin 1984, Johnson & Lunden 1986, Simmons 1990, Aveling & Snyman 1993), sugar beet (Hanse 2013), asparagus, onion, garlic (Gálvez et al. 2016), birdsfoot trefoil (*Lotus corniculatus*) (Seaney 1973), pear, parsley, lentil, lucerne (*Medicago sativa*) and a variety of other horticultural crops (Falloon et al. 1987, Koike et al. 2013, Lamprecht et al. 1984, Llorente & Montesinos 2006, Mentha 1998, Miller et al. 1978, Nasehi et al. 2013, Reis et al. 2011, Vakalounakis & Markakis 2013, Subedi et al. 2014). Leaf spot disease accompanied by *Stemphylium* sp. was first discovered on sugar beet (*Beta vulgaris*) in the Netherlands, and later, it spread rapidly throughout the country (Hanse 2013). Crous et al. (2016) formally named the causal agent of this leaf spot disease as *Stemphylium beticola*. *Stemphylium* blight caused by *S. botryosum* is becoming a serious threat to lentil cultivation (Subedi et al. 2014) and has been reported in Bangladesh, Egypt, Nepal, Syria and the USA (Bayaa & Erksine 1998). The causal agents of leaf spot in alfalfa and red clover are *S. alfalfa*, *S. botryosum*, *S. globuliferum*, *S. herbarum*, and *S. vesicarium* (Camara et al. 2002, Berg & Leath 1996). *Stemphylium vesicarium* also causes purple spot in asparagus and leaf spot in onion and garlic (Gálvez et al. 2016). *Stemphylium solani* is the responsible pathogen for grey leaf spot on tomato and potato (Ellis & Gibson 1975, Irwin 1984, Johnson & Lunden 1986, Simmons 1990, Aveling & Snyman 1993) *Stemphylium loti* has been reported as the causative agent for the most widespread foliar disease of birdsfoot trefoil (Seaney 1973). *Stemphylium* pathogens have been found from several vegetables and flowers, including asparagus (*Asparagus officinalis*), aster (*Aster* sp.), Chinese chives (*Allium tuberosum*), kalanchoe (*Kalanchoe blossfeldiana*), sweet pepper (*Capsicum annuum*), tomato (*Lycopersicon esculentum*), Welsh onion (*Allium fistulosum*), and white lace flower (*Ammi majus*) (Suzui 1973, Enjoji 1931, Ichikawa & Sato 1994, Tomioka et al. 1997, Shibata et al. 2000, Misawa 2009, Kurose et al. 2015, Tomioka & Sato 2011). *Stemphylium brassicicola*, *S. ixeridis* and *S. microsporum* have been reported from diseased leaves of *Ixeris denticulata*, *Brassica pekinensis*, and *Malus sieversii*, respectively, in Northwest China (Wang & Zhang 2009). Two species of *Stemphylium* have been described as causing a rot of apple (Ruehle 1930). *Stemphylium lycopersici* isolates has been obtained from diseased tomato, eggplant (*Solanum melongena*), pepper and lettuce (*Lactuca sativa*) (Nasehi et al. 2014). Koike et al. (2001) reported that *Stemphylium* was causing leaf spot symptoms on spinach.

Host specificity, pathogenicity, and disease severity

There is lack of information on the relationship between saprophytic and pathogenic populations of *Stemphylium* spp. as well as on the possible host-specificity of pathogenic isolates (Köhl et al. 2009). However, Koike et al. (2001) demonstrated that isolates of *S. botryosum* from spinach appear to infect only spinach, and *S. botryosum* isolates from other sources do not infect spinach, thus showing host specificity. Mehta (2001) observed genetic difference between cotton and tomato isolates of *S. solani* causing leaf blight, hence providing evidence that *S. solani* attacking cotton in Brazil belongs to a distinct genotype. Leaf spot disease starts with small, irregular, yellow spots on the leaves of host species. The yellow spots become necrotic from the centre of the lesion outwards with tissue turning brown and the spots spread throughout all leaves of the plant. Ultimately, heavily infected leaves will die (Basallote-Ureba et al. 1999, Crous et al. 2016). Early symptoms of *Stemphylium* infection on garlic leaves appear as small white spots and apical necrosis. These lesions soon develop into larger, elongate white spots that eventually become purple and water soaked (Basallote et al. 1993). Fungal pseudothecia are able to persist on crop residues and ascospores are the primary inoculum in the following season (Basallote-Ureba et al. 1998, 1999). Once the disease is established, conidia form in primary lesions and rapidly disperse to infect healthy plants, resulting in a large decrease in photosynthesis and therefore in bulb yield reduction (Zheng et al. 2010). The occurrence of this disease drastically reduces garlic yield every year, around 70%, in some fields in China (Zheng et al. 2010). Pseudothecia maturation and ascospore discharge are closely associated with high relative humidity and mild temperatures (Prados-Ligero et al. 1998).

Distribution

Both saprotrophic and pathogenic forms of *Stemphylium* occur on a wide range of host plants (Farr et al. 1989). Leaf blight caused by *Stemphylium* spp. (Basallote et al. 1993) has been described in many countries, including India (Raghayendra & Pavgi 1975), South Africa (Aveling & Naude 1992), Spain (Basallote et al. 1993), Australia (Suheri & Price 2000), China (Zheng et al. 2009), England (Ruehle 1930), Malaysia (Nasehi et al. 2014) and Turkey (Polat et al. 2012). *Stemphylium vesicarium* has been reported in Spain, whereas *S. solani* is the most prevalent species recorded in China. *Stemphylium vesicarium* has also been recorded from Po Valley in Italy causing brown spot on leaves and fruits of pear (Ponti et al. 1982). This disease was subsequently found in Spain and France in the late 1980s and first observations of brown spot in The Netherlands and Belgium were reported in the early 1990s (Llorente & Montesinos 2006, Polfliet 2002). *Stemphylium* leaf spot has become a huge challenge for California growers to overcome in producing large volumes of high quality, defect-free spinach (Koike et al. 2001) as well in Arizona, Delaware, Florida, Maryland and Quebec (Mou et al. 2008).

Molecular phylogeny (Table 1, Fig. 1)

Camara et al. (2002) used rDNA-ITS and glyceraldehyde-3-phosphate dehydrogenase (GPD) sequences to confirm the monophyly of the genus *Stemphylium*. An extensive phylogenetic study of *Pleospora* species with *Stemphylium* asexual morphs (Inderbitzin et al. 2009) left many unnamed and potentially new *Stemphylium* species. According to the one fungus-one name concept in the International Code of Nomenclature for algae, fungi and plants (ICN, McNeill et al. 2012), name changes in this genus became necessary. Woudenberg et al. (2017) revised the genus and accepted 28 species based on combined analyses of the ITS, gapdh and cmdA gene regions. ITS, gapdh and cmdA sequence data were analyzed by using 145 strains retrieved from the GeneBank following Woudenberg et al. (2017) (Table 1). Fig. 1 shows the phylogenetic placement of pathogenic isolates of *Stemphylium* species isolated from different host substrates and localities.

Table 1 Isolates used in this study for the analysis of combined ITS, gapdh, cmdA sequence data and their GenBank accession numbers. Bold accession numbers from ex-type strains.

Taxon	Strain no.	ITS	Gapdh	cmdA
Alternaria alternate	GV14-634a1	KU850502	KU850649	KU850790
Stemphylium amaranthi	CBS 124650	KU850503	KU850650	KU850791
	CBS 124651	KU850504	KU850651	KU850792
	CBS 124746	**KU850505**	**KU850652**	**KU850793**
	CBS 124750	KU850506	KU850653	KU850794
	CBS 124753	KU850507	KU850654	KU850795
	CBS 124984	KU850508	KU850655	KU850796
	CBS 124985	KU850509	KU850656	KU850797
	CBS 136589	KU850510	KU850657	KU850798
	CBS 338.73	KU850511	KU850658	KU850799
Stemphylium astragali	CBS 116583	KU850512	KU850659	KU850800
Stemphylium beticola	CBS 378.54	KU850513	KU850660	KU850801
	CBS 116599	KU850514	KU850661	KU850802
	CBS 133512	KU850515	KU850662	KU850803

Table 1 Continued.

Taxon	Strain no.	ITS	gapdh	cmdA
	CBS 133892	KU850516	KU850663	KU850804
	CBS 136590	KU850517	KU850664	KU850805
	CBS 136699	KU850518	KU850665	KU850806
	CBS 137492	KU850519	KU850666	KU850807
	CBS 141024	**KU850520**	**KU850667**	**KU850808**
	CBS 141025	KU850521	KU850668	KU850809
	CBS 141026	KU850522	KU850669	KU850810
	GV11-196a1-3	KU850523	KU850670	KU850811
	GV12-275a1	KU850524	KU850671	KU850812
	GV12-276a1	KU850525	KU850672	KU850813
	GV12-287a1	KU850526	KU850673	KU850814
	GV12-336a1	KU850527	KU850674	KU850815
	GV12-356a1	KU850528	KU850675	KU850816
	GV12-367a1	KU850529	KU850676	KU850817
	GV12-368a1	KU850530	KU850677	KU850818
	GV12-403a1	KU850531	KU850678	KU850819
	GV13-425a1	KU850532	KU850679	KU850820
	GV13-436c2	KU850533	KU850680	KU850821
	GV14-693a1	KU850534	KU850681	KU850822
	IFZ2013-024	KU850535	KU850682	KU850823
	IFZ2013-035	KU850536	KU850683	KU850824
	IFZ2014-020	KU850537	KU850684	KU850825
Stemphylium botryosum	**CBS 714.68**	**KC584238**	**AF443881**	**KU850826**
	CBS 116596	KU850538	KU850685	KU850827
Stemphylium callistephi	**CBS 527.50**	**KU850539**	**KU850686**	**KU850828**
Stemphylium canadense	**CBS 116602**	**KU850641**	**KU850782**	**KU850932**
	CBS 118081	KU850642	KU850783	KU850933
Stemphylium chrysanthemicola	**CBS 117255**	**KU850640**	**KU850781**	**KU850931**
Stemphylium drummondii	**CBS 346.83**	**GQ395365**	**KU850687**	**KU850829**
Stemphylium eturmiunum	CBS 668.80	KU850540	KU850688	KU850830
	CBS 109845	**KU850541**	**KU850689**	**KU850831**
	CBS 122124	KU850542	KU850690	KU850832
	CBS 122641	KU850543	KU850691	KU850833
	CBS 124652	KU850544	KU850692	KU850834
	CBS 133528	KU850545	KU850693	KU850835
	CBS 138495	KU850546	KU850694	KU850836
Stemphylium gracilariae	CBS 308.36	KU850547	KU850695	KU850837
	CBS 273.55	KU850548	KU850696	KU850838
	CBS 482.90	**KU850549**	**AF443883**	**KU850839**
	CBS 115179	KU850550	KU850697	KU850840
	CBS 115180	KU850551	KU850698	KU850841
	CBS 125060	KU850552	KU850699	KU850842
Stemphylium halophilum	**CBS 337.73**	**KU850553**	**KU850700**	**KU850843**
	CBS 410.73	KU850554	KU850701	KU850844

Table 1 Continued.

Taxon	Strain no.	ITS	gapdh	cmdA
Stemphylium ixeridis	**CBS 124748**	**KU850590**	**KU850737**	**KU850881**
Stemphylium lancipes	CBS 101217	KU850594	KU850741	KU850885
	CBS 116584	KU850595	AF443886	KU850886
	CBS 133314	KU850596	KU850742	KU850887
Stemphylium loti	**CBS 407.54**	**KU850597**	**KU850743**	**KU850888**
Stemphylium lucomagnoense	**CBS 116601**	**KU850629**	**KU850770**	**KU850920**
Stemphylium lycii	CBS 115192	KU850598	KU850744	KU850889
	CBS 116582	KU850599	KU850745	KU850890
	CBS 124982	KU850600	KU850746	KU850891
	CBS 125240	KU850601	KU850747	KU850892
	CBS 125241	**KU850602**	**KU850748**	**KU850893**
Stemphylium lycopersici	CBS 333.73	KU850603	KU850749	KU850894
	CBS 436.76	KU850604	KU850750	KU850895
	CBS 463.78	KU850605	KU850751	KU850896
	CBS 321.87	KU850606	KU850752	KU850897
	CBS 116585	KU850607	AY317010	KU850898
	CBS 116587	KU850608	KU850753	KU850899
	CBS 120325	KU850609	KU850754	KU850900
	CBS 120326	KU850610	KU850755	KU850901
	CBS 122639	**KU850611**	**KU850756**	**KU850902**
	CBS 122803	KU850612	KU850757	KU850903
	CBS 123008	KU850613	KU850758	KU850904
	CBS 124980	KU850614	KU850759	KU850905
	CBS 124981	KU850615	KU850760	KU850906
	CBS 124983	KU850616	KU850761	KU850907
	CBS 135778	KU850617	AY317026	KU850908
Stemphylium majusculum	**CBS 717.68**	**KU850618**	**AF443891**	**KU850909**
Stemphylium novae-zelandiae	CBS 138157	KU850630	KU850771	KU850921
	CBS 138295	**KU850631**	**KU850772**	**KU850922**
Stemphylium paludiscirpi	**CBS 109842**	**KU850620**	**KU850762**	**KU850911**
Stemphylium sarciniforme	CBS 335.33	KU850621	KU850763	KU850912
	CBS 364.49	KU850622	KU850764	KU850913
	CBS 110049	KU850591	KU850738	KU850882
	CBS 116579	KU850623	AF443892	KU850914
	CBS 116581	KU850592	KU850739	KU850883
	CBS 133723	KU850624	KU850765	KU850915
	CBS 136810	KU850593	KU850740	KU850884
	CBS 138345	KU850625	KU850766	KU850916
Stemphylium simmonsii	CBS 716.68	KU850632	KU850773	KU850923
	CBS 116598	KU850633	KU850774	KU850924
	CBS 116603	KU850634	KU850775	KU850925
	CBS 116604	KU850635	KU850776	KU850926
	CBS 133515	KU850636	KU850777	KU850927

Table 1 Continued.

Taxon	Strain no.	ITS	gapdh	cmdA
	CBS 133518	**KU850637**	**KU850778**	**KU850928**
	CBS 133894	KU850638	KU850779	KU850929
	CBS 134496	KU850639	KU850780	KU850930
Stemphylium solani	CBS 408.54	KU850626	KU850767	KU850917
	CBS 116586	**KU850627**	**KU850768**	**KU850918**
	CBS 118082	KU850628	KU850769	KU850919
Stemphylium symphyti	**CBS 115268**	**KU850643**	**KU850784**	**KU850934**
	CBS 118796	KU850644	KU850785	KU850935
	CBS 138069	KU850645	KU850786	KU850936
	CBS 138070	KU850646	KU850787	KU850937
Stemphylium trifolii	**CBS 116580**	**KU850647**	**KU850788**	**KU850938**
Stemphylium triglochinicola	**CBS 718.68**	**KU850648**	**KU850789**	**KU850939**
Stemphylium vesicarium	CBS 155.24	KU850555	KU850702	KU850845
	CBS 157.24	KU850556	KU850703	KU850846
	CBS 184.25	KU850557	KU850704	KU850847
	CBS 273.31	KU850558	KU850705	KU850848
	CBS 274.31	KU850559	KU850706	KU850849
	CBS 307.36	KU850560	KU850707	KU850850
	CBS 156.45	KU850561	KU850708	KU850851
	CBS 322.49	KU850562	KU850709	KU850852
	CBS 370.51	KU850563	KU850710	KU850853
	CBS 368.59	KU850564	KU850711	KU850854
	CBS 715.68	KU850565	KU850712	KU850855
	CBS 406.76	KU850566	KU850713	KU850856
	CBS 205.82	KU850567	KU850714	KU850857
	CBS 191.86	KC584239	AF443884	KU850858
	CBS 192.86	KU850568	KU850715	KU850859
	CBS 311.92	KU850569	KU850716	KU850860
	CBS 486.92	KU850570	KU850717	KU850861
	CBS 109843	KU850571	KU850718	KU850862
	CBS 109844	KU850572	KU850719	KU850863
	CBS 115182	KU850573	KU850720	KU850864
	CBS 115204	KU850574	KU850721	KU850865
	CBS 122640	KU850575	KU850722	KU850866
	CBS 123005	KU850576	KU850723	KU850867
	CBS 123803	KU850577	KU850724	KU850868
	CBS 124279	KU850578	KU850725	KU850869
	CBS 124747	KU850579	KU850726	KU850870
	CBS 124749	KU850580	KU850727	KU850871
	CBS 124751	KU850581	KU850728	KU850872
	CBS 124752	KU850582	KU850729	KU850873
	CBS 125242	KU850583	KU850730	KU850874
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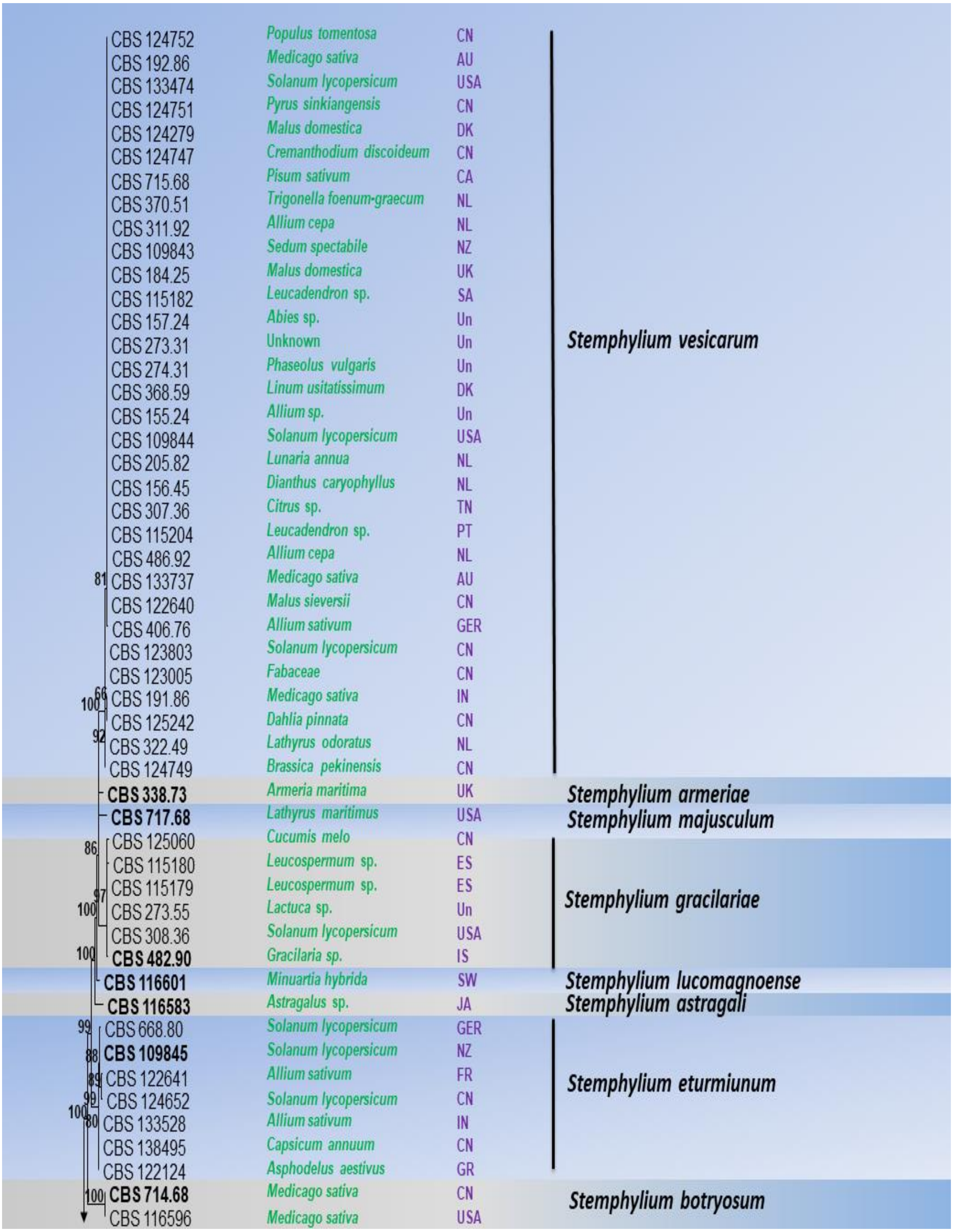
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CBS 274.31 Phaseolus vulgaris Un
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CBS 156.45 Dianthus caryophyllus NL
CBS 307.36 Citrus sp. TN
CBS 115204 Leucadendron sp. PT
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CBS 124749 Brassica pekinensis CN
Stemphylium vesicarum
CBS 338.73 Armeria maritima UK
Stemphylium armeriae
CBS 717.68 Lathyrus maritimus USA
Stemphylium majusculum
CBS 125060 Cucumis melo CN
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CBS 273.55 Lactuca sp. Un
CBS 308.36 Solanum lycopersicum USA
CBS 482.90 Gracilaria sp. IS
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CBS 116601 Minuartia hybrida SW
Stemphylium lucomagnoense
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Stemphylium astragali
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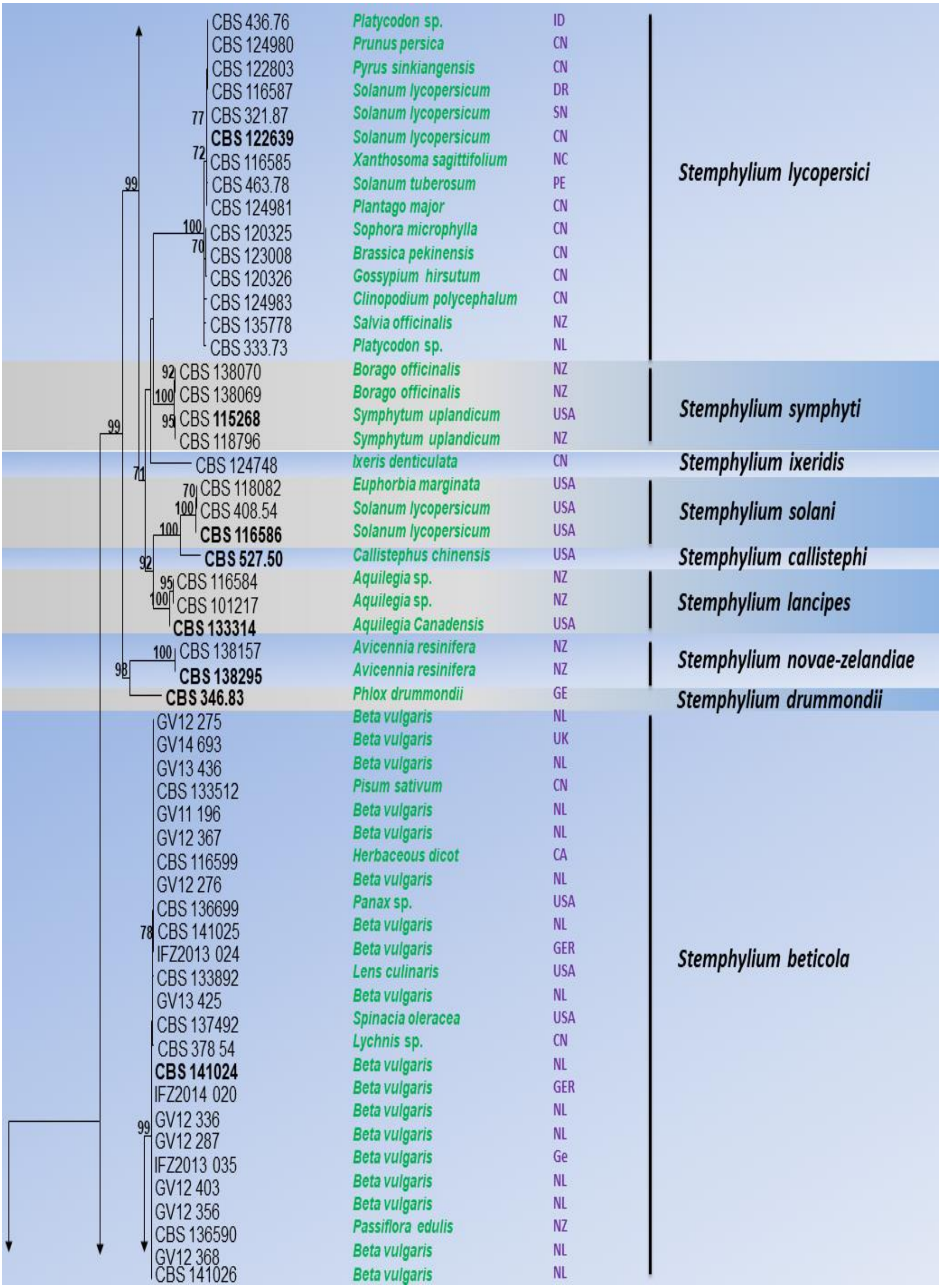
Stemphylium botryosum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Stemphylium lycopersici
92 CBS 138070 Borago officinalis NZ
100 CBS 138069 Borago officinalis NZ
95 CBS 115268 Symphytum uplandicum USA
CBS 118796 Symphytum uplandicum NZ
Stemphylium symphyti
CBS 124748 Ixeris denticulata CN
Stemphylium ixeridis
70 CBS 118082 Euphorbia marginata USA
100 CBS 408.54 Solanum lycopersicum USA
100 CBS 116586 Solanum lycopersicum USA
Stemphylium solani
CBS 527.50 Callistephus chinensis USA
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95 CBS 116584 Aquilegia sp. NZ
100 CBS 101217 Aquilegia sp. NZ
CBS 133314 Aquilegia Canadensis USA
Stemphylium lancipes
100 CBS 138157 Avicennia resinifera NZ
98 CBS 138295 Avicennia resinifera NZ
Stemphylium novae-zelandiae
CBS 346.83 Phlox drummondii GE
Stemphylium drummondii
99
99
71
92
GV12 275 Beta vulgaris NL
GV14 693 Beta vulgaris UK
GV13 436 Beta vulgaris NL
CBS 133512 Pisum sativum CN
GV11 196 Beta vulgaris NL
GV12 367 Beta vulgaris NL
CBS 116599 Herbaceous dicot CA
GV12 276 Beta vulgaris NL
CBS 136699 Panax sp. USA
78 CBS 141025 Beta vulgaris NL
IFZ2013 024 Beta vulgaris GER
CBS 133892 Lens culinaris USA
GV13 425 Beta vulgaris NL
CBS 137492 Spinacia oleracea USA
CBS 378 54 Lychnis sp. CN
CBS 141024 Beta vulgaris NL
IFZ2014 020 Beta vulgaris GER
99 GV12 336 Beta vulgaris NL
GV12 287 Beta vulgaris NL
IFZ2013 035 Beta vulgaris Ge
GV12 403 Beta vulgaris NL
GV12 356 Beta vulgaris NL
CBS 136590 Passiflora edulis NZ
GV12 368 Beta vulgaris NL
CBS 141026 Beta vulgaris NL
Stemphylium beticola

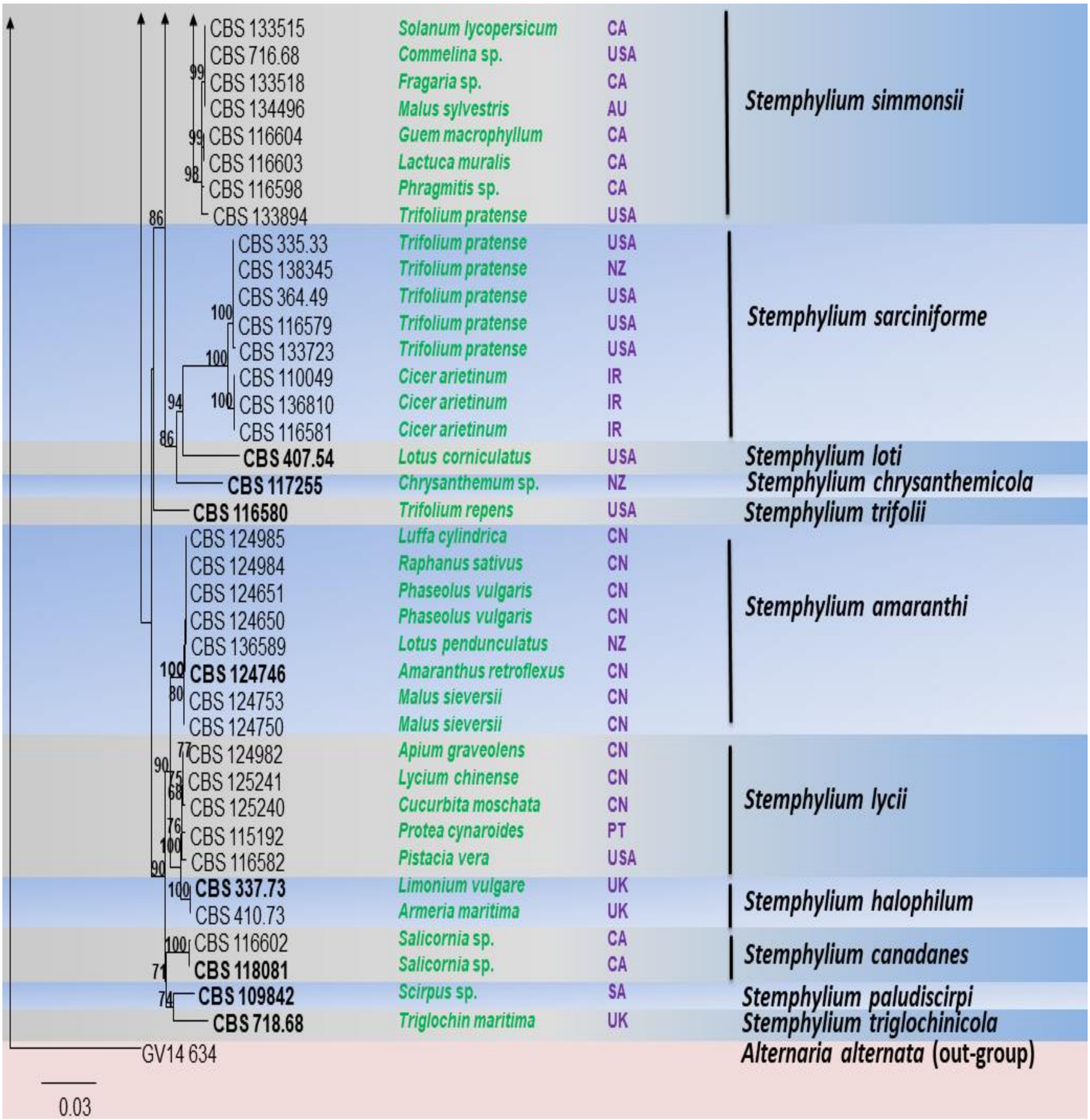

Fig. 1 – RAxML phylogenetic tree based on combined ITS, gapdh and cmdA sequence data from taxa of *Stemphylium*. Bootstrap support values for ML equal or greater than 65% are given above each branch. The tree is rooted to *Alternaria alternata* (GV14-634a1). AU: Australia; CN: China; DK: Denmark; DR: Dominican Republic; FR: France; GR: Greece; GER: Germany; IN: India; ID: Indonesia; IR: Iran; IS: Israel; JA: Japan; KA: Canada; NC: New Caledonia; NL: Netherlands; NZ: New Zealand; PE: Peru; PT: Portugal; SA: South Africa; ES: Spain; SN: Senegal; SW: Switzerland; TN: Tunisia; UK: United Kingdom; Un: Unknown; USA: America.

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