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Species concepts in *Calonectria* (*Cylindrocladium*)

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Abstract: Species of *Calonectria* and their *Cylindrocladium* anamorphs are important plant pathogens worldwide. At present 52 *Cylindrocladium* spp. and 37 *Calonectria* spp. are recognised based on sexual compatibility, morphology and phylogenetic inference. The polyphasic approach of integrating Biological, Morphological and Phylogenetic Species Concepts has revolutionised the taxonomy of fungi. This review aims to present an overview of published research on the genera *Calonectria* and *Cylindrocladium* as they pertain to their taxonomic history. The nomenclature as well as future research necessary for this group of fungi are also briefly discussed.

Key words: *Calonectria*, *Cylindrocladium*, species concepts, nomenclature, pathogenicity.

INTRODUCTION

The genus *Calonectria* (*Ca.*) was erected in 1867 by De Notaris, based on *Ca. daldiniana* collected on leaves of *Magnolia grandiflora* (*Magnoliaceae*), in Daldini, Italy (Rossman 1979a). Rossman (1979a) later reduced *Ca. daldiniana* to synonymy under *Ca. pyrochroa*, and defined this nectrioid fungus as having an ascocarp wall structure that is brightly coloured, changing to blood-red in 3 % KOH solution, warty to scaly and with a *Cylindrocladium* (*Cy.*) anamorph (Rossman 1993, Rossman *et al.* 1999). However, due to the restricted morphological characteristics of the teleomorph (Rossman 1979b, 1983), specimens can in many cases only be identified to species level if the anamorph is present (Schoch *et al.* 2000b, Crous 2002).

The anamorph genus *Cylindrocladium*, which is based on *Cy. scoparium,* was first described by Morgan (1892) in the U.S.A., where it was found growing as saprobe on a pod of *Gleditsia triacanthos*. Although Morgan (1892) failed to mention the stipe extension terminating in a vesicle of characteristic shape, he defined the genus as having branched conidiophores producing cylindrical conidia. This fungus has a wide distribution in sub-tropical and tropical regions of the world, and species are pathogenic to numerous plants (Crous 2002).

The aim of this review is to present an overview of published research on the genus *Calonectria* and their *Cylindrocladium* anamorphs. More specifically, the application of three types of species concepts is considered as they pertain to the taxonomic history of this genus. Although several species concepts (Mayden 1997) have been proposed, only the Morphological Species Concept (MSC), the Biological Species Concept (BSC) and the Phylogenetic Species Concept (PSC) are treated, as these have been most widely applied to *Calonectria*. Several reviews (Rossman 1996, Brasier 1997, Harrington & Rizzo 1999, Taylor *et al.* 1999, 2000, Seifert *et al.* 2000, Kohn 2005) have treated the various species concepts applied to the taxonomy of fungi and this topic is not treated other than in the manner in which it applies to *Calonectria.*

TAXONOMIC HISTORY

Calonectria resides in the *Nectriaceae*, one of three families in *Hypocreales*, an order that has been reviewed extensively (Rogerson 1970, Rossman 1983, Rossman *et al.* 1996, 1999). The *Nectriaceae* is circumscribed as having uniloculate ascomata that are orange to purple and not immersed in well-developed stromata (Rossman *et al.* 1999). The family includes approximately 20 genera of socio-economic importance and of these, *Calonectria* is most clearly distinguished from the others by its *Cylindrocladium* anamorphs and relevance as plant pathogens.

The first monograph of *Cylindrocladium* by Boedijn & Reitsma (1950), introduced seven *Cylindrocladium* species with one *Calonectria* connection. Later, in her treatment of *Calonectria*, Rossman (1983) recognised five species including the novel *Ca. ophiospora*. However, this species description did not include the anamorph state. The circumscribed type, *Ca. pyrochoa*, was also incorrectly reduced to synonymy with several other species based only on the teleomorph morphology. Peerally (1991a) highlighted this in a monograph of *Cylindrocladium*, where he regarded the anamorph morphology as important in distinguishing species of *Calonectria*. He subsequently recognised 10 *Calonectria* species with their *Cylindrocladium* anamorphs, including an additional 16 *Cylindrocladium* species not associated with a teleomorph. However, he mistakenly reduced *Cylindrocladiella*, a genus that accommodates *Cylindrocladium*-like species with small conidia (Boesewinkel 1982) and *Nectricladiella* teleomorphs, to synonymy with *Cylindrocladium* (Schoch *et al*. 2000b).

The monograph of *Cylindrocladium* by Crous & Wingfield (1994) entrenched the importance of anamorph characteristics in the taxonomy of *Calonectria* spp. In this monograph, 22

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Cylindrocladium species and one variety were recognised, associated with 16 *Calonectria* species. Five species were assigned to the genus *Cylindrocladiella* based on morphological characters of the holomorph. The focus on anamorph characteristics is perpetuated in the most recent monograph (Crous 2002), which recognised 28 *Calonectria* species, all associated with *Cylindrocladium* anamorphs and an additional 18 *Cylindrocladium* species for which teleomorph states were not known. Of the latter group, seven taxa were of doubtful authenticity. Presently, 37 *Calonectria* and 52 *Cylindrocladium* species are recognised (Table 1; Crous 2002, Crous *et al.* 2004b, 2006a; Gadgil & Dick 2004, Lombard *et al.* 2009, 2010).

A general search on MycoBank (www.mycobank.org; Crous *et al.* 2004a, Robert *et al.* 2005) and Index Fungorum (www.indexfungorum.org) resulted in a total of 291 and 261 name records respectively for *Calonectria*. A similar search for *Cylindrocladium* species on both electronic databases indicated a total of 98 and 93 names respectively.

Table 1. List of recognised *Calonectria* species and their respective *Cylindrocladium* anamorphs.

Teleomorph	Reference	Anamorph	Reference
Calonectria acicola Gadgil & M.A. Dick	Gadgil & Dick 2004	*Cylindrocladium acicola* Gadgil & M.A. Dick	Gadgil & Dick 2004
Calonectria asiatica Crous & Hywel-Jones	Crous *et al.* 2004b	*Cylindrocladium asiaticum* Crous & Hywel-Jones	Crous *et al.* 2004b
Calonectria avesiculata T.S. Schub., Ell-Gholl, Alfieri & Schoult.	Schubert *et al.* 1989	*Cylindrocladium avesiculatum* D.L. Gill, Alfieri & Sobers	Gill *et al.* 1971
Calonectria brassicae (Panwar & Bohra) L. Lombard, M.J. Wingf. & Crous	Lombard *et al.* 2009		
Calonectria brachiatica L. Lombard, M.J. Wingf. & Crous	Lombard *et al.* 2009		
Calonectria cerciana L. Lombard, M.J. Wingf. & Crous	Lombard *et al.* 2010		
Calonectria clavata Alfieri, El-Gholl & E.L. Barnard	El-Gholl *et al.* 1993b	*Cylindrocladium flexuosum* Crous	Crous *et al.* 1995
Calonectria colhounii Peerally	Peerally 1973	*Cylindrocladium colhounii* Peerally	Peerally 1973
Calonectria colombiensis Crous	Crous *et al.* 2004b	*Cylindrocladium colombiense* Crous	Crous *et al.* 2004b
Calonectria gracilipes Crous & Mchau	Crous *et al.* 1997a	*Cylindrocladium graciloideum* Crous & Mchau	Crous *et al.* 1997a
Calonectria gracilis Crous, M.J. Wingf. & Alfenas	Crous *et al.* 1997b	*Cylindrocladium pseudogracile* Crous	Crous *et al.* 1997b
Calonectria hederae G. Arnaud ex C. Booth	Booth & Murray 1960	*Cylindrocladium hederae* G. Arnaud ex Peerally	Peerally 1991a
Calonectria hongkongensis Crous	Crous *et al.* 2004b	*Cylindrocladium hongkongense* Crous	Crous *et al.* 2004b
Calonectria ilicicola Boedijn & Reitsma	Boedijn & Reitsma 1950	*Cylindrocladium parasiticum* Crous, M.J. Wingf. & Alfenas	Crous *et al.* 1993d
Calonectria indusiata (Seaver) Crous	Crous 2002	*Cylindrocladium theae* (Petch) Subram	Alfieri *et al.* 1972
Calonectria insularis C.L. Schoch & Crous	Schoch *et al.* 1999	*Cylindrocladium insulare* C.L. Schoch & Crous	Schoch *et al.* 1999
Calonectria kyotensis Terash.	Terashita 1968	*Cylindrocladium floridanum* Sobers & C.P. Seym.	Sobers & Seymour 1967
Calonectria leguminum (Rehm) Crous	Crous 2002	*Cylindrocladium leguminum* Crous	Crous 2002
Calonectria macroconidialis (Crous, M.J. Wingf. & Alfenas) Crous	Crous *et al.* 1999	*Cylindrocladium macroconidiale* (Crous, M.J. Wingf. & Alfenas) Crous	Crous *et al.* 1999
Calonectria madagascariensis Crous	Crous 2002	*Cylindrocladium madagascariense* Crous	Crous 2002
Calonectria mexicana C.L. Schoch & Crous	Schoch *et al.* 1999	*Cylindrocladium mexicanum* C.L. Schoch & Crous	Schoch *et al.* 1999
Calonectria morganii Crous, Alfenas & M.J. Wingf.	Crous *et al.* 1993a	*Cylindrocladium scoparium* Morgan	Morgan 1892
Calonectria multiseptata Crous & M.J. Wingf.	Crous *et al.* 1998b	*Cylindrocladium multiseptatum* Crous & M.J. Wingf.	Crous *et al.* 1998b
Calonectria naviculata Crous & M.J. Wingf.	Crous *et al.* 1994	*Cylindrocladium naviculatum* Crous & M.J. Wingf.	Crous *et al.* 1994
Calonectria ovata D. Victor & Crous	Victor *et al.* 1997	*Cylindrocladium ovatum* El-Gholl , Alfenas, Crous & T.S. Schub.	El-Gholl *et al.* 1993a
Calonectria pauciramosa C.L. Schoch & Crous	Schoch *et al.* 1999	*Cylindrocladium pauciramosum* C.L. Schoch & Crous	Schoch *et al.* 1999
Calonectria pseudoreteaudii L. Lombard, M.J. Wingf. & Crous	Lombard *et al.* 2010		
Calonectria pseudospathiphylli J.C. Kang, Crous & C.L. Schoch	Kang *et al.* 2001b	*Cylindrocladium pseudospathiphylli* J.C. Kang, Crous & C.L. Schoch	Kang *et al.* 2001b
Calonectria pteridis Crous, M.J. Wingf. & Alfenas	Crous *et al.* 1993c	*Cylindrocladium pteridis* F.A. Wolf	Wolf 1926
Calonectria pyrochroa (Desm.) Sacc.	Rossman 1979a	*Cylindrocladium ilicicola* (Hawley) Boedijn & Reitsma	Boedjin & Reitsma 1950
Calonectria queenslandica L. Lombard, M.J. Wingf. & Crous	Lombard *et al.* 2010		
Calonectria reteaudii (Bugnic.) C. Booth	Booth 1966	*Cylindrocladium reteaudii* (Bugnic.) Boesew.	Boesewinkel 1982

Table 1. (Continued).

Teleomorph	Reference	Anamorph	Reference
Calonectria rumohrae El-Gholl & Alfenas	El-Gholl *et al.* 1997	*Cylindrocladium rumohrae* El-Gholl & Alfenas	El-Gholl *et al.* 1997
Calonectria scoparia Ribeiro & Matsuoka ex Peerally	Peerally 1991a	*Cylindrocladium candelabrum* Viégas	Crous 2002
Calonectria spathiphylli El-Gholl, J.Y. Uchida, Alfenas, T.S. Schub., Alfieri & A.R. Chase	El-Gholl *et al.* 1992	*Cylindrocladium spathiphylli* Schoult., El-Gholl & Alfieri	Schoulties *et al.* 1982
Calonectria spathulata El-Gholl, Kimbr., E.L. Barnard, Alfieri & Schoult.	Crous & Wingfield 1994	*Cylindrocladium spathulatum* El-Gholl, Kimbr., E.L. Barnard, Alfieri & Schoult.	Crous & Wingfield 1994
Calonectria terrae-reginae L. Lombard, M.J. Wingf. & Crous	Lombard *et al.* 2010		
Calonectria variabilis Crous, B.J.H. Janse, D. Victor, G.F. Marais & Alfenas	Crous *et al.* 1993b	*Cylindrocladium variabile* Crous, B.J.H. Janse, D. Victor, G.F. Marais & Alfenas	Crous *et al.* 1993b
		Cylindrocladium angustatum Crous & El-Gholl	Crous *et al.* 2000
		Cylindrocladium australiense Crous & K.D. Hyde	Crous *et al.* 2006a
		Cylindrocladium canadense J.C. Kang, Crous & C.L. Schoch	Kang *et al.* 2001b
		Cylindrocladium chinense Crous	Crous *et al.* 2004b
		Cylindrocladium citri (H.S. Fawc. & Klotz) Boedijn & Reitsma	Boedjin & Reitsma 1950
		Cylindrocladium curvatum Boedijn & Reitsma	Boedjin & Reitsma 1950
		Cylindrocladium curvisporum Crous & D. Victor	Victor *et al.* 1997
		Cylindrocladium ecuadoriae Crous & M.J. Wingf.	Crous *et al.* 2006a
		Cylindrocladium gordoniae Leahy, T.S. Schub. & El-Gholl	Leahy *et al.* 2000
		Cylindrocladium hawksworthii Peerally	Peerally 1991b
		Cylindrocladium hurae (Linder & Whetzel) Crous	Crous 2002
		Cylindrocladium indonesiae Crous	Crous *et al.* 2004b
		Cylindrocladium leucothoës El-Gholl, Leahy & T.S. Schub.	El-Gholl *et al.* 1989
		Cylindrocladium malesianum Crous	Crous *et al.* 2004b
		Cylindrocladium multiphialidicum Crous, Simoneau & Risède	Crous *et al.* 2004b
		Cylindrocladium pacificum J.C. Kang, Crous & C.L. Schoch	Kang *et al.* 2001b
		Cylindrocladium penicilloides (Tubaki) Tubaki	Tubaki 1958
		Cylindrocladium pseudonaviculatum Crous, J.Z. Groenew. & C.F. Hill	Crous *et al.* 2002
		Cylindrocladium sumatrense Crous	Crous *et al.* 2004b

NOMENCLATURE OF *CALONECTRIA*

The nomenclature of pleomorphic fungi has been a topic of substantial debate during the course of the past two decades (Gams 1991, Cannon & Kirk 2000, Hawksworth 2004, 2005). The separate naming of anamorphs (mitotic morphs) and teleomorphs (meiotic morphs) has resulted in confusion, especially for non-taxonomists (Cannon & Kirk 2000). This is especially evident where teleomorph species epithets are different to those of their anamorphs and also where more than one anamorph (synanamorph) is found. The naming of fungal morphs based on the International Code of Botanical Nomenclature (ICBN; McNeill *et al.* 2005) and in particular following strict interpretation of Article 59 of the Code has now been unsatisfactory for many fungal groups due to our ability to connect morphs using molecular evidence, and there are increasing calls for further changes to be made.

Recent alterations to the Code at the ICBN meeting in Vienna allows for anamorphic fungi to be named in teleomorph genera, but these are vulnerable to be superseded by a connected teleomorph name in the future (Hawksworth 2004, McNeill *et al.* 2005, P. Cannon pers. comm.). Although there are several *Cylindrocladium* species without *Calonectria* connections (Crous 2002, Crous *et al.* 2004b, 2006a), we believe that new species should be described in *Calonectria* irrespective of whether a teleomorph is known or not. This follows a clear view based on phylogenetic inference that *Cylindrocladium* spp. all have *Calonectria* states (Schoch *et al.* 1999, 2000a, 2000b, Crous 2002, Crous *et al.* 2004b, 2006a). Following the approach of Crous *et al.* (2006b, 2008, 2009a, b) with other fungal groups, Lombard *et al.* (2009, 2010) recently described five new species in the genus *Calonectria*, irrespective whether the teleomorph was observed or not. Thus, for taxonomic purposes, *Cylindrocladium* species with known teleomorph states are referred to as *Calonectria* in this review.

IMPORTANCE OF *CALONECTRIA*

The genus *Calonectria* was initially regarded as a saprobe as no disease symptoms could be induced by inoculating a suspected host (Graves 1915). The first proof of pathogenicity of these fungi was provided by Massey (1917), and subsequently by Anderson (1919), who proved pathogenicity of *Ca. morganii* (as *Cy. scoparium*). Subsequently, *Calonectria* species have been associated with a wide range of disease symptoms on a large number of hosts worldwide (Crous 2002; Table 2; Figs 1–2). In the past, several authors have indicated that *Calonectria* species cause disease on plants residing in approximately 30 plant families (Booth & Gibson 1973, French & Menge 1978, Peerally 1991a, Wiapara *et al.* 1996, Schoch *et al.* 1999). Upon closer inspection, the number of plant families is actually closer to 100 (Table 2) and approximately 335 plant host species (Crous 2002). The plant hosts include important forestry, agricultural and horticultural crops and the impact of these plant pathogens has likely been underestimated.

The majority of disease reports associated with *Calonectria* species in forestry include hosts in five plant families, of which the most important are associated with *Fabaceae* (*Acacia* spp.), *Myrtaceae* (*Eucalyptus* spp.) and *Pinaceae* (*Pinus* spp.). Disease symptoms (Figs 1–2) include cutting rot (Crous *et al.* 1991, Crous 2002, Lombard *et al.* 2009, 2010), damping-off (Batista 1951, Cox 1953, Terashita & Itô 1956, Sharma & Mohanan 1982, Sharma *et al.* 1984, Crous *et al.* 1991, Brown & Ferreira 2000, Crous 2002, Taniguchi *et al.* 2008) leaf diseases (Cox 1953, Hodges & May 1972, Barnard 1984, Sharma *et al.* 1984, El-Gholl *et al.* 1986, Peerally *et al.* 1991a, Crous *et al.* 1993b, Crous & Wingfield 1994, Crous *et al.* 1998b, Schoch & Crous 1999, Schoch *et al.* 1999, Booth *et al.* 2000, Park *et al.* 2000, Crous & Kang 2001, Gadgil & Dick 2004), shoot blight (Sharma *et al.* 1984, Crous *et al.* 1991, 1998b, Crous & Kang 2001), stem cankers (Cox 1953, Sharma *et al.* 1984, 1985, Crous *et al.* 1991, Lombard *et al.* 2009) and root rot (Cox 1953, Hodges & May 1972, Cordell & Skilling 1975, Mohanan & Sharma 1985, Crous *et al.* 1991, Lombard *et al.* 2009). The majority of these diseases is associated with seedling and cutting production in forestry nurseries, but in a few cases *Cylindrocladium* species have also been reported from older, established commercial plantations. In these cases the pathogens have been reported to cause leaf diseases and shoot blight resulting in defoliation of trees leading to loss of vigour (Hodges & May 1972, Sharma *et al.* 1985, Booth *et al.* 2000, Park *et al.* 2000, Crous & Kang 2001, Crous 2002, Old *et al.* 2003, Rodas *et al.* 2005).

In agriculture, *Calonectria* species have been reported to cause diseases on several economically important crops. Several plant families of agricultural importance are susceptible to *Calonectria* infections, including *Fabaceae* and *Solanaceae*. Important diseases in these families are Cylindrocladium black rot of *Arachis hypogea* (peanut) and red crown rot of *Glycine max* (soybean) caused by *Ca. ilicicola* and *Ca. pyrochroa* in the USA (Bell & Sobers 1966, Beute & Rowe 1973, Rowe *et al.* 1973, Sobers & Littrell 1974, Rowe & Beute 1975, Phipps *et al.* 1976, Johnson 1985, Dianese *et al.* 1986, Berner *et al.* 1988, 1991, Culbreath *et al.* 1991, Porter *et al.* 1991, de Varon 1991, Hollowell *et al.* 1998, Kim *et al* 1998) and

Table 2. Plant families that are host to *Calonectria* species and number of known plant host species in each family (Crous 2002).

Host Plant family	Host species	Host Plant family	Host species	Host Plant family	Host species	Host Plant family	Host species
Actinidiaceae	2	*Cornaceae*	1	*Malipighiaceae*	2	*Pteridaceae*	1
Altingiaceae	1	*Crassulaceae*	1	*Malvaceae*	6	*Rhamnaceae*	1
Anacardiaceae	3	*Cupressaceae*	4	*Meliaceae*	2	*Rhizophoraceae*	1
Annonaceae	4	*Curcurbitaceae*	3	*Moraceae*	2	*Rosaceae*	10
Aparagaceae	1	*Cycadaceae*	1	*Musaceae*	2	*Rubiaceae*	2
Apiaceae	1	*Davalliaceae*	1	*Myristicaceae*	1	*Ruscaceae*	1
Apocynaceae	2	*Dennstaedtiaceae*	1	*Myrsinaceae*	1	*Rutaceae*	3
Aquifoliaceae	4	*Dilleniaceae*	1	*Myrtaceae*	31	*Salicaceae*	3
Araceae	5	*Dipterocarpaceae*	1	*Nelumbonaceae*	1	*Sapindaceae*	4
Araliaceae	2	*Dryopteridaceae*	2	*Nepenthaceae*	1	*Sapotaceae*	3
Arecaceae	21	*Ebenaceae*	1	*Nothofagaceae*	1	*Sarraceniaceae*	1
Araucariaceae	2	*Ericaceae*	14	*Nymphaeaceae*	1	*Saxifragaceae*	1
Aspleniaceae	1	*Euphorbiaceae*	6	*Oleaceae*	1	*Solanaceae*	4
Asteraceae	5	*Fabaceae*	57	*Onagraceae*	2	*Sterculiaceae*	2
Berberidaceae	2	*Fagaceae*	4	*Orchidaceae*	1	*Strelilziaceae*	2
Betulaceae	1	*Ginkgoaceae*	1	*Phytolaccaceae*	1	*Theaceae*	1
Bixaceae	1	*Juglandaceae*	2	*Pinaceae*	17	*Ulmaceae*	1
Bromeliaceae	3	*Lauraceae*	6	*Piperaceae*	1	*Verbenaceae*	1
Buxaceae	1	*Laxmanniaceae*	1	*Platanaceae*	1	*Vitaceae*	2
Caricaceae	2	*Lecythidaceae*	1	*Plumbaginaceae*	1	*Vochysiaceae*	1
Caryophyllaceae	1	*Leeaceae*	1	*Poaceae*	6	*Xanthorrhoeaceae*	1
Celastraceae	1	*Linaceae*	1	*Polygalaceae*	1	*Zingiberaceae*	1
Chenopodiaceae	1	*Lomariopsidaceae*	1	*Polygonaceae*	3		
Combretaceae	3	*Lythraceae*	1	*Polypodiaceae*	1		
Convolvulaceae	1	*Magnoliaceae*	2	*Proteaceae*	7		

Fig. 1. Disease symptoms associated with *Calonectria* (*Cylindrocladium*). A. Cutting rot of *Vallea stipolaris*. B. Cutting rot of *Eucalyptus* sp. C. Defoliated *Eucalyptus* trees in a plantation. D. Leaf and shoot blight of a *Eucalyptus* sp. E. Cylindrocladium leaf blight of a *Eucalyptus* sp. F. Leaf spots on a *Eucalyptus* sp. G–H. Stem cankers on twigs of a *Eucalyptus* sp. I–J. Root and collar rot of *Pinus* spp. K. Root rot of *Eucalyptus* sp. with conidiophores on the root surface.

Cylindrocladium tuber rot of *Solanum tuberosum* (potato) (Boedijn & Reitsma 1950, Bolkan *et al.* 1980, 1981) by *Ca. brassicae* (as *Cy. gracile*) in Brazil. Other diseases associated with *Calonectria* species on agricultural crops include root rot and leaf diseases of fruit bearing and spice plants (Jauch 1943, Wormald 1944, Sobers & Seymour 1967, Nishijima & Aragaki 1973, Milholland 1974, Krausz & Caldwell 1987, Hutton & Sanewski 1989, Anandaraj & Sarma 1992, Risède 1994, Jayasinghe & Wijesundera 1996, Risède & Simoneau 2001, Vitale & Polizzi 2008), post-harvest diseases of fruits (Fawcett & Klotz 1937, Boedijn & Reitsma 1950, Sepiah 1990, Fitzell & Peak 1992, Vaidya & Roa 1992, Sivapalan *et al.* 1998), root and crown rot of *Medicago sativa* (alfalfa) (Ooka & Uchida 1982, Hwang & Flores 1987), and sheath net blotch of *Oryza sativa* (rice) (Crous 2002).

On horticultural crops, *Calonectria* species have been reported mostly from the Northern Hemisphere, especially in gardens and ornamental commercial nurseries in Europe and Asia (Polizzi & Crous 1999, Polizzi 2000, Crous 2002, Henricot & Culham 2002, Pérez-Sierra *et al.* 2007, Polizzi *et al.* 2007a, b, Hirooka *et al.* 2008, Polizzi *et al.* 2009, Vitale *et al.* 2009). Hosts in this sector

include ornamental trees, shrubs and cut-flowers in several plant families, most commonly in *Arecaceae*, *Asteraceae*, *Ericaceae* and *Rosaceae*. A wide range of disease symptoms are recorded including crown-, collar- and root rot, leaf spots, and cutting rot (Massey 1917, Anderson 1919, Aragaki *et al.* 1972, 1988, Peerally 1991b, Uchida & Kadooka 1997, Polizzi & Crous 1999, Polizzi 2000, Crous 2002, Henricot & Culham 2002, Henricot & Beales 2003, Poltronieri *et al.* 2004, Lane *et al.* 2006, Pérez-Sierra *et al.* 2006, 2007, Polizzi *et al.* 2006a, b, 2007a, b, Vitale & Polizzi 2007, Aghajani *et al.* 2008, Hirooka *et al.* 2008, Vitale *et al*. 2008, Polizzi *et al.* 2009, Vitale *et al.* 2009).

MORPHOLOGY

Morphological or phenotypic characters have played a major role in the description of fungal species (Brasier 1997, Taylor *et. al.* 2000) and form the basis of new fungal descriptions as required by the ICBN (McNeill *et al.* 2005). In recent years, the use of morphological characters alone to delimit new species has been set aside to a large extent, with more focus being placed on biological and phylogenetic characters (Rossman 1996, Brasier 1997, Taylor *et al.* 2000). This trend is also evident in recent studies on *Calonectria* species (Crous *et al.* 2004b, 2006a).

The morphology of *Calonectria* and to a greater extent its anamorph, *Cylindrocladium*, has been important in the taxonomic history of these fungi. Prior to the 1990s, identification of species was based on morphological characteristics and to a lesser extent on sexual compatibility using standardised media (Boedijn & Reitsma 1950, Peerally 1991a, Crous *et al.* 1992, Crous & Wingfield 1994, Crous 2002). This resulted in the establishment of several species complexes, as many *Cylindrocladium* species are morphologically very similar. These include the *Ca. scoparia* complex (Schoch *et al.* 1999), *Ca. brassicae* (as *Cy. gracile*) complex (Crous *et al.* 2004b) and *Ca. kyotensis* complex (Crous *et al.* 2006a). Characteristics of the anamorphs that are extensively employed in identifications include vesicle shape, stipe extension length and macroconidial septation and dimensions (Fig. 3) (Boesewinkel 1982, Peerally 1991a, Crous & Wingfield 1994, Crous 2002). The morphological characteristics of the teleomorph (Fig. 4) that are important for identifications are ascospore septation and dimensions, ascospore number within the asci and perithecial colour. Perithecia of *Calonectria* species are morphologically very similar and these are not typically useful in identifications (Crous & Wingfield 1994, Crous 2002).

The use of biochemical techniques can also be used in phenotypic characterisation. These include substrate utilisation and cell wall polysaccharide analysis. The use of aminopeptidase specificity (Stevens *et al*. 1990) and utilisation of nitrogen and carbon (Hunter & Barnett 1978, Sharma *et al*. 1992) have been used successfully to separate several *Cylindrocladium* species. The use of polysaccharides obtained from cell walls of *Cylindrocladium* positively identified linkages between asexual species and their respective *Calonectria* teleomorphs (Ahrazem *et al*. 1997). However, this method has been found to have limited value as some species in complexes could not be distinguished (Crous 2002).

MATING COMPATIBILITY

Mating strategies have been employed in the taxonomy of *Calonectria* and have played an important role in identifying new species of the genus (Schoch *et al.* 1999, Crous 2002). Based on these studies, there are approximately 18 homothallic and 34 heterothallic species of *Calonectria* (Crous 2002, Crous *et al.* 2004b, Gadgil & Dick 2004, Crous *et al.* 2006a), with the heterothallic species showing a biallelic mating system (Schoch *et al.* 1999). Studies in the female fertility of *Cylindrocladium* by Schoch *et al.* (1999, 2000a, 2001a) have also shown that several species are self-sterile hermaphrodites requiring fertilisation from an opposite mating type. This is typical of heterothallic ascomycetes (Leslie & Klein 1996).

Several difficulties associated with applying the BSC have been highlighted (Brasier 1997, Taylor *et al.* 1999, 2000, Kohn 2005). The most relevant underlying problem occurs where genetically isolated fungal strains retain the ancestral ability to recombine to produce viable progeny (Brasier 1997). This phenomenon has also been found with several phylogenetic species that are closely related in *Calonectria*. Crous (2002), for example, showed that *Cy. hawksworthii*, *Ca. insularis* and *Ca. morganii* were capable of recombining, but that the progeny had low levels of fertility. Other mating studies done by Overmeyer *et al.* (1996) and Neubauer & Zinkernagel (1995) have found that induction of fertile perithecia requires the presence of an additional isolate that, however, does not contribute to the genetic make-up of the progeny. This clearly highlights the need for further studies regarding the mechanism of perithecial formation and recombination in *Calonectria*.

PHYLOGENY

Phylogenetic studies on *Calonectria* and its *Cylindrocladium* anamorphs have substantially influenced the taxonomy of these genera. Application of molecular techniques and particularly DNA sequence comparisons to distinguish between species has resulted in the recognition of numerous cryptic species. Several molecular approaches have been employed that include total protein electrophoresis (Crous *et al.* 1993a, El-Gholl *et al.* 1993a), isozyme electrophoresis (El-Gholl *et al.* 1992, 1997, Crous *et al.* 1998a), random amplification of polymorphic DNA (RAPD) (Overmeyer *et al.* 1996, Victor *et al.* 1997, Schoch *et al.* 2000a, Risède & Simoneau 2004) restriction fragment length polymorphisms (RFLP) (Crous *et al.* 1993b, 1995, 1997b, Jeng *et al.* 1997, Victor *et al.* 1997; Risède & Simoneau 2001) and DNA hybridisation (Crous *et al.* 1993b, 1995, 1997a, Victor *et al.* 1997). Although the above-mentioned techniques have been useful, DNA sequence comparisons and associated phylogenetic inference have had the most dramatic impact on the taxonomy of *Calonectria* and are most widely applied today.

In the first study using 5.8S ribosomal RNA gene and flanking internally transcribed spacers (ITS) sequences Jeng *et al.* (1997) were able to distinguish between *Cy. scoparium* and *Cy. floridanum* isolates. Subsequently, it was found that this gene region contains few informative characters (Crous *et al.* 1999, Schoch *et al.* 1999, Risède & Simoneau 2001, Schoch *et al.* 2001b). Therefore, the β-tubulin (Schoch *et al.* 2001b) and histone H3 (Kang *et al.* 2001a) gene regions have been applied in order to allow for improved resolution in separating species.

The first complete DNA sequence-based phylogenetic study using partial β-tubulin gene sequences (Schoch *et al.* 2001b)

Fig. 2. Disease symptoms associated with *Calonectria* (*Cylindrocladium*). A–D. Defoliation and yellowing associated with *Calonectria pseudonaviculata* infection on *Buxus* sp. at Paleis Het Loo in the Netherlands (upper part of hedge in A, arrows). B–D. Leaf yellowing and defoliation (note detaching leaves in D, arrows). E–H. *Calonectria ilicicola* causing Cylindrocladium black rot (CBR) on *Arachis hypogaea* in Georgia, U.S.A. F. Perithecia forming at the basal plant parts. G. Pods infected with tomato spotted wilt virus (left), healthy pods (middle), and pods infected with CBR (right). H. Field symptoms associated with CBR (photos with permission of T. Brenneman). I. Avocado roots infected with *Ca. ilicicola* (photo with permission of L. Forsberg). J. Seeding blight of *Callistemon citrinus* associated with *Ca. morganii* (photo with permission of G. Polizzi). K. Seedling rot of *Drosera* sp. associated with *Ca. pteridis* infection. L. Leaf spots of *Callistemon citrinus* associated with *Ca. pauciramosa* (photo with permission of G. Polizzi). M. *Arbutus unedo* associated with *Ca. pauciramosa* infection (photo with permission of G. Polizzi). N–O. Root rot and petiole lesions of *Spathiphyllum* sp. associated with *Ca. spathiphylli* infection (photo with permission from the late N.E. El-Gholl). P. Potato tuber infected with *Ca. brassicae*. Q–R. Leaf blight of *Eucalyptus* sp. associated with a mixed infection of *Ca. pteridis* and *Ca. ovata*.

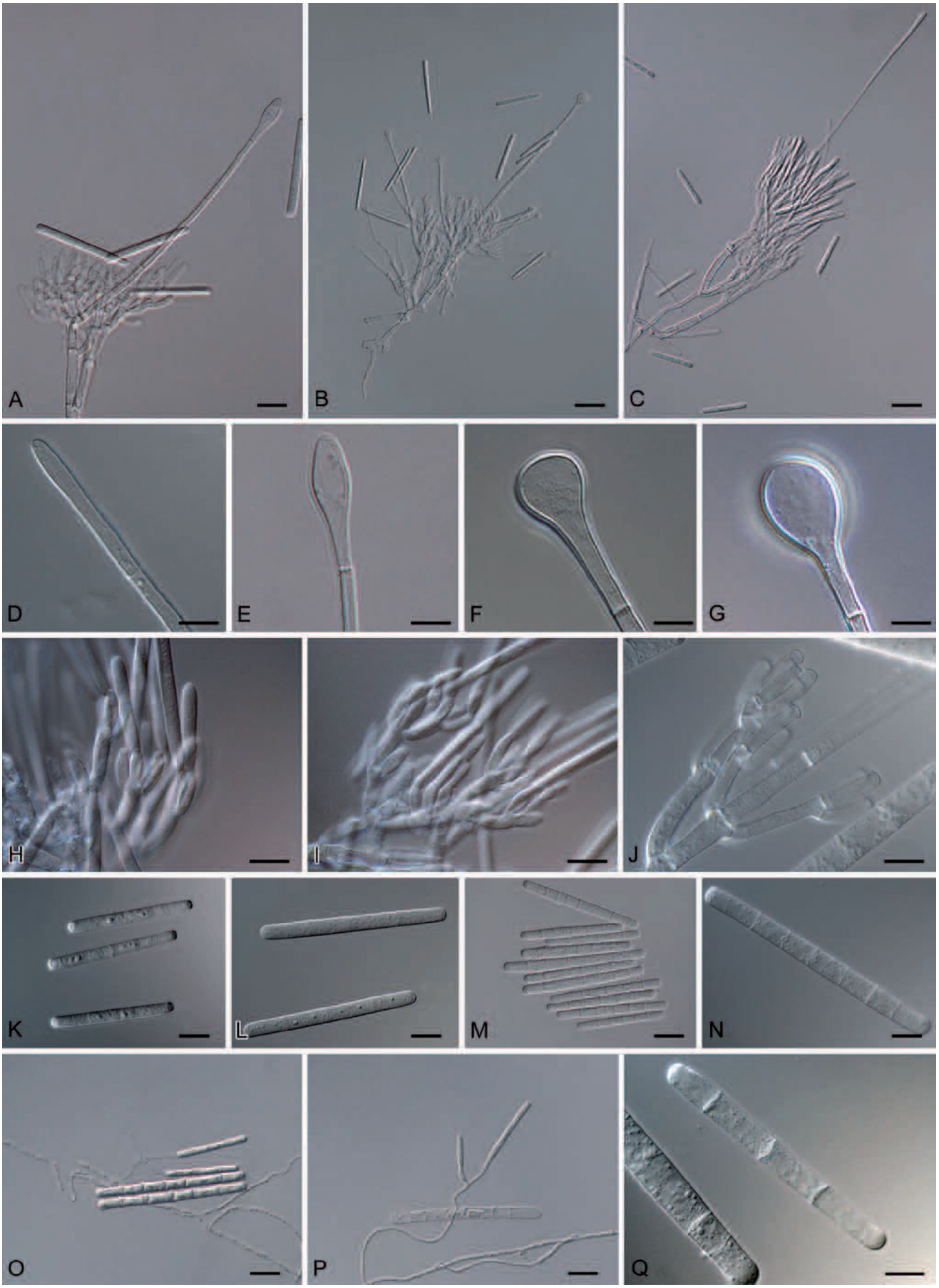

Fig. 3. Anamorph structures of *Calonectria*. A. Macroconidiophore of *Ca. pauciramosa*. B. Macroconidiophore of *Ca. hongkongensis*. C. Macroconidiophore of *Ca. brassicae*. D. Clavate vesicle of *Ca. reteaudii*. E. Obpyriform vesicle of *Ca. pauciramosa*. F. Sphaeropedunculate vesicle of *Ca. hongkongensis*. G. Pyriform vesicle of *Ca. morganii*. H. Fertile branches of *Ca. pauciramosa* with doliiform to reniform phialides. I. Fertile branches of a *Calonectria* sp. with elongate-doliiform to reniform phialides. J. Fertile branches of *Ca. reteaudii* with cylindrical to allantoid phialides. K. One-septate macroconidia of *Ca. pauciramosa*. L. Three-septate macroconidia of *Ca. colhounii*. M–N. Five to eight-septate macroconidia of *Ca. reteaudii*. O–P. Microconidiophores of *Ca. reteaudii*. Q. three-septate microconidium of *Ca. reteaudii*. Scale bars: B–C, M = 50 µm; A, O–P = 20 µm; D–L, N, Q = 10 µm.

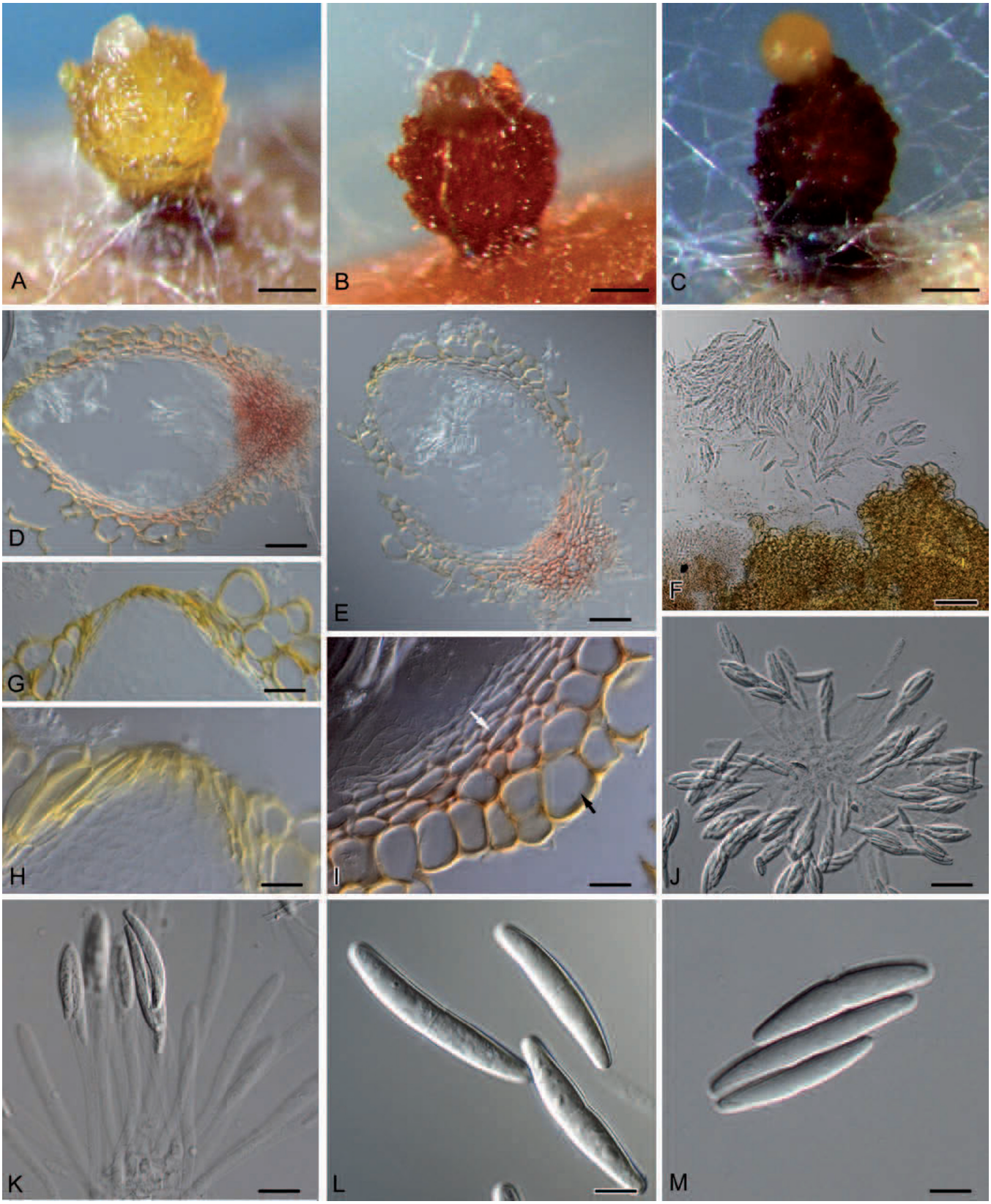

Fig. 4. Teleomorph structures of *Calonectria* spp. A. Yellow perithecium of *Ca. colhounii*. B. Orange to red perithecium of *Ca. pauciramosa*. C. Dark red perithecium of *Calonectria* sp. D–E. Vertical sections through perithecia. F. Squashed perithecium exuding ascospores. G–H. Ostiolar regions of perithecia. I. Vertical section through the wall of a perithecium showing the *textura globulosa* (black arrow) and *textura angularis* (white arrow) wall layers. J. Asci containing eight ascospores. K. Asci containing four ascospores. L–M. One-septate ascospores. Scale bars: A–C = 100 µm; F = 50 µm; J–K = 20 µm; D–E, G–I, L–M = 10 µm.

compared phenotypic, biological and phylogenetic concepts used in the taxonomy of *Cylindrocladium*. This also highlighted the fact that *Calonectria* represents a monophyletic lineage (Schoch *et al*. 2000b, 2001b). Subsequently, combined DNA sequence data for the ITS, β-tubulin and histone H3 gene regions have been widely used in studies relating to taxonomic issues surrounding *Cylindrocladium* and *Calonectria* (Crous *et al.* 1999, Schoch *et al.* 2000a, 2000b, Crous & Kang 2001, Kang *et al.* 2001a, 2001b, Henricot & Culham 2002, Crous *et al.* 2004b, 2006a, Lombard *et al.* 2009, 2010). Other partial gene sequences recently used include

translation elongation 1-alpha (TEF-1α) and calmodulin (Crous *et al.* 2004b, Lombard *et al.* 2010). However, insufficient data are currently available for these gene regions on GenBank (www.ncbi.nlm.nih.gov) to make them particularly valuable for comparative analysis.

A recent search in GenBank (March 2010) revealed a total of 734 partial gene sequences for *Calonectria* and *Cylindrocladium*. These include 311 for β-tubulin, 177 for histone H3, 159 for ITS, 39 for calmodulin, 36 for TEF-1α, five for large subunit RNA gene (LSU), three each for the high mobility group (HMG) box and peptidase synthetase and one for the small subunit RNA (SSU) gene. For *Cylindrocladium* and *Calonectria*, there are only six studies (Kang *et al.* 2001a, 2001b; Crous *et al.* 2004b, 2006a, Lombard *et al.* 2009, 2010) that provide files on TreeBase (www.treebase.org).

FUTURE RESEARCH

Population biology

Most studies on *Calonectria* have focused on the taxonomy, phylogeny and pathology of species. There have in contrast been relatively few studies treating the population biology of these fungi. This is unfortunate as population dynamics contributes considerable knowledge to a better understanding of population structure, distribution of genetic diversity, gene flow, centres of origin and mating strategies (McDonald 1997, Linde *et al.* 2002, Grünwald *et al.* 2003). An understanding of the population dynamics of *Calonectria* would contribute in determining the natural spread of these fungi as well as assist in phytosanitary and quarantine regulations. Another important aspect surrounding knowledge of *Calonectria* population dynamics is that this would contribute to plant breeding programmes and thus control of the many diseases that are caused by these fungi (McDonald 1997, Wright *et al.* 2006, 2007).

Limited research has been conducted on the population dynamics of *Calonectria*. To date only two studies (Wright *et al.* 2006, 2007) have reported on the development of polymorphic markers to characterise simple sequence repeats (SSRs) in loci of *Ca. ilicicola* (Wright *et al.* 2006) and *Ca. pauciramosa* (Wright *et al.* 2007). However, no study has yet been published on the population biology of either of these important pathogens using these markers. There is clearly a gap in this area of research concerning *Calonectria* spp. and future research on this topic should be encouraged.

Whole genome sequences

A relatively new and innovative technology employed in fungal genetics is the use of whole genome sequences of filamentous fungi. Whole genome sequencing has become relatively inexpensive and thus common in recent years. This revolutionary technology will promote our understanding of the mechanisms of gene function, conidiation, pathogenesis and sexual reproduction at the genotype level (Kupfer *et al.* 1997, Prade 1998, Yoder & Turgeon 2001, Foster *et al.* 2006, Cuomo *et al.* 2007). It is estimated that most filamentous fungi have a genome size of 30 to 40 Mb, containing approximately 8000 to 9000 genes (Kupfer *et al.* 1997, Prade 1998, Foster *et al.* 2006). There are currently several completed fungal genome sequences (http://www.broad.mit.edu/annotation/fungi/fgi/, Foster *et al.* 2006, Baker *et al.* 2008), including the model yeast *Saccharomyces cerevisiae* (Goffeau *et al.* 1996), plant pathogens and spoilage fungi such as *Aspergillus flavus* (Payne *et al.* 2006), *Fusarium graminearum* (http://www.broad.mit.edu, Cuomo *et al.* 2007), *Magnaporthe grisea* (Dean *et al.* 2005) and the model filamentous fungus *Neurospora crassa* (Galagan *et al.* 2003). Although there are currently over 300 ongoing filamentous fungal genome sequencing projects (http://www.genomesonline.org, Baker *et al.* 2008, Liolios *et al.* 2008), none include species of *Calonectria*.

The most closely related plant pathogen to *Calonectria* species currently being sequenced is *Haematonectria haematococca* (http://www.ncbi.nlm.gov). When the first *Calonectria* species is selected for whole genome sequencing, comparisons with *H. haematococca* could help to identify important genes in pathogenesis and sexual reproduction. Some *Calonectria* species that could be considered for genome sequencing include *Ca. pauciramosa*, based on its pathogenicity and importance on several plant hosts worldwide (Crous 2002), and *Ca. reteaudii*, one of the most important forest pathogens of South East Asia (Booth *et al.* 2000, Old *et al.* 2003).

CONCLUSIONS

Early studies on the taxonomy of *Calonectria* and *Cylindrocladium* focused on the use of MSC in combination with BSC. More recently, the wide availability of molecular techniques and particularly DNA sequence data have revolutionised the taxonomy of *Calonectria* and *Cylindrocladium.* Today, it is well accepted that the morphology of the *Cylindrocladium* state contributes most information to naming species and that these fungi all reside in *Calonectria*.

The first study to combine MSC, BSC and PSC concepts by Schoch *et al.* (1999) resulted in the identification of four species within a single species complex. Subsequently, several studies including the MSC, BSC and PSC have elucidated cryptic species in the genus (Kang *et al.* 2001a, 2001b, Henricot & Culham 2002, Crous *et al.* 2004b, 2006a, Lombard *et al.* 2009, 2010). Application of the BSC in the taxonomy of *Calonectria* has been found to be unreliable in some instances (Crous 2002). However, the implementation of MSC and PSC in combination provides powerful tool for taxonomic studies of these genera and it is likely that this will continue in future studies. Although several species complexes have been identified in *Calonectria*, more research is needed on the population level in order to study the gene flow between populations. Additional to this, more gene regions need to be identified and widely used in PSC. With the identification of several new species since 2002, an updated monograph is required to facilitate ease of identification.

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