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. pyrochoa, 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 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. ophiiospora. 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
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., Eli-Gholl, Alfieri & Schoult. | Schubert et al. 1989 | Cylindrocladium avesiculatum D.L. Gill, Alfieri & Sober | Gill et al. 1971 |
| Calonectria brassicaceae (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 cercicana 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 clothoumi Peerally | Peerally 1973 | Cylindrocladium clothoumi Peerally | Peerally 1973 |
| Calonectria colombiensis Crous | Crous et al. 2004b | Cylindrocladium colombiensis Crous | Crous et al. 2004b |
| Calonectria graciilipes Crous & Mchau | Crous et al. 1997a | Cylindrocladium graciloides Crous & Mchau | Crous et al. 1997a |
| Calonectria gracilis Crous, M.J. Wingf. & Alfenas | Crous et al. 1997b | Cylindrocladium pseudogracilis 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 insulana (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 morgani Crous, Alfenas & M.J. Wingf. | Crous et al. 1993a | Cylindrocladium scoparium Morgan | Morgan 1892 |
| Calonectria multiseptatum 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 pseudoreutaudii L. Lombard, M.J. Wingf. & Crous | Lombard et al. 2010 | Cylindrocladium pseudoreutaudii (Bugnic.) C. Booth | Crous et al. 2004b |
| Calonectria pseudopathiphylly J.C. Kang, Crous & C.L. Schoch | Kang et al. 2001b | Cylindrocladium pseudopathiphylly 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 | Boedijn & 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 Scholl., El-Gholl & Alfieri | Schouties et al. 1982     |
| Calonectria spathulatea El-Gholl, Kimbr., E.L. Barnard, Alfieri & Schout. | Crous & Wingfield 1994        | Cylindrocladium spathulatum El-Gholl, Kimbr., E.L. Barnard, Alfieri & Schout. | Crous & Wingfield 1994   |
| Calonectria terre-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 | Boedijn & Reitsma 1950  |                                               |                            |
| Cylindrocladium curvatum Boedijn & Reitsma | Boedijn & 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 hawkesworthii 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 malestianum 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. morgani (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. 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, Hodges & May 1972, Cordell & Skilling 1975, Mohanan & Sharma 1985, Crous & Kang 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. 1984, 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 barnyard (Arachis hypogea) black root of Arachis hypogea (peanut) 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 |
|-------------------|--------------|-------------------|--------------|-------------------|--------------|
| Actinidiaceae      | 2            | Combretaceae      | 1            | Malpighiaceae     | 2            |
| Altingiaceae       | 1            | Crassulaceae      | 1            | Malvaceae         | 6            |
| Anacardiaceae      | 3            | Cupressaceae      | 4            | Meliaceae         | 2            |
| Annnonaceae        | 4            | Curcurbitaceae    | 3            | Moraceae          | 2            |
| Aparagaceae        | 1            | Cucurbitaceae     | 3            | Moraceae          | 2            |
| Apliceae           | 1            | Cucurbitaceae     | 3            | Moraceae          | 2            |
| Apocynaceae        | 2            | Cucurbitaceae     | 3            | Moraceae          | 2            |
| Aquifoliaceae      | 4            | Dilleniaceae      | 1            | Myrtaceae         | 31           |
| Araceae            | 5            | Dilleniaceae      | 1            | Myrtaceae         | 31           |
| Arajaceae          | 2            | Dryopteridaceae   | 2            | Myrtaceae         | 31           |
| Arecaceae          | 21           | Ebenaceae         | 1            | Myrtaceae         | 31           |
| Araucaniaceae      | 2            | Ebenaceae         | 1            | Myrtaceae         | 31           |
| Aspleniacae        | 1            | Euphorbiaceae     | 6            | Olearaceae        | 1            |
| Asteraceae         | 5            | Fabaceae          | 57           | Olearaceae        | 1            |
| Berbecaceae        | 2            | Fabaceae          | 57           | Olearaceae        | 1            |
| Betulaceae         | 1            | Ginkgoaceae       | 1            | Olearaceae        | 1            |
| Bixaceae           | 1            | Juglandaceae      | 2            | Olearaceae        | 1            |
| Bromeliaceae       | 3            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Buxaceae           | 1            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Caricaceae         | 2            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Caryophyllaceae    | 1            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Celastraceae       | 1            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Chenopodiaceae     | 1            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Combretaceae       | 3            | Lamiaceae         | 6            | Olearaceae        | 1            |
| Convolvulaceae     | 1            | Lamiaceae         | 6            | Olearaceae        | 1            |
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 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 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 assexual species and their respective Calonectria telemorphs (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. spathiphyli* 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*. 

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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.
Species concepts in Calonectria (Cylindrocladium)

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

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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.
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. lilicola (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 (Kuper 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 (Kuper 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, Liiolios et al. 2008), none include species of Calonectria.

The most closely related plant pathogen to Calonectria species currently being sequenced is Haematonecota haematococca (http://www.ncbi.nlm.nih.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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