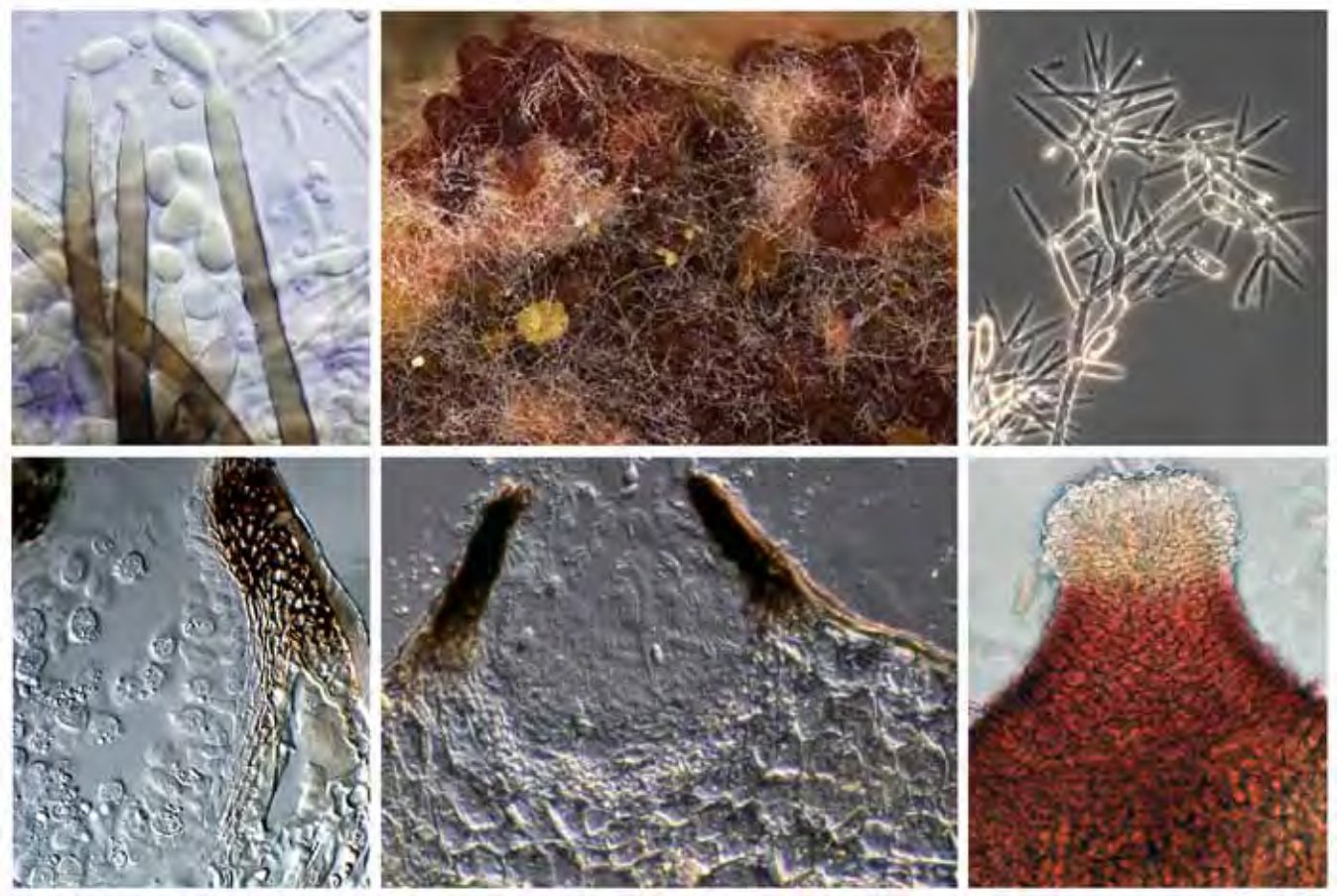
Studies in Mycology 68 (March 2011)

Phylogenetic revision of taxonomic concepts in the *Hypocreales* and other *Ascomycota*
- A tribute to Gary J. Samuels -

Amy Rossman and Keith Seifert, editors



CBS-KNAW Fungal Biodiversity Centre,
Utrecht, The Netherlands
An institute of the Royal Netherlands Academy of Arts and Sciences

Studies in Mycology

The Studies in Mycology is an international journal which publishes systematic monographs of filamentous fungi and yeasts, and in rare occasions the proceedings of special meetings related to all fields of mycology, biotechnology, ecology, molecular biology, pathology and systematics. For instructions for authors see www.cbs.knaw.nl.

Publication date: 22 March 2011

Published and distributed by CBS-KNAW Fungal Biodiversity Centre, P.O. Box 85167, 3508 AD Utrecht, The Netherlands. Internet: www.cbs.knaw.nl.
E-mail: info@cbs.knaw.nl.

ISBN/EAN : 978-90-70351-84-7
Online ISSN : 1872-9797
Print ISSN : 0166-0616

Cover: Top from left to right: Conidiophores of *Kylindria peruamazonensis* in culture. Pulvinate stromatic subiculum with perithecia of *Hypomyces aconidialis*. Topmost parts of conidiophores with conidiogenous cells and conidia of *Cladobotryum paravirescens*. Bottom from left to right: Vertical section through conidioma of *Guignardia korthalsellae*. Vertical section through ascoma of *G. korthalsellae*. Upper part of a perithecium of *Hypomyces virescens*.

PREFACE

Phylogenetic revision of taxonomic concepts in the *Hypocreales* and other *Ascomycota* - A tribute to Gary J. Samuels

This volume of Studies in Mycology is something of a successor to another issue of the same journal published a decade ago, "Molecules, Morphology and Classification: Towards Monophyletic Genera in the Ascomycetes' (vol. 45, edited by Seifert, Gams, Crous & Samuels 2000). In that issue, the authors grappled with questions of integrating the new phylogenetic information derived from DNA sequencing into a classification system that was already complicated by the need to accommodate fungal pleomorphy. In the intervening time, mycologists have become less tentative about handling this complexity. The present volume continues the trend of applying multigene phylogenetics to generic and species concepts, extending the higher taxonomic level studies of the Assembling the Fungal Tree of Life project into a more finely resolved realm.

There is another controversy brewing in the consciousness of contemporary ascomycete taxonomists, namely the issue of dual nomenclature, the practise that allows (and in some minds demands) the use of two or more Latin binomials for one fungal species, one for the teleomorph, if known, and the other(s) for the anamorph(s). This has been the focus of passionate discussion and debate in special sessions at the last three International Mycological Congresses. When we intiated this collection of papers in 2008, we were not intending for a particular theme to arise. We knew the papers would focus on Ascomycete systematics, and pay homage to the craft of our honoree, Gary Samuels, *i.e.* an attention to quality illustrations, complete descriptions, anamorph-teleomorph connections, and species-level molecular phylogenetics. But along the way, in one way or another, most of the authors found themselves facing the concept of dual nomenclature, most of them trying to work around it in their own way.

Although there is disagreement among mycologists about the need for a single name nomenclatural system, most would probably agree with the following statements:

A. Taxonomists should try to minimise name changes.
B. If name changes are proposed, a stable nomenclature should result.
C. Classifications and nomenclature should reflect phylogeny to the extent that this is practical.
D. If classifications and the resulting nomenclature reflect phylogeny, taxonomic and nomenclatural stability will result.

The usual criticism of any taxonomic change, or change to nomenclatural rules, is that the changes will lead to chaos, with confusion among users and a loss of credibility for the taxonomic endeavour as a whole. But our experience is that virtually all fungal taxonomists abide by the premises listed above, and it is disingenuous to suggest otherwise.

With Dual Nomenclature as the *status quo*, the authors of papers in this issue have adopted five different interpretations of One Fungus: One Name.

Option 1 – Strict priority. Strict application of priority of both generic names and species epithets, irrespective of whether these names were originally typified by anamorphic or teleomorphic elements. Following the lead primarily initiated by Lombard *et al*. (Stud. Mycol. 66, 2010), this approach was followed here by Gräfenhan *et al*. and Schroers *et al.* in their revisions of parts of *Fusarium sensu* Wollenweber and *Acremonium* by Summerbell *et al.*

Option 2 – Teleomorph priority with anamorphic species epithets. Transfer of anamorphic epithets to teleomorph genera for species that lack known teleomorphs. New teleomorph generic names are described when teleomorphs are discovered, irrespective of whether a previously described anamorph generic name exists.

This option maintains the primacy of teleomorph names at both the genus and species rank. It was exercised in part by Chaverri *et al*. in their revision of *Neonectria sensu lato*, and the associated anamorph genera *Cylindrocarpon* and *Campylocarpon.*

Option 3 – Teleomorph priority with earlier anamorph species epithets not considered.
Teleomorph genus and species name are both given priority. No attempt is made to revise anamorph genus or species names to determine if older names exist.

In common with Option 2, this option also maintains the primacy of teleomorph names and both the genus and species rank, but discounts known or unknown anamorph names from consideration in the construction of binomials. This practise was followed by Hirooka *et al*. in their revision of *Nectria cinnabarina,* in parts of the revision of *Neonectria* by Chaverri *et al*., the revision of *Plagiostoma* by Meija *et al*. and the description of the new species *Guignardia korthalsellae* by Sultan *et al*. Disregarding of anamorph names, however, does not always indicate a rejection of anamorph taxonomy *per se;* in the last example, there is no comprehensive revision of the anamorph genus *Phyllosticta* to enable the selection of possible earlier epithets for *G. korthalsellae*.

Option 4 – Teleotypification. Teleotypification of previously anamorphic names (genus or species) to holomorphic status.
This recently implemented provision of the ICBN in the Vienna Code (Art. 59.7) allows the status of an originally anamorphic name to be converted to holomorphic status by epitypification of its type specimen with a teleomorphic specimen. This provision cannot be used if an existing teleomorph is already named. As presently described in the ICBN, it is unclear whether this status is conveyed only to the species in question or to the generic name if the type species is teleotypified.

In this issue, this approach was followed by Réblová & Seifert, who changed the originally hyphomycetous status of *Sterigmatobotrys* to holomorphic status by epitypification.

Option 5 – Single species names but allowing two genera per clade.
Teleomorphic species are named in teleomorph genera and have only teleomorph-typified epithets; anamorphs are unnamed or referred to by their anamorph generic name. Anamorphic species are named in anamorph genera and have only anamorph-typified epithets. The result is that each species has a single name, but a monophyletic clade may have one teleomorph and one anamorph name associated with it. This has often been referred to as cross reference Nomenclature, where anamorph species epithets are dropped once the teleomorph is known, and anamorphs are then referred to only as *Anamorph-genus-name* of *Teleomorph-genus species epithet*.

This option is completely consistent with the requirements of the present Code. In this issue, Põldmaa followed this practise in her revision of tropical species of *Hypocrea* and related *Cladobotryum* anamorphs.

Which of these options, or practises derived from these, might ultimately be chosen to implement the concept of One Fungus : One Name remains for discussion amongst mycologists. We suggest that comparing options, including the maintenance of Dual Nomenclature, would be simplified if we could develop quantitative methods for evaluating each option objectively. ***Nomenclatural Parsimony***, a measure of the number of name changes needed to implement any particular system, should be an easy concept to define and to apply to each approach to single name nomenclature. Developing an algorithm for ***Nomenclatural Stability*** will probably be much more challenging, but the ability to compare the relative stability of particular kinds of nomenclatural changes should be a critical aspect of these discussions.

About this issue

This issue is not about nomenclature, rather it is about the phylogeny and taxonomy of several groups of Ascomycetes. The papers are authored by collaborators and students of Gary Samuels, who has devoted his career to furthering the study of Ascomycetes all over the world. In parallel with his career, we have divided the papers into two groups. The larger set of papers focuses on the taxonomy of the *Hypocreales*, the order that Gary cut his teeth on as a graduate student and continued to study for his whole career. He couldn't help dabbling though, and the second group of papers concern a diversity of Ascomycete orders and families, mirroring the many other papers that Gary has written.

The section on the *Hypocreales* includes four long papers revising generic and species concepts in the economically and biologically critical family, the *Nectriaceae*. The nominal genus *Nectria* is partly revised by Hirooka *et al*., with the well-known type species *N. cinnabarina* divided into four biological species, one of which is described as new. Chaverri *et al*. rework the *Neonectria* clade, which includes important plant pathogens often referred to the anamorph generic name *Cylindrocarpon,* providing a framework with five monophyletic genera. Gräfenhan *et al*. and Schroers *et al.* provide a similar phylogeny-based taxonomic framework to the prevailing concept of *Fusarium*. They show that this concept is not monophyletic and propose a new single-named nomenclatural system that recognises several genera. The paper by Põldmaa describes several new species of the family *Hypocreaceae* collected from the tropics, following the model established for the taxonomy of temperate species of this family established by the papers on *Hypomyces* published by Clark Rogerson & Gary Samuels. The paper by Summerbell *et al.* deals with a plesiomorphic anamorph that is broadly distributed in the Ascomycetes, but particularly prevalent in the *Hypocreales*, the hyphomycete form-genus *Acremonium*. This paper presents the first comprehensive overview of these anamorphs, providing taxonomic solutions for some groups, and pointing out many groups with lingering problems awaiting satisfying solutions.

The second set of papers deals with other groups of *Ascomycetes*. Réblová *et al.* determine that species of the anamorph genus *Monilochaetes* are phylogenetically diverse, although belonging primarily in the *Sordariomycetidae*. This revision results in the much-needed formal description of a new order for *Glomerella* and *Colletotrichum.* A teleomorph was discovered for the lignicolous *Sterigmatobotrys macrocarpa*, leading Réblová & Seifert to teleotypify this species. Huhndorf & Miller wrestle with the phylogeny of genera in the *Chaetosphaeriales,* describing a new species from New Zealand in the *Helminthosphaeriaceae*. Mejía *et al.* provide an account of the 25 accepted species of the genus *Plagiostoma* (*Gnomoniaceae, Diaporthales*) of which eight are new to science. Finally, Johnston *et al.* describe two new species on native New Zealand mistletoe in the dothideomycetous genera *Guignardia* and *Rosenscheldiella*.

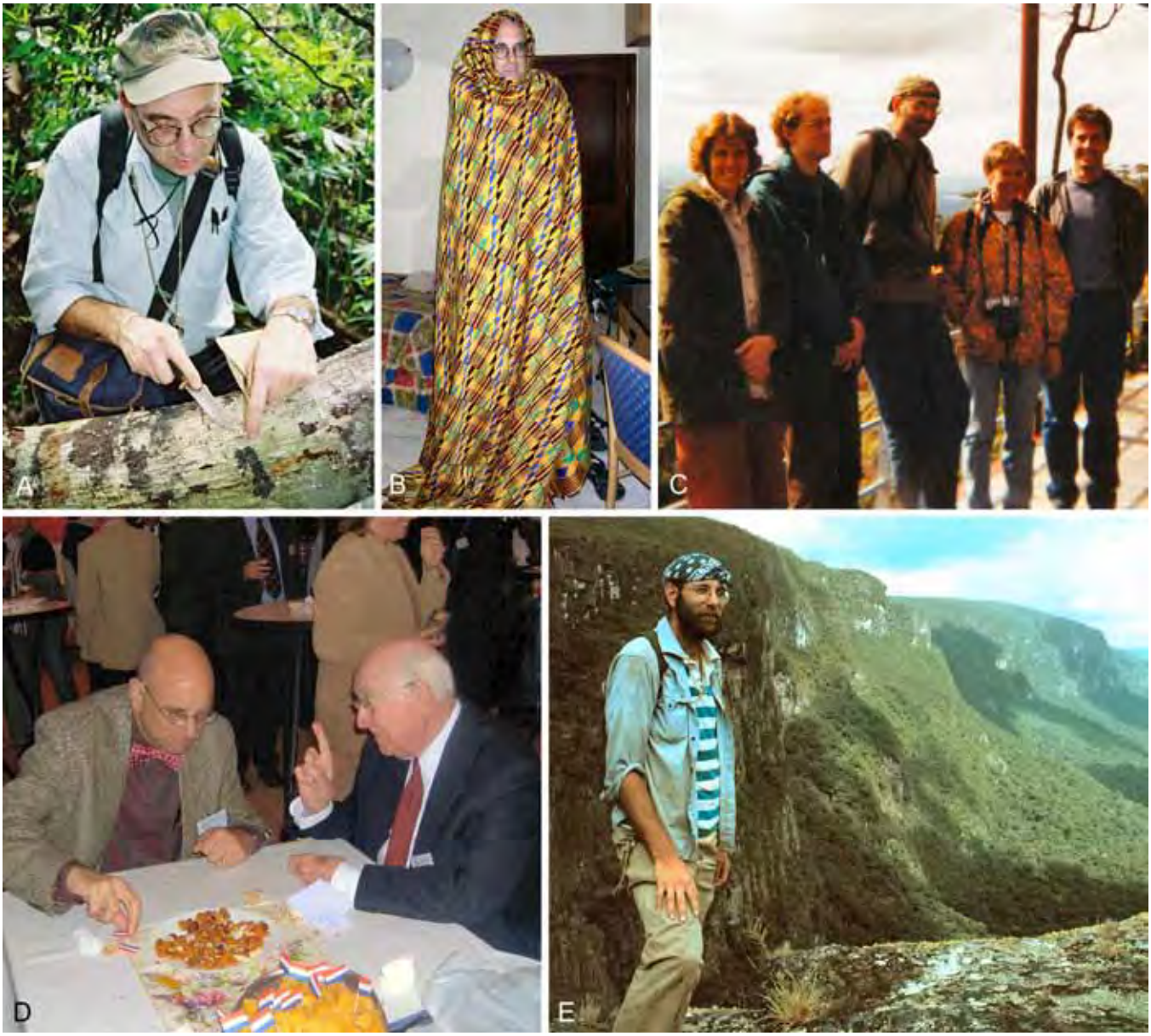
Reflections on the career of Gary Samuels

***Amy Rossman*:** I have known Gary for over 35 years since we first met on a collecting expedition in 1971 led by Dick Korf along with Don Pfister, Don Reynolds, and Kent Dumont. Gary was an older student, two years ahead of me in graduate school, and he suggested that I tackle the long-spored *Nectria*-like fungi while he polished off those with short spores. Thus, I had a thesis project. Throughout his career Gary has influenced other scientists inspiring them as he did me to work in many different groups of fungi. In truth, I think he would like to study all fungi, at least all of the pyrenomycetes and their anamorphs.

Gary's first job was in New Zealand where he relished the diversity of the many local undescribed fungi and set to work publishing on species ranging from the "bizzaro" discomycetes to his beloved *Hypocreales*. During this period in New Zealand he spent one-year with Emil Műller in Switzerland publishing on the connection of teleomorphs with asexual states for many new and unusual species. Throughout his career Gary collected fungi on field trips especially in the Neotropics and New Zealand, later in Asia. From these fresh collections he would isolate single ascospores using a micromanipulator in order to grow the fungus in culture often producing the asexual state. These cultures have served as the basis for many projects undertaken by his students and associates. Gary's philosophy was to collect everything and distribute his collections to specialists throughout the world.

One of Gary's contributions to mycology was collaborating with Clark Rogerson ensuring that Clark's extensive knowledge of *Hypomyces* was published. Their series of papers on *Hypomyces* on discomycetes, boletes, polypores, and mushrooms laid the groundwork for the continuing studies currently undertaken by Kadri Põldmaa. Like Clark Rogerson, Gary collaborates with amateur mycologists; for his latest invitation to a foray, he developed a field guide to the fungicolous fungi. This is a small book with one species described and illustrated on each page—just the handy reference book one needs to identify these fungi. For this one occasion, he spent about three weeks developing this useful identification manual.

In 1989 Gary Samuels joined the Systematic Mycology & Microbiology Laboratory at USDA Agricultural Research Service in Beltsville, MD, to work on the systematics of biological control fungi. At ARS his main research focus has been on *Hypocrea*/*Trichoderma,* a difficult group of fungi, and the most commonly used biological agents for controlling fungal diseases. His systematic knowledge of *Trichoderma* has resulted in the ability to distinguish species and to predict characteristics of unknown isolates. Working with David Farr, he developed an on-line system that provides descriptions and illustrations of the species of *Trichoderma* as well as a synoptic key that requires only minimal expertise to use. This was one of the first on-line identification systems for fungi. In addition, Gary has presented workshops on the identification of *Trichoderma* to plant pathologists in Cameroon, Peru, Thailand, and Vietnam, for which he developed a manual for the identification of *Trichoderma* especially for those working in biological control.



A. Gary carving specimen of hypocrealean fungus off a newly fallen tree trunk in a tropical forest. B. Gary dressing up in African fabric, Ghana, 2003. C. Kadri Põldmaa, Hans-Josef Schroers, Gary Samuels, Elke Lieckfeldt, and Pedro Crous take a break from collecting at Mt. Tomah, near Sydney, Australia, 1999. D. Emory Simmons advising Gary at the special symposium honoring Walter Gams held in Amsterdam, 2001. E. Gary was one of the first mycologists to collect fungi on a tepui in Venezuela, 1977.

Gary and his graduate student Hans-Josef Schroers conducted research on the genus *Clonostachys*, asexual state of *Bionectria,* resulting in a major monograph of this genus. Invaluable to those developing these fungi as biological control agents, this research has resulted in their increased use in the control of diseases of greenhouse plants. Another real-life problem that Gary solved involved the confusion of a disease of cultivated mushrooms known as green mold with a biological control agent. Initially the cause of the mushroom disease was identified as *Trichoderma harzianum*, a species commonly used as a biological control agent. This resulted in a conflict between the cultivated mushroom growers who want to prevent the spread of green mold and growers using *T. harzianum* in their fields as a biological control agent of crop plant diseases. Gary carefully studied the green mold pathogen, compared it with the biocontrol fungus, and showed that these fungi were two different species. He also developed a reliable, straightforward technique for distinguishing them.

Throughout his career Gary has actively participated in the Mycological Society of America (MSA). Following Clark Rogerson's influence about the importance of participation in the MSA, Gary served for over ten years as an Associate Editor of *Mycologia*, always giving each paper a fair and thorough review. This has included editing manuscripts written by non-English speakers so that they are acceptable, often spending days on one paper. Once he even sectioned and photographed a specimen so that an illustration of the teleomorph could be included - all this without any co-authorship. He has served on various MSA committees over the years including the one to review *Mycologia* when it first was increased in physical size with a new cover - this was considered very radical at the time. Gary was a willing participant in the rescue of the excess issues of *Mycologia* from the New York Botanical Garden and assemble of complete sets mailed to overseas mycological institutions. This involved lifting heavy boxes and putting them in order prior to assembling the sets, then packing them into new boxes all taking place in the dusty hot basement of our building.

Gary has greatly influenced the field of systematic mycology worldwide serving on the International Commission of the

A. Gary in Sri Lanka making friends with a snake. B. Gary in Cameroon showing fungi to guides, 2001. C. Keith Seifert (L) and Gary discussing weighty issues during a break from collecting in Mt. Tomah, Australia 1999. D. Gary taking a break from microscopy in the field.

Taxonomy of Fungi and on the editorial boards of three mycological journals, *Mycological Progress, Mycotaxon,* and *Sydowia*. He is widely known and well respected as evidenced by his frequent invitations to speak at national and international meetings. Gary was funded by the NSF Partnership in Enhancing Expertise in Taxonomy (PEET) programme through Pennsylvania State University where he trained three students and three research associates in the systematics of *Trichoderma* and related fungi. He is now a co-P.I. on a second PEET grant with one of the students (Priscila Chaverri) trained on the first grant. Numerous students and scientists from both inside and other the U.S. come each year to work with him usually for one to six months or longer. When they are here, he selflessly relinquishes his microscope system after patiently instructing them in its use while he does other work in the same room.

Gary is a world famous mycologist who has contributed enormously to the knowledge of the systematics of Ascomycetes. His research has resulted in monographs of important groups of fungi, mostly recently using multigene phylogenies to define species. His systematic research on biocontrol fungi has solved serious problems in agriculture in the U.S. and around the world. He has transferred that technology to plant pathologists through innovative web-based keys and through national and international workshops. Additionally, he has mentored a number of students and scientists who will provide a foundation for carrying on this important work into the future.

Gary is one of the people who enriched my career in mycology. We have not always agreed on such exciting topics as the generic circumscription of hypocrealean fungi or even which scientific names to apply to them but we have always respected each other's ideas and have gained enormously by working together for many years.

***Keith Seifert*:** At the 2008 meeting of the Mycological Society of America at the Pennsylvania State University, I had the chance to wear Gary Samuels's name tag at the banquet. Apart from the comedy of little Keith parading around with tall Gary's badge, which caused some double takes amongst our colleagues, I was proud to be so labelled for a time, even if it fooled no one. When Gary asked for his name tag back at the end of the evening, I refused to return it. It now sits as a prized possession in my collection of mycological memorabilia.

I have interacted with Gary throughout my career, from my MSc on. His skills as a field mycologist, his attention to establishing teleomorph-anamorph connections and considering the whole fungus in his taxonomic decisions, and his adoption of molecular techniques, have placed him at the forefront of ascomycete taxonomy. At every meeting I have attended with him, there is a retinue of neophyte ascomycete taxonomists from different cultures, shyly asking him questions and looking for his help. His willingness to share specimens, cultures, and ideas, and the always impeccable quality of his own published work have made him a role model for me.

My first contact with Gary was in 1980, when I asked him to collect jelly fungi for me in New Zealand, which when revived yielded cultures essential for my research, and even now remain the only extant cultures of these *Dacrymyces* species. When I was looking for a PhD post in 1982, Gary was one of the people I turned to. With unusual honesty, he told me that going outside America or Europe would be "academic suicide." I ended up at CBS in Holland, and Gary became my covert collaborator, sharing many cultures and specimens that greatly enriched my research. After meeting him in person for the first time at the 3rd International Mycological Congress in Tokyo, he invited me to coauthor his symposium paper from that meeting. This was an amazing opportunity for a graduate student, and the resulting review about correlations between teleomorph and anamorph genera in the *Hypocreales* was central to our subsequent work. My PhD committee agreed that I should be the sole author on my thesis monograph; otherwise, Gary would have been a coauthor on the book that was so important to starting my career.

Gary returned to the United States at about the same time that I returned to Canada. Those were unsettled years for us both, but again at about the same time we achieved employment stability, he in Beltsville, me at Agriculture & Agri-Food Canada. We continued to correspond, and I was one of many colleagues welcomed at the Samuels home in Laurel (some visitors stayed for months...). During one visit (where he also introduced me to the concept of fine bourbon), Gary spent a whole evening going over a manuscript he was handling as an associate editor for *Mycologia*. He went far beyond the usual call of duty as an editor, doing so much more than selecting reviewers and collating reviews. He always ensured that the manuscripts he handled were rigorously reviewed, and then vigorously edited to ensure that the work was presented in the best light, especially for authors whose language was not English.

Gary struggled with the adoption of molecular techniques to combine with his growing expertise in the anamorph genus *Trichoderma*. At the time he started this work, the enzymologists and biocontrol specialists who sought to exploit the species of this genus were using a nine species system published in 1968. My colleague John Bissett in Ottawa had applied a more refined morphological approach to the genus, but knowledge of its diversity was still very preliminary. At first Gary focused on isolating ascospores from the *Hypocrea* teleomorphs providing these strains to groups in several other labs who were exploring molecular markers. Continuing his fieldwork, he began accumulating anamorphic strains as well, including endophytic *Trichoderma* species from cacao - a complete surprise to those of us who dismissed this genus as a fast-growing, dirt-loving weed. About ten years ago, the pieces of the puzzle started to come together, resulting in a series of comprehensive monographs of many of the sections of this genus, involving many collaborators, with phylogenetic species concepts correlated with the

most detailed possible morphological observations on anamorphs and teleomorphs. He perfected a method of photographing the complexly branched conidiophores of *Trichoderma* species involving fluorescence microscopy; these illustrations were always accompanied by his characteristically precise line drawings.

Although Gary is mostly now known for his work on *Trichoderma*, his work on his beloved *Hypocreales* continued. This included his collaboration with his friend and colleague Amy Rossman, to produce the monographic revision on the *Genera of the Hypocreales*, and the identification guide to the *Hypocreales* of the southeastern United States (which we use almost daily in our lab). Gary has also worked on *Fusarium*, and, had I been more alert when I started my present job, I would have been working with him on this. With his knowledge of the teleomorphs, he has been a central figure in the development of a phylogenetic taxonomy in this genus, collaborating with David Geiser, Helgard Nirenberg, and Kerry O'Donnell in an ongoing attempt to settle issues of species concepts and nomenclature.

I cannot let a tribute to Gary go by without mentioning something else. He is interested in lots of things outside of science, and he is really a guy with a great sense of humour. Fans of James Trappe might disagree, but I think that Gary gave the funniest presentation in the history of the MSA. This happened in the late '80s, and was a consequence of one of those friendly collaborations that Gary got himself into so easily. He was actually giving the presentation as a favour to someone else, and, after the title slide, the projector broke. Rather than waiting for it to be fixed, Gary continued his talk, swooping his arms around and gesturing as he vividly described what was on the invisible slides, giving a very detailed description of the methods used to isolate fungi from caterpillar guts. The crowd was in stitches, and Gary was horrified that no one had taken him seriously, feeling that he had poorly represented his collaborators. But how many talks do *you* remember from twenty years ago?

Gary always revered his mentor Clark Rogerson, who introduced him to the *Hypocreales*, and we must also remember Emil Müller, with whom Gary did a post doc in Switzerland before going to New Zealand. This mentoring line goes from Rogerson and Müller through Gary and then outward to Hans-Josef Schroers and David Brayford and David Geiser and Priscila Chaverri and Sabine Huhndorf and Kerry O'Donnell and Kadri Põldmaa and Pedro Crous and Irina Druzhinina to name those that come easily to mind. And me. Gary has never been a university professor, yet his influence and impact are all over the practitioners of ascomycete taxonomy. A GenBank search reveals close to 2 000 sequences in GenBank with GJS as part of their collection number; this does not count sequences derived from Gary's cultures hidden under other numbers, such as the nearly 500 cultures that he has donated to the CBS culture collection.

Gary Samuels is a brilliant scientist, a generous mentor, a talented field mycologist, and a leader in our field. He is the mycologist's mycologist, the taxonomist's taxonomist. No hyperbole… he is my mycological hero.

The Editors March 2011

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.01

Studies in Mycology 68: 1–34. 2011.

Tropical species of *Cladobotryum* and *Hypomyces* producing red pigments

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Abstract: Twelve species of *Hypomyces/Cladobotryum* producing red pigments are reported growing in various tropical areas of the world. Ten of these are described as new, including teleomorphs for two previously known anamorphic species. In two species the teleomorph has been found in nature and in three others it was obtained in culture; only anamorphs are known for the rest. None of the studied tropical collections belongs to the common temperate species *H. rosellus* and *H. odoratus* to which the tropical teleomorphic collections had previously been assigned. Instead, taxa encountered in the tropics are genetically and morphologically distinct from the nine species of *Hypomyces/Cladobotryum* producing red pigments known from temperate regions. Besides observed host preferences, anamorphs of several species can spread fast on soft ephemeral agaricoid basidiomata but the slower developing teleomorphs are mostly found on polyporoid basidiomata or bark. While a majority of previous records from the tropics involve collections from Central America, this paper also reports the diversity of these fungi in the Paleotropics. Africa appears to hold a variety of taxa as five of the new species include material collected in scattered localities of this mostly unexplored continent. In examining distribution patterns, most of the taxa do not appear to be pantropical. Some species are known only from the Western Hemisphere, while others have a geographic range from southeastern Asia to Africa or Australia. The use of various morphological characters of anamorphs and teleomorphs as well as culture characteristics in species delimitation is evaluated. For detecting genetic segregation, partial sequences of the two largest subunits of the ribosomal polymerase perform the best in terms of providing informative sites and the number of well-supported groups recognised in the phylogenies. These are followed by the sequence data of the translation-elongation factor 1-alpha, while the ribosomal DNA ITS regions are of only limited use in distinguishing species and their phylogenetic relationships.

Key words: aurofusarin, biogeography, fungiolous ascomycetes, *Hypocreaceae, Hypocreales,* ITS rDNA, RPB1, RPB2, systematics, TEF1.
Taxonomic novelties: *Cladobotryum coriolopsicola* (R.F. Castañeda) K. Põldmaa, comb. nov.**,** *Hypomyces aconidialis* K. Põldmaa*,* sp. nov., *Hypomyces australasiaticus* K. Põldmaa*,* sp. nov., *Hypomyces gabonensis* K. Põldmaa*,* sp. nov., *Hypomyces samuelsii* K. Põldmaa, sp. nov., *Hypomyces virescens* G.R.W. Arnold & K. Põldmaa, sp. nov., *Cladobotryum heterosporum* K. Põldmaa, sp. nov., *Cladobotryum indoafrum* K. Põldmaa, sp. nov., *Cladobotryum paravirescens* K. Põldmaa, sp. nov., *Cladobotryum protrusum* K. Põldmaa, sp. nov., *Cladobotryum tchimbelense* K. Põldmaa, sp. nov.

INTRODUCTION

The fungicolous habit is manifested in many lineages across the fungal kingdom. The diversity of this lifestyle, highest in ascomycetes, reaches its peak in the order *Hypocreales*. Here, the most numerous group of exclusively fungicolous species is the genus *Hypomyces*, members of which live in association with different asco- and basidiomycetes. Whereas the best studied regions in terms of these fungi include Europe and the eastern coast of the USA, the species richness appears to be highest in the tropics, as for the other groups in the *Hypocreales* (Samuels 1996). As in many groups of fungi, the level of documentation and classification of fungal diversity in temperate regions far exceeds that known for the tropics. Põldmaa & Samuels (2004) summarised the main literature on tropical *Hypomyces* and related taxa. The present study has largely been inspired by recent works in the sister genus *Hypocrea/Trichoderma* in the *Hypocreaceae*. Detecting genetic segregation combined with detailed morphological observations has furthered the understanding of species delimitation and geographic distribution in many taxa in this intricate group of ascomycetes.

The present paper deals with species of *Hypomyces* that grow on various basidiomycetes and are characterised by red-coloured perithecia and/or colonies in culture. The colouration is due to the chinonic pigment, aurofusarin, first described as occurring in *Fusarium culmorum* (Ashley *et al*. 1937). Helfer (1991) studied the chromatographic pattern of several species of the *Hypomyces*-group suggesting that the red-pigmented species were closely related and introduced the term aurofusarin-group for them. The subsequent phylogenetic analyses of *Hypomyces* and related taxa, based on LSU rDNA data, supported a monophyletic group of the few included species producing the red pigment (Põldmaa *et al.* 1999, Põldmaa 2000, Põldmaa & Samuels 2004). This group, like others distinguished among the diverse fungicolous genus, comprises species with and without a known teleomorph. Most of the anamorphs of *Hypomyces* species growing on basidiomycetes other than boletes are accepted in the anamorph genus *Cladobotryum* (Rogerson & Samuels 1993) that, in turn, is connected only to this holomorphic genus. Despite the evidence on the congeneric nature of all the red-pigmented taxa treated in this study, the tradition of using separate generic names for pleo- and anamorphic species is followed until the monophyletic groups within this diverse complex of fungicolous fungi will be distinguished and named.

To date, 13 aurofusarin-producing species are known, three of which have a teleomorph. *Hypomyces rosellus* is the only one in which the teleomorph often accompanies the common anamorph in the temperate regions. Only the type collection from New Zealand is known for *H. dactylarioides*. In *H. odoratus,* a ubiquitous anamorphic fungus in Europe, the teleomorph has been obtained by crossing sexually compatible strains in culture (Arnold 1964). The remaining species are represented by single collections without a known teleomorph, described in the anamorph genera

Cladobotryum (= *Sibirina*) (Rogerson & Samuels 1993, Põldmaa 2000). Among the species known in tropical regions *Sibirina coriolopsicola, C. cubitense* and *C. virescens* have been described from Cuba (Castañeda-Ruiz 1987, Arnold 1987, 1988), while for *C. semicirculare* one collection was known also from Taiwan (Kirschner *et al*. 2007). Chen & Fu (1989) reported *Sibirina asterophora* and *S. purpurea* var. *asterophora* from China, while the type material of these species originates from Japan (Matsushima 1975, de Hoog 1978) or USA, Alabama (Gray & Morgan-Jones 1980), respectively.

Berkeley & Broome (1875) described *H. paeonius* as a roseous fungus from Sri Lanka. Although accepted by Petch (1912), the holotype, devoid of perithecia, does not confirm that it belongs to *Hypomyces*. Besides this doubtful taxon, no red-perithecial *Hypomyces* species have been described from the tropics. However, numerous teleomorphic specimens have been collected from the Americas for over a hundred years. A majority of these are preserved at The Mycological Herbarium of the New York Botanical Garden (NY) and lack cultures. These have been identified as *H. rosellus,* which was for a long time the only red-pigmented species of the genus with a described teleomorph, besides the neglected *H. paeonius*. Based on differences of the anamorph, a collection from Puerto Rico was published as *H. odoratus* (Rogerson & Samuels 1993). These authors state the absence of teleomorphic characters that would distinguish the two species, while admitting the possibility of error in identifying red-perithecial *Hypomyces* as *H. rosellus* in the absence of the anamorph. During recent decades, several new specimens of red-pigmented *Hypomyces/Cladobotryum* have been collected in various tropical areas of the world. Besides new localities in the well-sampled Central America, collecting has been carried out in Africa, Australia, Madagascar and southeastern Asia that all lacked records on the occurrence of these fungi. While some of the collections were easily distinguished as belonging to known species, many others presented difficulties in identification.

The present study aims to delimit species of *Hypomyces/ Cladobotryum* that produce red pigments and occur in the tropics, describing their phylogenetic relationships, anamorph-teleomorph connections, host range, and geographic distribution. To complete this task morphological examination of specimens and all available cultures was undertaken. For a majority of the cultures partial sequences of four gene regions (ITS rDNA, RPB1, RPB2, TEF1) were obtained and analysed. The results reveal the occurrence of at least a dozen red-pigmented species in various tropical areas of the world. Eight of them are described here as new species, while teleomorphs are described for two previously known anamorphic species. These data demonstrate that none of the studied tropical collections belongs to *H. odoratus* or *H. rosellus*. Neither are the distinguished tropical taxa closely related to these two and other temperate aurofusarin-producing species of *Hypomyces* and *Cladobotryum* that are not considered in detail in this study.

MATERIALS AND METHODS

Characterisation of morphology and cultures

Twenty-five or more ascospores and conidia were measured from each specimen/culture. The given ranges represent the mean values of specimens (two innermost numbers) and the limits of the 90 % range of estimated normal distribution observed in the single available or most divergent specimens (the two outermost numbers) being rounded to the nearest 0.5 µm. For rest of the structures, the absolute ranges are presented. Ascospore size is presented as the total length and width as well as the size of the main part (body) of the spore, including or excluding the apiculi and ornamentation, respectively. In both cases also the length/width ratio (Q) was estimated.

Ascospores or conidia were isolated onto 1.5 % malt extract agar (MEA). The descriptions and illustrations of species were made of cultures grown on Bacto (Detroit, USA) or Oxoid (Cambridge, UK) MEA in darkness or alternating 12 h/12 h darkness and fluorescent light at 25 ºC. Colony growth was measured from 9 cm-diam plastic Petri dishes into which a 4 × 4 mm plug taken from the edge of an actively growing colony was placed *ca.* 1 cm from the margin. Colony characters were evaluated also in cultures grown on cornmeal dextrose agar (CMD + 2 % dextrose), potato dextrose agar (PDA) and MEA from Merck (Darmstadt, Germany). Growth rates are presented as the colony radius on MEA in 4 d at 25 °C.

DNA extraction, PCR, and sequencing

Genomic DNA was extracted with High pure PCR template preparation kit (Roche Applied Science, Mannheim, Germany) according to the manufacturer's instructions or with TES buffer (200 mM Tris-HCl, pH = 7.6, 0.1 % SDS, 10 mM EDTA), followed by treatment with chloroform, isopropanol and ethanol. In the latter case DNA purification followed with GeneClean®III kit (Qbiogene, California, USA) or UltraClean™15 kit (Mo Bio Laboratory, California, USA), according to the manufacturer's instructions. PCR was set up using the following primers for amplification of the different gene regions: ITS and 5' end of the LSU rDNA: ITS1 and ITS4 or LR5 (White *et al*. 1990); RPB1: cRPB1Af and RPB1Cr (Castlebury *et al.* 2004); domains 6 and 7 of RPB2: RPB2-5f and RPB2-7cR (Liu *et al.* 1999); TEF1, part of the largest exon: EF1-983f (Carbone & Kohn 1999) and EF1-2218r (Rehner 2001). PCR was performed using Illustra TM puReTaq Ready-To-Go PCR Beads (GE Healthcare Europe GmbH, Freiburg, Germany) with an Eppendorf Mastercycler or Techne Genius thermocycler. The following amplification conditions were used: an initial denaturation at 95 °C for 3 min, followed by 35 cycles at 95 °C for 30 s, at 55 °C for 30 s, at 72 °C for 1 min increasing time 2 s per cycle, and a final extension at 72 °C for 10 min. For amplifying the protein-coding genes annealing temperatures from 57 to 60 °C were applied; in both RPB regions each step of the 35 cycles was prolonged to 1 min, while 30 s denaturation and annealing steps were applied in the 40 cycles used for TEF1. In the presence of multiple bands in the PCR products of the protein-coding genes, a touchdown program and/or cutting out the correct bands, followed by treatment with gel extraction DNA purification kit by Fermentas UAB (Vilnius, Lithuania), was used. Routinely PCR products were purified with Exo-SAP (GE Healthcare GmbH) according to the manufacturer's instructions. Sequencing was performed by MWG-Biotech AG (Ebersberg, Germany) or Macrogen Inc. (Seoul, Korea).

Alignments and phylogenetic analyses

Sequences of the ITS and LSU rDNA, RPB1, RPB2 and TEF1 regions were obtained from 61 cultures and two specimens. The majority of the sequenced material represented red-coloured *Hypomyces/Cladobotryum*. Sequences were obtained also from morphologically similar species lacking red pigments and closely related species with orange perithecia (*H. aurantius, H. lactifluorum* and *H. subiculosus*), the latter selected as the outgroup.

Sequence fragments were assembled and corrected using Sequencer v. 4.9 (Gene Codes Corp.). DNA sequences were submitted to European Molecular Biology Laboratory (EMBL) database with accession numbers, including those used from previous studies, listed in Table 1.

Alignments were performed using MAFFT v. 5.861 (Katoh *et al.* 2005), followed by manual adjustment in Genedoc v. 2.7 (Nicholas & *et al.* 1997). Maximum parsimony (MP) analyses were conducted in PAUP v. 4.0b10 (Swofford 2003) using 1000 heuristic searches with random taxon addition sequences, TBR branch swapping, and MulTrees on; the confidence of branching was assessed by 1000 bootstrap replicates applying 100 replicates with maxtrees set to 100. All characters were treated as unordered, equally weighted with gaps as missing data. MP trees were computed separately for each of the four gene regions as well as for the combined datasets of all four gene regions and the three protein-coding regions.

Bayesian inference of phylogeny was performed with MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) using the combined datasets with partitions defined according to the four gene regions. The GTR+Γ+I model was applied separately for each of the four data partitions, conducting two runs of the Markov chain Monte Carlo (MCMC) with four chains for 5 mln generations. Every 500th generation was sampled, discarding the generations before the run reached stationarity for computing of the consensus trees and posterior probability (PP) scores.

RESULTS

Phylogenetic analyses

The RPB1 dataset included 56 sequences and 713 characters of which 222 were parsimony-informative. The MP analysis yielded 615 trees. The RPB2 dataset of 62 sequences and 1 069 characters (342 parsimony-informative) resulted in 24 trees in the MP analysis. The TEF1 dataset of 63 sequences and 921 characters (165 parsimony-informative) yielded 112 MP trees. The ITS regions were sequenced for all 63 isolates with the smallest number of total and parsimony-informative characters, *i.e.* 612 and 92, respectively. Due to ambiguous alignment of some regions, 70 characters of ITS rDNA were excluded. MP analyses of the remaining 542 (74 parsimony-informative) characters resulted in 972 trees. In general, the topologies of the four consensus trees obtained in the separate analyses of the different gene regions (not shown) were in agreement, *i.e.* none of the strongly supported monophyletic groups (bs > 90 %) were in conflict with these clades on other gene trees. In the bootstrap analyses of the protein-coding genes 14 (RPB1), 17 (RPB2) or 11 (TEF1) strongly supported groups were distinguished. The bootstrap consensus of the ITS regions recognised only four groups in more than 90 % of the trees.

The combined dataset of four genes for 63 isolates included 3 246 characters of which 803 were parsimony-informative. MP analysis yielded 31 trees, the consensus of which is resolved in most parts. The topology generally concurs with the consensus tree obtained in Bayesian analysis of the combined dataset (Fig. 1). Therefore, support values for clades obtained in the bootstrap analysis are presented on the Bayesian tree. In several clades the support values were higher than observed in the bootstrap consensus trees in the analyses of individual genes. Exclusion of ITS rDNA from the combined dataset resulted in elevated support for some of the clades as well as revealed alternative relationships of two deeper branches discussed below.

Consensus trees of MP and Bayesian analyses of the four-gene combined dataset distinguish a well-supported clade of temperate taxa (clade II on Fig. 1), while all the tropical collections are included in its sister clade (clade I) or form basal lineages in regard to these two larger clades. The group comprising most of the species occurring in temperate areas (II) includes the best known red-coloured *Hypomyces* species, *H. rosellus* and *H. odoratus* together with other temperate species, each known only from type collection. These include *C. rubrobrunnescens* and *C. tenue* from Europe (Helfer 1991) as well as *C. multiseptatum* and *H. dactylarioides* from New Zealand (de Hoog 1978). The two European species form the sister-group of *H. rosellus,* which appears paraphyletic in regard to the two taxa from New Zealand.

The largest clade, comprising mostly tropical collections (Fig. 1 clade I), falls into two subclades (A, B) in the MP and Bayesian analyses. Among these, 10 of the well-supported groups or single-isolate lineages are considered to represent distinct species in accordance with morphological observations described below. Additional five isolates form third clade representing two tropical species. These form the moderately supported sister group of clade I in the consensus of MP trees obtained in the analyses of the combined four-gene and TEF1 datasets as well as in Bayesian and MP analyses based on the combined three coding genes. In the Bayesian phylogeny of the four-gene combined dataset this strongly supported clade (III in Fig. 1) is located in a more basal position. The remaining tropical, red-coloured *Hypomyces/ Cladobotrum* isolates (clade IV) are included in the most basal clades of the ingroup. The ex-type isolate of *C. penicillatum* from The Netherlands forms the sister-group to two tropical taxa but this relationship is not supported in any of the analyses.

The outgroup species with orange-coloured teleomorphs, *H. aurantius, H. lactifluorum,* and *H. subiculosus*, form a well-supported group. These three produce the pigment skyrin (Helfer 1991), that, likewise aurofusarin turns purple in KOH solution. These taxa formed the sister-group of the clade including red-pigmented species in previous analyses based mostly on LSU rDNA data and broader taxon sampling (Põldmaa 2000, Põldmaa & Samuels 2004, Jaklitsch *et al.* 2008). These studies revealed the clade of red-pigmented taxa to comprise also some *Hypomyces/Cladobotryum* species that lack red pigmentation but show similarities in anamorph characters to those observed in the aurofusarin-producing species. The ubiquitous temperate parasite of *Russulaceae*, *H. armeniacus* as well as *H. australis* and *H. khaoyaiensis* occuring on various aphyllophoroid basidiomycetes in the tropics, were included in this study. In the consensus trees of the Bayesian and MP analyses these species represent a monophyletic group that is well-supported only in the Bayesian analysis. In both trees it forms the unsupported sister-group of clade IV and *C. penicillatum*. However, Bayesian and MP analyses of combined data of the three protein-coding gene regions (excluding ITS rDNA) resulted in consensus trees in which the three pallid KOH-negative species formed the sister clade of all the KOH-positive, mostly red-pigmented species. Adding similar pallid taxa and further gene regions to the analyses is expected to raise the support to this sister-group relationship.

Morphology

Teleomorphs

The sexual state is described here for five species, including those found in nature for *H. australasiaticus* and *H. samuelsii.* In *H. aconidialis*, *H. gabonensis,* and *H. virescens* the teleomorph

Table 1. Strains and specimens of *Cladobotryum* and *Hypomyces* included in the phylogenetic analyses, their origin and numbers in the International Sequence Databases.

Species	Isolate or specimen number[1]	Isolate number in other collection[2]	Country of origin	GenBank accession numbers			
				RPB1	RPB2	TEF	ITS rDNA
C. asterophorum	CBS 676.77^T		Japan	FN868776	FN868649	FN868712	FN859395
C. cubitense	CBS 416.85^T	G.A. i1361	Cuba	FN868777	FN868650	FN868713	FN859396
	G.A. m643.w	TFC 98-35	Cuba	FN868778	FN868651	FN868714	FN859397
	TFC 2007-13	CBS 121646	Peru	FN868779	FN868652	FN868715	AM779857
	TFC 201293		Madagascar	FN868803	FN868676	FN868740	FN859422
	TFC 201294		Madagascar		FN868677	FN868741	FN859423
C. heterosporum	CBS 719.88^T	FSU 5514 (G.A. i1898)	Cuba	FN868780	FN868653	FN868716	FN859398
C. indoafrum	FSU 5807 (G.A. i3463)	CBS 127163	Republic of South Africa	FN868781	FN868654	FN868717	FN859399
	TFC 03-7	CBS 127162	Sri Lanka	FN868782	FN868655	FN868718	FN859400
	TFC 201277		Madagascar	FN868783	FN868656	FN868719	FN859401
	TFC 201286^T	CBS 127529	Madagascar		FN868686	FN868720	FN859402
	TFC 201295		Madagascar	FN868784	FN868657	FN868721	FN859403
	TFC 201336	CBS 127530	Uganda	FN868785	FN868658	FN868722	FN859404
C. multiseptatum	CBS 472.71^T		New Zealand	FN868786	FN868659	FN868723	FN859405
C. paravirescens	TFC 97-23 ^{T}	CBS 100366	Thailand	FN868787	FN868660	FN868724	FN859406
C. penicillatum	CBS 407.80^T		The Netherlands	FN868788	FN868661	FN868725	FN859407
C. protrusum	CBS 118999		Taiwan	FN868789	FN868662	FN868726	FN859408
	FSU 5044	HMAS 54138 (Chen68)	China	FN868790	FN868663	FN868727	FN859409
	FSU 5077	Chen 584	China	FN868791	FN868664	FN868728	FN859410
	FSU 5877	CBS 127165	Republic of South Africa	FN868792	FN868665	FN868729	FN859411
	G.A. i418 (IMI 165553)	CBS 127164	Zimbabwe	FN868793	FN868666	FN868730	FN859412
	TFC 201281		Madagascar	FN868794	FN868667	FN86873	FN859413
	TFC 201318^T	CBS 127531	Madagascar	FN868795	FN868668	FN868732	FN859414
C. purpureum	CBS 154.78^T		USA	FN868796	FN868669	FN868733	FN859415
C. rubrobrunnescens	CBS 176.92^T		Germany	FN868797	FN868670	FN868734	FN859416
C. semicirculare	CBS 705.88^T		Cuba	FN868798	FN868671	FN868735	FN859417
	TFC 03-3		Sri Lanka	FN868799	FN868672	FN868736	FN859418
C. tchimbelense	TFC 201146^T	CBS 127166	Gabon	FN868800	FN868673	FN868737	FN859419
C. tenue	CBS 152.92^T		Germany	FN868801	FN868674	FN868738	FN859420
Cladobotryum sp.	FSU 5046	Chen 339-2A	China	FN868802	FN868675	FN868739	FN859421
H. aconidialis	TFC 201215	CBS 127526	Gabon	FN995426	FN868710	FN868774	FN859455
	TFC 201334^T	CBS 127527	Madagascar		FN868711	FN868775	FN859457
H. armeniacus	TFC 02-86/2		France	FN868804	FN868678	FN868742	FN859424
H. aurantius	TFC 95-171		Estonia	FN868805	FN868679	FN868743	FN859425
H. australasiaticus	BPI 745759*		Thailand			FN868744	FN859426
	TFC 99-95	CBS 127153	Australia	FN868806	FN868680	FN868745	FN859427
	TFC 03-8^T	CBS 127152	Sri Lanka	FN868807	FN868681	FN868746	FN859428
H. australis	TFC 07-18	CBS 121663	Peru	FN868808	FN868682	FN868747	AM779860
H. dactylarioides	CBS 141.78^T		New Zealand	FN868809	FN868683	FN868748	FN859429
H. gabonensis	TFC 201256^T	CBS 127154	Gabon	FN868810	FN868684	FN868749	FN859430
H. khaoyaiensis	G.J.S. 01-304^T	CBS 113175	Thailand	FN868811	FN868685	FN868750	FN859431
H. lactifluorum	TAAM 170476*		USA	FN868812	EU710773	FN868751	FN859432
H. odoratus	C.T.R. 72-23	TFC 200102	USA	FN868813	FN868687	FN868752	FN859433
	G.A. m329	TFC 98-25	Germany	FN868814	FN868688	FN868753	FN859434
	TFC 03-16		Finland	FN868817	FN868691	FN868756	FN859437
	G.A. 05/93	TFC 05-93	Estonia	FN868816	FN868690	FN868755	FN859436
	TFC 200887		Estonia	FN868818	FN868693	FN868757	FN859439
H. rosellus	TFC 99-229		USA	FN868820	FN868695	FN868759	FN859441
	TFC 01-25		France	FN868821	FN868696	FN868760	FN859442
	TFC 200847		Estonia	FN868822	FN868692	FN868761	FN859438
	TFC 201071		Canary Islands	FN868823	FN86869	FN868762	FN859443
	G.A. 01/34	TFC 02-27	Russian Far East	FN868819	FN868694	FN868758	FN859440
H. samuelsii	CBS 536.88		Cuba	FN868824	FN868698	FN868763	FN859444
	TFC 200791	CBS 127155	West Indies		FN868699	FN868764	FN859445
	FSU 1010	G.A. i1716	Cuba		FN868701	FN868765	FN859447
	G.J.S. 96-41	CBS 127158	Puerto Rico	FN868825	FN868702	FN868766	FN859448
	G.J.S. 98-28^T	CBS 127157	Puerto Rico	FN868826	FN868703	FN868767	FN859449
	TFC 97-138	CBS 127159	Costa Rica	FN868827	FN868704	FN868768	FN859450
	TFC 2007-23	CBS 127160	Peru	FN868828	FN868705	FN868769	FN859451

Table 1. (Continued).

Species	Isolate or specimen number[1]	Isolate number in other collection[2]	Country of origin	GenBank accession numbers			
				RPB1	RPB2	TEF	ITS rDNA
H. subiculosus	TFC 97-166		Puerto Rico	FN868829	EU710776	FN868770	FN859452
H. virescens	G.A. i1899	CBS 127161	Cuba		FN868707	FN868771	FN859453
	G.A. i1906[T]	CBS 676.92	Cuba	FN868830	FN868708	FN868772	FN859454
Hypomyces sp.	G.A. m715.k	TFC 99-13	Azerbaidjan	FN868831	FN868709	FN868773	FN859455

[1] Numbers of strains/specimens from which DNA was extracted and sequences obtained.

[2] includes numbers of strains in personal collections, [T] ex-type cultures, * DNA isolated from specimen.

Abbreviations of culture collections and collectors: CBS = Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; FSU – Pilz-Referenz-Zentrum Jena, Institute of Microbiology, Friedrich Schiller University Jena, Germany; IMI – International Mycological Institute, CABI-Bioscience, Egham, Bakeham Lane, UK; TFC – Tartu Fungal Culture Collection, University of Life Sciences and University of Tartu, Tartu, Estonia; C.T.R. = Clark T. Rogerson, G.A. – Günter Arnold, G.J.S – Gary J. Samuels.

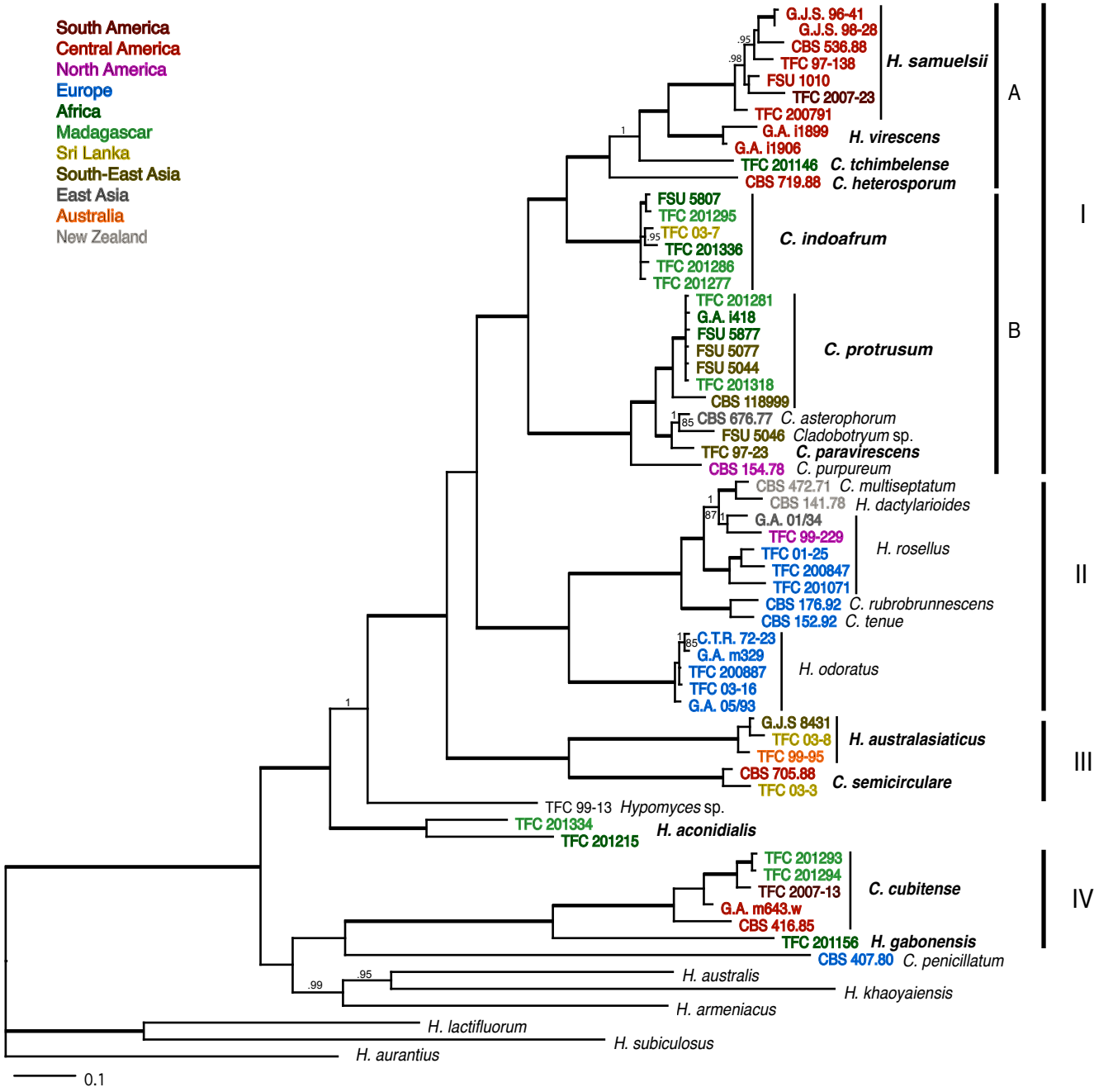

Fig. 1. Consensus tree obtained in partitioned Bayesian analysis of rDNA ITS regions and partial sequences of RPB1, RPB2 and TEF1 genes of *Hypomyces/Cladobotryum* producing red pigments. Names of tropical taxa are printed in bold. Font colours correspond to the geographic origin of the collection explained in the upper left hand side corner. Branches with posterior probability scores > 0.95 and bootstrap support > 95 % are in bold; in the case of individual values > 0.9 and > 85 %, these are given above and below the branches, respectively. Scale bar indicates subsitiutions per site.

has been obtained only in culture. In most species the subiculum develops as a scarce, arachnoid to profuse cottony, hyphal mat in which perithecia are formed. A restricted, pulvinate, stroma-like subiculum was observed only in cultures of *H. aconidialis.* In most species the perithecia are crimson to purplish red (11-12 C-D 6-8 according to Kornerup & Wanscher 1974). The subiculum is concolourous but usually much paler, appearing almost white in some collections. In the literature the colouration has also been described as (carmine-) red, pink, rosaceous lilac, and as "kirschrot" in German. The pigment reacts with aqueous KOH-solution, turning purple. Exceptional is the teleomorph of *H. gabonensis,* in which the subiculum and perithecia are buff-coloured with a faint colour change in KOH observed only in some parts of the subiculum. However, in cultures of this species, a KOH-positive, purplish red pigment develops. In all species the subiculum is composed of comparatively narrow, thin-walled hyphae, with only the cells surrounding the perithecia swollen. Perithecial anatomy is typical of most *Hypomyces* species growing on agaricoid and aphyllophoroid basidiomycetes (Rogerson & Samuels 1993, 1994, Põldmaa & Samuels 1999). The wall of the obpyriform perithecia is composed of a single region of thin-walled cells, compressed in the inner palisade and greatly swollen on the surface. The asci, containing eight, uniseriate, intact ascospores with ends overlapping, are released from the periphysate, ostiolar canal. The fusiform ascospores have a median septum, verrucose, warted or tuberculate wall and bear well-developed apiculi at their ends (Fig. 2).

The main differences observed among the teleomorphs were in the size of perithecia and ascospores. The largest perithecia, up to 600 µm high, occur in *H. gabonensis*. In this species the papilla is very prominent, reaching 250 µm in length. In *H. virescens* the perithecia, obtained only in culture, are 380–460 µm high and 280–350 µm wide. In the rest of the species the perithecia remain < 400 µm high and < 300 µm diam with the cylindrical to conical papillae not exceeding 140 µm in height.

Only in *H. samuelsii* are a fair number of teleomorphic specimens known. Ascospore size measured in seven specimens verified by cultures and sequence data revealed remarkable variation both in length and width (Fig. 3). Ranges of ascospore size in the single specimen of *H. virescens* and the two of *H. australasiaticus* overlap with that observed for *H. samuelsii*. Among the temperate species, the ascospore size of *H. odoratus* overlaps with that of these three tropical species, while *H. rosellus* differs from these by its considerably larger ascospores (Fig. 2). The mean values of spore size differ only slightly among the three tropical species as well as *H. odoratus* (Fig. 3) but the sample size is limited. The longest ascospores in *H. gabonensis* and smallest in *H. aconidialis* clearly distinguish these species from all the rest. Because the teleomorphs of three species of the group have been obtained only in culture and single specimens of species other than *H. samuelsii* are available, evaluating the statistical significance of spore size differences is premature. For the same reason, specimens from tropical America that share similar red-perithecia but lack anamorphs, can only tentatively be identified as belonging to *H. samuelsii* as discussed below.

Another feature distinguishing the treated species is the length/width ratio (Q) of ascospores. The ascospores of *H. gabonensis* are narrower than in other *Hypomyces* species discussed, with Q > 5. In the type specimens of *H. australasiaticus* and *H. virescens*, the mean value of Q ranges from 4.3 to 4.6, remaining less than 4.3 in *H. aconidialis, H. samuelsii* and most of the old collections lacking anamorph data. In *H. odoratus* and *H. rosellus* Q is 4.7 or 5.0–5.5, respectively.

All the treated tropical species are characterised by well-developed apiculi at the ends of ascospores (Fig. 2). These may vary from simple conical to hat-shaped with their tips mostly obtuse, rarely bent. Often these different forms are present in one specimen. Variation in size follows the pattern described for ascospores. The ranges and their mean values, mostly falling between 3 and 4 µm, vary considerably among the specimens of *H. samuelsii,* overlapping with those from all other species. At the same time, the temperate *H. odoratus* and *H. rosellus* are distinguished by smaller or larger apiculi with mean values < 2.7 or > 5.0 µm, respectively. The apiculi of *H. rosellus* are the most prominent, attenuating from a broad base to the very narrow tip. The apiculi of *H. gabonensis* are similar, yet narrower and shorter, with mean length of 4 µm.

So far, the ascospore measurements of *Hypomyces* have always been presented including the apiculi and ornamentation. However, these represent separate structures that may exhibit independent patterns of variation. Therefore, it would be correct to measure spore bodies separately from the apiculi and ornamentation. By comparing the mean values of length and width of the main part of the ascospores, differences similar to those described above for the inclusive measurements were observed among species. In most cases the size of the apiculi appears to be correlated with that of the main part of the ascospore. Yet in specimens of *H. samuelsii* and *H. rosellus* in which the longest apiculi cause the highest value of total length of ascospores, the mean value of the main part falls within the range observed for most other specimens. In *H. aconidialis* and *H. gabonensis* mean values of both measurements are among the smallest or largest detected in the group.

Anamorphs

On the natural substratum, structures associated with asexual reproduction are mostly formed on a delicate, whitish to buff mycelium bearing scattered, suberect to erect conidiophores. A well-developed, easily observable white mat, characteristic of the anamorphs of the temperate *H. odoratus* and *H. rosellus,* has been recorded only in the case of *C. semicirculare* infecting cultivated *Ganoderma* in Taiwan (Kirschner *et al.* 2007). Despite this, fast-growing, profusely conidiating colonies develop upon germination of ascospores or conidia in culture. On MEA the aerial mycelium appears whitish, buff or yellowish, the colouration being affected by the underlying strong pigmentation of the medium. The aerial mycelium is either scarce arachnoid or profuse and cottony, often without clear demarcation between aerial hyphae and conidiophores. The submerged hyphae mostly extend in a verticillate manner with branches regularly arising in opposite position in the agar, with an additional branch usually growing upwards. Once reaching above the agar, hyphae form alternating or opposite extensions that usually produce further branches. The whole branching system or only its uppermost parts should be called conidiophores. Their stipes, which arise from aerial hyphae at right angles, are often slightly wider and yellowish ochraceous, turning purple in KOH solution except for the uppermost part. The conidiophores branch verticillately or irregularly, sometimes dichotomously; branching is more or less symmetrical or repeatedly one sided (drepanoid). The branching, either uniformly distributed or confined to the top of the conidiophores giving these a tree-like aspect, is quite characteristic of each taxon. There can be up to four levels of side branches, the ultimate ones giving rise to conidiogenous cells. The conidiogenous cells are held in comparatively dense verticils in most species, being less numerous in lower than uppermost position.

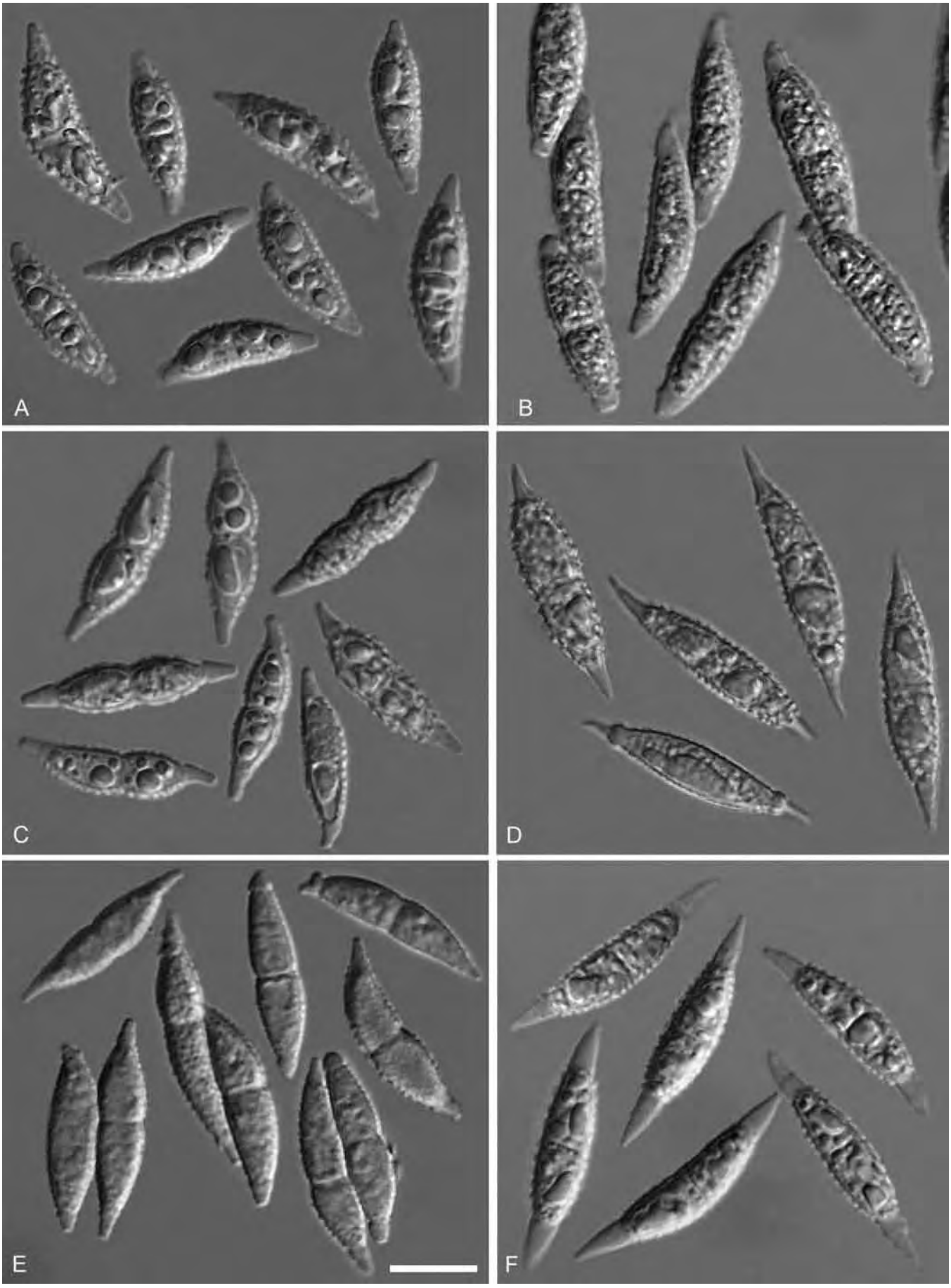

Fig. 2. Ascospores of red-coloured *Hypomyces*; all except *H. rosellus* from type collections. A. *H. samuelsii*. B. *H. virescens*. C. *H. australasiaticus*. D. *H. gabonensis*. E. *H. odoratus*. F. *H. rosellus*. (A. BPI 748258; B. TU 112905; C. TAAM 170757; D. TU 112024; E. Type JE; F. TAAM 161043). Scale bar on E = 10 µm applies to all figures.

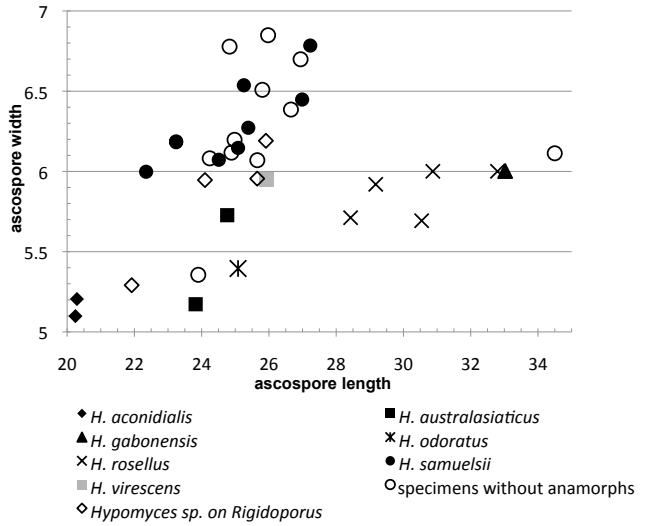

Fig. 3. Scatterplots of ascospore measurements of six red-coloured *Hypomyces*. The points represent mean values of specimens, units in µm.

Cylindrical or elongated-ampulliform conidiogenous cells deviate from the prevailing subulate form in which the cell is widest just above its base and attenuates gradually towards the apex. In contrast to the monoblastic, conidiogenous cells observed in most species, in *C. protrusum* their apices are slightly inflated or bear narrow elongations with several conidiogenous loci on irregular protrusions. Additional loci are observed also in the primary anamorph of *H. gabonensis* and occasionally in *C. heterosporum* and *C. paravirescens*.

Conidia observed in the anamorphs of tropical *Hypomyces* producing red pigments are often species-specific, while exhibiting high infraspecific variation and similarity among some of the taxa. Even though in a majority of species one to three septa are formed, single septate conidia can prevail in cultures of most of the species. Their shape varies from ellipsoidal to cylindrical, clavate, fusiform, obovoid or ovoid; the conidia are either straight or often curved in different ways with a part of almost circular conidia found in *C. semicirculare*. In *H. samuelsii* as well as in some other species, all forms are present either in a single or different strains. There is a tendency to form greenish conidia. Although prevailing in the *Trichoderma* anamorphs of the sister genus *Hypocrea*, in the *Cladobotryum* anamorphs of *Hypomyces* green conidia have been observed only in the anamorph of *H. viridigriseus*. The colouration is often faint and cannot always be observed even in conidial masses. However, the four species with greenish conidia do not constitute a monophyletic group indicating the homoplasious nature of this characteristic in the treated group. The conidial length and width as well as their ratio appear to be species-specific, with considerable range overlap observed among some taxa. The high variability of conidial size in *C. heterosporum* can be expressed by its coefficient of variation that exceeds 0.2, while it ranges from 0.01–0.15 in all other species (data not shown).

The differences in the width of the apex of the conidiogenous cell and that of the corresponding conidial hilum refer to retrogressive proliferation of the conidiogenous locus in most of the treated anamorphs. Specifically, width of these structures can vary to a considerable extent, reflecting their age and, in the case of hila, also formation order of successive conidia. Typically, the conidia are formed in an oblique position and held through their bases in imbricate chains. A single terminal conidiogenous locus usually produces two to five but never more than 10 conidia. The tips of conidia are pointed in different directions, giving the impression of star-like heads formed at the apices of conidiogenous cells. Distinct conidial columns composed of dozens of conidia held in one vertical plane are characteristic of the anamorph of *H. odoratus,* but are not found in the treated group. Neither are changes in the length of the conidiogenous cell and the width of its tip and conidial hila, also remarkable in *H. odoratus*. Likewise, annellidic tips of conidiogenous cells or those with a short rachis, both found in the anamorph of *H. rosellus*, are lacking in the tropical species. In *C. protrusum* each locus, formed at the tip of a small protrusion, presumably produces one conidium, with up to 12 conidia observed at the apex of each conidiogenous cell.

The anamorph of *H. gabonensis* provides an unusual phenomenon that illustrates the plasticity of the anamorphic state. The colonies on various media start growing by producing profusely branched conidiophores and comparatively small, 1-septate conidia from the uppermost and intercalary loci. Subsequently, a large-conidial anamorph, almost indistinguishable from *C. cubitense,* forms in most of the cultures at different times and location. Equally unique is *H. aconidialis,* representing the only species of the genus not found conidiating on the host or in the fresh isolations on different culture media.

Chlamydospores or thick-walled structures

Most of the species treated herein produce thick-walled, subglobose cells, referred to as chlamydospores, in nature as well as in culture. In nature they are found among the mycelium on which the conidiophores develop or near perithecia. In these fungal parasites chlamydospores obviously serve as survival structures to overcome periods between the availability of host fruiting bodies as well as unfavourable conditions like drought. Although seemingly more important for parasites of soft, ephermeral fruiting bodies of agarics, they are found also in cultures of species isolated from the more persistent basidiomata of wood-rotting aphyllophores. On natural substrata, the chlamydospores occur as single cells or are held in short simple chains. In cultures these can be followed by the formation of more complex aggregations. Generally, the chains of swollen and thick-walled cells grow out from a similar or simple intercalary cell on submerged or aerial hyphae. In some species the chains form branches and can develop into an irregular to globose mass of cells visible under the stereomicroscope. These are often light, almost colourless to pale ochraceous, soft, and lack inner structure characteristic of true sclerotia. The dark, tough, purplish brown sclerotia-like aggregations, common in temperate red *Hypomyces* species, were found only in *C. paravirescens* and *C. protrusum*.

Collections from tropical America lacking anamorph data

Over 20 specimens of red *Hypomyces* collected from tropical Central, North and South America in the 20th century are preserved at NY as *H. rosellus*. The US National Fungus Collection (BPI) holds fewer such specimens, some of which are accessioned as *H. odoratus*. Most of the specimens comprise purplish red perithecia developed in paler subiculum as typical of the members of the aurofusarin group of *Hypomyces*. The perithecia measure 300–430 µm in height and 200–340 µm in length, with papilla 50–150 µm high. Despite the similarity in perithecia, the morphology of ascospores clearly distinguishes all the studied mature collections from *H. rosellus*. The fusiform ascospores, 21.0–29.0 × (5.0–)5.5–7.5 µm, and their apiculi, 2.0–4.5(–5.5) µm, are shorter than in *H. rosellus*. Ascospore measurements, including the more diagnostic

mean values of length and width, fall in the range described for the cultured specimens of *H. samuelsii.* Moreover, the grossly warted to tuberculate ornamentation is similar to that observed in *H. samuelsii,* while in *H. rosellus* the ascospores are covered with fine low warts (Fig. 2). In addition, ascospore length covers the range observed in the type specimens of *H. odoratus* and *H. virescens,* teleomorphs of which have been observed only in culture. However, these two species differ from the described specimens at NY and BPI in smaller mean width of ascospores (Fig. 3), less prominent ascospore ornamentation and larger perithecia.

Four specimens at NY differ from the remaining collections in having ivory to buff, dense cottony subiculum with contrasting deep purplish red perithecia. These have been collected in the West Indies (Dominica), Guyana, and Puerto Rico, all growing on *Rigidoporus* sp. Their ascospore morphology and measurements, (19.0)–21.9–25.6(–29.0) × (5.0)–5.3–6.0(–7.0) µm, Q = (2.8–)3.4–4.4(–5.0), provide no distinction from *H. samuelsii*. However, the conidia (seen only in Setliff 1249), remind those of *C. cubitense*. In contrast, another specimen collected on *Datronia mollis* in Panama (Dumont-PA 2018) comprises ascospores that deviate from all other red perithecial *Hypomyces*. These resemble ascospores of *H. rosellus* but are even larger, measuring (31.0–)34.5(–38.0) × (5.5–)6.1–6.5 µm. Whether these collections represent two undescribed species or teleomorphs of known anamorphic species has to await furher collecting along with isolation of pure cultures.

None of the old specimens have been inoculated into pure culture but anamorph structures were sometimes observed in close proximity to the teleomorphs. Besides the collection on *Rigidoporus* sp., described above, the fusiform 3-septate conidia allowed their identification as *H. samuelsii*. Cylindrical-ellipsoidal 3-septate conidia and conidiogenous cells with a sympodial rachis at their apex, characteristic of *H. rosellus,* were not observed in any of the collections. Neither could the long chains of 1–3-septate cylindrical conidia produced from retrogressively proliferating conidiogenous cells be found, known only in *H. odoratus*.

In conclusion, the collections without and those with cultures provide no evidence on the occurrence of *H. odoratus* or *H. rosellus* in the tropics. Among the five teleomorphs described in this paper, those of *H. samuelsii* and *H. virescens* originate from tropical America. In addition to these two very similar teleomorphs, anamorphic *Cladobotryum cubitense*, *C. heterosporum* and *C. semicirculare,* have been found in Cuba. An immature teleomorph of *C. cubitense* was found accompanying the anamorph in a collection from Louisiana, USA, and it is likely that teleomorphs of the other two also grow in this region. As in other groups of fungi with limited variation in teleomorphs, old collections lacking anamorph data cannot always be unambiguously identified to species. However, considering the frequency of the recent samples of morphologically similar *H. samuelsii* and the fact that the teleomorphs of *H. virescens* and the three *Cladoboryum* species have never been found in nature, it is most likely that large part of the historical collections from tropical America represent *H. samuelsii.*

Culture characteristics

Most of the tropical red-coloured *Hypomyces* share the characters of fast growing, intensely coloured colonies on different media (Figs 4, 5). Colours and their succession are more or less identical in the strains studied, except for some species described below. On MEA whitish to buff mycelium develops after inoculation, with the colony reverse turning yellow in a few days. Usually in 2–4 wk, depending on the medium/brand and conditions, the colonies turn intensely red. The pigment, presumably aurofusarin in all these species, is most abundantly formed in submerged hyphae. Under the microscope, the colouration appears crimson to reddish or yellowish ochraceous, always turning purple in 3 % aquaeous KOH solution in which the pigment is partially dissolved from hyphae. In the isolates of *H. australasiaticus* and *C. semicirculare*, the pigmentation can be very pale, while *C. cubitense, C. heterosporum* and *H. gabonensis* differ in having a colony reverse that remains ochraceous for a long period. There is clearly a detectable KOH-reaction in all these species. In several isolates the ability to produce red pigments diminishes with age.

A majority of the observed strains and species grow fast on different media with obvious differences among the growth rates as well as optimum temperatures among the studied species (Fig. 6). All strains grow slowest at 15 °C with no growth observed at 35 °C. In several species the fastest growth is observed at 25 °C (*C. asterophorum, C. indoafrum, C. paravirescens, C. semicirculare, C. tchimbelense*). Many isolates of *H. australasiaticus, H. samuelsii, H. virescens, C. heterosporum,* and *C. protrusum* grow equally fast or even faster at 30 °C. Four of these species excluding *C. heterosporum* as well as *C. indoafrum* grow fastest at the four observed temperatures. Unlike other species the colony radius of *C. protrusum* exceeds 25 mm at 15 °C. On the contrary, *C. asterophorum, C. cubitense,* and *H. gabonensis* have slowest growth at all four temperatures. Because considerable infraspecific variation in growth, the values based on single strains should be interpreted with caution. For identification purposes three categories of growth rates can be distinguished, given here as the colony radius on MEA after 4 d at 25 °C. The fast growing species *C. indoafrum, C. paravirescens, C. protrusum, H. samuelsii,* and *H. virescens* exceed 50 mm, the slow growing *C. asterophorum, C. cubitense,* and *H. gabonensis* remain less than 20 mm, with intermediate values observed for the rest of the species.

Most species produce cottony, scarce to profuse, homogenous aerial mycelium on different media, while in others, profusely branching aerial hyphae or conidiophores form tufts throughout the colony (Fig. 4). Exceptional members of the group, *C. cubitense* and *H. gabonensis,* are characterised by slowly growing colonies, differing also in the pattern of colour change characteristic of the remaining taxa (Fig. 5). In these two species the colony reverse is intensely ochraceous, sometimes with an olivaceous tinge, turning purplish red in a few to several weeks. In both of these sister-species transfers resulted in subcolonies lacking the red pigment.

Several of the species produce odours detectable upon lifting the lid of the Petri dish. Often the smell is bitterish sweet, sometimes reminescent of camphour as described in the protologue of *H. odoratus* (Arnold 1964). The production and intensity of the smell depends on the medium and age of the strain. Because only some of the tropical strains were observed after their initial isolation, the data on strain odours is not extrapolated to species.

MEA was used as the standard medium for studying microscopic structures and colony characters because this medium guarantees optimal conidiation compared to CMD and PDA as well as the production of characteristic pigments. As observed in *Hypocrea/Trichoderma* strains (Jaklitsch 2009), the colony characters can vary depending on the brand of the extract used. MEA prepared from extract from Oxoid enhanced perithecial production, while extract from Bacto and Merck improved pigment production. For some strains, the anamorph structures were characterised on both media with no obvious differences observed.

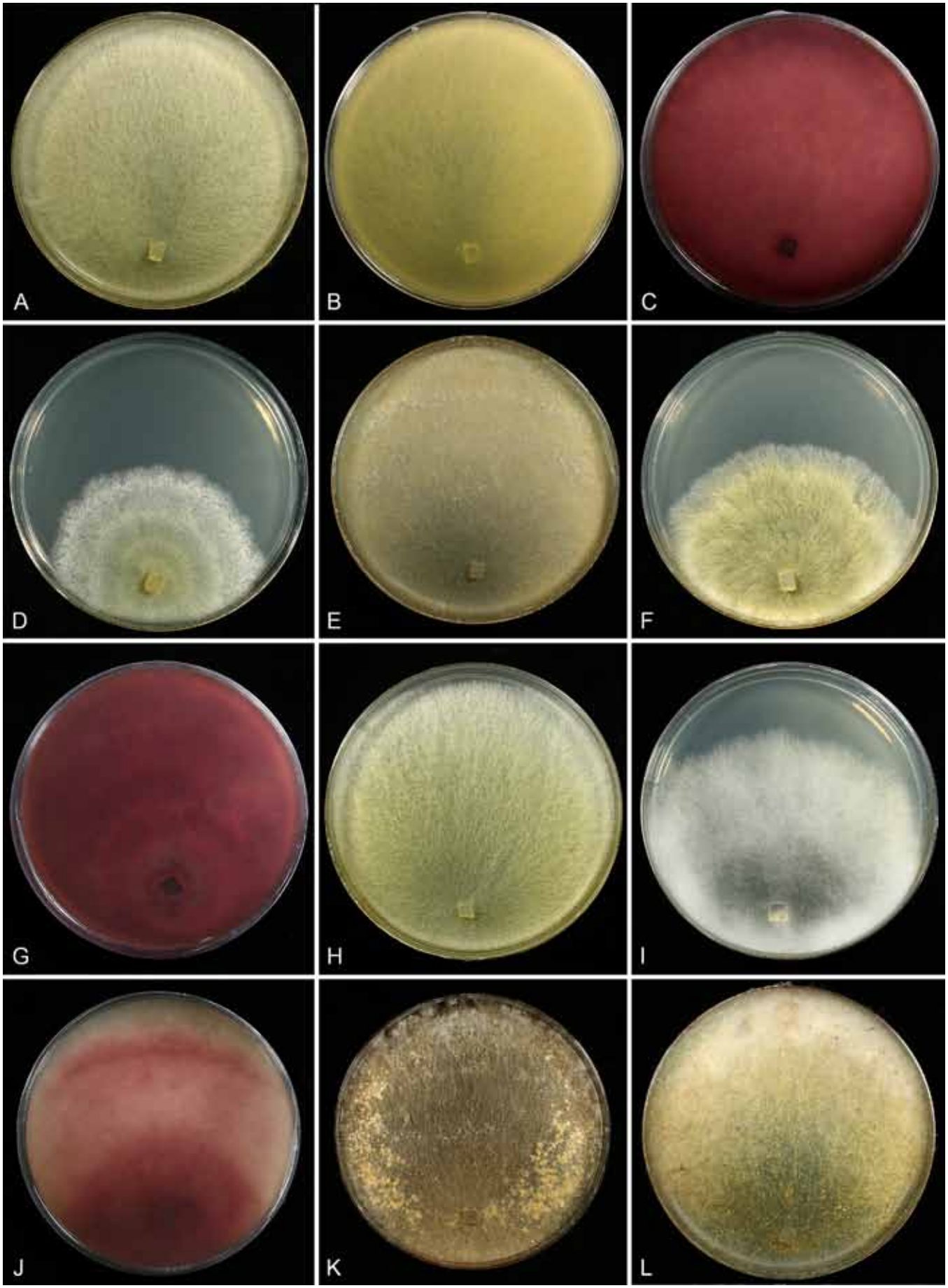

Fig. 4. Cultures of seven species of *Hypomyces/Cladobotryum* grown at 25 ºC in 12/12 h alternating darkness and fluorescent light. A–C. *H. samuelsii*. D, E. *H. virescens*. F, G. *C. heterosporum*. H. *C. indoafrum*. I, J. *C. semicirculare*. K. *C. protrusum*. L. *C. paravirescens*. (A–C. G.J.S. 98-28; D. G.A. i1899; E. G.A. i1906; F, G. CBS 719.88; H. TFC 03-7; I, J. CBS 705.88; K. FSU 5077; L. TFC 97-23; C, J on PDA, rest on MEA. A, B, D, F, H, I after 4 d; C, G, J. 2 mo; E, K, L. 1 mo).

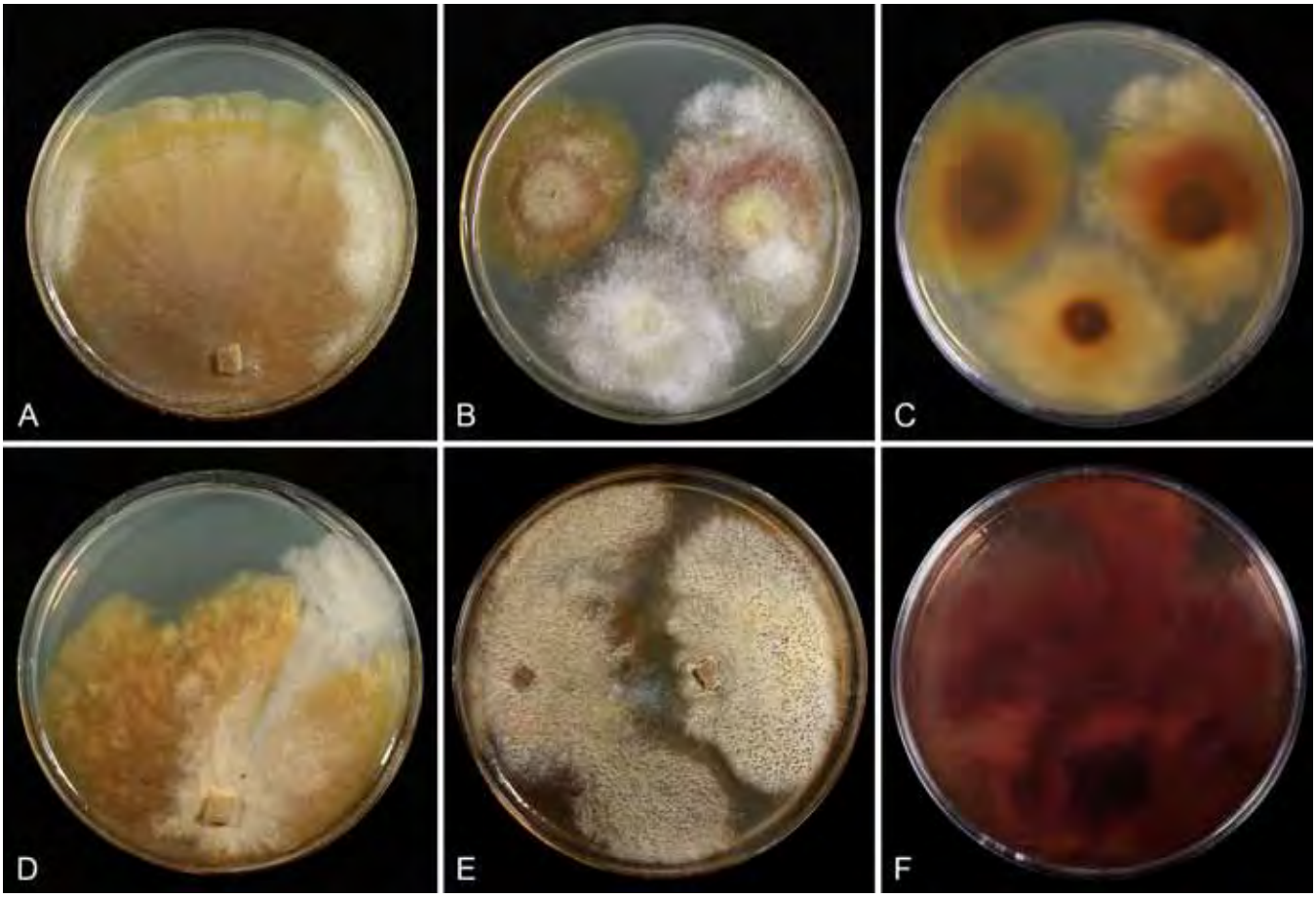

Fig. 5. Cultures of *C. cubitense* and *H. gabonensis* on MEA after 25 ºC grown in 12/12 h darkness and fluorescent light. A. *C. cubitense* G.A. i1361. B–F. *H. gabonensis* TFC 201156. B–D. Ochraceous colonies with the primary anamorph, white colonies/sectors with reddish reverse representing the secondary anamorph. (A, D grown for 1 mo; B, C, 2 wk; E, F 2 mo).

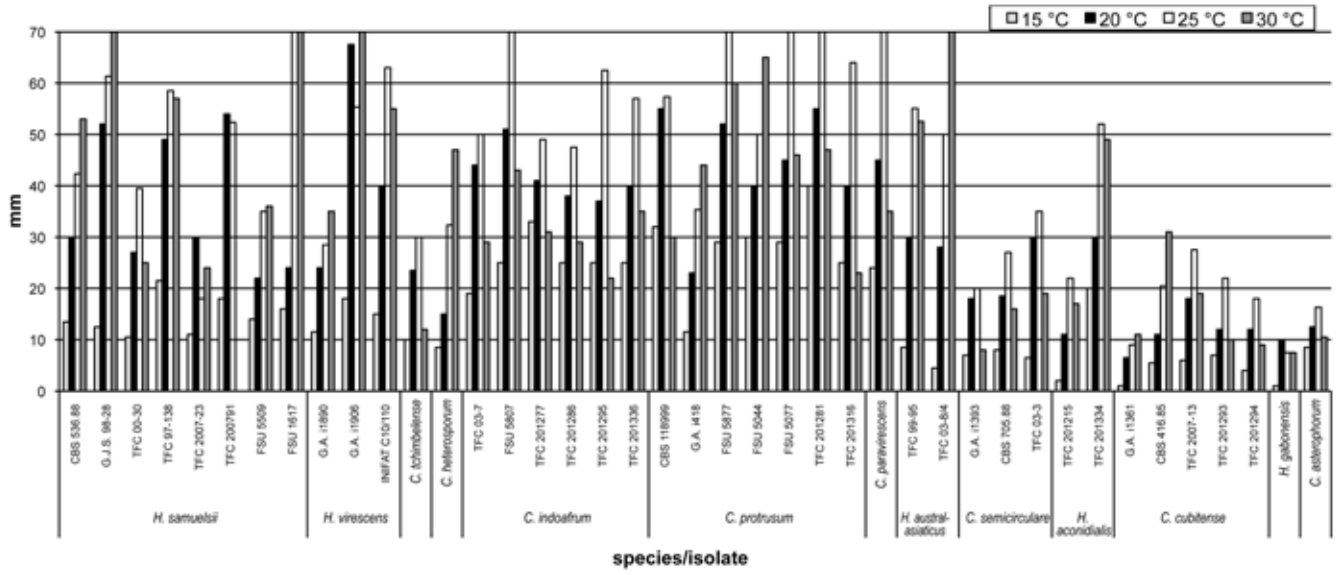

Fig. 6. Colony radius of 40 isolates of 12 tropical *Hypomyces/Cladobotryum* species and ex-type culture of *C. asterophorum* grown for 4 d on MEA at four different temperatures. Values represent means of 2–3 experiments.

On PDA the colony appearance is similar to that on MEA, with more intense colouration, turning from paler or darker egg-yolk yellow to crimson. The cottony aerial mycelium is generally more abundant, often reaching the lid of the Petri dish throughout the colony. On CMD all strains produce colonies with scarce aerial mycelium and the reverse turns bright yellow early. Generally the mycelium is homogenous with less conidiation than observed on other media. Only in *C. tchimbelense, C. heterosporum*, and one strain of *C. protrusum* growth is fasciculate.

Substrata

Species of the aurofusarin-group of *Hypomyces/Cladobotryum* grow on fruiting bodies of basidiomycetes belonging to specific taxonomic groups. The documented hosts represent saprotrophic, wood-decaying homobasidiomycetes, including species with soft, annual, or tough, perennial basidiomata either with poroid or gilled hymenophores. The host species belong to the families *Agaricaceae, Crepidotaceae, Pleurotaceae, Schizophyllaceae,* and *Tricholomataceae* in the *Agaricales* or to the *Coriolaceae, Cyphellaceae, Ganodermataceae, Lentinaceae, Polyporaceae,* and *Pterulaceae* in the *Polyporales*. Only *H. samuelsii* has also been collected on members of *Auriculariales* and *Hymenochaetales.*

While in temperate regions various ectomycorrhizal (EcM) taxa are frequently recorded as hosts of red-pigmented *Hypomyces/ Cladobotryum*, these have never been observed to parasitise EcM fungi in the tropics. Such differences may be due to the scarcity and patchy distribution of ectomycorrhizal trees in the tropical forests. The red species have been found also on bark, sometimes in association with black ascomata. In such cases observation on the actual host remains obscure because wood can always contains fungal hyphae.

Host preference apprears to characterise several taxa even if their host ranges are mutually not exclusive. *Hypomyces samuelsii*, with the most numerous available collections, grows on different kinds of fruiting bodies of members of various basidiomycete taxa. It is the only species of the group that has repeatedly been found on *Auricularia* spp., that are otherwise only infrequently parasitised (Põldmaa & Samuels 2004). *Cladobotryum semicirculare* appears to grow often on members of the *Polyporales*, while *H. australasiaticus* has yet been reported only on polypores including the not closely related *Antrodiella, Earliella,* and *Microporus*. The few collections of *C. tchimbelense* and *H. aconidialis* are on saprotrophic *Tricholomataceae*. Members of this family appear as preferred hosts also for *C. indoafrum* and *C. protrusum*. These differences may partially be explained by the state in which the parasite was found. The tropical red-pigmented *Hypomyces* follow the substrate pattern of *Hypomyces* species with *Cladobotryum* anamorphs, in which the anamorphs and teleomorphs can differ in their host range. While the anamorphs of several species can spread fast on soft ephemeral agaricoid basidiomata, the slower developing teleomorphs are only formed on more durable substrata. These include polyporoid basidiomata, wood or other substrata of the fungal host that were observed in all the studied teleomorphic collections except for one specimen of *H. samuelsii* on *Crepidotus* sp.

The anamorphs of temperate, red perithecial *Hypomyces* are causal agents of the cobweb disease responsible for epidemics in mushroom farms (McKay *et al.* 1999). In Taiwan *C. semicirculare* has been isolated growing on basidiomata of *Ganoderma* distributed as *G. tsugae* (Kirschner *et al.* 2007). Besides this record, we are not aware of similar cases in tropical regions.

Geographic distribution

The sparse data resulting from sporadic collecting activities of *Hypomyces* in the tropics support Samuels (1996) who stated that most species of the *Hypocreales* are either temperate or tropical and subtropical. From the phylogenies presented herein, it seems obvious that the species growing in various (sub)tropical areas of the world are distinct from the well-known temperate species to which many of the previous tropical collections had been attributed. This conforms to the pattern detected in some taxa of the sister genus *Hypocrea/Trichoderma* in which detailed studies have revealed more refined geographic distribution for many of the species (*e.g.* Jaklitsch *et al.* 2006, Samuels 2006). In red *Hypomyces/Cladobotryum* a number of closely related tropical species form the sister group of temperate taxa (Fig. 1, clades I and II, respectively). The rest of the tropical taxa represent earliest diverged lineages in the whole group that has also been observed in other hypocrealean fungi (*e.g.* O'Donnell *et al.* 2000).

The data presented here, as well as unpublished observations, reveal that none of the red-pigmented *Hypomyces/Cladobotryum* species crosses the line between holarctic and paleo- and/or neotropical distribution. Moreover, these results challenge the idea of pantropical distribution in most of the studied fungi. With two exceptions, the species occurring in tropical America have not been collected on other continents. The numerous collections of *H. samuelsii* suggest that this species is common in Central America. Thus far, *H. virescens* and *C. heterosporum* have been found only from Cuba but for *C. cubitense* records are added from Peru and Madagascar. In *C. semicirculare*, the genetic segregation between isolates from Central America and southeastern Asia suggests that morphological comparison coupled with analysing more variable gene regions may warrant the distinction of two species.

The remaining species in the treated group have not been found in the Western Hemisphere. *Hypomyces australasiaticus* has been collected in Australia, Sri Lanka and Thailand, while *C. paravirescens* is known only from its type specimen in Thailand. For the rest of the species at least some of the specimens originate from Africa. However, the scattered sites sampled on that continent give a mere hint of the great diversity of *Hypomyces* in the vast, unexplored areas. Namely, the few collections from Gabon, Republic of South Africa, Uganda and Zimbabwe belong to five new species that do not appear as closest relatives to each other. A dozen specimens collected from close localities in southeastern Madagascar belong to three of these taxa. Whereas *C. tchimbelense* and *H. gabonensis* are described from Gabon, *H. aconidialis* was also found in Madagascar. *Cladobotryum indoafrum*, common in Madagascar but collected also in southern Africa and Sri Lanka, is presumed to represent a species with an African-Indian distribution pattern. Even wider distribution is documented for *C. protrusum*, extending from southern Africa and Madagascar to southeastern China and Taiwan.

Despite the scarcity of data it is obvious from the phylogeny of the red-pigmented *Hypomyces* that different distribution events have resulted in the geographic pattern of extant taxa. The species occurring in temperate North America, *H. odoratus, H. rosellus* and *C. purpureum* do not show affinities to the several species found in tropical America. On the other hand, the clade comprising *C. asterophorum, C. protrusum* and *C. paravirescens* suggests extensive dispersal events related to speciation taking place along the tropical and temperate regions of eastern Asia. Disjunct distribution, described in saprotrophic and ectomycorrhizal

fungi (*e.g.* Matheny *et al.* 2009) is observed in *C. cubitense* and *C. semicirculare.* Also the sister taxa of *C. tchimbelense* from Africa, *H. samuelsii* and *H. virescens* grow in America. Similar African-South American disjunctions have been attributed to transoceanic dispersals in the *Fusarium graminearum*-group (O'Donnell *et al.* 2000). Estimating the divergence dates of lineages is required to understand whether also vicariance events have contributed to the observed distribution pattern as has been suggested for other groups of fungi (*e.g.* Hosaka *et al.* 2008, Matheny *et al.* 2009).

Species delimitation and phylogenetic relationships

The present study combines morphology, culture characteristics, and phylogenetic analyses of four gene regions for determining species and phylogenetic relationships among the red-pigmented *Hypomyces/Cladobotryum*. The analyses include pleomorphic taxa as well as those for which no teleomorph has been found. Tropical collections appear distinct from the temperate species, most of which form one clade (Fig. 1, clade II) comprising the common and well-known *H. odoratus* and *H. rosellus*. All the specimens from tropical areas of the world are distributed among other lineages. Most of them fall in the large clade I that appears as the sister-group to the temperate taxa in clade II. Members of this tropical clade share characters typical of the temperate taxa in producing fast-growing colonies that turn from yellow to purplish red in culture. Although all the isolates with greenish conidia are included in this clade, these do not form a monophyletic subclade. Moreover, none the four species forming green conidia reveal close affinities to another taxon sharing this feature. Neither do the studied green-conidial non-American isolates belong to *C. virescens* described from Cuba, the only previously known red-pigmented species producing green conidia. Therefore three new species, *C. indoafrum, C. paravirescens* and *C. protrusum*, are described based on material collected in Africa, Madagascar and southeastern Asia.

Clade I, including mostly tropical red *Hypomyces/Cladobotryum,* is composed of two subclades (Fig. 1). One of these, subclade A, includes five distinct lineages, each characterised by a unique combination of morphology. Members of three of the lineages are described below as new anamorphic species *C. heterosporum, C. indoafrum,* and *C. tchimbelense*. For the other two species, earlier known only from their anamorphic type material, teleomorphs are described herein. In *H. samuelsii*, previously known as *Sibirina coriolopsicola*, recently isolated and sequenced material provides evidence for the connection with teleomorphic specimens collected for over a hundred years. In *H. virescens,* the teleomorph has been obtained only in culture in a pairing of the only two known strains.

The sister-group, subclade B (Fig. 1), is well-supported but poses problems for species delimitation. Besides *C. purpureum*, described from North America, members of this subclade have been isolated outside the Western Hemisphere, mostly from tropical areas. The only other previously described species is *C. asterophorum,* known from the ex-type strain isolated from Japan. Characteristic of this strain is the production of polyblastic conidiogenous cells, a feature that is shared by most of the strains in subclade B. However, isolates forming several loci at the swollen apex of the conidiogenous cell do not form a monophyletic group. Rather, the ex-type isolate of *C. asterophorum* forms a strongly supported group with two strains characterised by monoblastic conidiogenous cells. The isolate TFC 97-23 from Thailand was previously reported as belonging to *C. virescens* (Põldmaa & Samuels 2004), while that from China (FSU 5046) was published as *Sibirina purpurea* var. *purpurea* (Chen & Fu 1989). Species delimitation is based on the correlation between genetic segregation and unique combinations of characters. The new species *C. paravirescens* and *C. protrusum* produce green conidia from poly- or monoblastic conidiogenous cells, respectively. *Cladobotryum asterophorum* differs in forming hyaline conidia from polyblastic cells.

As the well-supported sister-group of clades I and II, clade III (Fig. 1) is composed of tropical isolates that are often weakly pigmented and produce indistinct conidiophores. Molecular data support the distinction of *H. australasiaticus* with the longest conidia in the group from *C. semicirculare* with strongly curved conidia. A conidial isolate from Azerbaijan (TFC 99-13), forming an individual lineage, represents an undescribed species lacking a voucher specimen. A distinct lineage is formed of two isolates described as *H. aconidialis;* these are unique in lacking anamorph structures on natural substrate and culture media, while forming a discrete pulvinate subiculum with abundant perithecia reaching maturity in culture.

The most basal clade of the ingroup includes two tropical taxa (Fig. 1, clade IV) with limited production of red pigments. *Hypomyces gabonensis,* described here, forms the sister group to *C. cubitense*. These species differ in several aspects from other red-pigmented *Hypomyces/Cladobotryum*. Their colonies grow slowly on different media with intensive ochraceous colouration in *H. gabonensis*. The red pigments are absent or develop only in older cultures. While an immature teleomorph has been found for *C. cubitense* in nature, abundant buff-coloured perithecia with mature ascospores are produced in polysporic isolates of *H. gabonensis*.

KEY TO ANAMORPHS OF *HYPOMYCES*/*CLADOBOTRYUM* SPECIES PRODUCING RED PIGMENTS

1. Conidia observed on natural substratum and on standard culture media 2
1. Conidia not observed on natural substratum or on standard culture media ..... 10. *H. aconidialis*

2. At least part of conidia greenish 3
2. All conidia hyaline 6

3. Conidiogenous cells polyblastic, tips with protrusions ..... 6. *C. protrusum*
3. Conidiogenous cells monoblastic, tips simple 4

4. Conidia mostly uniformly cylindrical, mean l/w ratio > 3.0 ..... 2. *H. virescens*
4. Conidia mostly ellipsoidal or irregular in shape, often curved at base or both ends, mean l/w ratio < 3.0 5

5. Conidia mostly 1-septate, 2–3-septate conidia rare, conidial bases acuminate ..... 7. *C. paravirescens*
5. Conidia 1–3-septate, 2–3-septate conidia common, conidial bases rounded ..... 5. *C. indoafrum*

6. Aerial mycelium of long unbranched hyphae that form short lateral branches supporting verticils of conidiogenous cells; conidia slender, with mean l/w ratio > 4 ..... 8. *H. australasiaticus*
6. Aerial mycelium of moderately to profusely branched hyphae, usually forming long lateral branches that function as conidiophores with further branching, often confined to the apex; conidia with mean l/w ratio < 4 7

7. Conidia mostly 1-, rarely 2-septate 8
7. Conidia 1–3-septate, 3-septate conidia always present 10

8. Conidia > 20 µm long, > 7 µm wide ..... 3. *C. tchimbelense*
8. Conidia < 20 µm long, < 7 µm wide 9

9. Conidial shape homogenous, mostly one conidium at apex of conidiogenous cell ..... 12. *H. gabonensis*
9. Conidia variable in shape, 1–4 conidia at apex of conidiogenous cell ..... 4. *C. heterosporum*

10. Conidia ellipsoidal to fusiform, straight, slightly curved or twisted with ends curved in different direction ..... 1. *H. samuelsii*
10. Conidia ellipsoidal to clavate, often curved 11

11. Conidia ellipsoidal, often strongly curved to semicircular, held in radiating heads at the single locus at apex of conidiogenous cell, mean length < 19.5 µm, l/w ratio < 3.5 ..... 9. *C. semicirculare*
11. Conidia mostly cylindrical to clavate, less prominently curved, not appearing semicircular, held horizontally in imbricate chains at uppermost locus, occasionally also singly at intercalary loci, mean length > 19.5 µm, l/w ratio > 3.5 12

12. One type of conidiophore and conidia formed in culture ..... 11. *C. cubitense*
12. Cultures initially produce profusely branched conidiophores with 1-septate conidia on terminal and intercalary conidiogenous loci, followed by formation of moderately branched conidiophores producing larger 3-septate conidia from a single locus ..... 12. *H. gabonensis*

DESCRIPTIONS OF SPECIES

1. *Hypomyces samuelsii* K. Põldmaa, **sp. nov.** MycoBank MB518517. Figs 2A, 4A–C, 7.
Anamorph: ***Cladobotryum coriolopsicola*** (R.F. Castañeda) K. Põldmaa, **comb. nov.** MycoBank MB519537.
Basionym: *Sibirina coriolopsicola* R.F. Castañeda, Fungi Cubenses II, 10–11. 1987.

Etymology: Named to honour Gary J. Samuels whose long and extremely productive mycological career is mostly dedicated to the taxonomy of the *Hypocreales* with passion for *Hypomyces* among many others.

Perithecia in effuso subiculo dispersa, semiimmersa, coccinea purpurescentia, obpyriformia, (250–)270–370 × (160–)200–260 µm; papilla late conica, 65–120 µm alta, basi (60–)80–105 µm lata. Asci cylindrici, 130–160 × 7–9 µm. Ascosporae fusiformes, 21.0–23.2–27.6–29.0 × 5.0–6.1–6.8–8.0 µm, septo mediano, dense verrucatae, apiculo 2.5–3.3–4.4–5.5 µm longo. Conidiophora 100–400 µm longa, 7–12 µm lata. Cellulae conidiogenae cylindraceae vel subulatae, 25–45 µm longae, propre basin 4–6 µm latae, uno loco. Conidia ellipsoidea vel cylindracea, (late-) fusiformia, recta vel extremo extremibusque flexa, 15–30 × 6–8 µm, hyalina, 1–3(–4)-septata. Chlamydosporae 12–14 µm diametro, ochroleucae.

Subiculum with embedded perithecia widely effused over host or in small, < 1 cm diam patches, forming dense, cottony or sometimes scarce, arachnoid mat, whitish to pale crimson, buff to yellowish; hyphae hyaline to pale purplish red, 3–6 wide, with cells partially swollen to 17 µm diam, especially near the perithecia, thin-walled. *Perithecia* scattered in subiculum, semi-immersed to almost superficial, crimson to purplish red, turning purple in KOH with tip of papilla remaining hyaline and occasionally lower part of venter reddish brown; flask-shaped, (250–)270–370 × (160–)200–260 µm; *wall* 12–20 µm wide, composed of a single region of flattened thin-walled cells, cells greatly swollen, 12–20 µm diam, at surface; *papilla* prominent, broadly conical, 65–120 µm high, (60–)80–105 µm wide at base, with cells at surface 11–17 µm diam, attenuating to 30–60 µm at tip, tip obtuse with oblong-clavate cells, 6–14 × 3–4.5 µm reaching surface; ostiolar canal periphysate. *Asci* cylindrical, 130–160 × 7–9 µm, apex thickened, 0.5–1.5(–2.0) µm; ascospores uniseriate with ends overlapping. *Ascospores* fusiform, often inequilateral, (21.0–)23.2–27.6(–29.0) × (5.0–)6.1–6.8(–8.0) µm, Q = (3.2–)3.8–4.2(–4.9), main part of ascospore (14.5–)16.6–19.7(–22.5) × (4.5–)5.2–5.6(–6.0) µm, Q = (2.5–)3.2–3.5(–4.1); 1-septate, septum median; densely warted, warts to 1 µm high; apiculate, apiculi (2.5–)3.3–4.4(–5.5) µm long and (1.0–)1.6–2.4 (–3.0) µm wide at base, tips obtuse or sometimes acute.

Anamorph effused on host, also on subiculum. *Conidiophores* borne on scarce mycelium, erect, 100–400 µm long, 7–10 (–12) µm wide at base, tapering to 5–6 µm below uppermost verticil of conidiogenous cells, frequently septate, especially near base, thin-walled, hyaline, forming 1–2 verticils of conidiogenous cells. *Conidiogenous cells* held by 2–4, cylindrical to subulate, sometimes widest in middle, often constricted in upper part, 25–45 µm long, 4–6 µm wide near base, attenuating to 1–2 µm at apex, with one uppermost locus sometimes bearing a collarette. *Conidia* ellipsoidal to cylindrical, fusiform to broadly fusiform, occasionally long obovoid, equi- or inequilateral, straight or curved at one or both ends; 15–30 × 6–8(–10) µm; hyaline, apex sometimes refractive; 1–3(–4) septate; basal hilum small, central or slightly shifted to side. *Chlamydospores* of 2–4 cells, in lateral position on intercalary cells, subglobose, 12–14 µm diam, pale ochraceous, wall 1–1.5 µm thick, smooth.

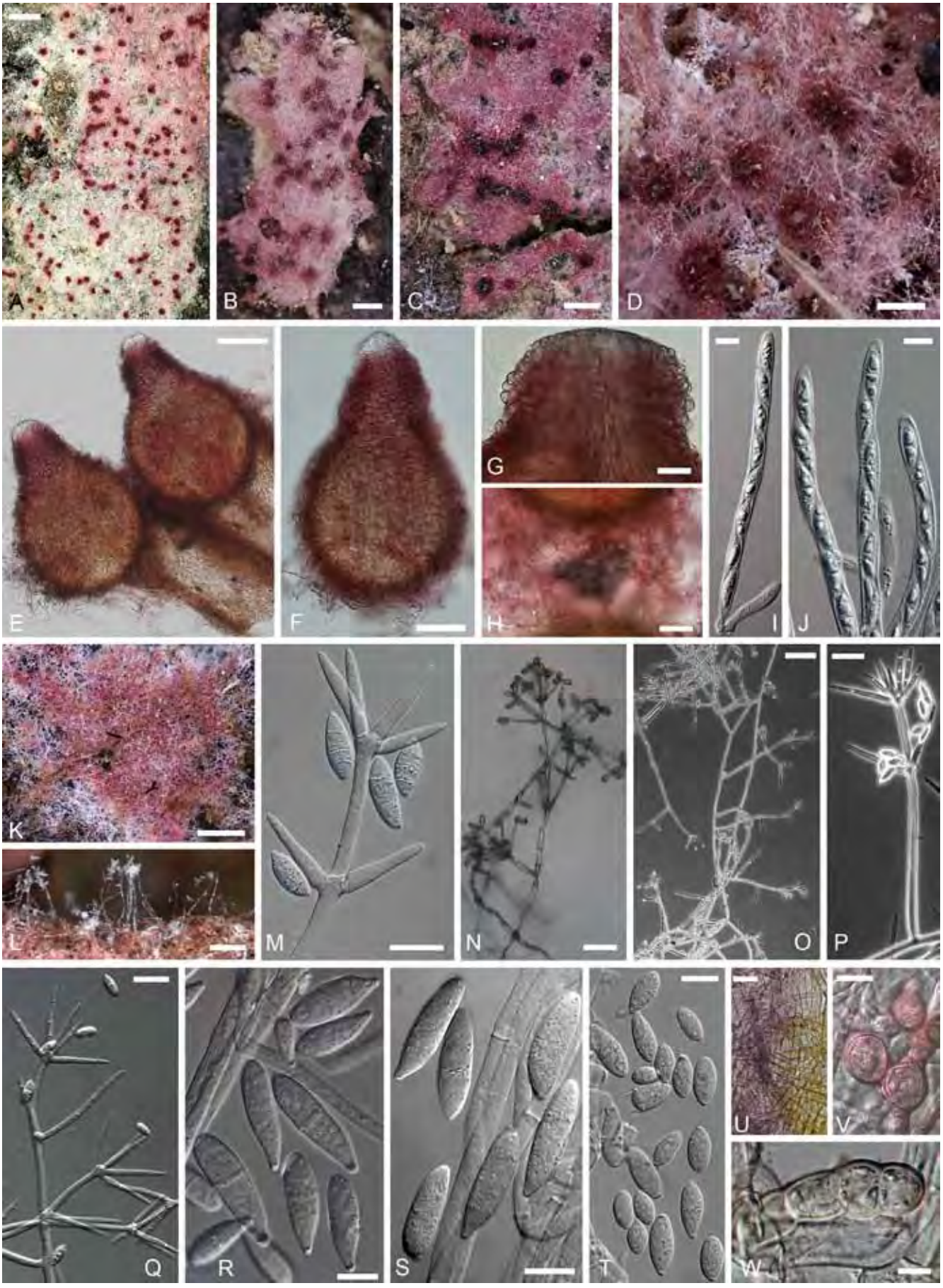

Fig. 7. *Hypomyces samuelsii*. A–D. Perithecia embedded in subiculum effused over the substratum. E. Two perithecia seated on host's pores. F. Perithecium. G. Perithecial papilla with ostiolar canal in the center and swollen cells on the surface. H. Swollen cells surrounding perithecia. I, J. Asci. K–M. Anamorph on the host. N–V. Anamorph in culture. N–Q. Conidiophores with verticillately placed conidiogenous cells bearing conidia at their tips. R–T. Conidia. U. Hyphae turning from initial yellow to purple in KOH. V, W. Chlamydospores. (A, H, I. TU 112902; B, G, J. BPI 749247; C, K. TFC 97-138; D, E. Holotype, BPI 748258; F. TU 112903; L, M. TU 112901; N, S, V. TFC 00-30; O–Q. TFC 200789; R, U. Ex-type culture, G.J.S. 98-28; T, W. G.J.S. 96-41). Scale bars: A = 1 cm; B, C = 500 µm; D, K, L = 250 µm; E, O = 100 µm; F, H = 50 µm; G, M, N, P, Q, U = 20 µm; I, J, R–T, V, W = 10 µm.

Colonies on MEA spreading fast, reaching 45–50 mm in 4 d; margin even or slightly fasciculate; reverse initially yellow, turning purplish red; yellowish brown, round or fan-shaped crystals and/or pigment patches with needle-like margins, turning deep purple in KOH, abundant in agar. *Odour* sweet or bitter-sweet, strong in recently isolated cultures, disappearing in old cultures. *Aerial mycelium* scanty to abundant, cottony, to 7 mm high or < 2mm in cultures producing teleomorph; mostly homogenous, occasionally with tufts; yellowish white, amber or buff, partially turning violet in KOH. Submerged hyphae often turning violet in KOH, cells infrequently swollen. *Conidiation* abundant in fresh isolates, becoming moderate to scarce in older strains. *Conidiophores* arising from aerial hyphae at right angles, not differentiated from these or distinct with main axis yellowish ochraceous, KOH+ and wall slightly thickened; ascending to suberect, 200–400(–1000) µm long, main axis near base 4–10 µm wide; branching profuse or sometimes sparse, verticillate or irregular, occasionally drepanoid, widely distributed, sometimes confined to uppermost parts, conidiophores then appearing irregularly tree-like in aspect; lateral branches formed at 1–2 levels, 1–4 developing from one point, 30–60 × 3.5–4.5 µm. *Conidiogenous cells* formed directly on conidiophores or from lateral branches that are often integrated in a previous verticil of conidiogenous cells, developing singly or (2–)3–6(–8) in a verticil, sometimes singly below verticil; subulate, 25–40 µm long, 2.5–4.5 µm wide near base, attenuating gradually to 0.8–2.0 µm at apex; aseptate; forming one conidiogenous locus at apex. *Conidia* ellipsoidal to fusiform, long obovoid *i.e.* droplet-shaped or sometimes widest in lower half (oblong-ovoid); equi- or inequilateral, straight but sometimes with basal or both ends curved; attenuated at base to a narrow but prominent central hilum, often attenuated also at apex; (9.5–)11.7–22.2(–26.5) × (4.0–)5.4–7.2 (–9.0) µm, Q = (1.6–)2.2–3.8(–4.6); 1–3-septate, in 1-septate conidia septum median or in upper 1/3 or 2/3; hyaline or occasionally with tinge of green when old, with refractive thickening at base or sometimes also at apex; formed obliquely from uppermost locus, held by (1–)2–3(–8) in imbricate chains appearing as radiating heads. *Chlamydospores* formed among aerial or submerged mycelium, hyaline; cells subglobose, 13–23 µm diam, wall 1–2 µm thick, smooth; 2–5 cells in intercalary chains or in lateral, irregular chains or sclerotia-like aggregations formed from an intercalary cell. Perithecia produced in abundance in recent cultures isolated from ascospores.

Substrata: Basidiomata of various wood-decaying members of *Agaricales, Hymenochaetales* and *Polyporales*, also on *Auriculariales*; in some collections host fungus not detected and then observed growing on bark, wood or associated with other ascomycetes.

Distribution: Tropical America.

Holotype: **Puerto Rico**, Luquillo, Chicken Farm, on *Phellinus* cf. *chryseus*, 10 June 1998, G.J. Samuels, BPI 748258, **ex-type** culture G.J.S. 98-28 = CBS 127157.

Specimens with living cultures examined: **Costa Rica**, Guanacaste Conservation Area, Santa Rosa National Park, on *Crepidotus* sp. and wood, 9 Oct. 1997, P. Chaverri & S. Salas, InBio 3-233, culture TFC 97-138 = CBS 127159; Guanacaste Conservation Area, Rincón de la Vieja Nat. Park, Pailas, on *Hexagonia glabra*, 1 July 1998, P. Chaverri & S. Salas InBio 5-183, culture IB8029 = TFC 00-30. **Cuba**, Guantanamo Prov., Imías, on *Coriolopsis* sp., 29 Apr. 1986, M. Camino, C 86/138, **Holotype** of *Sibirina coriolopsicola*, INIFAT, **ex-type** culture CBS 536.88; Sierra del Rosario, El Salon, on *Crepidotus* sp., 14 July 1984, G. Arnold A 84/790, culture FSU 1617 = m659; Soroa, on an agaric, 10 Nov. 1985, G. Arnold A 85/318, culture FSU 5509 = i1931; locality unknown, on *Pleurotus* sp., 1988, INIFAT Castañeda 87/261, culture G.A. i1716 = FSU 1010. **Peru**, Junin Dept., Chanchamayo Distr., Kimo, on fruitbodies of an agaricoid basidiomycete on a stem of a palm, 2 Mar. 2007, K. Põldmaa, TU 107212 (anamorph), conidial isolate TFC 2007-23 = CBS 127160). **Puerto Rico**, Caribbean National forest, Luquillo Mts, Trail to El Toro from Rte. 186, on wood, 24 Feb. 1996, G. J. Samuels & H. J. Schroers, BPI 749247, culture G.J.S. 96-41 = CBS 127158; Luquillo Mts., La Coca trail, on black mycelium on palm, 10 June 1998, P. Chaverri, BPI 748259, culture G.J.S. 98-29. **West Indies**, Martinique, Pointe La Philippe, on *Auricularia* cf. *polytricha* on bark of *Cyathea*, associated with *Gliocladium* sp., 19 Aug. 2007, C. L. Lechat 7259, TU 112901, conidial isolate TFC 200791 = CBS 127155; Anse Noire, on bark, 22. Aug. 2007, C. L. Lechat 7265, TU 112902, culture TFC 200793 = CBS 127156; same collecting data, JF07018, TU 112904, culture TFC 200790; Anse Noire, Les Anses d'Arlet, on bark of a dead standing stem and on black effused stromata incl. *Camillea* sp., 22 Aug. 2007, J. Fournier, JF07016, TU 112903, culture TFC 200789.

Specimens without living cultures but accompanied by dried cultures or anamorph on the host: **Cuba**, Santa Clara Prov., Santa Clara, on *Auricularia* sp., 17 Mar. 1905, F. S. Earle & W. Murrill 424, NY. **Jamaica**, Tray, on wood, 19 June 1909, A.E. Wight 473, NY, perithecia immature, anamorph present. **Puerto Rico**, Bosque Estatal de Guajataca Trail 1 to cave, on leaf litter, 24 Nov. 1992, S. M. Huhndorf 239, CTR 92-87, NY, dried culture BPI 747860. **USA**, Florida, Highlands Hammock, on a resupinate polypore, 1 Feb. 1937, C. L. Shear #288, BPI 630895; Rock Spa, on *Daedaleopsis confragosa*, 11 Jan. 1942, C. L. Shear, BPI 630911; Alachua Co., Univ. of Florida Horticultural Farm, 6 miles NW of Gainesville, on *Auricularia* sp., 26 Aug 1977, C. T. Rogerson 77-121, NY.

Notes: Most of the tropical collections of red perithecial *Hypomyces* at BPI were preserved as *H. odoratus*. Anamorphs studied in pure cultures, available for three of these, clearly differed from the anamorph of *H. odoratus* that is frequently found on mostly agaricoid basidiomycetes in Europe. Another specimen at NY (Huhndorf 239), accompanied by a dried culture and drawings representing similar morphology, had been published as one of first collections of *H. odoratus* in nature (Rogerson & Samuels 1994). Teleomorphs and anamorphs of these four specimens from Puerto Rico were similar to those collected in Costa Rica and the West Indies. Analyses of sequence data confirmed conspecificity of all the ascosporic isolates but revealed these not to be related to *H. odoratus*. The strongly supported monophyletic group comprised also three conidial isolates from Cuba, including the ex-type strain of *Sibirina coriolopsicola,* and one isolate from Peru. Based on these data, a new pleomorphic species, *Hypomyces samuelsii* is described.

Besides these collections of *H. samuelsii*, numerous specimens, including similar teleomorphs but lacking cultures, have been collected mostly from the the Caribbean region since the end of the nineteenth century. Several originate from Puerto Rico, with the oldest collection at NY dating back to 1899 (collected by G. P. Goll in Bairoa, Caguas). In 1930 a specimen has been sampled in the Luquillo mountains, as is a more recent collection with a living culture that was selected as the holotype of *H. samuelsii*. Rest of the specimens at NY originate from Cuba, Guatemala, Jamaica, USA (Florida, Louisiana) and the West Indies. While most of the specimens have been growing on various polypores, several were collected on *Auricularia* spp. as was a recent isolate from the West Indies. In most of these the morphology of the teleomorph and anamorph (if present) matches that of the cultured collections of *H. samuelsii*. The measurements of the conspicuously warted ascospores are described and compared to those of similar species in the section of "Collections from tropical America lacking anamorph data". It was concluded that large part of the old collections apparently belong to *H. samuelsii* which can be considered a common species at least in the tropical forests surrounding the Caribbean Sea.

Until now, *Sibirina coriolopsicola* was known from the type collection containing only the anamorph. In the original description only the anamorph on natural substratum was described. Despite scarce conidation in the ex-type culture, it produced the characteristic fusiform 1(–3)-septate conidia, slightly smaller than reported in the protologue, 13–26 × 4.5–8 µm. The main differences between the studied isolates and the protologue are the rarity of 2–3-septate conidia in culture and much smaller conidia in some of the strains, *e.g.* G.J.S. 96-41. The fusiform, sometimes twisted form of conidia is usually not as pronounced on culture media as it is on natural substratum. The moon-shaped conidia described in the protologue were not observed in culture nor on natural substrata. In several strains, including the ex-type culture of the anamorph and that of the holomorph of *H. samuelsii* designated here, 1-septate conidia were prevalent. The conidial size differs considerably among the studied strains, with minimal overlap in length of the short- and long-conidial isolates. Conidiation appears retrogressive; in the older cultures conidiogenous cells become shorter and their tips wider. The anamorph was originally described in *Sibirina,* presumably because of verticillately placed conidiogenous cells, but fits the expanded concept of *Cladobotryum* proposed by Rogerson & Samuels (1993). The recognition of *Sibirina* is not justified based on the molecular and morphological data provided here as well as in previous studies (Põldmaa 2003).

2. *Hypomyces virescens* G.R.W. Arnold & K. Põldmaa, **sp. nov.** MycoBank MB518518. Figs 2B, 4D, E, 8.
Anamorph: ***Cladobotryum virescens*** G.R.W. Arnold, Feddes Repertorium 98: 351. 1987.

Etymology: The epithet of the previously described anamorph referring to the greenish conidia.

Teleomorphosis crescens in MEA substrato; colonia crescens in subiculum. Perithecia dispersa, immersa, obpyriformia, 380–460 × 280–350 µm, coccinea purpurescentia; papilla brevi, cylindracea, 70–100 µm alta, basi 70–100 µm lata. Asci cylindrici, 160–180 × 7.0–8.5 µm. Ascosporae fusiformes, (22.0–)26.0(–30.0) × (5.0–)5.9(–7.0) µm, septo mediano, habentes densas breves verrucas, apiculo 2.5–4.5 µm longo.

Teleomorph produced in culture on MEA; colony becoming subiculum with embedded perithecia. *Subiculum* dense cottony mat, roseous with scattered buff patches; hyphae hyaline to pale crimson, KOH + purple, 2.5–4 µm wide, with cells surrounding perithecia often swollen to 15 µm in diam, thin-walled. *Perithecia* scattered in subiculum, immersed; flask-shaped, 380–460 × 280–350 µm; purplish red, in KOH base of papilla, upper part of venter turning purple with lower part of venter reddish brown; *wall* of a single region of flattened, thin-walled cells, at surface cells broadly ellipsoidal, 20–30 × 10–16 µm; *papilla* short, cylindrical, 70–100 µm high, 70–100 µm wide, apex obtuse with oblong-clavate cells, 5.5–8.0 µm diam at surface. *Asci* cylindrical, 160–180 × 7.0–8.5 µm, ascospores uniseriate with ends overlapping. *Ascospores* fusiform, equi- or inequilateral, (22.0–)26.0(–30.0) × (5.0–)5.9 (–7.0) µm, Q = (3.6–)4.4(–5.1); ascospore body (16.5–)19.5(–22.5) × (4.5–)5.2(–6.0) µm, Q = (3.0–)3.7(–4.5); 1-septate, septum median; densely covered with low warts to 0.5 µm high; apiculi 2.5–4.5 µm long, 2–3 µm wide at base, straight or sometimes hooked, simple or hat shaped, occasionally branched, tips obtuse or acute.

Colonies on MEA spreading fast to very fast, reaching (30–) 50–70 mm in 4 d, reverse first yellowish ochraceous or bright yellow, turning slowly into yellowish or reddish brown; margin even. *Odour* absent or sweetish. *Aerial mycelium* scanty to moderate, cottony, to 3 mm high or reaching the lid in some parts; homogenous or with small tufts; pale whitish buff or yellowish, becoming greenish with formation of conidia, hyphae partially turning purple in KOH. Submerged hyphae often turning purple in KOH, cells not swollen. *Conidiation* abundant, not diminishing with age. *Conidiophores* arising from aerial hyphae at right angles, not differentiated; ascending to suberect or erect, main axis 6–10 µm wide, brownish yellow, except tips, pigmented parts turning purple in KOH; branching profuse, verticillate, dichotomous, drepanoid or irregular, confined to upper half giving conidiophores tree-like aspect, forming tufts in colonies; often conidiophores borne as side branches from a verticil of conidiogenous cells, branching further at top; lateral branches, formed by 1–3 from one point, 20–30 × 3–4 µm. *Conidiogenous cells* developing mostly on short lateral branches, 3–6 in a verticil; subulate, aseptate, (25–)30.3–34.2 (–40) µm long, (2.5–)3.1–3.5(–4.0) µm wide near base, attenuating gradually to 0.6–1.2 µm at apex, straight or slightly curved at apex; producing one conidiogenous locus at apex. *Conidia* cylindrical or long ellipsoidal, sometimes narrowly clavate, equi- or inequilateral, straight or curved in lower half, often also attenuated towards base, (15.0–)20.6–23.6(–29.0) × (5.0–)6.1–6.5(–8.0) µm, Q = (2.5–) 3.4–4.0(–5.0); 1–3-septate, hyaline to pale green, pigmentation sometimes visible only in conidial masses, may be refractive at apex and hilum; hilum prominent, central or slightly off center; conidia produced obliquely from uppermost locus, (1–)2–3(–5) in radiating heads. *Chlamydospores* absent or formed in short lateral chains among aerial mycelium, cells globose, 9–16 µm diam, wall 1.0–1.5 µm thick; sclerotia-like aggregations absent.

Substrata: Wood-decaying basidiomycetes, wood.

Distribution: Central America.

Holotype: **Cuba**, G. Arnold, dried cultures with perithecia obtained from pairing isolates G.A. i1906 and G.A. i1899, data listed below, JE, isotypes BPI, TU 112905.

Cultures examined: **Cuba**, Matanzas Prov., Coliseo, on old decaying wood on the ground, 21 Feb. 1983, G. Arnold, A 83/244, holotype of the anamorph, permanent slide at JE, isotype HAJB, **ex-type** culture G.A. i1906 = TFC 98-37 = FSU 5526 = ATCC 66118 = CBS 676.92; Camaguey Prov., Moron, on *Schizophyllum commune*, 10 Oct. 1985, G. Arnold A 85/616-3, G.A. i 1899 = FSU 5525 = CBS 127161; Santiago de Las Vegas, on *Lentinellus* sp., 10 June 2010, R.F. Castañeda-Ruiz, INIFAT C10/110, culture TFC 201449.

Notes: *Cladobotryum virescens* was described based on a single collection from Cuba. Crossing the ex-type strain with another strain of this species from a different locality in Cuba by the author of the species in 1992 resulted in the production of perithecia in culture. This dried culture, deposited at JE (part of it as the isotype at TU), serves as the holotype of the teleomorph described herein. Another dried culture obtained from pairing the same two cultures is preserved at BPI. The ascospores formed in the perithecia of the two dried cultures differ to some extent. In the material at BPI ascospores are shorter and bear very low and broad apiculi, whereas in the holotype material, ascospores and apiculi are more slender with their tips acute. Formation of the teleomorph could not be repeated even when including the recently isolated strain in the pairing experiments.

The protologue describes the conidiogenous cells as producing one, seldom two conidia that are narrower (4.5–5.5 µm) than in current observations. In the isolates grown on MEA usually two to three, sometimes also four or five conidia are held at the tip of

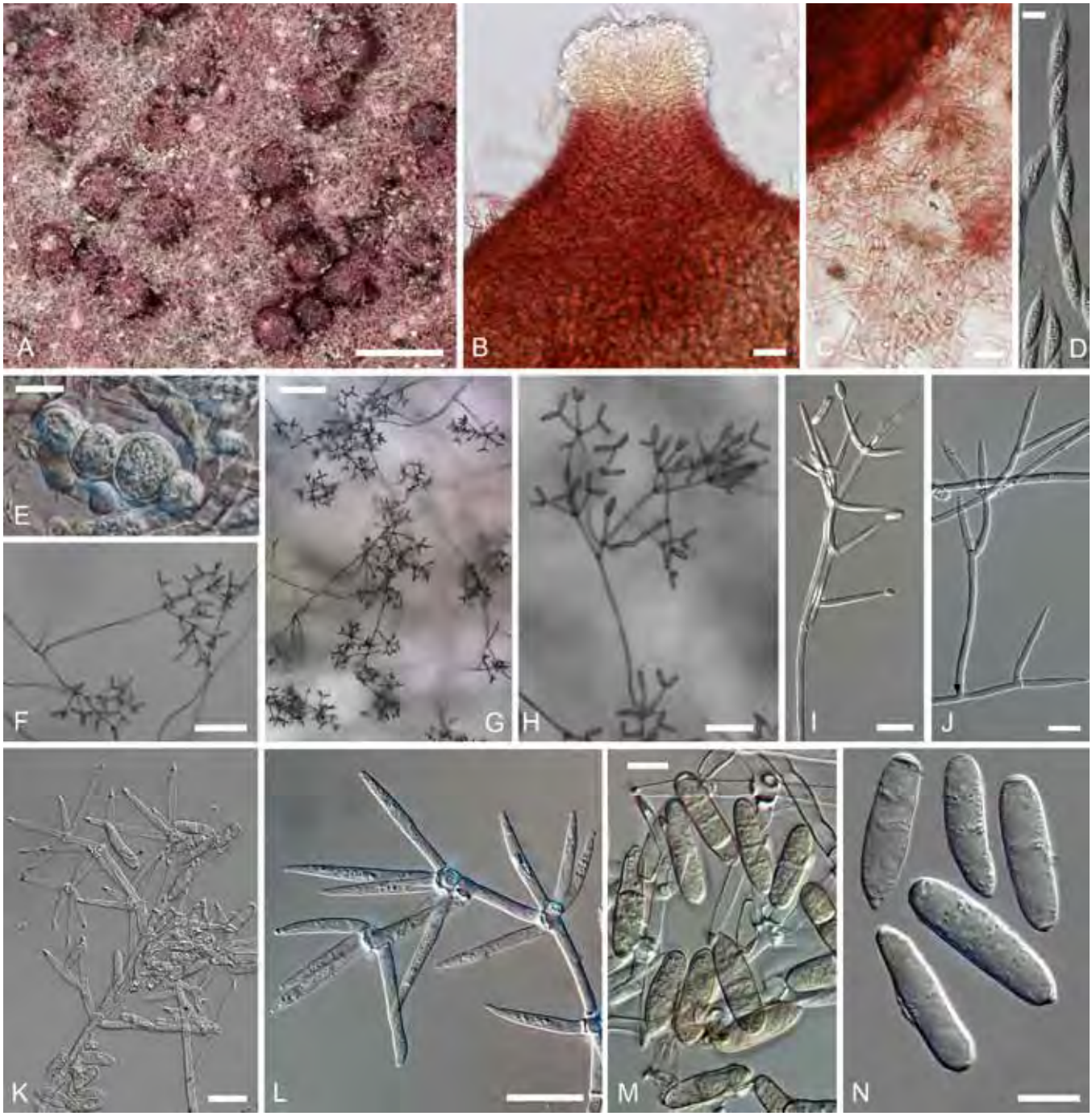

Fig. 8. *Hypomyces virescens*. A–D. Teleomorph from a dried culture on MEA. E–N. Anamorph on MEA. A. Perithecia embedded in the subiculum. B. Upper part of a perithecium. C. Base of a perithecium and subicular hyphae. F. Asci and ascospores. E. Chlamydospores among subiculum. F–J. Conidiophores with conidiogenous cells and conidia. K, L. Upper parts of conidiophores. M, N. Conidia. (A–E. Isotype, TU 112905; F–I, K–M. G.A. i1906; J, N INIFAT C10/110). Scale bars: A = 500 µm; F, G = 100 µm; H = 50 µm; B, C, I–L = 20 µm; D, E, M, N = 10 µm.

the conidiogenous cell. While on MEA 1-septate conidia prevail, a few 4–6-septate conidia were seen among the usual 3-septate ones on PDA. Although reported as lacking in the protologue, chlamydospores were found among the mycelium in the dried culture designated as the holotype.

In contrast to other red-pigmented *Hypomyces*, the isolates of *H. virescens* produce brownish rather than yellow pigments on different brands of MEA media. The final brownish red colouration develops quite late. Only on PDA the medium is initially yellow and starts to turn deep red after one wk. While G.A. i1906 is one of the fastest growing isolates among the red-pigmented *Hypomyces*, G.A. i1899 is characterised by considerably slower growth (Fig. 6).

Analyses of the four genes reveal *H. virescens* to be the sister-species of *H. samuelsii* (Fig. 1). The larger perithecia of *H. virescens* and ascospores with less pronounced ornamentation are the only differences observed between the two species (Figs 2, 3). Finding the teleomorph of *H. virescens* in nature would allow more precise comparison. The anamorphs of these two species, developing in culture, differ mainly in the colour and shape of conidia, being hyaline and often distinctively fusiform, sometimes also curved at both ends in *H. samuelsii.* The anamorph of *H. virescens* is distinguished by the green colouration of conidia easily observed in cultures due to profuse conidiation. It differs from other geen-conidial species by slender, comparatively regular, cylindrical, mostly straight, 1–3-septate conidia (Fig. 8M, N) formed from a single locus at the tip of the conidiogenous cell. Only the last formed conidium at the tip of each conidiogenous cell developing from a laterally displaced hilum is slightly curved at the base.

Fig. 9. *Cladobotryum tchimbelense*. A, B. Delicate mycelium on host gills. C. Chlamydospores. D–F. Conidiophores with conidiogenous cells and conidia. G. Conidia. H. Submerged hyphae turning purple in KOH. (A, B. Holotype, TU 112007; C–H. Ex-type culture TFC 201146 on MEA). Scale bars: A = 1 cm; B = 250 µm; C, E = 20 µm; D = 100 µm; F = 25 µm; G, H = 10 µm.

3. *Cladobotryum tchimbelense* K. Põldmaa, **sp. nov.** MycoBank MB518515. Fig. 9.

Etymology: Refers to the type locality in Gabon, Africa.

Mycelium tenue, lactescens, in hospitis lamellas; hyphae parce ramosae, septatae, 3–6 µm latae, hyalinae. Conidiophora et conidia n.v. In MEA substratum, conidiophora 200–1500 µm longa, 8–10 µm lata prope basin; conidiogenae cellulae subulatae vel fere cylindraceae, 25–50 µm longae, 3.5–5.0 µm latae prope basin, fascientes unum conidiogenum locum. Conidia ellipsoidea, fusiformes, clavata, obovoidea vel ovoidea, recta, basi attenuata, (16.0–)20.1(–24.0) × (7.5–)8.4(–9.5) µm, 1(–2)-septata, hyalina, (1–)2–3(–8) catenatae. Chlamydosporae subglobosae, 7–17 µm diametro, hyalinae vel ochrol.

Delicate whitish mycelium on lamellae of host; hyphae sparingly branched, septate, 3–6 µm wide, hyaline. Conidiophores and conidia not observed in nature. *Colonies on MEA* growing fast, reaching 40–65 mm in 4 d; reverse first yellow turning yellowish ochraceous or purple; margin even to fasciculate. *Odour* absent. *Aerial mycelium* scanty, arachnoid, 1–2 mm high; homogenous or forming mycelial tufts of variable size, to 1 cm diam; buff, turning ochraceous or salmon in compacted areas of 1–1.5 cm diam, turning purple in KOH. Submerged hyphae often turning purple in KOH. *Conidiation* abundant. *Conidiophores* arising from submerged and aerial hyphae, not differentiated or slightly wider at base, ascending to suberect, 200–1500 µm long, near base 8–10 µm wide with wall to 1.3 µm thick; branching sparse to moderate, mostly forming single side branches that function as conidiophores or shorter supporting branches of conidiogenous cells; supporting branches arising singly or by 2–3 from one point, 25–40 × 4–5 µm. *Conidiogenous cells* formed singly or by 2–3 directly on conidiophores, or 4–7(–12) in verticil at top of conidiophore and on lateral branches that can be integrated in verticil of previously formed conidiogenous cells; subulate to almost cylindrical, 25–50 µm long, 3.5–5.0 µm wide near base, attenuating gradually to 1–2.0 µm at the tip; aseptate or rarely with one septum in middle; forming one conidiogenous locus at tip. *Conidia* ellipsoidal to fusiform, clavate, obovoid, or ovoid, straight, equilateral, occasionally inequilateral, slightly curved at top, attenuated at base to a narrow, prominent or wider, indistinct central refractive hilum; (16.0–)20.1(–24.0) × (7.5–)8.4(–9.5) µm, Q = (2.0–)2.4(–2.8), 1(–2)-septate, septum median or in upper 2/3, hyaline; formed obliquely from uppermost locus, (1–)2–3(–8) in short imbricate chains that appear as radiating heads or columns in case of longer chains. *Chlamydospores* formed among aerial or submerged mycelium, hyaline to pale ochraceous, cells

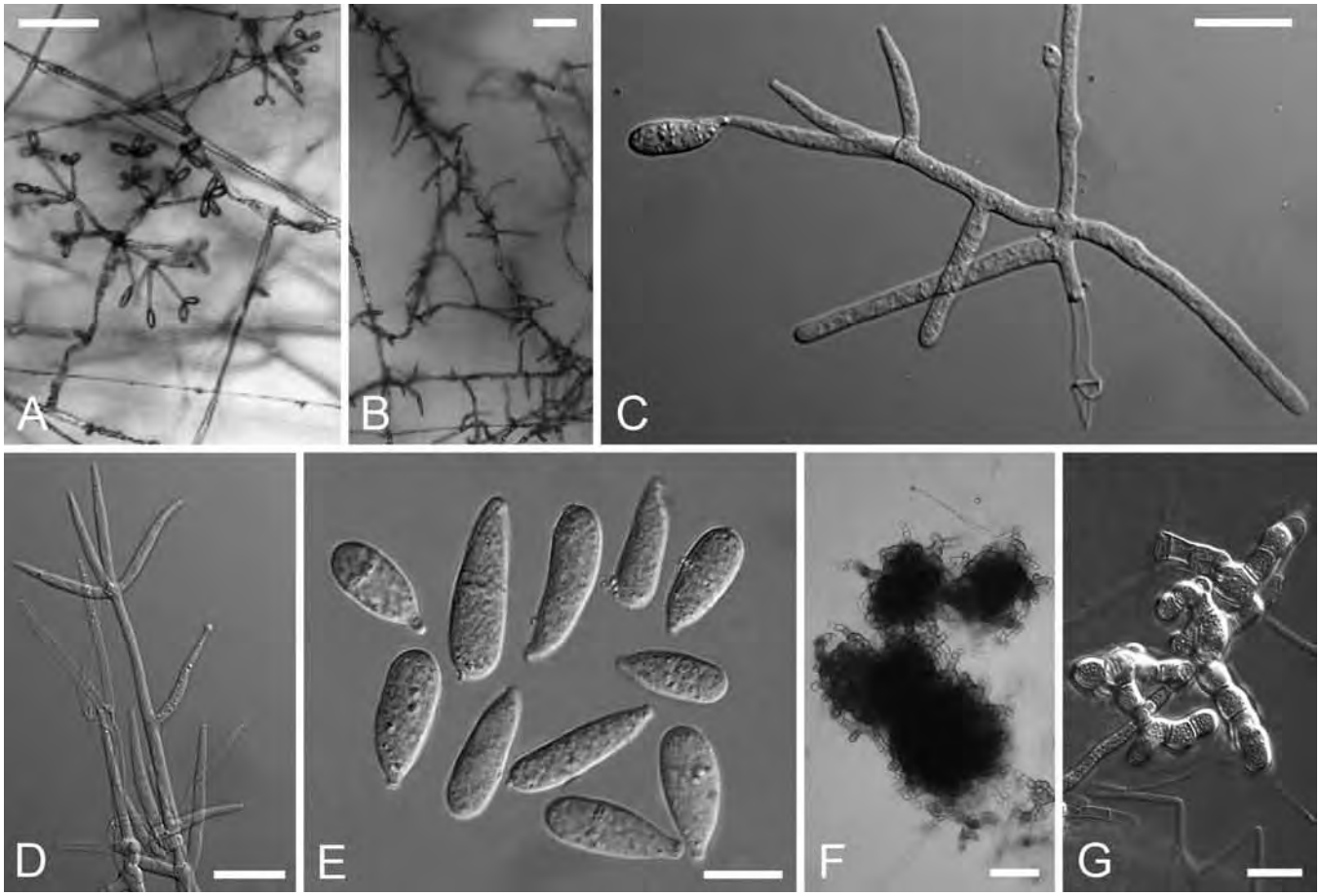

Fig. 10. *Cladobotryum heterosporum,* ex-type culture CBS 719.88 grown on MEA for 5 d. A. Conidiophores with verticillately arranged conidiogenous cells bearing radiating clusters of conidia. B. Hyphae with many short sterile lateral branches. C. Part of a conidiophore with two sterile branches. D. Top of a conidiophore. E. Conidia. F. Sclerotia-like aggregations above agar. G. Aggregations of thick-walled cells. Scale bars: A, B, F = 50 µm; C, D, G = 20 µm; E = 10 µm.

subglobose, 7–17 µm diam, wall 1–1.5 µm thick, intercalary on submerged hyphae or in long branching chains, sometimes forming soft pale orange-brown sclerotia-like aggregations in old cultures.

Substrata: Agaricoid basidiomata of *Tricholomataceae* growing on wood.

Distribution: Central Africa, known only from the type locality.

Holotype: **Gabon**, Crystal Mountains National Park, Tchimbele, on *Gymnopus* sp. on wood, 30 Apr. 2009, K. Põldmaa, TU 112007, **ex-type** culture TFC 201146 = CBS 127166.

Notes: *Cladobotryum tchimbelense* is distinguished by the monoblastic conidiogenous cells arranged in dense verticils as well as the ellipsoidal to fusiform, straight, mostly 1-septate conidia. It is similar to the anamorph of *H. samuelsii* in which especially the 3-septate conidia tend to be curved at one or both ends. Their conidial measurements overlap, with only the mean width in the single collection of *C. tchimbelense* falling outside the range of *H. samuelsii.* On MEA colonies of *C. tchimbelense* differ in having an uneven margin that is even more fasciculate on CMD, distinguishing the single known strain from others examined in this study. In old cultures on MEA main branches of the submerged hyphae contain conglomerations of brick-ochraceous pigment that partly diffuses into the medium resulting in patchy pigmentation of the agar.

4. *Cladobotryum heterosporum* K. Põldmaa, **sp. nov.** MycoBank MB518511. Figs 4F, G; 10.

Etymology: refers to the variable shape and size of conidia.

In MEA substratum, hyphae aeriae cum pluribus erectis libris extrematibus; conidiophora 7–8 µm lata. Cellulae conidiogenae subulatae vel fere cylindraceae, 25–40 µm longae, 2.5–3.5 µm latae prope basin, apice fascientes unum vel paucos conidiogenos locos, interdum ferentes parvam irregularem protuberationem. Conidia forma et amplitudine irregulares, ellipsoidea vel (angusta) clavata vel (ob)ovoidea, basi rotundata vel saepe attenuata ad hilum angustatum, vulgo aequilateralia et basi leviter curva, (12.0–)16.2(–20.5) x (4.5–)5.8(–7.0) µm, 1(–2)-septata, 2–5 aggregata in radiantibus capitulis. Chlamydosporae sublgobosae, 9–13 × 7–9 µm, hyalinae, catenatae vel sclerotiis aggregatae.

Colonies on MEA spreading moderately fast reaching 30–40 mm in 4 d; reverse initially yellowish ochraceous turning roseous or brownish red in 7–10 d, finally brownish red or crimson; margin even; pigment allocated in irregular patches in medium. *Odour* sweetish bitter or sweet, strong. *Aerial mycelium* scarce to moderate, homogenous or sometimes with small patches, 1–2(–5) mm high, buff; branching profusely with many erect free ends remeniscent of conidiophores, reaching lid of Petri dish, frequently also forming short, sterile lateral branches, 30–90 × 4–5 µm, divided by a few septa; hyphae hyaline to pale ochraceous, turning partially purplish in KOH. Submerged hyphae 4–6 µm diam, turning pinkish in KOH, cells not or irregularly swollen to 12 µm diam. Conidiation moderate. *Conidiophore*s not differentiated from aerial hyphae, sometimes arranged in tufts, suberect to erect, main axis 7–8 µm wide, thin-walled, hyaline; branching profuse, irregular. *Conidiogenous cells*

3–5(–8) in a verticil or occasionally 1–2 just below it; subulate to almost cylindrical, occasionally ampulliform, 25–40 µm long, 2.5–3.5 µm wide near base, attenuating gradually to 0.7–1.5 µm at tip, straight or occasionally curved at apex, aseptate, producing 1 or a few conidiogenous loci, mostly arranged at apex that sometimes bears small irregular protrusions. *Conidia* irregular in shape and size, ellipsoidal, clavate to narrowly clavate, ovoid or obovoid, base rounded or often attenuating to a narrow hilum, mostly equi-, seldom inequilateral, slightly curved at base, (12.0–)16.2(–20.5) x (4.5–)5.8(–7.0) µm; Q = (2.0–)2.9(–3.7), 1(–2)-septate, septum median or supramedian; hilum prominent, 1–1.5 × 1.3–1.7 µm, central or slightly off-center; held by 2–5 in radiating heads at apex of conidiogenous cell. *Chlamydospores* sublgobose, 9–13 × 7–9 µm, wall 0.7–1.2 µm, hyaline, forming chains of 2–6 cells in terminal position on lateral branches of submerged hyphae; often many chains formed from closely placed cells further developing into soft, almost hyaline sclerotia like-aggregations, held singly or 2–4 together in irregular clusters just above agar surface.

Holotype: **Cuba**, Soroa, on an agaric, 10 Oct. 1982, G. Arnold A 82/633, dried culture, TU 112906, **ex-type** culture G.A. i1898 = FSU 5514 = CBS 719.88.

Notes: *Cladobotryum heterosporum* is unique in the group due to the process of conidiation, small irregular conidia, and conidiophore system that forms abundant, short sterile side branches. The species can be differentiated through its mostly ellispoidal to clavate, 1-septate conidia that are variable in shape and size. Together with the primary anamorph described below for *H. gabonensis* in which the conidia are less than 15 µm, they share the shortest conidia in the group, being the only ones in which the conidial length does not exeed 20 µm.

Most of the conidiogenous cells in *C. heterosporum* bear 2–3 conidia at the apex. Often it is obvious that the conidia are held a short distance from each other, presumably as the result of each being formed from a different locus. This cannot be unequivocally stated as there are no clear denticles or scars demarcating the loci on the conidiogenous cells. Thus, it can only be presumed that each locus produces a single conidium, with the irregular protrusions, sometimes visible at the tips of conidiogenous cells, incorporating several loci. This is in agreement with the centrally based hilum, evident at the base of each conidium. Occasionally single conidia are seen also attached to the middle part of the conidiogenous cell that may be the result of the detached conidium sliding downwards after its release. Similar conidiogenesis has been observed in the anamorph of *H. orthosporus* (Põldmaa 1996, Põldmaa & Samuels 1999).

On CMD growth is fasciculate as in *C. tchimbelense*. On PDA *C. heterosporum* differs from most strains of the group in forming low, compact whitish, ochraceous to cocoa-brown aerial mycelium with reverse turning partially red or reddish brown in 1 wk. The sweet odour is also characteristic of *C. heterosporum*.

5. *Cladobotryum indoafrum* K. Põldmaa, **sp. nov.** MycoBank MB518510. Figs 4H, 11.

Etymology: refers to the geographic range of the species.

In MEA substratum, conidiophorae ascendentes vel (sub)erectae, 300–1500 µm longae, 8–10 µm latae. Cellulae conidiogenae subulatae, 20–45 µm longae et prope basin 3–5 µm latae, apice fascientes unum conidiogenum locum. Conidia forma irregulares, ellipsoidea vel cylindracea, aliquando clavata, recta vel in dimidio inferiore sparse curva, basi rotundata, (15.5–)18.9–24.5(–28.5) × (5.5–)5.9–7.5(–9.0) µm, 1–3(–4)-septata, primo hyalina, partim diluta viridescentes; conidia fascientes oblique in summo loco, (1–)2–4(–6) aggregata in radiantibus capitulis. Chlamydosporae fascientes in submersis hyphis.

Colonies on MEA spreading fast, reaching 50–70 mm in 4 d; reverse first yellow turning yellowish ochraceous to crimson; margin even; pigment patchy in agar. *Odour* absent. *Aerial mycelium* moderate, cottony, 1–5 mm high, homogenous; whitish yellowish buff, hyphae turning pinkish in KOH. Submerged hyphae turning violet in KOH, cells 5–9 diam, not swollen. Conidiation moderate. *Conidiophores* not differentiated from aerial hyphae or with distinguishable stipe, ascending to erect or suberect, 300–1500 µm long, main axis 8–10 µm wide near base, thin-walled, hyaline, not reacting in KOH; branching evenly distributed or confined to tip of conidiophore, giving it a tree-like aspect, verticillate, occasionally dichotomous, irregular or drepanoid; side branches sometimes incorporated in verticils of conidiogenous cells at lateral position, 1–4 arising from one point, 20–35 × 3.5–5 µm, aseptate or with 1 septum, branching further once or twice, uppermost branches 15–25 × 3.5–4.5 µm. *Conidiogenous cells* formed on lateral branches, 3–4(–6) in a verticil; subulate, 20–45 µm long and 3–5 µm wide near base, occasionally widest in middle, attenuating gradually or sometimes abruptly in upper quarter to 0.6–1.5 µm at tip; aseptate or occasionally longer ones with one septum in the middle; forming one, sometimes refractive conidiogenous locus at tip. *Conidia* of variable shape, ellipsoidal or cylindrical, occasionally suballantoid, clavate or with lower and/or upper half swollen, equi- or inequilateral, straight or curved in lower half, base rounded; (15.5–)18.9–24.5(–28.5) × (5.5–)5.9–7.5(–9.0) µm, Q = (2.1–)2.8–3.5(–4.1); 1–3(–4)-septate; hilum minute, narrow, 0.5–1.5 µm high and wide, central or slightly off center; first hyaline, partially turning pale green, white to pale green in mass; formed obliquely from uppermost locus, held by (1–)2–4(–6) in radiating heads. *Chlamydospores* formed on comparatively long, lateral branches of submerged hyphae, held by 2–10 in unbranched chains in terminal position; sclerotia-like aggregations absent.

Substrata: Basidiomata of *Agaricales* and *Polyporales*.

Distribution: Africa, Madagascar, South Asia.

Holotype: **Madagascar**, Anosy region, Tolagnaro distr., Manantantely, on *Neonothopanus* sp., 13 Mar. 2010, K. Põldmaa, TU 112289, **ex-type** culture TFC 201286 = CBS 127529.

Other specimens/cultures examined: **Madagascar**, Anosy region, Tolagnaro distr., Mandena Conservation Zone, littoral forest with *Uapaca, Intsia, Sarcolaena*, on a small agaricoid basidiomycete on a hanging branchlet, 11 Mar. 2010, K. Põldmaa, TU 112251, culture TFC 201277; same locality, on *Neonothopanus* sp., 18 Mar. 2010, K. Põldmaa, TU 112391, culture TFC 201319; same locality, on a decayed brown agaricoid basidiomycete, 18 Mar. 2010, E. Randrianjohany, TU 112487, culture TFC 201335; Petriky, littoral forest, on an agaricoid basidiomycete laterally attached to a living? trunk, 14 Mar. 2010, K. Põldmaa, TU 112338, culture TFC 201295. **Republic of South Africa**, Kwazulu-Natal Prov., Albert Falls Nature Reserve, on old aphyllophoralean basidiomycete, 15 Mar. 1995, G. Arnold A 95/12, culture G.A. i3463 = FSU 5807 = CBS 127163. **Sri Lanka**, Wagumba Prov., near Kurunegala, Aranyakele, 07°38'N, 80°25'E, on small agaricoid basidiomycetes, 12 Dec. 2002, K. Põldmaa, TAAM 170750, culture TFC 03-7 = CBS 127162. **Uganda**, Kibale National Park, on an aphyllophoralean basidiomycete, Mar. 2010, T. Tammaru, TU 112490, culture TFC 201336 = CBS 127530.

Notes: *Cladobotryum indoafrum* is characterised by tree-like conidiophores, monoblastic conidiogenous cells, and greenish, 1–3-septate conidia of variable shapes. In most of these features

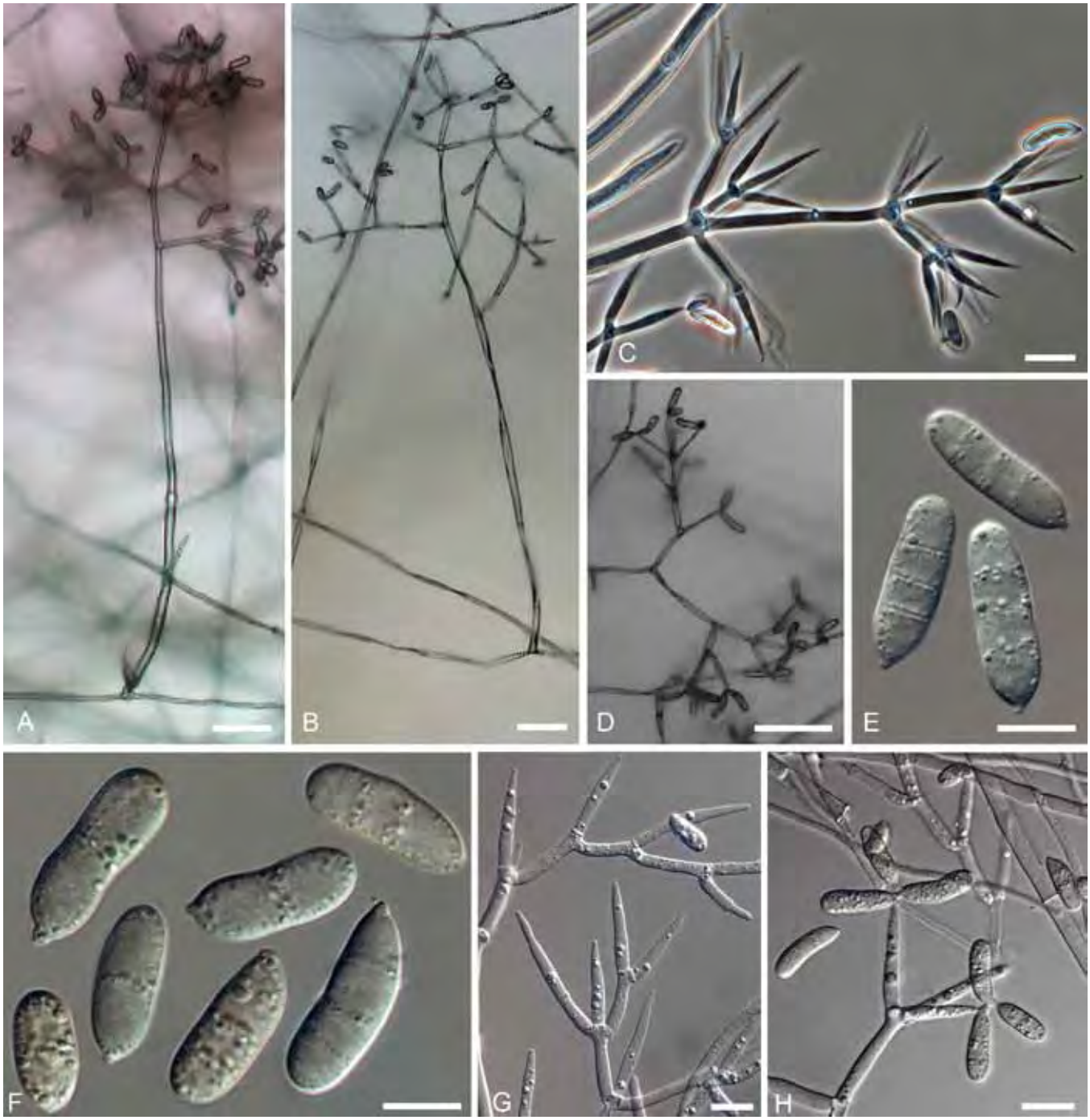

Fig. 11. *Cladobotryum indoafrum* on MEA. A, B. Conidiophores. C, D, G. Conidiogenous cells on short lateral branches at the apex of conidiophores. E, F. Conidia. H. Radiating heads of conidia at tips of two conidiogenous cells. A, F. TFC 03-7. B, D. Ex-type culture, TFC 201286. C, E. Holotype, TU 112289. G, H. FSU 5807. Scale bars: A, B, D = 50 µm; E–G = 10 µm; C, H = 25 µm.

it resembles the anamorphs of *H. virescens* and *H. paravirescens.* In *H. virescens* the conidia are much narrower, slightly longer, and very uniform in shape, being cylindrical and always straight. The conidial measurements of *H. paravirescens* overlap with those of *C. indoafrum* but in the former conidia are mostly 1-septate with their bases acuminate. The frequently curved, 3-septate conidia of *C. indoafrum* resemble those of *C. semicirculare,* which differs in producing much wider conidiogenous cells and conidia that remain hyaline. This newly descibed species was frequent in localities near Fort Dauphin in southeastern Madagascar suggesting that it might be a common species in other parts of its geographic range.

6. *Cladobotryum protrusum* K. Põldmaa, **sp. nov.** MycoBank MB518513. Figs 4K, 12.

= *Sibirina purpurea* var. *asterophora* J. D. Chen, Acta Mycologica Sinica 8: 129. 1989.

Etymology: refers to the morphology of the apex of conidiogenous cells that bears small protrusions from which conidia are formed.

In MEA substratum, conidiophora 200–700(–2000) µm longa, prope basin 7–9 µm lata. Cellulae conidiogenae subulatae, apice tumido et cum protubertionibus, ferentes aliquot locos, 25–45 µm longae, prope basin 3.5–5.0 µm latae. Conidia ellipsoidea vel cylindracea, interdum longo-clavatae vel fusiformes, (16.0–)20.0–23.0(–27.0) × (5.5–)6.2–7.9(–9.0) µm, basi attenuata, saepe curva in dimidio inferiore, (0–)1(–3)-septata, hyalina vel diluta flavovirentes; ≤ 12 conidia ad apicem cellulae conidiogenae. Chlamydosporae non visae; structurae aggregatae similes sclerotiis carentes vel fuliginosae, pseudoparenchymatae.

Fig. 12. *Cladobotryum protrusum*. A–E. Conidiophores with clusters of conidia. F. Conidia at tips of conidiogenous cells. G–I. Tips of conidiogenous cells bearing irregular protrusions. J, K. Conidia. (A, I. FSU 5044. B, D. Ex-type culture, TFC 201318. C. CBS 118999. E, H. FSU 5877. F, K. FSU 5077. G. IMI 165503. J. Holotype, TU 112389. A–I, K on MEA, J on natural substratum). Scale bars: A, B = 50 µm; C–E, H = 25 µm; F, G, I = 20 µm; J, K = 10 µm.

Colonies on MEA spreading fast to very fast, reaching 40–70 mm in 4 d; margin even; reverse first yellowish ochraceous, turning brick, brick-brown or purple. *Odour* absent or faint sweetish. *Aerial mycelium* scarce, cottony, 1–3 mm, to 4 mm high at margin, in some strains forming pinkish tufts, whitish yellowish buff, in some strains with olivaceous tinge, turning partially purple in KOH; submerged hyphae not or slightly swollen, (5–)7–10(–12) µm diam, yellowish ochraceous, becoming roseous to pale purple in KOH. Conidiation scarce to abundant. *Conidiophores* with a differentiated stipe, yellowish, becoming purplish in KOH; 200–700(–2000) µm long, 7–10 µm wide near base, branching moderately, confined to top of conidiophore, verticillate or occasionally drepanoid, forming one to two levels of branches; 2–4 branches producing conidiogenous cells formed from one point, sometimes in lateral position in a verticil of conidiogenous cells, 15–50 × 3–5 µm. *Conidiogenous cells* 2–5 in a verticil; subulate, attenuating slightly in upper part before formation of an irregular, often transversely placed or sometimes sublgobose conidiogenous elongation that bears several protrusions, protrusions formed also in subterminal position; 25–45 µm long, 3.5–5.0 µm wide near base, attenuating to 1.0–2.0 µm below protrusion where occasionally collarette is observed; terminal elongation with protrusions 1–2.5 µm high, 2–4(–7) µm wide. *Conidia* ellipsoidal, sometimes cylindrical, long clavate or fusiform, (16.0)–20.0–23.0(–27.0) × (5.5–)6.2–7.9(–9.0) µm, Q = (2.0–)2.6–3.3(–4.2), attenuating at base to a narrow but prominent central to laterally placed, sometimes refractive hilum, 1–2 µm long and 0.6–1.5 µm wide; inequi- or equilateral, often curved in lower half; (0–)1(–3)-septate, septum median or rarely sub- or supramedian; hyaline to pale yellowish green, white to pale green in mass; up to 12 conidia held at top of a conidiogenous cell. *Chlamydospores* not observed; in some isolates dark brown sclerotia-like aggregations scattered above agar, to 1 mm in diam, forming aggregations up to 7 mm in diam; context homogenous, pseudoparenchymatous, cells ellipsoidal to subglobose 13–19 × 12–14 µm, with wall 1.0–1.3 thick, yellowish ochraceous.

Substrata: Basidiomata of *Agaricales* and *Polyporales*, wood, and bark.

Distribution: Madagascar, southern Africa, southeastern Asia.

Holotype: **Madagascar**, Anosy region, Tolagnaro distr., Mandena Conservation Zone, eucalypt forest, 24.952 S, 47.002 E, on *Mycena* sp. on decorticated wood of a burnt dead trunk, 16 Mar. 2010, K. Põldmaa, TU 112389, **ex-type** culture TFC 201318 = CBS 12753.

Other specimens/cultures examined: **China**, Fujian Province, Sanmin, on *Agaricus bisporus*, Chen 68, culture HMAS 54138 = FSU 5044; Guangdong, on *Pleurotus ostreatus*), Chen 584, culture FSU 5077. **Madagascar**, Anosy region, Tolagnaro distr., Mandena Conservation Zone, littoral forest with *Uapaca, Intsia, Sarcolaena*, on *Neonothopanus* sp., 11 Mar. 2010, K. Põldmaa, TU 112269, culture TFC 201281; Mandena Conservation Zone, *Eucalyptus* forest, 24.952 S, 47.002 E, on *Neonothopanus* sp. on a stump, 16 Mar. 2010, K. Põldmaa, TU 112384, culture TFC 201316. **Zimbabwe**, Melfort, on cultivated *Agaricus* sp., 13. Mar. 1972, A. Rothwell, culture G.A. i418 = IMI 165503 = CBS 127164. **Republic of South Africa**, Kwazulu-Natal Prov., Kwambonambi State Forest Office, Arboretum, on bark of a lying trunk of *Eucalyptus* sp., 17 Mar. 1995, G. Arnold A 95/32.4, culture G.A. i3542 = FSU 5877 = CBS 127165. **Taiwan**, Taitung, Zhiben, on polypore and adjacent bark on dead wood, 15 Aug. 2002, R. Kirschner & H.-C. Kuo 1422, TNM, culture CBS 118999.

Notes: Isolates of this new species are similar in forming mostly pale yellowish green 1-septate conidia, often acuminate and curved at base. The conidia are formed on small protrusions at the apex of the conidiogenous cell. Although species having these characters occur in the group of red-coloured *Hypomyces/ Cladobotryum*, their unique combination clearly distinguishes *C. protrusum*. Two of the studied isolates, including that from Taiwan (Kirschner *et al.* 2007), had earlier been published as belonging to *C. asterophorum,* a species producing hyaline conidia from swollen apices of conidogenous cells. When reporting this species from China, Chen & Fu (1989) transferred it to *Sibirina*, based on the isolate Chen 584. For another strain (Chen 68), he described *S. purpurea* var. *asterophora*. This new variety was differentiated from the type by sympodial proliferation of the tips of conidiogenous cells and the formation of sclerotia. The morphological and molecular data reported herein strongly support the conspecificity of the strains from China with those from Madagascar and Zimbabwe as well as *C. asterophorum* and *C. purpureum* as distinct species (Fig. 1). These two taxa have not been found in the tropics and will be treated elsewhere together with other temperate red-coloured *Hypomyces/Cladobotryum*.

Most of the reported anamorphic isolates of *C. protrusum* differ from *C. asterophorum* by the tree-like conidiophores, profusely branched at the apex, protrusions formed at conidiogenous elongations that are often transversely placed at the apices of conidiogenous cells, and formation of greenish conidia. The conidia of *C. protrusum* are also slightly longer and much wider than in *C. asterophorum,* with 2–3-septate ones occurring among the prevailing conidia with one septum. A distinguishing feature is also the formation of up to 5 or 12 conidia at the apex of each conidiogenous cell in *C. asterophorum* and *C. protrusum,* respectively, as well as colony characters.

All the strains from Africa, China, and Madagascar exhibit only two bp difference among all the four gene regions studied. Despite the genetic homogeneity, considerable morphological variation was observed among the strains of *C. protrusum* from these distant regions. Namely, G.A. i3542 differs by having much less branched conidiophores that do not appear tree-like. In the isolates Chen 584 and TFC 201281 3–5 conidiophores are formed from one point on the aerial hyphae, with conidia remaining hyaline in the former. Both isolates from China are similar to the ex-type strain in the olive tinge of the aerial mycelium and in changing the agar reddish brown to dark-brown. In these strains, except for Chen 584, pinkish tufts are formed among aerial mycelium that develops into dark, tough sclerotia-like aggregations, common in *C. purpureum* (pers. obs.) and identical to those described in detail for *C. paravirescens*. In Chen 68 the terminal swellings or elongations on the conidiogenous cells are lacking or are much less developed than in other strains in which there are only a few subterminal protrusions. In this strain and TFC 201281 protrusions are scattered at the top of the conidiogenous cell with up to four denticles forming a subterminal ring in addition to the ones below.The strain from Taiwan isolated from a polypore and wood (CBS 118999) forms the sister-group to other strains, isolated from agaricoid basidiomycetes. Except for the somewhat larger mean conidial length (23 µm), it agrees morphologically with the other strains. While the greenish colouration of conidia is most obvious in the strain from IMI and Chen 68, they vary from hyaline to green in the other isolates. The colour is less intense than in *H. paravirescens* and *H. virescens,* with conidial masses often not appearing greenish when observed with the naked eye.

7. *Cladobotryum paravirescens* K. Põldmaa, **sp. nov.** MycoBank MB518512. Figs 4L, 13.

Etymology: refers to the similarity to the anamorph of *H. virescens* although phylogenetically not closely related.

In MEA substratum, conidiophora 300–600 µm longa, prope basin 6–9 µm lata. Cellulae conidiogenae subulatae, cum unum vel paucos conidiogenos locos, 25–35 µm longae, prope basin 4.0–5.0 µm latae. Conidia ellipsoidea, interdum clavatae, (18.0–)22.5(–27.5) × (6.5–)8.3(–10.0) µm, basi attenuata, saepe curva in dimidio inferiore, 1(–3)-septata, hyalina vel diluta flavovirentes; 2–3(–4) conidia ad apicem cellulae conidiogenae. Chlamydosporae sublgobosae, 14–17 × 12–14 µm, hyalinae vel ochraceae, catenatae; structurae aggregatae similes sclerotiis fuliginosae, pseudoparenchymatae.

Colonies on MEA spreading fast, reaching 70 mm in 4 d; reverse first ochraceous or yellow turning crimson; margin even. *Odour* absent. *Aerial mycelium* moderate, cottony, up to 4 mm high, reaching lid of Petri dish at margin; buff, obtaining greenish tinge with formation of conidia, hyphae turning purple in KOH. Submerged hyphae often turning purple in KOH, cells infrequently becoming swollen. Conidiation abundant, often in patches. *Conidiophores* not differentiated from aerial hyphae; ascending to suberect or erect, main axis 300–600 µm long, 6–9 µm wide, thin-walled, brownish yellow, except at apex, pigmented parts turning purple in KOH; branching moderate to profuse, verticillate or irregular, often drepanoid, mostly in uppermost part; conidiophores often borne as side branches from a verticil of conidiogenous cells, further branching at apex; lateral branches supporting 1–3 conidiogenous cells, 25–35 µm long and 4.0–5.0 µm wide, often integrated into a previously formed verticil. *Conidiogenous cells* 3–4(–6) in a verticil; subulate, 30–40 µm long, 3–4.5 µm wide near base, attenuating to 0.7–1.3 µm at apex; aseptate, forming one conidiogenous locus at tip or occasionally an additional locus on a small protrusion in the middle of cell or *ca.* 3–5 µm from tip. *Conidia* ellipsoidal, some slightly clavate, mostly inequi–, some equilateral, straight or curved in lower half, mostly attenuated towards base; **(**18.0–)22.5(–27.5) × (6.5–)8.3(–10.0) µm, Q = (2.2–)2.7(–3.3); 1(–3)-septate, septum median or sometimes sub- or supramedian; hyaline or pale yellowish green, pale green in conidial masses in culture; hilum prominent, narrow, refractive, central or laterally placed; *conidia* formed obliquely from uppermost locus, held by 2–3(–4) in radiating heads. *Chlamydospores* formed among submerged mycelium, cells subglobose, 14–17 × 12–14.5 µm, wall 0.7–1 thick, hyaline to pale ochraceous, in intercalary or lateral chains; dark brown sclerotia-like aggregations scattered above agar, to 1 mm diam, homogenous, pseudoparenchymatous, cells 13–19 × 12–14 µm, with wall 1.0–1.3 thick, yellowish ochraceous.

Substrata: Aphyllophoralean basidiomycete.

Distribution: Southeastern Asia, known only from the type locality.

Holotype: **Thailand**, Khao Yai National Park, Nature trail km 33 to Nong Pak Chi, on an aphyllophoralean basidiomycete, 1 Aug. 1997, K. Põldmaa, TAAM 169726, **ex-type** culture TFC 97-23 = CBS 100366.

Notes: *Cladobotryum paravirescens* is distinct in producing yellowish green, mainly 1-septate conidia with acuminate bases that are often curved. The colouration of conidia, led to the original identification of these two Thai collections as *C. virescens* (Põldmaa & Samuels 2004), previously the only known species producing red

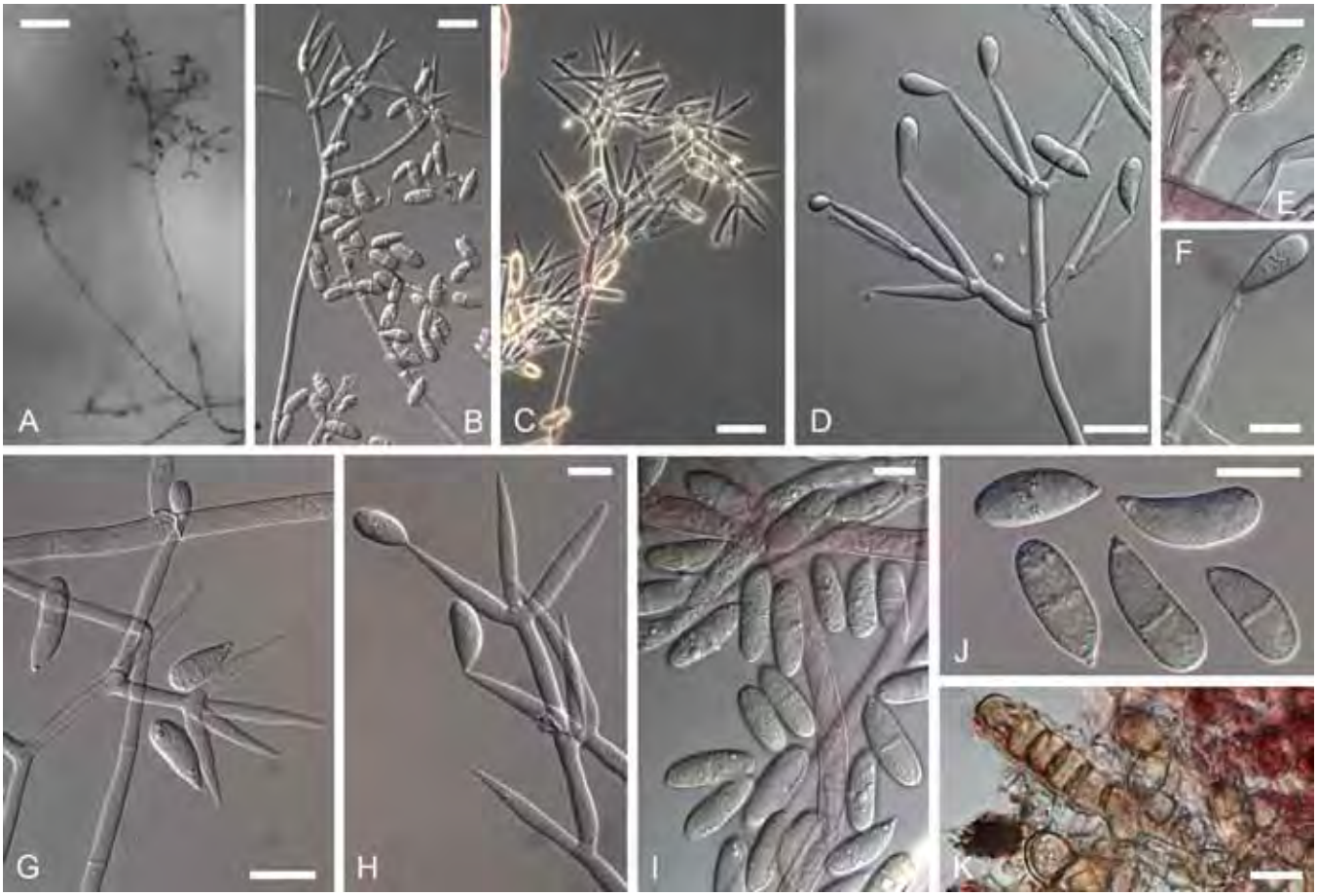

Fig. 13. *Cladobotryum paravirescens,* ex-type culture TFC 97-23 on MEA. A. Conidiophore. B–D. Topmost parts of conidiophores with conidiogenous cells and conidia. E, F. Conidiogenous cells with conidia at their tips. G, H. Conidiogenous cells formed in verticils. I, J. Conidia. K. Chlamydospores. Scale bars: A = 100 µm; B, C = 30 µm; D, G = 20 µm; E, F, H–K = 10 µm.

pigment and green conidia. Furthemore, the branching system of conidiophores and the mode of conidiation in the Thai specimen resembles those observed in *H. virescens*. The main distinguishing features include much broader, mostly ellipsoidal, 1-septate conida with curved acuminate bases in *C. paravirescens* compared to the narrow cylindrical, 1–3-septate, straight conidia of *H. virescens*. *Cladobotryum paravirescens* forms dark tough sclerotia-like aggregations, common in cultures of temperate species. Among other red-pigmented tropical *Hypomyces/Cladobotryum* these have been observed only in *C. protrusum*.

The molecular data presented herein clearly support the distinctness of *C. paravirescens* from *H. virescens*, revealing its affinities with an isolate from China (Chen 339-2A = FSU 5046) and the single known isolate of *C. asterophorum,* both of which produce hyaline conidia. The clade joining these three isolates forms the sister-group of *C. protrusum,* characterised by green conidia and prominent protrusions at the apices of conidiogenous cells. Among this group of species *C. paravirescens* is distinguished by having green conidia and conidiogenous cells with simple tips. Occasionally single inconspicuous outgrowths were observed in the middle or upper part of the conidiogenous cell. The frequently drepanoid branching of conidiophores resembles that described for *C. asterophorum* (de Hoog 1978). In contrast to this species, the conidia of *C. paravirescens* are green and wider, with a few 2-septate conidia usually present. In these features as well as the conidial shape and size, *C. paravirescens* is similar to *C. protrusum.* Although appearing most closely related to *C. paravirescens* (Fig. 1), the isolate Chen 339-2A differs in having hyaline, 0–1-septate, straight, ellipsoidal conidia that are smaller, (11.5–)15.7(–20.0) × (5.5–)6.6(–7.7), Q = (1.8–)2.4(–3.0). The conidiogenous cells attenuate into simple apices with one locus that forms 2–3 conidia. The isolate Chen 339-2A is similar to *C. paravirescens* in the abundant production of sclerotia-like aggregations which, however, are more light-coloured. This isolate was originally identified as *Sibirina purpurea* var. *purpurea* (Chen & Fu 1989). This species, now regarded as *C. purpureum,* was described from Alabama, USA. According to the morphology and phylogenetic analyses of molecular data, it is a distinct species. The Chinese strain Chen 339-2A probably represents an undescribed species, with additional strains reported by Chen & Fu (1989).

8. *Hypomyces australasiaticus* K. Põldmaa, **sp. nov.** MycoBank MB518515. Figs 2C, 14.

Etymology: refers to the presumable geographic range of the species.

Subiculum effusum super hospitis hymenophorum; perithecia dispersa, semidimmersa vel fere superficialia, obpyriformia, 330–400 × 260–300 µm, coccinea purpurescentia; papilla (55–)100–120 µm alta, basi (80–)100–130 µm lata. Asci cylindrici, 140–160 × 7–8. Ascosporae fusiformes, (20.5–)23.4–23.8(–26.0)× (4.5–)5.2–5.9(–6.5) µm, septo mediano, parietibus verrucosis, apiculo (2.0–)3.5–3.9(–4.6) µm longo. Conidiophora 3.5–5.5 µm lata; cellulae conidiogenae subulatae vel fere cylindraceae, 25–50 µm longae, basi 2.5–4.0 µm latae. Conidia cylindracea vel (oblonga) clavata, recta, (10.0–)15.8(–21.0) × (3.5–)5.2(–7.0), 1–3-septata, hyalina.

Subiculum effused over most of the host's hymenophore; thin, cottony, whitish to pink, crimson or purplish, turning purplish in KOH; hyphae 3–4 µm diam. *Perithecia* scattered among subiculum,

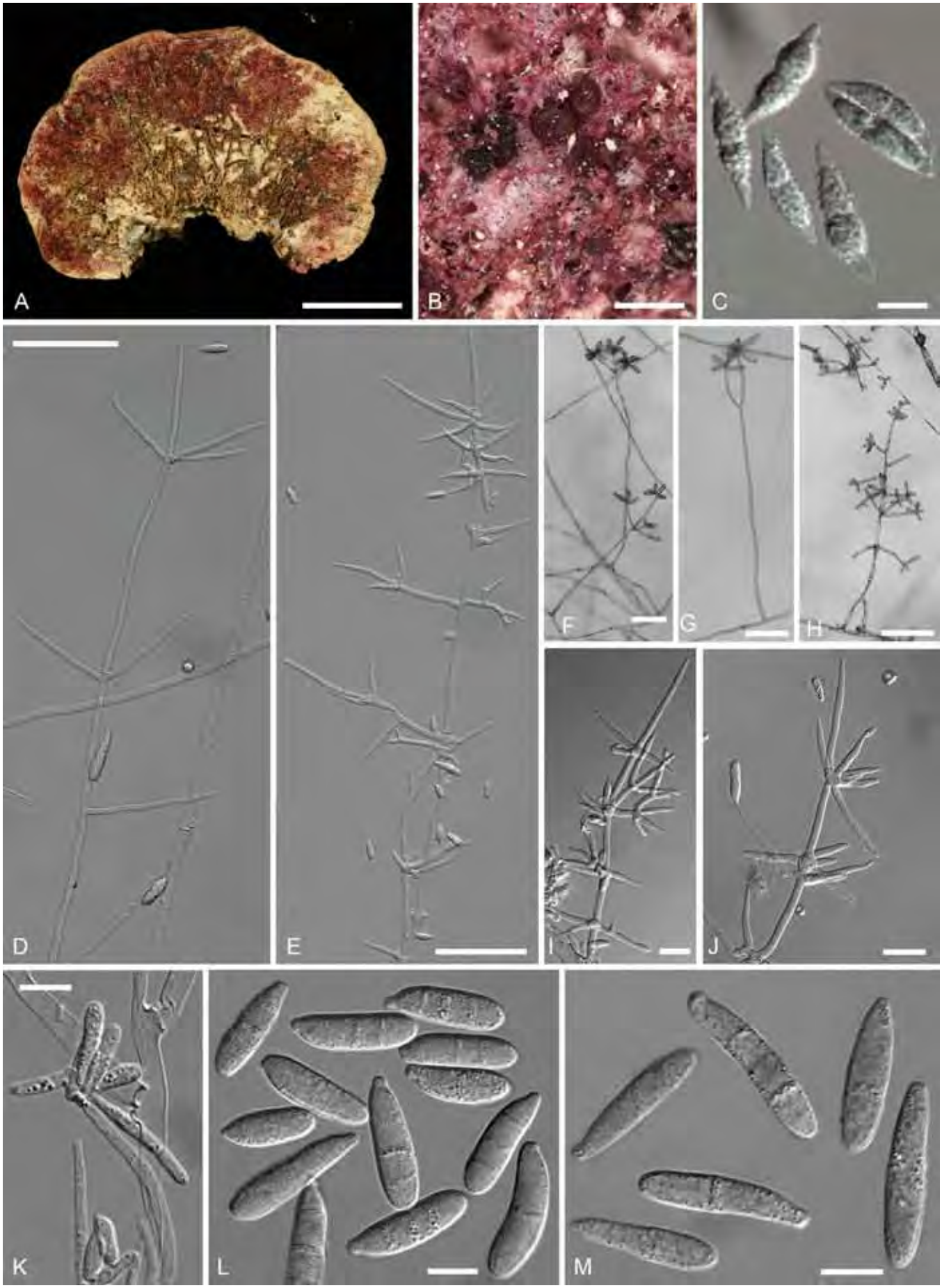

Fig. 14. *Hypomyces australasiaticus*. A. Teleomorph effused over the host's hymenophore. B. Perithecia scattered in the subiculum. C. Ascospores. D–J. Conidiophores with conidiogenous cells and conidia. K. Apex of a conidiogenous cell with a cluster of conidia. L, M. Conidia. (A, B. Holotype, TAAM 170757; C. BPI 745759; D, E, G–K, M. Ex-type culture, TFC 03-8; F, L. TFC 99-95; A, B on *Earliella scabrosa*, D–M on 7 d MEA). Scale bars: A = 1 cm; B = 0.5 cm; D–H = 50 µm; I, J = 20 µm. C, K–M = 10 µm.

singly or in groups of two to three, semi-immersed to almost superficial, obpyriform, 330–400 × 260–300 µm, crimson, turning purple in KOH, wall *ca*. 20 µm thick, with inner cells flattened, those on surface swollen, 17–27 × 15–15 µm, walls 1–2 µm thick; papilla conical, (55–)100–120 µm high, (80–)100–130 µm wide at base, tapering to 20–40 µm at apex, cells on surface of base swollen, 18–24 × 15–19 µm, apex obtuse. *Asci* cylindrical, 140–160 × 7–8 µm, apex slightly thickened, 1.0–1.5 µm; ascospores uniseriate with ends overlapping. *Ascospores* fusiform, inequilateral, (21.5–) 23.8–24.7(–27.0) × (4.5–)5.2–5.7(–6.5) µm, Q = (4.0–)4.3–4.6(–5.3), ascospore body (14.0–)16.1–17.1(–18.5) × (4.0–)4.4–4.6(–5.0) µm, Q = (3.0–)3.7–3.8(–4.3); septum median; wall verrucose to warted, warts discrete or confluent, 0.3–0.7 µm high; apiculi conical, occasionally hat-shaped or hooked, (2.5–)3.5–3.9(–4.5) µm long, (1.5–)2.0(–2.5) µm wide at base, apices obtuse.

Mycelium delicate, scarce, whitish, effused over host, apart from subiculum, bearing erect conidiophores with stipes 3.5–5.5 µm wide. *Conidiogenous cells* held by 1–3, subulate to almost cylindrical, 25–50 µm long, attenuating from 2.5–4.0 at base to 1–2.3 µm at apex. *Conidia* cylindrical or clavate to oblong clavate, (10.0–)15.8(–21.0) × (3.5–)5.2(–7.0), Q = (2.1–)3.1(–4.1), 1–3-septate, equilateral, straight, hilum mostly wide and laterally displaced or narrow and central.

Colonies on MEA growing fast, reaching 50–60 mm in 4 d; reverse first uncoloured, turning slowly reddish purple; margin even. *Odour* absent or sweet. *Aerial mycelium* abundant, cottony, to 7 mm high, homogenous, white, hyphae not changing colour in KOH. Submerged hyphae turning purple in KOH, cells not swollen. Conidiation moderate or abundant. *Conidiophores* not differentiated from aerial hyphae; ascending to suberect, to 1700 µm long, main axis 2.5–3 µm wide, thin-walled, unbranched but forming numerous short lateral branches, 19–24 × 2–3 µm, bearing verticils of conidiogenous cells or an additional level of supporting branches. *Conidiogenous cells* formed on supporting branches, sometimes directly on conidiophore, 3–6 in verticils, sometimes sinlgy or in pseudoverticils just below true verticil; subulate to almost cylindrical, 20–50 µm long and 1.5–3 µm wide near base, attenuated to 0.8–1.9 µm at apex; aseptate or occasionally with one septum in the middle, forming one conidiogenous locus at apex. *Conidia* oblong clavate, clavate, ellipsoidal or cylindrical, occasionally long fusiform, mostly equilateral, straight or curved in lower half; (15.0–)20.7–24.4(–35) × (3.5–)4.8–5.6(–6.5) µm, Q = (2.8–)3.7–5.1(–7.0), 1–3-septate, hyaline; hilum low, 0.5–1.3 µm high, narrow to very broad, 0.8–2.2 µm wide, central or slightly off-center; conidia formed obliquely from uppermost locus, 4–8(–10) in imbricate chains that appear as radiating heads. *Chlamydospores* and sclerotia-like aggregations absent.

Substrata: Basidiomata of *Polyporales*.

Distribution: Australia, south and southeastern Asia.

Holotype: **Sri Lanka**, Wagumba Prov., near Kurunegala, Aranyakele, 07°38'N, 80°25'E, on *Earliella scabrosa*, 12 Dec. 2002, K. Põldmaa, TAAM 170757, **ex-type** culture TFC 03-8 = CBS 127152.

Other specimens examined: **Australia**, Queensland, Daintree Nat. Park, Daintree Rainforest Environmental Centre, near Oliver Creek, on *Microporus affinis*, 27 Aug. 1999, K. Põldmaa, TAAM 170182, anamorph only, culture TFC 99-95 = CBS 127153. **Thailand**, Saraburi Province, Khao Yai National Park, Haew Narok, on *Antrodiella* sp., 13. Aug. 1996, G. J. Samuels 8431 & P. Chaverri, BPI 745759, accompanied by a dried culture; TU 112950; no living culture preserved.

Notes: Among the three collections of *H. australasiaticus,* only the one from Sri Lanka contains the teleomorph accompanied by a living culture. Therefore it was selected as the holotype despite the fact that the abundant perithecia are mostly overmature, asci have disintegrated, and many of the ascospores are swollen. In the Thai collection, ascospores are more slender, apiculi longer, and the ornamentation composed of larger confluent warts compared to the wider ascospores with more fine verrucose pattern observed in the specimen from Sri Lanka. The observed size variation may be the result of age differences when the specimens were dried. The material from Thailand also contains an anamorph that is absent in the specimen from Sri Lanka.

The teleomorph of this new species shares the typical features of the basidiomyceticolous members of *Hypomyces* with *Cladobotryum* anamorphs. It differs from the red tropical species with most similar teleomorphs, *H. samuelsii* and *H. virescens,* only by slightly smaller ascospores (Figs 2, 3). The characteristics of cultures and the anamorph provide further delimitors from related taxa. The cultures are distinct due to the abundant, white aerial mycelium from which arise very long, mostly unbranched conidiophore systems. These bear only very short lateral branches that form verticils of conidiogenous cells either directly or on a further level of supporting branches. Conidiogenous cells are narrow, tapering only slightly towards the apex. The conidiogenous locus produces numerous conidia that are held obliquely to almost horizontally with their bases connected, reminescent of the pattern observed in *C. cubitense* and the secondary anamorph type of *H. gabonensis*. *Hypomyces australasiaticus* is also distinct in the often clavate-shaped conidia. In these characteristic features the anamorph is reminiscent that of *H. polyporinus*, *H. pseudopolyporinus* (Rogerson & Samuels 1993, Põldmaa & Samuels 1999) and *H. puertoricensis* (Põldmaa *et al.* 1997). However, these species all have pallid, KOH-negative perithecia and cultures producing KOH-negative cocoa-brownish pigments. *Cladobotryum curvatum* (de Hoog 1978), known only from the type collection from Java, is similar to the anamorph of *H. australasiaticus* as well as to *C. cubitense* and *C. semicirculare.* However, conspecificity cannot be tested due to the lack of a living culture.

In the cultures obtained from the specimens from Australia and Sri Lanka, dimorphic conidia were observed. In addition to the comparatively long (up to 47 µm in older cultures), 1–3-septate conidia, small, 0–1-septate conidia measuring 10–17 × 3.5–6.0 µm, Q = 2.2–3.6 were found. These were abundant in one of the monosporic isolates from the Sri Lankan specimen.

Based on the few available collections *H. australasiaticus* is presumed to be distributed in southeastern Asia and Australasia. It is the sister species of *C. semicirculare*, some populations of which are apparently sympatric with *H. australasiaticus* in Asia. Their morphological similarities include indistinct conidiophores.

9. *Cladobotryum semicirculare* G.R.W. Arnold, R. Kirschner, Chee J. Chen, Sydowia 59: 118. 2007. Figs 4I–J, 15.

Mycelium whitish, effused on host; conidiogenous cells subulate, 12–24 µm long, 2–4 µm wide at base, 0.5–1.5 µm at tip, with tips sometimes curved; conidia (11.5–)15.0–18.5(–25.0) × (4.5–) 5.6–6.2(–8.0) µm, Q = (2.1–)2.7–3.0(–3.6); chlamydospores subglobose to globose, 13–15 µm diam, wall 1.0–1.5 µm thick, smooth.

Colonies on MEA spreading moderately fast, reaching 25–35 mm in 4 d; reverse ivory or uncoloured initially, turning yellowish

Fig. 15. *Cladobotryum semicirculare* on MEA. A–C. Upper parts of conidiophores bearing conidiogenous cells with conidia held in radiating heads. D, E. Verticillately placed conidiogenous cells. F–H. Conidia. I. Chlamydospore. (A, B, D, G, I. Ex-type culture, CBS 705.88; C, H. TFC 03-3; E. Isotype, IMI 394236; F. Holotype of *H. paeonius,* K(M) 168029). Scale bars: A–C = 30 µm; D = 15 µm; E–I = 10 µm.

buff or ochraceous, finally reddish brown; margin even. *Odour* absent or faint, reminescent of agarics. *Aerial mycelium* scanty or abundant, cottony, 2–7 mm high, homogenous, primary axes of hyphae wider than secondary branches, sometimes becoming moniliform or with single cells inflated, white, partially turning purple in KOH. Submerged hyphae with cells occasionally swollen, partially turning (pale) purplish red in KOH. Conidiation very abundant in fresh isolates, becoming moderate to scarce in old isolates. *Conidiophores* arising from aerial hyphae at right angles, not differentiated or wider from these, ascending to suberect, 70–450 µm long, main axis 3–5 µm wide; branching moderate, irregular or verticillate, mostly evenly distributed; lateral branches arising mostly singly from one point, 15–35 × 3–4 µm. *Conidiogenous cells* formed on conidiophores or supporting branches, 2–4 in a verticil, occasionally also formed singly just below verticil, verticils not always symmetrical, not all conidiogenous cells formed at same level; subulate, 20–40 µm long, 2–3 µm wide at base, attenuating gradually to 0.6–1.5 µm at apex, aseptate or sometimes with one septum, often slightly curved at apex, forming one conidiogenous locus at apex. *Conidia* ellipsoidal, clavate, sigmoid or semicircular, occasionally with two shallow branches at tip; inequilateral, often curved or straight, base rounded or acuminate, sometimes slightly attenuated at ends, then subfusiform; (12.0–)16.6–19(–25.5) × (4.5–)5.2–5.8(–7.2) µm, Q = (2.4–)3.2–3.4(–4.4), 1–3-septate, hyaline; with minute hilum of variable width, central or slightly off-center; formed obliquely from uppermost locus, held by 3–6(–8) in imbricate chains that appear as radiating heads. *Chlamydospores* formed among aerial mycelium, cells subglobose, 11–18 µm diam, wall 0.6–1.0 µm thick, ochraceous, in short chains on supporting cells or forming irregular clusters.

Substrata: Basidiomata of *Agaricales* and *Polyporales*.

Distribution: Central America, south and southeastern Asia.

Specimens/cultures examined: **Cuba**, Prov. Habana, Santiago de las Vegas, on old polypore, 9 Jan. 1985, G. Arnold A 85/185, isotype IMI 394236, **ex-type** culture CBS 705.88; same locality, on old agaric, 29 July 1985, G.A. A85/380, culture i1393; same locality, on *Lentinus scleropus*, 12 Aug. 1987, R. Castañeda, G. Arnold INIFAT C87/249, i 1715, CBS 533.88. **Sri Lanka**, on a resupinate polypore, Nov. 1867, G. H. K. Thwaites 127, K(M) 168028, ex herb. Berkeley, **holotype** of *H. paeonius*; K(M) 168029, ex herb. Broome, isotype of *H. paeonius*; Sabaragumuwa Prov., Sinharaja Man and Biosphere Reserve, Morning site, near bungalow in a forested slope, 06°24'N, 80°36'E, elev. 1035 m, 10 Dec. 2002, K. Põldmaa, TAAM 170728, culture TFC 03-2 = CBS 112421; Wagumba Prov., near Kurunegala, Aranyakele, 07°38'N, 80°25'E, on *Pterula* sp. cf. *P. typhuloides* on a decaying log, 12 Dec. 2002, K. Põldmaa, TAAM 170744, culture TFC 03-3.

Notes: Observations on the examined strains of *Cladobotryum semicirculare* generally match the protologue, except that the conidiophores and conidiogenous cells are much narrower and the conidia are wider. Kirschner *et al.* (2007) stated that strains from Cuba have larger conidia than those from Taiwan. According to my observations, conidia in the studied isotype measured (12.0–)18.5(–25.0) × (4.5–)6.2(–8.0) µm, Q = (2.3–)3.0(–3.6) and those in the ex-type strain (13.5–)18.6(–25.5) × (4.5–)5.8(–7.0) µm. In the strains from Sri Lanka conidia were slightly shorter and narrower, (11.5–)16.6(–21.0) × (4.5–)5.2(–7.0) µm. The latter agree with

the measurements given by Kirschner *et al.* (2007) for Taiwanese material for which no living strain is available. These morphological and genetic differences (data not shown) between the strains from Cuba and those from Asia indicate that these may represent two species sharing the unusual shape of conidia.

In *C. semicirculare* the branching of the conidiophorous system is much less pronounced than in most species of the group. The conidiogenous cells are usually held in the uppermost and one, seldom two, lower verticils that are formed on conidiophore-like branches of the aerial mycelium. Additional short branches supporting the verticils may also be involved. In this regard, *C. semicirculare* resembles the anamorph of its sister species, *H. australasiaticus* with even more poorly developed conidiophores. Conidiogenous cells of *C. semicirculare* with tips that are often curved are unique in the group. Although lower parts of the conidia are curved in several species, most often in *C. cubitense* and *C. indoafrum,* they are strongly curved, with some appearing almost circular in *C. semicirculare*.

Berkeley and Broome (1875) described *Hypomyces paeonius* based on material collected by Thwaites in Ceylon (= Sri Lanka) in 1867. The protologue describes a widely effused roseous fungus having subcymbiform spores with obtuse tips. In addition, conidia, resembling those of *H. rosellus* are mentioned. Upon examination of the holo- and isotype from Kew I could not find any perithecia or their initials among the purplish red mycelium covering a resupinate polypore. The same had been stated by Clark T. Rogerson and G. Arnold, whose notes are accompanying the type materials. These include also drawings (presumably by Berkeley) showing 1-septate curved ellipsoidal ascospores with obtuse ends, irregularly arranged in upper half of a clavate ascus. Although not suggestive of a species of *Hypomyces,* these could represent an immature collection of a member of this genus. Both the holo- and isotype material contain a well developed anamorph. The 1–3-septate ellipsoidal, often strongly curved hyaline conidia, measuring (11.5–)15.0(–18.5) × (4.5–)5.6(–7.0) µm with Q = (2.1–)2.7(–3.3), are formed on subulate conidiogenous cells, 10–22 µm long and attenuating from 2.0–4.5 µm at base to 0.5–1.5 µm at tip. With a proportion of conidia being semicircular, the anamorphs in these specimens clearly match the recently described *C. semicirculare*. Yet, because the holo- and isotype of *H. paeonius* do not contain teleomorph structures and the protologue with accompanying figures cannot unequivocally be considered as representing a species of *Hypomyces*, this material has to be regarded as a collection of the anamorphic *C. semicirculare* Petch (1912) accepted *H. paeonius* identifying two other specimens, collected from Sri Lanka at the beginning of 20th century, as belonging to this species. The strongly verrucose ascospores 25–30 × 5–7 µm and narrow-oval or clavate, 1–2-septate hyaline conidia, 15–28 × 5–6 µm, described by Petch (1912) match the characteristics of *H. australasiaticus*. However, the examination of one of these specimens [Petch 2345 = K(M) 168030] revealed ochraceous perithecia with faint purplish colour observed in KOH only at the base of the papilla and upper part of the venter. The ascospores inside asci appeared lanceolate or narrow-oval and non-apiculate as noted by Petch but the detached ascospores were grossly warted, bearing prominent, (2.0–)4.1(–6.0) µm long apiculi. These, as well as the ascospores, measuring (21.0–)26.5(–32.0) × (4.5–)5.9(–7.0) µm, Q = (3.6–)4.6(–5.5), were larger than in *H. australasiaticus*. Whereas no anamorph could be seen, the identity of this material remains unclear.

10. *Hypomyces aconidialis* K. Põldmaa, **sp. nov.** MycoBank MB518608. Fig. 16.

Etymology: indicates the absence of conidia, found neither on the host nor in culture.

Teleomorphosis crescens in MEA substrato; perithecia inclusa in pulvinato simile stromate subiculo. Perithecia dense aggregata, immersa, obpyriformia, 320–410 × 200–300 µm, rubra flavescentia; papilla conica, 90–140 µm alta, basi 90–130 µm lata. Ascosporae fusiformes, (13.0–)14.3–15.3(–16.5) × (3.5–)4.0–4.2(–5.0) µm, septo mediano, habentes densum breve tuberculare ornamentum; apiculo 2.0–3.0(–4.0) µm longo.

Teleomorph produced in culture on MEA; restricted patches turning into pulvinate stroma-like subiculum with embedded perithecia. Subiculum dense cottony mat, buff to roseous, of tightly interwoven hyphae; hyphae hyaline to pale crimson, turning purple in KOH, 2.5–4 µm wide, cells not swollen. *Perithecia* caespitose, immersed, flask-shaped, 320–410 × 200–300 µm; yellowish red, with whole perithecium or only the base of papilla turning purple in KOH; wall of a single region of flattened, thin-walled cells, at surface cells broadly ellipsoidal, 15–30 × 13–21 µm; papilla conical, 90–140 µm high, 90–130 µm wide at base, attenuating to 40–60 µm at apex, apex obtuse, with oblong-clavate cells, 5.0–8.0 µm diam at surface. *Ascospores* fusiform, equilateral, (18.0–)20.2–20.3(–22.5) × (4.5–)5.1–5.2(–5.5) µm, Q = (3.3–)3.9–4.0(–4.6); ascospore body (13.0–)14.3–15.3(–16.5) × (3.5–)4.0–4.2(–5.0) µm, Q = (2.9–)3.4–3.9(–4.5); 1-septate, septum median; densely tuberculate, ornamentation < 0.5 µm high; apiculi 2.0–3.0(–4.0) µm long, 1–2 µm wide at base, straight, simple or hat shaped, tips obtuse.

Colonies on MEA growing moderately fast to fast, reaching 25–50 mm in 4 d, reverse first yellowish ochraceous, turning slowly into yellowish or purplish red; margin even or fasciculate. *Odour* absent. *Aerial mycelium* moderate to profuse, cottony, to 3 mm high, homogenous or partly fasciculate, pale whitish or yellowish buff. Submerged hyphae partly turning purple in KOH, cells not swollen. Conidiation absent. Some parts of aerial hyphae becoming moniliform, with cells turning into chlamydospores, cells swollen, 9–15 µm diam, wall 1–1.5 µm thick, brownish yellow.

Substrata: Basidiomata of *Tricholomataceae (Agaricales*).

Distribution: Central Africa, Madagascar.

Holotype: **Madagascar**, Anosy region, Tolagnaro district, Mandena Conservation Zone, littoral forest with *Uapaca, Intsia, Sarcolaena*, on *Mycena* sp. on wood, 18 Mar. 2010, E. Randrianjohany, TU 112486, dried culture containing the teleomorph deposited together with anamorph material on natural host; **ex-type** culture TFC 201334 = CBS 127527.

Other specimen examined: **Gabon**, Crystal Mountains National Park, Tchimbele, on an agaricoid basidiomycete (*Tricholomataceae,* cf. *Gerronema*) on wood, 6 May 2009, K. Põldmaa, TU 112133, culture TFC 201215 = CBS 127526.

Notes: Both collections of *Hypomyces aconidialis* contain delicate whitish mycelium without any structures associated with conidiation. In the material from Gabon, there is scanty mycelium loosely attached to the gills of the host. In the holotype, more profuse mycelium covers most parts of the decayed host. In addition, there are small patches of subiculum with perithecial initials on a piece of adjacent wood.

This species appears unique because isolations from both collections do not form any conidiophores or conidia on any of the

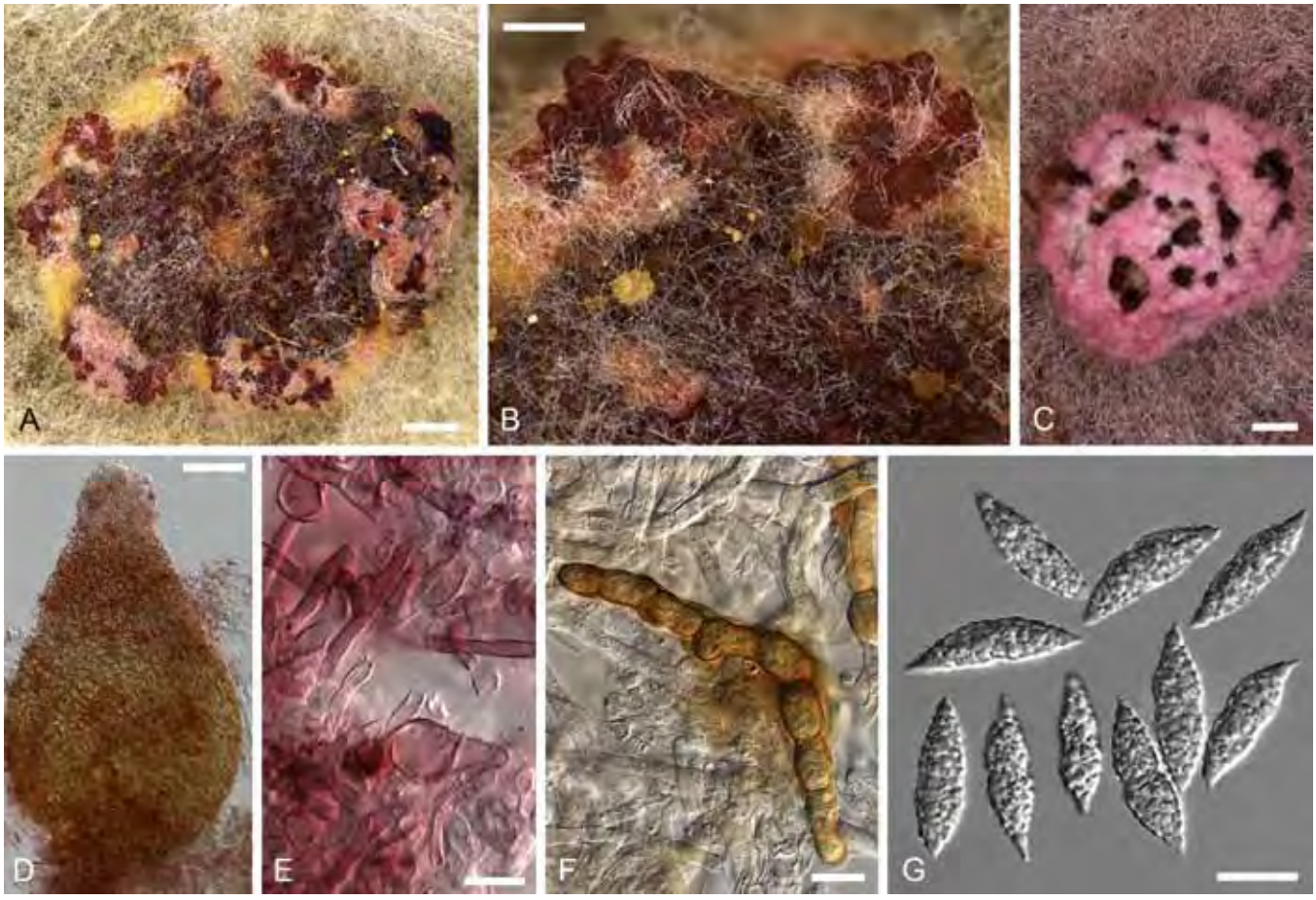

Fig. 16. *Hypomyces aconidialis*. A–C. Pulvinate stromatic subiculum with perithecia. D. Perithecium. E. Chains of chlamydospores. F. Cells at the surface of perithecium. G. Ascospores. (A, B, E–G. Ex-type culture, TFC 201334; C, D. TFC 201215). Scale bars: A, C = 1 mm; B = 500 µm; D = 50 µm; E–G = 10 µm.

three inoculated media. However, on MEA both strains produce pulvinate stroma-like subiculum with immersed perithecia. This feature distinguishes *H. aconidialis* from other red-perithecial species that all have effused, comparatively thin subiculum. The abundantly produced, mature ascospores with tuberculate ornamentation are smallest among the five tropical species for which the teleomorph has been observed (Fig. 3).

Cultures isolated from the holotype differ from the those isolated from the other specimen in having faster growing colonies, production of crystals in agar, and absence of fasciculate growth.

11. *Cladobotryum cubitense* R.F. Castañeda & G.R.W. Arnold, Feddes Repertorium 98: 414. 1987. Figs 5A, 17.

Mycelium on host cottony, buff, producing erect conidiophores, *ca.* 8 µm wide near base, branching at top; conidiogenous cells subulate, (15–)20–30 long, 2.5–4.0 µm wide in widest place, gradually attenuating to 0.8–1.8 µm at apex bearing one locus, held by 2–3 on short lateral branches. *Conidia* mostly cylindrical, some slightly curved, rarely sigmoid, (20.0–)23.7–25.0(–30.0) × (6.0–)6.6–7.0(–8.0) µm, Q = (2.9–)3.6(–4.3), hyaline, 3-septate; hilum laterally displaced, held transversely at the apex of conidiogenous cell.

Colonies on MEA spreading comparatively slowly, 15–25 mm in 4 d; margin even to slightly fasciculate; reverse first pale yellowish ivory or ochraceous, becoming paler purplish in some isolates. *Odour* absent or faint sweet. Conidiation abundant in fresh isolates. *Aerial mycelium* moderate, cottony, becoming compacted near inoculum, whitish to buff, 1–3 mm high. Submerged hyphae not swollen, turning purple in KOH. Aerial hyphae arising from agar, extending several millimeters, producing single branches at irregular intervals that function as conidiophores or branch further in irregular manner. *Conidiophores* not differentiated from aerial hyphae or with a well-defined stipe, ascending to suberect, 300–900 µm long, 7.5–9.0 µm wide near base, branched at top with one to three levels of branches ultimately bearing verticils of conidiogenous cells, hyaline or yellowish ochraceous, then turning purplish red in KOH; 2–4 branches supporting conidiogenous cells formed from one point, 18–35 × 2.5–4.0 µm. *Conidiogenous cells* held by 2–3, subulate or long ampulliform, occasionally attenuating slightly towards base, (15–)20–30(–50) µm long and 2–3.5 µm wide in widest place, gradually attenuating to 0.6–1.5 µm at apex bearing one locus. *Conidia* cylindrical, rarely ellipsoidal, often irregularly shaped, curved at base, lower half or middle, some sigmoid, (15.0–)19.5–25.0(–28.5) × (4.5–)5.5–7.5(–8.5) µm, Q = (2.1–)2.9–3.7(–4.6), hyaline, (1–)3-septate, hilum narrow to wide, central or at side of conidium, sometimes with a scar of attachment at base of conidium in opposite position to hilum; formed transversely from conidiogenous locus, held by 3–5(–12) in imbricate chains at apex of conidiogenous cell, rarely singly at intercalary loci on conidiophores. *Chlamydospores* abundant in old cultures, in and on agar, cells subglobose to globose, 10–30 µm diam, pale yellowish to ochraceous, wall 1–1.5 µm thick, smooth, held by a few to a dozen in chains or forming irregular clusters often held on thin-walled, hyaline supporting cell arising from an intercalary cell of aerial or submerged hyphae.

Substrata: Agaricoid, corticioid and cyphelloid basidiomata, wood.

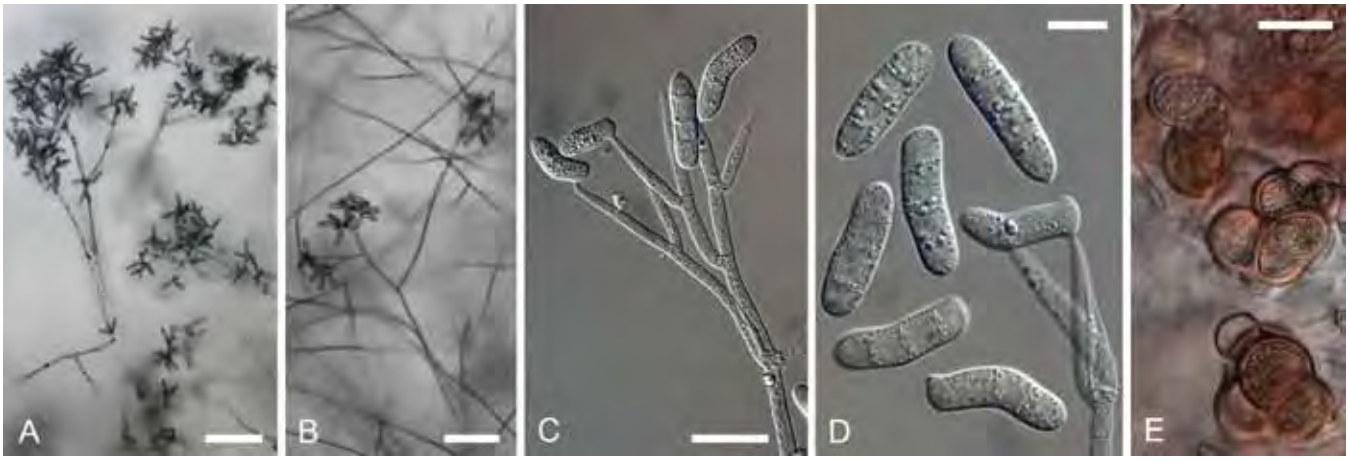

Fig. 17. *Cladobotryum cubitense*. A–C. Upper parts of conidiophores bearing conidiogenous cells with transversely placed conidia at their tips. D. Conidia. E. Chlamydospores. (A–D. TFC 07-13, 9 d on MEA; E. Ex-type culture, G.A. i1361, 3 mo on MEA). Scale bars: A = 100 µm; B = 50 µm; C, E = 20 µm; D = 10 µm.

Distribution: Tropical North, Central and South America, Madagascar.

Specimens and/or cultures examined: **Cuba**, Camagüey Prov., Sierra de Cubitas, Hoyo de Bonet, on dead fruiting bodies of an agaricoid basidiomycete, 6 Mar. 1985, R. Castañeda C85/29, **holotype**: INIFAT permanent slide, **ex-type** culture G.A. i1361 = CBS 416.85; Guantanamo Prov., Sierra de Imias, Las Cabezas del Arroyo Los Cacaos, on fruitbody of an old agaricoid basidiomycete, 9 Apr. 1984, G. Arnold, culture m643.w, GA 84/688-w white form, TFC 98-35. **Madagascar**, Anosy region, Tolagnaro distr., Petriky, littoral forest, on *Cyphellaceae*, 14 Mar. 2010, K. Põldmaa, TU 112334, culture TFC 201293; Mandena Conservation Zone, *Eucalyptus* forest, 24.952 S, 47.002 E, on wood next to *Rigidoporus* sp., 16 Mar. 2010, K. Põldmaa, TU 112379b, culture TFC 201294; same collecting data, on a corticioid basidiomycete on a living trunk of *Eucalyptus* sp., TU 112380, TFC 201315 = CBS 127528. **Peru**, Junin Dept., Chanchamayo Distr., Kimiri, on fruiting bodies of an agaricoid basidiomycete cf. *Lentinus sp.*, 2 Mar. 2007, K. Põldmaa, TU 107195, cultures TFC 2007-13 = CBS 121646. **USA**, Louisiana, near Walker, Livingston Parish, on a log, 23 Aug. 1960, C. T. Rogerson 60-189, NY, anamorph and immature teleomorph.

Notes: Characteristic of *Cladobotryum cubitense* are the comparatively long, narrow, clavate, mostly 3-septate conidia that are held horizontally at the tip of the conidiogenous cell. Indicative of the formation of conidia in long imbricate chains are the hila, often observed at the side of the conidia, close to the base. The more conidia are produced from one locus, the lower, wider and more laterally placed become the hila on the successive conidia. In most isolates part of the conidia are curved. Dinstinctive of the species are also the pale ochraceous, irregular aggregations of thick-walled swollen cells, often held on a thin-walled, hyaline supporting cell as in anamorphs of *Mycogone*. These are formed abundantly in old cultures. The more recently isolated strains from Madagascar and Peru differ from the two isolates from Cuba by the profuse branching of conidiophores, abundant conidiation, and much smaller conidiogenous cells.

All examined living cultures of *C. cubitense* have been isolated from the anamorph found in nature. In the collection from Louisiana, USA, the typical anamorph structures are accompanied by the teleomorph. It comprises buff subiculum with irregular pinkish patches effused over a resupinate polypore. The colour pattern of perithecia follows that of the subiculum, with the roseous perithecia turning pale purplish in KOH but the buff perithecia not changing colour. These characters fit the morphology expected for the sister taxon of *H. gabonensis*, described below. The red pigment is absent or less developed in both of these species that form the sister group to the rest of the red-coloured *Hypomyces*/*Cladobotryum*. In the specimen from Louisiana, the scattered perithecia are immersed except for the papilla that is mostly covered with a waxy cap of agglutinated extruded asci. The ascal content, however, has only started to differentiate, for what reason mature ascospores could not be observed. The oblong-clavate 1–4-septate conidia measure 20.0–40.0 × 6.5–9.0 µm and have a distinctive wide, often laterally placed flat base. The 0–1-septate and 30–50 µm long conidiogenous cells, attenuate from 3–5.5 µm at base to 1.5–2.5 µm at tip. While this collection is believed to represent *C. cubitense*, describing the teleomorph has to await for a collection with mature ascospores. Whether the four collections with pale subiculum but purplish red perithecia, described in the section describing uncultured collections, also belong to *C. cubitense* needs isolation of cultures from similar fresh collections on *Rigidoporus* spp.

Regarding colony characteristics, *C. cubitense* resembles *H. gabonensis* in which colonies grow more slowly, aerial mycelium is intensively buff, and the reverse remains ochraceous or turns pinkish. The type strain of *C. cubitense* was obtained consisting of a red and white form with the latter remaining uncoloured on different media. The conidial apparatus of *C. cubitense* is similar to that of the secondary anamorph of *H. gabonensis*, descibed below, and to the anamorph of *H. khaoyaiensis*. However, the latter has pallid, KOH-negative perithecia and does not produce red pigment in culture (Põldmaa & Samuels, 2004).

12. ***Hypomyces gabonensis*** K. Põldmaa, **sp. nov.** MycoBank MB518516. Figs 2D, 5B–F, 18.

Etymology: refers to the country of the type collection.

Mycelium tenue bubalinum, dependens sub hospitis hymenophoro; hyphae hyalinae, 7–9 µm diam. Conidia longo-clavata, cylindracea vel ellipsoidea, 15–30 × 5–7 µm, recta, hyalina, 1–3-septata. In MEA substratum, subiculum factum in partibus coloniae, tenue, hyphis 2.5–4.5 µm latis; perithecia fere superficiales, dispersa, obpyriformes, 400–600 × 300–400 µm, papilla cylindracea, 100–250 µm longa et basi 140–190 µm lata. Ascosporae fusiformes, (28.0–)30.7(–33.0) × (5.0–)5.7(–6.5) µm, septo mediano, subtiliter verrucosae, verrucis < 0.5 µm, apiculo (2.5–)4.0(–5.5) µm, angustatissimo, aciculari.

Mycelium delicate buff, hanging under host hymenophore, attached only from edge, of hyaline, frequently septate hyphae 7–9 µm diam, one simple, septate conidiogenous branch observed. Conidia long clavate, cylindrical or ellipsoidal, 15–30 × 5–7 µm, straight, hyaline, 1–3 septate, hilum narrow, central or wider, laterally displaced.

Teleomorph on MEA. Subiculum formed in parts of colony, thin, delicate; hyphae 2–4.5 µm wide, cells not swollen, buff, partially turning purple in KOH; *perithecia* semi-immersed to almost

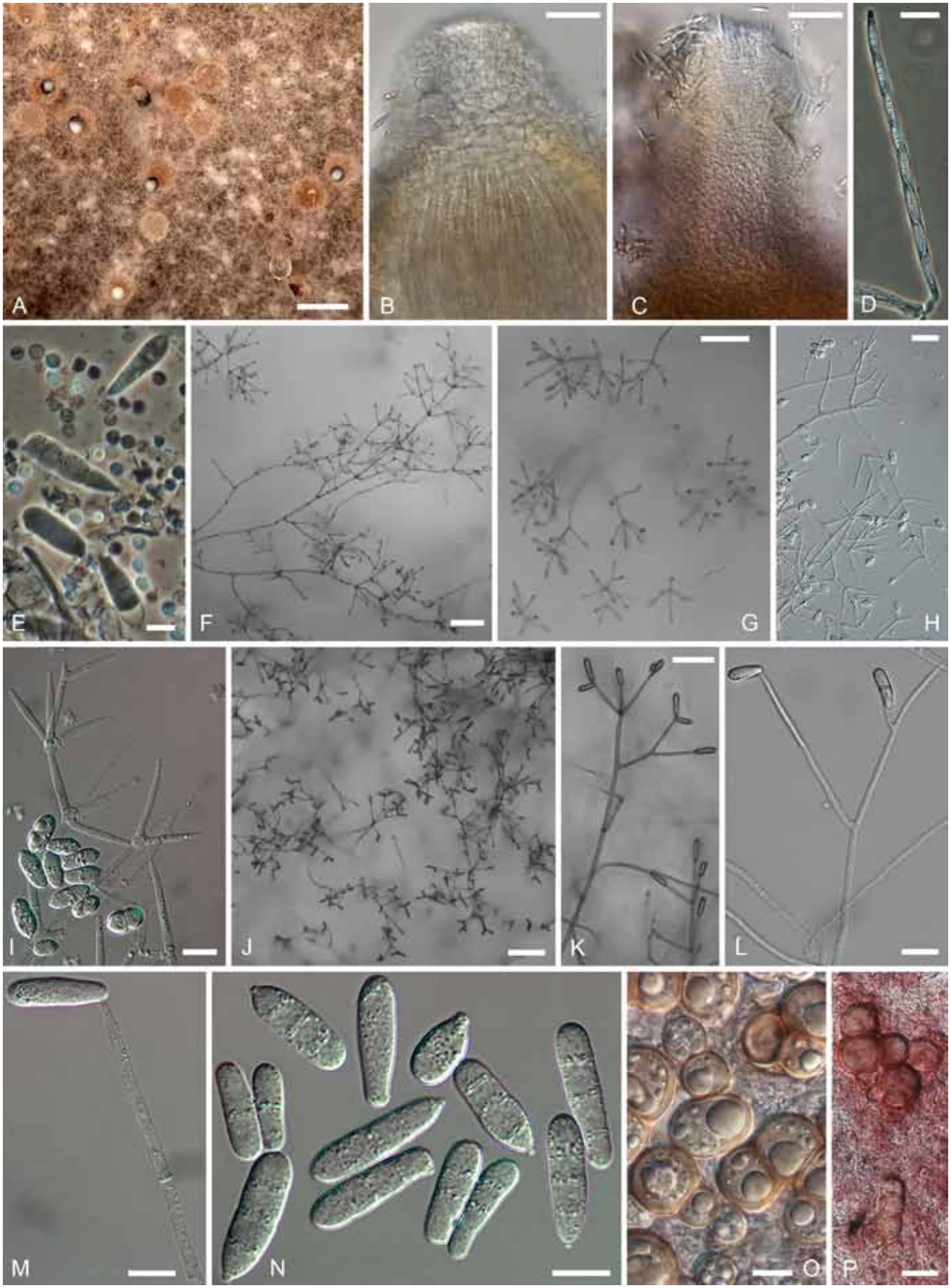

Fig. 18. *Hypomyces gabonensis*. A–D. Teleomorph formed in culture. A. Perithecia embedded in the subiculum. B–C. Upper parts of perithecia. D. Ascus. E. Conidia and basidiospores of the host on natural substratum. F–I. Conidiophores with verticillately placed conidiogenous cells and conidia formed first in culture. J–N. Conidiophores with sparingly placed conidiogenous branches and larger conidia produced after the first formed anamorph structures in culture. O, P. Chlamydospores among subiculum. (E. Holotype, TU 112024 on host; A–D, F–P. Ex-type culture, TFC 201156 on MEA; F–N. 12 d; A–D, O. 3 mo; P. 6 mo). Scale bars: A = 500 µm; F, G, J = 100 µm; B, C = 50 µm; H = 25 µm; D, K, L, P = 20 µm; E, I, M–O = 10 µm.

superficial on subiculum, scattered, obpyriform, 400–600 × 300–400 µm, buff to yellowish ochraceous, not reacting in KOH; papilla prominent, cylindrical, 100–250 µm long, 140–190 µm wide at base; cells at surface greatly swollen, 15–30 µm diam with wall 1.5–2.5 µm thick; surface cells at base of papilla 17–27 × 11–19 µm. *Asci* cylindrical, 180–210 × 6.5–7.5 µm, apex thickened, 1.5–2.5 µm, ascospores uniseriate with ends overlapping. *Ascospores* fusiform, (28.0–)33.0(–38) × (5.0–)6.0(–7.0) µm, Q = (4.6–)5.5(–6.4), main part (20.0–)23.0(–26.0) × (4.0–)5.0(–6.0) µm, Q = (4.0–)4.6(–5.3); (0–)1-septate, septum median; hyaline, becoming olivaceous-brown when old; finely verrucose, verrucae < 0.5 µm, not confluent; apiculi very narrow, needle-like, rarely with base wider, then hat-shaped, (3.5–)4.8(–6.3) µm long, (1.0–)1.5(–2.0) µm wide at base, ends acute, straight or sometimes curved.

Colonies on MEA spreading slowly, reaching 6–10 mm in 4 d, margin fasciculate. *Odour* absent. *Aerial mycelium* scarce, low, < 1 mm, compact, buff, hyphae turning purple in KOH; reverse yellowish ochraceous, turning darker, yellowish brown with age. Conidiation abundant. *Conidiophores* arising from submerged or aerial hyphae, ascending to suberect or erect, 300–750 µm long, branching profuse, mostly verticillate, often drepanoid, many verticils of conidiogenous cells producing one branch at lateral position, ending with a verticil or branching further several times; 1–4 lateral branches formed from one point, branches 23–30 × 2–3 µm. *Conidiogenous cells* borne on supporting branches, held in verticils by 2–7; subulate, 18–30 µm long, attenuating from 2–3 at base to 0.7–1.5 at apex, aseptate or sometimse with one septum in the middle; with one terminal, often with an additional intercalary conidiogenous locus formed on short denticle, often delimited below by a septum, denticles 1.0–2.5 µm high, 1.0–1.5 µm wide; intercalary loci forming also on stipes of conidiophores. *Conidia* ellipsoidal, ovoid or cylindrical, straight, (9.5–)12.5(–15.5) × (4.5–) 5.3(–6.0), Q = (1.8–)2.4(–3.0), (0–)1(–2)-septate, septum supramedian or median; hilum narrow, central; held by 1(–3) at uppermost or singly at intercalary loci.

Most colonies produce a *secondary anamorph*, developing in a section starting from inoculum or margin of existing colony. Mycelium whitish, growing faster than primary anamorph. *Odour* sweetish. *Aerial mycelium* moderate, sparse cottony, 1–3 mm high; reverse initially white, turning yellowish brown in a few days, finally brownish red to purplish brown (10–11 C–E 6–7). Conidiation abundant. *Conidiophores* arising from aerial hyphae, ascending, 350–1200 µm long, 4–5 µm wide near base, branching moderate, irregular or partly dichotomous. *Conidiogenous cells* or branches borne on lateral branches of conidiophore, rarely on conidiophore, 1–3 formed from one point, almost cylindrical, 35–55 µm long, attenuating from 2–3 at base to 0.7–1.7 at apex, with one terminal conidiogenous locus that produces first upright conidium, subsequent ones formed horizontally. *Conidia* cylindrical, long-clavate, seldom ellipsoidal, straight, (17.5–)22.9(–28.0) × (5.5–) 6.4(–7.0), Q = (2.7–)3.6(–4.5), (1–)3(–4)-septate; hilum narrow to wide, *ca.* 1 µm high and 1.5 µm wide, central, laterally displaced or shifted to side of conidium; held by 3–7 at apex of conidiogenous cells. *Chlamydospores* abundant in old cultures in and on the agar, cells subglobose to globose, 10–20 µm diam, pale brown, wall 1.0–2.5 µm thick, smooth, formed by a few to dozen in chains or irregular clusters often held on a smaller, hyaline thin-walled supporting cell.

Substrata: Resupinate basidiomata of *Polyporales*.

Distribution: Central Africa, known only from the type locality.

Holotype: **Gabon**, Crystal Mountains National Park, Tchimbele, on *Rigidoporus lineatus*, 1 May 2009, K. Põldmaa, **TU 112024**, dried culture containing the teleomorph deposited together with anamorph material on natural host; **ex-type** culture TFC 201156 = CBS 127154.

Notes: *Hypomyces gabonensis* was found as mycelium, loosely attached to the host, with relatively long, narrow 3-septate conidia (Fig. 18E). Although lacking teleomorph structures on the host, several conidial isolates produced perithecia in abundance. Therefore, *H. gabonensis* is described as a pleomorphic species with a dried culture containing both forms designated as the holotype.

The large, pallid perithecia (Fig. 18A–C) with long, slender ascospores clearly distinguish *H. gabonensis* from the other three teleomorphs described in this study. The perithecia lack any red colouration as well as the KOH reaction. However, red pigments are produced in the subicular hyphae and submerged mycelium, resulting in purplish colouration of the agar medium. The ascospores of *H. gabonensis* are remarkably long and narrow bearing long, very narrow needle-like apiculi at their ends (Figs 2D, 3). The ascospores resemble those of *H. rosellus* as well as *H. tegillum*. In the latter species, the ascospores and the apiculi are even longer than in *H. gabonensis*.

The cultures obtained from the germination of conidia are remarkable because of the formation of two types of anamorphs. To exclude the possibility of contamination, several isolations were made from single conidia as well as 16 ascospores. All the isolates started with the growth of profusely branching conidiophores bearing dense verticils of conidiogenous cells (Fig. 18F–H). The conidiogenous cells produce one, less frequently 2–3, ellipsoidal to ovate, 1- rarely 2–3-septate, conidia (Fig. 18I). These are formed either only at the single apical conidiogenous locus or also from a few additional loci on a short sympodium. While in *C. protrusum* the several conidiogenous loci are mostly arranged at the transversely placed elongation at the tip of the conidiogenous cell, a few closely formed terminal loci are seen in *C. heterosporum*. The widely distributed, single loci distinguish the primary anamorph of *H. gabonensis* from all other taxa treated in this study. An even more elongated denticulate rachis has been described in *Pseudohansfordia irregularis* (Arnold 1969) and *Cladobotryum stereicola* (Põldmaa & Samuels 1999). Occasionally the intercalary loci are scattered on the conidiophores, likewise observed in one isolate of *C. cubitense*.

Approximately 1 wk after inoculation several of the monosporic isolates start to form whitish mycelium that proceeds more quickly from one place of the primary yellowish ochraceous colony (Fig. 5D–F). Such mycelium bears long, loosely, yet profusely branched conidiophores with conidiogenous cells held singly or by 2–3 and forming one apical conidiogenous locus (Fig. 18J–M). These produce relatively long, cylindrical to long-clavate, 3-septate conidia (Fig. 18N). Such conidiophores are sometimes formed above the primary, profusely branched ones or are seen at the margins of colonies. This secondary anamorph is clearly distinct from the primary type. All the structures and mode of conidiation of the secondary anamorph are similar to those observed in the sister species *C. cubitense*. In both species conidia grow horizontally from the conidiogenous locus, while in all other species they develop obliquely. Consequently, narrow to wide hila are observed either centrally or laterally at base or often at the side of conidia. In *C. cubitense* the shape of conidia is often irregular due to variously curved conidia. In *H. gabonensis*, the straight conidia are uniform

in shape. The irregular clusters of chlamydospores associated with the secondary anamorph (Fig. 18O, P) are identical to those found in old cultures of *C. cubitense*. In *H. gabonensis* the yellowish ochraceous, later yellowish brown colouration of the reverse of colonies is much more intense and growth slower compared to *C. cubitense*. The anamorph of *H. gabonensis* presents a unique feature in the genus, producing two distinct anamorphs in culture. In the isolate of *C. cubitense* from Peru conidia appeared dimorphic, without differences observed in the conidiophorous system. Formation of secondary conidiophores and conidia has also been observed in *H. khaoyaiensis* and *C. dimorphicum*. In these species the smaller structures regularly precede or follow the characteristic primary anamorph. In *H. gabonensis* the two morphs represent distinct forms, which, on their own, could be described as different species of *Cladobotryum*. Isolates from single ascospores and conidia differ substantially in the timing and abundance of secondary anamorph production with the stimulation and mechanisms for their production remaining unknown.

ACKNOWLEDGEMENTS

I would like to thank the keen hypocreologists Gary J. Samuels and Günter Arnold for the many valuable discussions on these fungi and for sharing their collections of *Hypomyces* and *Cladobotryum*. Priscila Chaverri, Jacques Fournier, Christian Lechat and Rafael Castañeda Ruiz provided further specimens. I am indebted to Amy Y. Rossman for reviewing the manuscript, Christian Feuillet for preparing the Latin diagnoses, as well as to Leif Ryvarden and Erast Parmasto for identifying the polypores as hosts. Curators of the following herbaria and fungal culture collections are acknowledged for sending specimens and cultures: Ellen D. Bloch (NY), Erin McCray, Shannon Dominick (BPI), Begoña Aguirre-Hudson (K), Kerstin Voigt (FSU) and Walter Gams, previously at CBS. Several lab assistants helped with PCR. The study was supported by the Estonian Science Foundation grants (4994 and 6939), the Estonian Ministry of Education and Science (project SF0180012s09), and the European Union through the European Regional Development Fund (Centre of Excellence FIBIR).

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.02

A morphological and phylogenetic revision of the *Nectria cinnabarina* species complex

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Abstract: The genus *Nectria* is typified by *N. cinnabarina*, a wood-inhabiting fungus common in temperate regions of the Northern Hemisphere. To determine the diversity within *N. cinnabarina*, specimens and cultures from Asia, Europe, and North America were obtained and examined. Their phylogeny was determined using sequences of multiple loci, specifically *act,* ITS, LSU, *rpb1*, *tef1,* and *tub.* Based on these observations, four species are recognised within the *N. cinnabarina* complex. Each species is delimited based on DNA sequence analyses and described and illustrated from specimens and cultures. The basionym for *N. cinnabarina, Sphaeria cinnabarina,* is lectotypified based on an illustration that is part of the protologue, and an epitype specimen is designated. *Nectria cinnabarina s. str.* is recircumscribed as having 2-septate ascospores and long stipitate sporodochia. *Nectria dematiosa*, previously considered a synonym of *N. cinnabarina*, has up to 2-septate ascospores and sessile sporodochia or no anamorph on the natural substrate. A third species, *Nectria nigrescens,* has up to 3-septate ascospores and short to long stipitate sporodochia. One newly described species, *Nectria asiatica* with a distribution restricted to Asia, has (0–)1-septate ascospores and short stipitate sporodochia. Young and mature conidia developing on SNA were observed for each species. Mature conidia of *N. asiatica*, *N. cinnabarina*, and *N. nigrescens* but not *N. dematiosa* bud when the mature conidia are crowded. On PDA the optimal temperature for growth for *N. dematiosa* is 20 °C, while for the other three species it is 25 °C. Based on our phylogenetic analyses, three subclades are evident within *N. dematiosa*. Although subtle culture and geographical differences exist, these subclades are not recognised as distinct species because the number of samples is small and the few specimens are insufficient to determine if morphological differences exist in the natural environment.

Key words: *Ascomycota*, *Hypocreales*, molecular systematics, *Nectriaceae*, plant pathogen, type species.
Taxonomic novelty: *Nectria asiatica* Hirooka, Rossman & P. Chaverri, sp. nov.

INTRODUCTION

Nectria cinnabarina is the type species of the genus *Nectria* (*Hypocreales*, *Nectriaceae*). This species is characterised by red, globose, fleshy, warted perithecia that often become cupulate upon drying, 0–3-septate ascospores, and an anamorph referred to as *Tubercularia vulgaris* (Rossman *et al.* 1999). *Nectria cinnabarina* is a relatively common species that occurs on a range of hardwood trees and woody shrubs throughout the temperate regions of the Northern Hemisphere. It is occasionally considered to be a plant pathogen causing a disease on apple and other hardwood trees known as "coral spot" because of the pinkish sporodochia of its *Tubercularia* anamorph (Sinclair & Lyon 2005).

Nectria cinnabarina was originally described as *Sphaeria cinnabarina* by Tode (1791). When Fries (1849) sanctioned *Sphaeria cinnabarina,* he transferred this name to *Nectria*. *Nectria cinnabarina* was designated the lectotype species of the genus by Clements & Shear (1931). *Nectria* was conserved with this type species over *Ephedrosphaera* and *Hydropisphaera* (Cannon & Hawksworth 1983).

In studying the species of *Nectria* in the UK, Booth (1959) emphasised perithecial wall structure when he divided the large genus into groups. He included three species in what he referred to as the *Nectria cinnabarina* group: *N. cinnabarina*, *N. aurantiaca,* and *N. ralfsii*. When Rossman (1989) and Rossman *et al*. (1999) restricted *Nectria s. str.* to species congeneric with *N. cinnabarina*, they included *N. aurantiaca* and other species with a similar perithecial wall structure in *Nectria s. str. Nectria ralfsii* is now regarded a species of *Bionectria, B. ralfsii* (Schroers 2001).

Because of its morphological heterogeneity, 20 varieties and forms of *Nectria cinnabarina* exist as well as numerous synonyms. Wollenweber (1926, 1930) recognised three varieties of *N. cinnabarina*. *Nectria cinnabarina* var. *minor* was distinguished from the type variety by its smaller ascospores and conidia, while *Nectria cinnabarina* var. *dendroidea* has remarkably long, stipitate sporodochia. *Nectria cinnabarina* var. *ribis* (≡ *N. ribis*) was said to have larger ascospores and conidia than the other two varieties. Jøgensen (1952) published a monograph on *N. cinnabarina* and suggested that *Nectria ribis* was a "*nomen confusum*", being a mixture of *N. cinnabarina* and *N. berolinensis.* Despite detailed observations, he did not find differences among specimens of *N. cinnabarina*; however, he noted differences between specimens on non-*Ribes* hosts and those on *Ribes* that he recognised as *N. cinnabarina* var. *ribis*.

Tubercularia (Tode 1790) includes anamorphs of several species in the *Nectria cinnabarina* group (Booth 1959, Rossman 1983). *Tubercularia*, conserved based on *T. vulgaris,* was segregated from fungi with black sporodochia by Fries (1832). Saccardo (1886) divided species of *Tubercularia* into four groups based on differences in substrate; however, his taxonomic concept was revised by Paoletti (1887) who emphasised the acropleurogenously developing phialides. Petch (1940) organised and revised the British records of *Tubercularia*. Seifert (1985) provided a thorough account of *Tubercularia* accepting eight species including *T. vulgaris* with many synonyms.

Although Tode (1790, 1791) described and illustrated both *Sphaeria cinnabarina* and *Tubercularia vulgaris*, he did not recognise their relationship as states of one species. Later, Fries (1828) determined that these were the sexual and asexual states of the same species. Modern authors have confirmed that *N. cinnabarina* and *T. vulgaris* are manifestations of the same species (Seifert 1985, Rossman 1989).

Nectria cinnabarina is commonly regarded as a saprobe; as mentioned above, it sometimes causes cankers on hardwood trees and woody shrubs. The parasitic occurrence of *N. cinnabarina* was first reported by Mayr (1883), who considered this species to be parasitic on *Acer*, *Aesculus*, *Prunus*, *Robinia*, *Spiraea*, *Tilia,* and *Ulmus*. Many hardwood trees and woody shrubs around the world have been reported as hosts for *N. cinnabarina* (Sinclair & Lyon 2005). Jøgensen (1952) demonstrated that *N. cinnabarina* was a facultative parasite and saprobe, but could not differentiate pathogenic races. He mentioned the following genera as the most common hosts of *N. cinnabarina* in Denmark: *Acer*, *Aesculus*, *Carpinus*, *Fagus*, *Fraxinus*, *Malus*, *Prunus*, *Ribes*, *Tilia*, and *Ulmus*. Similarly the anamorph has been commonly reported on woody substrates in many plant families (Seifert 1985).

Based on our hypothesis that *Nectria cinnabarina* is heterogeneous and might comprise several species, detailed morphological and molecular phylogenetic analyses of this species were undertaken. Many isolates of freshly collected and herbarium specimens from around the world were analysed to define phylogenetic species within the *N. cinnabarina* species complex (NCSC). Each species is described and illustrated and a key is provided.

MATERIALS AND METHODS

Source and deposition of specimens and isolates

Fresh specimens of the teleomorph and anamorph were collected from which single ascospores or conidia were isolated. Specimens are deposited in the US National Fungus Collections (BPI), Beltsville, Maryland, USA, or elsewhere as indicated in Table 1. Specimens were also obtained from other herbaria as listed in the specimens examined; herbaria are indicated using abbreviations according to Holmgren & Holmgren (1998). To obtain cultures from fresh material, a suspension in sterilised water was made from ascospores or conidia from a crushed fruiting body, streaked onto 2 % (w/v) water agar (WA) with streptomycin (streptomycin sulfate; Sigma Chemicals, St. Louis, Missouri, USA) or Difco™ cornmeal dextrose agar (CMD; Difco, Detroit, Michigan, USA, cornmeal agar + 2 % w/v dextrose) supplemented with antibiotics 0.2 % each neomycin (neomycin trisulfate salt hydrate; Sigma Chemicals, St. Louis, Missouri, USA), and incubated at 25 °C. After 24 h, a single germinating ascospore or conidium was transferred directly to slants or plates of Difco™ potato dextrose agar (PDA) with a tungsten needle (Nissin EM Co., Tokyo, Japan). Representative isolates are preserved at the CBS Fungal Biodiversity Centre (CBS, Utrecht, Netherlands), and/or Genebank, National Institute of Agrobiological Sciences (NIAS, Tsukuba, Ibaraki, Japan). Isolates were also obtained from other culture collections, including the CBS Fungal Biodiversity Center and the Global Bioresource Center (ATCC, Manassas, Virginia, USA).

Table 1. Isolates and accession numbers used in the phylogenetic analyses.

Species	Isolate No.	Herbarium No.	Substrate/ Host	Country	GenBank Accession No.					
					act	ITS	LSU	*rpb1*	*tef1*	*tub*
Cosmospora coccinea	A.R. 2741, CBS 114050	BPI 802729	*Inonotus nodulosus*	Germany	GQ505967 [a]	HM484537	GQ505990 [a]	GQ506020 [a]	HM484515	HM484589
Cyanonectria cyanostoma	G.J.S. 98-127, CBS 101734	BPI 748307	*Buxaceae*	France	GQ505961 [a]	HM484558	FJ474081 [a]	GQ506017 [a]	HM484535	HM484611
Nectria antarctica	A.R. 2767, CBS 115033, ATCC 204178	BPI 746217	Dead stem of *Mahonia aquifolium*	USA	HM484501	HM484556	HM484560	HM484575	HM484516	HM484601
Nectria aquifolii	A.R. 4108, CBS 125147	BPI 880698	*Ilex aquifolium*	UK	HM484506	HM484538	HM484565	HM484579	HM484522	HM484590
Nectria asiatica	MAFF 241408	BPI 879980	Dead wood	Japan	–	HM484703	HM484744	HM484790	–	HM484815
	A.R. 4639, CBS 126568		Dead wood	China	–	HM484713	HM484727	HM484787	–	HM484811
	MAFF 241401	BPI 879978	Dead wood	Japan	HM484624	HM484716	HM484747	HM484788	–	HM484817
	MAFF 241435	BPI 879973	Bark of dead wood	Japan	HM484625	HM484709	HM484749	HM484794	–	HM484816
	MAFF 241399	BPI 879976	*Prunus* sp.	Japan	–	HM484715	HM484751	HM484791	–	HM484813
	MAFF 241448	BPI 879974	Dead twig	Japan	HM484626	–	HM484728	HM484793	–	HM484809
	MAFF 241398	BPI 879975	Dead wood of *Zelkova serrata*	Japan	HM484643	HM484702	HM484738	HM484792	–	HM484812
	MAFF 241439	BPI 879972	Bark of dead wood	Japan	HM484505	HM484701	HM484563	–	–	HM484604
	MAFF 241405	BPI 879979	Dead twig of *Prunus* sp.	Japan	–	HM484708	HM484748	HM484789	–	HM484814
	MAFF 241400	BPI 879977	Dead stem of *Sorbus commixta*	Japan	HM484623	HM484705	HM484743	HM484786	–	HM484818
Nectria aurigera	A.R. 3717, CBS 109874	BPI 841465	Twigs dead, *Fraxinus excelsior*	France	HM484511	HM484551	HM484573	HM484586	HM484521	HM484600
Nectria austroamericana	A.R. 2808, CBS 126114	BPI 746395	*Gleditsia triacanthos*	USA	GQ505960 [a]	HM484555	GQ505988 [a]	GQ506016 [a]	HM484520	HM484597

Table 1. (Continued).

Species	Isolate No.	Herbarium No.	Substrate/ Host	Country	GenBank Accession No.					
					act	ITS	LSU	*rpb1*	*tef1*	*tub*
Nectria balansae	A.R. 4446, CBS 123351	BPI 878477	*Coronilla* sp.	France	GQ505977 [a]	HM484552	GQ505996 [a]	GQ506026 [a]	HM484525	HM484607
Nectria balsamea	A.R. 4478, CBS 125166		*Pinus sylvestris*	Germany	HM484508	HM484540	HM484567	HM484580	HM484528	HM484591
Nectria berolinensis	A.R. 2776, CBS 126112	BPI 746346	Branches standing, *Ribes rubrum*	Austria	HM484510	HM484543	HM484568	HM484583	HM484517	HM484594
Nectria cinnabarina	A.R. 4327, CBS 125154		*Acer* sp.	Canada	HM484642	HM484688	HM484733	HM484778	HM484666	HM484824
	G.J.S. 91-111, CBS 713.97	BPI 1112880	*Acer* sp.	USA	HM484629	HM484693	HM484724	HM484777	HM484665	HM484825
	A.R. 4340, CBS 125156	BPI 878335	*Spiraea trilobata*	Canada	HM484635	HM484695	HM484756	HM484779	HM484664	HM484836
	A.R. 4341, CBS 125157	BPI 878311	*Acer saccharum*	Canada	HM484636	HM484687	HM484741	HM484780	HM484667	HM484822
	G.J.S. 91-109	BPI 1112878	*Fagus* sp.	USA	HM484633	HM484694	HM484723	HM484766	HM484670	HM484833
	A.R. 4379, CBS 125158	BPI 878313	Twigs	Ireland	HM484640	HM484696	HM484739	HM484772	HM484668	HM484830
	A.R. 4337, CBS 127668	BPI 878312	*Acer pseudoplatanus*	Denmark	HM484631	HM484690	HM484726	HM484775	HM484659	HM484826
	A.R. 4477, CBS 125165	BPI 879981	Dead twigs of *Aesculus* sp.	France	HM484503	HM484548	HM484562	HM484577	HM484527	HM484606
	A.R. 4496	BPI 878878	*Populus tremula*	Ukraine	HM484641	HM484712	HM484731	HM484768	HM484658	HM484831
	A.R. 4302, CBS 125150	BPI 878317	*Acer pseudoplatanus*	Austria	HM484627	HM484684	HM484736	HM484765	HM484654	HM484820
	ATCC 11432, CBS 255.47		Stem of *Ulmus* sp.	Netherlands	GQ505975 [a]	HM484710	GQ505997 [a]	GQ506027 [a]	HM484663	HM484832
	CBS 256.47		Twig of *Ulmus* sp.	Netherlands	HM484628	HM484692	HM484755	HM484769	HM484656	HM484828
	A.R. 4303, CBS 125151	BPI 878316	*Acer campestre*	Austria	HM484630	HM484686	HM484740	HM484776	HM484669	HM484821
	CBS 189.87		*Sorbus aria*	Germany	HM484644	HM484699	HM484746	HM484796	HM484671	HM484835
	A.R. 4397, CBS 125163	BPI 879983, C.L.L. 7027	*Acer* sp.	France	HM484638	HM484691	HM484742	HM484773	HM484661	HM484827
	A.R. 4381, CBS 125160	BPI 878310	Root	UK	HM484632	HM484685	HM484752	HM484774	HM484657	HM484837
	A.R. 4304, CBS 125152	BPI 879982	*Tilia* sp.	Denmark	HM484637	HM484698	HM484734	HM484767	HM484655	HM484829
	A.R. 4388, CBS 125161	BPI 878322	Twigs of *Acer pseudoplatanus*	Poland	HM484639	HM484689	HM484735	HM484771	HM484662	HM484823
	CBS 125115, G.J.S. 91-121	BPI 1112890	*Acer* sp.	USA	HM484634	HM484697	HM484753	HM484770	HM484660	HM484834
Nectria coryli	A.R. 4561, Y.H. 0815	BPI 880697	Twigs of *Rhus copallinum*	USA	HM484509	HM484539	HM484566	HM484581	HM484536	HM484596
Nectria cucurbitula	CBS 259.58		*Pinus sylvestris*	Netherlands	GQ505974 [a]	HM484541	GQ505998 [a]	GQ506028 [a]	HM484530	HM484592
Nectria dematiosa	CBS 126570, G.J.S. 94-37	BPI 749337	Bark	USA	HM484502	HM484557	HM484561	HM484576	HM484534	HM484603
	A.R. 4328, CBS 125155		*Acer* sp.	Canada	HM484616	HM484680	HM484725	HM484761	HM484648	HM484799
	CBS 279.48		*Acer pseudoplatanus*		–	HM484700	HM484754	HM484762	HM484649	HM484802
	CBS 278.48		*Ribes* sp.		HM484615	HM484682	HM484729	HM484760	HM484647	HM484800
	A.R. 4380, CBS 125159	BPI 878308	Twig	Poland	HM484614	HM484681	HM484722	HM484759	HM484650	HM484801
	A.R. 2699, CBS 125125	BPI 802212	Dead twig of *Acer macrophyllum*	Canada	HM484612	HM484676	HM484717	HM484757	HM484645	HM484797
	A.R. 2702, CBS 125127	BPI 802215	Dead twig of *Rosa* sp.	Canada	HM484613	HM484677	HM484719	HM484758	HM484646	HM484798
	MAFF 241430	BPI 879985	Branches standing	Japan	HM484617	HM484704	HM484750	HM484795	HM484653	HM484803
	A.R. 4638, CBS 127667		Unknown	China	–	HM484706	HM484718	HM484763	HM484651	HM484805
	MAFF 241416	BPI 879984	Attached branches of *Weigela coraeensis*	Japan	–	HM484714	HM484732	HM484764	HM484652	HM484804

Table 1. (Continued).

Species	Isolate No.	Herbarium No.	Substrate/ Host	Country	GenBank Accession No.					
					act	**ITS**	**LSU**	***rpb1***	***tef1***	***tub***
Nectria lamyi	A.R. 2779, CBS 115034	BPI 746349	*Berberis vulgaris*	Austria	HM484507	HM484544	HM484569	HM484582	HM484518	HM484593
Nectria miltina	A.R. 4391, CBS 121121	BPI 878442	Decaying leaves of *Agave americana*	Italy	HM484514	HM484547	HM484572	HM484587	HM484524	HM484609
Nectria nigrescens	A.R. 4282	BPI 878455A	Dead twig of *Acer* sp.	France	HM484619	HM484711	HM484745	HM484785	HM484673	HM484808
	A.R. 4211, CBS 125148	BPI 871083	Dead twig of dictyledonous tree	USA	HM484618	HM484707	HM484720	HM484781	HM484672	HM484806
	A.R. 4475, CBS 125164	BPI 878457	Twig of *Fagus sylvatica*	France	HM484504	HM484550	HM484564	HM484578	HM484526	HM484605
	AR 4565, CBS 127666	BPI 879986	Dead twig	USA	HM484620	HM484683	HM484730	HM484784	HM484674	HM484810
	A.R. 4213, CBS 125149	BPI 871084	Dead twig of *Betula lutea*	USA	HM484622	HM484679	HM484721	HM484782	HM484675	HM484819
	A.R. 4394, CBS 125162	BPI 878449	Twigs of *Celtis occidentalis*	Canada	HM484621	HM484678	HM484737	HM484783	–	HM484807
Nectria pseudocinnabarina	A.R. 4548	C.L.L. 8299	Unknown	French Guiana	–	HM484553	HM484574	HM484588	HM484529	HM484608
Nectria pseudotrichia	CBS 551.84		Unknown	Japan	GQ505976 [a]	HM484554	GQ506000 [a]	GQ506030 [a]	HM484532	HM484602
Nectria pyrrhochlora	A.R. 2786, CBS 125131	BPI 746398	*Acer campestre*	Austria	HM484512	HM484545	HM484570	HM484584	HM484519	HM484598
Nectria sinopica	CBS 462.83	CBS H-19479, CBS H-19485	*Hedera helix*	Netherlands	GQ505973 [a]	HM484542	GQ506001 [a]	GQ506031 [a]	HM484531	HM484595
Nectria zanthoxyli	A.R. 4280, CBS 126113	BPI 878445	*Crataegus* sp.	France	HM484513	HM484546	HM484571	HM484585	HM484523	HM484599
Thelonectria westlandica	G.J.S. 83-156, CBS 112464		*Dacrydium cupressinum*	New Zealand	GQ505959	HM484559	GQ505987 [a]	GQ506015 [a]	HM484533	HM484610

A.R.: Amy Y. Rossman, USDA-ARS MD USA; ATCC: American Type Culture collection, Manassas, VA, USA; BPI: U.S. National Fungus Collections USDA-ARS MD USA; CBS: Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; C.L.L.: Christian Lechat, Ascofrance, Villiers en Bois, France; G.J.S.: Gary J. Samuels, USDA-ARS MD USA; MAFF: MAFF Genebank, National Institute of Agrobiological Sciences, Ibaraki, Japan; Y.H.: Yuuri Hirooka, USDA-ARS MD USA.
[a]Sequences obtained from GenBank.

Morphological observations

For morphological characterisation of the teleomorph, the macromorphology of the perithecia and stroma was observed and described as follows: distribution of perithecia on the host; perithecium shape, colour and reaction to 3 % w/v potassium hydroxide (KOH) and 100 % lactic acid (LA) using a stereoscope (Zeiss, STEMI SV11, Jena, Germany). To observe internal and microscopic characteristics, the perithecia and stroma were sectioned by hand and rehydrated in water, KOH, and LA. Characteristics of asci and ascospores were observed by rehydrating the perithecia in water, removing part of the centrum with a fine glass needle, and placing it onto a glass slide. Microscopic observations were made using a compound microscope (Zeiss, Axioskop 2 Plus, Jena, Germany). To determine growth rates, colony colour, and odour, isolates were grown on PDA in 9-cm plastic dishes at 25 °C for 7 d in the dark. For observation of sporulating structures, the cultures were grown on a low nutrient agar (SNA; Nirenberg 1976). Cultures on SNA were incubated at 25 °C with alternating 12 h/ 12 h fluorescent light/darkness for 2–3 wk. Young conidia are those that develop after one or two d on SNA while mature conidia are 4–5 d old. To stimulate budding, mature conidia produced on SNA were suspended in distilled water and then streaked on SNA. After 24 h, budding mature conidia and germ tubes were produced. Images were captured with a Nikon DXM1200 digital camera. Some composite images were made with Helicon Focus v. 4.21.5 Pro (Helicon Soft, www.heliconfocus.com). All recognition of colour such as perithecia, ascospores, conidia, and top and reverse colony colour were described according to Kornerup & Wanscher (1978).

Statistical analysis

Measurements of continuous characters such as length and width were made using Scion Image software beta v. 4.0.2 (Scion Corporation, Frederick, Maryland, USA) and are based on up to 50 measurements for structures in each isolate. For morphological structures, descriptive statistics (minimum, mean, median, maximum, and standard deviation) were computed and variation of morphological characters displayed graphically using mean values and their corresponding 95 % confidence intervals. All computations were performed using Systat 10 (Systat Software, San José, California, USA). Only isolates for which all data were available were included in the analysis. Ranges are reported as mean values ± one standard deviation; the number of items measured is given in parentheses together with maximum and minimum.

Cardinal temperatures

Disks of 5 mm diam were cut from the edge of young colonies and placed in the centre of PDA plates, then incubated at temperatures from 15 to 35 °C at 5 °C intervals in complete darkness. Diameters of the colonies on three plates for each isolate at each temperature were measured daily for 1 wk.

Table 2. Genes/loci used in the phylogenetic analyses for members of the genus *Nectria*. Information on the primers, base pairs, PCR protocols, and models of nucleotide substitution are indicated.

Locus	Primers used (reference)	PCR protocol: Annealing temp. & cycles	Nucleotide substitution models	Included sites (# of excluded sites)	Phylogenetically informative sites (%)	Uninformative polymorphic sites	Invariable sites
Act	T*act*1, T*act*2 (Samuels *et al.* 2006)	65 °C, 30 s, 15´ 48 °C, 30 s, 30´	GTR+G	613 (127)	111 (18 %)	43	459
ITS	ITS5, ITS4 (White *et al.* 1990)	53 °C, 1 min, 35´	TIM3+I+G	539 (279)	62 (12 %)	52	425
LSU	LR5, LROR (Vilgalys n.d.)	53 °C, 1 min, 35´	TIM3+I+G	807 (150)	67 (8.3 %)	39	701
Rpb1	c*rpb1*a, *rpb1*c (Castlebury *et al.* 2004)	50 °C, 2 min, 40´	TIM2+I+G	590 (540)	233 (40 %)	65	292
Tef1	*tef1*-728, *tef1*-1567 (Carbone & Kohn 1999, Rehner 2001)	66 °C, 55 s, 9´ 56 °C, 55 s, 35´	GTR+I+G	645 (261)	142 (22 %)	43	460
Tub	β*tub*-T1, β*tub*-T2 (O'Donnell & Cigelnik 1997)	55 °C, 30 s, 35´	TPM3uf+I+G	479 (408)	192 (40 %)	32	255
Total				3673	807 (22 %)	274	2592

Table 3. Genes/loci used in the phylogenetic analyses for members of *Nectria cinnabarina* species complex (NCSC). Information on the primers, base pairs, PCR protocols, and models of nucleotide substitution are indicated.

Locus	Primers used (reference)	PCR protocol: Annealing temp. & cycles	Nucleotide substitution models	Included sites (# of excluded sites)	Phylogenetically informative sites (%)	Uninformative polymorphic sites	Invariable sites
Act	T*act*1, T*act*2 (Samuels *et al.* 2006)	65 °C, 30 s, 15´ 48 °C, 30 s, 30´	TrN+G	649 (91)	47 (7 %)	40	562
ITS	ITS5, ITS4 (White *et al.* 1990)	53 °C, 1 min, 35´	TrNef+G	475 (592)	38 (8 %)	19	418
LSU	LR5, LROR (Vilgalys n.d.)	53 °C, 1 min, 35´	TIM1+I+G	814 (260)	18 (2 %)	14	782
Rpb1	c*rpb1*a, *rpb1*c (Castlebury *et al.* 2004)	50 °C, 2 min, 40´	TrN+G	621 (123)	111 (18 %)	120	390
Tef1	*tef1*-728, *tef1*-1567 (Carbone & Kohn 1999, Rehner 2001)	66 °C, 55 s, 9´ 56 °C, 55 s, 35´	TrN+G	828 (186)	158 (19 %)	36	634
Tub	β*tub*-T1, β*tub*-T2 (O'Donnell & Cigelnik 1997)	55 °C, 30 s, 35´	TPM3uf+G	527 (135)	88 (17 %)	138	301
Total				3914	460 (12 %)	367	3087

DNA extraction, PCR, and sequencing

The forty-five cultures of *N. cinnabarina* used in the phylogenetic analyses (Table 1) and representatives of other species of *Nectria s. str.* were grown in Difco™ potato dextrose broth in 6 cm diam Petri plates for about 3 wk. Mycelial mats were harvested in a laminar flow hood and dried with clean, absorbent paper towels. DNA was extracted with Ultra Clean™ Plant DNA Isolation Kit (MO BIO Laboratories Inc., Solana Beach, California, USA).

Six loci were sequenced, namely a-actin (*act*) (Carbone & Kohn 1999), β-tubulin (*tub*) (O'Donnell & Cigelnik 1997), RNA polymerase II subunit one (*rpb1*) (Castlebury *et al.* 2004), the internal transcribed spacer (ITS) (White *et al*. 1990), large subunit nuclear ribosomal DNA (LSU) (Vilgalys n.d.), and translation elongation factor 1-a (*tef1*) (Carbone & Kohn 1999, Rehner 2001). The primers and PCR protocol information are listed in Tables 2 and 3. PCR products were cleaned with ExoSAP-IT® (USB Corporation, Cleveland, Ohio, USA) following the manufacturer's instructions. Clean PCR products were sequenced at the DNA Sequencing Facility (Center for Agricultural Biotechnology, University of Maryland, College Park, Maryland, USA) and at MCLAB (Molecular Cloning Laboratories, San Francisco, California, USA). Sequences were assembled and edited with Sequencher v. 4.9 (Gene Codes, Madison, Wisconsin, USA). Sequences are deposited in GenBank (Table 1).

Phylogenetic analyses

Sequences of the six genes were aligned with MAFFT v. 6 (Katoh 2008) and the alignment was visually improved with Mesquite v. 2.6 (Maddison & Maddison 2009). Maximum likelihood (ML) and Bayesian (BI) analyses were carried out with all sequences, first each locus separately, then with the combined/concatenated data sets. Representative members of the *Nectriaceae*, namely *Cosmospora coccinea*, *Cyanonectria cyanostoma*, and *Thelonectria westlandica,* were used as outgroups for inferring intrageneric relationships (Fig. 1). *Nectria balansae, N. pseudocinnabarina*, and *N. pseudotrichia* were used as outgroup taxa for the NCSC tree, including 45 isolates in the NCSC (Fig. 2). JMODELTEST (Posada 2008) was used to calculate the models of nucleotide substitutions of each gene/partition for the ML and BI analyses. The number of substitution schemes was set to 11, base frequencies +F, rate variation +I and +G, and the base tree for likelihood calculations was set to "ML

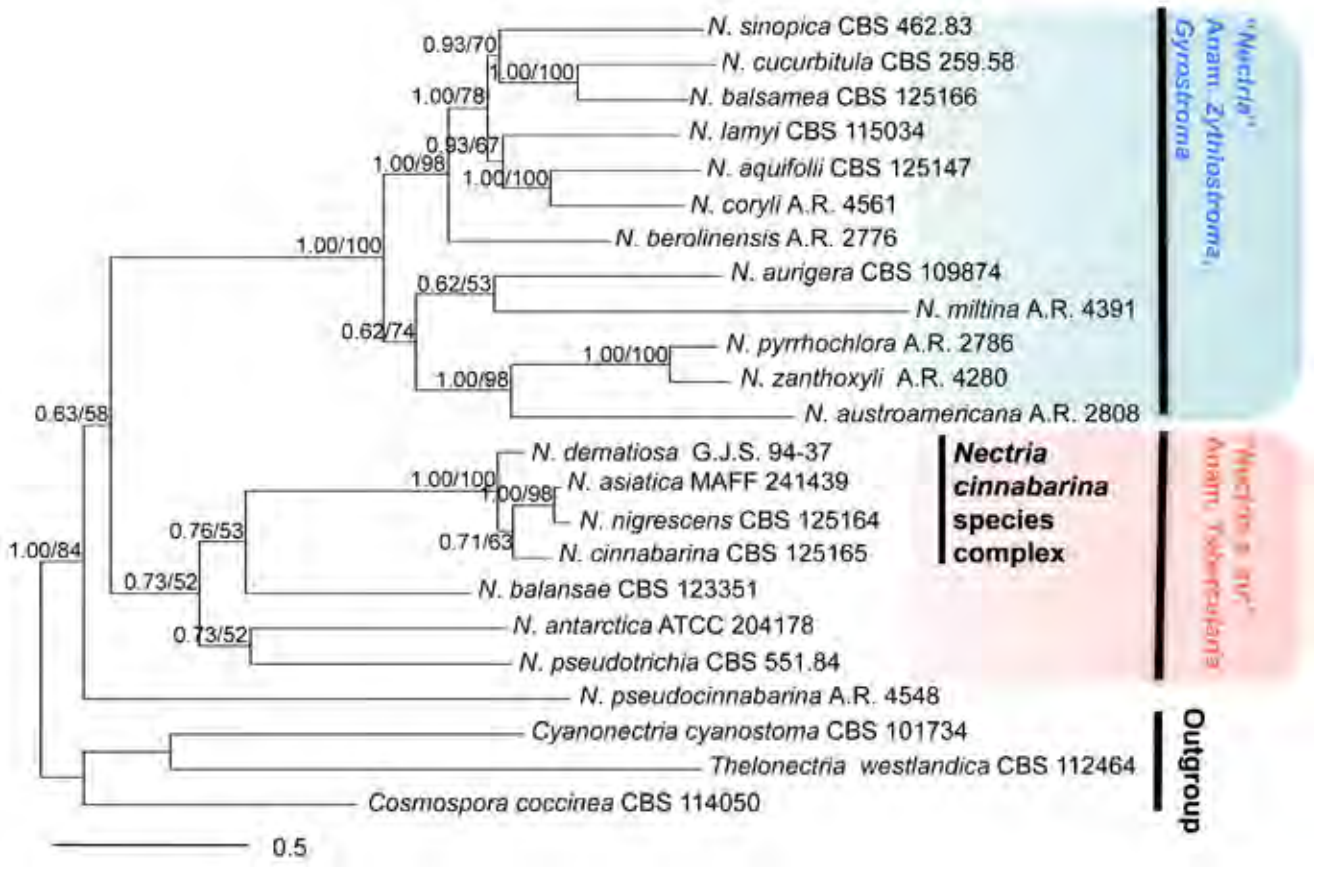

Fig. 1. Members of the genus *Nectria*. Combined *act*, *tub*, *rpb1*, ITS, LSU, *tef1* Bayesian cladogram (Ln −21514.704). BI posterior probabilities/ML bootstrap values indicated at branches.

optimised". 88 models were compared. After the likelihood scores were calculated, the models were selected according to the Akaike information criterion (AIC) (Posada & Buckley 2004). Under the AIC settings, the AICc corrected for smaller samples was selected. After jMODELTEST was run, likelihood settings for trees of the *Nectria* tree and NCSC tree were set to each gene (Tables 2, 3). For the ML and bootstrap analyses (BP), GARLI version 0.96 (Zwickl 2006) was computed through the Grid computing (Cummings & Huskamp 2005) and The Lattice Project (Bazinet & Cummings 2008), which includes clusters and desk tops in one integrated network (Myers *et al.* 2008). In GARLI, the starting tree was made by stepwise-addition and the number of runs or search replicates was set to 50. 2000 ML BP replicates were done in GARLI with the starting tree chosen randomly. Bayesian analysis (BI) was done using MrBayes v. 3.1.2 (Huelsenbeck *et al*. 2001, 2002). In MrBayes, data were partitioned by locus and the parameters of the nucleotide substitution models for each partition were set as described (Tables 2, 3). For this analysis, two independent analyses of two parallel runs and four chains were carried out for 5 000 000 generations using MrBayes. Analyses were initiated from a random tree and trees sampled every 100th generation. The first 20 % of the resulting trees were eliminated (= "burn in"). A consensus tree ("sumt" option) and posterior probabilities (PP) were calculated in MrBayes, which combines the results from both parallel runs. A reciprocal 70 % BP threshold was used to detect topological incongruence among genes/partitions (Mason-Gamer & Kellogg 1996, Reeb *et al*. 2004).

RESULTS

Phylogenetic analyses

Sequencing and alignment of the six loci for 23 taxa in *Nectria* resulted in 3 673 base pairs, 807 (22 %) phylogenetically informative, and 2 592 invariable sites; 325 sites presented unique non-informative polymorphic sites (Table 2). Sequencing and alignment of the six loci for 48 taxa for the NCSC tree included 3 914 base pairs, 460 (12 %) phylogenetically informative, and 3 087 invariable sites; 325 sites presented unique non-informative polymorphic sites (Table 3). Ambiguously aligned and poly-T/A regions were excluded from the analyses. For the species of *Nectria,* the ML and BI analyses of the combined six loci produced one tree with Ln likelihoods of –21393.478926 and −21514.704, respectively (Fig. 1). For the NCSC tree, ML and BI analyses produced one tree with Ln likelihoods of –11339.862470 and −11408.155, respectively (Fig. 2). The topologies of the ML and BI trees were congruent.

The topologies of each gene tree did not contradict each other, although the *tef1* tree does not include *N. asiatica* (results not shown). All individual gene trees reveal three clades in *N. dematiosa* species complex. Among these trees, the *act* tree provides the best resolution with best BP support as evidenced in the high BP and PP support in most nodes.

The combined ML and BI analyses of six loci indicated that *Nectria* comprises two major clades: species with *Tubercularia* anamorphs (0.73 BI PP, 52 % ML BP) and species with pycnidial anamorphs (1.00 BI PP, 100 % ML BP) (Fig. 1). All isolates initially identified as *N. cinnabarina* formed a monophyletic *Nectria-Tubercularia* clade supported by high BI PP and ML BP value (1.00 BI PP, 100 % ML BP).

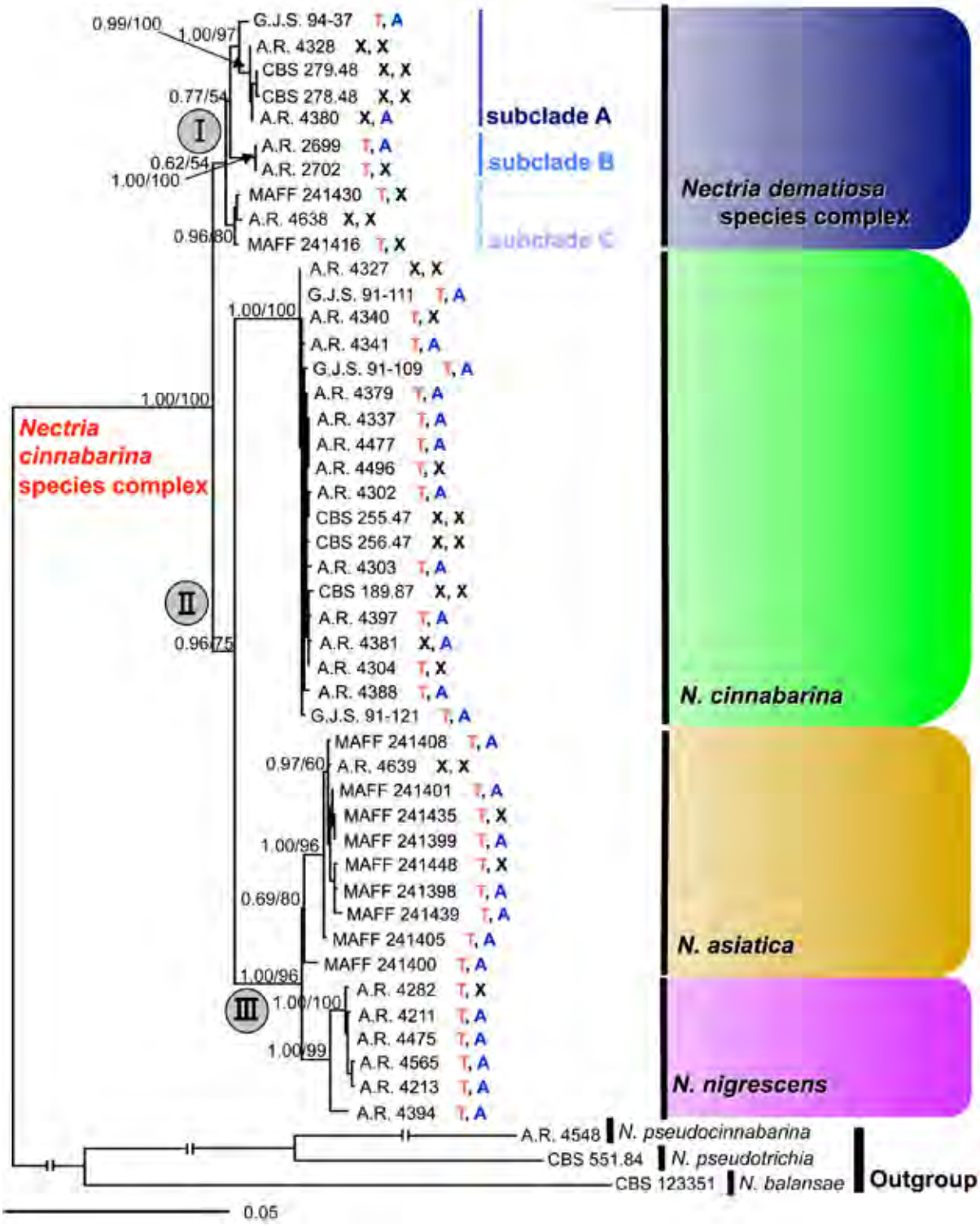

Fig. 2. Members of the *Nectria cinnabarina* species complex (NCSC). Combined *act*, *tub*, *rpb1*, ITS, LSU, *tef1* Bayesian cladogram (Ln −11408.155). BI posterior probabilities/ML bootstrap values indicated at branches. T: Teleomorph observed in the natural environment; A: Anamorph observed in the natural environment; X: no holomorph observed in the natural environment.

The combined ML and BI analyses of six loci using 45 isolates of the NCSC resolved four distinct species (Fig. 2). One major clade (clade II) included three species with high support (BI PP 0.96, ML BP 75 %). One of the species in clade II represents *N. cinnabarina s. str.* and includes the ex-epitype isolate from a hardwood tree in Europe with isolates on hardwoods in Europe and North America. *Nectria cinnabarina s. str.* is highly supported (BI PP 1.00, ML BP 100 %). A second segregate species occuring only in Asia is here described as a new species, *N. asiatica*. This species was supported by moderate values (BI PP 0.69, ML BP 80 %). A third species is recognised as *N. nigrescens*, previously considered a synonym of *N. cinnabarina*. *Nectria nigrescens* also occurs on hardwoods in Europe and North America. This species is highly supported (BI PP 1.00, ML BP 99 %). A fourth segregate species, recognised as *N. dematiosa* (clade I), a previous synonym of *N. cinnabarina*, constitutes a sister clade to clade II. Within *N. dematiosa,* three subclades are highly supported (BI PP 1.00, ML BP 97 % for subclade A; BI PP 1.00, ML BP 100 % for subclade B; and BI PP 0.96, ML BP 80 % for subclade C). However, clades I was poorly supported (BI PP 0.62, ML BP 54 % for clade I) (Fig. 2). *Nectria dematiosa* subclade A is known from Europe and North America, *N. dematiosa* subclade B is representated by two isolates from Canada, while *N. dematiosa* subclade C is known only from Asia.

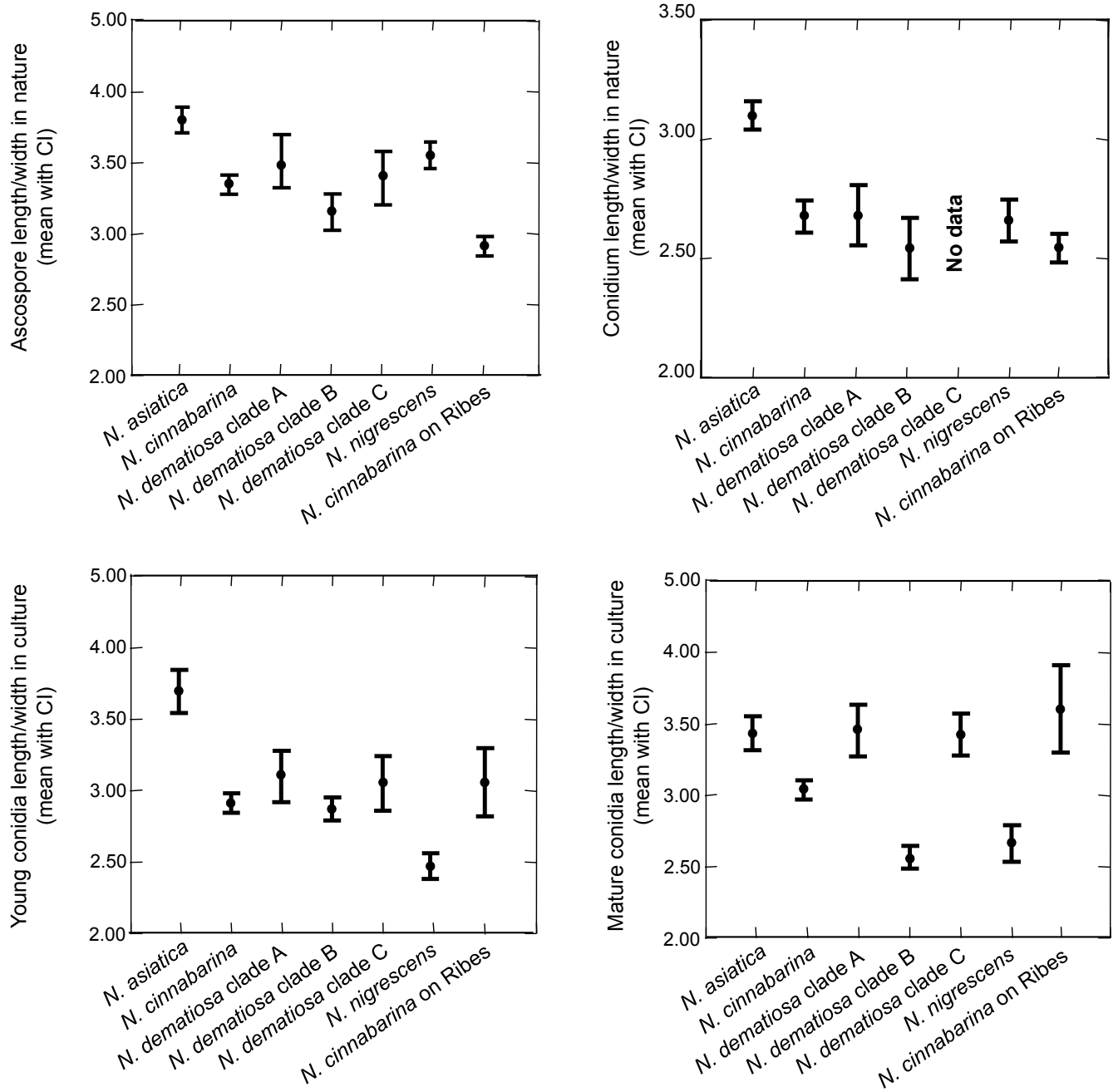

Fig. 3. Graphs of 95 % confidence intervals of length to width ratios of ascospores and conidia.

Morphological, colony growth, and temperature analyses

Morphological characters of the teleomorph and anamorph in the natural environment and cultural characteristics are useful in distinguishing species in the NCSC. Perithecial characters, such as colour, surface, and wall cell structure, are generally reliable for identifying the species complex, but not the segregate species. The perithecial wall surface of species in the NCSC is roughened, with conspicuous to small warts, 10–20 µm high, rarely smooth. In all species of the NCSC, the perithecial walls are about the same thickness and cell walls form similar *textura globulosa* or *t. angularis*; thus, perithecial wall structure is not useful in distinguishing species. Differences in ascospore septation correlate with phylogenetic species recognised in the NCSC. *Nectria asiatica* has up to 1-septate ascospores, *N. cinnabarina* and *N. dematiosa* have up to 2-septate ascospores, and *N. nigrescens* has up to 3-septate ascospores. The size ranges of ascospores in the four species overlap. However, in comparing 95 % confidence intervals of length/width ratios of ascospores on natural substrate, those of *N. asiatica* are greater than the other species while those of *N. cinnabarina* on *Ribes* are less than the other species (Fig. 3).

Anamorph characters on natural substrate, especially presence or absence and length of the stipe of the sporodochia, are useful in distinguishing species. A distinction is made here between sporodochia that are astipitate *i.e.* lack any kind of stipe and sporodochia that are stipitate having a short stipe, less than 800 µm high, or a long stipe, 700–1600 µm high. The sporodochia of *N. dematiosa* are astipitate. In clade II, which includes *N. cinnabarina*, *N. asiatica,* and *N. nigrescens,* the sporodochia are short to long stipitate. *Nectria asiatica* has short stipitate sporodochia, *N. cinnabarina* has long stipitate sporodochia, and *N. nigrescens* has short to long stipitate sporodochia. The long stipitate sporodochia of *N. cinnabarina* and *N. nigrescens* have marginal cells arranged in a palisade, while the short stipitate sporodochia of *N. asiatica* and *N. nigrescens* lack these cells.

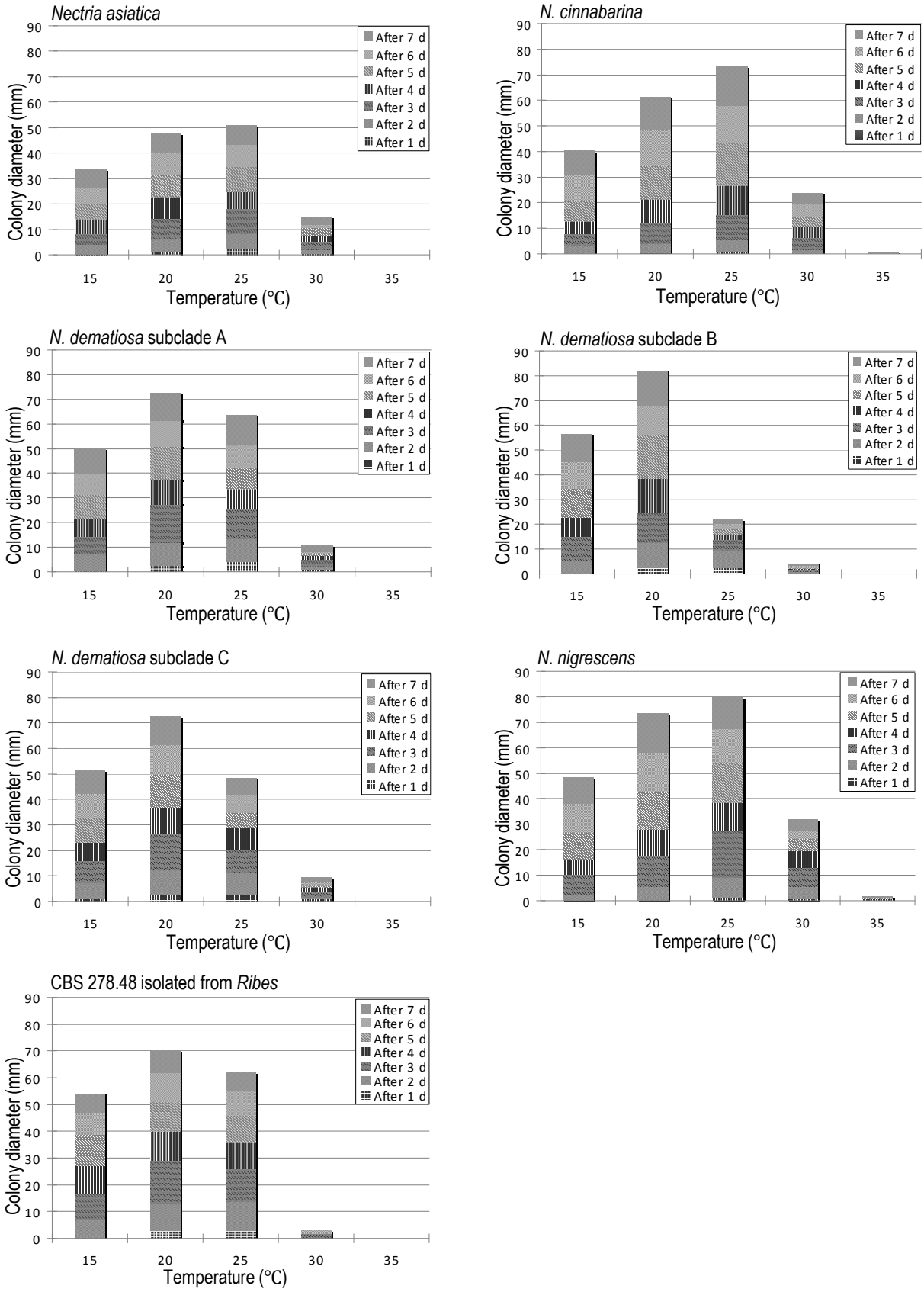

Fig. 4. Mycelial growth of NCSC at different temperatures on PDA.

Additional morphological characteristics of the anamorph were also evaluated. These characteristics include the number of conidiophore branches and conidial size in the natural environment. No differences were found between species. The sizes of conidia among the four species overlap; however, in comparing 95 % confidence intervals of length/width ratios of conidia on natural substrate, those of *N. asiatica* are larger than other members of the NCSC (Fig. 3).

The optimal temperature for growth on PDA for *N. dematiosa* is 20 °C while that for *N. asiatica, N. cinnabarina,* and *N. nigrescens* is 25 °C (Fig. 4). In macroscopic appearance these colonies look similar.

Conidia produced in culture show differences that correlate with species. The size of conidia varies considerably when grown on different media (CMD, PDA, and SNA). On SNA conidia were classified into two types, namely young and mature conidia. Mature conidia appear after 3 to 4 d and are defined by extreme swelling to twice their original size, becoming 1-septate, often including vacuoles. The 95 % confidence interval of length/width ratios of young conidia in culture of *N. asiastica* was larger than that of other species of the NCSC (Fig. 3). By observing mature conidia on SNA, we could distinguish species in the NCSC. Mature conidia of *N. cinnabarina* budded abundantly while those of *N. asiatica* and *N. nigrescens* rarely budded. Mature conidia of *N. dematiosa* did not bud at all. In evaluating the 95 % confidence intervals of length/width ratios of mature conidia in culture, *N. cinnabarina, N. dematiosa* subclade B, and *N. nigrescens* were smaller than other members of the NCSC. Each subclade in *N. dematiosa* can be distinguished by the morphology of the anamorph in culture. Mature conidia of subclade A produced almost straight germ tubes that do not penetrate the agar immediately, while mature conidia of subclades B and C produced sinuous germ tubes that penetrate the agar after germination. The 95 % confidence interval of length/width ratio of mature conidia of subclade B was statistically different from subclades A and C (Fig. 3). On PDA at 25 °C for 7 d, subclade B grew more slowly than subclades A and C (Fig. 4).

In summary, clades I includes *N. dematiosa* with subclades A, B and C. This species is characterised by ascospores that are generally 1-septate, rarely 0- or 2-septate, sessile sporodochia or anamorph lacking, mature conidia that do not bud, and an optimum growth temperature of 20 °C on PDA. Clade II includes *N. asiatica, N. cinnabarina* and *N. nigrescens,* all of which have short to long stipitate sporodochia, mature conidia that bud, although sometimes only rarely, and an optimum growth temperature of 25 °C on PDA. *Nectria cinnabarina* has 1-septate, rarely 0- or 2-septate ascospores, long stipitate sporodochia, and mature conidia that bud abundantly. *Nectria asiatica* has 1-septate, rarely 0-septate ascospores, short stipitate sporodochia, and mature conidia that seldom bud. *Nectria nigrescens* has 1-, 2-, or occasionally 3-septate ascospores, short to long stipitate sporodochia, and mature conidia that bud infrequently.

TAXONOMY

Based on our morphological and molecular analyses, the *N. cinnabarina* species complex is recognised as four distinct species, each of which is described and illustrated below. A key to these four species is provided.

Nectria asiatica Hirooka, Rossman & P. Chaverri, **sp. nov.** MycoBank MB516721. Fig. 5.
Anamorph: *Tubercularia vulgaris*-like.

Etymology: Asia + *-tica* - indicates the area from which this species is known.

Perithecia in cortice emortuo, solitaria vel gregaria, superficialia, subglobosa, 285–400 µm alta, 250–380 µm diam, rubella, KOH+, LA+. Asci unitunicati, clavate, apice simplici, 74–117 × 8.5–14.0 µm, octospori. Ascosporae ellipsoideae vel fusiformes, 10.5–19.0 × 3.0–6.0 µm, 0–1-septatae, hyalinae, laeves. Anamorphosis sporodochia discoida vel cylindrico-capitata, brevi-stipites, 250–800 mm alti, 300–2000 mm lati, atro-rubella vel raro niger, KOH+. Conidia oblonge ellipsoidea ad Cylindrica, 4.5–9.5 × 1.0–3.0 µm, hyalinae, leaves.

Holotype: **Japan**, Kanagawa Prefecture, Ashigarakami-gun, on dead wood, Oct. 2004, *Y. Hirooka,* holotype BPI 879972; ex-holotype culture MAFF 241439.

Teleomorph on natural substrata: *Mycelium* not visible around perithecia or on host. *Stromata* up to 1.0 mm high and 3 mm diam, erumpent through epidermis, whitish yellow to bay, sometimes darker red, KOH+ dark red, LA + yellow, pseudoparenchymatous; cells forming *textura angularis* to *t. prismatica* with cells oriented more or less vertically; cells 3–15 µm diam with walls 1–1.5 µm thick, intergrading with ascomatal wall. *Perithecia* superficial on well-developed stroma, solitary or caespitose, up to 20 on stroma, rarely clustered around base of stipitate sporodochia, subglobose to globose, 285–400 µm high × 250–380 µm diam (*n* = 39), red to reddish brown, sometimes cupulate upon drying, non-papillate, apical region darker, KOH+ dark red, LA+ yellow, surface with rough or concolourous warts, but sometimes smooth. *Perithecial surface cells* forming *textura globulosa* to *t. angularis*, with pigmented walls *ca.* 1.5 mm thick. *Perithecial wall ca.* 40–70 mm thick, of two distinct regions: outer region *ca.* 30–50 mm thick, intergrading with stroma, cells forming *textura globulosa* to *t. angularis*, walls pigmented, about 1.5 mm thick; inner region about 10–18 mm thick, of elongated, thin-walled, hyaline cells, forming *textura prismatica*. *Asci* unitunicate, (74–)89–101(–117) × (8.5–)10.0–12.5(–14.0) µm (*n* = 89), cylindrical to narrowly clavate, with an inconspicuous ring at apex, 8-spored, ascospores biseriate above, uniseriate below. *Ascospores* ellipsoidal to fusiform, straight, rarely slightly curved, hyaline, (0–)1-septate, (10.5–)14.5–17.5(–19.0) × (3.0–)3.5–5.0(–6.0) µm (n = 251), smooth-walled.

Anamorph on natural substrata: *Stromata* erumpent through epidermis, orange to red. *Sporodochial conidiomata* with stipe, superficial on well-developed stroma, smooth or cerebriform, scattered, solitary, or 2–4 gregarious, stipitate,, pustular, discoid or cylindrical-capitate, up to 250–800 mm high including stipe, 300–2000 mm diam, chestnut to black, sometimes whitish yellow to orange; *stipe* chestnut to black, sometimes dark green, up to 440–610 mm wide; *stipe cells* almost *textura angularis*, continuous with stroma, usually with wider cells in centre. *Hymenium* arising directly from *textura prismatica,* elongating from *textura angularis*, up to 110 µm long, of cells 2.0–7.0 µm wide, without curved margin. *Conidiophores* monoverticillate or rarely bi-verticillate, then developing acropleurogenously for 3–6 levels, strongly coiled, hyaline, rarely slightly pale green. *Phialides* intercalary, occurring below each septum, rarely terminal; *intercalary phialides* monophialidic, up to 3.5–7.5 µm long, 1.5–2.5 µm wide; *terminal cells* monophialidic, sometimes sterile, without collarettes. *Conidia* hyaline, narrowly long ellipsoidal to cylindrical, straight or slightly curved, non-septate, (4.5–)5.5–7.5(–9.5) × (1.0–)2.0–2.5(–3.0) µm (n = 258), smooth-walled.

Anamorph in culture: Optimum temperature for growth on PDA 25 °C, maximum temperature 30 °C; after 7 d at 25 °C colonies 40–75 mm diam (average 51 mm). *Colony surface* on PDA radiating sometimes wavy, slightly cottony with aerial mycelium, white to whitish saffron; *aerial mycelium* developing in a few isolates (CBS 125151, MAFF 241448); after 3 wk abundant white to whitish yellow sporodochial conidial masses produced; *reverse* white to slightly whitish yellow. *Odour* on PDA slightly fruity. Sporulation on SNA from *lateral phialidic pegs* on submerged or aerial hyphae, 3.0–5.0 µm long, 1.5–2.5 µm wide at base. *Aerial conidiophores* developing abundantly on aerial hyphae, unbranched, sometimes verticillate,

Fig. 5.A–R. *Nectria asiatica*. A. Perithecia and short stipitate sporodochia in the natural environment. B. Perithecia on nature. C. Median section of perithecium. D. Median section of perithecial wall. E. Ascus. F. 0–1 septates ascospores. G. Short stipitate sporodochium in the natural environment. H. Median section of short stipitate sporodochium. I. Edge of short stipitate sprodochium. J. Acropleurogenous conidiophores in the natural environment. K. Conidia in the natural environment. L. Aerial conidiophores and conidial mass on SNA. M. Lateral phialidic pegs and conidia on SNA. N. Short aerial conidiophores and conidia on SNA. O. Densely blanched aerial conidiophores and conidia on SNA. P. Mature conidia and young conidia on SNA. Q. Budding mature conidia on SNA. R. Budding and germinating mature conidia (arrow) that were streaked onto SNA. Scale bars: A, L = 1 mm; B, C, G, H = 300 µm; D, I = 100 µm; E, J, K, M, R = 30 µm; F, N, O, P, Q = 15 µm.

1–3 branched, becoming loosely to moderately densely branched, 6.0–25.5 µm long, 2.0–5.0 µm wide at base. *Conidiogenous cells* monophialidic, cylindrical, slightly tapering toward tip or narrowly flask-shaped with widest point in middle 7.5–22.5 µm long, 2.0–3.0 µm wide at base. *Young conidia* developing from monophialides on submerged or aerial hyphae, produced abundantly on slimy heads, non-septate, ellipsoidal, oblong to cylindrical, hyaline, smooth, straight or slightly curved, rounded at both ends, (4.0–) 6.0–12.0(–23.0) × (1.5–)2.0–3.0(–5.0) µm (*n* = 210). *Mature conidia* swollen, mostly 0-, rarely 1-septate, ellipsoidal, oblong or allantoid,

rarely ellipsoidal with slightly constricted centre, smooth, straight or slightly curved, rounded at both ends, germinating or budding mature conidia (7.0–)11.5–17.5(–25.5) × (3.0–)3.5–4.5(–6.0) µm (*n* = 168). *Chlamydospores* and *perithecia* not produced in culture.

Distribution: Asia (China, Japan).

Habitat: On dead woody substrata, known in this study from *Acer* sp., *Betula lutea*, *Prunus* sp., *Sorbus commixta*, and *Zelkova serrata*.

Specimens and isolates examined: **China**, on dead wood, W.Y. Zhuang, culture CBS 126568 = A.R. 4639. **Japan**, Kanagawa Prefecture, Ashigarakami-gun, on bark of dead wood, Oct. 2004, Y. Hirooka, BPI 879973, culture MAFF 241435; Kanagawa Prefecture, Ashigarakami-gun, on dead twig, Apr. 2005, Y. Hirooka, BPI 879974, culture MAFF 241448; Kumamoto Prefecture, Kikuchi city, Kikuchi valley on dead wood of *Zelkova serrata*, Dec. 2000, Y. Hirooka, BPI 879975, culture MAFF 241398; Kumamoto Prefecture, Kikuchi city, Kikuchi valley, on twig of *Prunus* sp., Dec. 2000, Y. Hirooka, BPI 879976, culture MAFF 241399; Hokkaido, kamigawa-gun, mie-cho, on dead stem of *Sorbus commixta*, Sep. 1999, Y. Ono, BPI 879977, culture MAFF 241400; Nagano Prefecture, Ina city, on dead wood, Aug. 7, 1999, Y. Ono, BPI 879978, culture MAFF 241401; Saitama Prefecture, Kawaguchi city, Angyo, on dead twig of *Prunus* sp., Sep. 2002, Y. Hirooka, BPI 879979, culture MAFF 241405; Tokyo, Setagaya-ku, Tokyo University of Agriculture, on dead wood, Oct. 2002, Y. Hirooka, BPI 879980, culture MAFF 241408.

Notes: *Nectria asiatica* is known only from China and Japan, a range it shares with *N. dematiosa* subclade C. To differentiate these species, it is necessary to consider morphological characters of both the teleomorph and anamorph. *Nectria asiatica* has up to 1-septate ascospores (Fig. 5F) and budding mature conidia on SNA (Fig. 5Q, R) while *N. dematiosa* subclade C has up to 2-septate ascospores (Fig. 7E) and mature conidia that do not bud on SNA (Fig. 7R–W). In addition, *N. asiatica* has an optimal temperature for growth of 25 °C on PDA while *N. dematiosa* including subclade C has an optimal temperature for growth of 20 °C on PDA (Fig. 4). Although *N. cinnabarina* and *N. nigrescens* also produce budding mature conidia, *N. asiatica* forms up to 1-septate ascospores and stipitate sporodochia shorter than the former two species.

Hara (1918) described *Nectria cinnabarina* f. *stromaticola* on *Dothichiza* sp. (*Dothioraceae, Dothideales*) in Japan. He did not mention a type specimen and one could not be located. Based on his original description, this species had superficial, red, warted perithecia, asci with eight ascospores, and 1-septate ascospores. No anamorph was mentioned; however, it seems possible that the black stroma of the *Dothichiza* sp. listed as the substrate was actually the dark sporodochia of a *Tubercularia* anamorph. Most specimens of *N. asiatica* collected in Japan have chestnut to black sporodochial conidiomata. Because no type specimen could be located, we do not consider *Nectria cinnabarina* f. *stromaticola* to be a synonym of *N. asiatica*.

One isolate (MAFF 241400) is phylogenetically distinct from the other isolates of *N. asiatica*; however, the BI posterior probabilities and ML bootstrap values are not high enough to clearly segregate this strain from *N. asiatica* (0.69 BI PP, 80 % ML BP) (Fig. 2). In addition, the specimen of this isolate forms up to 1-septate ascospores, short stipitate sporodochia, and ellipsoidal, budding mature conidia with slightly constricted centres, morphological characteristics typical of *N. asiatica*. Based on these morphological and molecular phylogenetic analyses, we include MAFF 241400 in *N. asiatica*.

Nectria cinnabarina (Tode : Fr.) Fr., Summa Veg. Scand. 2: 388. 1849. Fig. 6.

Basionym: *Sphaeria cinnabarina* Tode : Fr., Tode, Fungi Mecklenb. sel. 2: 9, 1791 : Fries, Syst. Mycol. 2: 412. 1823.

≡ *Cucurbitaria cinnabarina* (Tode : Fr.) Grev., Scot. Crypt. Fl. 3: 135. 1825.

= *Sphaeria tremelloides* Weigel, Obs. Bot. p. 46, 1772.

= *Sphaeria decolorans* Pers. : Fr., Persoon, Neues Magazin für Botanik, Rőmer 1: 83. 1794 : Fries, Syst. Mycol. 2: 412, 1823.

= *Sphaeria celastri* Fr., Elenchus Fungorum 2: 81. 1827.

= *Nectria russellii* Berk. & M.A. Curtis in Berkeley, Grevillea 4: 45. 1875.

= *Nectria offuscata* Berk. & M.A. Curtis in Berkeley, Grevillea 4: 45. 1875.

Anamorph: *Tubercularia vulgaris* Tode : Fr., Tode, Fungi Mecklenb. sel. 1: 18, 1790 : Fries, Syst. Mycol. 3: 464. 1832.

Teleomorph from natural substrata: *Mycelium* rarely visible around perithecia and on host. *Stromata* up to 2.0 mm high and 5 mm diam, erumpent through epidermis, whitish yellow to bay, KOH+ dark red, LA+ yellow, pseudoparenchymatous, cells forming *textura angularis* to *t. prismatica* with cells oriented more or less vertically; cells 5–20 µm diam, with 1–2 µm thick walls, intergrading with ascomatal wall. *Perithecia* superficial on well-developed stroma, solitary or caespitose, up to 25 on stroma, sometimes clustered around base of stipitate sporodochia, subglobose to globose, 275–400 µm high × 250–370 µm diam (*n* = 55), red to reddish brown, sometimes cupulate upon drying, non-papillate, apical region darker, KOH+ dark red, LA+ yellow, surface roughened with concolourous warts, but sometimes smooth. *Perithecial surface cells* forming *textura globulosa* or *t. angularis*, with walls pigmented *ca.* 1.5 mm thick. *Perithecial wall ca.* 40–60 mm thick, of two distinct regions: outer region *ca.* 35–55 mm thick, intergrading with stroma, cells forming *textura globulosa* or *t. angularis*, walls pigmented, *ca.* 1.5 mm thick; inner region *ca.* 15–20 mm thick, of elongated, thin-walled, hyaline cells, forming *textura prismatica*. *Asci* unitunicate, (81–)85–96(–105) × (7.5–)8.0–9.5(–11.0) µm (*n* = 129), cylindrical to narrowly clavate, with inconspicuous ring at apex, 8-spored, ascospores biseriate above, uniseriate below. *Ascospores* ellipsoidal to fusiform, straight, sometimes slightly curved, hyaline, (0–)1(–2)- septate, (11.5–)14.0–17.5(–21.5) × (3.0–)4.0–5.5(–7.0) µm (n = 558), smooth-walled.

Anamorph on natural substrata: *Stromata* erumpent through epidermis, pale yellow to orange, rarely reddish brown. *Sporodochial conidiomata* with stipe, superficial on well-developed stroma, smooth, cerebriform, or tubercularoid, scattered, solitary or 2–4 gregarious, stipitate, pustulate, discoid, or cylindrical-capitate, up to 700–1600 mm high including stipe, 300–2500 mm wide, white, whitish yellow to orange, sometimes darker red. *Stipe* white to whitish red, rarely darker red, up to 250–600 mm wide, solitary or 2–6 gregarious; *stipe cells* almost *textura angularis*, continuous with stroma, usually with wider cells in centre. *Hymenium* arising directly from *textura prismatica,* elongating from *textura angularis*, up to 150 µm long, of cells 2.5–5 µm wide; in stipitate forms marginal cells arranged in a palisade as described above for surface of stroma; curved margin, up to 100 µm long, of parallel hyphae 1.5–2.5 µm wide. *Conidiophores* monoverticillate or rarely bi-verticillate, then developing acropleurogenously for 3–10 levels, straight, curved. *Phialides* intercalary, occurring below each septum, or rarely terminal; *intercalary phialides* monophialidic, up to 3–9 µm long, 1.5–2 µm wide; *terminal cells* monophialidic, sometimes sterile, no collarettes. *Conidia* hyaline, narrowly long ellipsoidal to cylindrical, straight or slightly curved, non-septate, (4.0–)5.2–7.0(–8.5) × (1.3–)1.9–2.7(–3.4) µm (n = 355), smooth-walled.

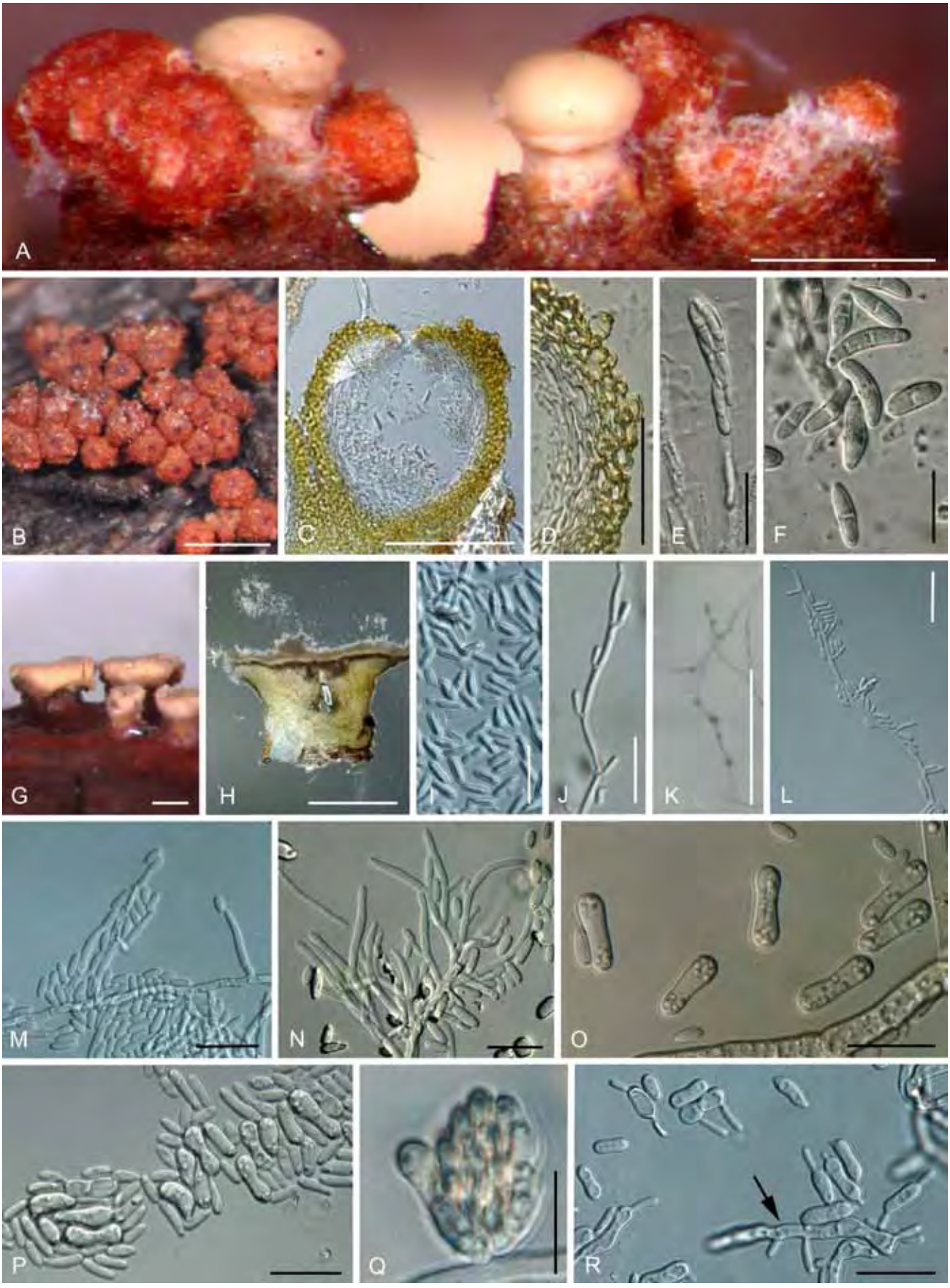

Fig. 6.A–R. *Nectria cinnabarina*. A. Perithecia and long stipitate sporodochia in the natural environment. B. Peritheica in the natural environment. C. Median section of perithecium. D. Median section of perithecial wall. E. Ascus. F. 0–2 septates ascospores. G. Long stipitate sporodochia in the natural environment. H. Median section of long stipitate sporodochia. I. Conidia in the natural environment. J. Acropleurogenous conidiophore in the natural environment. K. Aerial conidiophores and conidial mass on SNA. L. Lateral phialidic pegs on SNA. M. Aerial conidiophores and young conidia. N. Densely blanched aerial conidiophores and young conidia. O. Mature conidia on SNA. P. Budding mature conidia and secondly conidia on SNA. Q. Slimy head of young and mature conidia on lateral phialidic peg on SNA. R. Budding and germinating mature conidia (arrow) that were streaked onto SNA. Scale bars: A = 500 µm; C = 300 µm; D, = 100 µm; E, J, L, M, N, P, R = 30 µm; F, I, O, Q = 15 µm; B, G, H, K = 1 mm.

Anamorph in culture: Optimum temperature for growth on PDA 25 °C, maximum temperature 30 °C. After 7 d at 25 °C, colonies 60–85 mm (average 73 mm) diam. *Colony surface* radial, sometimes wavy, slightly cottony with aerial mycelium, white to whitish saffron; *aerial mycelium* developed, in some isolates (A.R. 4338, CBS 127668, CBS 125154, CBS 125157, CBS 125165) abundant, white to whitish yellow sporodochial conidial masses produced after 2 wk; *reverse* white to slightly whitish yellow. *Odour* on PDA slightly fruity. Sporulation on SNA from lateral phialidic pegs common, 1.5–4.5 µm long, 1.0–1.5 µm wide near aperture. *Aerial conidiophores* abundantly formed, unbranched, sometimes verticillate, 1–3 branched, becoming loosely to moderately densely branched, 5.5–38.0 µm long, 2.0–3.5 µm wide at base. *Conidiogenous cells* monophialidic, cylindrical and slightly tapering toward tip or narrowly flask-shaped with widest point in middle, 5–22 µm long, 2.0–3.2 µm wide at base. *Young conidia* formed from monophialides on submerged or aerial hyphae, formed abundantly on slimy heads or sporodochia, ellipsoidal, oblong to cylindrical, hyaline, smooth, straight or slightly curved with round at both end, non-septate, (3.0–) 5.5–9.0(–15.0) × (1.5–)2.0–3.0(–3.5) µm (*n* = 764), smooth-walled. *Mature conidia* swollen, mostly 0-, rarely 1-septate, allantoid, oblong, ellipsoidal, or ellipsoidal with strongly constricted centre, hyaline, smooth, straight or slightly curved, rounded at both ends, germinating and budding on media, (5.5–)10.5–17.0(–27.0) × (3.0–)4.0–5.0(–7.0) µm (*n* = 668). *Chlamydospores* rarely present, globose, subglobose, broadly ellipsoidal, 0(–1)-septate, solitary or chains, 8.5–12 µm diam. *Perithecia* not produced in culture.

Distribution: Europe (Austria, Denmark, France, Germany, Ireland, Netherlands, Poland, Sweden, Ukraine, UK) and North America (Canada, USA).

Habitat: On dead woody substrata including *Acer campestre*, *A. platanoides*, *A. pseudoplatanus*, *A. saccharum*, *Acer* sp., *Aesculus* sp., *Celastris scandens, Fagus* sp., *Gleditsia* sp., *Populus tremula*, *Sorbus aria*, *Spiraea trilobata*, *Tilia* sp., and *Ulmus* × *hollandica*.

Lectotype of Sphaeria cinnabarina *designated here*: figs 68a–e in the copy of Tode HJ (1791). Fungi Mecklenburgenses selecti. **2**: 9 associated with BPI.

Epitype of Sphaeria cinnabarina *designated here*. **France**: Villiers en Bois, on dead twigs of *Aesculus* sp., Feb. 13, 2008, C. Lechat, epitype BPI 879981 = C.L.L. 7152, ex-epitype culture CBS 125165 = A.R. 4477.

Additional type specimens examined: The type specimen of *Sphaeria tremelloides* exists at K but these specimens are no longer sent for examination. This name is retained as a synonym of *N. cinnabarina*. A lectotype for *Sphaeria decolorans* is designated here: Country unknown: on branch of *Acer platanoides*, ex Herb. Persoon, BPI 799523). Additional Persoon material examined: Country unknown: on bark of *Ribes rubrum*, Mougeot, ex Herb. Persoon, BPI 799524). The lectotype and additional specimens of *Sphaeria decolorans* were examined, but these lacked the anamorphic structures needed to identify species within the NCSC. This name is retained as a synonym of *N. cinnabarina*. Type specimen of *Sphaeria celastri*: **USA**, Philadelphia, on dead branch of *Celastrus scandens* L., coll. possibly L.D. Schweinitz, holotype Schweinitz Syn. PH 1421. Type of *Nectria russellii*: **USA** Massachusetts, Jan. 1856, J.L. Russell, holotype FH 284394. Lectotype of *Nectria offuscata* designated here: **USA**, South Carolina, on *Hibiscus syriacus* L., lectotype BPI, Michener Collection 32, Sheet 12.

Additional specimens and isolates examined: **Austria**, Vienna, 19th district, base of the mountain Kahlenberg, MTB 7763/2, on *Acer campestre* L., 25 May 2006, W. Jaklitsch, BPI 878316, culture CBS 125151 = A.R. 4303; Vienna, on *Acer pseudoplatanus* L., 25 May 2006, coll W. Jaklitsch, BPI 878317, culture CBS 125150 = A.R. 4302. **Canada**, Ontario, Ottawa, on *Acer* sp., 26 Sep. 2006, K.A. Seifert 961, culture CBS 125154 = A.R. 4327; Quebec, Gatineau Park, Lac Philippe sector, *ca.* 45°35'24"N 75°59'25"W, on *Acer saccharum* Marsh., 15 Sep. 2006, K.A. Seifert, W. Gams, T. Gräfenhan, BPI 878311, culture CBS 125157 = A.R. 4341; Quebec, Quebec City. Lake St. Charles, on *Spiraea trilobata* L., 18 Aug. 2006, G. Laflamme, BPI 878335, culture CBS 125156 = A.R. 4340. **Denmark**, on bark of *Tilia* sp., 21 May 2006, T. Laessoe, BPI 879982, culture CBS 125152 = A.R. 4304; Sjaelland, Gadevang, on *Acer pseudoplatanus* L., 25 Aug. 2006, W. Jaklitsch, BPI 878312, culture CBS 127668 = A.R. 4337. **France**, Chize, on *Acer* sp., Jan. 18, 2007, C. Lechat 7027, BPI 879983, culture CBS 125163 = A.R. 4397. **Germany**, on *Sorbus aria* (L.) Crantz, Oct. 1986, H. Reinartz, anamorph only, culture CBS 189.87. **Ireland**, Dublin, Phoenix Park 53°20'59.91"N 6°17'56.87"W, on twigs, 21 Sep. 2006, K. Seifert, BPI 878313, culture CBS 125158 = A.R. 4379. **Netherlands**, on stem of *Ulmus* sp., (culture CBS 255.47, ATCC 11432; on twig of *Ulmus* sp., culture CBS 256.47. **Poland**, Sudetes, Zlote Mts., Zloty Stok, on twigs of *Acer pseudoplatanus* L., 6 Jun. 2006, A. Chlebicki, BPI 878322, culture A.R. 4388. **Sweden**, Fries, Scleromyceti Sueciae no. 184 as *Sphaeria cinnabarina*, BPI 799329, BPI 799330, BPI 799331, UPS. **Ukraine**, Kharkov-city, University botanic garden, on fallen twigs of *Populus tremula* L., 3 Mar. 2007, A. Akulov, BPI 878878, culture A.R. 4496. **U.K**, Wales, Hafod, logged area, *ca.* 52°22'N 3°51'W, on root, 1 Oct. 2006, K. Seifert, BPI 878310, culture CBS 125160 = A.R. 4381. **USA**, Virginia, Giles Co., Cascades Recreation Site, 4 Mi N of Pembroke, Little Stony Creek, 37d2d'n, 80d35'w. alt. 840 meters, on *Acer* sp., 18 Sep. 1991, G.J. Samuels,C.T. Rogerson, S. Huhndorf, S. Rehner, BPI 1112890, culture CBS 125115 = G.J.S. 91-121; Virginia, Giles Co., Mountain Lake, alt. 1160 meters, 37d22'n,80d31'w, near hotel pond drain, on *Fagus* sp., 17 Sep. 1991, G.J. Samuels, BPI 1112878, culture G.J.S. 91-109; Virginia, Giles Co., Mountain Lake, alt. 1160 meters, 37d22'n, 80d31'w, near hotel, Pond Drain, on *Acer* sp., 17 Sep. 1991, G.J. Samuels, BPI 1112880, culture CBS 713.97 = G.J.S. 91-111.

Notes: *Nectria cinnabarina* is the type species of the genus *Nectria*. Tode (1791) described and illustrated the superficial, red, warted perithecia and 1-septate ascospores, but did not mention any detailed morphology of perithecial wall structure or stroma. Because the type specimen was lost, the name *Sphaeria cinnabarina* is lectotypified by the original illustration in the copy of Tode (1791) associated with BPI. A stipitate sporodochium with perithecia at the base is clearly illustrated by Tode (1791), thus assuring the identity of *N. cinnabarina*. Based on Article 7.8 of the ICBN (McNeill *et al.* 2006), an illustration from the protologue may serve as a lectotype, thus this lectotypification supersedes the neotypification by Rossman *et al.* (1999). We here epitypify *N. cinnabarina* with BPI 879981, a specimen collected in France with abundant mature perithecial and anamorph structures as well as a living culture.

Nectria cinnabarina can be identified by morphological characteristics of the teleomorph and anamorph in the natural environment and in culture. On natural substrate, *N. cinnabarina* has up to 2-septate ascospores and long stipitate sporodochia (Fig. 6A, F–H). Among species in the NCSC, *N. cinnabarina* is similar to *N. nigrescens* in having long stipitate sporodochia; however, *N. nigrescens* is distinct in having up to 3-septate ascospores. Unlike *N. asiatica, N. dematiosa*, and *N. nigrescens*, *N. cinnabarina* is distinguished in culture by abundant budding mature conidia that are ellipsoidal and strongly constricted in the centre (Fig. 6O, P).

Nectria dematiosa (Schwein.) Berk., Grevillea, 4: 16. 1875. Fig. 7.

Basionym: *Sphaeria dematiosa* Schwein., Trans. Amer. Philos. Soc. II, 4: 205. 1832.

≡ *Cucurbitaria dematiosa* (Schwein.) Kuntze, Revisio Generum Plantarum 3: 461. 1898.

= *Nectria sambuci* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 1890: 246. 1891.

= *Nectria cinnabarina* subsp. *amygdalina* P. Karst., Rev. Mycol. 37: 205. 1889.

≡ *Nectria amygdalina* (P. Karst.) Mussat in Saccardo, Syll. Fung. 15: 225. 1901.

Anamorph: *Tubercularia vulgaris*-like.

Teleomorph on natural substrata: *Mycelium* not visible around perithecia and on host. *Stromata* up to 0.3 mm high and 2 mm

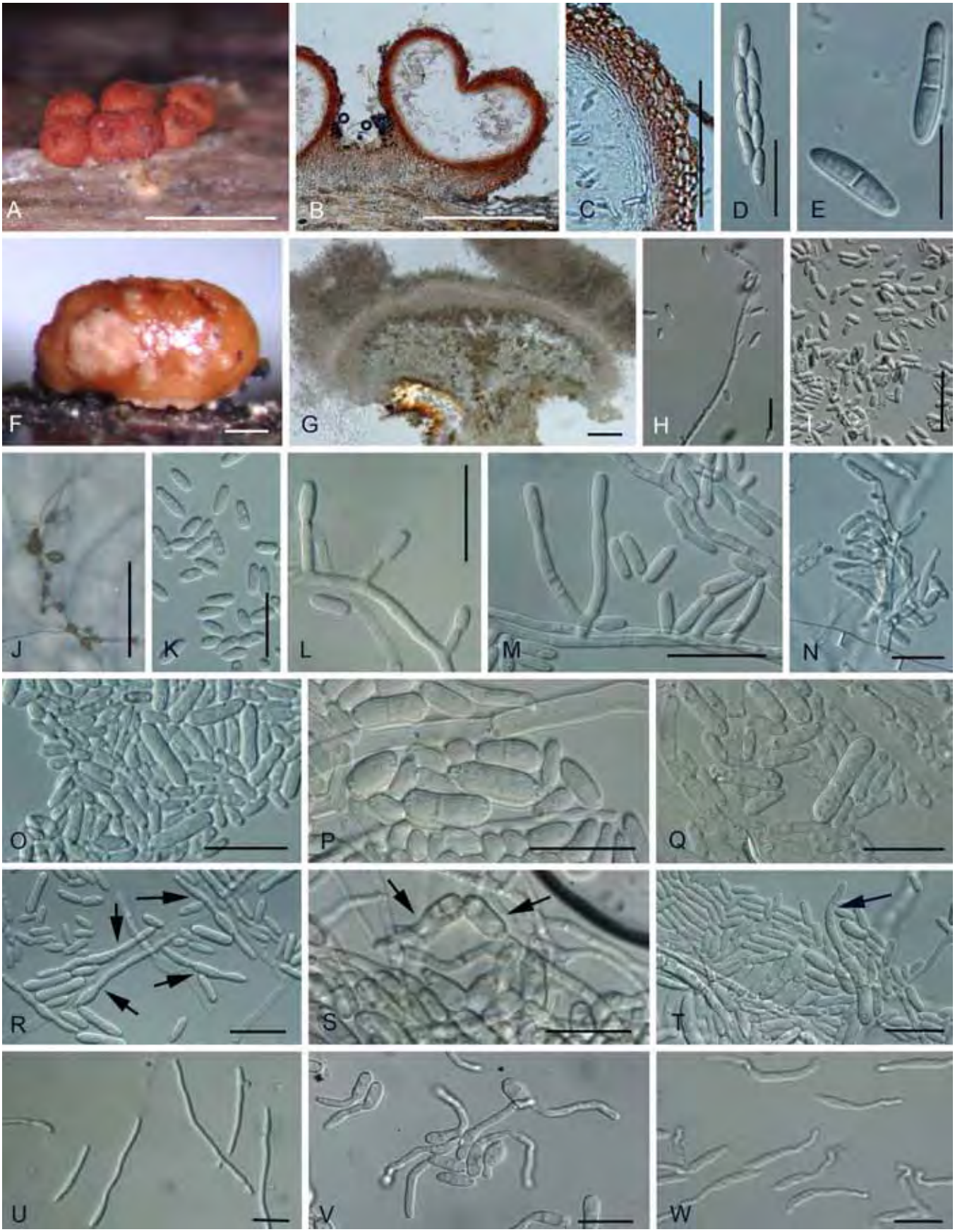

Fig. 7.A–W. *Nectria dematiosa* species complex. A. Perithecia in the natural environment. B. Median section of perithecium. C. Median section of perithecial wall. D. Ascus. E. 1–2 septates ascospores. F. Astipitate sporodochium in the natural environment. G. Median section of stipitate sporodochium. H. Acropleurogenous conidiophore in the natural environment. I. Conidia in the natural environment. J. Aerial conidiophores and conidial mass on SNA. K. Young conidia on SNA. L. Lateral phialidic pegs and young conidia on SNA. M. Short aerial conidiophores and conidia on SNA. N. Densely blanched aerial conidiophores on SNA. O. Mature conidia and young conidia of *N. dematiosa* subclade A. P. Mature conidia and young conidia of *N. dematiosa* subclade B. Q. Mature conidia and young conidia of *N. dematiosa* subclade C. R. Germinating mature conidia (arrows) of *N. dematiosa* subclade A on SNA. S. Germinating mature conidia (arrows) of *N. dematiosa* subclade B on SNA. T. Germinating mature conidia (arrow) of *N. dematiosa* subclade C on SNA. U. Germinating mature conidia of *N. dematiosa* subclade A that were streaked onto SNA. V. Germinating mature conidia of *N. dematiosa* subclade B that were streaked onto SNA. W. Germinating mature conidia of *N. dematiosa* subclade C that were streaked onto SNA. Scale bars: A, J = 1 mm; B = 300 µm; C, F, G = 100 µm; D, H, I, R = 30 µm; E, K, L–W = 15 µm.

diam, erumpent through epidermis, orange to bay, sometimes darker red, KOH+ dark red, LA+ yellow, pseudoparenchymatous, cells forming *textura angularis* to *t. prismatica* with cells oriented more or less vertically; cells 3–10 µm diam, with 1–1.5 µm thick walls, intergrading with the ascomatal wall. *Perithecia* superficial on well-developed, erumpent stroma, solitary or caespitose, up to 20 on a stroma, rarely clustered around sessile sporodochia, subglobose to globose, 260–380 µm high × 220–380 µm diam (*n* = 40), red to reddish brown, sometimes cupulate upon drying, non-papillate, apical region darker, KOH+ dark red, LA+ yellow, surface with rough or concolourous warts, but sometimes smooth. *Perithecial surface cells* forming *textura globulosa* or *t. angularis*, with walls pigmented, *ca.* 1.5 mm thick. *Perithecial wall ca.* 35–60 mm thick, of two distinct regions: outer region *ca.* 25–40 mm thick, intergrading with stroma, cells forming *textura globulosa* or *t. angularis*, walls pigmented, *ca.* 1.5 mm thick; inner region *ca.* 10–20 mm thick, of elongated, thin-walled, hyaline cells, forming *textura prismatica*. *Asci* unitunicate, (64–)77–91(–108) × (6.3–)9.4–11.0(–12.0) µm (*n* = 68), cylindrical to narrowly clavate, with an inconspicuous ring at apex, 8-spored, ascospores biseriate above, uniseriate below. *Ascospores* ellipsoidal to fusiform, sometimes long fusiform, straight or slightly curved, hyaline, smooth-walled, (0–)1(–2)-septate, (12.6–)15.2–17.2(–22.2) × (3.2–)4.3–5.7(–6.4) µm (*n* = 150); subclade A: (12.6–)13.9–16.9(–18.5) × (3.4–)3.9–4.9(–5.3) µm (*n* = 30); subclade B: (13.6–)14.7–17.9(–20.5) × (3.8–)4.7–5.7(–6.4) µm (*n* = 60); subclade C: (12.6–)14.3–18.9(–22.2) × (3.2–)4.3–5.7(–6.2) µm (*n* = 60).

Anamorph on natural substrata: *Stromata* erumpent through epidermis, orange to red. *Sporodochial conidiomata* without stipe, superficial on well-developed stroma, smooth, cerebriform or tubercularoid, scattered, solitary, rarely caespitose, astipitate, sessile, pustular, discoid or cylindrical-capitate, up to 200–700 mm high, 250–1000 mm wide, white, whitish yellow to orange, sometimes brown. *Hymenium* arising directly from *textura prismatica* elongating from *textura angularis*, up to 90 µm long, of cells 2.0–7.5 µm wide, not curved at margin. *Conidiophores* monoverticillate or sometimes bi-verticillate, then developing acropleurogenously for 3–6 levels, straight, curved hyaline. *Phialides* intercalary occurring below each septum, or rarely terminal; intercalary phialides monophialidic, 2.5–8.5 µm long, 1.3–2.4 µm wide at base; terminal cells monophialidic, sometimes sterile, no collarettes, 10.5–15 µm long, 2.3–2.8 µm wide at base. *Conidia* hyaline, narrowly long ellipsoidal to cylindrical, straight or slightly curved, non-septate, (4.5–)5.7–7.1(–8.8) × (1.7–)2.2–2.8(–3.1) µm (*n* = 60). Subclade A: (4.5–)5.5–7.1(–8.8) × (2.0–)2.2–2.6(–2.9) µm (*n* = 30), subclade B: (5.2–)5.8–7.0(–7.8) × (1.7–)2.3–2.9(–3.1) µm (*n* = 30), subclade C: none present.

Anamorph in culture: Optimum temperature for growth on PDA 20 °C, colonies 65–85 mm (average 70 mm) diam at 20 °C after 7 d, maximum temperature 30 °C. *Colony surface* on PDA, radial, sometimes wavy, slightly cottony with aerial mycelium, white to whitish saffron; aerial mycelium developing in a few isolates (CBS 125127, CBS 126570), white to whitish yellow sporodochial conidial masses produced after 2 wk; *reverse* white to slightly whitish yellow. *Odour* slightly fruity. Sporulation on SNA from lateral phialidic pegs on submerged or aerial hyphae common, 2.5–4.5 µm long, 1.5–3.0 µm wide at base. *Aerial conidiophores* occasionally developing on aerial hyphae, unbranched, sometimes verticillate, 1–2-branched, becoming loosely to moderately densely branched, 6.0–34 µm long, 2.1–4.5 µm wide at base. *Conidiogenous cells* monophialidic, cylindrical, slightly tapering toward tip or narrowly flask-shaped with widest point in middle, 8–26 µm long, 2.5–3.5 µm wide at base. *Young conidia* formed by monophialides on submerged or aerial hyphae, formed abundantly on slimy heads, non-septate, ellipsoidal, oblong to cylindrical, hyaline, smooth, straight or slightly curved with round at both ends, (4.1–)6.0–10.6(–17.3) × (1.6–)2.4–3.4(–5.1) µm (*n* = 496); subclade A: (4.6–) 5.9–10.1(–14.0) × (1.6–)2.3–3.1(–4.0) µm (*n* = 200); subclade B: (4.1–)6.0–10.6(–16.8) × (1.6–)2.4–3.6(–5.1) µm (*n* = 213); subclade C: (5.0–)6.5–11.5(–17.3) × (2.2–)2.6–3.4(–4.0) µm (*n* = 83). *Mature conidia* swollen, mostly 0-, rarely 1-septate, ellipsoidal, oblong or allantoid, rarely ellipsoidal, straight or slightly curved, rounded at both ends, germinating, never budding secondary conidia on media, (7.1–)10.0–17.4(–29.3) × (2.8–)3.8–5.6(–7.9) µm (*n* = 429); subclade A: (8.2–)10.7–19.1(–27.8) × (2.9–)3.6–5.0(–6.1) µm (*n* = 136); subclade B: (7.1–)9.7–16.7(–29.3) × (3.5–)4.3–6.1(–7.9) µm (*n* = 211); subclade C: (8.0–)10.7–15.9(–23.2) × (2.8–)3.3–4.7(–5.6) µm (*n* = 82). *Chlamydospores* and *perithecia* not produced in culture.

Distribution: Asia (China, Japan), Europe (Finland, Poland), New Zealand, North America (Canada, USA).

Habitat: On dead woody substrata including *Acer macrophyllum*, *A. pseudoplatanus*, *Acer* sp., *Morus* sp., *Prunus tenella, Ribes* sp., *Rosa* sp., *Sambucus nigra* ssp. *canadensis*, and *Weigela coraeensis*.

Lectotype of Nectria dematiosa *designated here*: **USA**, Pennsylvania, on *Morus* sp., Bethlehem, Schweinitz, lectotype BPI 799536, isolectotype BPI 799535 anamorph only. The two isotype specimens of *S. dematiosa* have sessile sporodochia; on BPI 799536 ascospores up to 2-septate were observed. This specimen has only 4 or 5 perithecia and a few sessile sporodochia.

Epitype of Nectria dematiosa *designated here*: **USA**, North Carolina, Highlands, Macon Co. Highlands Biological Station, Lake Ravenel, on bark, 31 Aug. 1994, G.J. Samuels & H.-J. Schroers, epitype BPI 749337, ex-epitype culture CBS 126570 = G.J.S. 94-37.

Additional type specimens examined. Holotype of *Nectria sambuci*: **USA**, Nebraska, Lincoln, on *Sambucus nigra* ssp. *canadensis*, Aug. 1888, H.J. Webber, holotype NY 00927949. Holotype of *Nectria cinnabarina* subsp. *amygdalina*: **Finland**, Mustiala, on dead branch of *Amygdalus nana*, now considered to be *Prunus tenella*, 28 May 1889, P.A. Karsten. Holotype H 6009374.

Specimens and isolate examined. **Canada**, British Columbia, Sidney, Dogwood, on dead twig of *Acer macrophyllum*, 2 May 1992, M.E. Barr, BPI 802212, culture CBS 125125 = A.R. 2699; British Columbia, Sidney, on dead twig of *Rosa* sp., 5 Feb. 1992, M.E. Barr, BPI 802215, culture CBS 125127 = A.R. 2702; Ontario, Ottawa, on *Acer* sp., K. Seifert 1450, culture CBS 125155 = A.R. 4328. **China**, Jun. 2009, W.Y. Zhuang, culture CBS 127667 = A.R. 4638. **Japan**, Gunma Prefecture, Seta-gun, Fujimi-son, on twig of *Weigela coraeensis* Thunb., May 2003, Y. Hirooka, BPI 879984, culture MAFF 241416; Tokyo, Okutama-gun, on twig, Nov. 2003, Y. Hirooka, BPI 879985, culture MAFF 241430. **New Zealand**, Otago, on dead twig of *Ribes sativum*, 1 Feb. 1948, BPI 880708. **Poland**, Bialowieza forest, NW part of the forest near Lipiny reserve, section 271c, alt. 170 m. 52°45'13''N 23°37'59''E, on twig, 21 May 2006, D. Karasinski and D. Ronikier, BPI 878308, culture CBS 125159 = A.R. 4380. **Unknown**: on *Acer pseudoplatanus*, culture CBS 279.48; on *Ribes* sp., culture CBS 278.48.

Notes: *Nectria dematiosa* is distinguished from other species of the NCSC by sessile sporodochia and ascospores that are up to 2-septate. Care must be taken in observing these characters, because the short stipitate sporodochia of *N. asiatica* and *N.*

nigrescens are often covered by a mass of conidia, thus appearing sessile. In addition, the 2-septate ascospores of *N. dematiosa* occur relatively infrequently (Fig. 7E). Additional differences include mature conidia of *N. dematiosa* that never bud on SNA (Fig. 7R–W). Finally, the optimum temperature for growth of *N. dematiosa* on PDA is 20 °C, while the optimum temperature for growth of *N. asiatica*, *N. cinnabarina*, and *N. nigrescens* is 25 °C (Fig. 4).

Our molecular phylogenetic analyses suggest that three subclades can be distinguished within *N. dematiosa* (Fig. 2). Some subtle differences among subclades were observed specifically differences in the shape and behavior of germ tubes, mycelial growth at 25 °C on PDA, and geographic range. Mature conidia of subclade A produce almost straight germ tubes that did not grow into the agar immediately, while mature conidia of subclades B and C produced sinuate germ tubes that grew into the agar after germination (Fig. 7U–W). The 95 % confidence intervals of mature conidial length/width ratio of subclade B were statistically different from subclades A and C (Fig. 3). According to mycelial growth at 25 °C for 7 d on PDA, subclade B showed slower growth than subclades A and C (20–30 mm vs. 40–70 mm) (Fig. 4).

For several reasons, we do not recognise these *N. dematiosa* subclades as distinct species. First of all, in subclade A the five collections from Canada, Poland and the USA contain only one specimen with the teleomorph (BPI 749337), while anamorphs on natural substrate were observed on only two specimens (BPI 749337, BPI 878308). In subclade B, there are only two specimens both collected in Canada (BPI 802212, BPI 802215). In addition, the anamorph of BPI 802215 was not found on natural substrate. Subclade C is known only from Asia and no anamorph was observed on natural substrate (Fig. 2). The number of samples available is relatively small and the few specimens were insufficient to determine if morphological differences exist and are constant on natural substrate.

Jøgensen (1952) found morphological differences between typical *N. cinnabarina* and *N. cinnabarina* on *Ribes*. Jøgensen (1952) also mentioned that the fungus grew faster than *N. cinnabarina* from other hosts. One isolate was obtained of *N.* '*cinnabarina*' on *Ribes* sp. (CBS 278.48). In growth trials this isolate showed growth similar to that of *N. dematiosa* subclade A (Fig. 4). Based on our phylogenetic analysis, this isolate falls in *N. dematiosa* subclade A with isolates collected on *Acer pseudoplatanus* and *Acer* sp.

Nectria nigrescens Cooke, Grevillea 7: 50. 1878. Fig. 8.

= *Nectria cinnabarina* f. *dendroidea* Fuckel, Fungi rhenani 2657. 1874.
≡ *Nectria cinnabarina* var. *dendroidea* (Fuckel) Wollenw., Angew. Bot. 8: 186. 1926.
= *Nectria cinnabarina* var. *minor* Wollenw., Angew. Bot. 8: 185. 1926.
= *Nectria meliae* Earle, Bull. Torrey Bot. Club 25: 364. 1898.
= *Nectria fuscopurpurea* Wakef., Kew Bull., p. 232. 1918.

Anamorph: *Tuberculariа vulgaris*-like.

Teleomorph on natural substrata: *Mycelium* rarely visible around perithecia and on host. *Stromata* up to 2.0 mm high and 4 mm diam, erumpent through epidermis, whitish yellow to bay, sometimes darker red, KOH+ dark red, LA+ yellow, pseudoparenchymatous, cells forming textura *angularis* to *t. prismatica* with cells oriented more or less vertically; cells 4–17 µm diam, with 1–1.5 µm thick walls, intergrading with the ascomatal wall. *Perithecia* superficial on well-developed stroma, solitary or caespitose, up to 20 on an erumpent stroma, rarely clustered around base of stipitate sporodochia, subglobose to globose, 265–420 µm high × 236–410 µm diam (*n* = 38), red to reddish brown, sometimes cupulate upon drying, non-papillate, apical region darker, KOH+ dark red, LA+ yellow, surface with rough or concolourous warts, but sometimes smooth. *Perithecial surface cells* forming *textura globulosa* or *t. angularis*, with walls pigmented *ca.* 1.5 mm thick. *Perithecial wall ca.* 40–65 mm thick, of two distinct regions: outer region about 25–45 mm thick, intergrading with stroma, cells forming *textura globulosa* or *t. angularis*, walls pigmented, *ca.* 1.5 mm thick; inner region *ca.* 7–18 mm thick, of elongated, thin-walled, hyaline cells, forming *textura prismatica*. *Asci* unitunicate, (62–)70–98(–113) × (6.5–)7.5–10.0(–11.5) µm (*n* = 63), cylindrical to narrowly clavate, with an inconspicuous ring at apex, 8-spored, ascospores biseriate above, uniseriate below. *Ascospores* ellipsoidal to fusiform, straight, sometimes slightly curved, hyaline, (0–)1(–3)-septate, (10.5–)13.5–18.0(–22.0) × (2.5–)3.5–5.5(–8.0) µm (*n* = 320), smooth-walled.

Anamorph on natural substrata: *Stromata* erumpent through epidermis, pale yellow to orange, rarely reddish brown. *Sporodochial conidiomata* with stipe, superficial on well-developed stroma, smooth, cerebriform or tubercularoid, scattered, solitary, or 2–4 gregarious, stipitate, pustular, discoid or cylindrical-capitate, up to 250–1700 mm high, 300–1700 mm wide, white, whitish yellow to orange, sometimes brown, red or dark red; *stipe* white to whitish red, rarely dark red, up to 340–640 mm wide; *stipe cells* almost *textura angularis*, continuous with stroma, usually with wider cells in centre. *Hymenium* arising directly from *textura prismatica* elongating from *textura angularis*, up to 120 µm long, of cells 2.5–6.0 µm wide, curved margin, up to 150 µm long, of parallel hyphae 1.5–2.5 µm wide. *Conidiophores* monoverticillate or rarely bi-verticillate, then developing acropleurogenously for 3–7 levels, straight to curved, sometimes coiled. *Phialides* intercalary, occurring below each septum, or rarely terminal; *intercalary phialides* monophialidic, up to 3.0–5.0 µm long, 1.0–2.0 µm wide; *terminal cells* monophialidic, sometimes sterile, no collarettes. *Conidia* hyaline, narrowly long ellipsoidal to cylindrical, straight or slightly curved, (4.7–)5.5–6.9(–8.4) × (1.6–)2.1–2.7(–3.0) µm (*n* = 343), non-septate.

Anamorph in culture: Optimum temperature for growth on PDA 25 °C, maximum temperature 35 °C, after 7 d colonies 70–85 mm (av. 80 mm) diam. *Colony surface* on PDA, radial, sometimes wavy, slightly cottony with aerial mycelium, white to whitish saffron; *aerial mycelium* developing only in CBS 125148, white to whitish yellow, sporodochial conidial masses produced after 2 wk; *reverse* white to slightly whitish yellow. *Odour* on PDA slightly fruity. Sporulation on SNA from *lateral phialidic pegs* on submerged or aerial hyphae common, 2.4–5.3 µm long, 1–1.9 µm wide near aperture. *Aerial conidiophores* abundantly developed on aerial hyphae, unbranched, sometimes verticillate, 1–2-branched, becoming loosely to moderately densely branched, 5.5–21.5 µm long, 2.0–3.0 µm wide at base. *Conidiogenous cells* monophialidic, cylindrical, slightly tapering toward tip or narrowly flask-shaped with widest point in middle, 9.5–17.0 µm long, 1.5–2.0 µm wide at base. *Young conidia* formed by monophialides on submerged or aerial hyphae, formed abundantly on slimy heads, non-septate, ellipsoidal, oblong to cylindrical, hyaline, smooth, straight or slightly curved with rounded ends, (3.0–)4.0–7.0(–14.5) × (1.5–)2.0–2.5(–3.5) µm (*n* = 250). *Mature conidia* swollen, mostly 0-, rarely 1-septate, ellipsoidal, oblong, or allantoid, rarely ellipsoidal with slightly constricted centre, hyaline, smooth, straight or slightly curved, rounded at both ends, germinating or budding secondary conidia on media, (5.0–)7.6–14.6(–24.3) × (2.3–)3.5–4.9(–6.6) µm (*n* = 180). *Chlamydospores* rare, globose, subglobose, broadly ellipsoidal, 0(–1)-septate, solitary or chains, 8.0–13.0 µm wide. *Perithecia* not produced in culture.

Fig. 8.A–S. *Nectria nigrescens*. A. Perithecia and short stipitate sporodochia in the natural environment. B. Peritheica in the natural environment. C. Median section of perithecia. D. Median section of perithecial wall. E. Ascus. F. One and three septatas ascospores. G. Long stipitate sporodochia in the natural environment. H. Median section of long stipitate sporodochium. I. Edge of long stipitate sporodochium. J. Acropleurogenous conidiophore in the natural environment. K. Conidia in the natural environment. L. Aerial conidiophores and conidial mass on SNA. M. Young conidia on SNA. N. Lateral phialidic pegs on SNA. O. Short and densely blanched aerial conidiophores, and conidia on SNA. P. Mature conidia and young conidia on SNA. Q, R. Budding mature conidia on SNA. S. Germinating mature conidia that were streaked onto SNA. Scale bars: A, G, H, L = 1 mm; B, C = 300 µm; D, I = 100 µm; E, J, K, O, R = 30 µm; F, M, N, P, Q, S = 15 µm.

Distribution: Europe (France, Germany, UK), North America (Canada, USA).

Habitat: On dead woody substrata including *Acer* sp., *Betula lutea*, *Celtis occidentalis*, and *Fagus sylvatica*.

Holotype of Nectria nigrescens: **USA**, South Carolina, on *Gleditsia* sp., S.C. Aiken, K 165219, Ravenel, American Fungi 2380a.

Epitype of Nectria nigrescens *designated here*. **USA**, North Carolina, Haywood Co., Great Smoky Mountains National Park, Purchase Knob. Cataloochees Divide Trail, alt. 5000 ft. 35°35'9.9"N 83°4'25.5"W, on dead twig of dictyledonous tree, 7 Sep. 2005, A.Y. Rossman, epitype BPI 871083, ex-epitype culture CBS 125148 = A.R. 4211.

Additional type specimens examined. Holotype of *Nectria cinnabarina* f. *dendroidea*: **Germany**, Fungi Rehnani 2657, FH. Holotype of *Nectria fuscopurpurea*: **UK**, Wisbech, on dead branch of *Prunus domestica* L., 1917, J.C.F. Fryer or A.D. Cotton, K 98615. Neotype of *Nectria meliae* designated here: **USA**, Alabama, on *Melia* sp., 1 Dec. 1896, C.F. Baker, BPI 552588.

Specimens and isolates examined: **Canada**, Ontario, Carleton Place, near the Mississippi River, on twigs of *Celtis occidentalis*, 31 Jun. 2007, T. Gräfenhan, BPI 878449, culture CBS 125162 = A.R. 4394. **France**, Foret le Chize, Les Essarts, on twig of *Fagus sylvatica*, 27 Nov. 2007, C. Lechat, BPI 878457, culture CBS 125164 = A.R. 4475; Foret le Chize, Puymardier, on dead twig of *Acer* sp., 18 May 2006, C. Lechat, BPI 878455A = C.L.L. 684, culture A.R. 4282. **USA**, Tennessee, Sevier Co., Great Smoky Mountains National Park. Alum Cave Bluff Trail, alt. 3900 ft. 35°37'43.3"N 83°27'32"W, on dead twig of *Betula lutea*, 8 Sep. 2005, A.Y. Rossman, BPI 871084, culture CBS 125149 = A.R. 4213; Vermont, Windham County, Putney, Fort Hill Road, along a stream in a wet site, on dead twig, 17 Oct. 2008, G.J. Samuels, BPI 879986, culture CBS 127668 = A.R. 4565.

Notes: *Nectria nigrescens* resembles *N. asiatica* and *N. cinnabarina* in producing short to long stipitate sporodochia and mature conidia that bud (Fig. 8A, G, H, Q, R). *Nectria nigrescens* has up to 3-septate ascospores, short or long stipitate sporodochia, and length/width ratios of young and mature conidia that are somewhat smaller than the other species of the NCSC (Figs 3, 8A, F, G, H). Budding mature conidia of *N. nigrescens* on SNA (Fig. 8Q, R) are less commonly observed than in *N. asiatica* and *N. cinnabarina*.

The name *N. cinnabarina* f. *dendroidea* was published on the label of Fuckel's Fungi Rhenani 2657, issued in 1874 (Pfister 1985). Fuckel (1874) provided a name on this label that referred to a previously published description of the specimen (Fuckel 1873). We examined photographs and a microscope slide of the exsiccati (Fuckel, Fungi Rhen. 2657 from FH) and determined this name to be a synonym of *N. nigrescens*. Wollenweber (1926) attributed his name *Nectria cinnabarina* var. *dendroidea* (Fuckel) Wollenw. to Fuckel (1873). Wollenweber (1926) noted the presence of long, stipitate sporodochia on the type specimen and was the first to regard this as an important characteristic. He described and illustrated both *N. cinnabarina* var. *dendroidea* and *N. cinnabarina* var. *minor* as having 1-septate ascospores. His later illustration of *N. cinnabarina* var. *minor* showed this variety with up to 3-septate ascospores (Wollenweber 1930, no. 778). Although Wollenwever (1926) did not document stipitate sporodochia of *N. cinnabarina* var. *minor*, his illustration showed well developed stroma (Wollenweber 1926, table 3, 21f). From these reasons, we include *N. cinnabarina* f. *dendroidea* and *N. cinnabarina* var. *minor* as synonyms of *N. nigrescens*.

The holotype specimen of *N. meliae* is lost, therefore, a specimen collected in the same year, on the same genus of host, and at the same place *i.e.* a topotype, specifically BPI 552588, is designated the neotype of *N. meliae*.

Our phylogenetic analyses suggest a sister-group relationship between *N. nigrescens* and CBS 125162, supported by high BI posterior probabilities and ML bootstrap (1.00 BI PP, 99 % ML BP) (Fig. 2). However, based on morphological characters in the natural environment and culture, CBS 125162 completely matches *N. nigrescens* and is regarded as *N. nigrescens*.

SPECIES EXCLUDED OR OF UNCERTAIN STATUS

Nectria cinnabarina* var. *ribis (Tode) Wollenw., Fusaria autographica delineata, Edn 1: no. 787. 1930.

Basionym: *Sphaeria ribis* Tode, Fungi Mecklenb. sel. 2: 31. 1791.

≡ *Hypoxylon ribis* (Tode) J. Kickx f., Fl. Crypt. Louvain p. 113. 1835.
≡ *Nectria ribis* (Tode) Nießl, Verh. Naturf. Vereins Brünn 3: 171. 1865.
≡ *Nectria ribis* (Tode) Rabenh. in Sacc., Syll. Fung. 2: 480. 1883.

Notes: *Nectria cinnabarina* var. *ribis* was originally described as *Sphaeria ribis* by Tode (1791). Because Tode's specimens were destroyed (Kirk *et al*. 2008), his illustrations are regarded as lectotype (tabula XII, fig. 103a–f). Tode (1791) described and illustrated smooth, pyriform perithecia immersed at the base of a well-developed stroma, possibly as a parasite, and thus do not belong in the *N. cinnabarina* species complex. Rather it appears to be related to *Cosmospora*.

Tremella purpurea L., Spec. Plant. 2: 1158. 1753.

Basionym: *Nectria purpurea* (L.) G.W. Wilson & Seaver, J. Mycol. 13: 51. 1907.

≡ *Cucurbitaria purpurea* (L.) Seaver, Mycologia 1: 184. 1909.

Notes: The name *Tremella purpurea* was listed as a synonym of *N. cinnabarina* (Rossman *et al*. 1999). However, according to Spencer *et al.* (2009), this name is invalid because the genus was not validly published by Linnaeus (1753). Names based on this invalidly published name are either invalid or illegitimate.

KEY TO THE SPECIES IN THE *NECTRIA CINNABARINA* SPECIES COMPLEX

On natural substrate

1. Ascospores up to 3-septate, 1-septate (91 %), 2-septate (5 %), 3-septate (4 %); sporodochia short (65 %) to long stipitate (35 %), 250–1700 µm high; Europe or North America ..... ***N. nigrescens***
1. Ascospores up to 1-, rarely 2-septate; sporodochia sessile or stipitate; Asia, Europe or North America **2**

2. Ascospores up to 1-septate; sporodochia less than 800 µm high, short stipitate; Asia ..... ***N. asiatica***
2. Ascospores up to 1- or rarely 2-septate (3 %); sporodochia sessile or long stipitate; Asia, Europe or North America **3**

3. Sporodochia 700–1600 µm high, long stipitate (70 %); Europe or North America ..... ***N. cinnabarina***
3. Sporodochia sessile or anamorph lacking; Asia, Europe or North America ..... ***N. dematiosa***

In pure culture

1. Mature conidia not budding on SNA after 7 d; optimum temperature for growth 20 °C on PDA ..... ***N. dematiosa,* subclades A–C**, go to **4**
1. Mature conidia budding on SNA after 7 d; optimum temperature for growth 25 °C on PDA **2**

2. Mature conidia ellipsoidal, strongly constricted, budding; Europe or North America ..... ***N. cinnabarina***
2. Mature conidia ellipsoidal, straight, or slightly curved, rarely slightly constricted, rarely budding; Asia, Europe or North America **3**

3. Young conidia averaging 10 µm long; mature conidia averaging 15 µm long; Asia ..... ***N. asiatica***
3. Young conidia averaging 5 µm long; mature conidia averaging 10 µm long; Europe or North America ..... ***N. nigrescens***

4. Germ tubes more or less straight, not penetrating agar immediately; Canada, Poland, USA ..... ***N. dematiosa* subclade A**
4. Germ tube sinuate, penetrating agar immediately after germination; Canada, China, Japan **5**

5. Mean of 95 % confidence intervals of mature conidial length/width ratio 2.5; mycelial growth 20–30 mm after 7 d at 25 °C; Canada ..... ***N. dematiosa* subclade B**
5. Mean of 95 % confidence intervals of mature conidial length/width ratio 3.5; mycelial growth 40–50 mm after 7 d at 25 °C; China, Japan..... ***N. dematiosa* subclade C**

DISCUSSION

Nectria cinnabarina and other species in the NCSC form a monophyletic group within *Nectria,* all having *Tubercularia* anamorphs (Fig. 1). The molecular analyses of the NCSC resolve four phylogenetically distinct species (Fig. 2), each of which is described and illustrated above.

The anamorph of *N. cinnabarina sensu lato* has been referred to as *Tubercularia vulgaris*. Many synonyms are known for *T. vulgaris* (Jøgensen 1952, Booth 1959, Seifert 1985) for which authentic and type specimens were examined by Seifert (1985). Although differences exist in stipe length in the natural environment and in size and shape of conidia in culture, it is not possible to determine which synonym of *T. vulgaris* represents each species in the NCSC. Thus, the anamorph of *N. cinnabarina* is referred to as *T. vulgaris*, while the anamorph of other species in the NCSC is referred to as *Tubercularia vulgaris*-like.

Seifert (1985) recognised that *T. vulgaris* in the natural environment had two types of sporodochia, *i.e.* sessile and stipitate sporodochia with marginal cells arranged in a palisade. These differences correlate with the species recognised here. Specifically, *N. dematiosa* has sessile sporodochia while *N. asiastica, N. cinnabarina,* and *N. nigrescens* have short to long stipitate sporodochia. Except for conidia in culture, no differences were found in other morphological characteristics of the anamorph including the number of conidiophore branches and conidial size in the natural environment. Morphological heterogeneity of conidia in culture was noted for many years (Mayr 1883, Brefeld 1891, Beck 1902, Jøgensen 1952). Beck (1902) observed conidia that were much larger than normal conidia and suggested that their size depended on the nutritional content of the media. To standardise cultural conditions, Jøgensen (1952) used a detached branch instead of artificial media. He determined that the range of conidial size was variable but not useful in distinguishing taxa within specimens identified as *N. cinnabarina*. By observing mature conidia on SNA, we could distinguish species in the NCSC including the subclades within *N. dematiosa*. Budding of mature conidia in culture was observed for *N. asiatica*, *N. cinnabarina,* and *N. nigrescens*, a characteristic not noted for other *Nectria*-like fungi. Differences in the size of mature conidia and the shape of its germ tube can be used to distinguish the subclades in the *N. dematiosa* clade.

Nectria cinnabarina sensu lato has been considered a cosmopolitan species (Farr & Rossman 2010). This study shows that *N. cinnabarina*, *N. nigrescens*, and *N. dematiosa* subclades A and B are widespread on hardwood trees and woody shrubs in Europe and North America, while *Nectria asiatica* and *N. dematiosa* subclade C are known only in Asia. *Nectria cinnabarina* has been reported in tropical regions and the Southern Hemisphere (Cunningham 1922, Tunstall 1923, Booth 1977, Debons *et al.* 1993), however, none of these reports could be confirmed because of the lack of specimens and cultures.

Species of the NCSC occur on a wide range of woody shrubs and trees in many families including the *Arecaceae* and *Pinaceae*; it is occasionally reported on herbaceous hosts (Farr & Rossman 2010). Most specimens used in this study were collected on newly killed branches suggesting that these fungi may exist as endophytes that then sporulate when the substrate dies (Wang *et al.* 2000). *Nectria cinnabarina sensu lato* causes a disease referred to as "coral spot *Nectria* canker" because of the conspicuous erumpent pink sporodochia of the anamorph (Sinclair & Lyon 2005). Trees and woody plants growing in plantations and nurseries or those damaged by frost or other causes appear to be especially susceptible. The pathogenicity of this fungus has been proven by host inoculation studies (Bedker & Blanchette 1984, Yasuda & Izawa 2007). Jøgensen (1952) demonstrated that *N. cinnabarina* was a facultative parasite and saprobe of mainly deciduous trees but was unable to correlate his results with specific hosts. Although *N. cinnabarina* and *N. nigrescens* produce chlamydospores, they are rarely found in soil.

Chaverri and Samuels (2003) used a morphological species concept (John & Maggs 1997, Kirk *et al.* 2008) and genealogical concordance phylogenetic species recognition (Taylor *et al.* 2000) to delimit *Hypocrea*/*Trichoderma* species with green ascospores. According to their species concept, each of the three subclades (A, B, and C) in *N. dematiosa* would be a distinct species. Even though we found that the subclades of *N. dematiosa* could be distinguished

by subtle anamorph characters in culture and by biogeography, we prefer not to give them names because of the small number of available specimens.

Our study clearly indicates that to define and characterise species in the *N. cinnabarina* species complex, an integrated approach should be used. The use of phylogenetic analyses of DNA sequences from six loci, observations and analyses of morphological characters of teleomorph and anamorph, mycelial growth, and geographical data indicates the existence of four species within the NCSC. This study will pave the way for understanding the evolutionary diversification and taxonomic implications of morphology using robust phylogenetic analyses and comprehensive character sampling.

ACKNOWLEDGEMENTS

The authors thank Dr Gary J. Samuels (USDA-ARS, Beltsville, Maryland, USA) for his contributions to the systematics of the hypocrealean fungi including discussions about the NCSC and other *Nectria*-like fungi. It is a distinct honour to publish our paper here. We thank the many mycologists who shared their fresh specimens and/or cultures of these fungi with us, specifically Alex Akulov, Margaret Barr, Alex Chlebicki, Walter Gams, Tom Gräfenhan, Walter Jaklitsch, Thomas Laessoe, Gaston Laflamme, Christian Lechat, Yasunori Ono, Gary Samuels, Hans-Josef Schroers, Keith Seifert, and Wen-ying Zhuang. We are indebted to Sato Toyozo, Takayuki Aoki, and Keisuke Tomioka (NIAS Genebank, National Institute of Agrobiological Sciences, Tukuba, Ibaraki, Japan), and Keiko T. Natuaki (Tokyo University of Agriculture) for sending and quickly depositing Japanese cultures. We also thank Orlando Petrini (Repubblica e Cantone Ticino, Bellinzona, Switzerland) for giving many ideas and advice about statistical analyses. We express sincere thanks to Andrew Minnis for providing nomenclatural advice and to our excellent technicians, Sasha Allen, Aimee Hyten and Tunesha Phillips. We also gratefully acknowledge the assistance of the curators and staff of the BPI, FH, H, TNS, K, NY, PH, SPA, and UPS. This study was supported in part by the United States National Science Foundation (NSF) PEET grant DEB-0731510 "Monographic Studies in the *Nectriaceae, Hypocreales*: *Nectria, Cosmospora*, and *Neonectria"* to University of Maryland (PIs: P. Chaverri, A.Y. Rossman, G.J. Samuels).

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.03

Studies in Mycology 68: 57–78. 2011.

Delimitation of *Neonectria* and *Cylindrocarpon* (*Nectriaceae, Hypocreales, Ascomycota*) and related genera with *Cylindrocarpon*-like anamorphs

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Abstract: *Neonectria* is a cosmopolitan genus and it is, in part, defined by its link to the anamorph genus *Cylindrocarpon*. *Neonectria* has been divided into informal groups on the basis of combined morphology of anamorph and teleomorph. Previously, *Cylindrocarpon* was divided into four groups defined by presence or absence of microconidia and chlamydospores. Molecular phylogenetic analyses have indicated that *Neonectria sensu stricto* and *Cylindrocarpon sensu stricto* are phylogenetically congeneric. In addition, morphological and molecular data accumulated over several years have indicated that *Neonectria sensu lato* and *Cylindrocarpon sensu lato* do not form a monophyletic group and that the respective informal groups may represent distinct genera. In the present work, a multilocus analysis (*act,* ITS, LSU, *rpb1*, *tef1, tub*) was applied to representatives of the informal groups to determine their level of phylogenetic support as a first step towards taxonomic revision of *Neonectria sensu lato*. Results show five distinct highly supported clades that correspond to some extent with the informal *Neonectria* and *Cylindrocarpon* groups that are here recognised as genera: (1) *N. coccinea*-group and *Cylindrocarpon* groups 1 & 4 (*Neonectria/Cylindrocarpon sensu stricto*); (2) *N. rugulosa*-group (*Rugonectria* gen. nov.); (3) *N. mammoidea/N. veuillotiana*-groups and *Cylindrocarpon* group 2 (*Thelonectria* gen. nov.); (4) *N. radicicola*-group and *Cylindrocarpon* group 3 (*Ilyonectria* gen. nov.); and (5) anamorph genus *Campylocarpon*. Characteristics of the anamorphs and teleomorphs correlate with the five genera, three of which are newly described. New combinations are made for species where their classification is confirmed by phylogenetic data.

Key words: Canker-causing fungi, molecular systematics, *Nectria*-like fungi, phylogeny, polyphasic taxonomy, root-rotting fungi, sequence analysis, systematics, taxonomy.
Taxonomic novelties: *Ilyonectria* P. Chaverri & C. Salgado, gen. nov.*; Ilyonectria coprosmae* (Dingley) P. Chaverri & C. Salgado, comb. nov.; *Ilyonectria liriodendri* (Halleen *et al*.) P. Chaverri & C. Salgado, comb. nov.*; Ilyonectria macrodydima* (Halleen, Schroers & Crous) P. Chaverri & C. Salgado, comb. nov.; *Ilyonectria radicicola* (Gerlach & L. Nilsoon) P. Chaverri & C. Salgado, comb. nov.; *Rugonectria* P. Chaverri & Samuels, gen. nov.; *Rugonectria castaneicola* (W. Yamam. & Oyasu) Hirooka & P. Chaverri, comb. nov; *Rugonectria neobalansae* (Samuels) P. Chaverri & Samuels, comb. nov.; *Rugonectria rugulosa* (Pat. & Gaill.) Samuels, P. Chaverri & C. Salgado, comb. nov.; *Thelonectria* P. Chaverri & C. Salgado, gen. nov.; *Thelonectria coronata* (Penz. & Sacc.) P. Chaverri & C. Salgado, comb. nov.; *Thelonectria discophora* (Mont.) P. Chaverri & C. Salgado, comb. nov.; *Thelonectria jungneri* (Henn.) P. Chaverri & C. Salgado, comb. nov.; *Thelonectria lucida* (Höhnel) P. Chaverri & C. Salgado, comb. nov.; *Thelonectria olida* (Wollenw.) P. Chaverri & C. Salgado, comb. nov; *Thelonectria trachosa* (Samuels & Brayford) Samuels, P. Chaverri & C. Salgado, comb. nov.; *Thelonectria veuillotiana* (Sacc. & Roum.) P. Chaverri & C. Salgado, comb. nov.; *Thelonectria viridispora* (Samuels & Brayford) P. Chaverri, C. Salgado, & Samuels, comb. nov.; *Thelonectria westlandica* (Dingley) P. Chaverri & C. Salgado, comb. nov.

INTRODUCTION

Species of *Neonectria sensu lato* and their anamorphs in *Cylindrocarpon* are common in tropical and temperate regions. They are generally found on bark of recently killed woody plants and sometimes on decaying herbaceous material (Samuels 1988, Samuels & Brayford 1990, Samuels *et al.* 1990, Samuels & Brayford 1993, 1994, Rossman *et al.* 1999, Castlebury *et al.* 2006). Some species of this genus are plant pathogens causing cankers, root rots, and other diseases on hardwood and coniferous trees, *e.g. Abies* and *Acer* cankers caused by *Neonectria castaneicola*; beech (*Fagus*) bark disease caused by *N. coccinea*, *N. ditissima* and *N. faginata*; black foot disease of grapevines (*Vitis*) caused by *N. liriodendri*; root rots caused by *N. radicicola*; and cankers caused by *N. rugulosa,* among others (Samuels & Brayford 1994, Hirooka *et al.* 2005, Kobayashi *et al.* 2005, Castlebury *et al.* 2006, Halleen *et al.* 2006). According to *Index Fungorum* (www.indexfungorum.org), 38 species have been placed in *Neonectria* and 143 in *Cylindrocarpon*. These numbers are underestimated because several species of *Nectria*-like fungi with *Cylindrocarpon* anamorphs have not been transferred to *Neonectria* (> 20 spp.). To date, the most comprehensive taxonomic works of *Neonectria* and species of *Nectria* having *Cylindrocarpon* anamorphs are those by Booth (1959, 1966) and Samuels, Brayford and collaborators (Samuels 1988, Brayford & Samuels 1993, Samuels & Brayford 1993, 1994, Brayford *et al.* 2004).

Species of *Neonectria sensu lato* are characterised by having perithecia that are subglobose to broadly obpyriform, smooth to roughened, red, becoming dark red in 3 % potassium hydroxide (KOH), and with an acute to constricted apex that is sometimes knobby; the perithecial wall is *ca*. 50 µm thick and generally composed of two regions, sometimes with an outer region that forms *textura epidermoidea*, that may or may not be covered with another region of cells; and the ascospores are hyaline, generally bicellular, rarely multi-cellular, and smooth or finely ornamented (Rossman *et al.* 1999). The anamorph of *N. ramulariae* (type of *Neonectria*) is *Cylindrocarpon obtusiusculum* and, consequently, species with the *Neonectria*-like morphology described above and *Cylindrocarpon* anamorphs have been classified as *Neonectria*. However, species that have been placed in *Neonectria* and species of *Nectria* having a *Cylindrocarpon* anamorph vary greatly in the morphology of their perithecia, some having perithecial walls < 50 µm or > 50 µm

thick, others warted, and others with various degrees of ascospore ornamentation. Some species of *Neonectria* are morphologically similar in perithecial morphology with differences seen only in the anamorph (Samuels *et al.* 2006b).

The morphological variation in *Neonectria* resulted in the subdivision of species into five informal groups, mostly based on perithecial characteristics: (1) *N. coccinea/galligena*-group (*Neonectria sensu stricto*) (Booth 1959); (2) *N. mammoidea*-group (*N. mammoidea* = *N. discophora* (Booth 1959); (3) *N. rugulosa*-group (Samuels & Brayford 1994); (4) *N. radicicola*-group (Booth 1959); and (5) *N. veuillotiana*-group (Brayford & Samuels 1993). Species in the *N. coccinea/galligena*-group are characterised by having few to numerous perithecia clustered on wood; perithecial walls are *ca*. 50 µm thick, composed of relatively thick-walled, small cells; and ascospores are generally smooth (Booth 1959). Species in the *N. mammoidea*-group were originally defined as having a distinctive perithecial wall that comprises a layer of hyphae that have thickened walls and are typically arranged radially, giving the appearance of a palisade (Booth 1959, Brayford *et al.* 2004). This characteristic generally results in smooth, shiny perithecia. In addition to the perithecial anatomy, the *N. mammoidea*-group has spinulose, often yellow-brown ascospores, and a non-microconidial anamorph. The *N. rugulosa*-group includes species with warted perithecia, a perithecial wall > 50 µm thick, composed of large, thick-walled cells, and striate ascospores (Samuels & Brayford 1994). The *N. radicicola*-group includes species that have smooth to slightly warted, usually solitary perithecia, the outer region of the perithecial wall composed of large, thin-walled cells, and smooth ascospores (Samuels & Brayford 1990). Species in the *N. veuillotiana*-group have perithecia with a flattened or knobby apex, perithecial walls composed of thick-walled cells, and tuberculate ascospores (Brayford & Samuels 1993). Mantiri *et al*. (2001) revised the informal groupings of *Neonectria* based on phylogenetic analyses of DNA sequence data. Group or clade I was *Neonectria sensu stricto* or the *N. coccinea/galligena*-group; clade II included the *N. mammoidea*-, *N. rugulosa*-, and *N. veuillotiana*-groups; and clade III was the *N. radicicola*-group.

Booth (1966) subdivided *Cylindrocarpon* into four groups based on the presence or absence of microconidia and chlamydospores. The first three *Cylindrocarpon* groups in Booth (1966) correlate with the three groups/clades in Mantiri *et al*. 2001 (Castlebury *et al.* 2006). Anamorphs in the *N. coccinea/galligena*-group (clade I in Mantiri *et al*. 2001) belong to *Cylindrocarpon* group 1, which have micro- and macroconidia but lack chlamydospores, except *N. ramulariae/C. obtusiusculum*, which has chlamydospores and lacks microconidia. *Cylindrocarpon obtusiusculum* was originally placed in *Cylindrocarpon* group 4 by Booth (1966). The type species of *Cylindrocarpon, C. cylindroides*, belongs in *Cylindrocarpon* group 1 (Booth 1966, Mantiri *et al.* 2001, Brayford *et al.* 2004, Halleen *et al.* 2004, Castlebury *et al.* 2006). Anamorphs in the *N. mammoidea/veuillotiana*-group (clade II in Mantiri *et al*. 2001) belong to *Cylindrocarpon* group 2 and are characterised by the lack of microconidia and chlamydospores. Anamorphs in *Cylindrocarpon* group 3 belong to the *N. radicicola*-group (clade III in Mantiri *et al*. 2001) and are characterised by the presence of microconidia and chlamydospores.

The anamorphic genus *Campylocarpon* was described by Halleen *et al*. (2004) for species resembling *Cylindrocarpon* with 3–5-septate, curved macroconidia and lacking microconidia. Halleen *et al*. (2004) segregated *Campylocarpon* from *Cylindrocarpon* based on molecular phylogenetic data that placed it more closely to *N. mammoidea*-group than to *Cylindrocarpon sensu stricto* (*N. coccinea*-group). Halleen *et al.* (2004) noted the similarity of *Campylocarpon* to the *Cylindrocarpon* anamorphs of species in the *N. mammoidea*-group.

Even though morphological and phylogenetic studies suggest that *Neonectria/Cylindrocarpon* represents more than one genus (Samuels & Brayford 1994, Mantiri *et al.* 2001, Brayford *et al.* 2004, Halleen *et al.* 2004, Hirooka *et al.* 2005, Castlebury *et al.* 2006, Halleen *et al.* 2006), formal taxonomic segregation of these groups has not been proposed. The objectives of the present study are to: (1) define *Neonectria sensu stricto*; (2) determine if *Neonectria/Cylindrocarpon* should be divided into multiple genera using phylogenetic analyses of multiple loci; and (3) recognise these species in monophyletic genera as a first step toward their taxonomic revision.

MATERIALS AND METHODS

Morphological characterisation

Specimens were obtained from U.S. National Fungus Collections (BPI), Steere Herbarium, New York Botanical Garden (NY), and Manaaki Whenua Landcare Research, New Zealand (PDD), and collected in fresh conidition from the field. Some cultures were obtained from the Centraalbureau voor Schimmelcultures (CBS), Utrecht, Netherlands. For morphological characterisation of the teleomorph, the macromorphology of the perithecia was observed and described using the following characters: distribution of perithecia on the host; perithecial shape, colour, and reaction to 3 % w/v potassium hydroxide (KOH) and 100 % lactic acid; perithecial wall structure; and colour and appearance of the perithecial apex. Colour standards are from Kornerup & Wanscher (1978). To observe internal and microscopic characteristics, the perithecia were rehydrated briefly in KOH, then supported by Tissue-Tek O.C.T. Compound 4583 (Miles Inc., Elkhart, Indiana, USA), and sectioned at a thickness of *ca*. 15 µm with a freezing microtome. Characteristics of asci and ascospores were observed by rehydrating the perithecia in 3 % KOH, removing part of the centrum with a fine glass needle, and placing it on a glass slide. Microscopic observations were made using an Olympus BX51 microscope and DP71 digital camera. Cultures were obtained by isolating asci containing ascospores on cornmeal-dextrose agar (CMD; Difco™ cornmeal agar + 2 % w/v dextrose supplemented with antibiotics 0.2 % each neomycin and streptomycin). Morphological observations of the colonies and anamorph in culture were based on isolates grown on Difco™ potato-dextrose agar (PDA) and SNA (low nutrient agar, Nirenberg 1976) for 3 wk in an incubator at 25 ºC with alternating 12 h/12 h fluorescent light/darkness. Measurements of continuous characters such as length and width for both anamorph and teleomorph were made using the beta 4.0.2 version of Scion Image software (Scion Corporation, Frederick, Maryland, USA). Continuous measurements are based on 10–30 measured units and are reported as the extremes (maximum and minimum) in brackets separated by the mean plus and minus one standard deviation.

DNA extraction, polymerase chain reaction (PCR), and sequencing

Strains listed in Table 1 were grown in Petri dishes (6 cm diam) containing Difco™ potato-dextrose broth. Plates were incubated

at 25 ºC for *ca*. 1 wk. DNA was extracted from the mycelial mat harvested from the surface of the broth. The PowerPlant™ DNA Isolation Kit (MO BIO Laboratories, Inc., Carlsbad, California, USA) was used to extract DNA from the samples. Other sequences used in the analyses were obtained from GenBank (Table 1).

DNA sequences of partial large subunit (LSU, *ca*. 900 bp) and complete internal transcribed spacers 1 and 2 (ITS, *ca*. 600 bp), including 5.8S of the nuclear ribosomal DNA; partial β-tubulin (*tub, ca*. 500 bp); α-actin (*act*, *ca*. 600 bp); RNA polymerase II subunit 1 (*rpb1*, *ca*. 700 bp); and translation elongation factor 1α (*tef1*, *ca*. 700 bp) were used in the phylogenetic analyses (Table 2). The primers used and PCR protocols are listed in Table 2. Each 25 µL PCR reaction consisted of 12.5 µL Promega GreenTaq™ Master Mix 2× (Promega Corporation, Madison, Wisconsin, USA), 1.25 µL 10 mM forward primer, 1.25 µL 10 mM reverse primer, 1 µL of the DNA template, 1 µL of dimethyl sulfoxide (DMSO), and 8 µL of sterile RNAase-free water. PCR reactions were run in an Eppendorf Mastercycler *ep* using the parameters detailed in Table 2. PCR products were cleaned with ExoSAP-IT® (USB Corporation, Cleveland, Ohio, USA). Clean PCR products were sequenced at the DNA Sequencing Facility (Center for Agricultural Biotechnology, University of Maryland, College Park, Maryland, USA). Sequences were assembled and edited with Sequencher v. 4.9 (Gene Codes, Madison, Wisconsin, USA). Sequences were deposited in GenBank as listed in Table 1.

Phylogenetic analyses

Sixty-nine strains and their corresponding DNA sequences were analysed. Not all strains had all six loci sequenced and some sequences were obtained from GenBank; see Table 1. Seven species in the *Bionectriaceae* were selected as the outgroup: *Emericellopsis glabra, Hydropisphaera fungicola, Lasionectria mantuana, Mycoarachis inversa, Nectriopsis exigua, Selinia pulchra,* and *Verrucostoma freycinetiae*. The included sequences were aligned with MAFFT v. 5 (Katoh *et al.* 2005) using the E-INS-i strategy. The alignment was improved by hand with Seaview v. 2.4 (Galtier *et al.* 1996) and MESQUITE v. 2.5 (Maddison & Maddison 2009). Gaps (insertions/deletions) were treated as missing data. Maximum Likelihood (ML) and Bayesian (BI) analyses were performed with all sequences, first with each gene/locus separately, and then with the combined data sets. A reciprocal 70 % BP threshold (Mason-Gamer & Kellogg 1996, Reeb *et al.* 2004) was used to determine if partitions could be combined into a single phylogeny.

JMODELTEST (Rannala & Yang 1996, Posada & Buckley 2004, Posada 2008) was used to select the models of nucleotide substitution for the ML and BI analyses. The number of substitution schemes was set to 11, base frequencies +F, rate variation +I and +G, and the base tree for likelihood calculations was set to "ML optimised." Once the likelihood scores were calculated, the models were selected according to the Akaike Information Criterion (AIC). After jMODELTEST was run, the parameters indicated in Table 2 were used for the ML and BI analyses.

GARLI v. 0.96 (Zwickl 2006) was used for the ML and bootstrap analyses through the Grid computing (Cummings & Huskamp 2005) and The Lattice Project (Bazinet & Cummings 2008), which includes clusters and desktops in one encompassing system (Myers *et al.* 2008). In GARLI, the starting tree was obtained by stepwise-addition and the number of runs or search replicates was set to 50. Bootstrap (BP) analyses were replicated 2000 times. BI analysis was done with MrBayes v. 3.1.2 (Rannala & Yang 1996, Mau *et al.* 1999, Huelsenbeck *et al.* 2001, Huelsenbeck *et al.* 2002). In MrBayes, data were partitioned by locus and the parameters of the nucleotide substitution models for each partition were set as described in Table 2. Two independent analyses of two parallel runs and four chains were carried out for 10 000 000 generations using MrBayes. Analyses were initiated from a random tree and trees were sampled every 100th generation. Convergence of the log likelihoods was analysed with TRACER v. 1.4.1 (beast.bio.ed.ac.uk/Tracer). The first 20 % of the resulting trees was eliminated (= "burn in"). A consensus tree ("sumt" option) and posterior probabilities (PP) were calculated in MrBayes. Phycas v. 1.1.2 (www.phycas.org) was used as another tree searching method and also to resolve possible polytomies ("Star Tree Paradox" problem), if any, as proposed by Lewis *et al*. (2005). Phycas uses reversible-jump MCMC to allow unresolved trees, *i.e.* with polytomies or very short and poorly supported branches, and fully resolved tree topologies to be sampled during a Bayesian analysis. Unresolved trees generally occur when the time between speciation events is so short or the substitution rate so low that no substitutions occurred along a particular internal edge in the true tree. The number of cycles in Phycas was set to 100 000, sampling every 100 cycles, and with a starting tree obtained randomly.

RESULTS

Molecular phylogenetic analyses

Multiple sequence alignment resulted in 4184 included base pairs, 1 359 (33 %) phylogenetically informative and 2 500 invariable sites; 325 sites presented unique non-informative polymorphic sites (Table 2). Ambiguously aligned regions were excluded from the analyses, especially in ITS, *tef1*, and *tub* loci, which possess highly variable regions, *i.e.* introns (Table 2). Phylogenetic analyses of six loci show high bootstrap (BP) and MrBayes posterior probabilities (PP) for most nodes in the combined cladogram, except for a few of the deeper nodes (Fig. 1). BI PPs were either 100 % (high support) or 50 % (low support). The negative log likelihoods (–Ln) for the ML, BI, and Phycas trees were 44603.27, 44959.23, and 44957.36, respectively. The reversible-jump MCMC run in Phycas resulted in a few improved posterior probabilities for some polytomies or poorly supported nodes in the ML or BI trees (Fig. 1). The reciprocal 70 % BP threshold used to determine topological conflicts between partitions resulted in complete congruence, that is, the topologies of each gene genealogy did not contradict each other (results not shown). This can be evidenced in the high BP and PP support found in most nodes (Fig. 1).

Species with *Cylindrocarpon*-like anamorphs are contained in two paraphyletic clades (Fig. 1): Clade A with the *N. rugulosa*-group, *N. mammoidea/veuillotiana*-groups, and *Campylocarpon* (72 % BP, 100 % PP) and Clade B with the *N. coccinea*- and *N. radicicola*-groups (97 % BP, 100 % PP). These clades correspond generally to those reported by Mantiri *et al*. (2001). Figure 1 also shows that some of the groups defined by Booth (1959) and Samuels & Brayford (1994), *i.e. N. mammoidea-, N. rugulosa-, N. coccinea-*, and *N. radicicola*-groups, are supported by high or moderately high BP and PP values. *Campylocarpon*, an anamorph genus with morphology similar to *Cylindrocarpon* especially to those anamorphs in the *N. mammoidea*-group (Halleen *et al*. 2004), clusters with the *N. mammoidea/veuillotiana*-group supported by BI PP (100 %).

Table 1. Isolates used in the phylogenetic analyses with their corresponding GenBank accession numbers.

Species (sexual/asexual state)**	Isolate	Isolate					
		ITS	LSU	*tef1*	*tub*	*act*	*rpb1*
Campylocarpon fasciculare	CBS 112613		HM364313			HM352881	HM364331
Campylocarpon pseudofasciculare	CBS 112679		HM364314			HM352882	HM364332
Cosmospora coccinea / 'Verticillium' olivaceaum	A.R. 2741 (= CBS 114050)	HM484537	AY489734*	HM484515	HM484589	GQ505967*	AY489667*
Cosmospora vilior / Acremonium berkeleyanum	A.R. 4215 (= CBS 126111)	HM484854	HM484869	HM484846	HM484875	HM484838	HM484872
Cosmospora viliuscula	G.J.S. 96-6 (= CBS 455.96)	HM484855	GQ506003*	HM484851	HM484876	GQ505966*	GQ506032*
Cosmospora sp.	G.J.S. 93-15	HM484856	GQ506006*	HM484849	HM484878	GQ505968*	GQ506035*
Cyanonectria cyanostoma / Fusarium sp.	G.J.S. 98-127 (= CBS 101734)	FJ474076*	FJ474081*	HM484611		GQ505961*	GQ506017*
Cylindrocarpon destructans var. *crassum* (I)	CBS 537.92				EF607079*		
Cyl. destructans var. *crassum* (I)	CBS 605.92	EF607078*			EF607065*		
Cyl. olidum (T)	CBS 215.67		HM364317			HM352884	HM364334
Emericellopsis glabra	A.R. 3614 (= CBS 125295)	HM484860	GQ505993*	HM484843	HM484879	GQ505969*	GQ506023*
Gibberella fujikuroi / Fusarium moniliforme	FM 94	FJ755697*					
Gibberella fujikuroi / Fusarium moniliforme	PMBMDF092	FJ798606*					
Haematonectria haematococca / Fusarium solani	NRRL 22277	AF178401*	AF178370*				
Haematonectria illudens / Fusarium illudens	NRRL 22090	AF178393*	AF178362*				
Haematonectria sp.	G.J.S. 93-47 (= CBS 125113)	HM484862	HM484870	HM484850	HM484880	HM484839	HM484873
Hydropisphaera fungicola	A.R. 4170 (= CBS 122304)	HM484863	GQ505995*	HM484845	HM484877	GQ505970*	GQ506025*
Lasionectria mantuana	A.R. 4029 (= CBS 114291)	HM484858		HM484844			
Leuconectria clusiae / Gliocephalotrichum bulbilium	ATCC 22228		AY489732*				AY489664*
Mycoarachis inversa	A.R. 2745 (= ATCC 22107)	HM484861	GQ505991*	HM484840	HM484882	GQ505972*	GQ506021*
Nectria antarctica	A.R. 2767 (= CBS 115033)	HM484556	HM484560	HM484516	HM484601	HM484501	HM484575
Nectria aquifolii	A.R. 4108 (= CBS 125147)	HM484538	HM484565	HM484522	HM484590		
Nectria aurigera	A.R. 3717 (= CBS 109874)	HM484551	HM484573	HM484521	HM484600	HM484511	HM484586
Nectria austroamericana / Gyrostroma austroamericanum	A.R. 2808 (= CBS 126114)	HM484555	GQ505988	HM484520	HM484597		
Nectria balansae	G.J.S. 86-117 (= CBS 125119)	HM484857	HM484868	HM484848	HM484874		HM484871
Nectria balsamea	A.R. 4478 (= CBS 125166)	HM484540	HM484567	HM484528	HM484591	HM484508	HM484580
Nectria berolinensis / "Tubercularia" berolinensis	A.R. 2776 (= CBS 126112)	HM484543	HM484568	HM484517	HM484594	HM484510	HM484583
Nectria cinnabarina (*dematiosa*) / *Tubercularia vulgaris*	CBS 278.48	HM484682	HM484729	HM484647	HM484800	HM484615	HM484760
Nectria coryli	Y.H. 0815 (= A.R. 4561)	HM484539	HM484566	HM484536	HM484596	HM484509	
Nectria cucurbitula / Zythiostroma pinastri	CBS 259.58	HM484541	GQ505998	HM484530	HM484592	GQ505974	GQ506028
Nectria lamyi	A.R. 2779 (= CBS 115034)	HM484544	HM484569	HM484518	HM484593	HM484507	HM484582
Nectria miltina	A.R. 4391 (= CBS 121121)	HM484547			HM484609	HM484514	HM484587
Nectria pseudotrichia / Tubercularia lateritia	CBS 551.84	HM484554		HM484532	HM484602	GQ505976	GQ506030
Nectria pyrrhochlora	A.R. 2786 (= CBS 125131)	HM484545	HM484570	HM484519	HM484598		
Nectria sinopica / Zythiostroma mougeotii	CBS 462.83	HM484542	GQ506001	HM484531	HM484595	GQ505973	GQ506031
Nectria zanthoxyli	A.R. 4280 (= CBS 126113)	HM484546	HM484571	HM484523	HM484599	HM484513	HM484585
Nectriopsis exigua / Verticillium rexianum	G.J.S. 98-32 (= CBS 126110)	HM484865	GQ505986*	HM484852	HM484883	GQ505979*	GQ506014*
Neo. castaneicola / Cyl. castaneicola (R)	TPPH 1	AB233175*					
Neo. coprosmae / Cyl. coprosmae (I)	G.J.S. 85-39 (= CBS 119606)	HM364301					
Neo. coronata / Cyl. coronatum (T)	A.R. 4505 (= CBS 125173)			HM364348	HM352862	HM352878	HM364328
Neo. discophora / Cyl. ianothele (T)	A.R. 4324 (= CBS 125153)	HM364294	HM364307	HM364345	HM352860	HM352875	HM364326
	A.R. 4499 (= CBS 125172)	HM364296	HM364309	HM364347		HM352877	HM364327
Neo. ditissima / Cyl. heteronemum	CBS 100316	HM364298	HM364311	HM364350	HM352864	HM352880	HM364330
Neo. fuckeliana / Cyl. cylindroides var. *tenue*	A.R. 3103 (= CBS 125133)	HM364291	HM446654	HM364342	HM352857	HM352872	
	A.R. 4109 (= CBS 119723)	HM364292	HM364305	HM364343	HM352858	HM352873	
	A.R. 4110 (= CBS 119200)	HM364293	HM364306	HM364344	HM352859	HM352874	
	A.R. 4480 (= 126652)	HM364295	HM364308	HM364346	HM352861	HM352876	
	G.J.S. 02-67 (= CBS 125109)	HM364300	HM364320	HM364354	HM352867	HM352886	
Neo. jungneri / Cyl. victoriae (T)	C.T.R. 71-244	HM364299	HM364319	HM364353	HM352866	HM352885	HM364336
Neo. liriodendri / Cyl. liriodendri (I)	CBS 112602	HM364302	HM364323		HM352853		
Neo. macrodidyma / Cyl. macrodydimum (I)	CBS 112615		HM364315			HM352883	HM364333
Neo. neobalansae / Cyl. sp. (R)	G.J.S. 85-219 (= CBS 125120)		HM364322		HM352869		
Neo. neomacrospora / Cyl. cylindroides var. *cylindroides*	CBS 198.62		HM364316	HM364351	HM352865		
	CBS 324.61		HM364318	HM364352	HM352854		HM364335
Neo. radicicola / Cyl. destructans (I)	A.R. 2553 (= ATCC 208837)	HM364290	HM364304	HM364341	HM352856	HM352871	HM364325
Neo. ramulariae / Cyl. obtusiusculum	ATCC 16237	HM364297	HM364310	HM364349	HM352863	HM352879	HM364329
	CBS 151.29	HM364303	HM364324	HM364340	HM352855		

Table 1. (Continued).

Species (sexual/asexual state)**	Isolate	Isolate					
		ITS	LSU	*tef1*	*tub*	*act*	*rpb1*
Neo. rugulosa / *Cyl. rugulosum* (R)	TPPH 32	AB233176*			AB237526*		
Neo. trachosa / *Cyl.* sp. (T)	CBS 112467		HM364312	HM364356			HM364339
Neo. veuillotiana / *Cyl. candidulum* (T)	G.J.S. 90-48 (= CBS 125118)			HM364357	HM352870	HM352888	HM364338
Neo. westlandica / *Cyl.* sp. (T)	G.J.S. 83-156 (= CBS 112464)		HM364321	HM364355	HM352868	HM352887	HM364337
Neocosmospora vasinfecta / *Acremonium*-like	A.R. 3587	HM484864		HM484842	HM484881		
Ophionectria trichospora / *Antipodium spectabile*	G.J.S. 01-206	HM484867		HM484847	HM484886		
	CBS 109876		AF543790*				AY489669*
Pseudonectria rousseliana / *Volutella buxi*	ATCC-MYA 627		U17416*				AY489670*
Rubrinectria olivacea / *Nalanthamala* sp.	CBS 102268	AY554219*	AY554244*		AY554238*		
Selinia pulchra /	A.R. 2812	HM484859	GQ505992*	HM484841	HM484884	GQ505982*	GQ506022*
Verrucostoma freycinetiae / *Acremonium*-like	MAFF240100/h523	HM484866	GQ506013*	HM484853	HM484885	GQ505984*	GQ506018*
Viridispora diparietispora / *Penicillifer furcatus*	CBS 114049		AY489735*				AY489668*

*Sequences obtained from GenBank.

** Letters in parenthesis represent their classification in the newly segregated genera. I: *Ilyonectria*; R: *Rugonectria*; T: *Thelonectria*.

Table 2. Genes/loci used in the phylogenetic analyses. Information on the primers, included bases pairs, PCR protocols, and models of nucleotide substitution are indicated.

Locus	Primers used (reference)	PCR protocol: Annealing temp. & cycles	Nucleotide substitution models	Included sites (# of excluded sites)	Phylogenetically informative sites (%)	Uninformative polymorphic sites	Invariable sites
ITS	ITS5, ITS4 (White *et al.* 1990)	53 °C, 1 min, 35´	GTR+G	670 (136)	230 (34 %)	95	345
LSU	LR5, LROR (Vilgalys n.d.)	53 °C, 1 min, 35´	TIM+I+G	915 (0)	142 (16 %)	44	729
Tef1	*tef1*-728, *tef1*-986 (Carbone & Kohn 1999)	66 °C, 55 s, 9´ 56 °C, 55 s, 35´	GTR+I+G	707 (524)	200 (20 %)	39	468
Tub	B*tub*-T1, B*tub*-T2 (O'Donnell & Cigelnik 1997)	55 °C, 30 s, 35´	HKY+I+G	535 (127)	260 (26 %)	49	226
Act	T*act*1, T*act*2 (Samuels *et al.* 2006)	65 °C, 30 s, 15´ 48 °C, 30 s, 30´	GTR+I+G	635 (0)	149 (15 %)	37	4498
Rpb1	c*rpb1*a, *rpb1*c (Castlebury *et al.* 2004)	50 °C, 2 min, 40´	GTR+I+G	722 (52)	378 (52 %)	61	283
Total				4184	1359 (33 %)	325	2500

The type species of *Neonectria, N. ramulariae,* and *Cylindrocarpon, C. cylindroides*, fall in the *N. coccinea*-group, *i.e. Neonectria/Cylindrocarpon sensu stricto* (94 % BP, 100 % PP) (Fig. 1), part of Clade B. This group also includes *N. ditissima* and *N. fuckeliana*. Morphological characteristics of the *Neonectria/Cylindrocarpon sensu stricto* clade include perithecia aggregated in an erumpent stroma, perithecial walls generally composed of two regions, somewhat ornamented ascospores, and macroconidia that are generally > 3-septate, cylindrical, and straight (Table 3). This clade is sister to the *N. radicicola*-group (Clade B). The monophyly of the *N. radicicola*-group is supported by 98 % BP and 100 % PP (Fig. 1). Characteristics of the teleomorph and anamorph clearly separate the *N. radicicola*-group from *Neonectria/Cylindrocarpon sensu stricto* (Table 3). Perithecia in the *N. radicicola*-group are superficial on the substrate and have a distinctive perithecial wall structure, smooth ascospores, and macroconidia that are straight, < 3-septate, with a prominent basal hilum.

The *N. rugulosa* group is sister to the *N. mammoidea/veuillotiana*-group and *Campylocarpon* (Clade A). The *N. rugulosa*-group is monophyletic (100 % BP, 100 % PP). It contains species with warted perithecia and a perithecial wall structure generally different that the *N. radicicola*-group and *Neonectria/Cylindrocarpon sensu stricto,* striate ascospores, microconidia, and no chlamydospores (Table 3). The clade that includes the *N. mammoidea/veuillotiana*-group is also supported by high BP and PP values (70 % BP and 100 % PP). Species in this clade have a perithecial wall comprised of thick-walled cells, a knobby or prominent apex, spinulose or tuberculate ascospores, and generally no microconidia or chlamydospores. *Campylocarpon* sequences form a distinct clade sister to the *N. mammoidea*-group and is supported by 100 % BP and 100 % PP. No teleomorph is known for *Campylocarpon*.

Table 3. Comparison of major diagnostic morphological characteristics between the newly segregated genera.

Character	*Campylocarpon* (Clade A)	*Rugonectria* (Clade A)	*Thelonectria* (Clade A)	*Ilyonectria* (Clade B)	*Neonectria* (Clade B)
Teleomorph groups (Booth 1959, Brayford & Samuels 1993, Samuels & Brayford 1994)	–	*N. rugulosa*-group	*N. mammoidea* /*veuillotiana*-groups	*N. radicicola*-group	*N. coccinea*-group
Anamorph groups (Booth 1966)	–		Group 2	Group 3	Groups 1 & 4
Arrangement of perithecia on substrate	Teleomorph unknown	Perithecia, formed on, or sometimes partially immersed within a stroma	Perithecia solitary or in groups, superficial, sometimes seated on an immersed inconspicuous stroma	Generally solitary and loosely attached to substrate	Perithecia clustered on wood, generally seated on an erumpent stroma
Perithecial apex	–	Non-papillate	Most species with a prominent, areolate (darkened) papilla, if not, then at least with a darkly pigmented apex	Broadly conical papilla	Blunt or acute apex, rarely papillate
Perithecial wall	–	Warted, 50–150 µm thick; outer region, including warts, of thick-walled (3–4 µm), globose, 10–20 µm diam; perithecial wall merging with surrounding stroma	Smooth or sometimes warted, 20–50 (–100) µm thick; outer region of intertwined hyphae or cells lacking a definite outline, *i.e. textura epidermoidea*	Generally smooth to slightly roughened, 35–50 µm thick; outer region of thin-walled, globose, large cells	Generally smooth and shiny, sometimes scurfy, 35–50 µm thick; outer region of small, angular to globose, thick-walled cells (*textura epidermoidea* in one species)
Ascospores	–	1-septate, striate	Generally 1-septate, smooth, rarely spinulose or striate	1-septate, smooth	1-septate, smooth or finely ornamented
Macroconidia shape	Fusiform, curved, often broadest at upper third, with rounded apical cells and flattened or rounded basal cells, inconspicuous hilum	Fusiform, curved, tapering towards ends (almost *Fusarium*-like), inconspicuous hilum	Fusiform, curved, often broadest at upper third, with rounded apical cells and flattened or rounded basal cells, inconspicuous hilum	Cylindrical, straight, rounded ends, prominent basal hilum	Cylindrical, generally straight, sometimes slightly curved toward ends, with rounded ends (except in one species, *N. fuckeliana*, which has fusiform straight conidia with pointed ends); inconspicuous hilum
Macroconidia septation	(1–) 3–5 (–6)-septate, average 4 septa	(3–) 5–7 (–9)-septate	(3–) 5–7 (–9)-septate, average 5	1–3-septate, rarely > 3-septate	3–7 (–9)-septate, average 5-septate
Macroconidia size	(24–) 35–60 (–62) × 6.5–9 µm	(35–) 48–85 × 5–10 µm	(35–) 40–90 (–110) × 4–8 (–11) µm	25–50 (–55) × 5–7.5 µm	35–65 (–110) × 4–7 (–8) µm
Microconidia shape	Absent	Ovoid to cylindrical, hilum inconspicuous	Microconidia rare (seen only on natural substrate)	Ellipsoidal, prominent basal hilum	Ellipsoidal to oblong, inconspicuous hilum
Microconidia size	Absent	(3–) 5–15 (–20) × 2–5 µm	–	3–15 × 2.5–5 (–6) µm	(2–) 6–10 (–15) × (1–) 2–5 (–6) µm
Chlamydospores	Uncommon	Absent	Uncommon (except in *T. olida* = *C. olidum*)	Abundant, generally intercalary, single or in chains, becoming brownish	Present in some species
Substrate	Pathogenic on roots and stems of grapevines	On bark of recently killed, dying or diseased trees, often causing cankers	On bark of recently killed, dying or diseased trees, often causing small cankers, sometimes on rotting roots	Generally a root pathogen. Anamorph common in the soil. Perithecia found mostly on decaying herbaceous material, sometimes branches or roots.	Generally on bark, sometimes causing cankers
Geographic distribution	South Africa, Uruguay	Widespread	Widespread, but more common in tropical regions	Widespread	Mostly in temperate regions

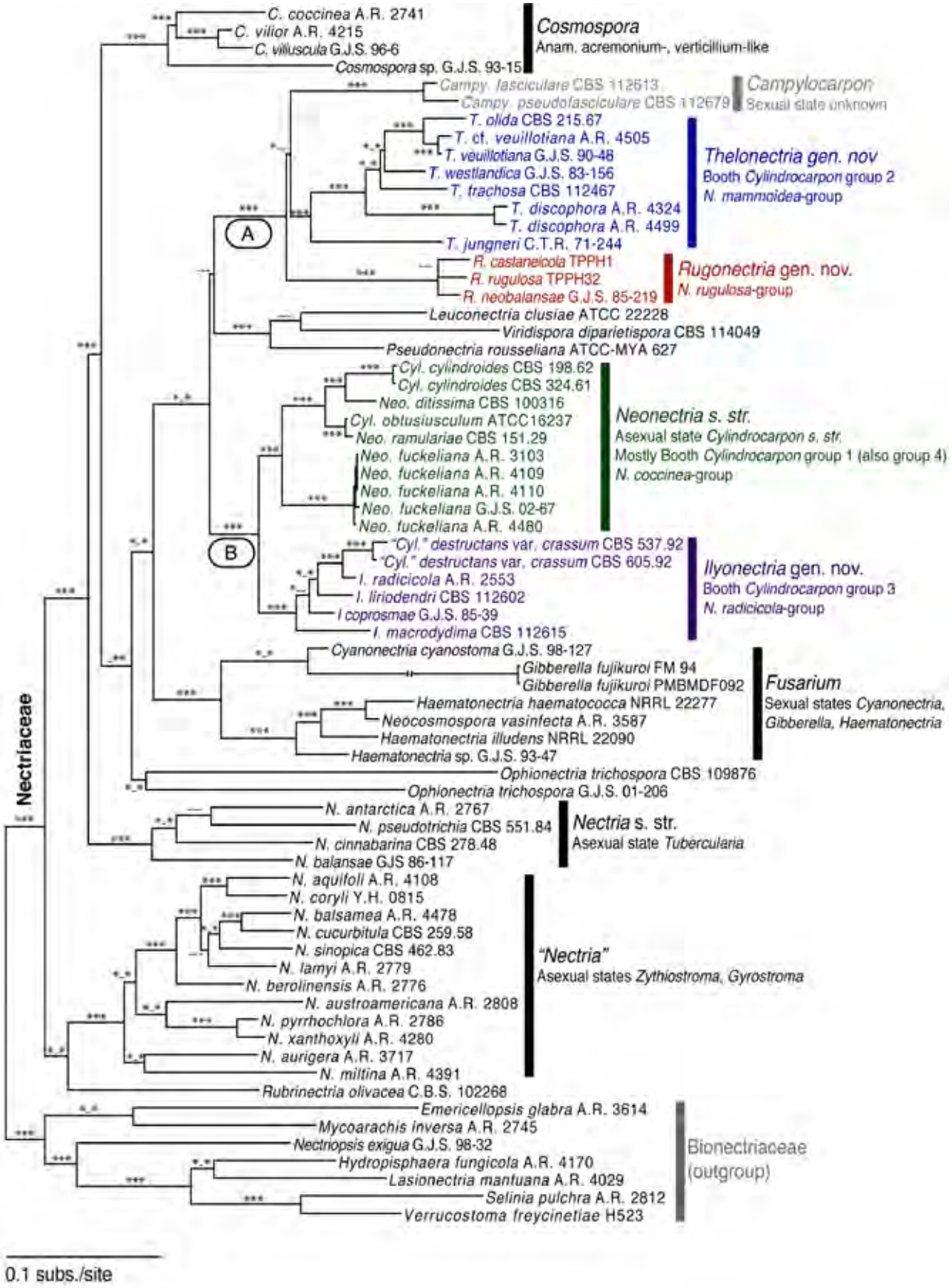

Fig. 1. Multilocus phylogenetic tree (Bayesian Inference) with the best log likelihood (-44959.23). Support values indicated at nodes. Bayesian posterior probabilities ≥ 90 %, Maximum Likelihood bootstrap ≥ 70 % and Phycas posterior probabilities ≥ 90 % indicated by ***. If less than those values, then indicated by -. *Cylindrocarpon*-like anamorphs are in two paraphyletic clades: A and B.

Morphological characterisation

Presence or absence of a stroma

In many cases perithecia are solitary, either seated directly on the substratum in the *N. radicicola*-group or on a minute basal stroma in the *N. mammoidea/veuillotiana*-group. In other cases, such as in *N. discophora* and *N. lucida*, perithecia are seated amidst erect hyphae that arise from a basal, almost inconspicuous stroma. A characteristic of *N. coccinea*, *N. fuckeliana* and other species of *Neonectria sensu stricto* and *N. rugulosa*-group is that they form in great numbers on a rather extensive, subcortical, basal stroma. An extensive stroma may also form in *N. jungneri*, but is not as conspicuous as in *Neonectria sensu stricto* and the *N. rugulosa*-group.

Perithecial wall

The perithecial wall of species of *Neonectria sensu lato* comprises at least two regions. The inner region is very thin, consisting of only a few layers of thin-walled, tangentially flattened cells lining the locule where the spores are formed. The outer regions vary. Essentially four distinctive types of outer perithecial walls are found among the groups studied here. In the *N. radiciola*-group the outer region of the perithecial wall is formed of one or two layers of large, round, thin-walled cells. This anatomy can be discerned even in whole mounts of perithecia. In species that have this anatomy, the surface of the perithecial wall, when seen in face view, is of large, round cells, mirroring what is seen in sections. The second perithecial wall anatomy consists of an outer region that is a palisade of short hyphae that are perpendicular to the locule, *e.g.* in the *N. mammoidea*-group. When seen in face view cells at the surface of the perithecium are small, < 5 µm diam. In some species, such as *N. trachosa* and *N. westlandica*, a superficial layer of large, angular cells that form warts obscure the palisade. When there is a palisade but no outer layer of large cells, the perithecial surface may be smooth and shiny. This wall anatomy typifies some members of the *N. mammoidea*-group, *e.g. N. discophora, N. lucida, N. westlandica;* and *N. fuckeliana* in *Neonectria sensu stricto*. The wall of species such as *N. coronata* or *N. jungneri*, both in the *N. mammoidea/veuillotiana*-group, which lacks any apparent cellular structure, is formed of intertwined hyphae having a seemingly random arrangement rather than a palisadal arrangement. The third perithecial wall type is characterised by the formation of thick-walled, round cells in the outer region that can be seen in section and in face view. This wall type characterises species of *Neonectria sensu stricto*. The fourth type of perithecial wall is that of the *N. rugulosa*-group. The perithecial wall is thick, 50–150 µm, with the outer region formed of several layers of cells, including warts, with small globose cells that are very thick-walled and merge with the surrounding stroma.

Ascospores

Although some species of *Neonectria* have been reported to have multiseptate ascospores (Rossman 1983, Samuels & Brayford 1993), the ascospores of the species included in the present study are bicellular. There is a tendency towards having spinulose ornamentation but there are exceptions. In species such as *N. veuillotiana* the ascospores may be nearly tuberculate. In *N. jungneri* the spores are coarsely striate. In *N. coronata* the spinules may be arranged in lines giving the appearance of striations. Ascospores of most species are hyaline, but, in *N. discophora, N. lucida*, and *N. westlandica,* the spores become pale yellow-brown. A species not included in the present study, *Nectria viridispora*, probably in the *N. mammoidea*-group, has green ascospores. Ascospores of species in *Neonectria sensu stricto* and the *N. radicicola*-group are smooth. Species in the *N. rugulosa*-group have striate ascospores, sometimes inconspicuous; cotton blue may be needed to observe these striations.

Paraphyses

The *Nectria*-type centrum (Luttrell 1951) is characterised by the formation of "apical paraphyses," filaments that originate in a meristem situated at the top of the locule. Typically these filaments have dissolved by the time the ascospores form but often chains of saccate cells may persist among maturing asci. Most species of *Neonectria sensu stricto* have filaments that appear to be free at the apex and thus resemble paraphyses. These paraphyses are septate and constricted at each septum. The paraphyses are abundant especially in *N. fuckeliana*.

Conidiophores and phialides

Most conidiophores, especially those that give rise to the macroconidia, are formed laterally from hyphae; they are irregularly branched or form fascicles. In the case of *Neonectria sensu stricto* and the *N. rugulosa*-group, the macroconidia are produced from irregularly branched conidiophores or fascicles, and the microconidia from simple, generally unbranched, conidiophores. In the case of the *N. radicicola*-group, macro- and microconidia apparently originate from the same type of conidiophore. These are simple, unbranched or sparsely branched, irregularly or verticillately branched, or rarely densely branched. The *N. mammoidea/veuillotiana*-group and *Campylocarpon* produce only macroconidia that originate from irregularly branched conidiophores or fascicles. The morphology of the phialides is highly conserved. Phialides are generally long and cylindrical or somewhat flask-shaped, but mostly long.

Macro- and microconidia

Although the average size of the macroconidia varies among the groups, there is significant overlap. *Campylocarpon,* the *N. radicicola*-group, and *Neonectria sensu stricto* have macroconidia 25–65 × 4–9 µm, smaller than those of the *N. mammoidea/veuillotiana*- and *N. rugulosa*-groups that are 40–90 × 4–10 µm. With respect to shape, species in Clade A (Fig. 1) have curved macroconidia and species in Clade B have straight macroconidia. Within Clade A, macroconidia of the *N. rugulosa*-group can be easily distinguished from those in *Campylocarpon* and the *N. mammoidea/veuillotiana*-group. Species in *N. rugulosa*-group have curved, fusoid macroconidia with tapering ends that are almost *Fusarium*-like. *Campylocarpon* and the *N. mammoidea/veuillotiana*-group also have curved macroconidia but with rounded ends. Even though the macroconidia of *Campylocarpon* and the *N. mammoidea/veuilotiana*-group are similar, they can be distinguished on the basis of septation. *Campylocarpon* has 3–5-septate macroconidia while the *N. mammoidea/veuilotiana*-group has 5–7-septate macroconidia. Regarding septation of macroconidia, most species have on average five septa, with exceptions. On average species of *Campylocarpon* have four septa, the *N. radicicola*-group have up to three septa with exceptions, and *N. jungneri* (*N. mammoidea*-group) has generally > 5 septa. Microconidial morphology is highly conserved. They are generally ellipsoidal, 0–1-septate and measure 3–15 × 2–5 µm. Only the *N. radicicola*-group has microconidia with a prominent hilum or abscission scar. No microconidia are formed in the *N. mammoidea/veuillotina*-group and *Campylocarpon*. Some species in *Neonectria*

sensu stricto may produce microconidia, but not as abundantly as in the *N. radicicola*- and *N. rugulosa*-groups. The only exception is *N. fuckeliana* in which microconidia are abundant and macroconidia are infrequently seen.

Chlamydospores

Chlamydospores are formed in the *N. radicicola*-group, in a few species in *Neonectria sensu stricto*, and are rarely formed in *Campylocarpon*. Species in the *N. rugulosa*-group rarely produce swollen and slightly pigmented hyphae that resemble chlamydospores. Most species in the *N. mammoidea/veuillotiana*-group do not produce chlamydospores, except in *Cylindrocarpon olidum*. The chlamydospores of the *N. radicicola*-group are generally intercalary, single or in chains, and yellow-brown. When produced in *Campylocarpon*, they are mostly terminal, single, or in chains of 2–3, and also yellow-brown.

Ecology

Species of *Neonectria sensu lato* and *Cylindrocarpon sensu lato* are either saprobes or plant pathogens. The only two known *Campylocarpon* species cause black foot disease of grapevines. Species in the *N. mammoidea/veuillotiana*-group are only known as saprobes growing on bark of recently killed woody trees. The only exception is *Cylindrocarpon olidum*, which has been reported as a root pathogen. Members of the *N. rugulosa*-group and *Neonectria sensu stricto* also grow on bark of recently killed trees and many species, *e.g. N. castaneicola, N. ditissima, N. faginata*, *N. rugulosa* among others, can cause cankers. In contrast, species in the *N. radicicola*-group are generally found in the soil and cause many root diseases. Based on the present study, the species that are commonly found in the soil causing root rots are the ones that produce chlamydospores. On the other hand, the species that grow on bark do not produce chlamydospores. Members of the *N. rugulosa*- and *N. radicicola*-groups are widespread, *N. mammoidea/veuillotiana*-group are mostly tropical and subtropical, *Neonectria sensu stricto* occur in temperate regions, and *Campylocarpon* is known only from South Africa and Uruguay (Abreo *et al*. 2010).

DISCUSSION

Genus concept

Several morphological characteristics of the teleomorphs and anamorphs have been used in defining informal groups in *Nectria sensu lato*. In the case of *Neonectria* and *Cylindrocarpon* groups (*e.g.* Booth 1959, 1966), they have been distinguished by the anatomy of the outer regions of the perithecial wall and presence or absence of microconidia and chlamydospores. Results from this study confirm previous suggestions that *Neonectria/Cylindrocarpon* is paraphyletic, comprising five independent lineages that may be interpreted as distinct genera. These segregate genera usually cannot be distinguished based on a single morphological or ecological character. However, the lineages or segregate genera correlate strongly with a combination of ecology and morphological characters of the perithecia and anamorphs (Table 3). Thus, the following genera are recognised: (1) *Neonectria/Cylindrocarpon sensu stricto* (*N. coccinea*-group); (2) *N. rugulosa*-group, hereafter *Rugonectria* gen. nov.; (3) *N. mammoidea/veuillotiana*-group, hereafter *Thelonectria* gen. nov.; (4) *N. radicicola*-group, hereafter *Ilyonectria* gen. nov.; and (5) *Campylocarpon.* The *Neonectria* and *Cylindrocarpon* groups defined by Booth (1959, 1966) based on morphological characters generally agree with the clades observed in the multilocus phylogeny (Fig. 1).

Based on the morphological similarity between *Campylocarpon* and *Thelonectria*, it could be argued that these two are congeneric. However, phylogenetic analyses do not support the monophyly of these two genera (short branch length, and low BP and PP supports, Fig. 1). Therefore, *Campylocarpon* and *Thelonectria* are recognised as separate. Several morphological and ecological traits aid in distinguishing these two genera (Table 3).

Although Clades A and B (Fig. 1) could be recognised as two genera, the multiple morphological and ecological traits of each of the five segregate genera are distinctive enough to justify their taxonomic subdivision. There are other similar cases in the Ascomycota. For example, although genera with fast-growing *Fusarium* anamorphs form a monophyletic group, they are still recognised as separate genera and have morphologically different teleomorphs (*e.g. Albonectria, Cyanonectria, Gibberella*, and *Haematonectria*) (O'Donnell 1996, Samuels *et al.* 2009, Luo & Zhuang 2010a). Another example is *Calonectria/Cylindrocladium* and related genera. *Glionectria/Gliocladiopsis, Nectricladiella/Cylindrocladiella,* and *Xenocalonectria/Xenocylindrocladium* all have similar anamorph and teleomorph morphology and were previously classified in *Calonectria*. Later they were segregated from *Calonectria/Cylindrocladium* based mostly on anamorph characteristics even though they form a monophyletic group (Rossman 1983, 1993, Schoch *et al.* 2000, Crous 2002, Samuels *et al.* 2009, Luo & Zhuang 2010a). A third example is *Botryosphaeria sensu lato*. Many recognised monophyletic anamorphic genera, *e.g. Fusicoccum*, *Lasiodiplodia,* and *Neofusicoccum* among others, are associated with *Botryosphaeria* teleomorphs, yet, *Botryosphaeria s. l.* forms a monophyletic group (Crous *et al.* 2006).

Results from the present study show that *Neonectria fuckeliana* clusters with *Neonectria/Cylindrocarpon sensu stricto*, and *T. jungneri* with *Thelonectria*. The branch lengths (substitutions/site) that separate these species from *Neonectria/Cylindrocarpon sensu stricto* and *Thelonectria*, respectively, are similar to the branch lengths between *Thelonectria* and *Rugonectria* (Fig. 1). This could be interpreted as evidence that *N. fuckeliana* or *T. jungneri* should be recognised as distinct genera. However, these species are not separated due to the lack of additional morphologically similar species and to avoid monotypic genera with further splitting of genera. It is possible that the addition of morphologically similar species will support the establishment of new genera.

Neonectria/*Cylindrocarpon sensu stricto*

Neonectria/Cylindrocarpon sensu stricto is characterised by having few to numerous perithecia clustered on wood and seated on an erumpent stroma; perithecial walls are generally composed of two regions with the outer region comprising small, thick-walled cells; generally septate paraphyses; smooth or finely ornamented ascospores; generally straight, typically 5-septate macroconidia with rounded ends; either microconidia or chlamydospores formed, generally not both; and, if microconidia are present, they are produced from simple, generally unbranched, conidiophores and lack a prominent abscission scar. Anamorphs of *Neonectria/Cylindrocarpon* belong in Booth's groups 1 and 4 (Booth 1966).

Neonectria/Cylindrocarpon sensu stricto species are mostly found in temperate regions on woody substrata, *e.g.* bark, often

causing cankers, and rarely found in soil. This genus includes species such as *N. coccinea/C. candidum, N. ditissima/C. heteronemum, N. faginata/C. faginatum, N. fuckeliana/C. cylindroides* var. *tenue, N. hederae/C. hederae, N. major/ Cylindrocarpon* sp., *N. neomacrospora/C. cylindroides, N. punicea/C. album,* and *N. ramulariae/C. obtusiusculum* (Castlebury *et al.* 2006). The monophyly of the *N. coccinea*-group was shown in Castlebury *et al*. (2006). Although some authors suggested that *N. fuckeliana* belongs in the *N. mammoidea*-group based on the morphology of the perithecia (Booth 1959, Brayford *et al.* 2004), this study supports more recent accounts that place this species close to *Neonectria sensu stricto* (Halleen *et al.* 2004, Castlebury *et al.* 2006, Luo & Zhuang 2010b).

The teleomorph of the type species of *Neonectria, N. ramulariae,* apparently has not been collected again since it was described by Wollenweber (1917) (Rossman *et al.* 1999). Rossman *et al*. (1999) examined the type specimen and noted that it had only immature perithecia along with its anamorph, *C. obtusiusculum* (= *C. magnusianum* Wollenw. 1928 non Wollenw. 1926). Domsch *et al*. (1980) followed Wollenweber (1928) in recognising *N. ramulariae* to be the teleomorph of *C. obtusiusculum* (then known as *C. magnusianum*), based on the anamorph present in the type specimen of *N. ramulariae*. Although Rossman *et al*. (1999) designated an iconotype for *N. ramulariae*, new collections of the anamorph and teleomorph are needed to better describe *N. ramulariae/C. obtusiusculum*. The morphology of *C. obtusiusculum* is similar to the anamorphs in *Ilyonectria*. However, the lignicolous habit, straight macroconidia, absence of microconidia, absence of a prominent basal abscission scar or hilum, and molecular phylogenetic analyses place *C. obtusiusculum* in *Neonectria/ Cylindrocarpon sensu stricto*.

The segregate genera: *Campylocarpon, Ilyonectria, Rugonectria,* and *Thelonectria*

A sister clade to *Neonectria/Cylindrocarpon, Ilyonectria* (*N. radicicola*-group), is described here based on *Ilyonectria radicicola* comb. nov. (anamorph *C. destructans*). Anamorphs in *Ilyonectria* belong in Booth's group 3 (Booth 1966). Contrary to *Neonectria/ Cylindrocarpon*, *Ilyonectria* and its anamorphs are common in the soil and rhizosphere or as agents causing root rots. Chlamydospores are generally present in species of *Ilyonectria,* possibly as an adaptation for survival in soil. Chlamydospores are generally absent in species that are associated with bark or cankers, *e.g. Neonectria, Rugonectria* and *Thelonectria*. Perithecia in *Ilyonectria* are not as commonly encountered as the anamorphs, and, if found, they are mostly on herbaceous substrata. The species of this genus are cosmopolitan and are found on a wide range of hosts.

Neonectria-like species included here in *Ilyonectria* are: *I. coprosmae/C. coprosmae, I. liriodendri/C. liriodendri, I. macrodydima/C. macrodydimum,* and *I. radicicola/C. destructans* (Samuels & Brayford 1990, Seifert *et al.* 2003, Halleen *et al.* 2004, 2006). The monophyly of species in *Ilyonectria*, viz. the *N. radicicola*-group, has also been shown in previous studies (Seifert *et al.* 2003, Halleen *et al.* 2004, 2006). These studies suggest that *C. destructans* is a species complex. Thus, defining *C. destructans sensu stricto* through the examination of many cultures derived from ascospores as well as cultures isolated directly from diverse substrata is a necessary future endeavour. Many other species have been described that may fit in *Ilyonectria*.

Rugonectria gen. nov. (*N. rugulosa*-group) is described here based on *Rugonectria rugulosa* comb. nov. (anamorph *C. rugulosum*). Members of the genus occur on recently killed or dying woody substrata, mostly bark, and are sometimes found causing cankers. Some species of *Neonectria* now included in *Rugonectria* are: *R. castaneicola/C. castaneicola*, *R. neobalansae,* and *R. rugulosa/C. rugulosum*. Another species that may fit in *Rugonectria* is *Nectria pulcherrima* (Samuels & Brayford 1994). This species has multiseptate, curved macroconidia with tapering ends, microconidia, and warted perithecia that are caespitose, somewhat immersed in an erumpent stroma, all characteristics of *Rugonectria*. This species is morphologically similar to *R. neobalansae*. A new combination has not been made due to the lack of DNA data to confirm its phylogenetic placement.

The new genus *Thelonectria* is established here to accommodate species in the *N. mammoidea*- and *N. veuillotiana*-groups. Species of *Thelonectria* are mostly tropical and subtropical, and are found on bark of recently killed or dying trees, often causing small cankers, rarely in soil except in one species, *C. olidum*. Some species included in this genus are: *T. coronata/C. coronatum, T. discophora/C. ianothele, T. jungneri/C. victoriae, T. lucida/C. lucidum, T. olida*, *T. trachosa, T. veuillotiana/C. candidulum, T. viridispora*, and *T. westlandica* (Mantiri *et al.* 2001, Brayford *et al.* 2004). Anamorphs in *Thelonectria* belong in Booth's group 2 (Booth 1966).

Although *Thelonectria* can generally be recognised by perithecia with prominent or darkened papilla, macroconidia that are curved with rounded ends, > 3-septate (average 5-septate), and absence of microconidia, some species deviate from this trend. For example, 3-septate macroconidia have been reported for *T. lucida* and *T. trachosa* (Booth 1966, Brayford *et al.* 2004). *Thelonectria trachosa* mostly forms 3-septate macroconidia, but > 3-septate macroconidia can be found in the same culture (Brayford *et al.* 2004). Brayford *et al*. (2004) reported that the majority of the *T. lucida* cultures formed > 3-septate macroconidia. Brayford *et al*. (2004) also suggested that *T. lucida* might comprise a species complex, thus, further taxonomic studies are needed to explain the morphological variation within this species. *Thelonectria lucida* and *T. trachosa* can be easily classified in *Thelonectria* based on the anatomy of the perithecia and curved macroconidia with rounded ends and absence of microconidia and chlamydospores. A similar case is *T. olida*, which produces 3–5-septate macroconidia and chlamydospores although Booth (1966) reports many > 3-septate macroconidia. This species is classified in *Thelonectria* based on the curved macroconidia with rounded ends and absence of microconidia. However, *T. olida* is difficult to distinguish from *Campylocarpon* based on morphology and ecology.

Conidia in *Campylocarpon* are similar to those in *Thelonectria*, as also reported by Halleen *et al*. (2004). The only morphological difference is the average number of septa in the macroconidia: four in *Campylocarpon* and five in *Thelonectria*. Despite the morphological similarity of the conidia, phylogenetic analysis distinguishes the two genera. *Campylocarpon* species were collected from diseased roots and stems of grapevines in South Africa. This is in contrast to most species of *Thelonectria*, which are found on above ground parts of woody plants. *Thelonectria olida,* associated with roots, is the exception.

Previous molecular phylogenetic studies (Mantiri *et al.* 2001, Brayford *et al.* 2004) did not show that the *N. rugulosa*-group was distinct from *N. mammoidea*-group, as suggested by Samuels & Brayford (1994). This was probably due to the few phylogenetically informative loci and few taxa that were used in those studies. The monophyly of the *N. rugulosa*-group (= *Rugonectria*) and its

close relationship to the *N. mammoidea/veuillotiana*-group (= *Thelonectria*) are shown here (Fig. 1). *Rugonectria* is distinguished from *Thelonectria* by perithecial anatomy, presence of microconidia in *Rugonectria*, and morphology of the macroconidia (Table 3).

As has been the case with several groups of fungi (Chaverri *et al.* 2003, Frisvad & Samson 2004, Schmidt *et al.* 2004, Samuels *et al.* 2006a, Chaverri *et al.* 2008, Degenkolb *et al.* 2008, Andersen *et al.* 2009), a multiphasic approach, *i.e.* using a combination of independently derived characters such as morphological, ecological, and molecular phylogenetic, is necessary to identify monophyletic groups with *Neonectria*/*Cylindrocarpon*-like morphology. For example, the presence of microconidia alone is not useful to identify groups with *Cylindrocarpon*-like morphology, because microconidia are always present in *Ilyonectria* and *Rugonectria*, sometimes present in *Neonectria*, and absent in *Thelonectria*, and their morphology is highly conserved. However, if characters are combined such as the presence of 3-septate, straight macroconidia with a prominent abscission scar, presence of chlamydospores, and perithecia with a particular wall anatomy, they can be used to classify a particular specimen as *Ilyonectria*. Thus, in this study our genus concept is based on a multilocus phylogenetic analyses correlated with a combination of multiple morphological and ecological characters. Each of the proposed genera is further described in the Taxonomy section.

Species of *Neonectria*/*Cylindrocarpon* of uncertain classification

In this study we present a general overview of genera with *Neonectria*/*Cylindrocarpon*-like morphology. There are still species classified in *Neonectria* and *Cylindrocarpon* that have teleomorph and anamorph morphology different than those presented here and also quite distinct from *Neonectria/Cylindrocarpon sensu stricto*. Additional specimens, cultures, and DNA sequences are needed to infer their phylogenetic position within the *Nectriaceae*. For example, *Neonectria macroconidialis* has morphological characteristics of both *Neonectria sensu stricto* and *Ilyonectria*. This species is not formally included in *Ilyonectria* because phylogenetic studies including this species in the ITS tree (Seifert *et al.* 2003, Halleen *et al.* 2004) show low bootstrap support for the clade with *N. macroconidialis* and other species in the *N. radicicola*-group. In contrast, the β-tubulin tree places *N. macroconidialis* basal and outside the *N. radicicola* complex. Therefore, the phylogenetic position of this species is uncertain. The straight macroconidia, prominent basal hilum, and anatomy of the perithecia suggest that *N. macroconidialis* belongs in *Ilyonectria*. However, the > 4-septate macroconidia, a characteristic of *Neonectria sensu stricto,* would be an exception if this species were included in *Ilyonectria*. This species and others previously placed in the *N. radicicola*-group (Samuels & Brayford 1990) are morphologically atypical of this group, specifically *N. austroradicicola/C. austrodestructans* and *N. radicicola* variant ex *Gahnia*.

Brayford & Samuels (1993) described three species of *Nectria* with *Cylindrocarpon*-like anamorphs and mentioned that they could not be classified in any of the then recognised groups of *Nectria*. *Nectria neblinensis* and *N. verrucospora* are distinct because they have macroconidia that are torpedo-like, viz. straight, wider near the middle or towards the base, and tapering and truncated at the ends. The perithecial wall anatomy somewhat resembles *Rugonectria*, but the ascospores in these two species are warted and not striate as in *Rugonectria*. Other species that have been placed in *Cylindrocarpon* that have torpedo-like macroconidia are *C. fusiforme*, *C. supersimplex*, and *N. laetidiscoides*; however, these are straight in the middle and the terminal cells taper almost to a point (Matsushima 1975, Samuels & Brayford 1993).

Several species previously classified in *Neonectria/Cylindrocarpon* are distinct from those treated here because they have phragmosporous ascospores, *e.g. N. fusispora*, *N. laetidisca*, *N. laetidiscoides*, *N. phaeodisca*, *N. philodendri*, *N. septospora* and *N. vermispora* among others (Rossman 1983, Samuels & Brayford 1993). Most of the above appear to belong in *Thelonectria*, or at least they are closely related, except *N. laetidiscoides* and *N. septospora*, which have distinct macroconidia.

Another species with uncertain affinity is *N. cinnamomea*. The perithecia do not change colour in 3 % KOH, a typical characteristic of members of the *Nectriaceae* (Brayford & Samuels 1993). In addition, the perithecial wall is completely different from the genera treated in this study or any other genus in *Nectriaceae*, and the ascospores have a conspicuous wrinkled sheath. The macroconidia are also distinct; they are curved, fusiform, and 3-septate.

Luo & Zhuang (2010b) described *Neonectria shennongjiana* based mostly on the distinctive macroconidia that are cylindrical-clavate to clove-shaped. The phylogenetic analysis in Luo & Zhuang (2010b) shows that *N. shennongjiana* may be closely related to *Neonectria sensu stricto*. Their parsimony cladogram reveals that *N. shennongjiana* clusters within *Neonectria sensu stricto* (BP 72 % if *N. fuckeliana* is included). However, in their phylogenetic tree based on parsimony analysis of two loci (ITS nrDNA and *tub*), the position of *N. shennongjiana* is not clear. The bootstrap value supporting the clade of *N. shennongjiana* and *C. obtusisporum* is low (62 %). Additional phylogenetic and taxonomic studies are needed to confirm if *N. shennongjiana* and other species with odd-shaped macroconidia belong in *Neonectria s.str*. Another species with clove-shaped macroconidia is described in the literature, *i.e. Nectria lugdunensis* (Webster 1959), the teleomorph of *Heliscus lugdunensis*.

TAXONOMY

Many of the species of *Neonectria sensu lato,* including those considered here, are known in both their teleomorph and anamorph states. Although Article 59 of the International Code of Botanical Nomenclature (ICBN) allows the use of two scientific names for some groups of pleomorphic fungi including ascomycetes, a trend exists toward the use of just one scientific name for each species regardless of the state manifested (Rossman & Samuels 2005, Rossman 2009). Additionally, generic names of asexual fungi are now being used in a narrower, phylogenetic sense rather than as broad form-genera that encompass unrelated fungi. For example, the genus *Verticillium sensu lato*, which traditionally included many species with verticillate branching, has been segregated into distinct phylogenetic genera in spite of morphological similarities. Recently, *Verticillium sensu stricto* was conserved with a different type so that it represents the plant pathogenic species such as *V. alboatrum* and *V. dahliae* (Zare *et al.* 2004). Moreover, other genera separated from *Verticillium sensu stricto* are now recognised based on distinctive morphological and ecological characteristics, *e.g. Lecanicillium* and *Pochonia* (Gams & Van Zaayen 1982, Zare *et al*. 2000, Gams & Zare 2001, Zare & Gams 2001a, b, Zare *et al*. 2001).

The anamorphs of *Neonectria sensu lato* have been classified in the genus *Cylindrocarpon*. Just as *Neonectria* is now conceived

in a narrow sense, the genus *Cylindrocarpon* is herein defined phylogenetically and restricted to only anamorphs of *Neonectria sensu stricto*. Thus, the anamorph name in *Cylindrocarpon* is listed for only those species that belong in *Neonectria sensu stricto*. However, for species in genera segregated from *Neonectria sensu lato* with an anamorph name in *Cylindrocarpon*, the scientific name of the anamorph is listed in quotes, *e.g.* "*Cylindrocarpon*" *destructans,* or as *Cylindrocarpon*-like, if no epithet exists, to indicate that it does not belong in *Cylindrocarpon sensu stricto*.

In this paper, some species described in *Cylindrocarpon* have no known teleomorph, but, phylogenetically, they fall into a recognised genus (*e.g. "C." olidum* = *Thelonectria olida* comb. nov). As permitted by the ICBN this scientific name is recombined in the new genus. Recent examples in the literature include Lombard *et al*. (2009), in which species are described in *Calonectria* despite the lack of known teleomorphs. Although it would be possible and correct according to ICBN Art. 59 to place these taxa into newly described or existing anamorph genera, this has not been done to avoid separating anamorph names from holomorph genera, which is redundant, confusing, and unnecessary. If and when a teleomorph were discovered for this species and a new name were proposed for it, at present, priority would be given to that teleomorph name rather than the anamorph name. Alternatively, the anamorph name could be epitypified with an element that represents the teleomorph in accordance with ICBN Art. 59.7. Given the confusion that has arisen because of the dual nomenclature associated with pleomorphic fungi and the usefulness of molecular systematics in determining the accurate taxonomic placement of asexually reproducing fungi, it would seem expedient to move toward the use of only one scientific name for all fungi.

KEY TO SEGREGATE GENERA OF *NEONECTRIA/CYLINDROCARPON*

1. Perithecia generally on herbaceous material, rarely on bark or woody parts; perithecia superficial, loosely attached to substratum; perithecial wall of two regions, outer region of thin-walled (*ca*. 1 µm), globose, large cells; ascospores smooth; anamorph in soil, generally associated with diseased roots; microconidia generally with a prominent abscission scar; chlamydospores present; macroconidia straight, generally < 3-septate, generally with a prominent abscission scar ..... *Ilyonectria*
1. Perithecia and macroconidia not as above 2

2. Perithecia smooth to slightly roughened, generally red, with a prominent papilla or non-papillate; ascospores generally smooth or slightly ornamented; microconidia present or absent; chlamydospores present or absent; macroconidia curved or almost straight, with rounded ends, generally 3–5-septate; on bark or roots 3
2. Perithecia conspicuously warted, orange-red, generally aggregated, with an inconspicuous papilla, perithecial wall 50–150 µm thick; ascospores striate; microconidia present; chlamydospores absent; macroconidia fusiform with tapering ends; generally on bark of recently killed trees or causing small cankers ..... *Rugonectria*

3. Perithecia clustered on wood, generally seated on an erumpent stroma, generally smooth and shiny, sometimes scurfy with a blunt or acute apex, rarely papillate; perithecial walls of 2–3 regions, outer region of small, angular to globose, thick-walled cells, rarely of *textura epidermoidea*; many species with septate paraphyses; ascospores ellipsoidal, smooth or finely ornamented; either microconidia or chlamydospores present; macroconidia generally straight or slightly curved toward ends, rarely clove-shaped, with rounded ends, rarely tapering, 5–7-septate; chlamydospores rare; on bark of recently killed trees or forming cankers ..... *Neonectria*
3. Perithecia mostly aggregated, generally smooth and shiny, with a prominent papilla; ascospores generally ornamented; microconidia and chlamydospores absent; macroconidia curved, often broadest at upper third, with rounded apical cells and flattened or rounded basal cells, 3–7-septate; on bark of recently killed trees, on small cankers, or diseased roots 4

4. Teleomorph unknown; macroconidia on average 4-septate; on diseased roots and stems of grapevines; generally pathogenic; macroconidia generally 3–5-septate (average 4); known from South Africa and Uruguay ..... *Campylocarpon*
4. Teleomorph common, on bark of recently killed trees or causing small cankers; perithecia superficial, most species with a prominent, darkened papilla, if not, then at least with a darkly pigmented apex; perithecial walls of 2–3 regions; outer region of intertwined hyphae or cells lacking a definite outline *i.e. textura epidermoidea*, with thickened and pigmented walls; ascospores mostly ornamented, becoming brownish at maturity; anamorphs rarely encountered apart from their teleomorph; macroconidia (4–)5–7(–9)-septate (average 5) (except *T. olida*; see section on Description of Genera) ..... *Thelonectria*

DESCRIPTION OF GENERA

In this paper five genera are described that have neonectria- and *Cylindrocarpon*-like morphology: *Campylocarpon* (teleomorph unknown); *Ilyonectria* gen. nov. (anam. *Cylindrocarpon*-like); *Neonectria sensu stricto* (anam. *Cylindrocarpon sensu stricto*); *Rugonectria* gen. nov. (anam. *Cylindrocarpon*-like); and *Thelonectria* (anam. *Cylindrocarpon*-like). New combinations are made only for those species that are confirmed to belong to the new genera based on molecular phylogenetic data presented here or in previous studies (Seifert *et al.* 2003, Brayford *et al.* 2004, Halleen *et al.* 2004, 2006, Castlebury *et al.* 2006).

CAMPYLOCARPON Halleen, Schroers & Crous, Stud. Mycol. 50: 449. 2004. Fig. 2.

Type: *Campylocarpon fasciculare* Schroers, Halleen & Crous, Stud. Mycol. 50: 449. 2004.

Teleomorph: Unknown.

Anamorph: *Cylindrocarpon*-like; microconidia not observed; chlamydospores rarely observed; conidiophores arising laterally from hyphae, irregularly branched conidiophores or forming fascicles; phialides cylindrical, (13–)15–20(–25) × (2–)3.5–4 µm; macroconidia

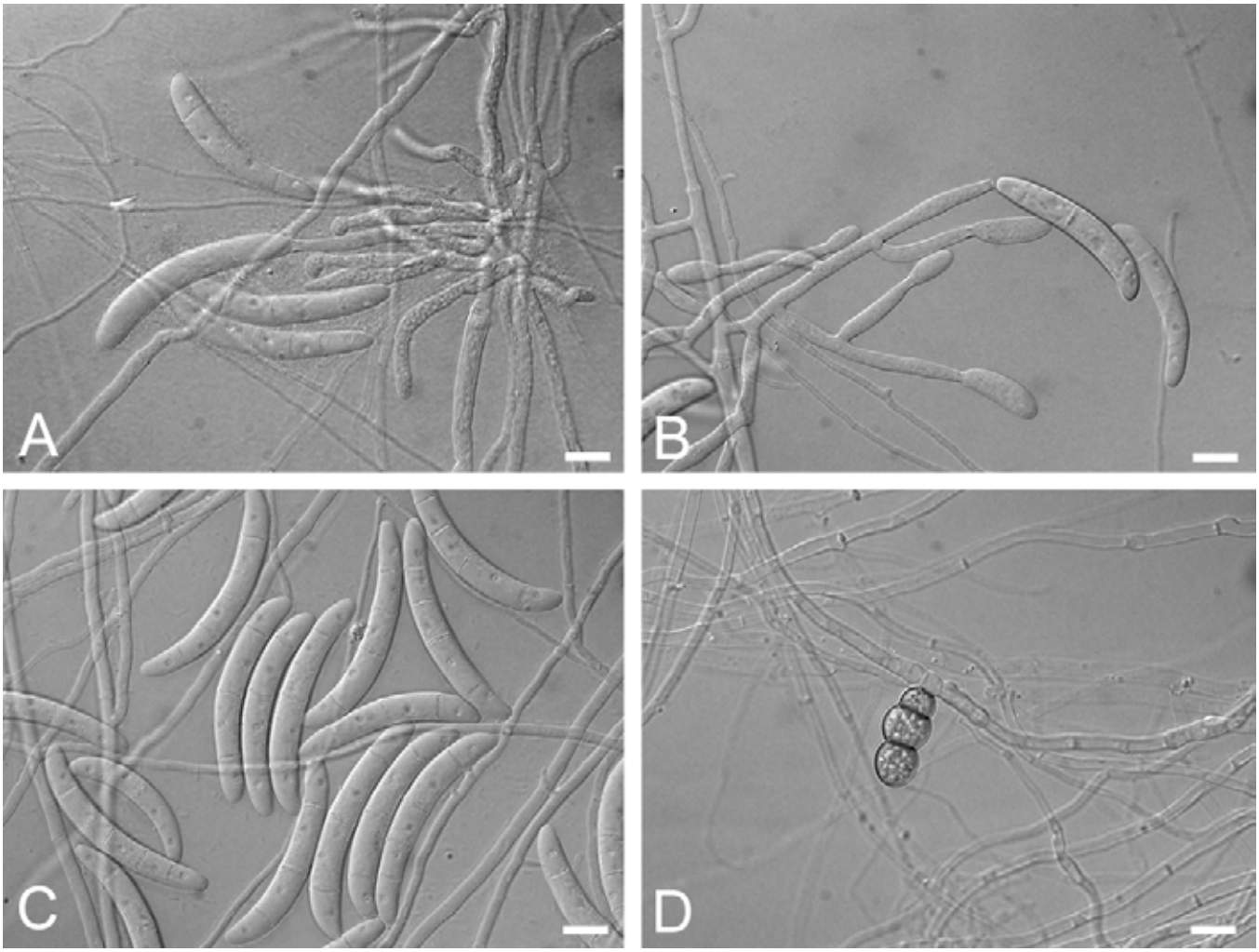

Fig. 2.A–D. *Campylocarpon*. A–C. *C. fasciculare* conidiophores and macroconidia (CBS 112613). D. *C. pseudofasciculare* chlamydospores (CBS 112679). Bars: 10 µm.

curved, often broadest at upper third, with rounded apical cells and flattened or rounded basal cells, (1–)3–5(–6)-septate (average 4), with inconspicuous hilum, (24–)35–60(–62) × 6.5–9 µm.

Habitat: On roots and stems of grapevines; generally pathogenic.

Distribution: Known from South Africa and Uruguay (Abreo *et al*. 2010).

Campylocarpon fasciculare Schroers, Halleen & Crous, Stud. Mycol. 50: 449. 2004.

Teleomorph: Unknown.

Habitat: On diseased roots, rootstock and stems of grapevines.

Distribution: South Africa.

Description and illustrations: Halleen *et al*. (2004).

Campylocarpon pseudofasciculare Halleen, Schroers & Crous, Stud. Mycol. 50: 451. 2004.

Teleomorph: Unknown.

Habitat: On asymptomatic grapevine roots.

Distribution: South Africa.

Description and illustrations: Halleen *et al*. (2004).

ILYONECTRIA P. Chaverri & C. Salgado, **gen. nov**. MycoBank MB518558. Fig. 3.

Type: *Ilyonectria radicicola* (Gerlach & L. Nilsson) Chaverri & C. Salgado.

Etymology: "ilyo" = Greek for "mud" or "dirt". The name is given because most species are found as soil inhabitants.

Ascomata superficialia, globosa vel sublobosa, verrucata vel squamosa, rubra, KOH+ phaeorubra, papilla conica vel subconica. Ascosporae ellipsoidea, 1-septatae, hyalinae, glabra. Anamorphosis cylindrocarpon-similis. Microconidia et chlamydosporae abundans. Phialide cylindrici. Macroconidia cylindrici, recte, hyaline, 1–3-septatae, hilum conspicue. Microconidia ellipsoidea vel oblonga, hyaline, 0–1-septatae, hilum conspicue. Typus: *Ilyonectria radicicola*.

Teleomorph: Perithecia superficial, loosely attached to substrate, red, KOH+, globose to subglobose, 175–350 µm diam, with a broadly conical papilla, scaly or slightly warted; perithecial wall of two regions, 35–50 µm thick: outer region 25–30 µm thick, of thin-walled, *ca*. 1 µm, globose, large cells; inner region of compressed, flattened cells. Ascospores ellipsoidal, 1-septate, smooth, hyaline.

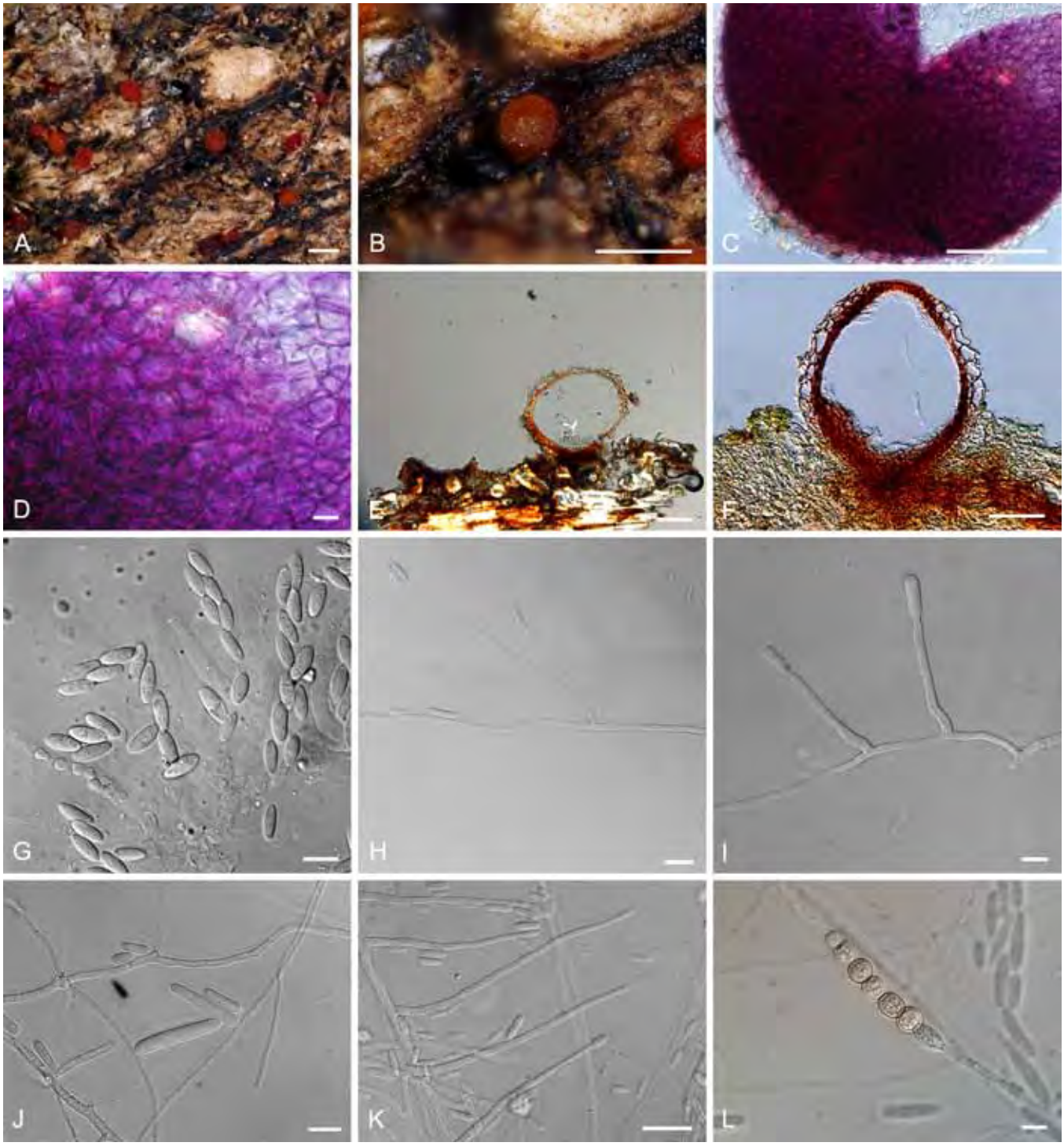

Fig. 3. *Ilyonectria*. A, B. *I. radicicola* perithecia (A.R. 2553). C, D. Crushed perithecium of *I. radicicola* showing perithecium wall surface (A.R. 2553**)**. E, F. Longitudinal section of perithecium (TFM FPH-7807) of *I. radicicola*. G. Asci and ascospores of *I. radicicola* (A.R. 2553). H–J. Conidiophores and conidia of *I. macrodydima* (CBS 112615). K. Conidiophores and conidia of *I. radicicola* (C.T.R. 71-76). L. Chlamydospores of *I. radicicola* (A.R. 2553). Bars: A, B = 500 µm; C, E, F = 100 µm; D, G, J, L = 10 µm; H, I = 20 µm; K = 50 µm.

Anamorph: *Cylindrocarpon*-like; microconidia and chlamydospores abundant; macro- and microconidia apparently originating from same conidiophores. Conidiophores 40–160 um long, generally simple, unbranched or sparsely branched, irregularly or verticillately branched, rarely densely branched. Phialides cylindrical, 15–40 (–50) × 1.5–3 µm. Macroconidia straight, hyaline, 1–3-septate, rarely > 3-septate, 25–50(–55) × 5–7.5 µm, generally with a prominent basal or lateral abscission scar or hilum. Microconidia ellipsoidal to ovoid, hyaline, 0–1-septate, with a lateral or basal hilum, 3–15 × 2.5–5(–6) µm. Chlamydospores abundant, generally intercalary, globose, single or in chains, becoming brownish.

Habitat: On roots, soil, woody and herbaceous plants, often pathogenic.

Notes: One potential existing generic name for this group is *Coleomyces* Moreau & M. Moreau that Booth (1966) listed as a synonym of *Cylindrocarpon*. The illustration in the original description of *Coleomyces*, based on *C. rufus* (Moreau & Moreau 1937), suggests that it belongs in the *N. radicicola*-group. However, in the original description the authors refer to this name as "*ad interim*." *Ad interim* means it is a provisional name and, according to the ICBN (Art. 34.1, Ex. 6), it is not validly published. The authors of

the present study were not able to find a later publication validating this name. Therefore, *Coleomyces* cannot be used for species in the *N. radicicola*-group.

Ilyonectria coprosmae (Dingley) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518559.
Basionym: *Nectria coprosmae* Dingley, Trans. Roy. Soc. New Zealand 79: 200. 1951.
≡ *Nectria radicicola* var. *coprosmae* (Dingley) Samuels & Brayford, Mycol. Res. 94: 438. 1990.
≡ *Neonectria coprosmae* (Dingley) Seifert, Phytopathology 93: 1541. 2003.
Anamorph: *"Cylindrocarpon" coprosmae* C. Booth, Mycol. Pap. 104: 16. 1966.
Basionym: *Cylindrocarpon destructans* var. *coprosmae* (C. Booth) Brayford & Samuels, Mycol. Res. 94: 438. 1990.

Habitat: On various decaying woody and herbaceous plants.

Distribution: New Zealand.

Descriptions and illustrations: Booth (1966) and Samuels & Brayford (1990).

Notes: Brayford & Samuels (1990) accepted this species as a variety of *Cylindrocarpon destructans*. However, Seifert *et al*. (2003) recognised it as a separate species. To better elucidate the taxonomic and phylogenetic relationship of *I. coprosmae*/*'C.' coprosmae* to *I. radicicola*/*'C.' destructans sensu stricto*, further detailed taxonomic studies are needed.

Ilyonectria radicicola (Gerlach & L. Nilsson) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518560.
Basionym: *Nectria radicicola* Gerlach & L. Nilsson, Phytopath. Z. 48: 225. 1963.
≡ *Neonectria radicicola* (Gerlach & L. Nilsson) Mantiri & Samuels, Canad. J. Bot. 79: 339. 2001.
Anamorph: "*Cylindrocarpon" destructans* (Zinssm.) Scholten var. *destructans*, Netherl. J. Plant Path. 70 suppl. (2): 9. 1964.
Basionym: *Ramularia destructans* Zinssm., Phytopathology 8: 570. 1918.
= *Cylindrocarpon radicicola* Wollenw., Fus. Autogr. Delin. 2: 651. 1924.
[= *Ramularia macrospora* Wollenw. Phytopathology 3: 222. 1913 non Fresen., Beitr. Mykol. 3: 88. 1863. *hom. illeg.*]
[= *Fusarium polymorphum* Marchal, Bull. Soc. Roy. Bot. Belgique 34: 145-148. 1895 non Matruchot, Rech. Dével. Mucéd. 84: 1892. *hom. illeg.*]

Habitat: On soil, roots, wood, and herbaceous debris.

Distribution: Cosmopolitan.

Descriptions and illustrations: Booth (1966, 1967), Samuels & Brayford (1990).

Ilyonectria liriodendri (Halleen *et al*.) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518561.
Basionym: *Neonectria liriodendri* Halleen, Rego & Crous, Stud. Mycol. 55: 232. 2006.
Anamorph: *"Cylindrocarpon" liriodendri* J.D. MacDon. & E.E. Butler, Pl. Dis. 65: 156. 1981.

Habitat: On diseased roots and rootstocks.

Distribution: France, Portugal, New Zealand, South Africa, USA.

Description and illustrations: Halleen *et al*. (2006).

Ilyonectria macrodidyma (Halleen, Schroers & Crous) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518562.
Basionym: *Neonectria macrodidyma* Halleen, Schroers & Crous, Stud. Mycol. 50: 446. 2004.
Anamorph: *"Cylindrocarpon" macrodidymum* Schroers, Halleen & Crous, Stud. Mycol. 50: 447. 2004.

Habitat: On diseased roots and rootstocks.

Distribution: Australia, Canada, New Zealand, South Africa.

Description and illustrations: Halleen *et al*. (2004).

NEONECTRIA Wollenw., Ann. Mycol. 15: 52. 1917. Fig. 4.

Type: *Neonectria ramulariae* Wollenw.
= *Chitinonectria* Morelet, Bull. Soc. Sci. Nat. Archéol. Toulon Var 178: 6. 1969. Type: *Ch. coccinea* (Pers. : Fr.) Morelet (≡ *Sphaeria coccinea* Pers. : Fr., ≡ *Neonectria coccinea* (Pers. : Fr.) Rossman & Samuels).
Anamorph: *Cylindrocarpon* Wollenw., Phytopathology 3: 225. 1913. Type species *Cylindrocarpon cylindroides* Wollenw.
[= *Fusidium* Link : Fr., Syst. Mycol. 1: x1. 1821 : 3(2): 480. 1832 *nomen rejiciendum*]

Teleomorph: Perithecia clustered on wood, generally seated on an erumpent stroma, red, KOH+ dark red, yellow in lactic acid, generally smooth and shiny, sometimes scurfy, subglobose to broadly obpyriform, 200–400 µm diam, generally not collapsing when dry, with a blunt or acute apex, rarely papillate. Perithecial walls of 2–3 regions, generally 35–50 µm thick: outer region of small, angular to globose, thick-walled cells, rarely of *textura epidermoidea*; inner region of flattened thin-walled cells. Paraphyses when present, septate, slightly constricted at each septum. Ascospores ellipsoidal, smooth or finely ornamented, 1-septate, hyaline, sometimes becoming pale brown at maturity.

Anamorph: Either microconidia or chlamydospores present. Macroconidia produced from irregularly branched conidiophores or fascicles. Phialides cylindrical, typically 10–20(–30) µm long. Macroconidia hyaline, smooth, generally straight, sometimes slightly curved toward ends, with rounded ends except in one species, *N. fuckeliana*, which has fusiform conidia with pointed ends, 3–7(–9)-septate, mostly 5-septate, lacking a prominent scar or basal hilum, 35–65(–110) × 4–7(–8) µm. Microconidia produced from simple, generally unbranched conidiophores, short or long; microconidia hyaline, smooth, ellipsoidal to oblong, 0–1-septate, mostly unicellular, (2–)6–10(–15) × (1–)2–5(–6) µm. When present, chlamydospores globose to subglobose, hyaline.

Habitat: Generally on bark, sometimes causing cankers. Mostly in temperate regions.

Representative species: *N. coccinea*/*C. candidum, N. ditissima*/*C. heteronemum, N. faginata*/*C. faginatum, N. fuckeliana*/*C. cylindroides* var. *tenue, N. hederae*/*C. hederae, N. major*/*Cylindrocarpon* sp., *N. neomacrospora*/*C. cylindroides, N. punicea*/*C. album,* and *N. ramulariae*/*C. obtusiusculum.*

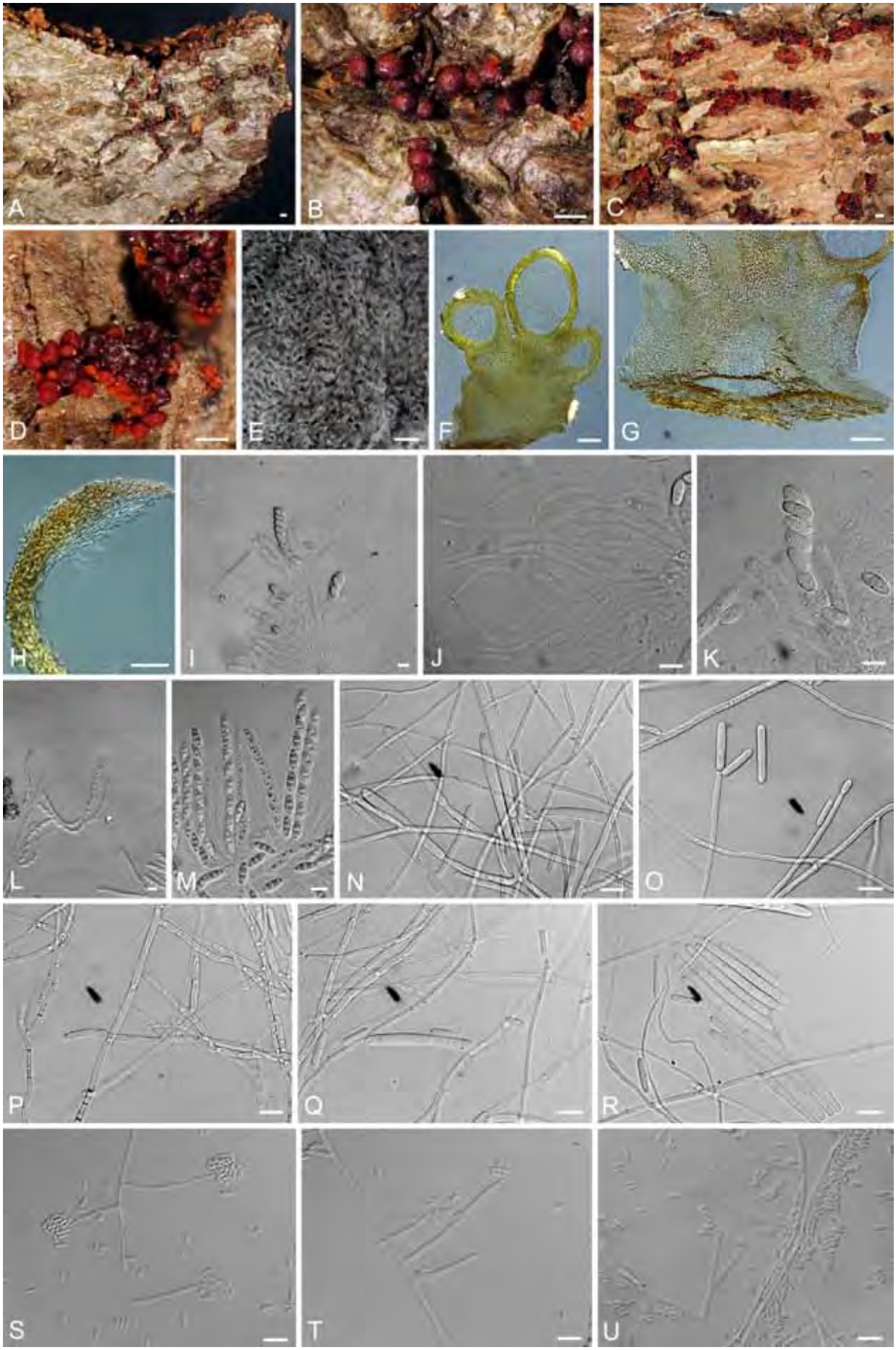

Fig. 4. *Neonectria.* A, B. *N. ditissima* perithecia (A.R. 3690 = BPI 870951). C, D. *N. fuckeliana* perithecia (A.R. 3103 = BPI 842140). E. Top view of surface of *N. fuckeliana* perithecium (A.R. 3103 = BPI 842140). F–H. Longitudinal section of *N. ditissima* perithecia (A.R. 3690 = BPI 870951). I. Asci and ascospores of *N. ditissima* (A.R. 3703 = BPI 871120). J. Paraphyses of *N. ditissima* (A.R. = BPI 871120). K. Asci and ascospores of *N. ditissima* (A.R. 3703 = BPI 871120). L, M. Asci and ascospores of *N. fuckeliana* (A.R. 3103 = BPI 842140). N–R. Conidiophores and macroconidia of *N. ditissima* (A.R. 3692 = CBS 119521 = BPI 871119). S–U. Conidiophores and microconidia of *N. fuckeliana* (G.J.S. 02-67 = CBS 125109 = BPI 842434). Bars: A, C = 1 mm; B, D = 500 µm; E, I–U = 10 µm; F, G = 100 µm; H = 50 µm.

Notes: Three names exist that could be considered synonyms of *Cylindrocarpon*, *i.e. Allantospora*, *Cylindrodendrum*, and *Heliscus* (Booth, 1966). The protologue and illustrations of *Allantospora* suggest that it is probably not congeneric with *Cylindrocarpon* (Wakker 1895). Wakker (1895) illustrated this genus based on the type species, *A. radicicola,* as having *Verticillium*-like conidiophores and small, allantoid conidia. Therefore, this synonymy is doubtful. *Cylindrodendrum* could also be considered a synonym of *Cylindrocarpon*, based on the cylindrical conidia although many other genera in the *Hypocreales* have cylindrical conidia. The original description and illustration of this genus based on the type species, *Cylindrodendrum album,* shows that most characteristics are quite distinct from *Cylindrocarpon* (Bonorden 1851). In *Cylindrodendrum,* the conidiophore branches have sterile, terminal elongations that are generally hooked, phialides with a swollen base and narrow neck, and relatively small conidia that are not septate. Regarding *Heliscus* as a possible synonym of *Cylindrocarpon*, Luo & Zhuang (2010b) placed the morphologically similar species, *Neonectria shennongjiana*, close to *Neonectria/ Cylindrocarpon sensu stricto*. However, more studies are needed to confirm if *Heliscus* is congeneric with *Cylindrocarpon.* If it is congeneric, then, *Heliscus* is an older name (1880) and thus would have priority over *Cylindrocarpon*. Due to the extensive use of the name *Cylindrocarpon*, its economic importance, and some doubts about the phylogenetic placement of *Heliscus*, the authors of the present study would argue for conservation of *Cylindrocarpon* over *Heliscus*.

RUGONECTRIA P. Chaverri & Samuels, **gen. nov**. MycoBank MB518563. Fig. 5.

Etymology: "rugo" = Latin for "wrinkled". The perithecial wall surface for species of this genus is warted or rugose.

Type: *Rugonectria rugulosa* (Pat. & Gaill.) Chaverri, C. Salgado & Samuels.

Ascomata superficialia vel gregaria in stromatae, ascomata globosa vel sublobosa, verrucata vel tuberculata, rubra, KOH+ phaeorubra, non papillata. Ascosporae ellipsoidea vel oblongata, 1-septatae, hyalinae vel pallide brunneae, striatae. Anamorphosis Cylindrocarpon-similis. Phialide cylindrici. Macroconidia fusiformes, hyaline, (3–)5–7(–9)-septatae, hilum inconspicue. Microconidia ellipsoidea vel cylindrici, hyaline, 0–1-septatae, hilum inconspicue. Chlamydosporae absens. Typus: *R. rugulosa*.

Teleomorph: Perithecia solitary or in groups, formed on or sometimes partially immersed within a stroma. Perithecia globose to subglobose, warted, non-papillate, orange to red, dark red in KOH+, yellow in lactic acid. Perithecial wall 50–150 µm thick, generally of two indistinct regions: outer region including warts with cells circular, 10–20 µm diam, cell walls 3–4 µm thick, merging with surrounding stroma; inner region with cells becoming progressively flattened, thinner, and less pigmented toward locule. Ascospores ellipsoidal to oblong, striate, hyaline, or sometimes yellowish, bicellular.

Anamorph: *Cylindrocarpon*-like; microconidia present; chlamydospores lacking. Macroconidia arising laterally from hyphae, irregularly branched conidiophores or in fascicles, generally with a short base. Phialides from macroconidiophores cylindrical, 15–25 × 3–5 µm. Macroconidia curved, fusiform, tapering towards ends, (3–)5–7(–9)-septate, with inconspicuous hilum, (35–)48–85 × 5–10 µm. Microconidia produced from simple monophialidic or sparsely branched conidiophores, scattered, *ca*. 20–100 µm long. Phialides from microconidiophores cylindrical, 20–40 × 3–4 µm. Microconidia ovoid to cylindrical, with rounded ends, generally blunt, 0–1-septate, hyaline, (3–)5–15(–20) × 2–5 µm, lacking a prominent basal hilum.

Habitat: On bark of recently killed, dying or diseased trees, often causing cankers.

Rugonectria castaneicola (W. Yamam. & Oyasu) Hirooka & P. Chaverri, **comb. nov.** MycoBank MB518564.
Basionym: *Nectria castaneicola* W. Yamam. & Oyasu, Sci. Rep. Hyogo Univ. Agric. Biol. 3: 17. 1957.
≡ *Neonectria castaneicola* (W. Yamam. & Oyasu) Tak. Kobay. & Hirooka, J. Gen. Plant Pathol. 71: 126. 2005.
Anamorph: *"Cylindrocarpon" castaneicola* Tak. Kobay. & Hirooka, J. Gen. Plant Pathol. 71: 126. 2005.

Habitat: On bark of conifers, generally causing cankers.

Distribution: Japan.

Description and illustrations: Kobayashi *et al*. (2005).

Rugonectria neobalansae (Samuels) P. Chaverri & Samuels, **comb. nov.** MycoBank MB518565.
Basionym: *Nectria neobalansae* Samuels, Mem. N. Y. Bot. Gard. 59: 60. 1990.
Anamorph: *Cylindrocarpon*-like.

Habitat: On bark of living and recently killed trees.

Distribution: Indonesia, known only from the type locality.

Description and illustrations: Samuels *et al*. (1990).

Notes: *Rugonectria neobalansae* is distinct in being almost completely immersed in an orange-red stroma and having, large striate ascospores.

Rugonectria rugulosa (Pat. & Gaill.) Samuels, P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518566.
Basionym: *Nectria rugulosa* Pat. & Gaill., Bull. Soc. Mycol. France 4: 115. 1888 [1889].
≡ *Neonectria rugulosa* (Pat. & Gaill.) Mantiri & Samuels, Canad. J. Bot. 79: 339. 2001.
= *Nectria congoensis* Sydow *in* Hennings *in* Wildeman Mycetes. Ann. Mus. Congo. Bot. V. Études Syst. Geog. Bot. Flore du Bas- et du Moyen Congo 14. 1909.

Anamorph: *"Cylindrocarpon" rugulosum* Brayford & Samuels, Sydowia 46: 146. 1994.

Habitat: On bark of living and recently killed trees, sometimes causing cankers.

Distribution: Pantropical.

Descriptions and illustrations: Samuels *et al.* (1990), Samuels & Brayford (1994).

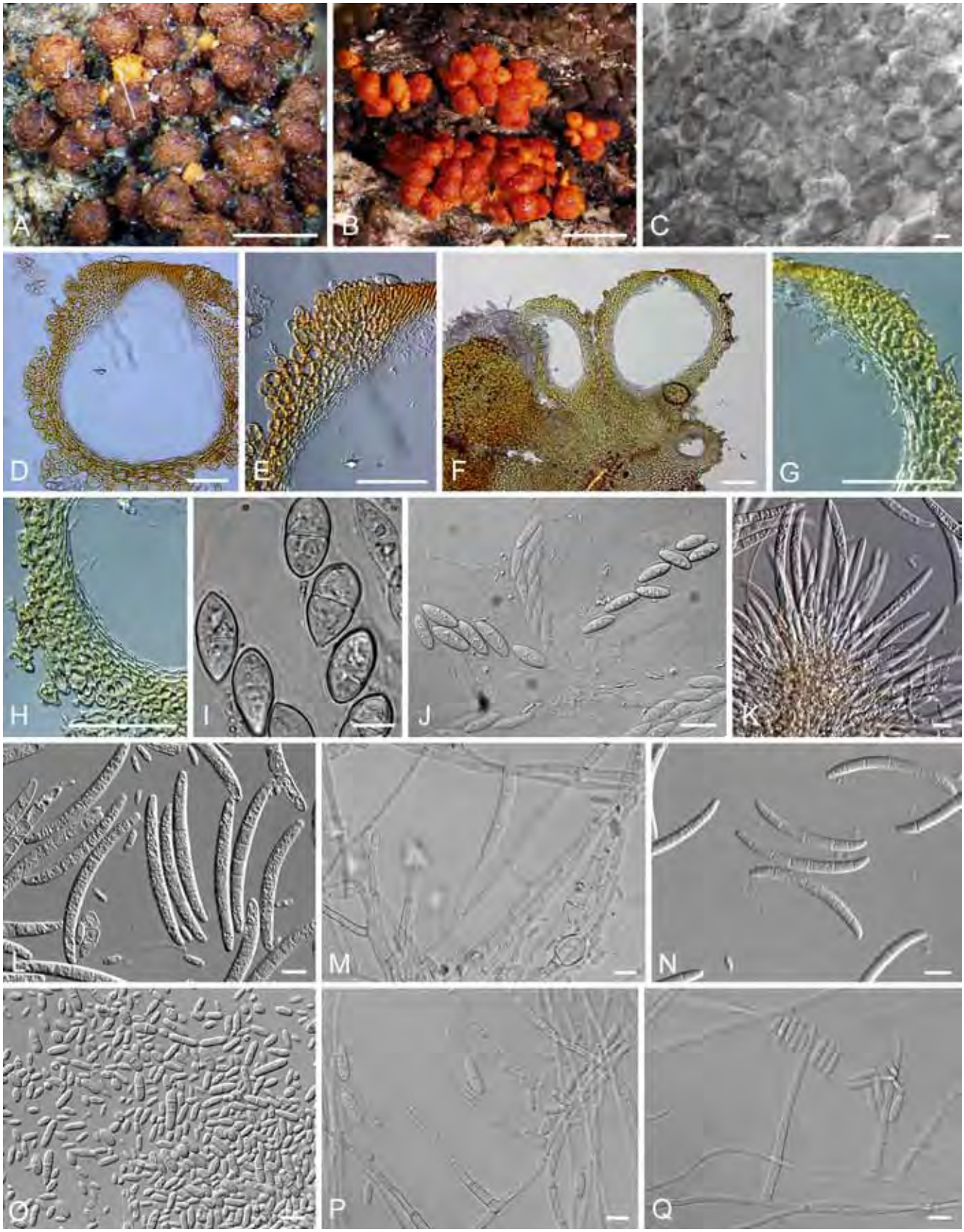

Fig. 5. *Rugonectria*. A. Perithecia of *R. neobalansae* (G.J.S. 85-219, NY). B. Perithecia of *R. rugulosa* (G.J.S. 90-238 = BPI 1107399). C. Top view of surface of *R. rugulosa* perithecium (G.J.S. 90-238 = BPI 1107399). D, E. Longitudinal section of *R. neobalansae* perithecium (G.J.S. 85-219, NY). F–H. Longitudinal section of *R. rugulosa* (G.J.S. 90-238 = BPI 1107399). I. Ascospores of *R. neobalansae* (G.J.S. 85-219, NY). J. Asci and ascospores of *R. rugulosa* (G.J.S. 90-238 = BPI 1107399). K, L. Conidiophores and macroconidia of *R. castaneicola* (MAFF 237284). M. Conidiophores and macroconidia of *R. rugulosa* (G.J.S. 09-1337). N. Macroconidia of *R. rugulosa* (MAFF 241491). O. Microconidia of *R. castaneicola* (MAFF 237284). P, Q. Conidiophores and microconidia of *R. rugulosa* (09-1337). Bars: A, B = 1 mm; C, I–Q = 10 µm; D–H = 100 µm.

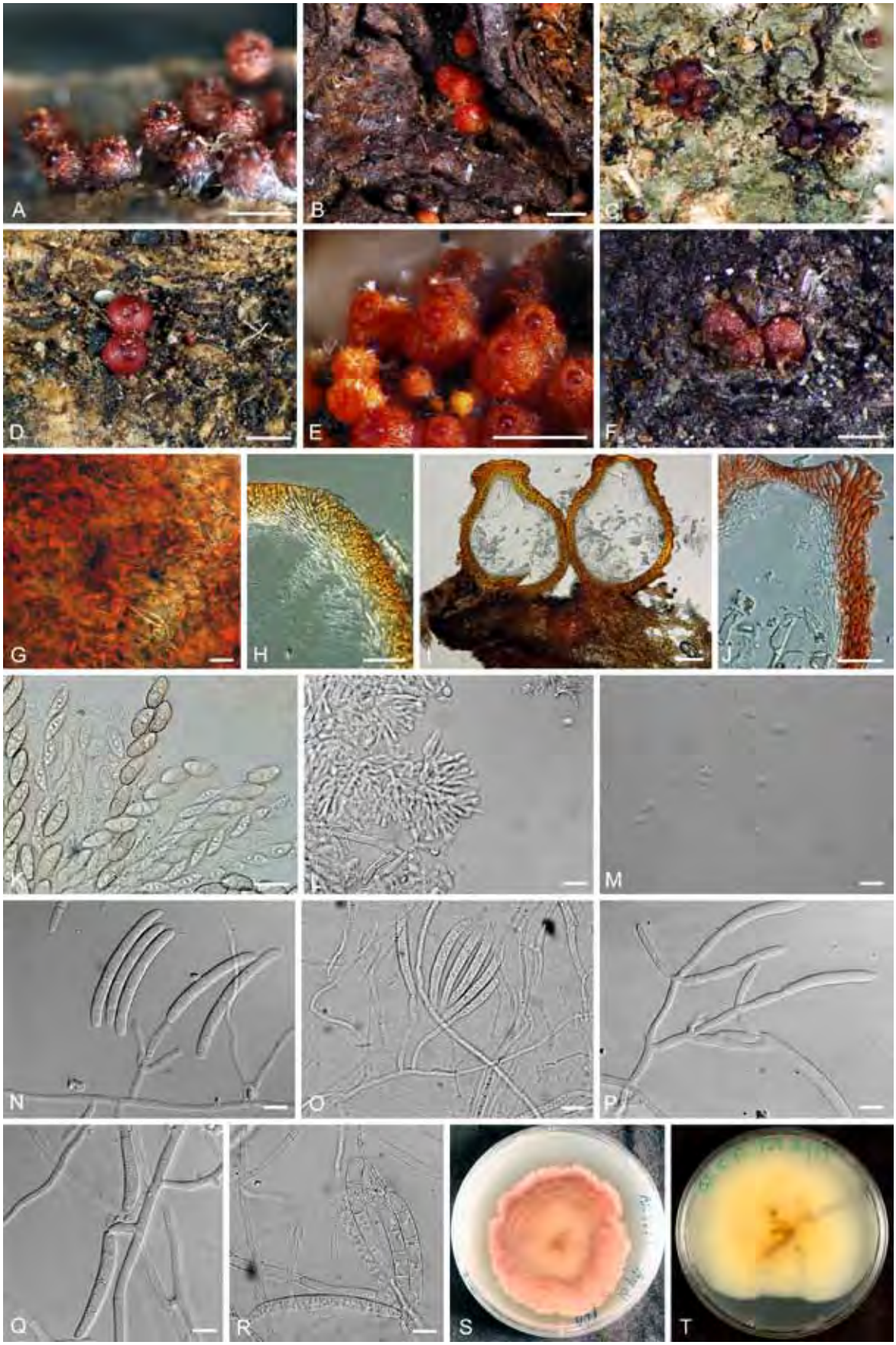

Fig. 6. *Thelonectria*. A. *T. veuillotiana* perithecia (A.R. 4505 = BPI 878946). B. *T. discophora* perithecia (A.R. 4499 = BPI 878945). C. *T. jungneri* perithecia (C.T.R. 71-244, NY). D. *T. lucida* perithecia (C.T.R. 72-180, NY). E. *T. veuillotiana* perithecia (G.J.S. 90-48 = BPI 1107127). F. *T. westlandica* perithecia (G.J.S. 83-156, PDD). G. Top view of surface of *T. veuillotiana* perithecium (A.R. 4505 = BPI 878946). H. Longitudinal section of *T. discophora* perithecium (A.R. 4499 = BPI 878945). I, J. Longitudinal section of *T. veuillotiana* perithecium (G.J.S. 90-48 = BPI 1107127). K. Asci and ascospores of *T. lucida* (C.T.R. 72-180, NY). L, M. Conidiophores and conidia of *T. veuillotiana* on natural substrate (G.J.S. 90-48 = BPI 1107127). N. Conidiophores and macroconidia of *T. discophora* (A.R. 4499 = BPI 878945). O. Conidiophores and macroconidia of *T. olida* (CBS 215.67**)**. P. Conidiophores and macroconidia of *T. veuillotiana* (G.J.S. 90-48 = BPI 1107127). Q. Conidia of *T. trachosa* (CBS 112467). R. Macroconidia of *T. westlandica* (G.J.S. 83-156, PDD). S. Reverse colony of *T. discophora* on PDA (A.R. 4499 = BPI 878945). T. Reverse colony of *T. veuillotiana* on PDA (G.J.S. 90-48 = BPI 1107127). Bars: A–F = 500 µm; G, K–R = 10 µm; H, J = 50 µm; I = 100 µm.

THELONECTRIA P. Chaverri & C. Salgado, **gen. nov**. MycoBank MB518567. Fig. 6.

Etymology: "thelo" – Greek for "nipple". Many species in this genus have a raised, papilla that is sometimes darkened, and thus resembles a nipple.

Type species: *Thelonectria discophora* (Mont.) P. Chaverri & C. Salgado (new combination made below).

Ascomata superficialia vel gregaria, ascomata globosa vel sublobosa, glabra, rubra, KOH+ phaeorubra, atropapillata. Ascosporae ellipsoidea vel oblongata, 1-septatae, hyalinae, glabra. Anamorphosis Cylindrocarpon-similis. Phialide cylindrici. Macroconidia fusiformes, curva, saepe triente apicali latiore, cellulis apicalibus rotundatis et cellulis basalibus rotundatis vel complanatis, hyaline, (3–)5–7(–9)-septatae, hilum inconspicue. Microconidia absens. Chlamydosporae absens. Typus: *T. discophora*.

Teleomorph: Perithecia superficial, sometimes seated on an immersed inconspicuous stroma, smooth or sometimes warted, sometimes shiny, globose, subglobose, or pyriform to elongated, 300–600 µm diam, most species with a prominent, areolate (darkened) papilla, if not, then at least with a darkly pigmented apex; perithecial walls of 2 or 3 regions, 20–50(–100) µm thick: outer region of intertwined hyphae or cells lacking a definite outline *i.e. textura epidermoidea*, with thickened, pigmented walls; inner region of thin-walled, non-pigmented, flattened cells. Ascospores mostly smooth, rarely spinulose or striate, hyaline, becoming brownish at maturity, generally 1-septate.

Anamorph: *Cylindrocarpon*-like; microconidia rare, sometimes seen on natural substrata; chlamydospores rare, abundant in one species; conidiophores arising laterally from hyphae, irregularly branched conidiophores or forming fascicles; phialides cylindrical, 10–25 × 3–6 µm; macroconidia curved, often broadest at upper third, with rounded apical cells and flattened or rounded basal cells, (3–)5–7(–9)-septate, with inconspicuous hilum, (35–)40–90(–110) × 4–8(–11) µm.

Habitat: On bark of recently killed, dying or diseased trees, often causing small cankers, sometimes on rotting roots.

Thelonectria coronata (Penz. & Sacc.) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518568.
Basionym: *Nectria coronata* Penz. & Sacc., Malpighia 11: 510. 1897.
≡ *Neonectria coronata* (Penz. & Sacc.) Mantiri & Samuels, Canad. J. Bot. 79: 339. 2001.
Anamorph: "*Cylindrocarpon" coronatum* Brayford & Samuels, Sydowia 46: 91. 1993.

Habitat: On bark, often associated with small cankers.

Distribution: Probably pantropical.

Descriptions and illustrations: Brayford & Samuels (1993); Samuels & Brayford (1994)

Thelonectria discophora (Mont.) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518569.
Basionym: *Sphaeria discophora* Mont., Ann. Sci. Nat. Bot. II 3: 353. 1835.
≡ *Neonectria discophora* (Mont.) var. *discophora* Mantiri & Samuels, Canad. J. Bot. 79: 339. 2001.
= *Nectria tasmanica* Berk. in Hooker, Flora Tasmaniae 2: 279. 1860.
= *Nectria mammoidea* W. Phillips & Plowr. Grevillea 3: 126. 1875.
≡ *Creonectria mammoidea* (W. Phillips & Plowr.) Seaver, Mycologia 1: 188. 1909 (as *Creonectria mammoides*).
= *Nectria nelumbicola* Henn., Verh. Bot. Vereins. Prov. Brandenburg 40: 151. 1898.
= *Nectria umbilicata* Henn., Hedwigia 41: 3. 1902.
= *Nectria mammoidea* var. *rugulosa* Weese, Akad. Wiss. Wien Math.-Naturw. Kl., Abt. 1, 125: 552. 1916.
= *Nectria mammoidea* var. *minor* Reinking, Zentralbl. Bakteriol., Abt. 2, 94: 135. 1936.
= *Creonectria discostiolata* Chardón, Bol. Soc. Venez. Ci. Nat. 5: 341. 1939.
= *Nectria pinea* Dingley, Trans. Roy. Soc. New Zealand 79: 198. 1951.
Anamorph: "*Cylindrocarpon" ianothele* var. *majus* Wollenw., Z. Parasitenk. (Berlin) 1: 161. 1928.
= *Cylindrocarpon ianthothele* var. *minus* Reinking, Zentralbl. Bakteriol., Abt. 2, 94: 135. 1936.
= *Cylindrocarpon ianthothele* var. *rugulosum* C. Booth, Mycol. Pap. 104: 25. 1966.
= *Cylindrocarpon pineum* C. Booth, Mycol. Pap. 104: 26. 1966.

Habitat: On bark and twigs of recently killed trees, rarely on palm trunks.

Distribution: Cosmopolitan.

Description and illustrations: Brayford *et al*. (2004).

Thelonectria jungneri (Henn.) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518570.
Basionym: *Nectria jungneri* Henn., Bot. Jahrb. Syst. 22: 75. 1897.
= *Nectria eustoma* Penz. & Sacc., Malpighia 11: 509. 1898 [1897]
= *Nectria leucoloma* Starbäck, Bih. Kongl. Svenska Vetensk.-Akad. Handl. 25: 28. 1899.
= *Nectria cinereopapillata* Henn. & Nyman in Warburg, Monsunia 1: 161. 1900 [1899]
= *Nectria striatospora* Zimm., Centralbl. Bakteriol. II, 7: 105. 1901.
= *Nectria azureostiolata* Doi, Mem. Nat. Sci. Mus. Tokyo 10: 23. 1977.
Anamorph: "*Cylindrocarpon" victoriae* Wollenw., Z. Parasitenk. (Berlin) 1: 161. 1928.

Habitat: On bark of recently killed or dying trees.

Distribution: Pantropical.

Description and illustrations: Samuels *et al*. (1990).

Thelonectria lucida (Höhn.) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518571.
Basionym: *Nectria lucida* Höhn., Akad. Wiss. Wien math. Naturw. Kl., Abt. 1, 118: 289. 1909.
≡ *Neonectria lucida* (Höhn.) Samuels & Brayford, Mycologia 96: 590. 2004.
Anamorph: "*Cylindrocarpon" lucidum* Booth, Mycol. Pap. 104: 21. 1966.

Habitat: On bark of recently killed or dying trees, rarely on vines.

Distribution: Asia, New Zealand, South America, North America, probably cosmopolitan.

Description and illustrations: Brayford *et al*. (2004).

Thelonectria olida (Wollenw.) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518572.
Basionym: *Ramularia olida* Wollenw., Phytopathology 3: 223. 1913.
≡ *Cylindrocarpon olidum* var. *olidum* (Wollenw.) Wollenw., Fus. Autogr. Del., ed. 1: 471. 1916.
= *Cylindrocarpon curvatum* Hochapfel in Wollenw., Z. Parasitenk. 3: 495. 1931.

Teleomorph: Unknown.

Habitat: On rotting roots of various plants.

Distribution: Probably widespread.

Descriptions and illustrations: Booth (1966), Brayford (1987).

Notes: This species is somewhat different from the rest of *Thelonectria* in having shorter macroconidia, fewer septa, and abundant chlamydospores. However, it also has similarities with *Thelonectria*. *Thelonectria olida* has short conidiophores, lacks microconidia, and has curved macroconidia with rounded ends. Molecular phylogenetic data presented here also places this species in *Thelonectria*.

Thelonectria trachosa (Samuels & Brayford) Samuels, P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518573.
Basionym: *Neonectria trachosa* Samuels & Brayford, Mycologia 96: 592. 2004.
Anamorph: *Cylindrocarpon*-like

Habitat: On bark of unknown conifer.

Distribution: Scotland, only known from the type locality.

Description and illustrations: Brayford *et al*. (2004).

Thelonectria veuillotiana (Sacc. & Roum.) P. Chaverri & C. Salgado, **comb. nov**. MycoBank MB518574.
Basionym: *Nectria veuillotiana* Sacc. & Roum. in Désmazières, Rev. Mycol. (Toulouse) 2: 189. 1880.
≡ *Dialonectria veuillotiana* (Sacc. & Roum.) Cooke, Grevillea 12: 110. 1884.
≡ *Cucurbitaria veuillotiana* (Sacc. & Roum.) Kuntze, Revis. Gen. Pl. (Leipzig) 3: 462. 1898.
≡ *Neonectria veuillotiana* (Sacc. & Roum.) Mantiri & Samuels, Canad. J. Bot. 79: 339. 2001.
= *Sphaerostilbe sanguinea* Fuckel, Symb. Myc. App. 3: 22. 1877.
Anamorph: "*Cylindrocarpon" candidulum* (Sacc.) Wollenw., Z. Parasitenk. 1: 160. 1928.
≡ *Atractium candiduli* Sacc., Syll. Fung. (Abellini) 2: 512.1883.

Habitat: On bark of recently killed trees, rarely on wood or leaves.

Distribution: Probably widespread.

Description and illustrations: Brayford & Samuels (1993).

Thelonectria viridispora (Samuels & Brayford) P. Chaverri, C. Salgado, & Samuels, **comb. nov.** MycoBank MB518575.
Basionym: *Neonectria viridispora* Samuels & Brayford, Mycologia 96: 592. 2004.
Anamorph: *Cylindrocarpon*-like.

Habitat: On bark of *Ochroma*.

Distribution: Ecuador, only known from the type locality.

Description and illustrations: Brayford *et al.* (2004).

Thelonectria westlandica (Dingley) P. Chaverri & C. Salgado, **comb. nov.** MycoBank MB518576.
Basionym: *Nectria westlandica* Dingley, Trans. Roy. Soc. New Zealand 79: 201. 1951.
≡ *Neonectria westlandica* (Dingley) Samuels & Brayford, Mycologia 96: 595. 2004.
Anamorph: *Cylindrocarpon*-like.

Habitat: On bark of dicotyledonous trees, sometimes gymnosperms.

Distribution: New Zealand.

Description and illustrations: Brayford *et al*. (2004)

ACKNOWLEDGEMENTS

We appreciate the nomenclatural advice given by Drew Minnis (USDA). We also greatly appreciate the assistance of Adam Bazinet (UMD) in the use of the GRID-computing system. This study was funded by a grant from United States National Science Foundation (PEET program) DEB-0925696: "Monographic Studies in the *Nectriaceae, Hypocreales*: *Nectria, Cosmospora*, and *Neonectria"* to University of Maryland (P. Chaverri, G.J. Samuels & A.Y. Rossman).

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.04

Studies in Mycology 68: 79–113. 2011.

An overview of the taxonomy, phylogeny, and typification of nectriaceous fungi in *Cosmospora*, *Acremonium*, *Fusarium*, *Stilbella*, and *Volutella*

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Abstract: A comprehensive phylogenetic reassessment of the ascomycete genus *Cosmospora* (*Hypocreales, Nectriaceae*) is undertaken using fresh isolates and historical strains, sequences of two protein encoding genes, the second largest subunit of RNA polymerase II (*rpb2*), and a new phylogenetic marker, the larger subunit of ATP citrate lyase (*acl1*). The result is an extensive revision of taxonomic concepts, typification, and nomenclatural details of many anamorph- and teleomorph-typified genera of the *Nectriaceae,* most notably *Cosmospora* and *Fusarium.* The combined phylogenetic analysis shows that the present concept of *Fusarium* is not monophyletic and that the genus divides into two large groups, one basal in the family, the other terminal, separated by a large group of species classified in genera such as *Calonectria, Neonectria,* and *Volutella*. All accepted genera received high statistical support in the phylogenetic analyses. Preliminary polythetic morphological descriptions are presented for each genus, providing details of perithecia, micro- and/or macro-conidial synanamorphs, cultural characters, and ecological traits. Eight species are included in our restricted concept of *Cosmospora*, two of which have previously documented teleomorphs and all of which have *Acremonium*-like microconidial anamorphs. A key is provided to the three anamorphic species recognised in *Atractium*, which is removed from synonymy with *Fusarium* and epitypified for two macroconidial synnematous species and one sporodochial species associated with waterlogged wood. *Dialonectria* is recognised as distinct from *Cosmospora* and two species with teleomorph, macroconidia and microconidia are accepted, including the new species *D. ullevolea.* Seven species, one with a known teleomorph, are classified in *Fusicolla*, formerly considered a synonym of *Fusarium* including members of the *F. aquaeductuum* and *F. merismoides* species complex, with several former varieties raised to species rank. Originally a section of *Nectria*, *Macroconia* is raised to generic rank for five species, all producing a teleomorph and macroconidial anamorph. A new species of the *Verticillium*-like anamorphic genus *Mariannaea* is described as *M. samuelsii*. *Microcera* is recognised as distinct from *Fusarium* and a key is included for four macroconidial species, that are usually parasites of scale insects, two of them with teleomorphs. The four accepted species of *Stylonectria* each produce a teleomorph and micro- and macroconidial synanamorphs. The *Volutella* species sampled fall into three clades. *Pseudonectria* is accepted for a perithecial and sporodochial species that occurs on *Buxus*. *Volutella s. str.* also includes perithecial and/or sporodochial species and is revised to include a synnematous species formerly included in *Stilbella*. The third *Volutella*-like clade remains unnamed. All fungi in this paper are named using a single name system that gives priority to the oldest generic names and species epithets, irrespective of whether they are originally based on anamorph or teleomorph structures. The rationale behind this is discussed.

Key words: Article 59, *Buxus*, codon model, holomorph concept, unitary nomenclature, synnematous hyphomycetes.
Taxonomic novelties: New genus: *Macroconia* (Wollenw.) Gräfenhan, Seifert & Schroers. **New species:** *Dialonectria ullevolea* Seifert & Gräfenhan, *Fusicolla violacea* Gräfenhan & Seifert, *Mariannaea samuelsii* Seifert & Bissett, *Microcera rubra* Gräfenhan & Seifert. **New combinations:** *Atractium holubovae* (Seifert, S.J. Stanley & K.D. Hyde) Seifert, *Atractium crassum* (Wollenw.) Seifert & Gräfenhan, *Cosmospora arxii* (W. Gams) Gräfenhan & Schroers, *Cosmospora berkeleyana* (P. Karst.) Gräfenhan, Seifert & Schroers, *Cosmospora butyri* (J.F.H, Beyma) Gräfenhan, Seifert & Schroers, *Cosmospora cymosa* (W. Gams) Gräfenhan & Seifert, *Cosmospora khandalensis* (Thirum. & Sukapure) Gräfenhan & Seifert, *Cosmospora lavitskiae* (Zhdanova) Gräfenhan & Seifert, *Cosmospora viridescens* (C. Booth) Gräfenhan & Seifert, *Fusicolla acetilerea* (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert, *Fusicolla aquaeductuum* (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers, *Fusicolla epistroma* (Höhn.) Gräfenhan & Seifert, *Fusicolla matuoi* (Hosoya & Tubaki) Gräfenhan & Seifert, *Fusicolla merismoides* (Corda) Gräfenhan, Seifert & Schroers, *Macroconia cupularis* (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, *Macroconia gigas* (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, *Macroconia leptosphaeriae* (Niessl) Gräfenhan & Schroers, *Macroconia papilionacearum* (Seaver) Gräfenhan & Seifert, *Macroconia sphaeriae* (Fuckel) Gräfenhan & Schroers, *Microcera diploa* (Berk. & M.A. Curtis) Gräfenhan & Seifert, *Microcera larvarum* (Fuckel) Gräfenhan, Seifert & Schroers, *Pseudonectria buxi* (DC.) Seifert, Gräfenhan & Schroers, *Stylonectria purtonii* (Grev.) Gräfenhan, *Stylonectria wegeliniana* (Rehm) Gräfenhan, Voglmayr & Jaklitsch, *Volutella citrinella* (Ellis & Everh.) Seifert, *Volutella consors* (Ellis & Everh.) Seifert, Gräfenhan & Schroers. **New name:** *Stylonectria carpini* Gräfenhan.

INTRODUCTION

This paper focuses on phylogenetic and taxonomic reassessment of the prevailing concept of the ascomycete genus *Cosmospora* (*Nectriaceae, Hypocreales*) (Samuels *et al*. 1991, Rossman *et al*. 1999). This genus has been assumed to be polyphyletic because of its anamorphic and biological diversity, a fact recently reinforced by phylogenetic studies on a limited sampling of species (Zhang & Zhuang 2006, Luo & Zhuang 2008, Samuels *et al.* 2009). The majority of described *Cosmospora* species have *Acremonium*-like or *Fusarium*-like anamorphs, but hyphomycetous anamorphs classified in *Chaetopsina, Cylindrocladiella, Gliocladiopsis, Mariannaea, Penicillifer, Stilbella, Verticillium,* and *Volutella* have also been associated with the genus (Samuels *et al.* 1991 as *Nectria* subgenus *Dialonectria,* Rossman *et al.* 1999). The prevailing concept of *Cosmospora* is unified by the teleomorph, which tends to be relatively nondescript, with usually solitary, astromatic, smooth, thin-walled perithecia, often orange or reddish, and changing to dark red in KOH, and 1-septate ascospores in a cylindrical ascus with a simple apex of refractive apical ring; for convenience we will refer to this concept as *Cosmospora sensu* Rossman.

Before DNA-based phylogenetic studies significantly influenced fungal taxonomy, anamorph taxonomy in the *Hypocreales* had shifted away from classical form-taxa towards a practice that correlated teleomorphic and anamorphic generic concepts (Samuels

& Seifert 1987). Preceding the segregation of *Nectria sensu* Booth into many teleomorph genera in three families, Rossman (1993) suggested the delimitation of each teleomorph genus with one anamorph genus, the so-called 1:1 genus concept. Taxonomic equivalency between linked teleomorph and anamorph genera was proposed for several groups of the *Bionectriaceae*, *Nectriaceae,* and *Hypocreaceae*. Within the *Cosmospora* complex, for example, this rationale was used in the corresponding generic concepts for *Nectricladiella* (teleomorph), with *Cylindrocladiella* (anamorph) (Schoch *et al.* 2000), and *Chaetopsinectria* (teleomorph) with *Chaetopsina* (anamorph) (Luo & Zhuang 2010).

Booth's broad concept of *Nectria* dominated for 30 years; he recognised "groups" of species including the Episphaeria group (Booth 1959). This group, with additional species, was revised first as *Nectria* subgenus *Dialonectria* by Samuels *et al.* (1991), and then elevated to generic rank as *Cosmospora* (Rossman *et al.* 1999). The latter is typified by *C. coccinea* (= *Nectria cosmariospora,* not *Nectria coccinea,* which is a different fungus), which Saccardo (1883) listed as the only member of *Nectria* subgenus *Cosmospora*. *Cosmospora coccinea* produces orange, solitary, superficial perithecia and verrucose, brownish ascospores; its anamorph is *Verticillium olivaceum* (Gams 1971).

The relationship of the prevailing concept of *Cosmospora* with the generic concept of the economically important anamorph genus *Fusarium* is significant. In the present taxonomic system, about 20 *Fusarium* species or varieties are linked to *Cosmospora sensu* Rossman (Gräfenhan *et al.* 2008). There has been a reluctance to apply the 1:1 genus concept or strict monophyly to the present generic concept of *Fusarium,* which exhibits a striking lack of correlation with teleomorph/holomorph generic concepts in the *Nectriaceae.* Species with teleomorphs classified in other orders of ascomycetes were excluded from *Fusarium* some time ago, namely *Microdochium nivale* (*Xylariales,* Samuels & Hallett 1983) and *Plectosporium tabacinum* (*Glomerellales,* Palm *et al.* 1995). As now delimited, *Fusarium* is still linked to six teleomorph genera in the *Nectriaceae*, *i.e. Albonectria*, *Cosmospora*, *Cyanonectria*, *Gibberella* (the teleomorph genus associated with the type species of *Fusarium*), and *Haematonectria,* with some species remaining in *Nectria sensu* Booth. Members of a seventh genus, *Neocosmospora*, fall into the *Fusarium solani*/*Haematonectria* clade (O'Donnell *et al.* 2008), but no *Fusarium*-like macroconidia are produced by these species.

Throughout the modern history of *Fusarium,* taxonomists have consistently recognised the distinctiveness of several groups of species first considered as discrete taxonomic sections by Wollenweber (1931). Most species of sections *Eupionnotes, Macroconia, Pseudomicrocera,* and *Arachnites* produce characteristic colonies *in vitro*, growing slower and producing less aerial mycelium than species of other sections (Gerlach & Nirenberg 1982), often with spreading orange, macroconidial slime known as pionnotes. As shown for most taxonomic sections of *Fusarium*, sections *Eupionnotes* and *Macroconia* are polyphyletic (O'Donnell 1993, Torzilli *et al.* 2002, Schroers *et al.* 2009). Some of the morphological characters used to define these sections, including macroconidial shape and colony characters *in vitro*, are plesiomorphic and shared by distantly related species. For *Acremonium*-like anamorphs, a similar or even more complex pattern of plesiomorphy is known; preliminary revisions to that generic concept are presented by Summerbell *et al.* (2011).

Although there have been discussions of narrowing the generic concept of *Fusarium* at specialist symposia, arguments have not been presented in print nor have nomenclatural changes been proposed. The prevailing concept of *Fusarium* is essentially that of Wollenweber (1931) and Wollenweber & Reinking (1935) with the exclusion of some species; for convenience we refer to this concept as *Fusarium sensu* Wollenweber. The need to reevaluate more than 20 anamorph generic names considered synonyms of *Fusarium* has caused some hesitancy in modifying this concept; these type studies are initiated here. Previous studies provided inconclusive phylogenetic evidence to demonstrate the distinctiveness of the *Gibberella* and *Cosmospora* clades, but sampled inadequately from other anamorph and teleomorph genera in the *Nectriaceae* (O'Donnell 1993, Zhang & Zhuang 2006, Luo & Zhuang 2008, Samuels *et al.* 2009). We sampled more broadly here, including 93 species originally assigned to about 11 teleomorph and 13 anamorph genera.

Our phylogenetic analysis, combined with morphological and ecological considerations, suggests the recognition of about 13 well supported lineages within *Cosmospora sensu* Rossman that can be recognised at the generic level. *Fusarium sensu* Wollenweber splits into two major groups, which we will refer to as the "terminal *Fusarium* clade" centred on *Gibberella*, and a collection of lineages in the basal part of the *Nectriaceae* that we will refer to as the "basal *Fusarium*-like clades". In the latter, we resurrect the genera *Dialonectria*, *Fusicolla*, *Microcera*, and *Stylonectria* for species and varieties of the former *Fusarium* sections *Arachnites*, *Eupionnotes*, *Macroconia*, *Pseudomicrocera*, and *Submicrocera*, *Acremonium* section *Nectroidea*, and several fungicolous, entomogenous, and soil-borne species classified in *Cosmospora sensu* Rossman. *Cosmospora s. str.* is redelimited as a morphologically and phylogenetically restricted genus including only species with anamorphs originally ascribed to *Acremonium* or *Verticillum*. We raise *Nectria* sect. *Macroconia* to generic rank for a small group of species with large *Fusarium*-like macroconidia and minute perithecia. We epitypify the classical hyphomycete genus *Atractium*, sometimes listed as a synonym of *Fusarium*, and consider two other anamorph genera associated with *Cosmospora,* namely *Mariannaea* and *Volutella.*

The result is a revision of the *Cosmospora sensu* Rossman clade into segregate genera that should provide phylogenetic clarity to subsequent monographic revisions and facilitate the description of new species in appropriate genera. The basal *Fusarium*-like clades, for the most part the slow growing pionnotal species formerly associated with *Cosmospora sensu* Rossman, are distributed in seven monophyletic genera, six of them provided with pre-existing generic names. Another paper concerns genera of the terminal *Fusarium* clade, including the former *Nectria desmazieri,* with teleomorphs that morphologically are somewhat *Cosmospora*-like (Schroers *et al.* 2011).

In common with the papers by Schroers *et al*. (2011) and Summerbell *et al.* (2011), we adopt a single-name nomenclature, employing the oldest available generic name in combination with the oldest available species epithet, irrespective of whether these names could be interpreted as teleomorphic or anamorphic. In some cases these cross-morph combinations violate Article 59. In our opinion, the International Code of Botanical Nomenclature (ICBN, McNeill *et al.* 2006) should be like any legal code and be governed by its own basic principles. This is analogous to a constitution; when laws within a legal structure are found to be unconstitutional, they are rejected. Art. 59 violates Principle III of the ICBN, that the correct name is based on priority of publication. We give precedence to the Principles rather than the contradictory article and essentially reject Art. 59 as unconstitutional. According to Art. 59, when a valid and legitimate name is transferred into a genus

that does not match its karyological type, *i.e.* an anamorph epithet is moved into a teleomorph genus or visa versa, the name can be considered superfluous or incorrect or contrary to Art. 59.1, but the resulting binomial is still valid and legitimate. By this interpretation, combination of a valid, legitimate anamorph-typified epithet to a teleomorph-typified generic name or a valid teleomorph-typified epithet to an anamorph-typified generic name, results in a binomial that is incorrect for the holomorph. Incorrect names may become correct later (*cf.* Art. 52.3) provided they have a valid/legitimate basionym and the part of the Code (*i.e.* Art. 59) that makes the names incorrect is changed. According to the title of Chapter VI of the Code, Art. 59 only applies to pleiomorphic fungi, *i.e.* species where both the teleomorph and anamorph(s) are known. In this interpretation, names for monomorphic species resulting from the transfer of anamorph epithets into teleomorph-typified genera or visa versa would be correct, valid, and legitimate. In this paper, we explicitly state which names may be "incorrect" according to this interpretation of the present Code. However, we hope that the growing support for single name nomenclature that was evident at the International Mycological Congresses in 2002, 2006, and 2010 will discourage anyone from attempting to "correct" them.

MATERIALS AND METHODS

Fungal isolates and herbarium specimens

Ninety-three taxa of *Nectriaceae* were included in the phylogenetic study with *Acremonium lichenicola* selected as outgroup (Table 1) based on prior analyses (Gräfenhan *et al.* 2008). Morphological observations of colonies and anamorph characters are based on strains grown on potato-dextrose agar (PDA; Difco), cornmeal agar (CMA; Acumedia, Lansing, Michigan) and synthetic low nutrient agar (SNA; Nirenberg 1976) in the laboratory at room temperature (about 22–25 °C) under ambient light conditions. Measurements for some structures are presented as a range of one standard deviation above and below the calculated mean, with extreme observed values given in parentheses, and the number of measured structures noted. Colour codes refer to Kornerup & Wanscher (1978). Herbarium abbreviations are from Holmgren *et al.* (1990). Abbreviations of culture collections follow the World Federation of Culture Collections code (wdcm.nig.ac.jp/wfcc).

DNA extractions, PCR and DNA sequencing

DNA extractions were performed using UltraClean Microbial DNA Isolation Kits (MO BIO Laboratories Inc., Carlsbad, California) from mycelium scraped from colonies grown on PDA using a sterile scalpel. DNA concentration and quality were determined by Nanodrop ND-1000 spectrometer (Thermo Scientific, Wilmington, Delaware) and preparations were diluted to 1–5 ng/µL of DNA template.

The second largest subunit of the RNA polymerase II (*rpb2*) was amplified following the protocol of de Cock & Lévesque (2004) using the primer combinations 5F2/7cR and 7cF/11aR (O'Donnell *et al.* 2007) in a total reaction volume of 20 µL. PCR products of the larger subunit of the ATP citrate lyase (*acl1*, Nowrousian *et al.* 2000) was amplified using the newly designed primers acl1-230up (5'-AGC CCG ATC AGC TCA TCA AG-3') and acl1-1220low (5'-CCT GGC AGC AAG ATC VAG GAA GT-3') in a total reaction volume of 20 µL following the same protocol. PCR reactions were placed in an Eppendorf thermal cycler (Westbury, New York) and processed with the following temperature profile for the *rbp2* regions: 3 min at 95 °C (initial denaturation), 5 cycles 45 s at 95 °C (denaturation), 45 s at 60 °C (annealing), 2 min at 72 °C (extension), followed by 5 cycles with annealing at 58 °C, followed by 30 cycles with annealing at 54 °C, with a final extension 8 min at 72 °C. The temperature profile for the *acl1* region was as follows: 3 min at 95 °C, 5 cycles 45 s at 95 °C, 45 s at 64 °C, 2 min at 72 °C, followed by 5 cycles with annealing at 62 °C, followed by 30 cycles with annealing at 56 °C, with a final extension 8 min at 72 °C. For forward and reverse strands, sequencing reactions were performed directly without cleaning PCR amplicons, using a BigDye sequencing kit (Applied Biosystems, Foster City, California) on an ABI3130 DNA Analyzer (Applied Biosystems). The following profile was used for the sequencing reactions: 95 °C for 3 min, then for 40 cycles at 95 °C for 30 s, 50 °C for 15 s, 60 °C for 2 min. Contig sequences were assembled using Sequencher v. 4.9 (Gene Codes Corporation, Ann Arbor, Michigan) and aligned manually using BioEdit 7 (Hall 1999). Protein coding DNA sequences were aligned along the reading frame of the corresponding amino acid sequence and divided into 3 partitions, *rpb2* region 5–7, *rpb2* region 7–11, and *acl1*. Intergenic spacer regions and introns of the *rpb2* and *acl1* gene sequences could not be reliably aligned and were excluded from the final alignment. Additional ITS sequences were generated for some of the species mentioned below using the methods described by Nguyen & Seifert (2008).

All DNA sequences generated in this study are deposited in GenBank (accession numbers listed in Table 1 and in the Taxonomy part as barcodes). We have designated some of these as "DNA barcodes" when they represent type, authentic, or thoroughly validated strains.

Phylogenetic analyses

The combined and partitioned data set of the protein encoding regions of *rpb2* and *acl1* was used to search for the best maximum likelihood (ML) tree employing the GARLI v. 1 software (Zwickl 2006) implemented by the CIPRES project at the San Diego Supercomputer Center (www.phylo.org). The best-fit substitution model under the Akaike information criterion (Akaike 1974) was determined by using Modeltest v. 3.7 (Posada & Crandall 1998) and PAUP v. 4.0b10 (Swofford 2003). The GTR + I + G nucleotide substitution model was selected, which assumes an estimated proportion of invariant sites and 8 gamma-distributed rate categories to account for rate heterogeneity across sites. 100 independent ML heuristic phylogenetic analyses were performed using a starting tree generated by stepwise-addition (attachmentspertaxon = 2) and 10 000 generations without topology improvement parameter.

To correct for positive and divergent selection in molecular evolution of protein encoding DNA sequences, ML analyses were performed with GARLI using a codon substitution model that considers the ratio of nonsynonymous (dN) to synonymous (dS) rates of nucleotide substitution (dN/dS = ω). The GTR-like substitution model was selected with F3×4 codon frequencies (observed frequency at each codon position) and dN/dS values and proportions falling in three discrete categories $\omega 1 < \omega 2 < \omega 3$ (M3 model with site classes $K = 3$, Yang *et al.* 2000). Ten independent ML heuristic phylogenetic analyses were performed using a starting tree generated by stepwise-addition (attachmentspertaxon = 2) and 10 000 generations without improving the topology parameter.

Table 1. Taxa used in molecular phylogenetic analysis.

Unitary names used in phylogenies	Teleomorph name (most recent)	Anamorph name (most recent)	Strain †	Other No. †	Collector/ Depositor	Country	Substratum	GenBank Accession No. ‡			
								rpb2	*acl1*	ITS	LSU
Acremonium lichenicola W. Gams		*Acremonium lichenicola* W. Gams	CBS 425.66*		K.W. Gams	Germany	*Betula* sp., old leaf	HQ897724	HQ897861	–	–
Acremonium macroclavatum Ts. Watan.		*Acremonium macroclavatum* Ts. Watan.	CBS 123922*	MAFF 238162	T. Watanabe	Japan	Soil	HQ897740	HQ897876	HQ897806	–
Acremonium tsugae W. Gams		*Acremonium tsugae* W. Gams	CBS 788.69*		J.E. Bier	Canada	*Tsuga heterophylla*	HQ897728	HQ897865	–	–
"Albonectria" albida (Rossman) Guu & Y.M. Ju	*Albonectria albida* (Rossman) Guu & Y.M. Ju		BBA 67603*	ATCC 44543; BBA 65209; C.T.R. 71-110	C. T. Rogerson	Jamaica	Bark of woody stem	HQ897738	HQ897874	HQ897804	–
Albonectria albosuccinea (Pat.) Rossman & Samuels	*Albonectria albosuccinea* (Pat.) Rossman & Samuels		BBA 64502*	ATCC 44544; C.T.R. 71-188; NRRL 20459	C.T. Rogerson	Venezuela	Wood	HQ897699	HQ897837	HQ897788	U34554
Albonectria rigidiuscula (Berk. & Broome) Rossman & Samuels	*Albonectria rigidiuscula* (Berk. & Broome) Rossman & Samuels	*Fusarium decemcellulare* Brick	CBS 122570	BPI 863840; G.J.S. 01-170	G.J. Samuels	Cameroon	Bark	HQ897760	HQ897896	HQ897815	–
"Albonectria" verrucosa (Pat.) Rossman & Samuels	*Albonectria verrucosa* (Pat.) Rossman & Samuels		CBS 102163	ATCC 208923; BBA 64786; G.J.S. 84-426	G.J. Samuels	Venezuela	Recently cut bamboo	HQ897784	HQ897920	–	–
Atractium crassum (Wollenw.) Seifert & Gräfenhan		*Fusarium merismoides* var. *crassum* Wollenw.	CBS 180.31*	NRRL 20894	H.W. Wollenweber	Germany	Water tap	HQ897722	HQ897859	–	U88110
Atractium stilbaster Link		*Stilbella fusca* (Sacc.) Seifert	DAOM 215627		K.A. Seifert	Canada / Quebec	Cut stump	HQ897748	HQ897884	–	HQ843769
Chaetopsina penicillata Samuels	*Chaetopsinectria chaetopsinae-penicillatae* (Samuels) J. Luo & W.Y. Zhuang	*Chaetopsina penicillata* Samuels	CBS 608.92*	ATCC 56205; G.J.S. 77-21	G.J. Samuels	New Zealand	*Beilschmiedia tawa*, bark	HQ897709	HQ897847	HQ897798	–
Cosmospora arxii (W. Gams) Gräfenhan & Schroers		*Acremonium arxii* W. Gams	CBS 748.69*		K.W. Gams	Germany	*Hypoxylon* sp.	HQ897725	HQ897862	–	–
Cosmospora butyri (J.F.H. Beyma) Gräfenhan, Seifert & Schroers		*Tilachlidium butyri* J.F.H. Beyma	CBS 301.38*	MUCL 9950	Knudson	Denmark	Butter	HQ897729	HQ897866	–	–
Cosmospora coccinea Rabenh.	*Cosmospora coccinea* Rabenh.	*Verticillium olivaceum* W. Gams	CBS 341.70		K.W. Gams	Germany	Hymenium of *Inonotus nodulosus* on *Fagus sylvatica*	HQ897777	HQ897913	HQ897827	–
Cosmospora cymosa (W. Gams) Gräfenhan & Seifert		*Acremonium cymosum* W. Gams	CBS 762.69*		K.W. Gams	Germany	*Inonotus radiatus*, decaying fruiting body	HQ897778	HQ897914	HQ897828	–
Cosmospora khandalensis (Thirum. & Sukapure) Gräfenhan & Seifert		*Cephalosporium khandalense* Thirum. & Sukapure	CBS 356.65*	ATCC 16091; IMI 112790; MUCL 7974	M.J. Thirumalachar	India	*Bambusa* sp., decaying stem	HQ897723	HQ897860	–	–
Cosmospora lavitskiae (Zhdanova) Gräfenhan & Seifert		*Gliomastix lavitskiae* Zhdanova	CBS 530.68*	ATCC 18666; IMI 133984	L.A. Beljakova	Ukraine	Plant debris on surface soil	HQ897726	HQ897863	–	–
"Cosmospora" stegonsporii Rossman, D.F. Farr & Akulov	*Cosmospora stegonsporii* Rossman, D.F. Farr & Akulov		CBS 122305*	A.R. 4385; BPI 878274	A.Y. Akulov	Ukraine	*Stegonsporium pyriforme* on bark	HQ897733	HQ897869	–	–
Cosmospora cf. *viridescens* (C. Booth) Gräfenhan & Seifert	*Nectria* cf. *viridescens* C. Booth		CBS 102433		M. Reblova	Czech Republic	*Tilia* sp., dead tree	HQ897712	HQ897850	–	–

Table 1. (Continued).

Unitary names used in phylogenies	Teleomorph name (most recent)	Anamorph name (most recent)	Strain †	Other No. †	Collector/ Depositor	Country	Substratum	GenBank Accession No. ‡			
								rpb2	*acl1*	ITS	LSU
Cosmospora sp.			CBS 213.70		K.W. Gams	Poland	*Fomitopsis pinicola*	HQ897727	HQ897864	–	–
Cyanonectria buxi (Fuckel) Schroers, Gräfenhan & Seifert	*Gibberella buxi* (Fuckel) G. Winter	*Fusarium buxicola* Sacc.	BBA 64985		M.E. Noordeloos	Netherlands	*Buxus sempervirens*	HQ897746	HQ897882	HQ897809	–
Cyanonectria cyanostoma (Sacc. & Flageolet) Samuels & Chaverri	*Cyanonectria cyanostoma* (Sacc. & Flageolet) Samuels & Chaverri		BBA 70964*	BPI 748307; CBS 101734; G.J.S 98-127	G.J. Samuels & F. Candoussau	France	*Buxus sempervirens*, bark	HQ897759	HQ897895	HQ897814	FJ474076
Cylindrocladium sp.			CBS 125514	K.A.S. 1732	K.A. Seifert	New Zealand	Soil under *Leptospermum scoparium*	HQ897735	HQ897871	HQ897801	–
Cylindrodendrum sp.			DAOM 226786	K.A.S. 872	K.A. Seifert	Australia / New South Wales	Rotten wood	HQ897750	HQ897886	–	HQ843773
Dialonectria cf. *episphaeria* (Tode : Fr.) Cooke	*Cosmospora* cf. *episphaeria* (Tode : Fr.) Rossman & Samuels		CBS 125494	DAOM 235830; T.G. 2006-11	T. Gräfenhan	Canada / Ontario	Old ascomycete stromata on deciduous tree	HQ897756	HQ897892	HQ897811	–
Dialonectria ullevolea Seifert & Gräfenhan		*Fusarium aquaeductuum* var. *medium* Wollenw.	CBS 125493	DAOM 235827; T.G. 2007-56	T. Gräfenhan	USA / Pennsylvania	Ascomycete on *Fagus americana*	HQ897782	HQ897918	–	–
"Fusarium" cavispermum Corda		*Fusarium cavispermum* Corda	BBA 64137	CBS 184.77; NRRL 20837; NRRL 22279	T. Nilsson	Sweden	Untreated pine pole	HQ897762	HQ897898	–	–
"Fusarium" ciliatum (Alb. & Schw.) Link		*Fusarium ciliatum* (Alb. & Schw.) Link	BBA 62172	ATCC 16068; ATCC 24137; CBS 191.65; CBS H-12687; IMI 112499; NRRL 20431	H. Richter	Germany	On *Fagus sylvatica*	HQ897764	HQ897900	HQ897818	AF228349
"Fusarium" dimerum Penz.		*Fusarium dimerum* Penz.	CBS 254.50	NRRL 36384	Mack	Netherlands	Man, sputum	HQ897695	–	EU926279	–
"Fusarium" domesticum (Fr.) Bachm.		*Fusarium domesticum* (Fr.) Bachm.	CBS 116517	NRRL 29976	K. O'Donnell	Switzerland	Cheese	HQ897694	–	EU926219	–
Fusarium graminearum Schwabe	*Gibberella zeae* (Schwein.) Petch	*Fusarium graminearum* Schwabe	NRRL 31084	PH-1		USA / Michigan	*Zea mays*	FGSG02659[o]	FGSG06039[o]	–	–
"Fusarium" lunatum (Ellis & Everh.) Arx		*Fusarium lunatum* (Ellis & Everh.) Arx	BBA 63199	CBS 632.76; NRRL 20690; NRRL 37067	W. Gerlach	Germany	*Gymnocalcium damsii*	HQ897766	HQ897902	HQ897819	–
"Fusarium" melanochlorum (Casp.) Sacc.		*Fusarium melanochlorum* (Casp.) Sacc.	CBS 202.65	ATCC 16069; B 700014030; BBA 62248; NRRL 36353	H. Richter	Austria	Branch canker on *Fagus sylvatica*	HQ897769	HQ897905	–	AF228353
"Fusarium" merismoides var. *chlamydosporale* Wollenw.		*Fusarium merismoides* var. *chlamydosporale* Wollenw.	CBS 179.31*	NRRL 20839	H.W. Wollenweber	USA / Wisconsin	*Ostrya virginiana*	HQ897721	–	–	U88109
"Fusarium" nematophilum Nirenberg & G. Hagedorn		*Fusarium nematophilum* Nirenberg & G. Hagedorn	BBA 70838		A. Westphal	USA / California	*Beta vulgaris / Heterodera schachtii*	HQ897693	HQ897834	HQ897786	–

Table 1. (Continued).

Unitary names used in phylogenies	Teleomorph name (most recent)	Anamorph name (most recent)	Strain †	Other No. †	Collector/ Depositor	Country	Substratum	GenBank Accession No. ‡			
								rpb2	*acl1*	ITS	LSU
Fusarium sambucinum Fuckel	*Gibberella pulicaris* (Fr.) Sacc.	*Fusarium sambucinum* Fuckel	BBA 70569		H.I. Nirenberg	Germany	*Humulus lupulus*	HQ897751	HQ897887	–	–
Fusarium sublunatum Reinking		*Fusarium sublunatum* Reinking	BBA 62431*	CBS 189.34; NRRL 13384; NRRL 20840	O.A. Reinking	Costa Rica	Soil of banana plantation	HQ897780	HQ897916	HQ897830	–
Fusarium verticillioides (Sacc.) Nirenberg	*Gibberella moniliformis* Wineland	*Fusarium verticillioides* (Sacc.) Nirenberg	NRRL 20956	FGSC 7600; FRC M-3125		USA / California	*Zea mays*	FVEG09286°	FVEG04667°	–	–
"Fusarium" sp.			DAOM 235648	BBA 62195; CBS 119875; K.A.S. 2872; MRC 1652	R. Schneider	Germany	*Solanum lycopersicum*	HQ897698	HQ897836	HQ897787	–
Fusicolla acetilerea (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert		*Fusarium merismoides* var. *acetilereum* Tubaki, C. Booth & T. Harada	BBA 63789*	IMI 181488; NRRL 20827	Miyoshi	Japan	Polluted soil	HQ897701	HQ897839	HQ897790	U88108
Fusicolla aquaeductuum (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers		*Fusarium aquaeductuum* var. *aquaeductuum* (Radlk. & Rabenh.) Lagerh.	BBA 63669	CBS 734.79; NRRL 20686	W. Gerlach	Germany	Drinking water	HQ897742	HQ897878	–	–
Fusicolla betae (Desm.) Bonord.		*Fusarium betae* (Desm.) Sacc.	BBA 64317*		C. Bauers	Germany	On young plants of *Triticum aestivum*	HQ897781	HQ897917	–	–
Fusicolla epistroma (Höhn.) Gräfenhan & Seifert		*Fusarium epistroma* (Höhn.) C. Booth	BBA 62201*	IMI 85601; NRRL 20439	W.G. Bramley	UK	Ascomycete on *Betula* sp.	HQ897765	HQ897901	–	AF228352
Fusicolla matuoi (Hosoya & Tubaki) Gräfenhan & Seifert	*Cosmospora matuoi* Hosoya & Tubaki	*Fusarium matuoi* Hosoya & Tubaki	CBS 581.78	ATCC 18694; MAFF 238445; NRRL 20427	T. Matsuo	Japan	*Albizzia julibrissin*	HQ897720	HQ897858	–	–
Fusicolla violacea Gräfenhan & Seifert		*Fusarium merismoides* var. *violaceum* W. Gerlach, *nom. inval.*	CBS 634.76*	BBA 62461; NRRL 20896	D. Ershad	Iran	*Quadraspidiotus perniciosus* on living on branch of *Prunus domestica*	HQ897696	–	–	U88112
Geejayessia atrofusca (Schw.) Schroers & Gräfenhan	*Nectria atrofusca* (Schwein.) Ellis & Everh.	*Fusarium staphyleae* Samuels & Rogerson	CBS 125482	DAOM 238118; T.G. 2006-01	T. Gräfenhan	Canada / Ontario	*Staphylea trifolia*, twigs	HQ897775	HQ897911	HQ897825	–
Geejayessia celtidicola Gräfenhan & Schroers			CBS 125481	DAOM 238129; T.G. 2006-29	T. Gräfenhan	Canada / Ontario	*Celtis occidentalis*, twigs	HQ897772	HQ897908	HQ897822	–
Geejayessia cicatricum (Berk.) Schroers	*Nectria cicatricum* (Berk.) Tul. & C. Tul.		CBS 125550	CBS H-20375; H.J.S. 1374	H.-J. Schroers & M. Žerjav	Slovenia	*Buxus sempervirens*, twigs	HQ897697	HQ897835	–	–
Geejayessia desmazieri (Becc. & De Not.) Schroers, Gräfenhan & Seifert	*Nectria desmazieri* Becc. & De Not.	*Fusarium fuckelii* Sacc.	CBS 313.34	NRRL 20474	E.W. Mason	UK	*Buxus sempervirens*, dead twig	HQ897703	HQ897841	HQ897792	U88125
Geejayessia zealandica (Cooke) Schroers	*Cosmospora zealandica* (Cooke) Samuels & Nirenberg	*Fusarium zealandicum* Nirenberg & Samuels	BBA 65034	BPI 802575; CBS 101913; G.J.S. 86-509	G.J. Samuels	New Zealand	*Plagianthus*, timber	HQ897745	HQ897881	HQ897808	–
Haematonectria illudens (Berk.) Samuels & Nirenberg	*Haematonectria illudens* (Berk.) Samuels & Nirenberg	*Fusarium illudens* C. Booth	BBA 67606	G.J.S. 82-98; NRRL 22090	G.J. Samuels	New Zealand	*Beilschmiedia tawa*	HQ897692	HQ897833	AF178393	AF178362
Haematonectria ipomoeae (Halst.) Samuels & Nirenberg	*Haematonectria ipomoeae* (Halst.) Samuels & Nirenberg	*Fusarium striatum* Sherb.	BBA 64379	NRRL 22147	H.I. Nirenberg	Germany	*Passiflora edulis*	HQ897753	HQ897889	–	–

Table 1. (Continued).

Unitary names used in phylogenies	Teleomorph name (most recent)	Anamorph name (most recent)	Strain †	Other No. †	Collector/ Depositor	Country	Substratum	GenBank Accession No. ‡			
								rpb2	*acl1*	ITS	LSU
Heliscus lugdunensis Sacc. & Therry	*Nectria lugdunensis* J. Webster	*Heliscus lugdunensis* Sacc. & Therry	CBS 125485	DAOM 235831; T.G. 2008-07	T. Gräfenhan	USA / Arizona	*Populus fremontii*, twigs in stream	HQ897731	HQ897867	–	–
Heliscus submersus H.J. Huds.		*Heliscus submersus* H.J. Huds.	CBS 394.62*		H.J. Hudson	UK		HQ897707	HQ897845	HQ897796	–
Macroconia leptosphaeriae (Niessl) Gräfenhan & Schroers	*Cosmospora leptosphaeriae* (Niessl) Rossman & Samuels	? *Fusarium sphaeriae* var. *majus* Wollenw.	CBS 100001	CBS H-6030	L. Rommelaars	Netherlands	On *Leptosphaeria* on dead stem of *Urtica dioica*	HQ897755	HQ897891	HQ897810	–
Macroconia papilionacearum (Seaver) Gräfenhan & Seifert	*Cosmospora papilionacearum* (Seaver) Rossman & Samuels	**?** *Fusarium gigas* Speg.	CBS 125495	DAOM 238119; T.G. 2007-03	T. Gräfenhan	USA / Florida	Black ascomycete on *Fabaceae*	HQ897776	HQ897912	HQ897826	–
Macroconia sp.			CBS 125496	T.G. 2008-08	T. Gräfenhan	USA / Arizona	*Quercus* sp., branch in stream of water	HQ897732	HQ897868	–	–
Mariannaea elegans (Corda) Samson	? *Nectria mariannaeae* Samuels & Seifert	*Mariannaea elegans* (Corda) Samson	DAOM 226709	K.A.S. 948	K.A. Seifert	Canada / Ontario	*Betula* sp., wood	HQ897747	HQ897883	–	HQ843768
Mariannaea samuelsii Seifert & Bissett			DAOM 235814*	CBS 125515; K.A.S. 1307	J. Bissett	Guatemala	Soil under *Podocarpus*	HQ897752	HQ897888	HQ843767	HQ843766
Microcera coccophila Desm.		*Fusarium coccophilum* (Desm.) Wollenw. & Reinking	CBS 310.34	NRRL 13962	H.W. Wollenweber	Italy	Scale insect on *Laurus nobilis*	HQ897705	HQ897843	HQ897794	–
Microcera diploa (Berk. & M.A. Curtis) Gräfenhan & Seifert	*Cosmospora diploa* (Berk. & M.A. Curtis) Rossman & Samuels	*Fusarium coccidicola* Henn.	BBA 62173	CBS 735.79; NRRL 13966	W. Gerlach	Iran	*Quadraspidiotus perniciosus* on living on branch of *Prunus domestica*	HQ897763	HQ897899	HQ897817	–
Microcera larvarum (Fuckel) Gräfenhan, Seifert & Schroers		*Fusarium larvarum* Fuckel	CBS 169.30	NRRL 22102	H.W. Wollenweber	Japan	Aphids on *Pyrus communis*	HQ897717	HQ897855	–	–
Microcera rubra Gräfenhan & Seifert		*Fusarium larvarum* var. *rubrum* W. Gerlach, *nom. inval.*	BBA 62460*	CBS 638.76; NRRL 20475; NRRL 22111; NRRL 22170	W. Gerlach	Iran	*Quadraspidiotus perniciosus* on living on branch of *Prunus domestica*	HQ897767	HQ897903	HQ897820	–
Nalanthamala diospyri (Crand.) Schroers & . M.J. Wingfield		*Nalanthamala diospyri* (Crand.) Schroers & . M.J. Wingfield	CBS 429.89	ATCC 22206	B.S. Crandall	USA / Mississippi	*Diospyros virginiana*	HQ897718	HQ897856	–	–
"Nectria" cinereopapillata Henn. & E. Nyman	*Nectria cinereopapillata* Henn. & E. Nyman		CBS 264.36		H.W. Wollenweber	Sierra Leone	*Cassia sieberiana*	HQ897710	HQ897848	HQ897799	–
"Nectria" diminuta Berk.	*Cosmospora diminuta* (Berk.) Rossman & Samuels		CBS 114636	BPI 864173; G.J.S. 00-181	G.J. Samuels	USA / North Carolina	*Quercus virginiana*, dead tree	HQ897758	HQ897894	HQ897813	–
"Nectria" cf. *flavoviridis* (Fuckel) Wollenw.	*Nectria flavoviridis* (Fuckel) Wollenw.		BBA 65542		G.J. Samuels	USA / New York	On fungus on decorticated wood	HQ897702	HQ897840	HQ897791	–
"Nectria" magnoliae M.L. Lohman & Hepting	*Nectria magnoliae* M.L. Lohman & Hepting		CBS 380.50*	BPI 552527	G.H. Hepting	USA / North Carolina	*Liriodendron tulipifera*	HQ897713	HQ897851	–	–
Nectria miltina (Mont.) Mont.	*Nectria miltina* (Mont.) Mont.		CBS 125499	T.G. 2008-02	T. Gräfenhan	USA / Arizona	*Yucca elata*	HQ897730	–	–	–
Nectria nigrescens Cooke	*Nectria nigrescens* Cooke		CBS 125500	DAOM 235832; T.G. 2006-18	T. Gräfenhan	Canada / Ontario	*Acer* sp., twig	HQ897757	HQ897893	HQ897812	–
Nectria pseudotrichia Berk. & M.A. Curtis	*Nectria pseudotrichia* Berk. & M.A. Curtis	*Tubercularia lateritia* (Berk.) Seifert	DAOM 235820	T.G. 2007-41	T. Gräfenhan	USA / Florida	Dead herbaceous plant	HQ897706	HQ897844	HQ897795	–

Table 1. (Continued).

Unitary names used in phylogenies	Teleomorph name (most recent)	Anamorph name (most recent)	Strain †	Other No. †	Collector/ Depositor	Country	Substratum	GenBank Accession No. ‡			
								rpb2	*acl1*	ITS	LSU
"Nectria" rishbethii C. Booth	*Cosmospora rishbethii* (C. Booth) Rossman & Samuels		CBS 496.67*	IMI 070248b; MUCL 4133	J. Rishbeth	UK	*Pinus sylvestris*, stump	HQ897714	HQ897852	–	–
"Nectria" rubropeziza Wollenw.	*Nectria rubropeziza* Wollenw.		CBS 234.31*		H.W. Wollenweber	USA / Maryland	Tree trunk	HQ897708	HQ897846	HQ897797	–
"Nectria" setofusariae Samuels & Nirenberg	*Nectria setofusariae* Samuels & Nirenberg	*Fusarium setosum* Nirenberg & Samuels	CBS 635.92	A.R. 3333; BBA 65063; BPI 1113176; G.J.S. 88-12	A.Y. Rossman	French Guiana	Bark of recently cut tree	HQ897704	HQ897842	HQ897793	–
"Nectria" ventricosa C. Booth	*Nectria ventricosa* C. Booth	*Fusarium ventricosum* Appel & Wollenw.	BBA 62452	CBS 748.79; NRRL 20846; NRRL 22113	K.H. Domsch	Germany	Wheat field soil	HQ897761	HQ897897	HQ897816	L36613
"Nectria" ventricosa C. Booth	*Nectria ventricosa* C. Booth	*Fusarium ventricosum* Appel & Wollenw.	CBS 430.91	NRRL 25729	U. Kuchenbäcker	Germany	*Robinia pseudoacacia*, twig	HQ897771	HQ897907	–	–
Nectria sp.			CBS 125498	T.G. 2006-33	T. Gräfenhan	Canada / Ontario	*Abies balsamea*	HQ897737	HQ897873	HQ897803	–
Neocosmospora vasinfecta E.F. Sm.	*Neocosmospora vasinfecta* E.F. Sm.		NRRL 22166	ATCC 62199	L.M. Carris	USA / Illinois	*Heterodera glycines*	EU329497	–	DQ094319	DQ236361
Neonectria coccinea (Pers.) Rossman & Samuels	*Neonectria coccinea* (Pers.) Rossman & Samuels	*Cylindrocarpon candidum* (Link) Wollenw.	CBS 125484	DAOM 235835; T.G. 2007-17	T. Gräfenhan	Germany	*Fagus sylvatica*	HQ897785	HQ897921	HQ897832	–
Neonectria ditissima (Tul. & C. Tul.) Samuels & Rossman	*Neonectria ditissima* (Tul. & C. Tul.) Samuels & Rossman	*Cylindrocarpon heteronema* (Berk. & Broome) Wollenw.	CBS 125486	DAOM 235836; T.G. 2006-21	T. Gräfenhan	Canada / Ontario	*Fagus americana*, branch	HQ897774	HQ897910	HQ897824	–
Neonectria fuckeliana (C. Booth) Castl. & Rossman	*Neonectria fuckeliana* (C. Booth) Castl. & Rossman		CBS 239.29*	IMI 039700	H.W. Wollenweber	UK	*Picea sitchensis*, bark	HQ897711	HQ897849	–	–
Pseudonectria buxi (DC.) Seifert, Gräfenhan & Schroers	*Pseudonectria rousseliana* (Mont.) Wollenw.	*Volutella buxi* (DC.) Berk.	CBS 125483	T.G. 2007-69A	K.W. Gams	Spain	*Buxus sempervirens*, leaves	HQ897719	HQ897857	HQ897800	–
"Pseudonectria" pachysandricola B.O. Dodge	*Pseudonectria pachysandricola* B.O. Dodge	*Volutella pachysandricola* B.O. Dodge	DAOM 195309		E.J. Mathers	USA / Florida	*Pachysandra* sp., nursery stock	HQ897743	HQ897879	HQ897807	–
Pseudonectria sp.			BBA 71336		H.I. Nirenberg	Germany	*Buxus sempervirens*, leaves	HQ897741	HQ897877	–	–
Stylonectria cf. *applanata* Höhn.	*Nectria applanata* var. *succinea* Höhn.		CBS 125489	T.G. 2008-24	T. Gräfenhan	Canada / Ontario	Ascomycete on *Betula* sp.	HQ897739	HQ897875	HQ897805	–
Stylonectria carpini Gräfenhan	*Nectria applanata* Fuckel		DAOM 235819	W.J. 3013	H. Voglmayr	Austria	On *Melanconis spodiaea* on *Carpinus betulus*	HQ897773	HQ897909	HQ897823	–
Stylonectria purtonii (Grev.) Gräfenhan	*Cosmospora purtonii* (Grev.) Rossman & Samuels		DAOM 235818	T.G. 2007-30	T. Gräfenhan	Germany	On small branches of *Picea abies*	HQ897783	HQ897919	HQ897831	–
Stylonectria wegeliniana (Rehm) Gräfenhan, Voglmayr & Jaklitsch	*Cosmospora wegeliniana* (Rehm) Rossman & Samuels		CBS 125490	WU 29855	H. Voglmayr	Austria	Stromata of *Hapalycystis bicaudata* on *Ulmus glabra*	HQ897754	HQ897890	–	–
Stylonectria sp.			CBS 125491	T.G. 2007-21	T. Gräfenhan	Germany	Ascomycete on *Carpinus / Ulmus* ?	HQ897779	HQ897915	HQ897829	–
Thelonectria discophora (Mont.) P. Chaverri & C. Salgado	*Neonectria discophora* (Mont.) Mantiri & Samuels	*Cylindrocarpon ianthothele* var. *majus* Wollenw.	CBS 125487	DAOM 235837; T.G. 2007-34	T. Gräfenhan	Germany	*Aesculus hippocastanum*	HQ897700	HQ897838	HQ897789	–
Thelonectria lucida (C. Booth) P. Chaverri & C. Salgado		*Cylindrocarpon lucidum* C. Booth	DAOM 226723	K.A.S. 1007	K.A. Seifert	Canada / British Columbia	*Pseudotsuga menziesii*, root	HQ897734	HQ897870	–	–

Table 1. (Continued).

Unitary names used in phylogenies	Teleomorph name (most recent)	Anamorph name (most recent)	Strain †	Other No. †	Collector/ Depositor	Country	Substratum	GenBank Accession No. ‡			
								rpb2	*acl1*	ITS	LSU
Volutella ciliata (Alb. & Schwein.) Fr.		*Volutella ciliata* (Alb. & Schwein.) Fr.	DAOM 226718	K.A.S. 972	J.A. Traquair	Canada / Ontario	Agricultural soil	HQ897736	HQ897872	HQ897802	–
Volutella citrinella (Cooke & Massee) Seifert	*Cosmospora stilbellae* (Samuels & Seifert) Rossman & Samuels	*Stilbella aciculosa* (Ellis & Everh.) Seifert	DAOM 226720	K.A.S. 978	R.J. Bandoni & A.A. Bandoni	Canada / British Columbia	*Solanum tuberosum*, debris	HQ897770	HQ897906	HQ897821	HQ843771
Volutella consors (Ellis & Everh.) Seifert, Gräfenhan & Schroers	*Cosmospora consors* (Ellis & Everh.) Rossman & Samuels	*Volutella minima* Höhn.	CBS 328.77	C.T.R. 72-347	C.T. Rogerson	USA / North Carolina	*Magnolia fraseri*, old inflorescence	HQ897716	HQ897854	–	–
Volutella consors (Ellis & Everh.) Seifert, Gräfenhan & Schroers	*Cosmospora consors* (Ellis & Everh.) Rossman & Samuels	*Volutella minima* Höhn.	CBS 139.79		G.H. Boerema	Netherlands	Decaying orchid bulb	HQ897715	HQ897853	–	–

† — A.R. = Amy Y. Rossman personal collection; ATCC = American Type Culture Collections, Manassas, Virginia, USA; B = Mycological Herbarium at the Botanical Museum, Berlin, Germany; BBA = Julius Kühn-Institute, Institute for Epidemiology and Pathogen Diagnostics, Berlin & Braunschweig, Germany; BPI = U.S. National Fungus Collections, USDA, ARS, Beltsville, Maryland, USA; CBS = Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; C.T.R. = Clark T. Rogerson personal collection; DAOM = Canadian National Mycological Herbarium and Culture Collection, AAFC, Ottawa, Ontario, Canada; FGSC = Fungal Genetics Stock Center, School of Biological Sciences, University of Missouri, Kansas City, Missouri, USA; FRC = Fusarium Research Center, Department of Plant Pathology, Penn State University, University Park, Pennsylvania, USA; G.J.S. = Gary J. Samuels personal collection; H.J.S. = Hans-Josef Schroers personal collection; IMI = CABI Bioservices, Egham, Surrey, UK; K.A.S. = Keith A. Seifert personal collection; MAFF = Microbial Culture Collection, National Institute of Agrobiological Sciences, Tsukuba, Japan; MRC = Microbial Culture Collection, South African Medical Research Council, Tygerberg, South Africa; MUCL = (Agro)Industrial Fungi & Yeasts Collection, Université Catholique de Louvain, Louvain-la-Neuve, Belgium; NRRL = ARS Culture Collection, USDA, NCAUR, Peoria, Illinois, USA; T.G. = Tom Gräfenhan personal collection; W.J. = Walter Jaklitsch personal collection; WU = Herbarium, Department of Plant Systematics and Evolution, Faculty of Life Sciences, University Vienna, Austria.

* — Type or other authentic material.

‡ — GenBank accession numbers beginning with HQ were newly generated. All other sequences were obtained from GenBank.

° — Locus number in the *Fusarium* genome database (http://www.broad.mit.edu/annotation/fungi/fusarium)

Non-parametric bootstrapping of 1 000 ML pseudo-replicates of the data was used to assess clade support with GARLI. Because of the extended time necessary for ML bootstrap analysis under the M3 codon model, the measure of clade support was calculated using the parameters of the GTR + I + G nucleotide model given above. ML bootstrap probabilities (ML-BP) for the splits were mapped onto the best phylogenetic tree inferred under the M3 codon substitution model using SumTrees of the DendroPy v. 3.7 phylogenetic computing library (Sukumaran & Holder 2010).

Bayesian posterior probabilities (PP) were obtained from the combined and partitioned *rpb2*/*acl1* data set using MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003) implemented by the CIPRES project (see above). The GTR + I + G substitution model was selected assuming an estimated proportion of invariant sites and 4 gamma-distributed rate categories to account for rate heterogeneity across sites. Two independent Markov chain Monte Carlo analysis (MCMC) runs each with 4 chains were performed simultaneously. The analysis was run for 10 000 000 generations, sampling every 1 000 generations for a total of 10 001 trees. The first 1 500 000 generations were discarded as burn-in. Each of the two independent MCMC runs yielded 8 501 trees from each partition. The resulting six tree files (total 51 006 trees) were used to calculate PPs. These posterior probabilities were mapped onto the best phylogenetic tree using SumTrees of the DendroPy package.

Heuristic searches for the most parsimonious (MP) trees using PAUP v. 4.0b10 (Swofford 2003) were based on 1 026 parsimony informative, unordered and equally weighted characters; gaps were treated as missing data. Starting trees were obtained via 100 stepwise, random addition sequences. Other settings included auto-increase for MAXTREES, the tree-bisection-reconnection branch-swapping algorithm, the MULTREES option, and assigning any possible character state to an internal node with STEPMATRIX. MP bootstrap probabilities (MP-BP) were assessed by 1 000 heuristic pseudoreplicates using the same settings as above but with 20 stepwise, random addition sequences. By using SumTrees of the DendroPy package, the MP-BP support for the splits were mapped onto the best phylogenetic tree.

RESULTS

Sequence alignment

The combined and partitioned data set of two protein encoding genes for 93 taxa and outgroup consisted of 2 250 bp, translating to 750 amino acids. The *rpb2* sequences (1 764 bp) had two coding regions (*rpb2* 5–7 and *rpb2* 7–11) with an intergenic spacer, which was removed from the final alignment. The *acl1* amplicon comprised a coding region of 420 bp and a single intron of 200–500 bp, which was also removed.

Phylogenetic analyses

One hundred independent ML analyses under the GTR + I + G nucleotide substitution model of the combined and partitioned data set (*rpb2* 5–7 with 488 parsimony-informative characters, *rpb2* 7–11 with 387 parsimony-informative characters, and

acl1 with 206 parsimony-informative characters) resulted in a single best ML tree with −lnL = −57,309.9782 (not shown). The parameters for the GTR + I + G model of the *rpb2* 5–7 partition were as follows: Estimated base frequencies; A = 0.2098, C = 0.2885, G = 0.2691, T = 0.2326; substitution rates AC = 2.104, AG = 6.386, AT = 2.011, CG = 0.767, CT = 9.725, GT = 1.000; proportion of invariable sites I = 0.3861; gamma distribution shape parameter α = 0.8858. The parameters for the GTR + I + G model of the *rpb2* 7–11 partition were as follows: Estimated base frequencies; A = 0.2033, C = 0.3050, G = 0.2538, T = 0.2379; substitution rates AC = 1.680, AG = 7.167, AT = 2.089, CG = 0.914, CT = 10.966, GT = 1.000; proportion of invariable sites I = 0.5253; gamma distribution shape parameter α = 0.8815. The parameters for the *GTR + I + G* model of the *acl1* partition were as follows: Estimated base frequencies; A = 0.1774, C = 0.3655, G = 0.2369, T = 0.2202; substitution rates AC = 0.982, AG = 2.844, AT = 0.638, CG = 0.839, CT = 7.876, GT = 1.000; proportion of invariable sites I = 0.4834; gamma distribution shape parameter α = 0.9192.

Ten independent ML analyses under the codon substitution model (M3 with *K* = 3) of the combined and partitioned data set (*rpb2* 5–7 with 294 parsimony-informative characters, *rpb2* 7–11 with 292 parsimony-informative characters, and *acl1* with 145 parsimony-informative characters) resulted in a single best ML tree with −lnL = −54,991.4885 (Fig. 1). The parameters for the M3 codon model of the *rpb2* 5–7 partition were as follows: 61 empirical codon frequencies (F3×4 method); substitution rates AC = 1.234, AG = 2.380, AT = 1.222, CG = 0.743, CT = 2.758, GT = 1.000; and three estimated nonsynonymous rate categories ω1 = 0.0020 with p1 = 0.6471, ω2 = 0.0726 with p2 = 0.2452, ω3 = 0.3214 with p3 = 0.1077. The parameters for the M3 codon model of the *rpb2* 7–11 partition were as follows: 61 empirical codon frequencies (F3×4 method); substitution rates AC = 1.023, AG = 2.820, AT = 1.177, CG = 0.933, CT = 2.489, GT = 1.000; and three estimated non-synonymous rate categories ω1 = 0.0020 with p1 = 0.8918, ω2 = 0.0925 with p2 = 0.0985, ω3 = 0.5436 with p3 = 0.0097. The parameters for the M3 codon model of the *acl1* partition were as follows: 61 empirical codon frequencies (F3×4 method); substitution rates AC = 1.863, AG = 3.515, AT = 1.290, CG = 1.264, CT = 3.346, GT = 1.000; and three estimated non-synonymous rate categories ω1 = 0.0031 with p1 = 0.8025, ω2 = 0.1007 with p2 = 0.1211, ω3 = 0.4420 with p3 = 0.0763. These dN/dS ratios (ω < 1) verify a significant departure from neutrality (ω ≈ 1) of the *rpb2* and *acl1* data partitions implying natural selection against changes of amino acids in the encoding genes studied.

In comparison, the best ML tree for the M3 codon model received a significantly better negative-log likelihood score than the best ML tree under the GTR + I + G nucleotide substitution model. The topology of the phylograms did not differ for the clades studied. Only some basal lineages such as "*Nectria*" *diminuta*, "*N.*" *rubropeziza*, and "*Pseudonectria*" *pachysandricola* grouped differently using different substitution models, probably a result of long branch attraction.

Similarily, heuristic searches of the parsimony analysis yielded a single most parsimonious tree (not shown), which did not have a significantly different topology than that of the ML analyses. The MP tree was 14 023 steps with a consistency index (CI) of 0.152, a retention index (RI) of 0.492, a rescaled CI (RC) of 0.075, and a homoplasy index (HI) of 0.848.

1 000 ML pseudoreplicates, two independent MCMC analyses, and 1 000 heuristic bootstrap replicates of the combined and partitioned data set conducted with GARLI, MrBayes and PAUP, respectively, yielded majority consensus trees with highly concordant topologies (not shown) similar to that of the best ML tree generated for the M3 codon model. Internodes with significant clade support are drawn in thicker lines on the best ML tree topology (Fig. 1). Nodes were considered strongly supported when ML bootstrap proportions (ML-BP) is ≥ 75 %, Bayesian posterior probabilities (PP) is ≥ 0.95, and MP bootstrap proportions (MP-BP) is ≥ 75 % (Lutzoni *et al*. 2004).

Polyphyly of *Cosmospora sensu* Rossman

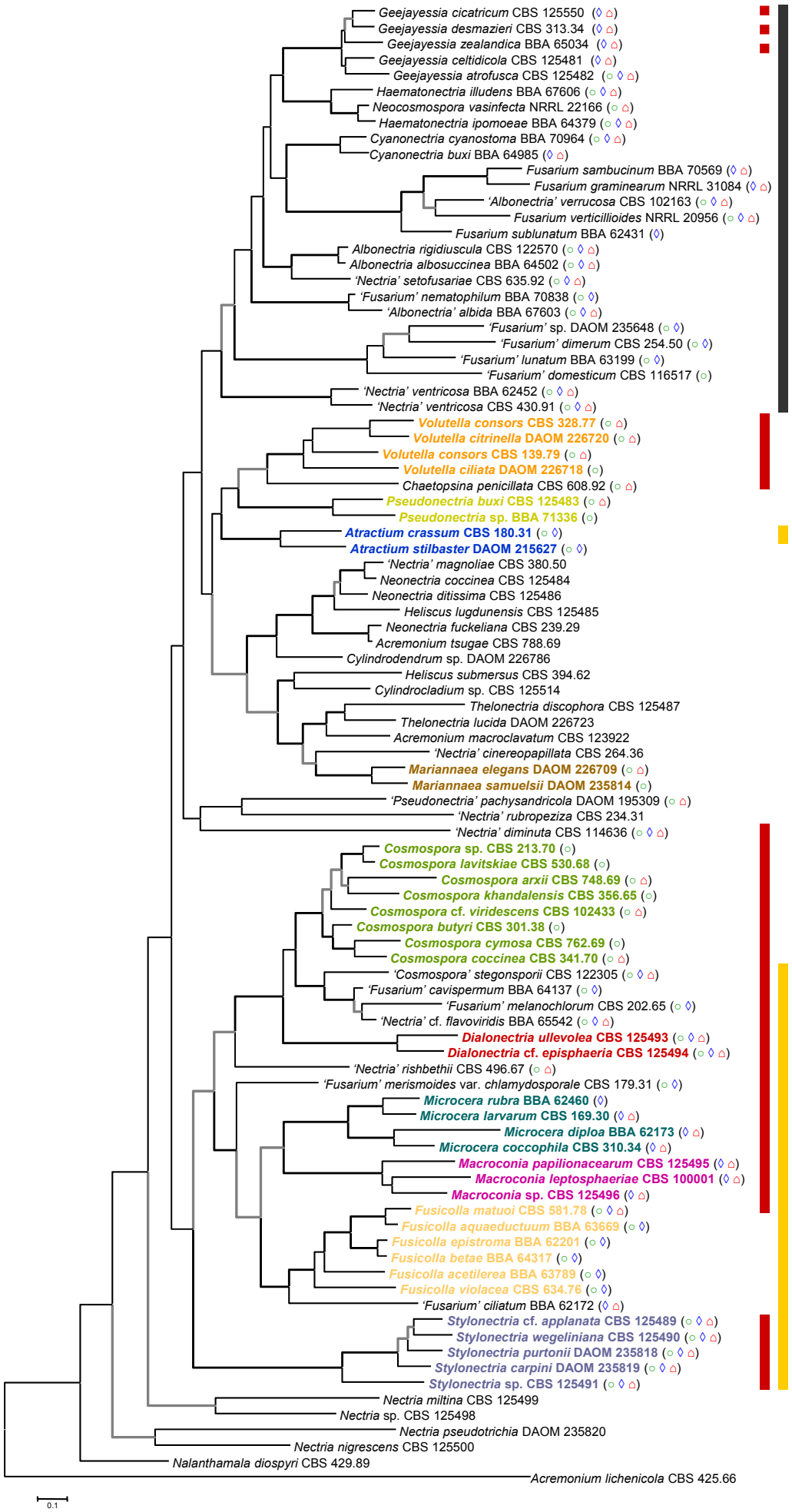
In the best ML tree (Fig. 1), species formerly placed in *Cosmospora sensu* Rossman fall into several major clades. The first major clade includes *Volutella* with four strains of three species, *V. ciliata*, *V. citrinella* (*"Cosmospora" stilbellae*) *and V. consors* (*"C." consors*), in a strongly supported clade. *Chaetopsina penicillata* (= *Chaetopsinectria* or *"Cosmospora" chaetopsinae-penicillatae*) is a well supported sister species of *Volutella,* confirming the close phylogenetic relationship of *Chaetopsina* and *Volutella* (Zhang & Zhuang 2006, Luo & Zhuang 2010). Although not strongly supported, the *Volutella*/*Chaetopsina* group is the sister clade to a diverse fungal clade consisting of species of *Calonectria*, *Cylindrodendrum*, *Heliscus*, *Mariannaea*, and *Neonectria*.

The second major clade includes species formerly classified as *Nectria applanata*, *Cosmospora purtonii*, and *C. wegeliniana*. This clade is strongly supported and comprises species having ascomata with perithecial walls mainly consisting of two regions, and which are probably host-specific. These species are transferred to *Stylonectria* in the taxonomic section below.

The third and largest clade includes several subclades including the type species of *Cosmospora*, *C. coccinea,* and species with *Fusarium*-, *Acremonium*- and *Verticillium*-like anamorphs, which are classified in *Cosmospora sensu stricto*, *Dialonectria*, *Fusicolla*, *Macroconia*, and *Microcera* below. *Cosmospora coccinea* forms a strongly supported clade with other well-known species of the genus with *Acremonium*-like anamorphs, such as *C. butyri, C. cymosa,* and *C. viridescens*. This clade contains a group of species with similar microconidial anamorphs and a fairly constant ecological niche, delineating the new generic concept of *Cosmospora s. str.* Basal to *Cosmospora* is the strongly supported *Dialonectria* clade, which contains *D. episphaeria* and a new species, *D. ullevolea*. With *"Nectria" rishbethii* as a sister species, this subclade is delimited from another strongly supported subclade with species of *Macroconia* and *Microcera*, and *Fusicolla matuoi*. *Macroconia* and *Microcera* are sister clades, and include species such as *Macroconia papilionacearum* and *Mac. leptosphaeriae* as well as *Microcera coccophila*, *Mic. diploa*, and *Mic. larvarum*. These subclades, together with a few "residual" species classified in *Fusarium* such as *"F." cavispermum*, *"F." ciliatum*, *"F." melanochlorum*, and *"F." merismoides* var. *chlamydosporale*, are all phylogenetically distinct from the terminal *Fusarium* clade discussed below.

The terminal *Fusarium* clade contains a group of fungi with *Cosmospora*-like teleomorphs, of which only *"Nectria" zealandica* was formally combined in *Cosmospora* (Nirenberg & Samuels 2000).

Fig. 1. (p. 89). Maximum likelihood (ML) tree under the M3 codon model inferred from combined *rpb2* + *acl1* gene sequence data set. Negative-log likelihood (-lnL) of the ML tree is −54,991.4885. Branches with ML-BP and MP-BP values of > 75 % and PP scores > 0.95 are in bold. Internodes that are supported with individual values of ML-BP or MP-BP > 75 % or PP scores > 0.95, respectively, are drawn in bold and grey. Symbols following strain numbers indicate different morphs known for the species: ○ = microconidial state, ◊ = *Fusarium*-like macroconidial state, ⌂ = teleomorph. Vertical bars in red indicate members of *Cosmospora sensu* Rossman *et al.* (1999), yellow bars taxa of the basal *Fusarium*-like clade, and a dark grey bar species of the terminal *Fusarium* clade, respectively.


Geejayessia cicatricum CBS 125550 (◊ ⌂)
Geejayessia desmazieri CBS 313.34 (◊ ⌂)
Geejayessia zealandica BBA 65034 (◊ ⌂)
Geejayessia celtidicola CBS 125481 (◊ ⌂)
Geejayessia atrofusca CBS 125482 (○ ◊ ⌂)
Haematonectria illudens BBA 67606 (○ ◊ ⌂)
Neocosmospora vasinfecta NRRL 22166 (○ ⌂)
Haematonectria ipomoeae BBA 64379 (○ ◊ ⌂)
Cyanonectria cyanostoma BBA 70964 (○ ◊ ⌂)
Cyanonectria buxi BBA 64985 (◊ ⌂)
Fusarium sambucinum BBA 70569 (◊ ⌂)
Fusarium graminearum NRRL 31084 (◊ ⌂)
'Albonectria' verrucosa CBS 102163 (○ ◊ ⌂)
Fusarium verticillioides NRRL 20956 (○ ◊ ⌂)
Fusarium sublunatum BBA 62431 (◊)
Albonectria rigidiuscula CBS 122570 (○ ◊ ⌂)
Albonectria albosuccinea BBA 64502 (○ ◊ ⌂)
'Nectria' setofusariae CBS 635.92 (○ ◊ ⌂)
'Fusarium' nematophilum BBA 70838 (○ ◊)
'Albonectria' albida BBA 67603 (○ ◊ ⌂)
'Fusarium' sp. DAOM 235648 (○ ◊)
'Fusarium' dimerum CBS 254.50 (○ ◊)
'Fusarium' lunatum BBA 63199 (○ ◊)
'Fusarium' domesticum CBS 116517 (○)
'Nectria' ventricosa BBA 62452 (○ ◊ ⌂)
'Nectria' ventricosa CBS 430.91 (○ ◊ ⌂)
Volutella consors CBS 328.77 (○ ⌂)
Volutella citrinella DAOM 226720 (○ ⌂)
Volutella consors CBS 139.79 (○ ⌂)
Volutella ciliata DAOM 226718 (○)
Chaetopsina penicillata CBS 608.92 (○ ⌂)
Pseudonectria buxi CBS 125483 (○ ⌂)
Pseudonectria sp. BBA 71336 (○)
Atractium crassum CBS 180.31 (○ ◊)
Atractium stilbaster DAOM 215627 (○ ◊)
'Nectria' magnoliae CBS 380.50
Neonectria coccinea CBS 125484
Neonectria ditissima CBS 125486
Heliscus lugdunensis CBS 125485
Neonectria fuckeliana CBS 239.29
Acremonium tsugae CBS 788.69
Cylindrodendrum sp. DAOM 226786
Heliscus submersus CBS 394.62
Cylindrocladium sp. CBS 125514
Thelonectria discophora CBS 125487
Thelonectria lucida DAOM 226723
Acremonium macroclavatum CBS 123922
'Nectria' cinereopapillata CBS 264.36
Mariannaea elegans DAOM 226709 (○ ⌂)
Mariannaea samuelsii DAOM 235814 (○)
'Pseudonectria' pachysandricola DAOM 195309 (○ ⌂)
'Nectria' rubropeziza CBS 234.31
'Nectria' diminuta CBS 114636 (○ ◊ ⌂)
Cosmospora sp. CBS 213.70 (○)
Cosmospora lavitskiae CBS 530.68 (○)
Cosmospora arxii CBS 748.69 (○ ⌂)
Cosmospora khandalensis CBS 356.65 (○)
Cosmospora cf. viridescens CBS 102433 (○ ⌂)
Cosmospora butyri CBS 301.38 (○)
Cosmospora cymosa CBS 762.69 (○)
Cosmospora coccinea CBS 341.70 (○ ⌂)
'Cosmospora' stegonsporii CBS 122305 (○ ◊ ⌂)
'Fusarium' cavispermum BBA 64137 (○ ◊)
'Fusarium' melanochlorum CBS 202.65 (○ ◊)
'Nectria' cf. flavoviridis BBA 65542 (○ ◊ ⌂)
Dialonectria ullevolea CBS 125493 (○ ◊ ⌂)
Dialonectria cf. episphaeria CBS 125494 (○ ◊ ⌂)
'Nectria' rishbethii CBS 496.67 (○ ⌂)
'Fusarium' merismoides var. chlamydosporale CBS 179.31 (○ ◊)
Microcera rubra BBA 62460 (◊)
Microcera larvarum CBS 169.30 (◊ ⌂)
Microcera diploa BBA 62173 (◊ ⌂)
Microcera coccophila CBS 310.34 (◊ ⌂)
Macroconia papilionacearum CBS 125495 (◊ ⌂)
Macroconia leptosphaeriae CBS 100001 (◊ ⌂)
Macroconia sp. CBS 125496 (◊ ⌂)
Fusicolla matuoi CBS 581.78 (○ ◊ ⌂)
Fusicolla aquaeductuum BBA 63669 (○ ◊)
Fusicolla epistroma BBA 62201 (○ ◊)
Fusicolla betae BBA 64317 (○ ◊)
Fusicolla acetilerea BBA 63789 (○ ◊)
Fusicolla violacea CBS 634.76 (○ ◊)
'Fusarium' ciliatum BBA 62172 (◊ ⌂)
Stylonectria cf. applanata CBS 125489 (○ ◊ ⌂)
Stylonectria wegeliniana CBS 125490 (○ ◊ ⌂)
Stylonectria purtonii DAOM 235818 (○ ◊ ⌂)
Stylonectria carpini DAOM 235819 (○ ◊ ⌂)
Stylonectria sp. CBS 125491 (○ ◊ ⌂)
Nectria miltina CBS 125499
Nectria sp. CBS 125498
Nectria pseudotrichia DAOM 235820
Nectria nigrescens CBS 125500
Nalanthamala diospyri CBS 429.89
Acremonium lichenicola CBS 425.66
0.1

The terminal clade includes *"Nectria" desmazieri* and *"N." atrofusca,* and is dealt with in more detail by Schroers *et al*. (2011).

As a singleton, "*Nectria" diminuta* does not group with any of the clades mentioned above. In all analyses under various substitution models (data not shown), *"N." diminuta* fell neither in the terminal *Fusarium* clade nor the basal *Fusarium*-like clade nor any of the *Cosmospora sensu* Rossman groups (Fig. 1). This positional artifact may be caused by long-branch attraction or a paucity of parsimony-informative characters for the basal taxa in the combined DNA sequence data set.

Polyphyly of *Fusarium sensu* Wollenweber

The genus *Fusarium* is taxonomically linked to the teleomorph genus *Gibberella*, because they share the same species as type, *F. sambucinum* and *G. pulicaris*. In nature, *Gibberella* teleomorphs occur less frequently than their *Fusarium* anamorphs (Rossman *et al.* 1999). In the ML tree (Fig. 1), the *Gibberella* clade, representing *Fusarium* in the strict sense and including the type species in addition to *F. graminearum*, *F. sublunatum*, and *F. verticillioides*, is strongly supported. In Fig. 1 and Schroers *et al*. (2011), *Gibberella* is the sister clade to *Cyanonectria*. The terminal *Fusarium* clade in Fig. 1, including species with teleomorphs described in *Albonectria*, *Cyanonectria*, *Gibberella*, *Haematonectria*, and *Neocosmospora*, did not receive a statistically significant support similar to that obtained in other phylogenetic analyses (Schroers *et al.* 2009). The basal lineage of the terminal *Fusarium* clade is represented by the *"Nectria" ventricosa* species complex. Within the terminal *Fusarium* group*,* members of *Albonectria* and the *Haematonectria/ Neocosmospora* species complex as well as the species pair "*Albonectria*" *albida* and "*Fusarium*" *nematophilum* always formed strongly supported groups.

The basal *Fusarium*-like clade, with numerous members formerly classified in *Fusarium* sections *Arachnites*, *Eupionnotes*, *Macroconia*, *Pseudomicrocera*, and *Submicrocera*, is phylogenetically and phenotypically distinct from the terminal *Fusarium* clade mentioned above. The basal clade splits into several subclades similar to what is described above for *Cosmospora sensu* Rossman. Therefore we have given these groups genus rank in the taxonomy part below.

Another genus of *Fusarium*-like species is represented by *Atractium*. *Atractium crassum* (*"Fusarium" merismoides* var. *crassum*) did not fall within the basal or terminal *Fusarium* clades. Together with *Atractium stilbaster*, it forms a strongly supported sister lineage to a group of fungi including species of *Chaetopsina*, *Pseudonectria*, and *Volutella.*

Polyphyly of *Volutella sensu lato*

As mentioned above, *Volutella* and *Chaetopsina* form a well supported lineage that is distinct from *Cosmospora s. str.* and the basal *Fusarium*-like clade. The type of the genus *Pseudonectria*, *P. buxi*, together with another similar species (BBA 71336), form a strongly supported sister group to the *Volutella*/*Chaetopsina* lineage. *Chaetopsina* separates *Pseudonectria* from species of *Volutella s. str*. In contrast to the above-mentioned clades, *"Pseudonectria" pachysandricola* and "*Nectria" rubropeziza* comprise a fairly well supported clade that branches off near the root of the tree and that separates the basal from the terminal *Fusarium* clade (Fig. 1). Thus, *'"P." pachysandricola* is only distantly related to the type species of *Pseudonectria* and the *Volutella s. str.* group.

DISCUSSION

In revising the taxa associated with *Cosmospora sensu* Rossman, we focused on both teleomorph and anamorph phenotypes and ecological parameters guided by molecular phylogenetics. Resolving the taxonomy and nomenclature of *Cosmospora* requires resolving the phylogenetic relationships of many species presently included in *Fusarium sensu* Wollenweber. Previously published phylogenies of *Fusarium, e.g.* Summerbell & Schroers (2002), O'Donnell *et al*. (2010), sampled sparingly from teleomorphs of the *Nectriaceae* associated with other anamorph genera. It is clear from the analysis presented here in Fig. 1 and elsewhere in this volume by Chaverri *et al.* (2011), that as presently defined, *Fusarium* is not monophyletic. The basal *Fusarium*-like lineages and terminal *Fusarium* clade are separated by other genera that represent large genetic and taxonomic diversity. Although the sampling of species outside of the core *Fusarium* clade exceeds that of previous studies, this is still a relatively small subsample of these other genera. For example, *Cylindrocladium,* represented by one species here, includes about 50 known species, and the *Cylindrocarpon* clade including the teleomorph genera *Ilyonectria, Neonectria, Rugonectria,* and *Thelonectria,* and the anamorph genus *Campylocarpon* (see Chaverri *et al.* 2011), has at least 70 species. *Volutella,* discussed below, is probably similarly speciose, although no comprehensive revision exists. The hyphomycete genera *Cylindrodendrum, Heliscus,* and *Mariannaea* and many *Acremonium*-like species also occur in this clade.

In our analyses based on two genes including a standard barcode marker for *Fusarium*, *rpb2*, and a new phylogenetic marker, *acl1,* statistical support is weak for the backbone of the phylogenetic tree. Similar problems exist with published nuclear ribosomal large subunit trees, *e.g.* Summerbell & Schroers (2002), Zhang & Zhuang (2006), and Luo & Zhuang (2008). In the five gene analysis by Chaverri *et al*. (2011), the statistical support for the backbone of the *Nectriaceae* is stronger, and the few members sampled in the basal *Fusarium*-like clade and terminal *Fusarium* clade both form well-supported, distinct monophyletic groups. It would be preferable if the bootstrap and probability support for the relative arrangment of these clades were stronger, but in a polyphasic treatment, this is only one kind of evidence. Although molecular analyses do not strongly support our conclusion that the basal and terminal clades of *Fusarium* are phylogenetically distinct, there are also no data to support the taxonomic hypothesis that *Fusarium sensu* Wollenweber is monophyletic. Thus, neither monophyly nor the 1:1 teleomorph:anamorph genus argument supports the classical concept of *Fusarium.* We are confident that additional DNA sequencing data will add support to our conclusion that these major clades diverged long ago. Our decision results in a monophyletic concept of *Fusarium s. str.,* although the terminal *Fusarium* clade retains some problematic groups that will require further consideration (*cf.* Schroers *et al.* 2011). Additional sampling of outlying *Fusarium*-like species will undoubtedly lead to the recognition of other genera.

The *Hypocreales* is an anamorph rich order, with the majority of holomorphic species having at least one anamorph, and with many apparently solely anamorphic species. One of the main character suites of the *Nectriaceae* are sporodochial anamorphs with slimy macroconidia produced from phialides, which are broadly distributed in the family and probably represent the plesiomorphic condition. The three best known macroconidial groups were placed in the classical genera *Fusarium sensu* Wollenweber*, Cylindrocarpon,*

Table 2. Anamorphic genera reported as synonyms of *Fusarium* and interpretation of their type species according to present knowledge.

Generic name	Type species	Synonymy proposed by	Identity of type species	Present status
Fusisporium Link 1809	*F. aurantiacum* Link 1809 : Fr.	Wollenweber (1916)	*F. graminum* Corda or *F. sporotrichioides* Sherb.	= *Fusarium*, Gams & Nirenberg 1989
Atractium Link 1809	*A. stilbaster* Link 1809	Wollenweber & Reinking (1935)	*A. stilbaster* Link	Distinct genus in *Nectriaceae,* this paper
Selenosporium Corda 1837	*S. tubercularioides* Corda 1837 ≡ *Fusarium tubercularioides* (Corda) Sacc. 1886	Lindau (1910), Wollenweber & Reinking (1935)	*F. avenaceum* (Corda) Sacc. or *F. lateritium* Nees	= *Fusarium*, Holubová-Jechová *et al.* 1994
Microcera Desm. 1848	*M. coccophila* Desm. 1848	Wollenweber & Reinking (1935)	*M. coccophila* Desm.	Distinct genus in *Nectriaceae,* this paper
Pionnotes Fr. 1849	*P. capitata* (Schw.) Fr. 1849 ≡ *Fusarium capitatum* Schw. 1832	Wollenweber & Reinking (1935)	*Dacrymyces* sp. (PH!)	= *Dacrymyces,* Seifert *et al.* in prep.
Fusicolla Bonord. 1851	*F. betae* (Desm. : Fr.) Bonord. 1851 ≡ *Fusisporium betae* Desm. 1830 : Fr.	Wollenweber (1916), Wollenweber & Reinking (1935)	*Fusicolla betae* (Desm.) Bonord.	Distinct genus in *Nectriaceae,* this paper
Sporotrichella P. Karst. 1887	*S. rosea* P. Karst. 1887	Wollenweber & Reinking (1935)	*F. sporotrichioides* Sherb.	= *Fusarium*
Lachnidium Giard 1891	*L. acridiorum* Giard 1891	Saccardo (1901), Wollenweber & Reinking (1935)	*F. solani* complex	= *Fusarium*
Discocolla Prill. & Delacr. 1894	*D. pirina* Prill. & Delacr. 1894	Wollenweber & Reinking (1935)	*F. lactis* Pirotta & Riboni	= *Fusarium*
Septorella Allesch. 1897	*S. salaciae* Allesch. 1897	Höhnel (1912)	Unknown	Status uncertain
Trichofusarium Bubák 1906	*T. rusci* Bubák 1906 ≡ *Fusarium roseum* var. *rusci* Sacc. 1886	Wollenweber & Reinking (1935), Sutton (1986)	*Pycnofusarium rusci* D. Hawksw. & Punith.	Considered distinct by Schroers (pers. comm.)
Ustilaginoidella Essed 1911	*U. musaeperda* Essed 1911	Brandes (1919)	*F. oxysporum* complex	= *Fusarium*
Stagonostroma Died. 1914	*S. dulcamarae* (Pass.) Died. 1914 ≡ *Stagonospora dulcamarae* Pass. 1890	Sutton (1977)	Unknown	Status uncertain
Fusariopsis Horta 1919	*F. derrienii* Horta 1919	Dodge (1935)	Unknown	Unknown
Discofusarium Petch 1921	*D. tasmaniense* (McAlpine) Petch 1921 ≡ *Microcera tasmanica* McAlpine 1904 ≡ *Fusarium tasmanicum* (McAlpine) Rossman 1983	Rossman (1983)	*"Fusarium"* anamorph of "*Nectria*" *coccidophaga* (Petch) Rossman 1983	Unknown
Pseudomicrocera Petch 1921	*P. henningsii* (Koord.) Petch 1921 ≡ *Aschersonia henningsii* Koord. 1907	Wollenweber & Reinking (1935)	*Microcera diploa*	= *Microcera,* this paper
Fusidomus Grove 1929	Not designated	Sutton (1977)	Unknown	Status uncertain
Infrafungus Cif. 1951	*I. micropus* (Sacc.) Cif. 1951 ≡ *Fusarium micropus* Sacc. 1921	Wollenweber & Reinking (1935)	*Fusarium lateritium* complex	= *Fusarium*
Euricoa Bat. & H. Maia 1955	*E. dominguesii* Bat. & H. Maia 1955	Summerbell & Schroers (2002)	*F. solani* complex	
Hyaloflorea Bat. & H. Maia 1955	*H. ramosa* Bat. & H. Maia 1955	W. Gams (pers. comm.)	*F. solani* complex	= *Fusarium*
Pseudofusarium Matsush. 1971	*P. fusarioideum* Matsush. 1971 = *Pseudofusarium semitectum* (Berk. & Rav.) Matsush. 1975	Pascoe (1990)	*F. semitectum* auct.	*Fusarium*, Matsushima 1980
Pycnofusarium Punith. 1973	*P. rusci* D. Hawksw. & Punith. 1973	Sutton (1986)	*Pycnofusarium rusci* D. Hawksw. & Punith.	= *Trichofusarium*, Schroers (pers. comm.)

and *Cylindrocladium,* the latter now treated by its teleomorph generic name, *Calonectria* (Lombard *et al.* 2010). Often, macroconidial anamorphs are accompanied by microconidial, *Acremonium*-like synanamorphs, with small ameroconidia produced from phialides and enveloped in slime. These are probably also plesiomorphic in the family and homologous to similar "microconidial" anamorphs in other families of the order. In some lineages, macroconidia seem to have disappeared, while in other lineages, microconidia seem to have disappeared. Verticillate anamorphs occur in some clades, in particular *Chaetopsina* and *Mariannaea*, presumably derived from *Acremonium*-like progenitors. In addition to micro- and macroconidia, mesoconidia have been described in a few species of *Fusarium* (Pascoe 1990) as intermediate between micro- and macroconidia, but dry and produced from holoblastic conidiogenous cells, while megaconidia were described by Crous & Seifert (1998) in a few species of *Calonectria,* significantly larger than macroconidia and produced only under some cultural conditions.

Fusarium-like conidia occur in several orders of *Ascomycota* (Seifert 2001). In the *Nectriaceae,* the phylogenetic distribution of this character is disjunct. Because the phylogenetic backbone of the family is weakly supported in most analyses including ours, there are two possible interpretations for the distribution of the *Fusarium*-like conidium. If the *Fusarium*-like conidium is plesiomorphic in the *Nectriaceae*, then the cylindrical macroconidia of *Calonectria* and *Neonectria* were derived from it, and the taxa delimited by the ancestral *Fusarium*-like conidium have become paraphyletic. Alternatively, but perhaps less probable, the *Fusarium*-like conidium has evolved several times in the family, and the taxon delimited by this character is polyphyletic.

A practical problem with dividing *Fusarium* is the existence of 22 generic names sometimes considered synonyms (Table 2). These names must be considered in any division of the genus, which means that the identities of their type species in modern terms must be understood. Many of the synonyms come from the work of Wollenweber, whose herbarium studies are largely documented in his series *Fusarium autographice delineata* (Wollenweber 1916). Unfortunately, Wollenweber did not rigorously employ a type concept that conforms with today's standards, and we have discovered that many of his interpretations cannot be verified. The status of some of the 22 synonyms can be evaluated on the basis of existing knowledge and we examined type specimens of relevant genera for this study (Table 2); the precise status of a few of these genera remains uncertain. We focused on older generic synonyms, seriously considering *Atractium* (1809), *Microcera* (1848), *Pionnotes* (1849), and *Fusicolla* (1851).

We considered two scenarios to resolve the para/polyphyly of *Fusarium*. The first was to adopt broad generic concepts and to maintain the two main lineages as genera, *i.e.* the terminal lineage including the type species of *Fusarium*, and the basal *Fusarium*-like lineage that includes most of the species attributed to *Cosmospora sensu* Rossman. The perithecial walls of the species of these two clades have clearly different micromorphology. Cultures generally differ in colony morphology and growth rates, produce different metabolites, and the species have different ecological preferences, especially host specificity. However, this separation was unsatisfactory because these two large clades themselves lacked convincing statistical support, and the amount of morphological diversity incorporated in both of these large clades was huge, rendering the resulting taxonomy meaningless from a practical point of view. In particular, the generic name *Cosmospora* would be supplanted by the oldest available name *Microcera*, resulting in a genus incorporating many large, phylogenetically well-supported clades, some of which are sufficiently well-defined ecologically and morphologically to be recognised as distinct genera on their own. In this broad concept of *Microcera*, anamorphs with *Fusarium*-like macroconidia would still not be monophyletic, because of the existence of a large clade of microconidial, *Acremonium*-like anamorphs that is terminal within this basal clade.

The second option was to adopt the genera as well-supported, ecologically or morphologically distinct clades within the basal lineage. Although this results in more genera, the concepts are more homogenous and the system is practical. We followed this second approach, and the details of the generic names adopted are included in the Taxonomy section below. Fortunately, we were able to assign existing generic or subgeneric taxa to most of the clades. *Cosmospora* is retained for the clade with *Acremonium*-like microconidial anamorphs, and *Microcera* is reintroduced in something similar to its nineteenth century delimitation, as a genus of insect pathogens producing striking, flame-like conidiomata, usually on scale insects. Despite the number of genera segregated, this revision keeps the core of common, economically important *Fusarium* species intact. Of the species included in the popular Nelson *et al*. (1983) system and its more speciose successor (Leslie *et al.* 2006), only the *F. aquaeductuum* and *F. merismoides* species complexes are removed to *Fusicolla.* The more difficult decision concerning the generic fate of the *Fusarium solani* species complex remains to be decided.

Both Gams & Nirenberg (1989) and Seifert (2001) emphasised the importance of delimiting genera using polythetic concepts, *i.e.* concepts based on the occurrence of variable sets of shared characters with no single character considered essential for inclusion. Although we provide preliminary descriptions below, the development of robust polythetic diagnoses for the genera remains a work in progress. This is just the beginning of a taxonomic reevaluation of *Fusarium* and morphologically similar genera that, with increased sampling and more genomic analysis, will result in the recognition and definition of additional segregate genera. This revision provides a foundation for the discovery and phylogenetic classification of a large amount of presently unrecognised diversity representing both holomorphic and anamorphic species.

It is unfortunate that our decision to attempt to implement a single name nomenclature to these fungi coincides with what may be equally a controversial decision to split *Fusarium.* In general, *Fusarium* workers have had little interest in teleomorphs and most will have no reluctance to abandon a dual nomenclature of little relevance to them. Because teleomorphs are rarely seen in culture, except for that of *F. graminearum,* they are considered the domain of taxonomic specialists and their nomenclatural primacy is an historical annoyance. The introduction of single scientific names for polythetically characterised holomorphs and the recognition of a single nomenclaturally valid name for all taxonomic ranks seem inevitable steps towards the stabilisation of fungal taxonomy (Rossman & Samuels 2005). We encourage mycologists to accept our proposed nomenclature as a sincere attempt to provide a functional single-name system that respects the principles of the ICBN and refrain from attempting to perpetuate a dual nomenclatural system where it is unlikely to be used by most scientists working on the practical aspects of these fungi.

TAXONOMY

In this section, we consider the classification, nomenclature, and typification of the species examined in our phylogenetic studies and implement the taxonomic conclusions discussed above. Where possible, we have examined holotype specimens, other authentic material, and/or ex-type cultures, as well as material conforming to the concepts of Wollenweber. When feasible, we designate lectotype or epitype specimens to stabilise species concepts and provide living material for further studies. Many species are pleomorphic having a teleomorph, a macroconidial, *Fusarium*-like anamorph, and a microconidial or *Acremonium*-like anamorph, or any combination of these. The morphs recorded for each species are indicated on Fig. 1. The species are not redescribed here. In some cases, species concepts applied by various authors deviate from the strict concept of the species as typified. Therefore, we refer only to descriptions and illustrations already published that represent the species indicated by the typification.

Atractium Link : Fr., Mag. Ges. naturf. Freunde, Berlin 3: 10 (tab. I, fig. 11), 1809 : Fries, Syst. Mycol. 1: xli, 1821.

Type species: ***Atractium stilbaster*** Link 1809.

Emended generic diagnosis

Teleomorph unknown. *Conidiophores* aggregated into sporodochia or synnemata, nonstromatic; in culture, sometimes becoming pionnotal. When produced synnemata determinate, pale brown, composed of a stipe of parallel hyphae and a divergent capitulum of conidiophores giving rise to a slimy conidial mass; differentiated marginal hyphae absent. Conidiophore branching once or twice monochasial, 2-level verticillate, monoverticillate or irregularly biverticillate. *Conidiogenous cells* monophialidic, hyaline, subulate, with conspicuous periclinal thickening. Conidial masses yellow to orange. *Conidia* (0–)1–5-septate, clavate, obovoid or gently curved, rarely ellipsoidal, with a rounded apical cell, and somewhat conical basal cell, lacking a differentiated foot. *Chlamydospores* produced in culture by some species. Cultures growing relatively slowly, usually less than 30 mm diam in 14 d, with little aerial mycelium.

One of the commonly cited synonyms of *Fusarium* is the name *Atractium*, described immediately following and on the same page as its more famous cousin. The original diagnosis for *Atractium* and its type species *A. stilbaster* reads:

"*Atractium. Stroma elongatum, capitatum. Sporidia fusiformia, non septata, capitulo instrata.* Stroma stilbiforme, sporidia eadem quae Fusidiorum. Contextus stromatis, uti videtur, tenue floccosus, floccis parallelis. Capitulum sub microscopio composito, aqua

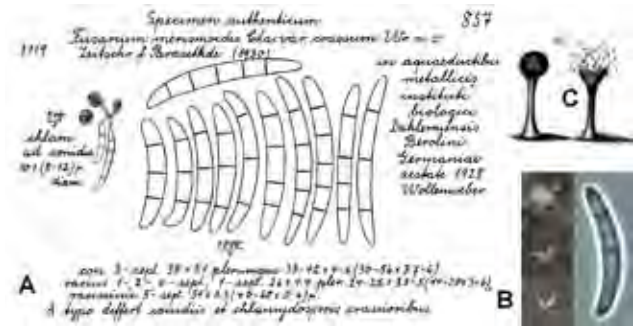


Fig. 2. *Atractium* species. A. *Atractium crassum*, as illustrated in the protologue by Wollenweber (1930). B. *Atractium stilbaster*, original drawing by Ditmar accompanying the protologue of *Atractium*, designated here as lectotype for *A. stilbaster*. C. *Atractium crassum,* digital photographs of living conidiomata (left) and a conidium (right) from a collection made in Ontario, Canada (K.A.S. 809).

adfusa, in sporidia fere diffluit. Unica species, nondum descripta. *A. stilbaster,* stipite cylindrico, capitulo globoso, utroque glabro lutescente. In truncis fagorum caesorum occurrit, vix ulta ½ lin. longa, fugax, stipite facili evanescente et capitulo in sporidia diffluente. Rarius invenit am. Ditmar. Iconem v. fig. 11."

The protologue includes a drawing by Ditmar (reproduced here as Fig. 2B), which shows what could either be a capitate, synnematous fungus, similar to *Stilbella* or possibly a myxomycete with a ruptured sporangium as seen in species of *Trichia* and many other genera, growing on a stump of *Fagus*. Link was confused about the septation of conidia of *A. stilbaster.* The protologues for both *Fusarium* and *Atractium* explicitly state, "Sporidia fusiformia, nonseptata…". Link (1816) added two more species to *Atractium* that Nees (1817) transferred to *Fusarium* without explanation. Link (1825) adjusted his observation and reported septate conidia in *A. stilbaster*, transferring it to *Fusarium*, and implicitely modifying his original species concept, and thus the generic concept of *Atractium*, to include species with septate conidia. These reinterpretations led subsequent authors, such as Berkeley, Fuckel, and Saccardo, whose systematic philosophy would not allow synnematous species to be included in the sporodochial genus *Fusarium,* to place synnematous *Fusarium*-like species in *Atractium*. In the 19th century, the prevailing concept of *Atractium* evolved to represent pale or colourful synnematous fungi with slimy conidial masses, usually with falcate, septate conidia. Tulasne & Tulasne (1861, 1865) noted the similarity of *Atractium* and *Microcera* (reintroduced below), and Petch (1921) commented on the modification of Link's original concept to include species with septate conidia. The species added to *Atractium* were often associated with the teleomorph genus *Sphaerostilbe,* the species of which were revised by Seifert (1985a).

Following the work of Wollenweber & Reinking (1935), who equated *A. stilbaster* with *Fusarium aquaeductuum* var. *medium* (now *Dialonectria ullevolea,* see below), *Atractium* was usually listed as a synonym of *Fusarium.* The proposed synonymy is curious because this species does not produce synnemata, the dominant feature of Link's drawing of *A. stilbaster.* There is no reason to follow Wollenweber & Reinking's interpretation and no evidence that Wollenweber, in his work for either *Die Fusarien* or *Fusarium autographice deliniata,* saw authentic material of *A. stilbaster*.

We were unable to locate authentic material of *A. stilbaster,* the original species of *Atractium,* from the herbaria of Link (B), Persoon (L) or Fries (UPS, UPS-Fries). The drawing with the protologue must be regarded as the lectotype; it shows what we interpret as a capitate, synnematous fungus (Fig. 2). The confusion over whether or not the conidia were septate, described above, is instructive in the interpretation of the identity of this fungus. To fix the application of the name, an epitype specimen should be designated of a synnematous fungus occurring on wood of *Fagus* in Germany. Seifert (1985a) provided a description and illustration of a fungus he called *Stilbella fusca*, a common, synnematous fungus on water-saturated, decayed wood, including trunks of *Fagus*, in northern Europe including Germany. It is the most frequently collected species attributed to the pre-1985 concept of *Didymostilbe*, and was often reported as *D. eichleriana*. This species produces slimy, obovate to obclavate conidia that are usually curved, from long phialides on branched conidiophores. The present concept includes specimens with predominantly aseptate conidia, but most specimens have only 1-septate conidia (Seifert 1985a). This species thus matches both Link's original concept and his subsequent revised concept of *A. stilbaster* in all salient details, especially noting that other authors included it in *Atractium*. A culture of this fungus isolated from bark in Germany, CBS 410.67, is thus selected as the epitype for *A. stilbaster*, applying *Atractium* for this clade identified in Fig. 1.

The three species of *Atractium* accepted here are all associated with water in some way. *Atractium stilbaster* and *A. holubovae* (not known in culture) are associated with water saturated decaying wood, and *A. crassum* was isolated twice from drinking water in Germany.

In our phylogenetic analysis (Fig. 1), two species (*A. stilbaster* and *A. crassum*) form a well-supported monophyletic clade in the *Nectriaceae*. The clade is also basal to *Chaetospina*, *Pseudonectria*, and *Volutella* as discussed below.

We did not attempt a systematic reevaluation of the 24 species attributed to *Atractium*, but a summary of present knowledge is presented in Table 3.

No teleomorphs are conclusively known for this genus, and there are no other published names that could be applied to this clade. Seifert (1985a) discussed the association of *A. stilbaster* with "*Nectria" flavoviridis* and *Sphaerostilbe fusca*, concluding that the reported association of this teleomorph and anamorph was probably coincidental. Our reexamination of the type material suggests that the KOH– perithecia on the specimen are more likely to represent the teleomorph of a species of *Fusicolla*, the macroconidia of which also occur on the specimen, rather than the teleomorph of *A. stilbaster.*

KEY TO ACCEPTED *ATRACTIUM* SPECIES

1. Conidia mostly (0–)1–3 septate; synnematous conidiomata produced 2
1. Conidia mostly 3(–5) septate; synnemata not produced ..... *A. crassum*

2. Conidia 37–49 × 4–5.5 µm; phialides 30–54 × 1.5–2.5 µm ..... *A. holubovae*
2. Conidia 15–25 × 2–4.5 µm, phialides 20–40 × 1.5–2.5 µm ..... *A. stilbaster*

Table 3. Species attributed to *Atractium* and their current status. Basic nomenclatural data from *Index Fungorum* (www.indexfungorum.org).

Species, authority and year of publication	Status	Reference
A. aurantiacum (Corda) Bonord. 1851	Unknown	–
A. brunaudiana Sacc. 1883	Unknown	–
A. candiduli Sacc. 1883	= *Cylindrocarpon candidulum* (Sacc.) Wollenw.	–
A. ciliatum Link 1816	Basionym of *"Fusarium" ciliatum* (Link) Link	This paper
A. cristatum Demelius 1923	Unknown	–
A. cronartioides Speg. 1883	Unknown	–
A. flammeolum Höhn. 1915	*Nomen dubium*	Seifert 1985a
A. flammeum Berk. & Ravenel 1854	= *Microcera coccophila* Desm.	This paper
A. flavoviride Sacc. 1883	Synonym of *A. stilbaster*	Seifert 1985a
A. fuscum Sacc. 1883	Synonym of *A. stilbaster*	Seifert 1985a
A. gelatinosum (Pers.) Sacc. 1886	No type in L, *nomen dubium*	Seifert 1985a
A. indicum Chona & Munjal 1956	Unknown	–
A. lusitanicum Sousa da Câmara & Luz 1941	Unknown	–
A. micropus (Pers.) Sacc. 1886	No type in L, *nomen dubium*	Seifert 1985a
A. olivaceum Kunze & J.C. Schmidt 1817	No type in B, *nomen dubium*	Seifert 1985a
A. pallens Nees 1818	Type in B examined, is a coelomycete	This paper
A. pallidum Bonord. 1851	Unknown	–
A. pallidum Berk. & M.A. Curtis 1868	Unknown	–
A. pulvinatum Link 1816	Type in B examined, not an *Atractium*	This paper
A. rigidum Bonord. 1864	Unknown	–
A. stilbaster Link 1809	Accepted species	This paper
A. therryanum Sacc. 1879	Anamorph of *Dermea morthieri* (Fuckel) Nannf.	Groves 1946
A. trematis Hansf. 1944	Unknown	–
A. tubericola Sacc. & Peglion. 1902	Unknown	–

Accepted species

Atractium stilbaster Link 1809, Mag. Ges. naturf. Freunde, Berlin 3: 10.

Basionym: *Fusarium stilbaster* (Link) Link in Willdenow, Sp. pl., Edn 4 6(2): 106. 1825 (1824).

= *Atractium fuscum* Sacc., Syll. Fung. 2: 514. 1883.

≡ *Stilbella fusca* (Sacc.) Seifert, Stud. Mycol. 35: 77. 1985.

See Seifert (1985a, as *Stilbella fusca*) for other synonyms.

Typification: Illustration published in Mag. Ges. naturf. Freunde, Berlin 3 as tab. I, fig. 11, **lectotype** designated here, reproduced here as Fig. 2B. **Epitype** of *A. stilbaster* designated here: **Germany,** Bayrischer Wald, Rachelseewand, on bark, Jul. 1967, W. Gams, CBS 410.67.

Other material examined: See Seifert (1985a). **Canada**, Quebec, Gatineau Park, Lac Bourgeous, on cut end of stump, Jul. 1992, K.A. Seifert, DAOM 215627.

Notes: Seifert (1985a) provided illustrations and a complete description of this species. The variability in conidium dimensions and septation reported by Seifert (1985a) may indicate the existence of several closely related but possibly morphologically diagnosable species.

Atractium crassum (Wollenw.) Seifert & Gräfenhan**, comb. & stat. nov.** MycoBank MB519420.

Basionym: *Fusarium merismoides* var. *crassum* Wollenw., Fus. autogr. del. 3: 857. 1930. (The publication of the same species in *Zeitschrift für Parasitenkunde* 3(3): 308. 1931 was apparently after the cited 1930 publication).

Typification: **Germany**, Berlin, isolated from drinking water, 1928, H.W. Wollenweber 3119, **lectotype** designated here, CBS. **Ex-type** cultures CBS 180.31 = NRRL 20894. GenBank barcodes: HQ897722 (*rpb2*), HQ897859 (*acl1*).

Notes: This species was described and illustrated by Wollenweber (1930, reproduced here as Fig. 2A), Wollenweber & Reinking (1935), and Gerlach & Nirenberg (1982). The strains described by the latter authors are now degenerated, and the following details come from their description. Fresh cultures grow slowly, 15–30 mm diam after 10 d on PDA, and sometimes produce *Coremium*-like structures. The macroconidia are gently curved with a rounded to somewhat conical basal cell and a rounded apical cell; there is no foot to the basal cell. They are mostly 3–5-septate; 3-septate conidia average 52 × 5 µm (ranging 37–60 × 4.5–5.5), 4–5-septate 60 × 5.5 µm (50–65 × 5-6), 1–2 septate 31 × 4.5 µm (25–37 × 3–6). Chlamydospores are terminal, intercalary or in conidia, round, 7–12 µm diam.

A second culture, BBA 62257, was illustrated by Gerlach (1972) and Gerlach & Nirenberg (1982) but is no longer available. A dried culture kept in the CBS herbarium is designated as lectotype above, because it is the only known original material. Wollenweber's published illustration of the type strain (Fig. 2A) represents the macroconidia of his taxon well. Epitypification must await the isolation of a fresh culture and specimen that can demonstrate the salient morphological features more completely than the existing cultures.

This species developed in damp chambers on small twigs collected from cold, running river water in Ontario, Canada, but the cultures were not preserved and the fungus cannot be relocated on the original specimen. Attempts to recollect and reisolate the fungus from the same locality were unsuccessful. The conidiomata on the natural substrate were glistening white and flame-shaped; the bundles of parallel macroconidia give the appearance of minute synnemata (Fig. 2C). However, little conidiomatal tissue is actually produced, and the phialides arise from a typical, *Fusarium*-like sporodochium of interwoven but not stromatic hyphae and conidiogenous cells.

Atractium holubovae (Seifert, S.J. Stanley & K.D. Hyde) Seifert, **comb. nov.** MycoBank MB519421.

Basionym: *Stilbella holubovae* Seifert, S.J. Stanley & K.D. Hyde, Sydowia 47: 258, 1995.

Typification: **Philippines**, Negros Occiental, Bario Caliban, Caliban River, on submerged wood, Dec. 1994, K.D. Hyde & E. Arimas, **holotype** DAOM 214961.

Notes: This species was described and illustrated by Seifert *et al.* (1995) in the absence of pure cultures and is transferred here on the basis of its morphological similarity with *A. stilbaster*. It is known from the holotype and two subsequent records on submerged wood collected from streams in Asia (Sivichai *et al*. 2002, Fryar *et al*. 2004).

Cosmospora Rabenh., Hedwigia 2: 59. 1862.

Type species: ***Cosmospora coccinea*** Rabenh. 1862.

Stroma inconspicous or absent. *Perithecia* scattered to gregarious, pyriform with an acute or apical papilla, collapsing cupulate or pinched when dry, orange red or bright red, turning dark red in KOH+, smooth walled, usually 150–450 µm high. *Asci* cylindrical to narrowly clavate, with an apical ring, 8 uniseriate or partly biseriate ascospores. *Ascospores* initially hyaline but becoming yellow brown to reddish brown, 1-septate, becoming tuberculate when mature. *Conidiophores Acremonium*-like, either lateral phialides on somatic hyphae, or with one or two layers of monochasial branching, or verticillate, hyaline. *Phialides* monophialidic, cylindrical to subulate, hyaline. *Microconidia* ellipsoidal, oblong or clavate or slightly allantoid, aseptate, hyaline, in slimy heads. *Macroconidia* absent. *Chlamydospores* usually not seen, but produced on some media.

Colonies on PDA slow growing, 15–25 mm diam in 14 d at room temperature, surface powdery, felt-like, floccose, cottony, white, pale pink, ochre to olivaceous green, sporulation usually abundant, arising directly from agar surface or from sometimes abundant aerial mycelium.

Habitat: On fruiting bodies and stromata of other fungi, *e.g. Fomitopsis, Hypoxylon, Inonotus, Stereum*, often isolated from soil.

Notes: About 65 species have been attributed to *Cosmospora sensu* Rossman. This concept is relatively broad, encompassing a great deal of anamorphic variability, although the teleomorph morphology is relatively conserved, with small, orange or reddish KOH+ perithecia with thin walls, cylindrical asci with or without an apical ring, and eight, uniseriate, 1-septate ascospores; stroma development is usually limited. Our phylogenetic analyses (Fig. 1) identify several distinct lineages within the prevailing concept of *Cosmospora*. New teleomorph genera have already been proposed for some lineages, namely *Nectricladiella* (a synonym of the anamorphically typified genus *Cylindrocladiella*) and *Chaetopsinectria* (a synonym of the anamorphically typified genus *Chaetopsina*). In general, well-supported clades correlate with anamorph types, although *Fusarium*-like anamorphs are found in several lineages.

Here, we propose a more restricted concept for *Cosmospora*, limiting it to the clade of species surrounding the type, *C. coccinea*, which have only microconidial, *Acremonium*-like anamorphs and tend to occur on other fungi. Other microconidial genera recognised are *Mariannaea* and *Volutella*. The clades with *Fusarium*-like anamorphs are reclassified below in the reintroduced genera *Dialonectria*, *Fusicolla,* and *Microcera,* with *Macroconia* elevated to generic rank from its previous sectional rank in *Nectria*. A small residue of species remains in *Cosmospora sensu* Rossman that are not redisposed here.

Although several of the new combinations propose the transfer of an anamorph typified name to a teleomorphically typified genus, as explained in the Introduction, the results are correct, legitimate, and valid for those species that are not pleomorphic, *i.e.* those that lack a teleomorph and are outside Art. 59 of the ICBN.

Accepted species

Cosmospora coccinea Rabenh., Hedwigia 2: 59. 1862 [non Nectria coccinea (Pers.) Fr. 1849].

= *Verticillium olivaceum* W. Gams, Cephalosporium-*artige Schimmelpilze*, p. 129. 1971.

Typification: **Germany**, near Laubach, on rotting pores of a polypore, Solms, Fungi europaei no. 459, **lectotype** BPI designated by Rossman *et al.* 1999.

Other material examined: **Germany**, Bayrischer Wald, Arberseewand, on hymenium of *Inonotus nodulosus* on *Fagus sylvatica*, Aug. 1967, W. Gams 680, CBS 341.70 = VKM F-2863; Kr. Plön, near Dobersdorf, on hymenium of *Inonotus radiatus* on *Alnus*, Oct. 1965, W. Gams 1104, CBS 343.70; Eifel, Geeser Wald near Gerolstein, on *Inonotus radiatus*, Sep. 1970, W. Gams, CBS 841.70; Eifel, Geeser Wald near Gerolstein, on *Inonotus radiatus*, Sep. 1970, W. Gams, CBS 983.70 = VKM F-2862; Neubrandenburg, Kleppelshager Forst near Friedland, on *Inonotus radiatus*, Oct. 1978, P. Hübsch H78/40, CBS 704.79; Bayern, on *Inonotus nodulosus*, dead crust, on fallen branch of *Fagus sylvatica*, 1993, T.R. Lohmeyer & R. Boesmiller 93/62, A.R. 2741 = BPI 802729 = CBS 114050; Nordrhein-Westfalen, Detmold, Krebsteich, on *Inonotus nodulosus* on *Fagus sylvatica*, Apr. 2007, T. Gräfenhan 2007-37, DAOM 235821.

Notes: For descriptions, illustrations, and additional taxonomic synonyms of the microconidial anamorph, see Gams (1971); the teleomorph is briefly described by Rossman *et al.* (1999).

Cosmospora arxii (W. Gams) Gräfenhan & Schroers, **comb. nov.** MycoBank MB519422.

Basionym: *Acremonium arxii* W. Gams, Cephalosporium-*artige Schimmelpilze*, p. 123. 1971.

Typification: **Germany**, Niedersachsen, near Wilhelmshaven, Neuenburger Urwald, on *Hypoxylon* sp., May 1965, W. Gams, **holotype** CBS H-6635, **ex-type** culture CBS 748.69 GenBank barcodes: HQ897725 (*rpb2*), HQ897862 (*acl1*).

Other material examined: **Germany**, Nordrhein-Westfalen, Kamen, Heerener Holz, on *Hypoxylon* on *Fagus*, Apr. 2007, T. Gräfenhan 2007-22, DAOM 235822; Nordrhein-Westfalen, Detmold, Externsteine, on *Hypoxylon* on *Fagus sylvatica*, Apr. 2007, T. Gräfenhan 2007-28, DAOM 235823; Nordrhein-Westfalen, Detmold, Donoper Teich, on *Hypoxylon* on *Fagus sylvatica*, Apr. 2007, T. Gräfenhan 2007-29, DAOM 235824 & T.G. 2007-33, DAOM 235825; **USA**, Pennsylvania, near Salt Springs State Park, on *Hypoxylon* on *Acer*, May 2007, T. Gräfenhan 2007-55, DAOM 235826.

Notes: The teleomorph of *Cosmospora arxii* is commonly found on *Hypoxylon* spp. on *Fagus* in North America and Europe, but has not been described yet; its morphology is similar to that of *C. viridescens*. For a description, illustrations, and discussion of the microconidial anamorph, see Gams (1971) and notes under *C. berkeleyana* below.

Cosmospora berkeleyana (P. Karst.) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519423.

Basionym: *Verticillium berkeleyanum* P. Karst., Meddeland. Soc. Fauna Fl. Fenn. 18: 64. 1891.

≡ *Acremonium berkeleyanum* (P. Karst.) W. Gams, Netherlands J. Pl. Pathol. **88**: 76. 1982.

Typification: **Finland**, near Mustiala, on *Stereum hirsutum* on *Betula*, Oct. 1890, P.A. Karsten 2310, **holotype** H.

Notes: For a description and discussion of this microconidial species, see Karsten (1891) and Gams & Zaayen (1982).

Although some have considered the teleomorph to be the heterotypic *Hypomyces berkeleyanus* Plowr. & Cooke (≡ *Sphaerostilbella berkeleyana* (Plowr. & Cooke) Samuels & Candoussau), our observations complicate the situation considerably. Because our phylogenetic results suggest that this is a species complex, the proposed synonyms applied to the teleomorph-anamorph connections for *Cosmospora berkeleyana* need to be re-evaluated (Fig. 1). These synonyms include *Acremonium butyri*, *Cephalosporium khandalense*, *Gliomastix lavitskiae*, *Nectria vilior*, and *N. viridescens* (Gams 1971, Samuels *et al.* 1990, Rossman *et al.* 1999). In our phylogenetic analysis, all of these putative synonyms can be interpreted as distinct species of *Cosmospora*.

Cosmospora berkeleyana, C. vilior, and *C. viridescens* have often been considered synonymous, but this now seems unlikely and each name must be re-evaluated. Samuels *et al.* (1990, 1991) studied and discussed the type material of *C. vilior* on a valsaceous stroma from Brazil. Because no fresh material from subtropical South America is available, we are unable to reinterpret Samuels' concept in phylogenetic terms. *Cosmospora viridescens* was described from a fungal host on *Salix* in Europe and thus may have distinct host relationships and geographical distribution. Possible morphological distinctions between these two teleomorphs are discussed below under *C. viridescens.*

Gams & Zaayen (1982) studied a recent specimen and culture identified as *Acremonium berkeleyanum*, which was unavailable for our study (**The Netherlands**, Oostelijk Flevoland, Abbert-bos, perceel O66, on *Stereum hirsutum*, July 1981, W. Gams, CBS 501.81). A similar fungus producing perithecia and the characteristic greenish *Acremonium*-like anamorph on basidiocarps of *S. hirsutum* on *Alnus rubra* is common in British Columbia, Canada (Seifert, unpubl. data).

Until species limits can be more clearly established, we prefer not to epitypify *C. berkeleyana* or *C. vilior.* The diversity of substrates and broad geographic distribution recorded for *C. berkeleyana* (Gams 1971, www.cbs.knaw.nl/databases) suggest that additional phylogenetic species await discovery in this complex.

Cosmospora butyri (J.F.H. Beyma) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519428.
Basionym: *Tilachlidium butyri* J.F.H. Beyma, Zentralbl. Bakteriol., 2 Abt. 99: 388. 1938.

≡ *Acremonium butyri* (J.F.H. Beyma) W. Gams, Cephalosporium-*artige Schimmelpilze*, p. 126. 1971.

Typification: **Denmark**, Copenhagen, butter, Knudsen, **holotype** CBS H-6601, **ex-type** cultures CBS 301.38 = MUCL 9950. GenBank barcodes: HQ897729 (*rpb2*), HQ897866 (*acl1*).

Notes: No teleomorph is known, but see notes under *C. berkeleyana* above. This microconidial species is described, illustrated, and discussed by van Beyma (1938) and Gams (1971). As noted by Summerbell *et al.* (2011), there may be more than one fungus preserved as CBS 301.38; we have not examined the holotype specimen.

Cosmospora cymosa (W. Gams) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519429.
Basionym: *Acremonium cymosum* W. Gams, Cephalosporium-*artige Schimmelpilze,* p. 131. 1971.

Typification: **Germany**, Schleswig-Holstein, Kr.Rendsburg, Enkendorfer Gehölz, on decaying *Inonotus radiatus*, Oct. 1965, W. Gams, **lectotype** designated here CBS H-5054, **isotype** CBS H-6603, **ex-type** culture CBS 762.69. GenBank barcodes: HQ897778 (*rpb2*), HQ897914 (*acl1*).

Other material examined: **Germany**, Kr.Plön, Dobersdorfer Wald, on *Inonotus radiatus* on *Alnus glutinosa*, June 1965, W. Gams 512A, CBS H-8146, CBS 258.70.

Notes: For description and illustrations of this microconidial anamorphic species, see Gams (1971). No teleomorph is known.

Cosmospora khandalensis (Thirum. & Sukapure) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519430.
Basionym: *Cephalosporium khandalense* Thirum. & Sukapure, Mycologia 58: 359. 1966.

Typification: **India**, Maharashtra, Khandala, on decaying stem of *Bambusa*, Aug. 1964, M.J. Thirumalachar, **holotype** HACC 148, **isotype** CBS H-15076, **ex-type** cultures ATCC 16091 = CBS 356.65 = IMI 112790 = MUCL 7974. GenBank barcodes: HQ897723 (*rpb2*), HQ897860 (*acl1*).

Notes: The microconidial anamorph of this species as typified here is described and illustrated by Sukapure & Thirumalachar (1966) and discussed by Gams (1971). See notes above under *C. berkeleyana.*

Cosmospora lavitskiae (Zhdanova) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519431.
Basionym: *Gliomastix lavitskiae* Zhdanova, Mikrobiol. Zhurn. 28: 37. 1966.

Typification: **Ukraine**, Poltawa region, on plant debris from rhizosphere soil of *Zea mays*, July 1961, **holotype** D.K. Zabolotny Institute of Microbiology and Virology of the National Academy of Sciences of Ukraine, **ex-type** cultures ATCC 18666 = CBS 530.68 = IMI 133984 = VKM F-1324. GenBank barcodes: HQ897726 (*rpb2*), HQ897863 (*acl1*).

Notes: The microconidial anamorph of the species is described and illustrated by Zhdanova (1966) and discussed by Gams (1971). No teleomorph is known. See notes above under *C. berkeleyana.*

Cosmospora viridescens (C. Booth) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519432.
Basionym: *Nectria viridescens* C. Booth, Mycol. Papers 73: 89. 1959.

Typification: **UK**, England, Yorkshire, Sawley Woods, on black pyrenomycete on branches of *Salix*, Apr. 1954, C. Booth, **holotype** IMI 56736, **isotype** DAOM 83074.

Notes: The microconidial anamorph and teleomorph of this species as typified are described, illustrated, and discussed by Booth (1959) and Gams (1971).

Cosmospora viridescens is morphologically similar to *C. vilior*, but the latter has tuberculate ascospores, compared to the spinulose ascospores of *C. viridescens* (Samuels *et al.* 1990). Both species have *Acremonium*-like anamorphs with green colonies, and their perithecia occur on black, valsaceous stromata. Ascospore isolates made from perithecia collected on stromata of *Hypoxylon* and *Ustulina* in temperate areas often yield green colonies similar to *C. viridescens*, but are probably different from the tropical or subtropical species identified as *C. vilior*. Furthermore, differences in substrate specificity and geographic distribution support the distinction of *C. viridescens* from the other *Cosmospora* species mentioned above.

Cosmospora viridescens cannot be correlated with any described *Acremonium* species, nor can any of the described *Acremonium* species in this complex be unequivocally connected

to any of the described teleomorphic species. Of the species in this complex with names based on anamorphic types, only *C. arxii* unequivocally has a known teleomorph, but it has apparently never been named.

Dialonectria (Sacc.) Cooke, Grevillea 12: 109. 1884. MycoBank MB1491.

Type species: ***Dialonectria episphaeria*** (Tode : Fr.) Cooke 1884 as *D. sanguinea*.

Stroma inconspicous or absent. *Perithecia* scattered and solitary or in small groups, pyriform with a short acute or round apical papilla, collapsing cupulate or pinched when dry, orange red to carmine red, turning dark red in KOH+, smooth-walled, usually < 200 µm high. *Asci* cylindrical to narrowly clavate, with an apical ring, 8 uniseriate ascospores. *Ascospores* hyaline to pale brown, 1-septate, smooth or becoming tuberculate when mature. *Conidiophores* initially as lateral phialides on somatic hyphae, sometimes verticillate, hyaline. *Phialides* monophialidic, subulate to subclavate, hyaline. *Microconidia* ellipsoidal to clavate, aseptate, hyaline, abundant. *Macroconidia*, if present, subcylindrical, moderately curved, slightly narrowing toward each end, apical cell often slightly hooked with a more or less pointed tip, basal cell not or scarcely pedicellate, predominantly 3–5-septate, hyaline, mostly thin-walled. *Chlamydospores* not observed.

Colonies on PDA slow growing, 25–50 mm diam in 14 d at room temperature, surface smooth, white to orange, aerial mycelium sparse, often becoming pionnotal, *i.e.* with abundant sporulation occuring in slimy masses over colony surface, often without discrete sporodochia.

Habitat: Mostly growing on stromata of other ascomycetes on deciduous trees.

Notes: *Dialonectria* was introduced first as a subgenus of *Nectria* and was revised in that context by Samuels *et al.* (1991), with a delimitation that more or less correlated with what the same authors later assigned to *Cosmospora sensu* Rossman. With the more restricted delimitation of *Cosmospora* adopted above, we also propose a restricted concept of *Dialonectria* around its type species, *D. episphaeria*. Most of the ~45 other species ascribed to *Dialonectria* by various authors have been reassigned or synonymised with other species by students of *Nectria* over the past 30 years.

Several phylogenetically distinct lineages are known within the *D. episphaeria* complex, one of which is described as a new species below.

Accepted species

Dialonectria episphaeria (Tode : Fr.) Cooke as *D. sanguinea*, Grevillea 12: 110. 1884.

Basionym: *Sphaeria episphaeria* Tode : Fr., Tode, Fungi Mecklenb. Sel. 2: 21. 1791 : Fries, Syst. Mycol. 2: 454. 1823.

≡ *Nectria episphaeria* (Tode : Fr.) Fr., Summa Veg. Scand. 2: 388. 1846.

≡ *Cucurbitaria episphaeria* (Tode : Fr.) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.

≡ *Fusarium episphaeria* (Tode) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 32: 662. 1945.

≡ *Cosmospora episphaeria* (Tode : Fr.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 121. 1999.

Typification: Origin unknown, **lectotype** designated by Booth (1959) in L 0112704, Herb. Lugd. Bat. 910267659 ex Herb. Persoon, **isotype** TNS.

Notes: For description, illustrations, and discussion of the teleomorph, see Booth (1959). The anamorph produces micro- and macroconidia and is described by Gerlach & Nirenberg (1982) and Nelson *et al.* (1983).

The morphological species *Dialonectria episphaeria* splits into at least five phylogenetic lineages, which share similar phenotypic traits (Gräfenhan *et al.* 2008). There is presently no fresh, well-characterised material on *Diatrype* on *Crataegus* from northern Germany suitable for epitypification. The anamorph of *D. episphaeria* was often reported as or referred to as *Fusarium aquaeductuum* var. *medium, e.g.* Gerlach & Nirenberg 1982, but we consider this to represent a different phylogenetic species that is described below as a new species.

Dialonectria ullevolea Seifert & Gräfenhan, **sp. nov.** MycoBank MB519433. Fig. 3A–J.

= *Fusarium aquaeductuum* var. *medium* Wollenw., Fus. autogr. del., no. 844. 1930.

Etymology: K.A.S. recalls impassioned discussion on the topic of dividing *Fusarium* with P. Crous, K. O'Donnell, M. Stadler, and B. Summerell during the 7th International Mycological Congress in Oslo, Norway, August 2002; this is commemorated with *Dialonectria ullevolea,* named for the Ullevol pub, where this discussion occurred.

Coloniae in agaro CMA perithecia fertilia, aurantiaco-rubra vel rubra formantes; perithecia pyriformia, papilla brevi praedita, Dialonectriae episphaeriae similia, ascosporis dilute brunneis, bicellularibus, (8.7–)9.7–11(–12.5) × (3.7–)4–4.5(–4.8) µm. Conidiophora primum phialides simplices ex hyphis orientes, deinde irregulariter ramosa, nonnumquam verticillata. Monophialides subulatae vel subclavatae, 8–20 × 1.5–2.3 µm. Conidia copiosa in pionnote conidiophororum aggregatorum vel in conidiophoris singulis, tenuitunicata, hyalina: microconidia ellipsoidea vel clavata, unicellularia, (3–)3.5–5(–6.5) × 1–1.5(–1.7) µm, fere copiosa; macroconidia plerumque 3–5-septata, 1-septata: 10–25 × 1.5–2 µm, 3-septata: (20–)30–42(–48) × (1.8-)2–2.5(–2.7) µm, 4–5-septata: (30–)37–43.5(–50) × (1.8-)2–2.5(–2.7) µm, 6–7-septata: 40–48(–52) × (2–)2.3–2.7 µm, subcylindrica, modice curvata, utrinque paulo angustata, sursum saepe paulo uncinata et plus minusve acutata; ad basim vix an non pedicellata. Coloniae in agaro PDA lente crescentes, 25–30 mm diam. post 14 dies, dilute aurantiae vel griseo-aurantiae. Mycelium aerium absens vel appressum, pionnotes aurantia iuxta coloniam mediam. Corpora sclerotialia absentia.

On CMA, the type culture forms fertile, orange red to bright red *perithecia*, pyriform each with a short apical papilla, morphologically similar to *Dialonectria episphaeria* as described by Booth (1959); *ascospores* pale brown, 1-septate, (8.7–)9.7–11(–12.5) × (3.7–)4–4.5(–4.8) µm (n = 50).

Colonies slow-growing on PDA, 25–30 mm diam in 14 d at room temperature. Surface light orange (5A5) to greyish orange (5B5) in colony centre, whitish at margin, margin smooth to broadly lobed. Reverse similar in colour but less bright with a slightly yellowish tinge (6A4 to 6B5). *Aerial mycelium* sparse or occasionally with floccose spots, lacking or appressed at margin. *Sporulation* in orange pionnotal masses, first observed near colony centre. Sclerotial bodies not observed.

In culture on CMA: *Conidiophores* initially unbranched, with phialides arising laterally from hyphae, later irregularly or occasionally verticillately branched. *Phialides* monophialidic, subulate to subclavate, 8–20 × 1.5–2.3 µm, hyaline. *Conidia* produced abundantly in pionnotes of aggregated conidiophores or on single conidiophores, delicate, hyaline. *Microconidia* ellipsoidal to clavate, aseptate, (3–)3.5–5 (–6.5) × 1–1.5(–1.7) µm (n = 30), hyaline, abundant. *Macroconidia* subcylindrical, moderately curved, slightly narrowing toward each end,

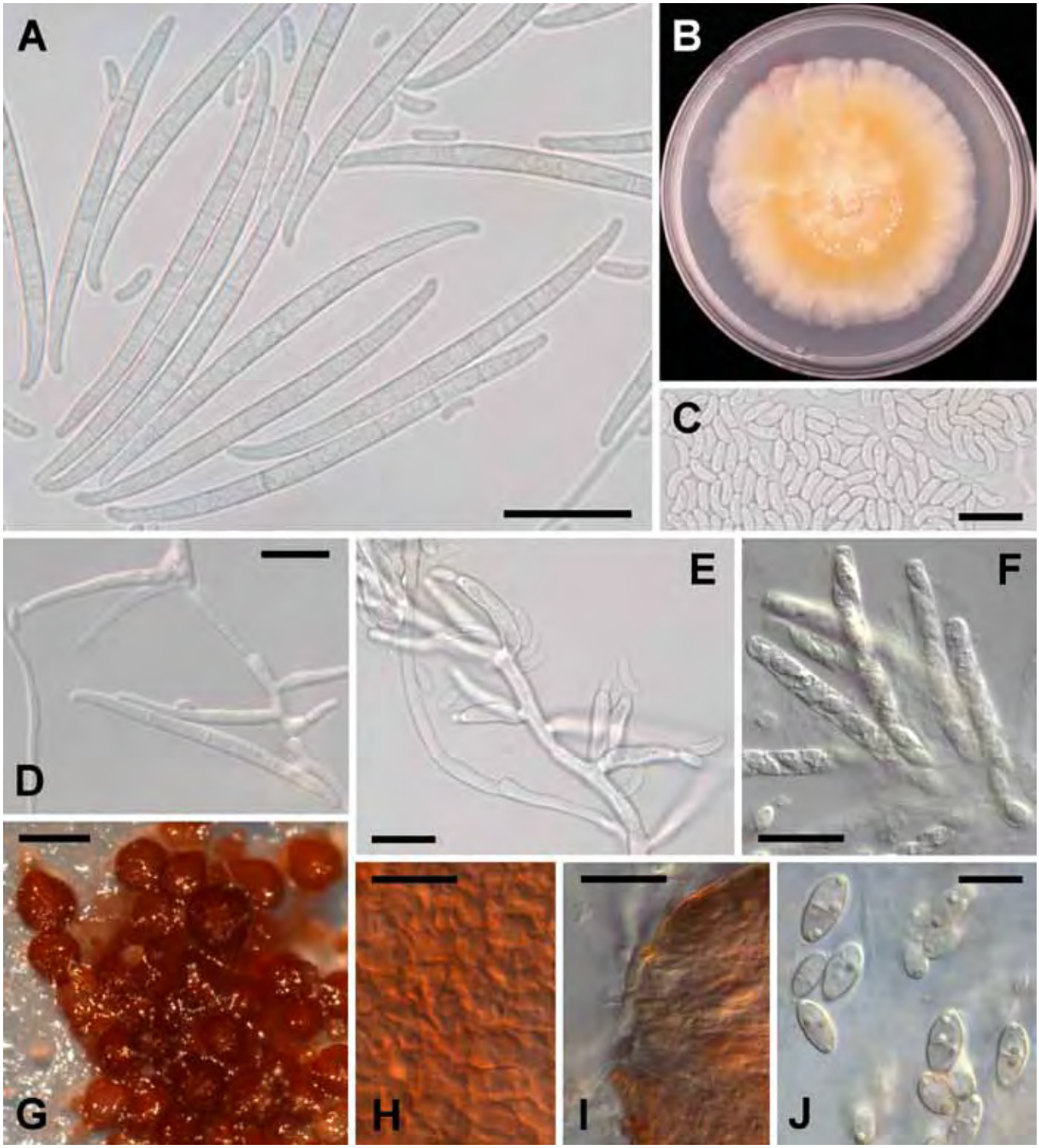


Fig. 3.A–J. *Dialonectria ullevolea*, ex-type strain (BBA 64549). A. Micro- and macroconidia formed on CMA after 18 d. B. Colony surface on PDA after 1 mo. C. Microconidia formed on CMA after 18 d. D–E. Phialides bearing microconidia on agar surface (D) and submerged (E) on CMA after 14 d. F. Cylindrical asci with obliquely uniseriate ascospores. G. Pyriform perithecia in culture on CMA after 50 d. H. Cells at surface of perithecial wall mounted in water. I. Perithecial apex mounted in water. J. Ascospores in optical section mounted in water. Scale bars: C, D, E, J = 10 µm; A, F, H, I = 20 µm; G = 200 µm.

apical cell often slightly hooked with a more or less pointed tip; basal cell not or scarcely pedicellate, predominantly 3–5-septate, 1-septate: 10–25 × 1.5–2 µm (n = 5), 3-septate: (20–)30–42(–48) × (1.8-)2–2.5(–2.7) µm (n = 40), 4–5-septate: (30–)37–43.5(–50) × (1.8-)2–2.5(–2.7) µm (n = 30), 6–7-septate: 40–48(–52) × (2–)2.3–2.7 µm (n = 25). *Chlamydospores* not observed.

Typification: **Netherlands**, Baarn, Groeneveld, perithecia on branch of *Fagus sylvatica*, July 1984, K.A. Seifert 357, **holotype** CBS H-3565, **ex-type** cultures BBA 64549 = CBS 512.84 = NRRL 20688. GenBank barcodes: HQ897749 (*rpb2*), HQ897885 (*acl1*).

Other material examined: **USA**, Pennsylvania, near Salt Springs State Park, on pyrenomycete stroma on *Fagus*, May 2007, T. Gräfenhan 2007-56, DAOM 235827; **Canada**, Quebec, Mayo, Forêt la Blanche, on pyrenomycete stroma on deciduous tree, Oct. 2007, T. Gräfenhan 2007-72, DAOM 235828.

Notes: To preserve the taxonomic concept of *F. aquaeductuum* var. *medium sensu* Wollenweber (1930), we typify *Dialonectria ullevolea* with an isolate from *Fagus sylvatica* collected in The Netherlands. The species produces a teleomorph and both microconidial and macroconidial synanamorphs; it seems to be pan-temperate and has been collected in Europe and North America.

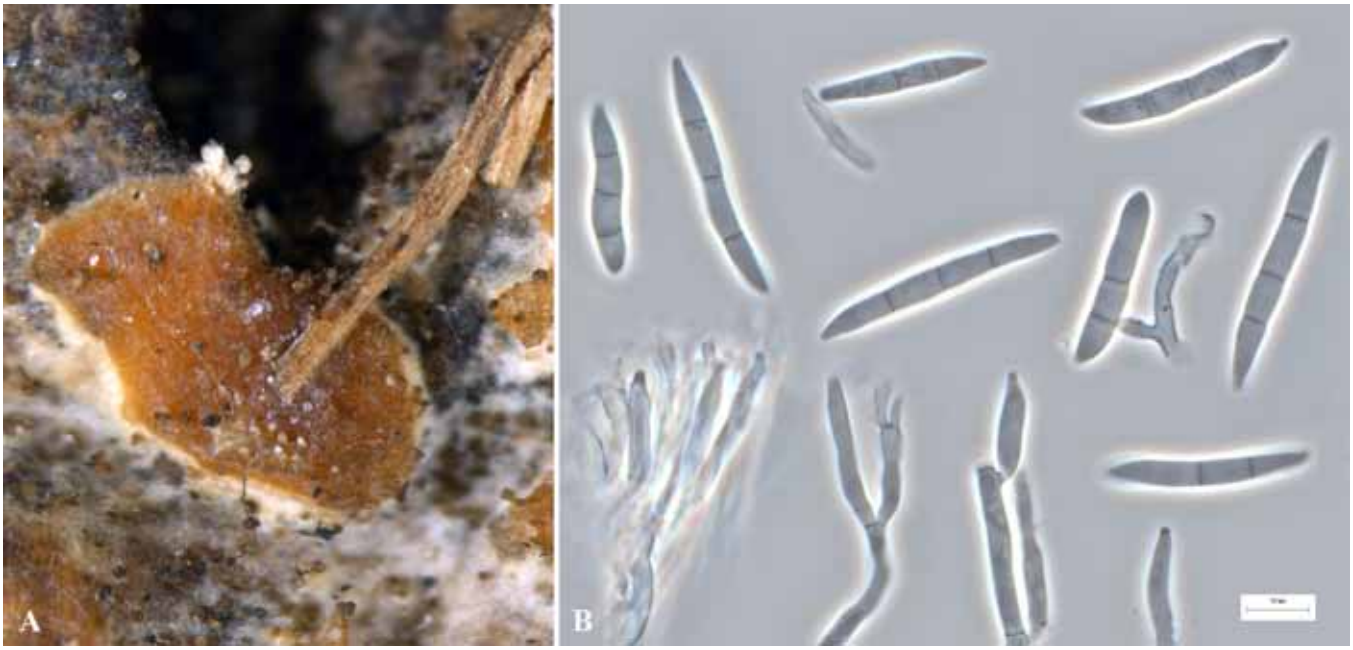


Fig. 4. *Fusicolla betae,* lectotype (K). A. Sporodochium. B. Conidia and phialides. Scale bar in B = 10 µm.

Fusicolla Bonord., *Handbuch der allgemeinen Mykologie* p. 150. 1851.

Type species: ***Fusicolla betae*** (Desm.) Bonord. 1851.

Stroma erumpent from host with hyphae forming a slimy, pale orange sheet over the substratum, with perithecia fully or partially immersed. *Perithecia* scattered to gregarious, or in small groups, globose to pyriform with a short acute or disk-like papilla, pinched when dry, yellow, pale buff to orange, KOH–, smooth walled, usually 100–200 µm high. *Asci* cylindrical to narrowly clavate, with an apical ring, 8 uniseriate ascospores. *Ascospores* hyaline to pale brown, 1-septate, smooth or becoming slightly verrucose when mature. *Conidiophores* initially as lateral phialides on somatic hyphae, sometimes monochasial, verticillate or penicillate, hyaline. *Phialides* monophialidic, cylindrical to subulate, hyaline. *Microconidia* sparse or absent, ellipsoidal to allantoid, aseptate, hyaline. *Macroconidia* falcate, more or less straight, or moderately to clearly curved, slightly narrowing toward each end, apical cell often hooked with a more or less pointed tip, basal cell slightly pedicellate, predominantly 1–3-septate, or 3–5-septate, in one species up to 10-septate, hyaline, mostly thin-walled. *Chlamydospores* absent, sparse, or abundant, when present globose, single, in pairs or chains, sometimes in macroconidia.

Colonies on PDA slow growing, 30–55 mm diam in 14 d at room temperature, surface smooth, whitish to pale brown, pink or orange, sometimes with violet or reddish-brown tones, often entirely pionnotal; *aerial mycelium* sparse or abundant, turf-like, felt-like, or coremioid if with violet or reddish-brown tones.

Habitat: On soil or plant matter in contact with soil, on woody material, slime flux of trees, sometimes on stromata of other fungi, in flowing water including drinking water and sewage.

Notes: *Fusicolla* has generally been considered a synonym of *Fusarium* (see notes under *F. betae* below), but is adopted here for elements of the *F. aquaeductuum* and *F. merismoides* species complexes. Some of the varieties attributed to those two species by other authors are raised to species rank. The application of the name *Fusarium merismoides* var. *chlamydosporale* remains uncertain at this time, while *F. merismoides* var. *crassum* is transferred to *Atractium* above.

Eight other species were described in *Fusicolla* before the genus was synonymised with *Fusarium* by Wollenweber (1916, see below), six of them by Karsten. We have not seen the type specimens of any of these species, which have apparently not been revised since their original descriptions.

Accepted species

Fusicolla betae (Desm.) Bonord., *Handbuch der allgemeinen Mykologie* p. 150. 1851. Fig. 4.

Basionym: *Fusisporium betae* Desm., Ann. Sci. Nat., Bot., Sér. 1, 19: 436. 1830.

≡ *Fusarium betae* (Desm.) Sacc., Michelia 2: 132. 1880.
≡ *Pionnotes betae* (Desm.) Sacc., Syll. Fung. 4: 726. 1886.
≡ *Pionnotes rhizophila* var. *betae* (Desm.) De Wild. & Durieu, Prodr. Fl. Belg. 2: 367. 1898.

Typification: **France**, on tuber of *Beta vulgaris*, spring 1826, Desmazières, **lectotype** designated here K(M) 167520, Plantes Cryptogames du Nord de la France, no. 305; **epitype** designated here: **Germany**, Schleswig-Holstein, Kiel, on young plants of *Triticum aestivum*, Jan. 1983, C. Bauers, preserved culture BBA 64317. GenBank barcodes: HQ897781 (*rpb2*), HQ897917 (*acl1*).

Other material identified: **Germany**, northern Germany, rotting potato tuber, E. Langerfeld DE 8, FRC E-0114 = MRC 2196 = NRRL 47186. **Turkey**, roots of *Papaver*, 2007, G. Turhan, T.G. 2007-70. **UK**, on *Beta vulgaris,* IMI 105043 = NRRL 22133.

Notes: Morphologically, *Fusicolla betae* closely resembles other members of the *Fusicolla merismoides* species complex, and critical taxonomic reevaluation of this complex is required to develop reliable species concepts.

There has been confusion over the identity of this species with two independent concepts in the literature. Wollenweber (1916, no. 99, 100) probably studied type material of *Fusisporium betae*, but later listed the species as synonym of *Fusarium merismoides* irrespective of precedence of the older species epithet (Wollenweber & Reinking 1935). Following this, the genus *Fusicolla*

was usually listed as a synonym of *Fusarium, e.g.* Carmichael *et al*. 1980. Alternatively, Chupp (1954, p. 111) cited *Fusarium betae* and "*Fusidium betae* Desm." (probably a *lapsus* for *Fusisporium*) as synonyms of *Cercospora beticola*. He cited only the type of *C. beticola* and types of other *Cercospora* names synonymised with *C. beticola*; types of the *Fusarium*/*Fusidium* names were not cited. We conjecture that he proposed the synonymy based on the identity of the host and a general congruence in conidial size and septation. Crous & Braun (2003) followed the latter synonymy including *Fusisporium betae* as a synonym of *Cercospora apii s. lat.;* they also did not see type material (U. Braun, pers. comm.). Our studies of the lectotype designated above confirm that Desmaziéres' fungus produces sporodochia, phialides, and *Fusarium*-like conidia identical to those of the epitype selected above.

Fusicolla acetilerea (Tubaki, C. Booth & T. Harada) Gräfenhan & Seifert, **comb. et stat. nov.** MycoBank MB519434.

Basionym: *Fusarium merismoides* var. *acetilereum* Tubaki, C. Booth & T. Harada, Trans. Brit. Mycol. Soc. 66: 355. 1976.

Typification: **Japan**, Osaka, near Osaka University, soil, 1973, T. Miyoshi, **holotype** IFO 30040, **ex-type** cultures IMI 181488 = BBA 63789 = NRRL 20827. GenBank barcodes: HQ897701 (*rpb2*), HQ897839 (*acl1*).

Other material identified: **Australia**, soil, FRC E-0052 = NRRL 13261, FRC E-0120 = NRRL 47187, FRC E-0121 = NRRL 47188, ICMP 10485 = NRRL 39744, IMI 175962 = NRRL 22137. **Philippines**, Nueva Vizcaya, FRC E-0164 = NRRL 47201. **South Africa**, soil, FRC E-0130 = NRRL 47191, FRC E-0136 = NRRL 47193, FRC E-0205 = NRRL 47210, FRC E-0226 = NRRL 47215, FRC E-0229 = NRRL 47844, FRC E-0257 = NRRL 47222, FRC E-0265 = NRRL 47224, FRC E-0287 = NRRL 47231, FRC E-0288 = NRRL 47232. **Zambia**, soil, FRC E-0208 = NRRL 47212.

Notes: This species produces both macroconidia and microconidia. The holotype is described, illustrated, and discussed by Tubaki *et al.* (1976) and Gerlach & Nirenberg (1982).

Fusicolla aquaeductuum (Radlk. & Rabenh.) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519435.

Basionym: *Selenosporium aquaeductuum* Radlk. & Rabenh., Kunst- Gewerbe-Blatt 49: 10. 1863.

≡ *Fusarium aquaeductuum* (Radlk. & Rabenh.) Lagerh., Centralbl. Bakteriol. Parasitenk. 9: 655. 1891.

Typification: **Germany**, Bayern, München, water fountain near Gasteigberg, Nov. 1862, L. Radlkofer, **lectotype** designated here B 700014034. A permanent slide prepared by Radlkofer and sent to Wollenweber is selected here as the lectotype of *Selenosporium aquaeductuum*; it is the only known authentic material. **Epitype** designated here: **Germany**, Berlin-Dahlem, Julius-Kühn-Institute (formerly BBA), isol. ex plugged water tap in BBA, May 1985, H.I. Nirenberg, **ex-type** cultures BBA 64559 = CBS 837.85 = NRRL 20865 = NRRL 37595. GenBank barcodes: HQ897744 (*rpb2*), HQ897880 (*acl1*).

Other material examined: **Germany**, Berlin, drinking water, 1974, W. Gerlach, BBA 63669 = CBS 734.79 = NRRL 20686; **The Netherlands**, Baarn, rubber tubing, 1953, A.L. van Beverwijk, CBS H-12677, CBS 268.53 = NRRL 22115.

Notes: No teleomorph is known for this species. For a description, illustrations, and discussion of the microconidial and macroconidial synanamorphs of this species as epitypified here, see Gerlach & Nirenberg (1982).

In Radlkofer (1863), two figures illustrate *Selenosporium aquaeductuum*, one showing 1–2(–4)-septate conidia borne on phialides. Wollenweber (1916) studied a permanent slide originally prepared by Radlkofer and drew the fungus with 1-septate and 3–4-septate conidia. On the herbarium sheet with that slide, Wollenweber noted the presence of two *Fusarium* species, *F. aquaeductuum* with 1-septate conidia, 18–22 × 1.5–2 µm and *F. biasolettianum* with 3-septate conidia, 30–55 × 2–2.5 µm. Based on similarities of the phenotype and substrate preferences, we classify *Fusarium aquaeductuum* in *Fusicolla*.

Wollenweber & Reinking (1935) included *Microcera brachyspora* Sacc. & Scalia as a synonym of *F. aquaeductuum*, but this should be confirmed with type studies.

Wollenweber (1931) linked *Fusarium aquaeductuum* var. *aquaeductuum* to "*Nectria" episphaeria* var. *coronata* (syn. *"Nectria" purtonii,* see below); subsequently this anamorph-teleomorph connection was accepted by Booth (1959), Gerlach and Nirenberg (1982), Samuels *et al.* (1991), and Rossman *et al.* (1999). According to our phylogenetic results, *"Nectria" purtonii* is not a member of *Fusicolla* but belongs to *Stylonectria*. The reported anamorph-teleomorph connection could not be confirmed here.

Fusicolla epistroma (Höhn.) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519436.

Basionym: *Dendrodochium epistroma Höhn.,* Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 118: 424. 1909.

≡ *Fusarium epistroma* (Höhn.) C. Booth as *F. epistromum*, *The Genus* Fusarium p. 66. 1971.

Typification: **Germany**, Brandenburg, "Schmidt's Grund" near Tamsel, on old stromata of *Diatrypella favacea* on branches of *Betula*, Nov. 1906, P. Vogel, Sydow's Mycotheca germanica 648 *Hymenula epistroma*, **lectotype** B 700014042 designated here, **isotypes** FH 00286649, K, S F40143. **Epitype** designated here: **UK**, England, Yorkshire, Aberford & Gundale, on *Diatrypella* on *Betula*, Apr. 1961, C. Booth, IMI 85601, **ex-type** cultures ATCC 24369 = BBA 62201 = NRRL 20461 = NRRL 20439. GenBank barcodes: HQ897765 (*rpb2*), HQ897901 (*acl1*).

Other material examined: **Germany**, Triglitz, 1907, O. Jaap, herb. von Höhnel 3087, FH 00286650.

Notes: For descriptions, illustrations, and discussion of the micro- and macroconidial synanamorphs of this species, see Booth (1971) and Gerlach & Nirenberg (1982).

An anamorph-teleomorph connection of *F. epistromum* with *Nectria* ("*Cosmospora"*) *magnusiana* was suggested by Höhnel (1909) and later followed by Jaap (1910), Booth (1959), Gerlach & Nirenberg (1982), and Samuels *et al.* (1991). Höhnel (1909) based his assumption on the observation that both fungi occurred on the same host fungus, *Diatrypella favacea*. However, he did not collect or observe the teleomorph together with his *Dendrodochium epistroma*. Wollenweber (1924, No. 539) studied a specimen of *N. magnusiana* collected by Jaap (Fungi selecti exs. 418) and questioned the link with Höhnel's anamorphic fungus. Booth's (1959) report of the anamorph-teleomorph connection included a drawing of the anamorph that lacks attribution to a specimen, but looks much like Wollenweber's *Fusaria autographice delineata* no. 539. The conidiophores and conidia are similar, having subulate phialides and non-septate, oblong to allantoid conidia. We compared Rehm's type material (S F84956, B 700014041) to the description given by Samuels *et al.* (1991) based on Jaap's exsiccati. In contrast to the latter, the KOH– ascomatal wall of the type specimen appears slightly verrucose and the colour is dark orange-brown with an obtuse apex and an ostiolar area that becomes almost black. Mature ascospores of *Nectria magnusiana* measure (12–)13–14.5(–15.5) × (5.5–)5.8–6.5(–6.8) µm and are significantly wider than those of the Jaap exsiccata studied by Samuels *et al.* (1991). The type material of *N. magnusiana* is reminiscent of *Neonectria* or *Nectria s.str*. An anamorph was associated with the same stroma from which perithecia developed. Its buff-coloured hymenium bears oblong-ellipsoidal microconidia conidia, 3.5–8 × 1–2 µm. These microconidia

match those observed in two authentic collections of *Dendrodochium epistroma* (Sydow's Mycotheca Germanica 648 and Jaap's Fungi Selecti Exsiccati 349). Booth (1959) and Samuels *et al.* (1991) concluded that *D. epistroma* is the anamorph of *N. magnusiana*, both being host specific to *Diatrypella favacea.* Only a few *Fusarium*-like macroconidia were found on the type material of *Dendrodochium epistroma*, but macroconidia were lacking on the hymenium of the type collection of *N. magnusiana*. Interestingly, in culture the ex-type isolate of *Fusicolla epistroma* produces predominantly 3-septate conidia, rarely microconidia. From this, it remains unclear whether the associated anamorph on the type material of *N. magnusiana* is *Fusicolla epistroma*. Therefore, we decided to designate the epitype for *F. epistroma* based on Booth's material and not to consider the older species name *Nectria magnusiana* for this species.

Fusicolla matuoi (Hosoya & Tubaki) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519437.
Basionym: *Fusarium matuoi* Hosoya & Tubaki, Mycoscience 45: 264. 2004.

≡ *Cosmospora matuoi* Hosoya & Tubaki, Mycoscience 45: 262. 2004.

[= *Fusarium splendens* Matuo & Takah. Kobay., *nom. nud.*, Trans. Mycol. Soc. Japan 2(4): 13. 1960].

Typification: **Japan**, Honshu, Yamagata Pref., Mamurogawa-machi, Mogami-gun, on *Albizia julibrissin*, Oct. 1958, T. Kobayashi, **holotype** TNS F-11127, **ex-type** culture MAFF 410976.

Other material examined: **Iran**, Prov. Gilan, near Bandarepahlavi, on rotting stalk of *Zea mays*, Oct. 1968, D. Ershad, BBA 62154 = FRC E-0089 = NRRL 47180. **Japan**, on *Albizia julibrissin*, Oct. 1959, T. Kobayashi, ATCC 18694 = CBS 581.78 = MAFF 238445 = NRRL 20427.

Notes: For a description, illustrations, and discussion of the teleomorph and micro- and macroconidial synanamorphs of this species, see Hosoya & Tubaki (2004).

Fusicolla merismoides (Corda) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519438.
Basionym: *Fusarium merismoides* Corda, Icon. Fung. 2: 4. 1838.

Typification: **Czech Republic**, Prague, on very wet shards of a plant pot, winter 1836, Corda, **holotype** PRM 155493.

Notes: *Fusicolla merismoides* is morphologically well characterised and has been widely accepted as a distinctive species (Wollenweber 1931, Booth 1971, Gerlach & Nirenberg 1982, Nelson *et al.* 1983, Leslie *et al.* 2006, Domsch *et al.* 2007); these authors provide descriptions, illustrations, and discussion of the macroconidial anamorph of this species. The morphological species concept was established by Wollenweber & Reinking (1935), who synonymised numerous taxa with *Fusarium merismoides* var. *merismoides*. Unlike *F. betae*, which is mainly known from roots and tubers of plants, *F. merismoides* is commonly isolated from soils, polluted water, slime fluxes of trees, rotting plant material, and many other substrates. Gräfenhan *et al.* (2008) discovered several phylogenetic lineages in the *F. merismoides* morphological species, including some ascospore isolates; the same conclusion can be drawn from publically available sequences attached to this name. We studied Corda's type material deposited in PRM and could not come to a satisfying conclusion on the selection of an appropriate epitype based solely on the macroconidial characteristics. Moreover, after examination of authentic material of *Fusarium biasolettianum* (PRM 155487), we could not confirm the reported synomymy with *Fusicolla merismoides* (Wollenweber & Reinking 1935). Macroconidia of *Fusarium biasolettianum* have almost an pointed

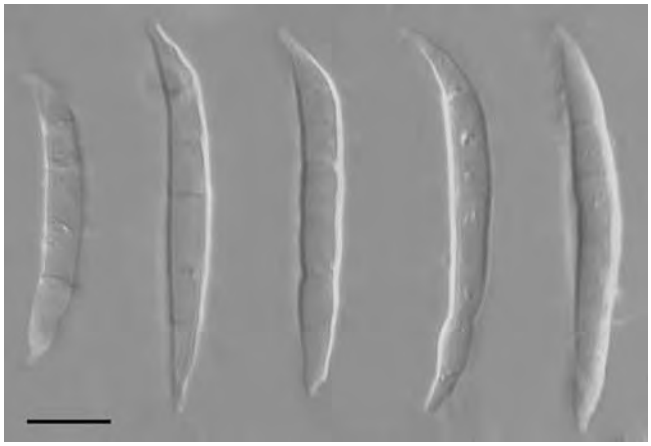


Fig. 5. *Fusarium biasolettianum*, authentic material (PRM 155487). Macroconidia. Scale bar = 10 µm.

and slightly hooked apical cell and a pedicellate basal cell (Fig. 5) that rather resemble macroconidium characteristics of *Fusarium s. str.* species. Rossman *et al.* (1999) mentioned *Chrysogluten biasolettianum nom. rej.,* but there is no nomenclatural connection between this teleomorphic fungus and *F. biasolettianum;* the coincidental epithets indicate only that they were named in honour of the Italian botanist B. Biasoletto.

Most of the varieties within *F. merismoides* are distinct species, either within *Fusicolla* or in sister genera.

Fusicolla violacea Gräfenhan & Seifert, **sp. nov.** MycoBank MB519439.

= *Fusarium merismoides* var. *violaceum* W. Gerlach, Phytopathol. Z. 90: 34. 1977. *nom. inval.* Art. 37.

Latin description in Gerlach, Phytopath. Z. 90: 34-35. 1977 under the name "*Fusarium merismoides* var. *violaceum*".

Typification: **Iran**, Prov. Gilan, near Rasht, on *Quadraspidiotus perniciosus* (San José insect) scaleon dying twig of *Prunus domestica*, Nov. 1968, W. Klett, **holotype** CBS 634.76, permanently cryopreserved culture, **ex-type** cultures BBA 62461 = NRRL 20896. GenBank barcodes: HQ897696 (*rpb2*).

Notes: For descriptions, illustrations, and discussion of the micro- and macroconidial synanamorphs of this species, see Gerlach (1977) and Gerlach & Nirenberg (1982).

The taxon was not validly published because the author did not designate a holotype, instead listing one living strain with accession numbers in two culture collections as "Cultura typica".

Macroconia (Wollenw.) Gräfenhan, Seifert & Schroers, **gen. et stat. nov.** MycoBank MB519441.
Basionym: *Nectria* sect. *Macroconia* Wollenw., Angew. Bot. 8: 179. 1926. MycoBank MB519440.

Type species: ***Nectria leptosphaeriae*** Niessl in Krieger 1886, here recognised as *Macroconia leptosphaeriae* (Niessl) Gräfenhan & Schroers.

Stroma inconspicous or absent. *Perithecia* solitary, subglobose with or without a small apical papilla, collapsing cupulate when dry, orange to carmine red, KOH+ dark red to violet, sometimes with hyphal hairs arising from outer wall, usually 100–250 µm high. *Asci* cylindrical to narrowly clavate, with a simple apex, 8 uniseriate to partially biseriate ascospores. *Ascospores* yellowish, 1-septate, smooth or becoming striate when mature. *Conidiophores* initially as lateral phialides on somatic hyphae, later monochasial to

verticillate, hyaline. *Phialides* monophialidic, cylindrical to subulate, hyaline. *Microconidia* absent or very rare, when present ellipsoidal to allantoid, hyaline. *Macroconidia* robust, subcylindrical to moderately curved, apical cell conical or hooked, basal cell mostly conspicuously pedicellate, 3–7(–14)-septate, hyaline, mostly thick-walled. *Chlamydospores* absent or rare, when present globose, single, in pairs, or in chains in hyphae.

Colonies on PDA slow- or very slow-growing, 7–10 or ~ 45 mm diam in 14 d at room temperature, whitish to orange or reddish brown; aerial mycelium abundant, with discrete pink, orange or reddish brown sporodochia or small pionnotes.

Habitat: Mostly growing on stromata of other ascomycetes on herbaceous plants or deciduous trees.

Notes: Based on the section name originally in *Nectria* (Wollenweber 1926), but also used as a "Gruppe" in *Fusarium* (Wollenweber & Reinking 1935), we raise *Macroconia* to generic rank here for five species with large *Fusarium*-like macroconidia and minute perithecia.

Accepted species

Macroconia leptosphaeriae (Niessl) Gräfenhan & Schroers, **comb. nov.** MycoBank MB519442.
Basionym: *Nectria leptosphaeriae* Niessl in Krieger, Fungi Saxonici Exsiccati. Die Pilze Sachsen's 4: No. 165. 1886.
≡ *Cucurbitaria leptosphaeriae* (Niessl) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.
≡ *Hypomyces leptosphaeriae* (Niessl) Wollenw., Fus. autogr. del., Edn 1: No. 57. 1916.
≡ *Lasionectria leptosphaeriae* (Niessl) Petch, Trans. Brit. Mycol. Soc. 21: 267. 1938.
≡ *Cosmospora leptosphaeriae* (Niessl) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 122. 1999.
? = *Fusarium sphaeriae* var. *majus* Wollenw., Fus. autogr. del. No. 859. 1930.

Typification: **Germany**, Sachsen, Königstein Fortress, church yard, on *Leptosphaeria doliolum* on stems of *Urtica dioica*, Sept. & Oct. 1885, W. Krieger, Krieger's Fungi saxonici 165, **lectotype** designated here K(M) 165805, **isotype** B, BPI, K.

Other material examined: **Canada**, Ontario, Ottawa, Britannia, near Mud Lake, on *Leptosphaeria* on dead stem of *Urtica dioica*, July 2008, T. Gräfenhan 2008-15, DAOM 235833. **Italy**, Latio, ancient Etruscan village Corviano near Bomarzo, on *Leptosphaeria* on dead stem of *Urtica dioica*, Aug. 2008, T. Gräfenhan 2008-19, DAOM 235834. **The Netherlands**, Tilburg, on *Leptosphaeria* on dead stem of *Urtica dioica*, L. Rommelaars, CBS 100001, CBS-H 6030.

Notes: For description and illustration of the macroconidial anamorph and teleomorph of this species, see Weese (1916), Wollenweber (1916, No. 57; 1926; 1930, No. 859), Booth (1959, 1971), and Samuels *et al.* (1991).

The distinction between *Macroconia leptosphaeriae* and *M. sphaeriae* is based on the size of ascospores and conidia in the type collections. According to Wollenweber (1926), the ascospores of the type material of *M. leptosphaeriae* are smaller (14–18 × 5–5.5 µm) than those of *M. sphaeriae* (19–25 × 5.8–6.5 µm). These observations were partly confirmed by Samuels *et al.* (1991), who discussed the history and synonymy of the species. Five-septate conidia of *M. leptosphaeriae* measure 74–105 × 5–7 µm, whereas 5-septate conidia of *M. sphaeriae* are 45–73 × 4.5–5.5 µm (Wollenweber 1926). Further morphological studies of fresh collections from *Leptosphaeria* on *Urtica* are needed to confirm these species boundaries in these two species of *Macroconia.* Also, the occurrence of cellular hairs or sterile appendages on ascomatal walls needs to be reviewed critically. Therefore, we refrain from designating epitype material for *M. leptopshaeriae* here.

Macroconia cupularis (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519443.
Basionym: *Cosmospora cupularis* J. Luo & W.Y. Zhuang, Fungal Diversity 31: 88. 2008.

Typification: **China**, Zhejiang, Hangzhou, Taihuyuan, 500 m alt., on fruitbodies of a black ascomycete (*Stylodothis* sp.) on twigs of an unidentified tree, Sep. 2005, J. Luo and W.Y. Li 6790-2, **holotype** HMAS 97514, **ex-type** culture HMAS 173240. GenBank barcodes: EF121864 (*ITS*), EF121870 (*28S rDNA*).

Notes: For description, illustrations, and discussion of the teleomorph and macroconidial anamorph of this species, see Luo & Zhuang (2008). Its inclusion in *Macroconia* is inferred from the morphology and sequences provided in the protologue, although we did not include the species in our own analysis.

Macroconia gigas (J. Luo & W.Y. Zhuang) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519444.
Basionym: *Cosmospora gigas* J. Luo & W.Y. Zhuang, Fungal Diversity 31: 85. 2008 non *Fusarium gigas* Speg., Anales Soc. Ci. Argent. 22: 221. 1886.

Typification: **Taiwan**, Nantou, Huisun Forestry Farm, 700 m alt., on rotten stem of bamboo associated with other fungi, Aug. 2005, W.Y. Zhuang 6598, **holotype** HMAS 99592, **ex-type** culture HMAS 173239; **paratype** *ibid*., W.Y. Zhuang, *6595*, HMAS 97513. GenBank barcodes: EF121863 (*ITS*), EF121869 (*28S rDNA*).

Notes: For description, illustrations, and discussion of this teleomorph and macroconidial anamorph of this species, see Luo & Zhuang (2008). Its inclusion in *Macroconia* is inferred from the morphology and sequences provided in the protologue, although we did not include the species in our own analysis.

Macroconia papilionacearum (Seaver) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519445.
Basionym: Nectria papilionacearum Seaver, Mycologia 1: 62. 1909.
≡ *Cosmospora papilionacearum* (Seaver) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 124. 1999.
? = *Fusarium gigas* Speg., Anales Soc. Ci. Argent. 22: 221. 1886.

Typification: **USA**, Missouri, Lebanon, on living *Lespedeza* with *Parodiella perisporioides*, Jul. 1887, Kellerman 1003, **lectotype** NY designated by Samuels *et al.* 1991.

Other material examined: **USA**, Florida, Tampa, near Hillsborough River State Park, on pyrenomycete on *Fabaceae*, Dec. 2006, T. Gräfenhan 2007-03, CBS 125495 = DAOM 238119.

Notes: For a description, illustrations, and discussion of the teleomorph, see Samuels *et al.* (1991). Our material collected in Florida closely resembles the description of *M. papilionacearum* given by Samuels *et al.* (1991), except for the smooth ascospores; the specimen from Florida has striate ascospores. In culture, the macroconidial anamorph of the Florida collection corresponded with the sketchy descriptions of *Fusarium gigas* (Wollenweber 1916, Wollenweber & Reinking 1935, Booth 1971, Gerlach & Nirenberg 1982). We found no anamorphic structures during our examination of the type material of *Fusarium gigas* (**Paraguay**, Arroyo-Guazu, on sterile pyrenomycete on culm of *Bambusaceae*, Jan. 1882, B. Balansa, Pl. du Paraguay 3471, Spegazinni's Fungi Guaranitici 426, B 700014033, B 700014032, PAD). The synonymy of *M. papilionacearum* with the macroconidial anamorph

represented by the name "*Fusarium*" *gigas* should be confirmed using fresh South American material.

Macroconia sphaeriae (Fuckel) Gräfenhan & Schroers, **comb. nov.** MycoBank MB519446.

Basionym: *Fusarium sphaeriae* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 370. 1870.

? = *Nectria leptosphaeriae* var. *macrospora* Wollenw., Angew. Bot. 8: 187. 1926.

Typification: **Germany**, Hessen, Rheingau, Reichartshausen near Oestrich-Winkel, on *Leptosphaeria (Sphaeria) dioica* on *Urtica dioica*, in spring, L. Fuckel, Fuckel Fungi Rhenani 212, **lectotype** designated here G 00111017, **isotypes** B, DAOM 126601 = Herb. Barbey-Boissier 2634.

Notes: The macroconidial anamorph and the teleomorph of this species is described, illustrated, and discussed by Wollenweber (1916, No. 58; 1926). The proposed new combination moves an anamorphically typified epithet into a teleomorphically typified genus, resulting in a valid, legitimate but technically incorrect name under the present Art. 59.

Macroconia sphaeriae can be distinguished from *M. leptosphaeriae* by its larger ascospores and smaller conidia (Wollenweber 1926; see *M. leptosphaeriae* above). The lectotype material in G had a few ascomata, but the two perithecia studied contained neither asci nor ascospores. The isotype material lacked teleomorph structures. We follow Wollenweber's (1926) conclusion and treat the two as separate species.

Mariannaea G. Arnaud ex Samson, Stud. Mycol. 6: 74. 1974.

Type species: ***Mariannaea elegans*** (Corda) Samson 1974.

Stroma absent or inconspicuous. *Perithecia* solitary, globose with a flat apex, not collapsing or collapsing by lateral pinching when dry, pale yellow, orange or brown, KOH–, smooth or finely roughened, 250–350 µm high. *Asci* cylindrical to narrowly clavate, with a sometimes inconspicuous apical ring, 8 uniseriate or apically biseriate ascospores. *Ascospores* hyaline, 1-septate, smooth to spinulose when mature. *Conidiophores* verticillate to penicilliate, hyaline, with conidiogenous cells arising directly from the stipe or from whorls of metulae on lower parts of the stipe, the stipe hyaline or yellowish brown at the base, often roughened at the base. *Phialides* monophialidic, flask shaped, hyaline, usually with obvious periclinal thickening and inconspicuous collarettes. *Conidia* aseptate, hyaline, in imbricate chains that eventually collapse to form slimy heads. *Chlamydospores* produced by some species.

Notes: *Mariannaea* is a common hyphomycete genus in soil and on woody substrates, and includes mononematous species with verticillate conidiophores, phialidic conidiogenous cells, and often imbricate chains of aseptate conidia. The genus was validly published by Samson (1974) and his concept is accepted for this anamorph typified genus, with the addition of teleomorph characters above. Although the conidia are small, the conidiophores and conidia are not comparable to microconidia of the *Fusarium* complex, and the genus is included here because of the similarity of its teleomorph to the *Cosmospora* complex. In common with many of the teleomorph-anamorph connections discussed in this paper, the exact identities of the relevant morphs are imprecise. A teleomorph of a fungus similar to *M. elegans* was described from specimens collected in Jamaica and Venezuela as *"Nectria" mariannaea* by Samuels & Seifert (1991). Although it is *Cosmospora*-like, the name was not transferred by Rossman *et al*. (1999) and remains misclassified in *Nectria.* As discussed below, it seems unlikely that *"N." mariannaea* is the teleomorph of *M. elegans s. str.*, and we are unable to infer its identity with any other of the named anamorphic species. An LSU sequence for the ex-type culture of *N. mariannaeae* was deposited in GenBank (AY554242) by Schroers *et al.* (2005); the LSU of the ex-type of *M. samuelsii* (HQ843766) differs by 5 substitutions from *N. mariannaeae*, and 3 substitutions from *M. aquaticola*. Thus, given the limited amount of variation in the ITS and LSU normally seen in the *Nectriaceae,* the phylogenetic data suggest that *M. aquaticola, N. mariannaeae* and *M. samuelsii* represent different species. We elect not to describe a new genus for *N. mariannaeae*, preferring to use the older *Mariannaea* as a holomorphic genus. Transferring it to *Mariannaea* would create a tautonym (Art. 23.4), thus, we have elected to leave this name in limbo until its taxonomic status can be more thoroughly evaluated.

Some of the species described in *Mariannaea* do not belong to the *Nectriaceae,* but to the *Cordycipitaceae* (Liang 1991, Liu *et al*. 2002). A phylogenetic analysis of internal transcribed spacer sequences of nectriacious *Mariannaea* species was provided by Li *et al*. (2009) and suggests the existence of four species, including the type, *M. elegans,* a variety distinguished from the type that seems to be distinct at the species level, *i.e. M. aquaticola, M. camptospora,* and *M. elegans* var. *punicea.* To this we add a fifth species, *M. samuelsii* described below.

Mariannaea samuelsii Seifert & Bissett, **sp. nov.** MycoBank MB519447. Fig. 6.

Coloniae in agaro malto et peptono confecto post 7 dies 21 mm diam, aureo-brunneae vel brunneolo-aurantiae; in agaro farina avenae confecto 28–29 mm diam, sub luce aurantio-griseae, obscuritate griseo-aurantiae. Conidiophora 100–200 µm longa, stipite 2–3.5 µm lato, bis vel ter verticillata, verticillos terminales (2–)3–5 phialidum, in verticillis subterminalibus 25–35 µm distantibus 1–3 phialides ferentia; raro phialides singulae circa 20 µm longae ex hyphis repentibus orientes. Phialides 12–30 µm longae, in parte latissima 2–3.5 µm latae, subulatae, in summo periclinaliter inspissatae, collari inconspicuo cylindrico praeditae. Conidia 3.5–7.5 × 2.5–3.5 µm, late fusiformia vel ellipsoidea, symmetrica, sed saepe asymmetrice ex apertura conidiogena protrusa, hyalina, levia, in catenis imbricatis saepe collabentibus adhaerentia. Holotypus DAOM 235814 (cultura dessicata).

On Blakeslee's MEA: *Conidiophores* arising from the agar surface, from aerial hyphae or fascicles, mostly 100–200 µm long, the axis 2–3.5 µm wide, branching 2–3 level verticillate, with a terminal whorl of (2–)3–5 phialides, and 1–2 lower nodes of 1–3 phialides spaced 25–35 µm apart, sometimes with a basal branch that repeats the pattern of 1–2 levels of verticillate branching, rarely with phialides single and terminal on an intercalary cell about 20 µm long. *Phialides* 12–30 µm long, 2–3.5 µm wide at broadest part (19.8 +/- 0.9 × 2.9 +/- 0.06, n = 25), subulate, sometimes with base slightly swollen, often longest in basal whorls, periclinal thickening obvious with phase contrast, collarette inconspicuous, about 1 × 1 µm, cylindrical. *Conidia* 3.5–7.5 × 2.5–3.5 µm (6.0 +/- 0.2 × 3.1 +/- 0.06, n = 25), broadly fusiform or ellipsoidal, L/B ratio about 2–2.5, symmetrical but often sitting asymmetrically on conidiogenous aperture, hyaline, smooth-walled, in imbricate chains that quickly collapse into hyaline, slimy heads. *Chlamydospores* rarely produced, globose to ellipsoidal, hyaline, ~5–10 × 3–5 µm, in chains of up to five cells.

Colonies on Blakeslee's MEA after 7 d about 21 mm diam, golden brown to brownish orange (5–6D6) in centre, fading towards entire margin, planar, with sparsely lanose aerial mycelium and fascicles, reverse concolourous; sporulation more intense on MEA in presence of 12:12 h fluorescent light:continuous darkness, agar surface mealy. On OA 28–29 mm diam, orange gray (5B2)

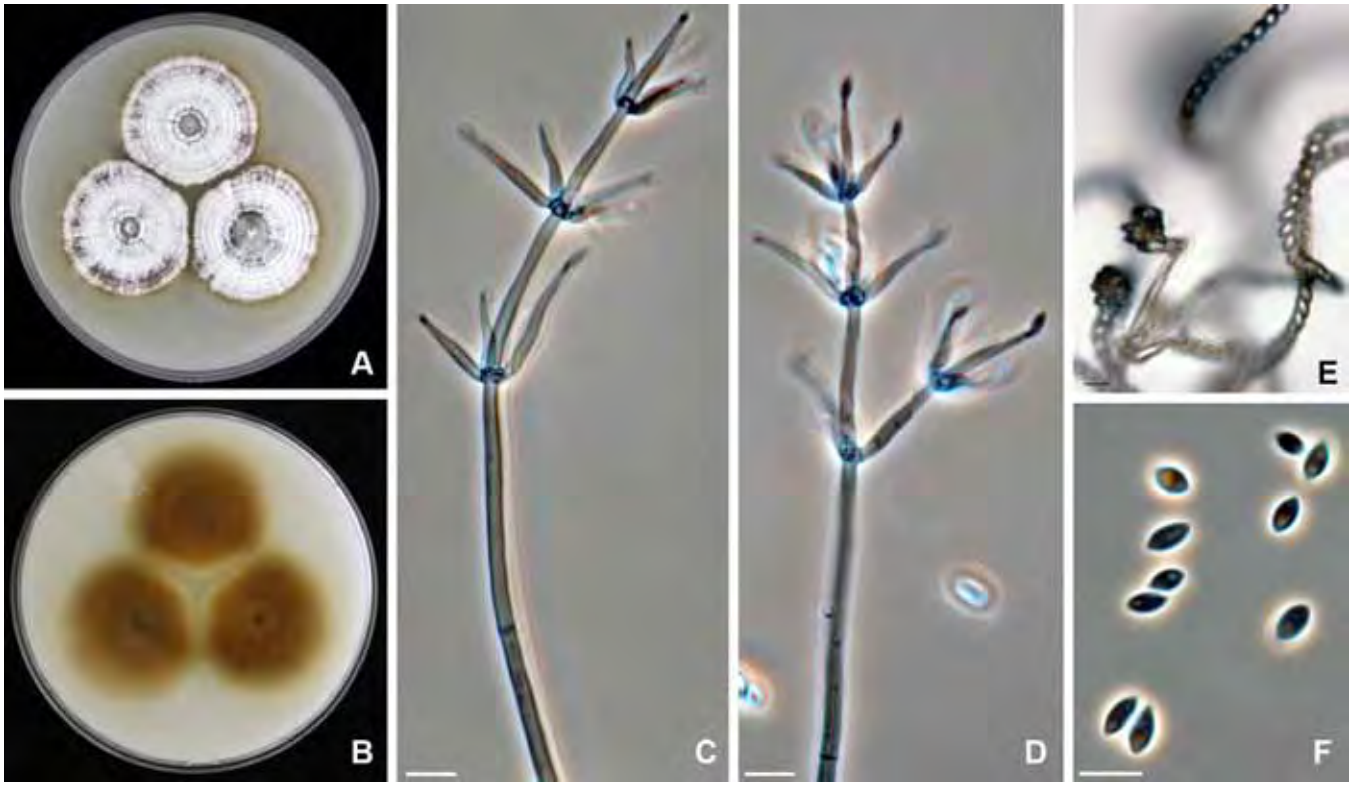


Fig. 6. *Mariannaea samuelsii*, ex-type strain. A, B. Obverse and reverse of 14 d old colony on oatmeal agar. C, D. Conidiophores showing verticillate branching. E. Imbricate conidial chains. F. Conidia. Scale bars = 10 µm.

in light, and grayish orange (5D2) in dark, fading towards entire, thin margin, with moderately dense lanose aerial mycelium and fascicles, reverse concolourous.

Typification: **Guatemala**, Zacapa Prov., San Lorenzo Mt., isolated from soil under *Podocarpus* sp., surface litter and humus horizons, containing roots, 0–2 cm, 12 Jul. 1986, John Bissett, herb. DAOM 235814, **ex-type** culture CBS 125515. GenBank barcodes: HQ843766 (*28S rDNA*), HQ843767 (*ITS*), HQ897752 (*rpb2*), HQ897888 (*acl1*).

Notes: *Mariannaea samuelsii* is morphologically similar to *M. elegans*, the type of the genus (Samson 1974), and the recently described *M. aquaticola* (Li *et al*. 2009) in producing verticillate conidiophores and imbricate chains of fusiform conidia. The conidiophores of *M. aquaticola* and *M. samuelsii* are generally less elaborately branched than those of *M. elegans,* and lack basal roughening. The size ranges of the conidia of these three species overlap, with conidia of *M. samuelsii* (3.5–7.5 × 2.5–3.5 µm) intermediate in length between the shorter conidia of *M. elegans* (4–6 × 1.5–2.5 µm) and the longer conidia of *M. aquaticola* (5–10 × 2–4.5 µm). *Mariannaea elegans* produces chlamydospores, which have not been seen in *M. aquaticola* and are rarely and sparsely produced in *M. samuelsii.*

Mariannaea samuelsii differs by four base-pair substitutions (two in the ITS1, two in the ITS2) from *M. aquaticola*, its sister species.

Microcera Desm., Ann. Sci. Nat., Bot., sér. 3, 10: 359. 1848.
= *Pseudomicrocera* Petch, Trans. Brit. Mycol. Soc. 7: 164. 1921.

Type species: ***Microcera coccophila*** Desm. 1848.

Stroma and/or white byssus covering host. *Perithecia* solitary or in groups, globose, with a blunt papilla, collapsing cupulate or pinched when dry, orange to dark red, KOH+ dark red or violet, finely roughened, 200–400 µm high. *Asci* cylindrical to narrowly clavate, with an apical ring, 8 uniseriate ascospores. *Ascospores* hyaline to pale yellow-brown, 1(–3)-septate, smooth or becoming tuberculate when mature. *Conidiophores* initially as lateral phialides on somatic hyphae, later monochasial, verticillate to penicilliate, hyaline, usually forming discrete sporodochia or synnemata on the host. *Phialides* monophialidic, cylindrical to subulate to subclavate, hyaline. *Microconidia* absent. *Macroconidia* pale, orange, pink or bright red in mass, subcylindrical, moderately curved, or conspicuously curved, apical cell often slightly or conspicuously hooked, basal cell scarcely to conspicuously pedicellate, mostly (0–)3–5-septate, but up to 12 septate in one species, hyaline, mostly thick-walled. *Chlamydospores* not observed.

Colonies on PDA slow growing, 18–35 mm diam in 14 d at room temperature, surface smooth, felt-like or floccose, whitish to bright orange-red, sometimes with violet or vinaceous tones; *aerial mycelium* sparse or appressed, sporulation occurring in sporodochia or sometimes in slimy masses (pionnotes).

Habitat: Mostly parasites of scale insects, also reported on aphids, adelgids, and sometimes isolated as saprobes from soil or plant debris.

Notes: Along with *Atractium* discussed above, *Microcera* was a generic name used for synnematous *Fusarium*-like fungi, but in this case mostly parasites of scale insects. Our phylogenetic analysis confirms the significance of this ecological association, and the genus is here redefined to include additional non-synnematous species associated with scale insects, some of which are sometimes also found on other substrates. Until the 1920's, the generic name *Microcera* was widely used for entomogenous species with slender, falcate conidia (McAlpine 1899, 1904; Parkin 1906; Trabut 1907; Miyabe & Sawada 1913; Petch 1921). The original concept of *Microcera* included one species, *M. coccophila*, based on two collections made by Roberge near Caen, France. Desmazières did not

Table 4. Species attributed to *Microcera* and their current status. Basic nomenclatural data from *Index Fungorum* (www.indexfungorum.org).

Species, authority and year of publication	Status	Reference
M. acuminata (Ellis & Everh.) Höhn. 1919	= *Fusarium acuminatum*	Wollenweber & Reinking 1935
M. aurantiicola Petch 1921	= *M. larvarum*	This paper
*M. brachyspor*a Sacc. & Scalia 1904	? = *Fusicolla aquaeductuum*	Wollenweber & Reinking 1935
M. ciliata (Link) Wollenw. 1916	= *"Fusarium" ciliatum,* status unclear	–
M. clavariella Speg. 1886	= *Cladosterigma fusispora* Pat.	Seifert 1985b
M. coccidophthora Petch 1921	= *Fusarium tasmanicum* (McAlpine) Rossman 1983	Rossman 1983
M. coccophila Desm. 1848	Accepted species	This paper
M. curta Sacc. 1909	= *M. larvarum*	This paper
M. erumpens Ellis & Everh. 1894	Unknown	–
M. fujikuroi Miyabe & Sawada 1913	= *M. diploa*	This paper
*M. henningsi*i (Koord.) Petch 1914	= *M. diploa*	This paper
M. massariae Sacc. 1886	= *"Fusarium" ciliatum,* see above	Wollenweber & Reinking 1935
M. merrillii Syd. 1914	= *M. diploa*	This paper
M. mytilaspidis McAlpine 1904	= *Fusarium lateritium* var. *longum*	Wollenweber & Reinking 1935
M. orthospora Syd. 1924	= *Mycogloea orthospora* (Syd.) R. McNabb ex Dingley 1989	Dingley 1989
M. parlatoriae Trab. 1907	= *M. larvarum*	This paper
M. pluriseptata Cooke & Massee 1888	= *M. coccophila*	This paper
M. rectispora Cooke & Massee	= *Tetracrium rectisporum* (Cooke & Massee) Petch 1921	Petch 1921
M. tasmanica McAlpine 1904	= *Fusarium tasmanicum* (McAlpine) Rossman 1983	Rossman 1983
M. tonduzii Pat. 1912	= *M. larvarum*	This paper

mention perithecia on these specimens, but from the conidial shape he inferred a close relationship with *Fusarium*. Tulasne & Tulasne (1861, 1865) studied these and additional specimens from the type and other locations. They redescribed the species as a holomorph as *Sphaerostilbe flammea*, but concluded that Desmazières' *Microcera* was a "*Stilbum*" with long, curved, *Fusarium*-like macroconidia. Petch (1921) revised this group of entomogenous species and studied the type material of *M. coccophila,* finding perithecia on well-developed stromata associated with the synnemata of the anamorph. Mature perithecia were red with ascospores measuring 12–18 × 5–7 µm (Petch 1921).

The taxonomic synonymy of *Microcera* with *Fusarium* followed the work of Wollenweber. Wollenweber (1916) first classified *F. ciliatum* in *Microcera,* based on his study of two herbarium specimens originally identified as *Fusarium pallens* (Wollenweber 1916; 1st edition, No. 435, 436). Later, Wollenweber & Reinking (1935) discarded *Microcera* and placed its species in *Fusarium*. In his first monographic revision of *Fusarium*, Wollenweber (1931) did not consider *M. coccophila*, but subsequently revised his generic concept profoundly (Wollenweber & Reinking 1935). Then, *M. coccophila,* along with species described in other genera such as *Atractium*, *Discofusarium*, *Fusidium*, *Fusisporium*, *Fusoma*, *Microcera*, *Pionnotes*, *Pseudomicrocera,* and *Selenosporium* were placed in *Fusarium*. Of these, only the type species of *Pseudomicrocera* (*Ps. henningsii*) would now be considered a member of the *Microcera* clade. After Wollenweber's work, *Microcera* was included as a synonym in major revisions of *Fusarium, e.g.* Booth (1971), Gerlach & Nirenberg (1982), Nelson *et al.* (1983), and Leslie *et al.* (2006).

Twenty species were included in *Microcera* by various authors, and the present status of most species is known (Table 4). We presently accept four species, which can be keyed out as follows.

KEY TO SPECIES OF *MICROCERA*

1. Macroconidia straight to slightly curved, up to 140 µm long, up to 12 septate ..... *M. coccophila*
1. Macroconidia distinctly curved, usually less than 120 µm long, mostly 3–5 septate 2

2. Macroconidia slender, 40–120 µm long ..... *M. diploa*
2. Macroconidia usually less than 40 µm long 3

3. Agar colonies with red pigments ..... *M. rubra*
3. Agar colonies lacking red pigments ..... *M. larvarum*

Accepted species

Microcera coccophila Desm., Ann. Sci. Nat., Bot., Sér. 3, 10: 359. 1848. Fig. 7A, B.

Basionym: *Tubercularia coccophila* (Desm.) Bonord., Abh. Geb. Mykol., p. 96. 1864.

≡ *Fusarium coccophilum* (Desm.) Wollenw. & Reinking, *Die Fusarien*, p. 34. 1935.

≡ *Fusarium episphaeria* f. *coccophilum* (Desm.) W.C. Snyder & H.N. Hansen, Amer. J. Bot. 32: 662. 1945.

= *Microcera pluriseptata* Cooke & Massee in Cooke, Grevillea 17: 43. 1888.

Typification: **France**, Normandy, near Caen, on *Eulecanium tiliae* (nut scale) on living and young trunks of *Salix* and *Fraxinus excelsior*, Feb. 1847, M. Roberge, **lectotype** designated here K (M) 165807, Plantes Cryptogames de France, Ed. II, Ser. I, No. 1350, **isotypes** P, K (M) 165806, Plantes Cryptogames de France Ed. I, Ser. I, No. 1750.

Additional material examined: **Japan**, Saitama, Hiki-gun, Ogawa-machi, on scale insect on *Broussonetia kazinoki* × *B. papryifera*, Jul. 1993, G. Okada.

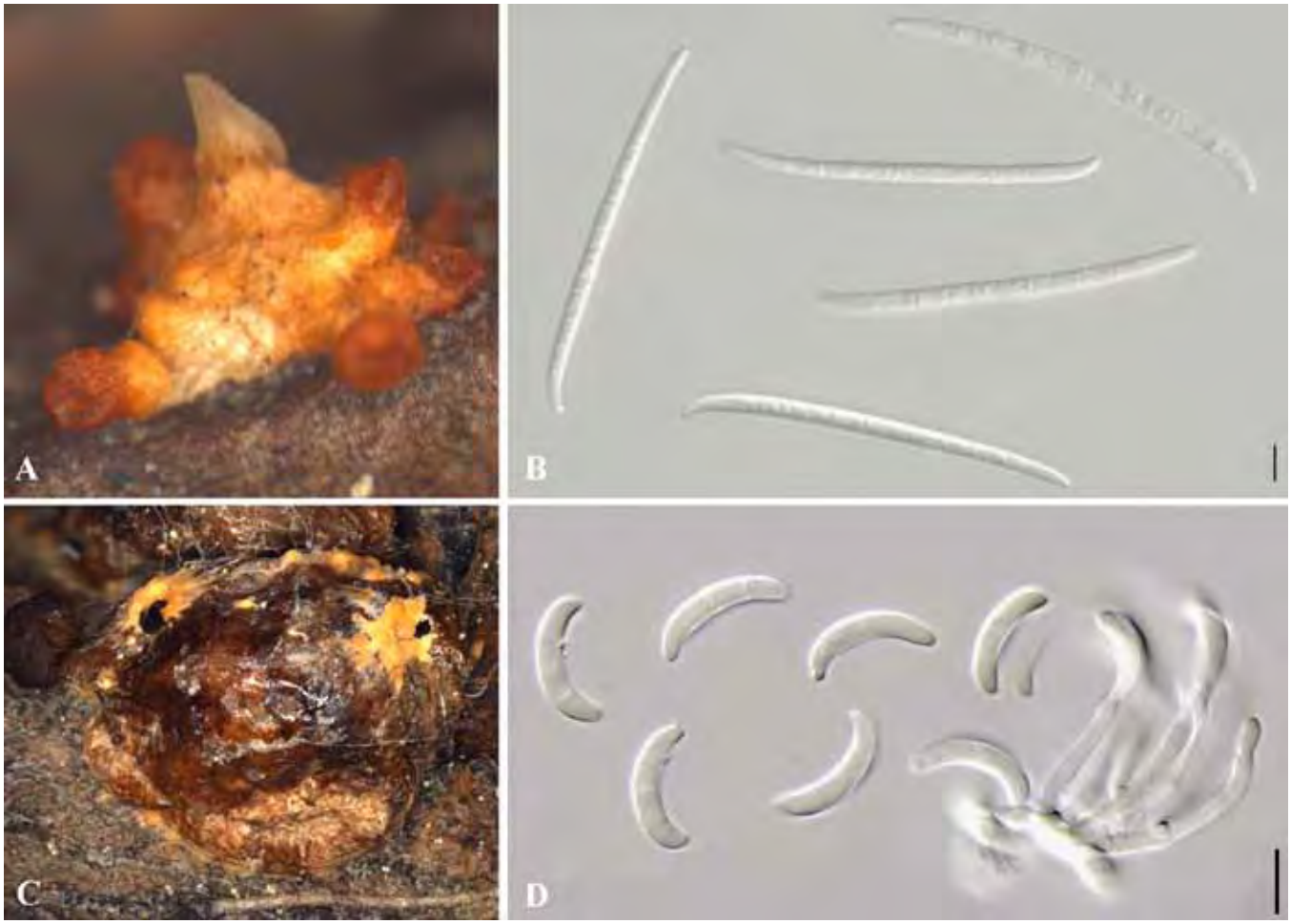


Fig. 7. Two *Microcera* species. A, B. *Microcera coccophila.* A. Habit, with conical red perithecia on a stroma growing over scale insect and flame-like synnema emerging from the top. B. Macroconidia. C, D. *M. larvarum*. C. Flame-like conidiomata on scale insect. D. Conidia. Scale bars = 10 µm.

Notes: The macroconidial anamorph and the teleomorph of this species as lectotypified here is described and discussed in detail by Petch (1921). For description, illustrations, and further taxonomic synonyms of the anamorph, see Gerlach & Nirenberg (1982).

There has been confusion about synonymies and anamorph-teleomorph connections between this fungus, *M. diploa*, and *M. larvarum*. Petch (1921) synonymised the anamorphic name *Atractium flammeum* Berk. & Ravenel with *Microcera coccophila,* arguing that *Sphaerostilbe flammea* Tul. & C. Tul. represented the holomorph of *M. coccophila* and that *Sphaerostilbe coccophila* Tul. & C. Tul. was actually a different species, *M. larvarum* (as "*Nectria" aurantiicola*). He cited two Desmazières exsiccati of *M. coccophila*, namely Plantes Cryptogames de France, Ed. I, Ser. I, No. 1750 and *ibid.* Ed. II, Ser. I, No. 1350. Our reexamination of the latter confirms Petch's observation that mature perithecia have 1-septate ascospores, 12–18 × 5–7 µm, associated with the anamorph. "*Nectria*" *flammea* reportedly has larger ascospores (Dingley 1951, 15–24 × 6–10 µm; Booth 1971, 1981b, 16–20 × 7.5–10 µm). The anamorph-teleomorph connection of *Microcera coccophila* with "*Nectria*" *flammea* needs to be critically reevaluated.

Gräfenhan *et al.* (2008) noted the occurrence of several phylogenetic species among anamorph and teleomorph collections that are morphologically similar to *M. coccophila*, *M. diploa*, and *M. larvarum*.

Microcera diploa (Berk. & M.A. Curtis) Gräfenhan & Seifert, **comb. nov.** MycoBank MB519448.

Basionym: *Nectria diploa* Berk. & M.A. Curtis, J. Linn. Soc., Bot. 10: 378. 1869.

≡ *Cucurbitaria diploa* (Berk. & M.A. Curtis) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.

≡ *Creonectria diploa* (Berk. & M.A. Curtis) Seaver, Mycologia 1: 190. 1909.

≡ *Calonectria diploa* (Berk. & M.A. Curtis) Wollenw., Angew. Bot. 8: 193. 1926.

≡ *Cosmospora diploa* (Berk. & M.A. Curtis) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 121. 1999.

= *Fusarium coccidicola* Henn. [as "*coccideicola*"], Bot. Jahrb. Syst. 34: 57. 1904.

= *Aschersonia henningsii* Koord., Bot. Untersuch. Java p. 213. 1907.

≡ *Microcera henningsii* (Koord.) Petch, Ann. Roy. Bot. Gard. Peradeniya 5: 533. 1914.

≡ *Pseudomicrocera henningsii* (Koord.) Petch, Trans. Brit. Mycol. Soc. **7**: 164. 1921.

= *Microcera fujikuroi* Miyabe & Sawada, J. Coll. Agric. Tohoku Imp. Univ. 5: 83. 1913.

= *Microcera merrillii* Syd., Ann. Mycol. 12: 576. 1914.

Typification: **Cuba**, on individual scale insects on bark, C. Wright 606 ex Herb. Berk., Fungi Cubensis Wrightiana 767, **lectotype** K designated by Booth 1971, **isotypes** FH 00286651, FH 00286652, NYS.

Notes: The holotype of this species is consistent with the descriptions of the teleomorph by Booth (1971) and Rossman (1983). The macroconidial anamorph is described by Booth (1971), Gerlach & Nirenberg (1982), and Rossman (1983). As explained in the introduction, under the present Art. 59, the proposed new combination results in a technically incorrect but valid and legitimate name.

Microcera diploa is an entomogenous species reported from many tropical and subtropical regions (Booth 1971, Rossman 1983), commonly found on various scale insects sitting on several plant species. Booth (1971) studied the type collection and reported pustules of perithecia on a stroma associated with the anamorph. From our observations of the same material, it is clear that the stromata developed over individual scale insects. In agreement with Rossman (1983), we follow Booth's decision to interpret the Cuban specimen as the type of *Nectria diploa*. Several *Fusarium* species were synonymised with *M. diploa*, namely *F. derridis*, *F. juruanum*, and *F. pentaclethrae*, which were described only from herbaceous material (Wollenweber & Reinking 1935). We studied Hennings' material (*F. derridis* = B 700014017; *F. juruanum* = B 700014035, B 700014036; *F. pentaclethrae* = B 700014037), and none seem to be insect-associated. Therefore, we reject these synonymies, except for *F. coccidicola* as listed above.

Microcera larvarum (Fuckel) Gräfenhan, Seifert & Schroers, **comb. nov.** MycoBank MB519449. Fig. 7C, D.

Basionym: *Fusarium larvarum* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 369. 1870.

= *Microcera parlatoriae* Trab., Bull. Agric. Algérie Tunisie 13: 33. 1907.
= *Microcera curta* Sacc., Ann. Mycol. 7: 437. 1909.
= *Microcera tonduzii* Pat., Bull. Soc. Mycol. France 28: 142. 1912.
= *Microcera aurantiicola* Petch, Trans. Brit. Mycol. Soc. 7: 163. 1921.

Typification: **Germany**, Hessen, Rheingau, near Oestrich-Winkel, on larva cuticles of insects on apple trees, in spring, L. Fuckel, **lectotype** designated here G 00111015 **Epitype** designated here: **Iran**, Prov. Gilan, near Rasht, on *Quadraspidiotus perniciosus* (San José insect) scale on *Prunus domestica*, Oct. 1968, W. Gerlach & D. Ershad, **epitype** BBA, **ex-type** cultures BBA 62239 = CBS 738.79 = MUCL 19033 = NRRL 20473. GenBank barcodes: HQ897768 (*rpb2*), HQ897904 (*acl1*).

Notes: For descriptions, illustrations, and further taxonomic synonyms of the teleomorph and macroconidial anamorph of this species, see Petch (1921), Wollenweber (1931), Booth (1971, 1981a, c), and Gerlach & Nirenberg (1982).

Our phylogenetic analysis and that of Bills *et al.* (2009) clearly indicate that the two varieties of *M. larvarum* segregated by Gerlach (1977) warrant species rank; *M. larvarum* var. *rubrum* is recognised as a distinct species below. Bills *et al.* (2009) studied parnafungin production by species of this complex, and their data suggest that perhaps two additional phylogenetic species may exist in this group.

The synonymy of *Microcera larvarum* with "*Nectria*" *aurantiicola* cited by Booth (1971, 1981a), Gerlach & Nirenberg (1982), and Rossman *et al.* (1999) should be critically reviewed.

Microcera rubra Gräfenhan & Seifert, **sp. nov.** MycoBank MB519450.

= *Fusarium larvarum* var. *rubrum* W. Gerlach, Phytopath. Z. 90: 38. 1977. *nom. inval.* Art. 37.

Latin description in Gerlach, Phytopath. Z. 90: 38. 1977 under the name "*Fusarium" larvarum* var. *rubrum*.

Typification: **Iran**, Prov. Gilan, near Rasht, on *Quadraspidiotus perniciosus* (San José insect) scale on *Prunus domestica*, Oct. 1968, W. Gerlach & D. Ershad, **holotype** CBS H-714, **ex-type** cultures BBA 62460 = CBS 638.76 = NRRL 20475 = NRRL 22111 = NRRL 22170. GenBank barcodes: HQ897767 (*rpb2*), HQ897903 (*acl1*).

Notes: For descriptions, illustrations, and discussion of this macroconidial species, see Gerlach (1977) and Gerlach & Nirenberg (1982); for phylogenetic relationships, see Bills *et al.* (2009).

The taxon was not validly published because the author did not designate a holotype, instead listing one living strain with accession numbers in two culture collections as "Cultura typica".

Pseudonectria Seaver, Mycologia 1: 48. 1909.

Type species: ***Pseudonectria rousseliana*** (Mont.) Clements & Shear 1931, here recognised as *P. buxi* (DC.) Seifert, Gräfenhan & Schroers.

Notes: *Pseudonectria* as presently circumscribed is not monophyletic (Fig. 1), with two species branching out in separate clades in the *Nectriaceae*. The type species of *Pseudonectria,* together with an undescribed taxon, forms a sister clade to *Atractium*. The second species, "*Pseudonectria*" *pachysandricola* together with "*Nectria*" *diminuta* and "*N.*" *rubropeziza*, falls between the terminal and basal *Fusarium*-like clade. Therefore, only one species is presently recognised in this genus, with the teleomorph typifying the oldest available generic name *Pseudonectria* 1909, and the anamorph representing the type of the later generic name *Chaetodochium* 1932. There is presently no acceptable generic name for "*Pseudonectria*" *pachysandricola*, which is well described and illustrated by Dodge (1944) and Rossman *et al*. (1993).

The anamorphs of *Pseudonectria* are fairly well understood pathogens on the *Buxaceae* (Bezerra 1963, Rossman *et al*. 1993), but these species are usually cited under their anamorph names, *i.e.* "*Volutella*" *buxi* and "*V." pachysandricola*. Because these species do not share common morphological characters with *Volutella s. str.* (see below) and are phylogenetically distinct, these anamorph names should not be used. The phylogenetic relationship of a biologically and morphologically similar species described from *Ruscus aculeatus*, "*V." rusci*, remains unresolved.

Pseudonectria buxi (DC.) Seifert, Gräfenhan & Schroers, **comb. nov.** MycoBank MB519451.

Basionym: *Tubercularia buxi* DC., Flore française, Edn. 3 (Paris) 6: 110. 1815.

≡ *Chaetostroma buxi* (DC.) Corda, Icon. Fung. 2: 30. 1838.
≡ *Volutella buxi* (DC.) Berk., Outl. Brit. Fungi p. 340. 1860.
≡ *Chaetodochium buxi* (DC.) Höhn., Mitt. bot. Inst. tech. Hochsch. Wien 9: 45. 1932.
= *Pseudonectria rousseliana* (Mont.) Clements & Shear, *Genera of Fungi* p. 280. 1931.
≡ *Nectria rousseliana* Mont. in Castagne, Cat. P1. Marseille Suppl. p. 44. 1851. For additional obligate synonyms, see Rossman *et al*. 1993.

Notes: Bezerra (1963) and Rossman *et al*. (1993) redescribed and illustrated both the anamorph and teleomorph of *P. buxi,* a common pathogen of *Buxus sempervirens.* The conidia of the anamorph tend toward fusiform, a shape not seen in species of *Volutella s. str.,* and the sporodochia tend to be broadly attached to the substratum. These are subtle characters, and at present we cannot suggest robust morphological characters to unequivocally distinguish the anamorphs of *Pseudonectria* from *Volutella*. However, the teleomorphs are rather different, with the perithecia of *Volutella* being red and those of *Pseudonectria* being green.

Because this fungus has a known teleomorph and anamorph, Art. 59 applies, and our transfer of an anamorphically typified epithet to a teleomorphically typified generic name is technically incorrect according to the present ICBN, but it is valid and legitimate.

Stylonectria Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 124: 52. 1915.

Type species: ***Stylonectria applanata*** Höhn. 1915.

Stroma thin, whitish or yellow, hyphal or subiculum-like. *Perithecia* gregarious in groups of up to 20, subglobose, pyriform to

subcylindrical, with a rounded or broad, circular, flat disc on a venter-like neck, sometimes laterally collapsing when dry, pale yellow, orange-red, orange-brown, or pale to dark red, KOH+ dark red to purple, yellow in lactic acid, smooth, usually shiny, slightly iridescent, 150–250(–350) µm high. *Perithecial wall* consisting of two regions: inner region of hyaline, thin-walled, compressed, elongate cells; outer region of distinct, isodiametric to oblong, angular or globose, thick-walled cells. *Asci* cylindrical to clavate, apex simple or with a ring, with 8 uniseriate, biseriate or irregularly disposed ascospores. *Ascospores* hyaline or yellow to pale brown, 1-septate, cylindrical to allantoid or ellipsoidal, smooth or tuberculate, generally thick-walled. *Conidiophores* initially formed mostly as unbranched phialides on somatic hyphae, occasionally loosely branched, sometimes forming small sporodochia. *Phialides* monophialidic, almost cylindrical to subcylindrical, often with a distinct collarette. *Microconidia* sparsely produced, allantoid to lunulate, slightly to strongly curved, aseptate, in slimy heads. *Macroconidia* orange in mass, subcylindrical or moderately to strongly curved, falcate, mostly 0–1-septate, apex narrower than base, apical cell blunt or hooked, basal cell not or scarcely pedicellate. *Chlamydospores* not observed.

In culture on PDA slow- to very slow-growing, 10–30 mm diam in 14 d at room temperature, surface white, later becoming off-white to pale or bright orange, occasionally with orange sporodochia; aerial mycelium mostly lacking, if present, sparse and appressed margin smooth to broadly lobed

Habitat: Restricted to stromata of ascomycetes, mainly in the *Diaporthales*.

Notes: *Stylonectria* was described by Höhnel (1915) as an anamorph genus with the type and only species, *S. applanata*, for which the teleomorph was considered to be "*Nectria" applanata* var. *succinea*. Booth (1959) presented convincing evidence that Höhnel (1915) actually was dealing with a teleomorphic fungus, which was further explained by Rossman *et al.* (1999). Species of *Stylonectria* are considered to be host specific, probably to the fungal host, which itself may be host specific to the plant.

Accepted species

Stylonectria applanata Höhn., Sitzungsber. Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 124: 52. 1915.

= *Nectria applanata* var. *succinea Höhn., Sitzungsber.* Kaiserl. Akad. Wiss., Wien, Math.-Naturwiss. Kl., Abt. 1, 124: 51. 1915.

Typification: **Austria**, Niederösterreich, near Sonntagsberg, on stromata of *Melogramma bulliardii* on dead twigs of *Corylus avellana*, Aug. 1914, P. Strasser, **lectotype** designated here FH 00286663.

Notes: For descriptions and discussion of the teleomorph, microconidial anamorph, and macroconidial synanamorph of this species, see von Höhnel (1915) and Weese (1916).

Von Höhnel (1915) distinguished "*Nectria*" *applanata* var. *succinea* from "*N.*" *applanata* var. *applanata* based on the pale yellow colour of the translucent perithecia. Otherwise, the two varieties were described with identical macro- and microscopic characters. Because host specificity is an important character for distinguishing species of *Stylonectria* (*cf.* Gräfenhan 2009), we recognise *S. applanata* as a distinct species from *S. carpini,* described below, *i.e. Nectria applanata* var. *applanata*.

Stylonectria carpini Gräfenhan, **nom. nov.** MycoBank MB519452.

≡ *Nectria applanata* Fuckel, Jahrb. Nassauischen Vereins Naturk. 25–26: 310. 1871 (1872).

≡ *Cucurbitaria applanata* (Fuckel) O. Kuntze, Rev. Gen. Plant. 3: 460. 1898.

≡ *Dialonectria applanata* (Fuckel) Petch, Trans. Brit. Mycol. Soc. 25: 170. 1941.

Etymology: The species epithet is derived from the plant host genus *Carpinus*.

Typification: **Germany**, Hessen, Rheingau, Aepfelbach im Oestricherwald, on black pyrenomycete on decaying, corticated branches of *Carpinus betulus*, L. Fuckel, Fuckel Fungi Rhenani 2356, **lectotype** designated here G 00111018, **isotypes** B 700014054, FH 00286648, K, DAOM 119800 = Herb. Barbey-Boissier 862.

Other material examined: **Austria**, Niederösterreich, Gießhübl, Wasserspreng, Talgrund, (Finsterer Gang), MTB 7863/1, on *Melanconis spodiaea* on *Carpinus betulus*, Aug. 2006, H. Voglmayr W.J. 3013, DAOM 235819. **Germany**, Schleswig-Holstein, near Stegelkamp, Naturwaldzelle Endern, on pyrenomycete on *Carpinus betulus*, Aug. 2008, T. Gräfenhan 2008-17, DAOM 235829.

Notes: This species produces both a micro- and a macroconidial synanamorph in addition to a teleomorph. Our examination of Höhnel's type material of *Stylonectria applanata* (FH 00286663) and that of Fuckel's "*Nectria*" *applanata* (G 00111018) suggests the two species are not conspecific, but both are species of *Stylonectria;* the latter is therefore renamed here.

The distribution of *Stylonectria carpini* corresponds to the distribution of *Carpinus betulinus* in Europe. In North America, a different species of *Stylonectria* occurs on a black pyrenomycete on the congeneric native host, *Carpinus caroliniana,* and has a microconidial anamorph in culture and a distinctly different teleomorph. Collections made from a pyrenomycete on *Betula* are morphologically similar to *S. carpini* but phylogenetically distinct.

Stylonectria purtonii (Grev.) Gräfenhan, **comb. nov.** MycoBank MB519453.

Basionym: *Sphaeria purtonii* Grev., Scot. Crypt. Fl. 6: 23. 1828.

≡ *Nectria purtonii* (Grev.) Berk., Outl. Brit. Fung. p. 394. 1860.

≡ *Dialonectria purtonii* (Grev.) Cooke, Grevillea 12: 110. 1884.

≡ *Cucurbitaria purtonii* (Grev.) O. Kuntze, Rev. Gen. Plant. 3: 461. 1898.

≡ *Cosmospora purtonii* (Grev.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 124. 1999.

Typification: **UK**, Scotland, Edinburgh, Rosslyn Woods, on black pyrenomycete on small branches of coniferous tree, 1820, Greville, **lectotype** E designated by Booth 1958.

Other material examined: **France**, Provence, St. Remy, on old stromata of pyrenomycete on *Coronilla emerus*, Oct. 1974, W. Gams, culture CBS 717.74. **Germany**, Nordrhein-Westfalen, Detmold, Externsteine, on small branches of felled trees of *Picea abies*, Apr. 2007, T. Gräfenhan 2007-30, DAOM 235818.

Notes: For descriptions, illustrations, and further taxonomic synonyms of the teleomorph as well as microconidial and macroconidial synanamorphs of this species, see Booth (1959) and Samuels (1976).

Stylonectria wegeliniana (Rehm) Gräfenhan, Voglmayr & Jaklitsch, **comb. nov.** MycoBank MB519454.

Basionym: *Nectria episphaeria* var. *wegeliniana* Rehm, Hewigia 30: 260. 1891.

≡ *Dialonectria wegeliniana* (Rehm) Petch, Trans. Brit. Mycol. Soc. 21: 266. 1938 as *D. wegeliana*.

≡ *Cosmospora wegeliniana* (Rehm) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 131. 1999.

Typification: **Switzerland**, Heimiswyl bridge near Bern, on *Hapalocystis bicaudata* (= *Pseudovalsa berkeleyi*) on dry branches of *Ulmus*, Oct. 1887, Wegelin, Rehm Ascomyceten 1045, **lectotype** designated here S F86597, **isotype** NY.

Other material examined: **Austria**, Niederösterreich, Distr. Mödling, Comm. Hinterbrühl, Wassergspreng, Finsterer Gang west of Gießhübl, margin of a forest road, elev. 400 m, map grid 7863/3, on *Hapalocystis bicaudata* on corticated dead branches of *Ulmus glabra* attached to the living tree, May 2009, H. Voglmayr, WU 29855, culture CBS 125490.

Notes: This species produces microconidia and macroconidia in culture; the teleomorph was only found in nature. For a description, illustrations, and discussion of the species, see Weese (1916).

Volutella Tode 1790 : Fr. 1832. Fungi Mecklenb. Sel. 1: 28. 1790 : Syst. Mycol. 3: 458, 466 1832, *nom. cons.* [non *Volutella* Forsk. 1775 (*Lauraceae*)]

Type species: ***Volutella ciliata*** (Alb. & Schw. : Fr.) Fr. 1832, *typus cons.*

Perithecia nonstromatic, pyriform, collapsing by lateral pinching or not collapsing when dry, brownish orange to brownish red, yellow in 100 % lactic acid, darkest around papilla, hyphal hairs covering surface, hyaline, thick walled. *Perithecial wall* 15–25 um wide, with two intergrading layers of angular cells; cells next to centrum thin walled; cells of layer region thick walled. *Asci* narrowly clavate to broadly cylindrical, apex with or without refractive ring, eight-spored. *Ascospores* fusiform or biconic, equally or unequally 2-celled, smooth or finely roughed, hyaline, white in mass, obliquely uniseriate or partially biseriate near base, completely filling each ascus. *Conidiophores* aggregated into sporodochia or synnemata, with an inconspicuous basal stroma; unbranched, hyaline setae around margin of conidiomata. *Synnemata*, when produced, determinate, pale, composed of a stipe of parallel hyphae and a divergent capitulum of conidiophores giving rise to a slimy conidial mass; differentiated marginal hyphae absent. *Conidiophore branching* once or twice monochasial, 2-level verticillate, monoverticillate or irregularly biverticillate. *Conidiogenous cells* monophialidic, hyaline, subulate, usually with conspicuous periclinal thickening. *Conidial masses* slimy, white, yellow, orange or pink. *Conidia* aseptate, hyaline, ellipsoidal, ovate or oblong. *Chlamydospores* produced in culture by some species. *Verticillium*-like synanamorph present in some species: *Conidiophores* hyaline, with 2 or more whorls of conidiogenous cells; phialides and conidia with similar characters to those described for the conidiomata. Agar cultures growing relatively slowly, usually less than 30 mm diam in 14 d, with little aerial mycelium.

Notes: *Volutella* is a classical hyphomycete genus that has received little study, despite the common occurrence and broad distribution of its species. The genus is typified by *V. ciliata*, which has sporodochial conidiomata with conspicuous hyaline, thick-walled, unbranched, spine-like setae, phialidic conidiogenous cells arising from more or less penicillately branched conidiophores, and ameroconidia accumulating in a profuse, colourful slime. Domsch *et al*. (2007) provided a general overview of the type and a few other soil-borne species of the genus. In anticipation of a more comprehensive revision of *Volutella*, the inclusion of one synnematous species in this genus is discussed here.

Volutella s. str. should be restricted to the clade that includes the type species, *V. ciliata*, *V. consors* (referred to as *V. minima* by Domsch *et al*. 2007), and the synnematous *V. citrinella*. The teleomorphs associated with *Volutella* provide clues to its polyphyly. "*Cosmospora*" *consors* was reported as the teleomorph of *V. ciliata* by Samuels (1977, as *Nectria consors*); the identity of the anamorph was later changed to *V. minima* by Domsch *et al*. (2007). This species differs from *V. ciliata* primarily by its cylindrical conidia. *Volutella citrinella,* considered at more length below, has a similar teleomorph, "*Nectria*" *stilbellae*. Neither teleomorph genus is appropriate, with *Cosmospora* now restricted to species with *Acremonium*-like anamorphs, discussed above, and *Nectria* is restricted to species with *Tubercularia* anamorphs (Hirooka *et al.* 2011). We have elected not to describe a new teleomorph genus for this clade, preferring to refer to these fungi by the oldest available generic name *Volutella*. As noted by Summerbell *et al*. (2011) in their discussion of *Trichothecium*, replacing a classic and well known generic name with a virtually unknown teleomorphically typified generic name would be taxonomically capricious. The other two holomorphic species with anamorphs attributed to *Volutella* are species presently classified in *Pseudonectria* (see above), which produce setose perithecia and aseptate ascospores, rather different than the smooth- or rough-walled perithecia and 1-septate ascospores of *V. citrinella* and *V. consors.*

The synnematous fungus *V. citrinella* was formerly known as *Stilbella aciculosa* (Seifert 1985a) but is more appropriately classified in *Volutella.* There have been scattered comments in the literature about synnematous species of *Volutella,* including the comment by Domsch *et al*. (2007) that some strains or species are "short stipitate". Thus, the inclusion of synnematous species only subtly alters the existing generic concept. Although there was scant mention of *Volutella* in the monograph of the synnematous genus *Stilbella* by Seifert (1985a), it was included in the key to *Stilbella*-like genera because of these observations by other authors.

Few of the approximately 120 described species of *Volutella* have been revised, and most species were seldom reported after their original descriptions. A preliminary survey of type specimens accessioned in K by Seifert (unpublished) suggests that many of the described species represent *Colletotrichum*, *Sarcopodium,* and other anamorphic genera. Comparatively few species that conform to the modern concept were uncovered. However, given the morphological variation we have seen in unidentifed specimens and cultures, we suggest *Volutella s. str.* will ultimately include many more species.

Accepted species

Volutella ciliata (Alb. & Schwein.) Fr., Syst. Mycol. 3: 467. 1832.
Basionym: *Tubercularia ciliata* Alb. & Schwein., Consp. fung. p. 68. 1805.

Typification: We were unable to locate authentic material of *T. ciliata*; the sole specimen in the Schweinitz herbarium (PH) dates to a later publication (Schweinitz 1822). Because this name is formally conserved, careful attention must be paid to appropriate typification, and we chose not to propose a neotype or epitype here.

Volutella consors (Ellis & Everh.) Seifert, Gräfenhan & Schroers**, comb. nov.** MycoBank MB519455.
Basionym: *Dialonectria consors* Ellis & Everh., J. Mycol. 4(12): 122. 1888.
≡ *Nectria consors* (Ellis & Everh.) Seaver, Mycologia 1: 61. 1909.
≡ *Nectriella consors* (Ellis & Everh.) Sacc., Syll. fung. 9: 941. 1891.
≡ *Cosmospora consors* (Ellis & Everh.) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 119. 1999.
? = *Volutella comata* Ellis, Bull. Torrey Bot. Club 9: 20. 1892.

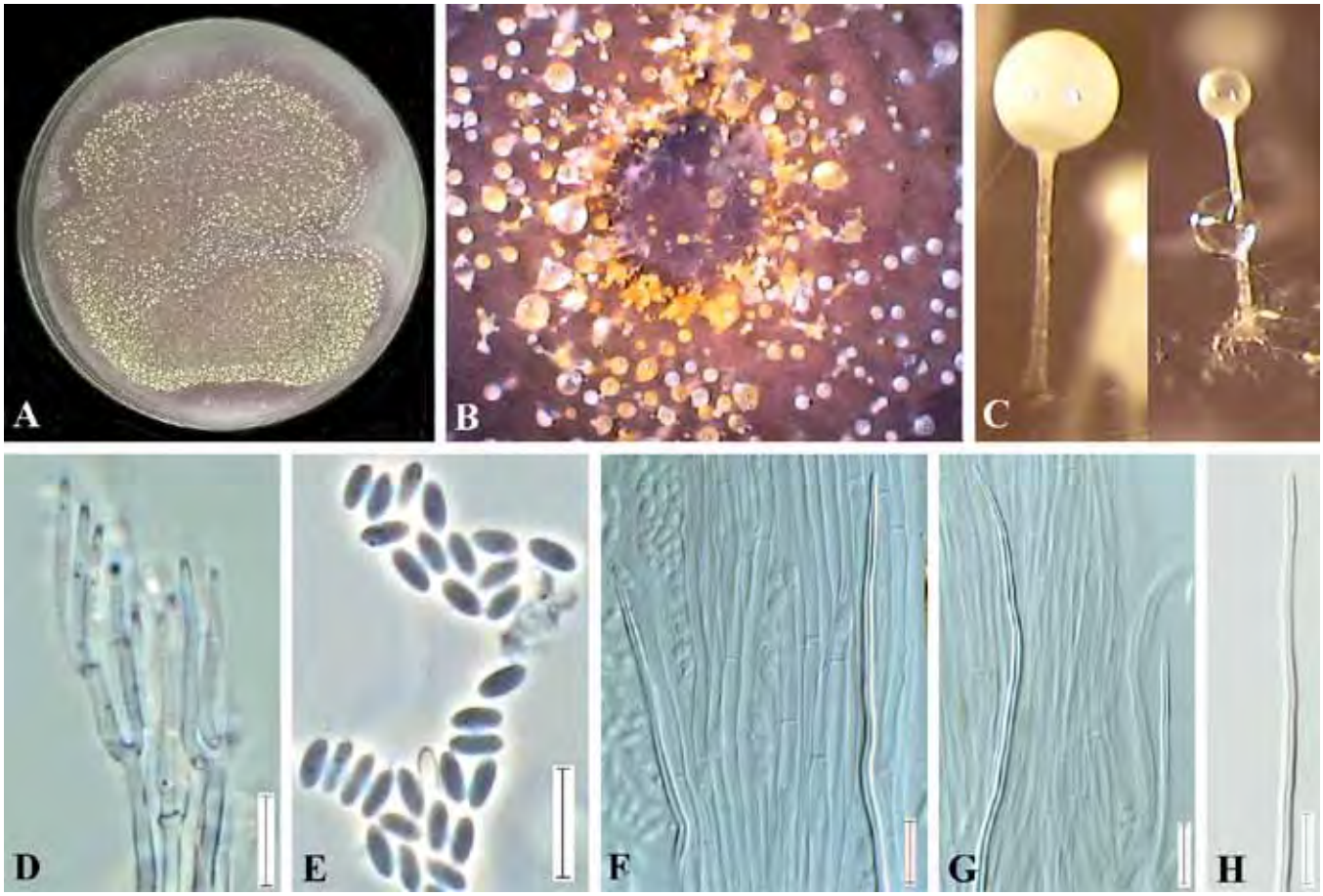


Fig. 8. *Volutella citrinella*, colony and microscopic characters. A, B. Colony on oatmeal agar showing typical purple pigment and yellowish slime of the synnemata. C, D. Determinate synnemata developed in culture. E. Conidiophores. F. Conidia. G, H, I. Seta-like marginal hypha in culture (DAOM 226716, 165570). Scale bars = 10 µm.

? = *Volutella minima* Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1, 118: 1543. 1909.

Typification: **USA**: Louisiana, St. Martinsville, Sep. 1888, Langlois 1485. **Holotype** NY (examined by Samuels 1977).

Material examined: *Volutella comata.* **USA**, New Jersey, Newfield, on fallen petioles on *Robinia*, June 1881, Ellis North American Fungi no. 811. **Isotypes** DAOM, K.

Notes: *Volutella consors* predates the commonly used name for this morphological species, *V. minima* and the newly synonymised *V. comata*. As noted in the Introduction, the transfer of a teleomorph typified name into an anamorph genus creates a technically incorrect name that is nevertheless valid and legitimate.

Several morphological variants of this species exist including specimens with reddish brown sporodochial tissues and white conidial masses as in the isotypes of *V. comata* or white stipes and bright yellow conidial masses as in several specimens from India in CBS-H and IMI 205174, as *Stilbella* sp. In addition, some living strains have *Verticillium*-like synanamorphs as noted but not illustrated by Matsushima (1975) and visible in the strain CBS 552.89. This is probably a species complex, and the synonymies with *V. minima* and *V. comata* should be reevaluated in future studies.

Volutella citrinella (Cooke & Massee) Seifert, **comb. nov.** MycoBank MB519456. Fig. 8.

Basionym: *Stilbum citrinellum* Cooke & Massee, Grevillea 16: 81. 1887.

= *Stilbum aciculosum* Ellis & Everhart, J. Mycol. 1: 153. 1885.

≡ *Stilbella aciculosa* (Ellis & Everhart) Seifert, Stud. Mycol. 27: 44. 1985 non *Volutella aciculosa* (Ellis & Harkn.) Sacc., *Syll. fung.* 4: 687. 1886.

= *Nectria stilbellae* Samuels & Seifert, Sydowia 43: 250. 1991.

≡ *Cosmospora stilbellae* (Samuels & Seifert) Rossman & Samuels in Rossman, Samuels, Rogerson & Lowen, Stud. Mycol. 42: 125. 1999.

For other synonyms, see Seifert (1985a) under *Stilbella aciculosa.*

Notes: The holomorph was described and illustrated by Samuels & Seifert (1991). Seifert (1985a) noted that the hyphae of the synnema stipes of this species sometimes become slightly thick-walled, and, if they diverge from the synnema, may appear somewhat seta-like. With the sister relationship of *V. citrinella* to *V. ciliata* revealed by the phylogenetic analysis, the taxonomic significance of this morphological observation becomes clear. Examination of three cultures of this fungus and reexamination of a slide of the holotype of *Stilbum aciculosum* revealed thickened hyphae with nearly occluded lumina in all of them. These hyphae (Fig. 7F–H) are 1.5–3 µm wide with cell walls thickened up to 1 µm at the base, thinning towards the acute apex. They are common on specimens from nature. In culture, they are less frequent sometimes giving the synnemata a slightly hirsute appearance, but they generally do not penetrate into the capitulum.

In addition to the distributional records provided by Seifert (1985a), specimens have since been examined originating in Grenada, New Zealand, and South Africa.

ACKNOWLEDGEMENTS

This study would have been impossible without the tremendous contributions of Gary J. Samuels. His habit of sharing collections selflessly and his holistic approach to describing fungi make him a role model for both beginning and experienced mycologists. He could have been easily a co-author of this study, but then we could not have written this acknowledgement for him!

We thank Kerry O'Donnell for providing unpublished DNA sequences (*rpb2*) for many *Fusicolla* and *Microcera* strains deposited with NRRL. We enjoyed numerous fruitful discussions with Scott Redhead on interpretations of Article 59 of the ICBN but assume full responsibility for the nomenclatural decisions made here. We thank the curators of the herbaria B, DAOM, G, FH, K, L, PAD, PH, PRM, S, and UPS for the loan of type and other material or for searching for relevant material. We are especially indebted to Harrie Sipman at the Botanical Museum in Berlin for providing information on fungal specimens deposited by H. Richter and H.W. Wollenweber.

We appreciate the continued support of and consultation with our mentor Prof. W. Gams, who prepared the Latin diagnosis for *M. samuelsii,* while proclaiming his horror at the nomenclatural mutations proposed here by his devoted former students.

We are grateful for DNA sequencing by Gerry Louis-Seize, and for the support from the Canadian Collection of Fungal Cultures. Last but not least, we thank W. Jaklitsch and H. Voglmayr for permission to study their specimens of *Stylonectria* and the examination of type material of *S. wegeliniana*.

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.05

Studies in Mycology 68: 115–138. 2011.

A revision of *Cyanonectria* and *Geejayessia* gen. nov., and related species with *Fusarium*-like anamorphs

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Abstract: A revision of *Fusarium*-like species associated with the plant genus *Buxus* led to a reconsideration of generic concepts in the *Fusarium* clade of the *Nectriaceae*. Phylogenetic analyses of the partial second largest subunit of the RNA polymerase II (*rpb2*) and the larger subunit of the ATP citrate lyase (*acl1*) gene exons confirm the existence of a clade, here called the terminal *Fusarium* clade, that includes genera such as *Fusarium sensu stricto* (including its *Gibberella* teleomorphs), *Albonectria*, *Cyanonectria,* "*Haematonectria*", the newly described genus *Geejayessia,* and "*Nectria*" *albida*. *Geejayessia* accommodates five species. Four were previously classified in *Nectria sensu lato*, namely the black perithecial, KOH– species *G. atrofusca* and the orange or reddish, KOH+ *G. cicatricum*, *G. desmazieri* and *G. zealandica. Geejayessia celtidicola* is newly described. Following our phylogenetic analyses showing its close relationship with *Cyanonectria cyanostoma*, the former *Gibbera buxi* is recombined as the second species of *Cyanonectria*. A three gene phylogenetic analysis of multiple strains of each morphological species using translation elongation factor 1 α (*tef-1*), *rpb2* and *acl1* gene exons and introns confirms their status as distinct phylogenetic species. Internal transcribed spacer of the ribosomal RNA gene cluster and nuclear large ribosomal subunit sequences were generated as additional DNA barcodes for selected strains. The connection of *Fusarium buxicola*, often erroneously reported as the anamorph of *G. desmazieri*, with the bluish black and KOH+ perithecial species *C. buxi* is reinstated. Most *Cyanonectria* and *Geejayessia* species exhibit restricted host ranges on branches or twigs of *Buxus* species, *Celtis occidentalis,* or *Staphylea trifolia*. Their perithecia form caespitose clusters on well-developed, mostly erumpent stromata on the bark or outer cortex of the host and are relatively thin-walled, mostly smooth, and therefore reminiscent of the more or less astromatous, singly occurring perithecia of *Cosmospora, Dialonectria,* and *Microcera*. The cell walls in outer- and inner layers of the perithecial walls of *Cyanonectria* and *Geejayessia* have inconspicuous pore-like structures, as do representative species of *Albonectria, Fusarium sensu stricto*, "*Haematonectria*", and "*Nectria*" *albida*. The taxonomic significance of these structures, which we call Samuels' pores, is discussed.

Key words: Holomorph concept, nomenclature, peridial pores, taxonomy.
Taxonomic novelties: *Geejayessia* Schroers, Gräfenhan & Seifert, gen. nov., *Geejayessia celtidicola* Gräfenhan & Schroers, sp. nov., *Cyanonectria buxi* (Fuckel) Schroers, Gräfenhan & Seifert, comb. nov., *Geejayessia atrofusca* (Schw.) Schroers & Gräfenhan, comb. nov., *Geejayessia cicatricum* (Berk.) Schroers, comb. nov., *Geejayessia desmazieri* (Becc. & De Not.) Schroers, Gräfenhan & Seifert, comb. nov., *Geejayessia zealandica* (Cooke) Schroers, comb. nov.

INTRODUCTION

Species of *Fusarium* are of major agricultural, economic, and health importance because of their mycotoxin production and roles as crop and opportunistic human pathogens (Marasas *et al.* 1984, Summerbell 2003) or saprobes isolated from soil or decaying plant substrates (Domsch *et al.* 2007). Some *Fusarium*-like species inhabit lichens, other fungi, and insects, but many of these species are phylogenetically distantly related to *F. sambucinum*, the type species of *Fusarium*. Some of these were classified in *Cosmospora* by Rossman *et al.* (1999), and now placed in re-circumscribed genera such as *Dialonectria*, *Fusicolla*, *Macroconia*, *Microcera,* and *Stylonectria* in this volume, Gräfenhan *et al.* (2011).

Fusarium species typically sporulate readily and grow moderately fast in culture. Perithecia are formed *in vitro* by a few species, often only after crossing of compatible mating types using special media and incubation conditions (Leslie 1991). Accordingly, the main *Fusarium* monographers of the 20th and 21st centuries were predominantly teleomorphically challenged and anamorph names are widely used (Wollenweber & Reinking 1935, Gerlach & Nirenberg 1982, Nelson *et al.* 1983, Gams *et al.* 1997, Leslie & Summerell 2006, Domsch *et al.* 2007). However, a parallel holomorphic system was initiated by other taxonomists, sometimes with less exposure to plant pathology and the *Fusarium* literature, and numerous *Fusarium* holomorphs were integrated taxonomically into the *Nectriaceae, Hypocreales,* under a variety of teleomorphic names, most notably *Gibberella* (Booth 1959, Samuels 1976, Samuels *et al.* 1990, 1991, Samuels & Brayford 1994, Rossman *et al.* 1999). The taxonomic segregation of species included in the broad concept of *Nectria sensu* Booth (1959) into distinct genera (Rossman *et al.* 1999), crystallised with the recognition or resurrection of holomorphic genera such as *Albonectria*, *Cosmospora*, *Cyanonectria, Gibberella*, *Haematonectria,* and *Neocosmospora* (Rossman *et al.* 1999, Samuels *et al.* 2009), all with the exception of the latter at least with some *Fusarium*-like anamorphs. This holomorphic system implied that the generic concept of *Fusarium* might not be monophyletic or that additional genera might be necessary to delimit monophyletic, morphologically homogenous, or natural species groups. Samuels *et al.* (2009) and the accompanying paper by Gräfenhan *et al.* (2011) provide evidence for a monophyletic *Fusarium* clade, once the species related to the revised concepts of *Cosmospora, Dialonectria, Fusicolla, Macroconia*, *Microcera,* and *Stylonectria* are removed; for convenience, we refer to this as the terminal *Fusarium* clade based on its position in the *Nectriaceae* in the phylogenetic analysis of Gräfenhan *et al.* (2011). In that study, this terminal *Fusarium* clade received low support in phylogenetic analyses and included several

strongly supported phylogenetic lineages within it. Typically, the statistically supported phylogenetic clades corresponded in a nearly 1:1 fashion with taxonomic groupings earlier established on the basis of teleomorph (Samuels 1976, Samuels *et al.* 2001) and/or anamorph characters (Gerlach & Nirenberg 1982).

The taxonomic placements of some species formerly included in *Nectria sensu* Booth, including the black perithecial *N. atrofusca*, the orange *N. desmazieri,* and the red *N. zealandica* (the latter also included in *Cosmospora sensu* Rossman *et al.* 1999) are particularly puzzling. "*Nectria*" *atrofusca*, which has a macroconidial, *Fusarium*-like anamorph, cannot convincingly be placed phylogenetically among other species with darkly pigmented perithecia, in particular the large and well-known genus *Gibberella* (Samuels & Rogerson 1984, O'Donnell 1993, Samuels *et al.* 2009). Therefore, it remained classified in Booth's broadly delimited concept of "*Nectria*", although its perithecia and macroconidial *Fusarium* anamorph are morphologically dissimilar to species of *Nectria sensu stricto* (Hirooka *et al.* 2011). The second species, "*N.*" *desmazieri,* was placed in the *N. episphaeria* species group by Booth (1959), but was not accepted as a species of *Nectria* subgenus *Dialonectria* by Samuels *et al.* (1991), nor was it transferred to *Cosmospora* by Rossman *et al.* (1999). Nirenberg & Samuels (2000) compared the third species, the plant-associated "*N.*" *zealandica,* with the scale insect pathogens now classified by Gräfenhan *et al.* (2011) as *Microcera diploa* and *M. flammea.* This might have suggested reclassification in *Cosmospora sensu* Rossman *et al.* (1999), but it has perithecia in caespitose clusters on well-developed stromata, atypical for *Cosmospora*.

The anamorphs of these three species are *Fusarium*-like and some anamorphic names have been proposed for them. Deviating descriptions and concepts exist for *Fusarium buxicola*, considered the anamorph of "*N.*" *desmazieri* by Wollenweber & Reinking (1935), Booth (1959, 1971), and Gerlach & Nirenberg (1982). Saccardo (1883) had proposed *F. buxicola* as the anamorph of an additional bluish-black perithecial species, '*Gibbera*' *buxi*, and the subsequent association with the orange or brownish orange perithecial species "*N.*". *desmazieri* is mysterious. Wollenweber & Reinking (1935) classified *F. buxicola* and "*N.*" *desmazieri* in *Nectria* section *Macroconia*, which Wollenweber (1926) erected for "*Nectria" stilbosporae*, "*N." leptosphaeriae* and "*N." aurantiicola,* currently classified as "*Fusarium*" *expansum*, *Macroconia leptosphaeriae* and *Microcera larvarum* by Gräfenhan *et al.* (2011).

Our study began with newly obtained collections of nectrioid fungi on species of *Buxus* and *Celtis* in Europe and North America. This led us to revise the taxonomy of the "*N.*" *desmazieri* species group, a monophyletic clade within the terminal *Fusarium* clade according to phylogenetic analyses (Samuels *et al.* 2009, Gräfenhan *et al.* 2011). We describe this clade as a new genus *Geejayessia,* with the former *N. cicatricum* as its type species, and including the former "*N.*" *atrofusca*, "*N.*" *desmazieri*, "*N.*" *zealandica,* and a new species collected on *Celtis occidentalis, G. celtidicola*; henceforth in this paper the *Geejayessia* names are used. The morphological and anatomical characters of the teleomorphs are compared with those of other teleomorphs in the terminal *Fusarium* clade. Specifically, perithecial wall layers and surface roughening are analysed, characters that were used, for example, when Booth (1959) placed *G. desmazieri* in the *N. episphaeria* species group.

Following the arguments of Gräfenhan *et al.* (2011) and similar opinions of others (Seifert & Samuels 2000, Cannon & Kirk 2000, Rossman & Samuels 2005), we have adopted a single name nomenclatural system in this paper. None of the species recognised here are solely anamorphic, and the oldest available species epithets are all teleomorphic. Therefore, all of the binomials adopted for species in this paper are valid, legitimate, and nomenclaturally correct according to the present International Code of Botanical Nomenclature (McNeill *et al.* 2006). We consider the available *Fusarium* binominals as synonyms of the names in *Cyanonectria* and the newly described genus *Geejayessia* and its anamorphs as *Fusarium*-like, and not part of our taxonomic concept of *Fusarium sensu stricto.*

MATERIALS AND METHODS

Specimens and strains

Dried reference specimens were obtained from the herbaria BPI, DAOM, G, K, M, and W. Herbarium abbreviations are from Holmgren *et al.* (1990). Cultures were obtained from the culure collections at the CBS Fungal Biodiversity Centre (CBS, Utrecht, the Netherlands), Eastern Cereal and Oilseed Research Centre (DAOM, Ottawa, Canada), and the Julius Kühn-Institute, Institute for Epidemiology and Pathogen Diagnostics (BBA, Berlin & Braunschweig, Germany).

Dead or decaying twigs attached to healthy *Celtis occidentalis* trees, *Buxus sempervirens* bushes, or detached twigs found below these trees, were examined for nectriaceous teleomorphs. Perithecia and supporting substrate were removed from specimens, rehydrated in water, embedded in Tissue Tek 4583 O.C.T.™, sectioned at –20 ºC and 6–16 µm thickness using a Leica Cryotome CM 1850, and mounted in Shear's fluid (Gams *et al.* 1998). Microscopic structures such as conidia, phialides, asci, ascospores, details of stromata and walls of perithecia, etc. were studied with a Zeiss Imager microscope using differential interference contrast and luminance coded with 0.45 or, rarely, 1.0 gamma correction in the Zeiss AxioVision software v. 4.6, or an Olympus BX50 compound microscope. Anamorphic structures were studied in water, and teleomorphic structures in water, Shear's, 2 % KOH or 85–90 % lactic acid. Other methods for the study of micro- or macroscopical characters of strains including morphometrical analyses are described elsewhere (Schroers *et al.* 2009).

For ascospore isolates, single perithecia were squashed in a drop of sterile water. The resulting ascospore suspension was collected either with a 1 mL propipettor or a glass pasteur pipette with its tip sterilised and extended using an alcohol flame; the suspension was spread by moving the pipette over the surface of synthetic nutrient-poor agar (SNA; Nirenberg 1976) with penicillin and streptomycin (Gams *et al.* 1998). The next day isolated germinating ascospores were located under a compound microscope at low magnification or a dissecting microscope at high magnification and transferred to fresh media. For mycelial or conidial specimens, cultures were isolated by plating a piece of *Buxus* root surface sterilised with 70 % ethanol onto potato dextrose agar (PDA, Biolife, Italy) with penicillin and streptomycin or by streaking out macroconidia obtained from sporodochia on decaying *Buxus* branches.

For taxonomic studies, cultures were studied on agar media in 9 cm vented, plastic Petri dishes. Strains were grown on SNA with small pieces of sterile carnation leaves (CL) or *Buxus* leaves or twigs on the surface (SNA/CL or SNA/B). Growth rates were determined after 7 d on PDA (Difco, USA) incubated at 15, 20, 25, 30, and 35 ºC. Colony colours were scored on the same medium after 14 d or later using Kornerup & Wanscher (1978). For the

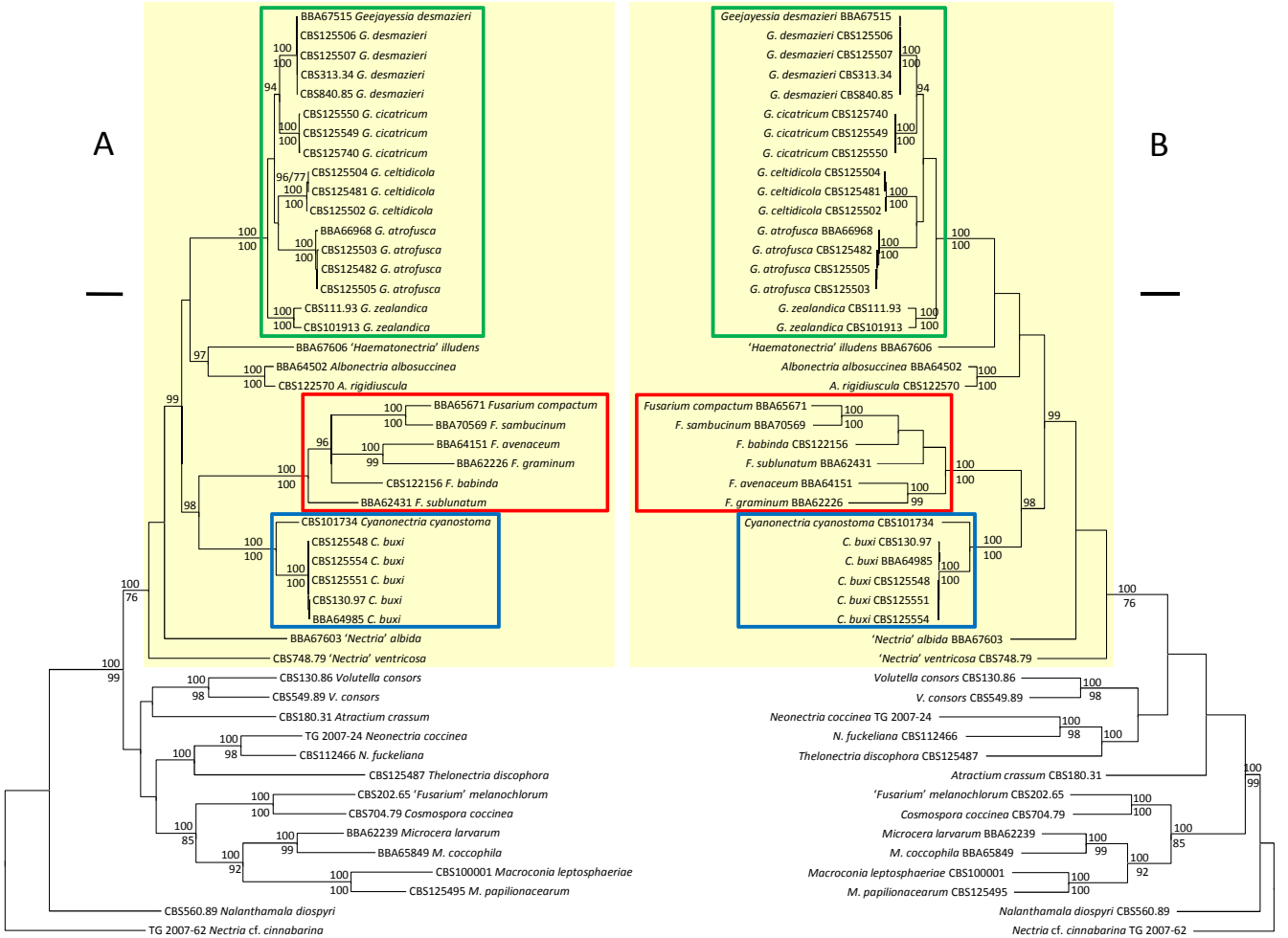

Fig. 1. Phylogrammes showing generic relationships in the terminal *Fusarium* clade inferred from partial sequences of the second largest subunit of the RNA polymerase II and the larger subunit of ATP citrate lyase gene exons using *Nectria* cf. *cinnabarina* as outgroup. A. Majority rule consensus tree of a Bayesian Markov chain Monte Carlo sampling. B. One of 145 equally parsimonious trees. Numbers above branches are Bayesian posterior probabilities multiplied by 100 (p.p. > 90 are shown); those below lines are parsimony bootstrap proportions (> 70 % are shown). *Fusarium sensu stricto* is demarcated by a red frame, *Geejayessia* by green, *Cyanonectria* by blue, and the terminal *Fusarium* clade by yellow. Scale bars: A 0.05 substitutions per site, B 50 steps.

preparation of voucher material, cultures were first dried in a Christ LMC-2 lyophiliser and then killed with formalin as described by Gams *et al.* (1998).

The species included in the genus-level phylogenetic evaluation of the terminal *Fusarium* clade (Fig. 1) were *Nectria* cf. *cinnabarina*, **USA**, Pennsylvania, Salt Springs State Park, on *Fagus grandifolia*, T. Gräfenhan, May 2007, TG 2007-62, DAOM [HQ728160 (*rpb2*), HQ728179 (*acl1*)] (outgroup); *Nalanthamala diospyri*, **USA**, Tennessee, Readyville, wood of *Diospyros virginiana*, M.J. Wingfield, CBS 560.89 [HQ728156 (*rpb2*), HQ728175 (*acl1*)]; *Fusarium avenaceum*, **Germany**, north Germany, *Solanum tuberosum*, tuber, E. Langerfeld, August 1980, BBA 64151 [DNA barcodes: HQ728167 (*rpb2*), HQ728186 (*acl1*)]; *Fusarium babinda*, **Spain**, Morga, *Pinus radiata*/*Hylurgops palliates*, P. Romòn, CBS 122156 [HQ728168 (*rpb2*), HQ728187 (*acl1*)]; *Fusarium compactum*, **Sudan**, seed of *Gossypium barbadense*, G. Ibrahim, June 1989, BBA 65671 [HQ728165 (*rpb2*), HQ728184 (*acl1*)]; *Fusarium graminum*, **Iran**, Prov. Mazandaran, near Babol, *Claviceps*, on ear of *Paspalum dilatatum*, W. Gerlach & D. Ershad, October 1968, BBA 62226 [HQ728166 (*rpb2*), HQ728185 (*acl1*)]; *Microcera larvarum*, **Iran**, Prov. Guilan, near Rasht, *Quadraspidiotus perniciosus*, on living on branch of *Prunus*, W. Gerlach & D. Ershad, October 1968, BBA 62239 [HQ728163 (*rpb2*), HQ728182 (*acl1*)]; *Microcera coccophila*, **New Zealand**, Croesus Track, tree bark, H.I. Nirenberg, June 1991, BBA 65849 [HQ728158 (*rpb2*), HQ728177 (*acl1*)]; *Macroconia leptosphaeriae*, **Netherlands**, Tilburg, on *Leptosphaeria* sp./dead stem of *Urtica dioica*, L. Rommelaars, as ‚*Fusarium sphaeriae*', CBS 100001 [HQ728164 (*rpb2*), HQ728183 (*acl1*)]; "*Fusarium*" *melanochlorum*, **Austria**, on branch canker of *Fagus sylvatica*, W. Gerlach, CBS 202.65 (= ATCC 16069, BBA 9831, DSM 62248) [HQ728162 (*rpb2*), HQ728181 (*acl1*)]; *Cosmospora coccinea*, **Germany**, Neubrandenburg, Kleppelshager Forst near Friedland, on *Inonotus radiatus*, P. Hübsch, 22 Oct 1978, CBS 704.79 [HQ728161 (*rpb2*), HQ728180 (*acl1*)]; *Neonectria coccinea*, **Germany**, Brandenburg, Stolpe, *Fagus sylvatica*, T. Gräfenhan, March 2007, TG 2007-24, DAOM [HQ728159 (*rpb2*), HQ728178 (*acl1*)]; *Neonectria fuckeliana*, **Switzerland**, KT. Graubunden, vic. Zuoz, along Ova d'Arpiglia, on branches of *Picea* sp., 6 Sep 1990, CBS 112466 (= IMI 342667) [HQ728157 (*rpb2*), HQ728176 (*acl1*)]; *Volutella consors*, **India**, Karnataka, Agumbe, on *Agave americana*, V. Rao, Oct 1985, CBS 130.86 [HQ728155 (*rpb2*), HQ728174 (*acl1*)]; *Volutella consors*, Brazil; Pará, 200 km SE from Belém, Capitão Poço, soil, L. Pfenning, CBS 549.89 [HQ728154 (*rpb2*), HQ728173 (*acl1*)]. Gräfenhan *et al.* (2011) list strain data and GenBank accession numbers for "*Haematonectria*" *illudens* (BBA 67606), *Albonectria albosuccinea* (BBA 64502), *A. rigidiuscula* (CBS 122570), *Fusarium sambucinum* (BBA 70569), *F. sublunatum* (BBA 62431), "*Nectria*"

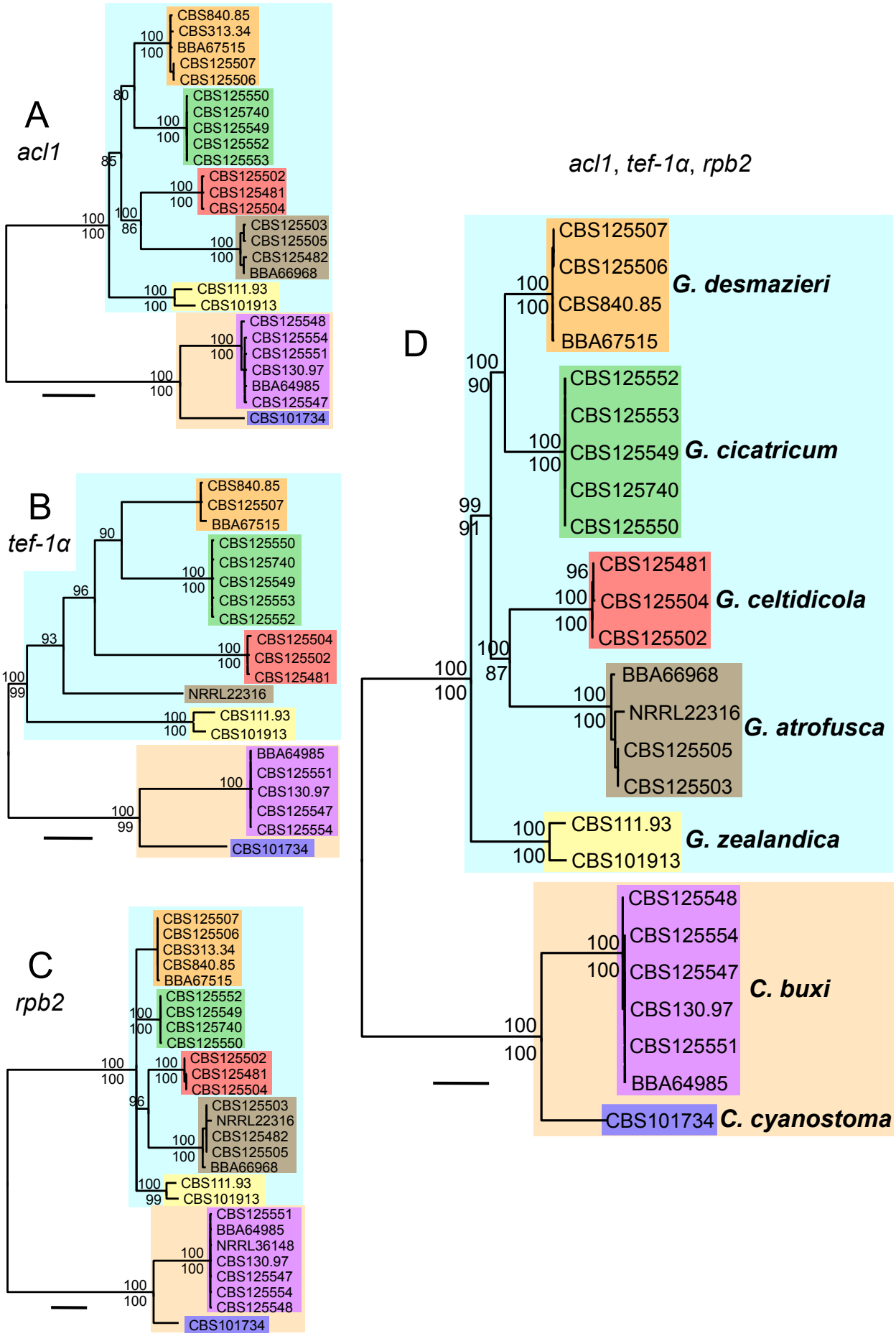

Fig. 2. Phylogrammes showing individual gene phylogenies and combined phylogeny of species of *Geejayessia* and *Cyanonectria*. Majority rule consensus trees of Bayesian Markov chain Monte Carlo sampling inferred from introns and exons of the ATP citrate lyase (*acl1*, A), translation elongation factor 1 alpha (*tef-1*α, B), and the second largest subunit of the RNA polymerase II (*rpb2*, C). D. Phylogramme based on the combined data sets of the three genes. Numbers above branches are Bayesian posterior probabilities multiplied by 100 (p.p. > 90 are shown). Numbers below the branches are parsimony bootstrap proportions (> 70 % are shown). Scale bars: 0.04 substitutions per site.

albida (BBA 67603), "*Fusarium*" *ventricosum* (CBS 748.79), *Thelonectria discophora* (CBS 125487), and *Atractium crassum* (CBS 180.31)].

The sequences HM068357 (*rpb2*, NRRL 36148, O'Donnell *et al.*, unpubl. data, as "*Nectria desmazieri*"), EU329502 (*rpb2*, NRRL 22316, O'Donnell *et al.* 2008), and AF178361 (*tef-1α*, NRRL 22316, O'Donnell *et al.*, unpubl. data) were included in the three gene analysis for testing phylogenetic species boundaries (Fig. 2B, C).

DNA sequencing

Following the methods of Gräfenhan *et al.* (2011), partial sequences of the second largest subunit of the RNA polymerase II (*rpb2*) flanked by the primers 5F2/7cR (O'Donnell *et al.* 2007) and the larger subunit of ATP citrate lyase (*acl1*) were generated for strains not included in that study. In addition, sequences of the internal transcribed spacer regions 1 and 2 and the 5.8S nuclear ribosomal DNA (ITS rDNA), partial nuclear ribosomal large subunit DNA (LSU rDNA), and the partial nuclear translation elongation factor 1-alpha (*tef-1α*), were sequenced following published protocols (Schroers *et al.* 2005, 2009). For *tef-1α*, we used an initial denaturation step at 94 °C for 3 min, 35 cycles of 94 °C for 60 s, 54 °C for 60 s, 72 °C for 90 s and a final extension at 72 °C for 6 min. Sequencing reactions were performed at the Macrogen sequencing facility (Seoul, Korea). Newly generated sequences were deposited at GenBank under accession numbers HM626622–HM626690 and HQ728144–HQ728187.

Phylogenetic analyses

Two data sets were assembled. The first data set combined sequences of *rpb2* (948 bp alignment) and the exon regions of the *acl1* (477 bp alignment) to address the generic relationships of the terminal *Fusarium* clade (Fig. 1A, B). The second analysis included *rpb2, acl1,* and *tef-1α* gene exons and introns of multiple strains of each species to evalute species boundaries by geneological concordance.

Bayesian phylogeny (BP) inferences with MrBayes v. 3.1.2 (Ronquist & Huelsenbeck 2003) implemented substitution models selected according to the akaike information criterion calculated with the software jmodeltest based on 24 models (Guindon & Gascuel 2003, Posada 2008). The software MrBayes v. 3.1.2 was run for 10 M generations with four Markov chains sampled every 100 generations starting from a randomly selected tree. A 50 % majority rule consensus tree and posterior probabilities for each split was calculated after excluding the first 25000 sampled trees. In analyses of combined data (Figs 1A, 2D), stationary nucleotide frequencies, relative rates of substitution, alpha shape parameter of the gamma distribution, and the proportion of invariable sites was estimated in MrBayes independently for each of the partitions, and the site specific rates were set variable. Trees illustrating the relationships of the species (Fig. 2A–D) were rooted at the longest split using the tools provided in the software MEGA (Tamura *et al.* 2007) after they were inspected unrooted using the software TreeView (Page 1996).

Heuristic searches for shortest trees in parsimony analyses (PA) generated with PAUP v. 4.0b10 (Swofford 2003) were based on parsimony informative, unordered, and equally weighted characters; gaps were treated as missing data. Starting trees were obtained with 1 000 (Fig. 1B analyses) or 1 0000 (Fig. 2 analyses) stepwise, random addition sequences. Other settings included the treebisection-reconnection branch-swapping algorithm and the MULTREES option. Branch robustness was assessed by 1000 heuristic bootstrap replicates using the same settings, but with 10 stepwise, random addition sequences. A MAXTREE setting of 1 000 was effective for bootstrap analyses of the combined data sets summarised in Fig. 1B and Fig. 2D and the analyses of the *rpb2* gene (Fig. 2C). Either fewer than 1000 trees were collected or an automatically increased MAXTREE setting was adopted for the other parsimony analyses.

For the second set of analyses, the phylogenetic relationships of strains identified as *Cyanonectria cyanostoma*, '*Fusarium buxicola*', *F. staphyleae*, *G. atrofusca, G. desmazieri*, *G. zealandica*, and others isolated from *Buxus sempervirens* or *Celtis occidentalis* were estimated from the aligned DNA sequences of the individual genes (Fig. 2A–C). The combined data sets (Fig. 2D) comprised the *acl1* (915 bp alignment) and *tef-1α* (751 bp) gene exons and introns and the *rpb2* gene fragment (1033 bp alignment). Strain data and sequence accession numbers are listed in the Taxonomy section below. Sequences of the ITS and LSU rDNA were generated only for representatives of the ingroup taxa and are cited in the taxonomic part below as DNA barcodes. Phylogenetic analyses based on these sequences (not shown) were consistent with the inferences summarised in Fig. 2. They also included AF178423 and AF178392 (ITS and LSU, NRRL 22316; O'Donnell *et al.*, unpublished), U88116 (LSU, NRRL 20428; O'Donnell 1993) and U88125 (LSU, NRRL 20474; O'Donnell 1993).

RESULTS

A General Time Reversible plus Gamma model and gamma distribution of rate variation with a proportion of invariable sites (GTR+G+I) was selected for each of the individual data sets of the 48 taxon analyses (Fig. 1A). The proportion of invariable sites was 0.4170 in the *rpb2* gene (*acl1*: 0.5510). The shape parameter of the gamma distribution was 0.9300 (*rpb2*) and 1.4020 (*acl1*) across sites. In modeltest analyses, basefrequencies were calculated as 0.2456, 0.2658, 0.2599, 0.2288 for A, C, G, T, respectively (*rpb2*) and 0.2098, 0.3162, 0.2601, 0.2139 (*acl1*); substitution rates were AC = 1.3301, AG = 3.6324, AT = 1.2458, CG = 0.6151, CT = 7.6227, GT = 1.000 (*rpb2*) and 1.1272, 2.6353, 0.4595, 1.1210, 10.9535, 1.0000 (*acl1*). The most negative likelihood (−lnL) score was –15.758.620 for the combined analysis. The overall topologies of the 48 equally most parsimonious trees did not differ significantly from each other. Based on 590 parsimony-informative characters (PIC), they were 3 330 steps in length and had a consistency index (CI) of 0.305 and a retention index (RI) of 0.620.

Based on the partial *rpb2* and *acl1* loci, phylogenetic analyses identified a statistically moderately or strongly supported clade [Bayesian posterior probability (B-PP), 1.00; maximum parsimony bootstrap proportion (P-BP), 76 %], here called the terminal *Fusarium* clade. This included various subclades, most corresponding with previously identified holomorph genera or other taxonomic groups with *Fusarium*-like anamorphs (Fig. 1A, B). The parallel analyses by Gräfenhan *et al.* (2011) obtained no significant statistical support for the terminal *Fusarium* clade, but showed that taxa with *Fusarium*-like macroconidia cannot be regarded monophyletic. In all analyses, the terminal *Fusarium* clade excludes phylogenetically distantly related *Fusarium*-like species, most of which are currently classified in *Dialonectria*, *Fusicolla, Macroconia*, *Microcera*, or *Stylonectria* (Gräfenhan *et al.*

2011) or as "*Nectria*" *diminuta* (Hirooka *et al.* 2008). Equivocally strong statistical support B-PP, 1.00 and P-BP, 100 % (Fig. 1A, B) or maximum likelihood bootstrap proportions ≥ 75 %, B-PP ≥ 0.95, and P-BP ≥ 75 % (Gräfenhan *et al.* 2011: fig. 1), was obtained for the subclades nested within the terminal *Fusarium* clade. These include (i) *Fusarium sensu stricto* including but not restricted to species with teleomorphs often classified in *Gibberella* and various species groups (Summerbell & Schroers 2002, O'Donnell *et al.* 2007, Schroers *et al.* 2009, O'Donnell *et al.* 2010), (ii) "*Haematonectria*" mostly with *Fusarium solani* like anamorphs (Rossman *et al.* 1999, O'Donnell 2000, O'Donnell *et al.* 2008), (iii) *Albonectria* (Rossman *et al.* 1999), (vi) the "*Fusarium*" *dimerum* species group (Schroers *et al.* 2009) and "*Fusarium*" *domesticum* (anamorphic *Rodentomyces* Doveri *et al.* 2010), (vii) *Cyanonectria* (Samuels *et al.* 2009, this paper), and (viii) *Geejayessia*, described below for "*N.*" *desmazieri* and its allies.

The genus-level analysis confirmed that several holomorphs in the terminal *Fusarium* clade previously classified in *Nectria* ("*N.*" *atrofusca*, "*N.*" *cicatricum*, "*N.*" *desmazieri* and "*N.*" *ventricosa*) are distantly related to *Nectria sensu stricto*. The species of the *Fusarium* section *Macroconia sensu* Wollenweber & Reinking (1935) or Gerlach & Nirenberg (1982) belong either to *Cyanonectria* (as "*Fusarium buxicola*") and *Geejayessia* or to the distantly related genera *Microcera* (*M. coccophila*) or *Macroconia* (*M. leptosphaeriae* and *M. gigas*).

The species-level phylogenetic analyses based on introns and exons of the individual (Fig. 2A–C) and combined (Fig. 2D) *acl1*, *tef1* and *rpb2* genes were based on a Hasegawa-Kishino-Yano plus Gamma (HKY+G) (*acl1*) or a General Time Reversible plus Gamma substitution model (GTR+G) (*tef1*, *rpb2*) with a proportion of invariable sides set to 0 for all. The shape parameter of the gamma distribution was 0.6150 (*acl1*), 0.4030 (*tef1*) and 0.2390 (*rpb2*) across sites. In modeltest analyses, basefrequencies were calculated as 0.2054, 0.2795, 0.2527, 0.2624 for A, C, G, T, respectively, (*acl1*), 0.2251, 0.3004, 0.2293, 0.2452 (*tef1*) and 0.2521, 0.2637, 0.2630, 0.2213 (*rpb2*); for *acl1* a kappa = 5.0494 (ti/tv = 2.5475) was calculated; substitution rates were AC = 0.9777, AG = 1.8456, AT = 1.0869, CG = 0.5516, CT = 3.6992, GT = 1.0000 (*tef1*) and 0.9601, 3.2151, 0.8718, 0.4166, 7.8738, 1.0000 (*rpb2*). The most negative likelihood (−lnL) score was –9239.02 for the combined analysis and –3138.52, –2.957.743 and –3.140.872 for the individual data sets of the *acl1*, *tef1* and *rpb2*, respectively. Parsimony analyses yielded 18240 equally most parsimonious trees 1 083 steps long with a CI of 0.814 and a RI of 0.943 and were based on 711 PIC (Fig. 2D). The following tree scores were retrieved when *acl1* (256 PIC), *tef1* (223 PIC) and *rpb2* (232 PIC) sequences were analysed individually: CI, 0.861, 0.773, 0.822; (RI) 0.965, 0.911, 0.959; number of steps, 353, 388, 338; number of equally parsimonious trees, 156, 28, 28 098. The inferences provided evidence for close relationships among *Geejayessia desmazieri, G. cicatricum, G. celtidicola,* and *G. atrofusca* with *G. zealandica* forming the root of the genus *Geejayessia*. The strain NRRL 36148 was re-identified as *Cyanonectria buxi* (Fig. 2C, based on *rpb2* sequences).

Analyses of aligned LSU- and ITS rDNA sequences obtained in our study (results not shown) confirmed the equally rDNA based conclusions of Samuels *et al.* (2009), which showed *Geejayessia* and *Cyanonectria* as distinct phylogenetic lineages within the terminal *Fusarium* clade. The phylogenetic analyses by Samuels *et al.* (2009) placed *Cyanonectria cyanostoma* in a moderately supported sister group relationship with *Fusarium sensu stricto*. According to rDNA based comparisons, we confirm the identity of NRRL 20474 (GenBank U88125) as *G. desmazieri*, and NRRL 22316 (AF178392), used in phylogenetic analyses by O'Donnell (1993) and Samuels *et al.* (2009), as *G. atrofusca*.

Ten to 15 nucleotide substitutions or indels in the ITS rDNA distinguish the new species *G. celtidicola* from *G. zealandica*, and the species pair *G. desmazieri* and *G. cicatricum* from each other. *Geejayessia desmazieri* differs from *G. cicatricum* by 2 substitutions in the ITS rDNA. The ITS rDNA of *G. atrofusa* differs from that of the other species by 29–33 substitutions or indels.

TAXONOMY

Cyanonectria Samuels & Chaverri, Mycol. Progress 8: 56. 2009.
Anamorph: *Fusarium*-like

Type species: *Cyanonectria cyanostoma* (Sacc. & Flageolet) Samuels & Chaverri, Mycol Progress 8: 56. 2009.

Basionym: *Nectria cyanostoma* Sacc. & Flageolet, Rendi Congr. Bot. Palermo 1902: 53. 1902.

Stromata reduced, minute or more or less well developed, prosenchymatous, typically consisting of hypha-like cells. *Perithecia* gregarious or caespitose, smooth, thin-walled, unevenly coloured, apex darkly pigmented, dark bluish purple or bluish black, main body less intensely dark bluish or red to reddish brown; colours in KOH becoming darker, in lactic acid changing from bluish black to red or from red or reddish brown to yellow. *Ascospores* 1-septate, ellipsoidal with gently tapering ends, more or less hyaline or pale yellow brown, smooth. *Macroconidia* (1–)5–7(–8)-septate, gently curved throughout or with a subcylindrical central middle part, pedicellate, with a hooked apical cell; formed in off-white, cream slimy masses, sometimes on sporodochia on branched conidiophores, terminating in whorls of monophialides. *Microconidia* not observed. *Chlamydospores* absent or rarely formed in cells of aging macroconidia. Cultures on PDA in *C. cyanostoma* pale coloured, cream, or somewhat yellowish but at 30 ºC with somewhat greyish blue surface or, in *C. buxi*, dark brown, reddish brown, greenish grey, with a greyish blue, pastel violet or light blue surface.

Notes: When describing the monotypic genus, Samuels *et al.* (2009) restricted *Cyanonectria* for a species with spectacularly bicoloured perithecia characterised by a bluish purple papilla and a red perithecial body. The anamorphic characters were narrowly defined in their genus concept. For example, unpigmented, white colonies on SNA and PDA were described. With *Gibbera buxi* and its *Fusarium buxicola* anamorph a unicoloured, bluish black or bluish purple perithecial species forming surprisingly dark colonies on PDA is added to the genus necessitating an emended generic concept for *Cyanonectria*.

Cyanonectria buxi (Fuckel) Schroers, Gräfenhan & Seifert, **comb. nov.** MycoBank MB519485. Figs 3, 4.
Basionym: *Gibbera buxi* Fuckel, Jahrb. Nassauischen Vereins Naturk. 27–28: 32. 1873.
≡ *Gibberella buxi* (Fuckel) G. Winter, Rabenh. Krypt.-Fl. 2: 103. 1887.
≡ *Lisea buxi* (Fuckel) Sacc., Syll. Fung. 2: 518. 1883.
= *Fusarium buxicola* Sacc., Syll. Fung. 2: 518. 1883.

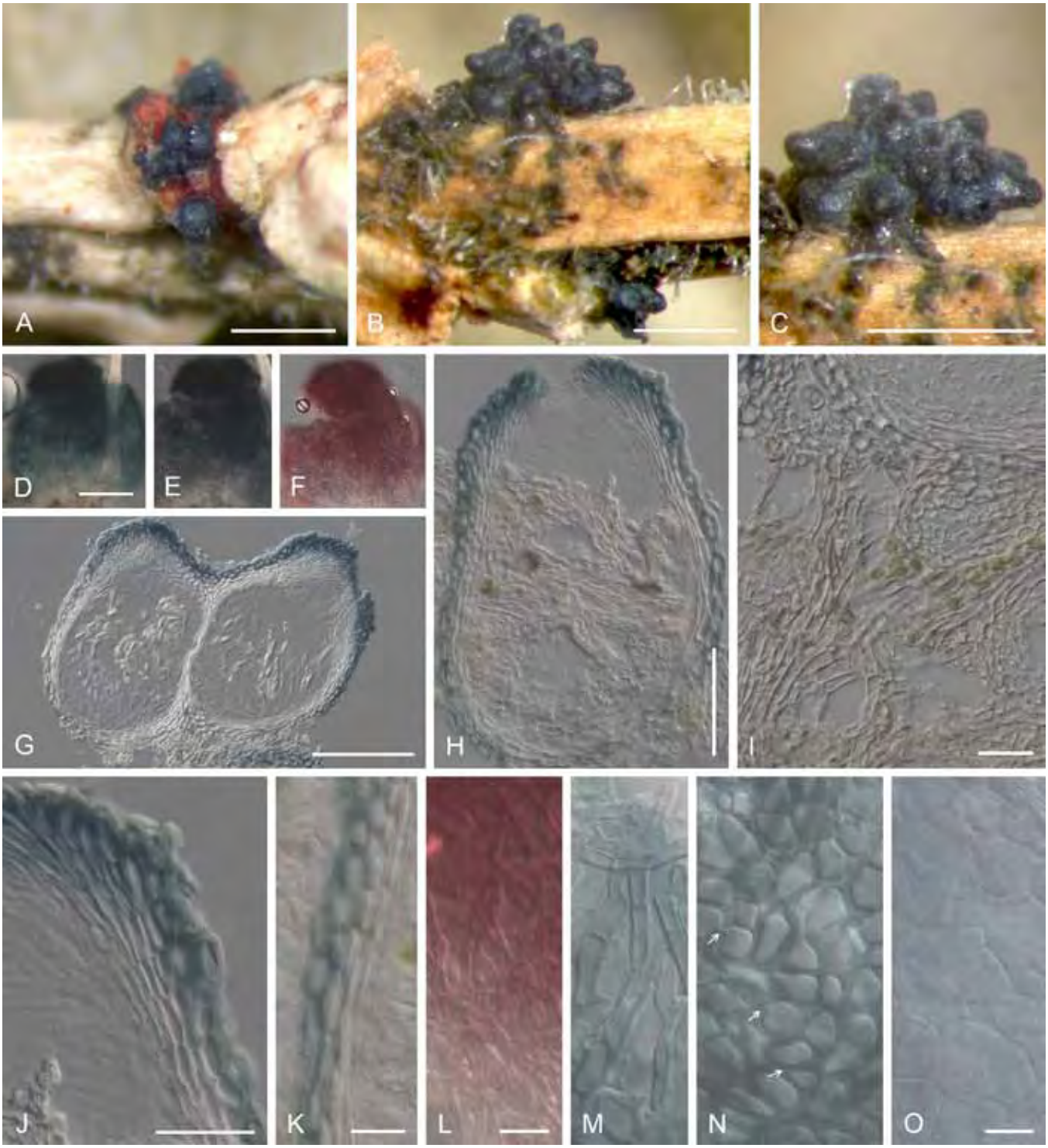

Fig. 3. *Cyanonectria buxi*, perithecia on the natural substrate. A–C. Habit on *Buxus* twigs. D–F. Colour change in perithecium in water (D), replaced with 2 % KOH (E) and then lactic acid (F), showing the reduced reaction towards the base of perithecium (E, F). G, H, J, K. Median longitudinal section through perithecia (G, H), ostiolar (J) and lateral perithecial walls (K). I. Longitudinal section through hyphal stroma supporting perithecia. L–O. Face view of perithecial wall. L. Hyphae covering perithecia reacting to lactic acid in a similar manner as the perithecium. M. Hypha-like cells on the surface of perithecia. N. Outermost cells of the main perithecial wall region with Samuels pores. O. Innermost cells of the perithecial wall. G–K in Shears; L in 2 % KOH; M–O in water. A, D–F, L–O CBS H-20380; B, C, G–K CBS H-20379. Scale bars: A–C = 500 µm; D (also applies to E, F), G = 100 µm; H = 50 µm; I–L 20 = µm; O (M, N) 10 = µm.

Stromata prosenchymatous, cells 3–5 µm wide, with at least some hypha-like cells, arranged in an irregular *textura porrecta*. *Perithecia* solitary or in groups of 20 or more seated on a stroma formed on bark of small twigs, leaf or terminal twig axils; smooth; broadly ampulliform to obpyriform, with a short neck or broadly ellipsoidal; dark bluish purple or bluish black, main body less intensely dark, not red, somewhat darker blue in 2 % KOH, purplish red in lactic acid; in longitudinal section 200–250 µm high, 130–150 µm wide. Hyphae continuous with cells of stroma continous with wall of lower part of perithecia, 4–6(–8) µm wide, with walls to 2 µm thick. *Perithecial wall* of a single region, 15–20 µm wide or subapically 20–35 µm, consisting of *ca.* 3 layers of cells; in face view, cell walls of outer and inner layers with pores, 1–1.5 µm wide in outer layers, 0.5 µm thick or less in inner layers; cells in outer layers angular, (8–)11(–14) × (6.5–)8(–9.5) µm, arranged in a *textura angularis*, in inner layers subglobose to angular, (10–)14(–22) × (5.5–)10.5(–14.5) µm, arranged in a *textura angularis*; cells in longitudinal sections subglobose to angular, flatter towards

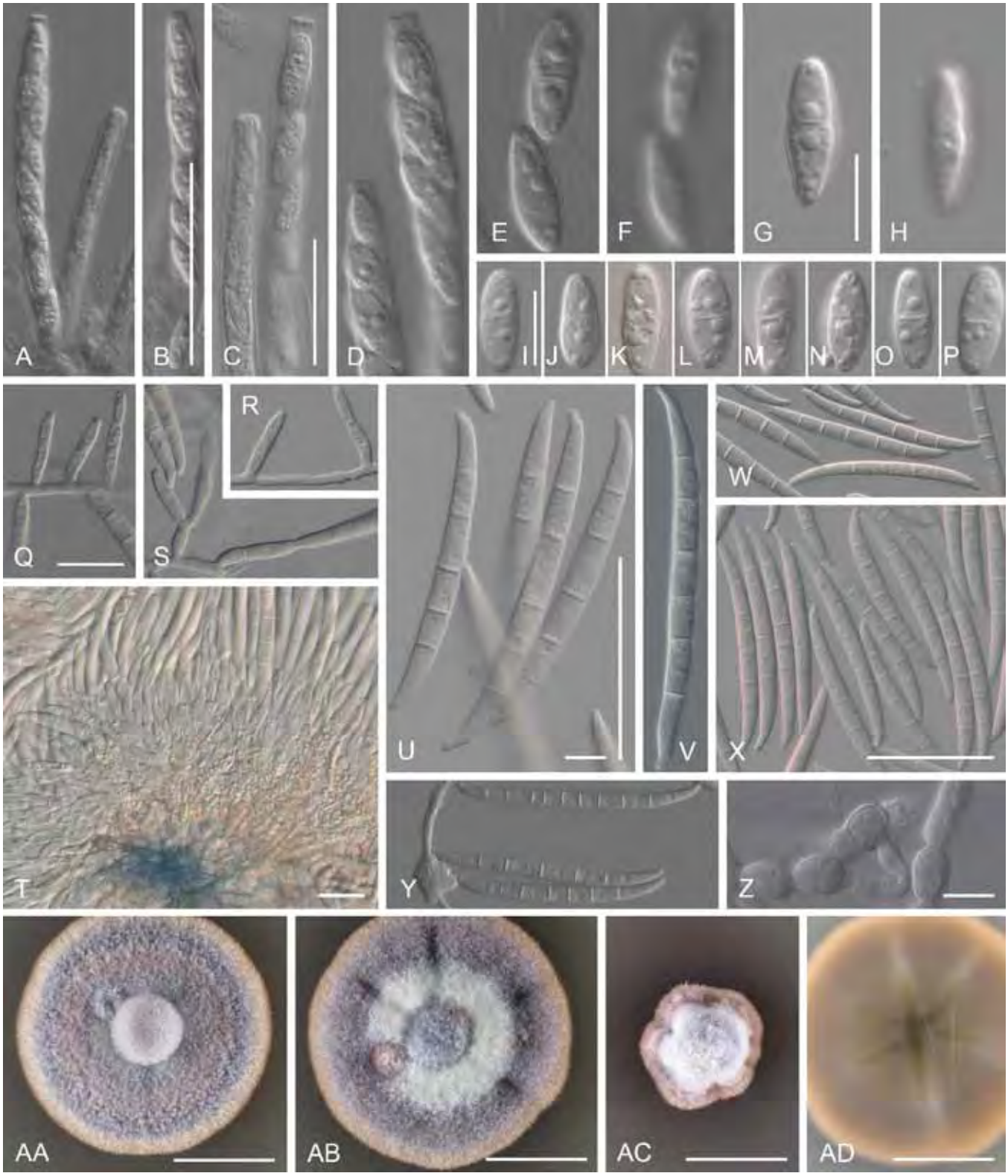

Fig. 4. *Cyanonectria buxi*, spores and spore forming cells. A–D. Asci with a somewhat flattened apex, with or without a visible refractive ring. E, G, I–P. Ascospores. F, H. Ascospore surface. Q–S. Monophialides formed by immersed mycelium. T. Sporodochium. U–Y. Macroconidia. Z. Chlamydospores derived from macroconidium. AA–AC. Surface of PDA colonies after 14 d at 20, 25 and 30 ºC. AD. Reverse of colony illustrated in AB. A–P CBS H-20379; Q–S. CBS 130.97; T, Y CBS 109638; U CBS 125554; V CBS 125551; W CBS 30.97; X, AA–AD BBA 64985; Z CBS 125547. A–P, from natural substrate. Q–Z, from SNA/B. Scale bars: B (also applies to A), X (W, Y) 50 = µm; C (D), Q (R, S), T 20 = µm; G (E, F, H), I (J–P), Z 10 = µm; U (V) = 50 and 10 µm; AA–AD = 10 mm.

centrum. *Asci* cylindrical or narrowly clavate, with rounded or flattened apex, with or without visible refractive ring, eight-spored, with mostly overlapping uniseriate or somewhat biseriate above and uniseriate ascospores below, 80–100 × 9–12 µm. *Ascospores* equally 2-celled, rarely 2-septate, ellipsoidal with somewhat tapering ends, smooth, unpigmented, (12–)13–14–14.5(–17) × (4–)5–5–5.5(–6.5) µm.

Colonies on PDA after 7 d around 12–16 mm diam (20 ºC) or 15–20 mm (25 ºC); optimum 20–25 ºC, maximum between 30 and 34 ºC, no growth observed at 35 ºC. Colony reverse at 15 ºC, 14–21 d on PDA reddish brown to somewhat dark brown (8E7–8F7) or brownish to greenish grey (8F2, 30F2) with or without a reddish brown (8E7) pigment visible outside margin, at 20–25 ºC dark green or greyish green (25F4) to brownish black (8F6) or brownish to greenish grey

(8F2, 30F2), typically without pigment visible outside margin. Colony surface on PDA with felt-like to cottony mycelium, greyish green to greyish blue or pastel violet (19A4) to light blue (20A5), with or without small or large watery droplets of exudates, with or without off-white sporodochial masses of conidia; on SNA unpigmented or, in older colonies, greenish grey (25B2–25C2), surface smooth or with fine cottony mycelium, greyish blue in centre of colony, with concentrically arranged pale yellow, off-white or somewhat greyish blue, to 5 mm diam conidial masses. Aerial and submersed mycelium and hyphae of sporodochia becoming purplish red in lactic acid. Conidiation on SNA along submersed hyphae or from sporodochia forming within 14 d or later on surface of SNA or on pieces of carnation leaves or *Buxus* twigs placed on SNA; submersed sporulation by solitary monophialides or on sparsely branched conidiophores. *Monophialides* cylindrical, 14–21 µm long, 2.5–3.5 µm wide at base, *ca.* 2.5 µm near aperture; *sporodochia* of branched conidiophores with solitary or whorls of 2–3 terminal monophialides; base of older sporodochia bluish; phialides of sporodochia cylindrical or bottle-shaped, (9–)15.5–17.5–19.5(–23) µm long, (2.5–)3–3–3.5(–4) µm wide at base, (3–)3.5–4–4(–4.5) µm in middle, (2–)2–2.5–2.5(–3) µm wide near conidiogenous aperture. *Microconidia* not observed. *Macroconidia* formed in off-white or pale yellow or somewhat greyish blue slimy masses, typically with central and basal part nearly straight, rarely gently curved throughout, with a more or less pronounced pedicellate foot cell and an inequilateral fusoid or hooked apical cell, (1–4)5–7(–8) septate: 5-septate (46–) 77.5–82–87(–99.5) × (5.5–)6.5–7–7(–8) µm, 6-septate (77.5–)83–87–90.5(–100) × (6–)7–7–7.5(–8) µm, 7-septate 86.5–101 × 6.5–8 µm. *Chlamydospores* formed from cells of macroconidia, subglobose, 6–11 × 6–8 µm; mycelial chlamydospores not observed.

Characters of holotype, G 00111019, and isotype, G 00111020, of *G. buxi,* identical to details reported above except as follows: *Perithecia* turning brownish in KOH, only weakly reddish brown or reddish in lactic acid. Immature ascal ascospores 1-septate. *Macroconidia* associated with perithecial clusters, 5-septate 70–76.6 × 6.5 µm, 6-septate 75 × 6.5 µm.

Habitat: On decaying or dead terminal twigs still attached to living *Buxus sempervirens* trees; perithecia sometimes co-occurring with those of *G. cicatricum* (Figs 3A, 5B).

Distribution: Europe (Belgium, France, Germany, Slovenia).

Typification: Lectotype of *Gibbera buxi* and *Fusarium buxicola* designated here: **Germany**, Nassau (today, Hesse), Oestrich, K.W.G.L. Fuckel, Herbier Fuckel 1894, G 00111019. *Isotypes* of *Gibbera buxi*: DAOM 126623, G 00111020, G00111021, all Herbier Fuckel 1894, Herbier Barbey-Boissier 886. Specimens have sporodochia and clustered, solitary perithecia on a minutely developed stroma; asci of the sampled material are immature and free ascospores were not seen. *Epitype* for *Gibbera buxi* designated here: **Slovenia**, between Domžale and Kamnik, Arboretum Volčji Potok, prealpine zone, on decaying terminal twig still attached to a living *Buxus sempervirens* var. *elegantissima* tree, July 2009, H.-J. Schroers 1398 & M. Žerjav, CBS H-20379, filed with dried SNA/B culture of CBS 125551, ex-epitype strain, isolated from ascospore of CBS H-20379.

Additional specimen and strains examined: **Belgium**, C. Crepel, CBS 109638. **France**, Dépt. Jura, Bois de la Rochette near Nogna, on leaf litter, 24 Sep 1996, H.-J. Schroers, CBS 130.97. **Netherlands**, on *Buxus sempervirens*, 1987, M.E. Noordeloos, BBA 64985. **Slovenia**, between Domžale and Kamnik, Arboretum Volčji Potok, prealpine zone, on decaying terminal twig with bluish black perithecia still attached to *ca.* 80 year-old, living *Buxus sempervirens* tree, July 2009, H.-J. Schroers 1400 & M. Žerjav, CBS H-20380, derived ascospore culture CBS 125554; Ljubljana, nursery, isolated from roots of potted, small bush of *Buxus sempervirens*, April/March 2009, M. Žerjav 15574, CBS 125548; decaying branch still attached to wilting, small bush of *Buxus sempervirens*, 2007, H.-J. Schroers, CBS 125547.

DNA sequences generated: ITS rDNA (CBS 125554: HM626660, 125551: HM626661, 125548: HQ728144). LSU rDNA (CBS 125554: HM626672, 125551: HM626673). *acl1* (CBS 130.97: HM626622, 125548: HM626623, 125554: HM626629, 125551: HM626630, 125547: HQ728172). *tef-1α* (CBS 125554: HM626649, 125551: HM626648, 125547: HQ728152, 130.97: HQ728150, BBA 64985: HQ728151). *rpb2* (CBS 130.97: HM626690, 125548: HM626687, 125554: HM626688, 125551: HM626689, 125547: HQ728169). See Gräfenhan *et al.* (2011) for others included in Fig. 1.

Notes: *Cyanonectria buxi* is characterised by bluish black perithecia that turn somewhat brown in KOH and reddish in lactic acid, 1-septate ascospores, and relatively long, wide macroconidia. Ex-ascospore isolates and several conidial isolates form dark, greyish-blue cultures on PDA. Measurements of macroconidia of *C. buxi* overlap with those of *Geejayessia cicatricum*, the latter of which forms pale colonies. The macroconidia are longer than those of *G. desmazieri* and members of the *F. lateritium* complex.

Fuckel (1873) described *Gibbera buxi* as a bluish or violaceous black perithecial fungus with 1-septate ascospores. He considered its anamorph similar and related to that of *Nectria gibbera* but did not propose anamorph names for either species. Saccardo (1883) accepted *G. buxi* as distinct and suggested its combination in *Lisea* in which he placed *Gibberella*-like species with 1-septate ascospores (see also Rossman *et al.* 1999). He also described the anamorph of *Lisea buxi* as *Fusarium buxicola,* for which he literally copied Fuckel's description of the anamorph of *N. gibbera,* an act he repeated later for *F. fuckelii* (Saccardo 1886). Saccardo (1883) clearly attributed the name *F. buxicola* to Fuckel's bluish black perithecial fungus and referred to the location where Fuckel collected *G. buxi*. Apparently in error, *F. buxicola* was later used instead for the anamorph of the orange perithecial *G. desmazieri* and its synonym *Nectria gibbera* (Wollenweber & Reinking 1935, Booth 1959, 1971, Gerlach & Nirenberg 1982). Booth (1971) listed *Fusarium lateritium* var. *buxi* as the anamorph of the incorrectly cited "*Gibberella buxi* Fuckel, Symb. Mycol., Nacht. 2: 32, 1873" (apparently confusing *Gibberella* and *Gibbera*) but the ascospores of *F. lateritium* var. *buxi* reportedly have three septa (Booth 1971).

The genetic and nomenclatural connection between *Fusarium buxicola* and *Gibbera buxi* is re-established here, based on recent collections of bluish black, smooth perithecia forming mature asci and 1-septate ascospores (Figs 3A–D, 4A–P). These new specimens exhibit similar characters to those observed on the lectotype and isotypes of *G. buxi*. The few macroconidia observed associated with the perithecia or stromata in the authentic material are identical to macroconidia formed in cultures of the epitype. Perithecia of *G. buxi* have an intensely pigmented ostiolar region but their lower parts appear less intensely pigmented (Fig. 3C, D) probably because of relatively thin lateral perithecia walls (Fig. 3G, H, K). Its original material, however, turns somewhat brownish in KOH and only weakly reddish or brownish reddish in lactic acid while our recent gatherings become more intensely bluish black in KOH (Fig. 3E) and bright red in lactic acid (Fig. 3F, L). Perhaps this reflects immaturity of the perithecia on the type specimens of *G. buxi*, a thought further supported by the fact that no discharged ascospores were visible.

Cyanonectria buxi is well characterised by its greyish blue colonies on PDA, which we observed in all strains. Gerlach & Nirenberg (1982) observed only cream, amber, or fawn to brown and noted blue or verdigris, spotted pigmentation as seldom occurring. It is therefore possible that their concept of *F. buxicola* was based on a heterogeneous selection of strains, probably including

G. cicatricum and *G. desmazieri*, or that some degeneration had occurred. *Cyanonectria buxi* forms longer and wider and partly more-septate macroconidia than *G. celtidicola* and *G. desmazieri.* Macroconidia of *C. buxi* and *G. cicatricum* are similar in size and number of septa.

Cyanonectria buxi has been reported rarely. We collected its teleomorph in July; Fuckel (1873) reported it as very rare and also found perithecia in the summer. Several isolations from conidia or mycelium and one from surface sterilised roots indicate that it is commonly associated with *Buxus sempervirens*. A surprising observation in our study is that perithecia of *C. buxi* can apparently co-occur with those of *G. cicatricum* on what appears to be the same perithecial stroma (Figs 3A, 5B).

Cyanonectria cyanostoma (Sacc. & Flageolet) Samuels & Chaverri, Mycol. Progr. 8: 56. 2009.
Basionym: *Nectria cyanostoma* Sacc. & Flageolet, Atti del Congr. bot. di Palermo: 53. 1902.

Description and illustrations: Samuels *et al.* (2009).

Material studied: CBS 101734 = BBA 70964, GJS 98-127, ex epitype strain, see Samuels *et al.* (2009).

DNA sequences generated: LSU rDNA (CBS 101734: HM626671). *tef-1α* (CBS 101734: HM626647). See Gräfenhan *et al.* (2011) for others included in Fig. 1.

Geejayessia Schroers, Gräfenhan & Seifert, **gen. nov.** MycoBank MB519479.
Anamorph: *Fusarium*-like

Etymology: In honour of Gary J. Samuels, in recognition of his contributions to our knowledge of hypocrealean holomorphs, acknowledging the thousands of specimens and strains he collected and isolated, known universally by their G.J.S. collecting numbers, which he made freely available to his many colleagues.

Perithecia e stromate in substratis erumpente exorientia, superficialia dense coarctata, subglobosa, ovoidea vel obpyriformia, superficie levia vel minute verrucosa, coccinea, aurantiaca vel atra, KOH– vel KOH+. Tunica perithecii ex uno strato composite. Asci 8 spori, cylindrici vel clavate. Ascosporae ellipsoideae, uniseptatae, verruculosae ali leviae, hyalinae vel pallide brunneae. Coloniae fere celeriter crescentes, incoloratae, pallide luteae, pallide aurantiacae veil pallide ochraceae; reversum pigmento rubro carens. Mycelium aerium in agaro parcum, albidum. Sporodochia ad superficiem agari SNA, in foliis Dianthi caryophylli vel foliis et ramis Buxi sempervirentis formata. Monophialides sporodochiales plus minusve cylindricae. Microconidia absentia vel praesentia, 0–1 septata, ovoidea vel ellipsoidea, allantoidea vel fusiformia. Macroconidia sporodochialia 3–multi septata, modice curvata vel quasi recta et apicales rostrata et curvata. Chlamydosporae absentes.

Stromata erumpent, byssoid or densely prosenchymatous, typically of densely packed hyphae, bearing either perithecia or well-developed sporodochia. *Perithecia* caespitose on bark of decaying twigs or dead buds of woody hosts, often on dead twigs still attached to living host, mostly smooth, smooth to warted in one species, thin-walled, uniformly coloured or with a darker ostiolar region when dry, pale orange, brownish to reddish orange, bright red or black, reacting to KOH and lactic acid, unless black, then hardly reacting. *Ascospores* 1-septate, ellipsoidal, with gently tapering or broadly rounded ends, pale brown or yellowish brown, smooth or verruculose at maturity. *Macroconidia* observed in all species, 3- to multi-septate, relatively long when 3-septate, either gently curved throughout with dorsal wall somewhat more curved or with a subcylindrical middle part, always conspicuously pedicellate, with an inequilaterally fusoid and more or less hooked apical cell; formed in slimy yellowish or orange masses on branched, frequently sporodochial conidiophores, terminating in whorls of monophialides. *Microconidia* usually absent; when present, then oblong ellipsoidal, gently curved, rounded at both ends or with an asymmetrical hilum. *Chlamydospores* not seen. Cultures on nutritionally rich media such as PDA about 15–20 mm diam after 7 d at 20–25 °C, pale coloured, cream, yellowish, orange, brownish orange or with some greyish hues.

Type species: *Geejayessia cicatricum* (Berk.) Schroers, Stud Mycol. 68: 124. 2011.

Geejayessia cicatricum (Berk.) Schroers, **comb. nov.** MycoBank MB519481. Figs 5, 6.
Basionym: *Sphaeria sanguinea* var. *cicatricum* Berk., Mag. Zool. Bot. 1: 48. 1837.
≡ *Nectria cicatricum* (Berk.) Tul. & C. Tul., *Selecta Fungorum Carpologia: Nectriei- Phacidiei- Pezizei* 3: 77. 1865.

Stromata formed within bud leaves or erumpent through substrate, prosenchymatous, cells 3–5 µm wide, with at least some hypha-like cells, arranged in an irregular *textura porrecta*; hyphae connecting cells of stroma and wall of lower part of perithecia, 2.5–7 µm wide, with walls less than 1 µm thick. *Perithecia* crowded in groups of 5 to > 50, smooth, broadly ampulliform with a short neck or broadly ellipsoidal, bright red with concolourous ostiolar region, deep violet in 2 % KOH, yellowish orange in lactic acid; in longitudinal section 160–260 µm high, 125–250 µm wide. *Perithecial wall* with a single region, (12–)13.5–18(–21) µm wide or, subapically 20–30 µm wide, consisting of 3–5 layers of cells; in face view, cell walls 1–1.5 µm thick in outer layers, 0.5 µm thick or less in inner layers, with pores in all layers; cells in outer layers angular to lobed, (9–)12.5(–18) × (6–)9(–13.5) µm, arranged in a *textura epidermoidea* or *t. angularis*, subglobose to angular in inner layers, (10–)16.5(–23.5) × (7.5–)10–11.5(–16) µm, arranged in a *textura angularis*; in longitudinal section, cells subglobose to angular, narrow towards centrum. *Asci* cylindrical or clavate, with a broadly rounded or flattened apex, with a minute refractive ring, eight-spored, mostly overlapping uniseriate or biseriate above and uniseriate below, (65.5–)73–92.5(–103) × (8–)10–11(–13.5) µm. *Ascospores* equally 2-celled, broadly ellipsoidal to ellipsoidal, slightly constricted at septum, verruculose, hyaline or pale brown, (9.5–)11.5–12–13(–14.5) × (4.5–)5.0–5.5–6(–6.5) µm.

Colonies on PDA after 7 d at 20 and 25 °C 15–20 mm diam; optimum for growth 25 °C, maximum 30–34 °C, no growth at 35 °C. Colony reverse lacking red pigments, after 14–21 d on PDA at 15–25 °C with weak pigment production, pale to light yellow (4A3-4A5), at 30 °C somewhat pale orange. Colony surface on PDA with pustules or cushions of white aerial mycelium to 15 mm diam, with scattered sporodochia covered with pale yellow conidial masses, smooth at margin, wax-like, pale yellow (4A2–4A3); on SNA hyaline, typically smooth or occasionally with pustules of white mycelium. Conidiation on SNA inconspicuous, first along submersed hyphae, within 14 d or later from sporodochia formed on the agar surface or on CL or B. *Sporodochia* with a hymenium of branched conidiophores with solitary phialides or whorls of 2–3 terminal monophialides; metulae anastomosing; cells of stroma densely packed, arranged in an irregular *textura porrecta*. *Phialides* more or less cylindrical, tapering towards apex, on SNA (18.5)–22–26.5(–31) µm long, 3–4 µm wide at base and in middle, 2–2.5 µm wide near the conidiogenous aperture; on PDA to 45 µm long, 3–4.5 µm wide at base and 2.5–3.5 µm wide near

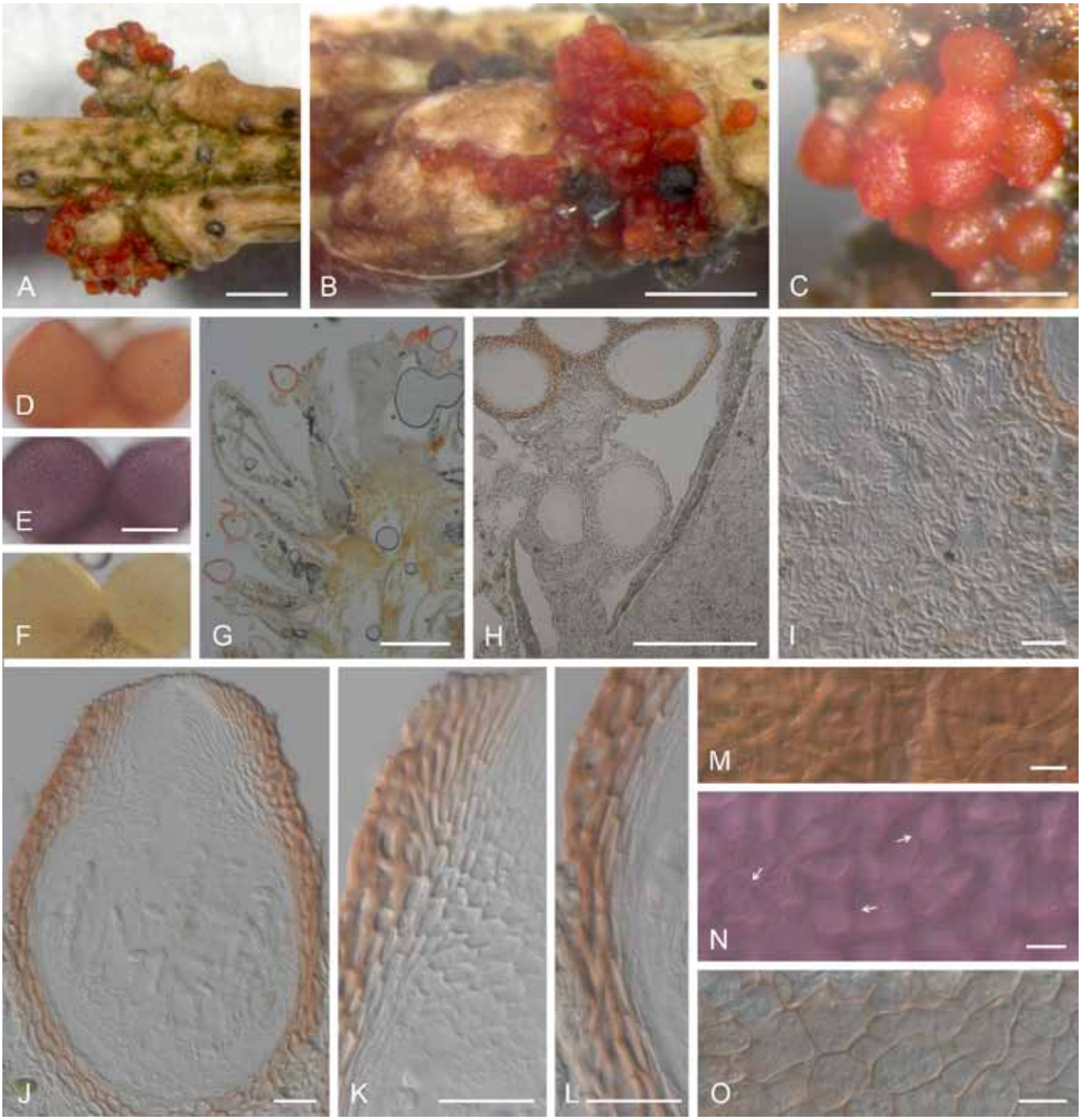

Fig. 5. *Geejayessia cicatricum*, perithecia on the natural substrate. A–C. Habit on decaying buds of *Buxus sempervirens*. D–F. Colour change in perithecium in water (D), replaced with 2 % KOH (E) and then lactic acid (F). G, H. Longitudinal section through decaying bud. I. Longitudinal section through stroma supporting the perithecia, with hypha-like cells. J–L. Median longitudinal sections through perithecia (J), ostiolar region (K) and lateral perithecial wall (L). M–O. Face views of perithecial wall. M. Cells on the surface of perithecia having hyphal or setose characteristics. N. Outermost cells of the main perithecial wall region with Samuels pores. O. Innermost cells of perithecial wall. C rehydrated in water, G–L in Shears, M, O in water, N in 2 % KOH. A, C, G–L, CBS H-20375; B, D–F, CBS H-20376; M–O, CBS H-20377. Scale bars: A–C, G = 500 µm; E (D, F) = 100 µm; H = 200 µm; I–L = 20 µm; M–O = 10 µm.

conidiogenous aperture. *Microconidia* not observed. *Macroconidia* formed in pale yellow slimy masses, typically gently curved throughout, less commonly almost straight, with pronounced pedicellate foot cell, and a more or less inequilaterally fusoid, hooked apical cell, (2–)5–7(–8) septate: 5-septate (55–)73–81–92(–107) × (6–)6.5–7–7.5(–8.5) µm; 6-septate (88–)98.5–103–107(–124) × (7–)7.5–7.5–8(–8.5) µm; 7-septate 88–125 × 6.5–9 µm. *Chlamydospores* not observed.

Habitat: On decaying or dead buds, axils of dead leaves or twigs or sometimes on decaying, subterminal twigs still attached to living *Buxus sempervirens* trees; perithecia sometimes co-occurring with those of *C. buxi* (Figs 3A, 5B).

Distribution: Europe (Slovenia, England).

Typification: Isotype of *Sphaeria sanguinea* var. *cicatricum*: **Sine loco** but presumably England based on the name of the publication, on stems of ?*B. sempervirens*, ex herb. M.J. Berkeley, K(M) 160064. Epitype of *Sphaeria sanguinea* var. *cicatricum* designated here: **Slovenia**, between Domžale and Kamnik, Arboretum Volčji Potok, prealpine zone, on dead buds or bark of decaying, terminal twig still attached to *ca.* 80 year-old, living *B. sempervirens* tree, July 2009, H.-J. Schroers & M. Žerjav, CBS H-20374, twig with perithecial stromata filed together with dried SNA culture of ex-epitype ascospore isolate CBS 125549.

Additional specimen and strains examined: Same location as the epitype. On dead buds or decaying terminal twig still attached to living *B. sempervirens* tree, CBS H-20376, ascospore culture CBS 125552; CBS H-20377, ascospore culture CBS 125553; CBS

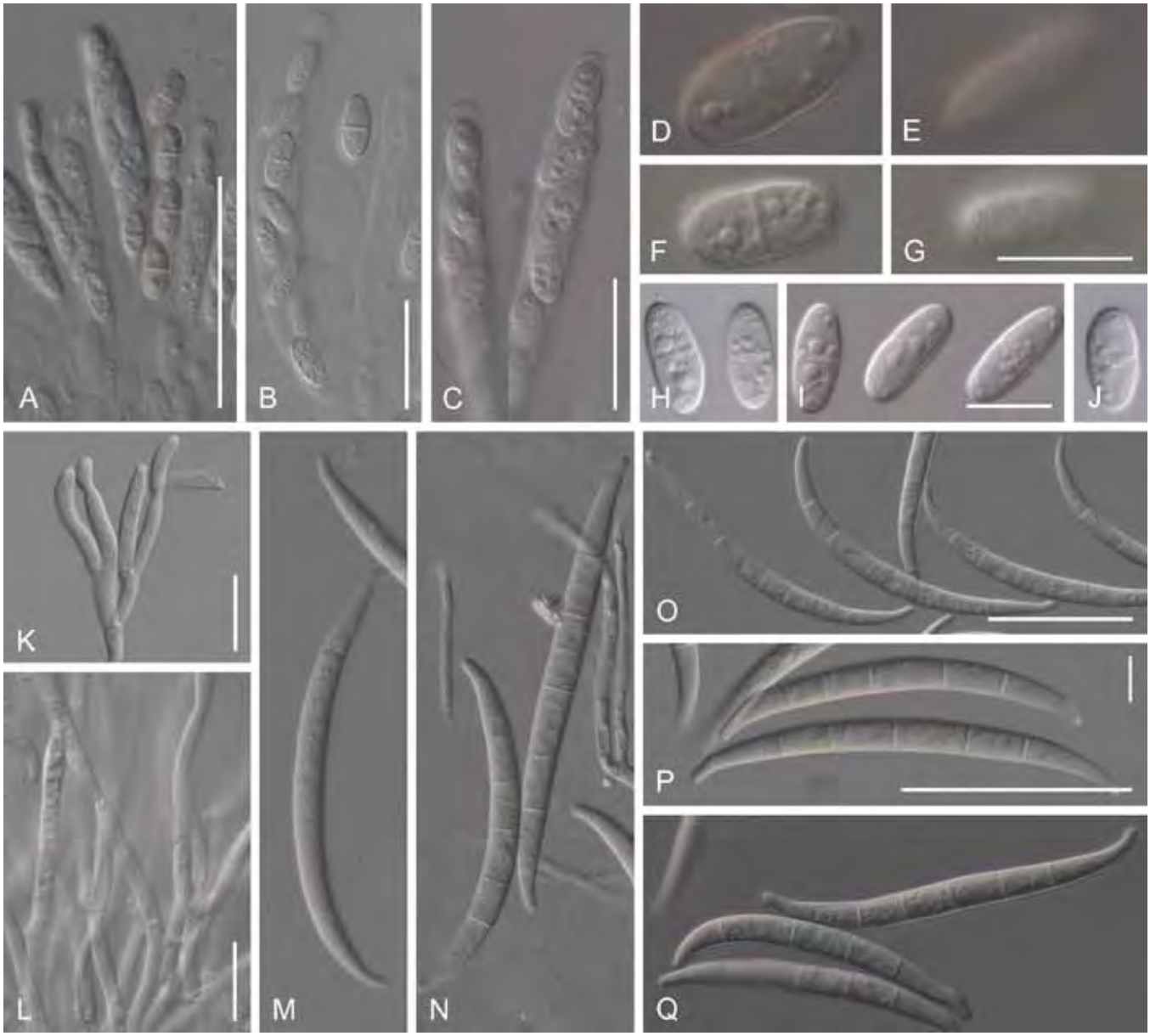

Fig. 6. *Geejayessia cicatricum*, spores and spore forming cells. A–C. Asci with broadly rounded or slightly flattened apex, with visible refractive ring. D–J. Ascospores, with E, G showing surface roughening. K, L. Branched conidiophores and monophialides from sporodochia with anastomosing cells. M–Q. Macroconidia. A–J, M from natural substrate. K, N–Q from SNA, SNA/CL or SNA/B. L from PDA. A–J, L, CBS H-20374; K, N, P, Q, CBS 125549; M, CBS 125552; O, CBS 125550. Scale bars: A, O 50 = µm, B, C, K, L = 20 µm, G (applies also to D–F), I (H, J) = 10 µm, P (M, N, Q) = 50 and 10 µm.

H-203801, ascospore culture CBS 125740; on *B. sempervirens* var. *elegantissima*, July 2009, H.-J. Schroers & M. Žerjav, CBS H-20375, ascospore culture CBS 125550.

DNA sequences generated: ITS rDNA (CBS 125553: HM626653, 125550: HM626654, 125740: HM626655, 125552: HQ728145). LSU rDNA (CBS 125553: HM626665, 125550: HM626666, 125740: HM626667). *acl1* (CBS 125740: HM626635, 125549: HM626636, 125552: HQ728171, 125553: HQ728170). *tef-1α* (CBS 125553: HM626645, 125550: HM626642, 125549: HM626643, 125552: HM626644, 125740: HM626646). *rpb2* (CBS 125740: HM626680, 125549: HM626679, 125552: HQ728153). See Gräfenhan *et al.* (2011) for other strains included in Fig. 1.

Notes: The morphological distinctions between *G. cicatricum* and *G. desmazieri* are discussed in the notes for *G. desmazieri*. Based on the collections available including the isotype, *G. cicatricum* occurs on dead buds specifically on decaying or dead terminal branches of *Buxus sempervirens*, whereas the majority of *G. desmazieri* specimens suggest a habitat on thicker, subterminal branches, with perithecia forming on bark. Although the niche of these species may overlap, there are no indications that they co-occur. The width of macroconidia from the type specimen of *Sphaeria sanguinea* var. *cicraticum* (K 160064) were wider than macroconidia of *G. desmazieri,* confirming the usefulness of this character for distinguishing the species.

Geejayessia atrofusca (Schw.) Schroers & Gräfenhan, **comb. nov.** MycoBank MB519483. Fig. 7.

Basionym: *Sphaeria atrofusca* Schw., Trans. Amer. Philos. Soc. ser. 2. 4: 206. 1832.

≡ *Nectria atrofusca* (Schw.) Ellis & Everhart, N. Amer. Pyrenomyc.: 99. 1892.

= *Fusarium staphyleae* Samuels & Rogerson, Brittonia 36: 84. 1984.

Habitat: On bark of twigs of *Staphylea trifolia*, associated with twig blight (Samuels & Rogerson 1984).

Description and illustrations: Samuels & Rogerson (1984).

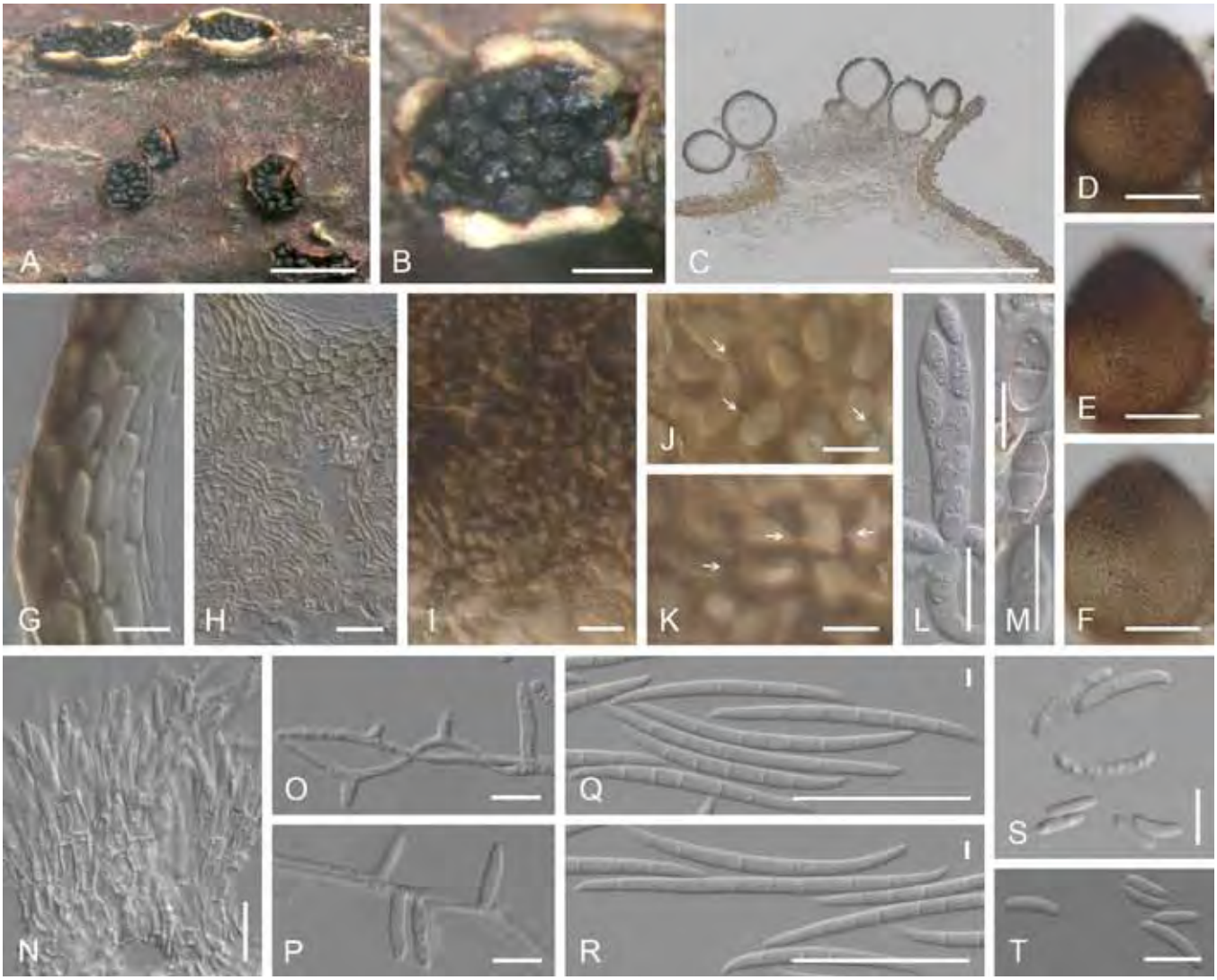

Fig. 7. *Geejayessia atrofusca*. A, B. Habit of perithecia on twigs of *Staphylea trifolia*. C, G, H. Longitudinal section through perithecial stroma (C), lateral perithecial wall (G), stroma composed of hypha-like cells (H). D–F. Colour change in perithecium in water (D), replaced with 2 % KOH (E) and then lactic acid (F). I. Hypha-like cells continuous with cells of the stroma covering base of perithecium. J, K. Face view of outermost cells of perithecial wall with Samuels pores (arrows). L. Ascus. M. Ascospores, the bottom one showing surface. N. Sporodochium. O, P. Mononematious, simple conidiophores, phialides. Q, R. Macroconidia. S, T. Aseptate or 1-septate microconidia. A–M, CBS H-20381, from natural substrate; N–T, CBS 125505 ex ascospores of CBS H-20381 on SNA/CL. Scale bars: A = 1 mm; B, C = 500 µm; D–F = 100 µm; G, J, K, M, O, P, S, T = 10 µm; H, I, L, N = 20 µm; Q, R = 50 and 5 µm.

Material studied: **Canada**, Ontario, Ottawa, Petrie Island, riverine forest, on twig of *Staphylea trifolia*, Oct. 2006, T. Gräfenhan T.G. 2006-01, DAOM 238118, ascospore isolate CBS 125482; same as above: T.G. 2006-01A, conidial isolate CBS 125503; Nov. 2008, T.G. 2008-34, ascospore isolate CBS 125505. **USA**, New Jersey, Palisade Interstate Parkway, *Staphylea trifolia*, C.T. Rogerson 81-53, BBA 66968.

DNA sequences generated: ITS rDNA (CBS 125505: HM626659). LSU rDNA (CBS 125505: HM626674). *acl1* (CBS 125503: HM626627, 125505: HM626628, BBA 66968: HM626637). *rpb2* (CBS 125503: HM626683, 125505: HM626682, BBA 66968: HM626681). See Gräfenhan *et al.* (2011) for other strains included in Fig. 1.

Notes: The almost black perithecia and weak reaction of their pigments to KOH are distinctive features of *Geejayessia atrofusca.* As noted in the discussion of phylogeny, this species does not belong to *Gibberella*, despite the similar colouration of perithecia on the natural substratum. *Geejayessia atrofusca* is clearly a member of this new genus based on combined LSU- and ITS analysis (Samuels *et al.* 2009) and the combined *rpb2* and *acl1* analysis (Fig. 1). *Geejayessia atrofusca* forms non-septate or sparsely septate microconidia on SNA. In the other species of *Geejayessia*, no such microconidia were observed. Samuels & Rogerson (1984) described *F. staphyleae* from cultures grown from ascospores isolated from *G. atrofusca*; thus the genetic connection between the teleomorph and anamorph covered by these two names is clear.

Geejayessia celtidicola Gräfenhan & Schroers, **sp. nov.** MycoBank MB519482. Figs 8, 9.

Etymology: In reference to the substrate of this species, *Celtis occidentalis*.

Perithecia e stromate in substratis lignosis erumpente exorientia, superficialia vel interdum partim semi-immersa, dense coarctata, ovoidea vel obpyriformia, breviter papillata, levia, intense rubida, *ca.* 200–250 µm alta, 120–210 µm lata in 2 % KOH purpurascentia, luteo-aurantia in acido lactico. Stromata prosenchymatica cellulae partim hyphales. Tunica perithecii ex uno strato composita, 15–25 µm crassa ad latus, cellulae exteriores angulares vel lobatae, (6.5–)9.5(–14) × (5–)6.5(–11) µm, interiores subglobosae vel angulares, (9.5–)14(–18.5) × (6.5–)10(–13.5) µm; cellulae contiguae pseudoporis connexae. Asci cylindrici vel clavati, apice anulo refringente carentes, 70–87.5–94 × 6–10–13.5 µm. Ascosporae ellipsoidea, uniseptatae, leves vel eximie verruculosae, hyalinae vel pallide brunneae, (10.5–)12.5–13.5–14(–16.5) × (4.5–)5–5.5–6(–6.5) µm. Coloniae fere celeriter crescentes, in agaro PDA incoloratae vel pallide luteae 15–25 °C, pallide brunneoaurantiacae 30 °C, reversum pigmento rubro

Fig. 8. *Geejayessia celtidicola*, perithecia on the natural substrate, holotype. A, B. Habit on bark of Celtis occidentalis. C, D. Colour change in perithecium in 2 % KOH (C) then replaced by lactic acid (D). E. Longitudinal section of erumpent stroma and perithecia. F–I. Face view of perithecial wall. F. Cells on the surface of perithecia showing hyphal or setose characteristics. G, H. Outermost cells of the main perithecial wall with Samuels pores. I. Intermediate cells of the perithecial wall. J–L. Median longitudinal sections of perithecia or perithecial walls. M. Longitudinal section through stroma supporting the perithecia showing hypha-like cells. B. after rehydration in water; E, H, J–M in Shears; F, G, I in water. Scale bars: A = 500 µm; B, E = 200 µm; C, D = 100 µm; F–I = 10 µm; J–M = 20 µm.

carens. Mycelium aerium in agaro PDA et SNA parcum vel in parte media pulvinos albos formans. Sporodochia post 14 dies vel postea in foliis Dianthi caryophylli vel ad superficiem agari SNA formata, hemisphaerica. Monophialides sporodochiales plus minusve cylindricae, (12–)20–22–25(–34) µm longae, 2–3 μm latae ad basim, 1.5–2 µm latae ad apicem. Microconidia absentia. Massae conidiorum sporodochialium in agaro SNA hemisphaericae, albidae vel pallide aurantiacae. Macroconidia sporodochialia (1–)3–5(–8)-septata, cellulae basilares pediformes, latissimae in medio, cellulae centrales et basilares quasi rectae, apicales rostratae et curvatae vel utrinque modice curvata; conidia 3-septata (34.5–)54–58–62(–70) × (3.5–)4–4.5–4.5(–5) µm; 4-septata (56–)60.5–64–67.5(–75) × (4–)4.5–4.5–4.5(–5) µm; 5-septata (55–)63–67.5–74(–78.5) × (4–)4.5–5–5(–5.5); 6-septata 66–82.5 × 4.5–5.5; 7-septata 71–84 × 5–5.5; 8-septata 74.5–93 × 5–5.5 µm. Chlamydosporae absentes.

Stromata erumpent through bark, prosenchymatous, cells 3–5 µm wide, with at least some hypha-like cells, arranged in an irregular *textura porrecta*; hyphae connecting cells of stroma to wall of lower part of perithecia, either arranged in a network or as terminal hyphae, 18.5–45 long, 6–7.5 µm wide near base, with walls to 2 µm wide. *Perithecia* crowded in groups of up to 15, seated on surface of or with base partly immersed in stroma, smooth, broadly ampulliform with a short neck or broadly ellipsoidal, dark red with a darker red ostiolar region, dark purple red in 2 % KOH, yellowish orange in lactic acid; in longitudinal sections 200–250 µm high, 120–210 µm wide. *Perithecial wall* consisting of a single region, 15–25 µm thick or, subapically, 30–35 µm, of 3–5 layers of cells; in face view, cell walls 1–1.5 µm thick in outer layers, 0.5 µm thick or less in inner layers, with pores in all layers; cells in outer layers lobed to angular, (6.5–)9.5(–14) × (5–)6.5(–11) µm, arranged in a *textura angularis* to *t. epidermoidea*, in inner layers subglobose to angular, (9.5–)14(–18.5) × (6.5–)10(–13.5) µm, arranged in a *textura angularis*; in longitudinal section, cells subglobose to angular, flatter towards

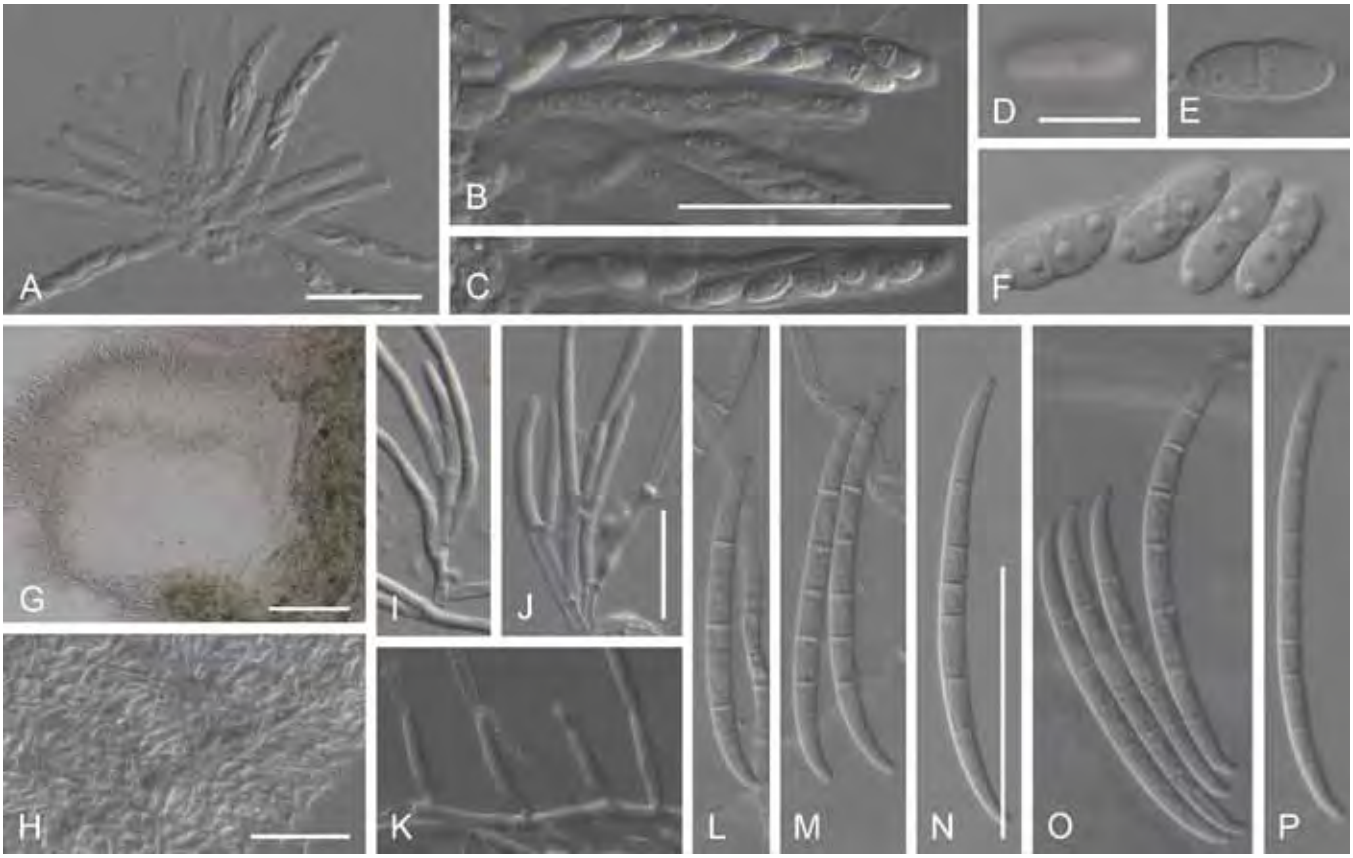

Fig. 9. *Geejayessia celtidicola*, spores and spore forming cells. A–C. Asci with rounded apex, lacking refractive ring. D. Ascospore surface. E, F. Ascospores. G. Longitudinal section of sporodochium. H. Hymenial tissue of base of sporodochial stroma. I–K. Monophialides on branched conidiophores from sporodochial hymenium, I, J. With anastomoses. L–P. Macroconidia. A–F. Holotype CBS H-20378; G–K, P CBS 125502; L, M, O, CBS 125504; N, CBS 125481. Scale bars: A, B (applies also to C), N (L, M, O, P) = 50 µm; D (E, F) = 10 µm; G =100 µm; H, J (I, K) = 20 µm.

centrum. *Asci* cylindrical or clavate, with rounded apex, without a visible refractive ring, eight-spored, overlapping uniseriate or biseriate above and uniseriate below, 70–87.5–94 × 6–10–13.5 µm. *Ascospores* equally 2-celled, ellipsoidal, slightly constricted at septum, smooth or finely verruculose, hyaline or pale brown, (10.5–)12.5–13.5–14(–16.5) × (4.5–)5–5.5–6(–6.5) µm.

Colonies on PDA after 7 d at 20 and 25 °C 25 mm diam; optimum for growth 20–25 °C, maximum 30–34 °C, no growth at 35 °C. Colony reverse lacking red pigments, after 14–21 d on PDA at 15–25 °C without obvious pigment production, yellowish white to pale yellow (3–4A2–3), at 30 °C weakly greyish to brownish orange (5B4, 6C7). Colony surface on PDA smooth, wax-like because of dense spreading mycelium; aerial mycelium sparse, felt-like, produced in central half of colony or restricted to pustules; aerial mycelium on SNA present in central half of colony, white, loosely branched or felt-like, absent towards margin. Conidiation on SNA beginning within 14 d or later, inconspicuous, along submersed hyphae or from sporodochia on CL, later on surface of SNA and from aerial mycelium. Sporodochia on CL consisting of a well-developed stroma covered with dense, *ca.* 100 µm high hymenium of phialides and anastomosing cells of conidiophores; cells of subhymenium densely packed, prosenchymatous. *Conidiogenous cells* monophialidic, 2-level or twice monochasial, more or less cylindrical but tapering towards apex, (12–)20–22–25(–34) µm long, 2–3 µm wide at base, 1.5–2 µm wide near conidiogenous aperture. *Microconidia* not observed. *Macroconidia* formed in off-white or pale yellow slimy masses, with pronounced pedicellate foot cell and almost equilateral fusoid, hooked apical cell, gently and equally curved towards both ends or with central and basal part nearly straight, (1–)3–5(–8) septate: 3-septate (34.5–)54–58–62(–70) × (3.5–)4–4.5–4.5(–5) µm; 4-septate (56–)60.5–64–67.5(–75) × (4–)4.5–4.5–4.5(–5) µm; 5-septate (55–)63–67.5–74(–78.5) × (4–)4.5–5–5(–5.5) µm; 6-septate 66–82.5 × 4.5–5.5; 7-septate 71–84 × 5–5.5 µm; 8-septate, 74.5–93 × 5–5.5 µm. *Chlamydospores* not observed.

Habitat: On bark of dead twigs and branches in the canopy of living *Celtis occidentalis*.

Distribution: North America (Canada: Ontario).

Typification: Holotype of *Geejayessia celtidicola*: **Canada**, Ontario, Ottawa, Petrie Island, riverine forest, on dead branches in the canopy of a living *Celtis occidentalis* tree, Nov. 2008, T. Gräfenhan 2008-32, CBS H-20378, twig with perithecial stromata; ex-type culture CBS 125502.

Additional specimens and strains examined: **Canada**, Ontario, same general location and habit as the holotype, Nov. 2006., T. Gräfenhan 2006-29, DAOM 238129, ascospore isolate CBS 125481; Ontario, Carleton Place, riverine forest, Nov. 2006, T. Gräfenhan 2006-35, DAOM 238130, ascospore isolate CBS 125504.

DNA sequences generated: ITS rDNA (CBS 125504: HM626656, 125502: HM626657). LSU rDNA (CBS 125504: HM626668, 125502: HM626669). *acl1* (CBS 125504: HM626624, 125502: HM626625). *tef-1α* (CBS 125504: HM626639, 125502: HM626638, 125481: HQ728149). *rpb2* (CBS 125504: HM626686, 125502: HM626685). See Gräfenhan *et al.* (2011) for other strains included in Fig. 1.

Notes: In addition to host differences, the dark red perithecia of *Geejayessia celtidicola* distinguish this species from its phylogenetic relatives *G. cicatricum* and *G. desmazieri***.** The shape

and size of its macroconidia are reminiscent of *G. desmazieri*, but they are longer and more frequently septate. PDA cultures of *G. celtidicola* are relatively darkly pigmented at 30 °C, compared with those of *G. cicatricum* and *G. desmazieri*. On PDA, cultures form comparatively little aerial mycelium. The shapes and sizes of the macroconidia in *G. celtidicola* and *G. zealandica* are similar. The 3-septate macroconidia in *G. zealandica* are mostly less than 4 µm and its 5-septate macroconidia can be up to 5 µm wide (Nirenberg & Samuels 2000), whereas the 3-septate macroconidia of *G. celtidicola* are mostly 4–5 µm wide and have a similar width to the 5-septate macroconidia formed on SNA.

Fusarium celtidis produces almost straight macroconidia on fruits of *C. occidentalis* in North America (Ellis & Tracy 1890), whereas those of *G. celtidicola* are frequently gently curved throughout. The shape and substratum of *F. celtidis* suggest the *F. lateritium* complex as noted by Booth (1971) following Wollenweber & Reinking (1935). *Fusarium sphaeriaeforme*, described from bark of *Celtis australis* in Italy, differs from *G. celtidicola* by its shorter macroconidia (Saccardo 1892).

Geejayessia desmazieri **(**Becc. & De Not.) Schroers, Gräfenhan & Seifert, **comb. nov.** MycoBank MB519480. Figs 10, 11.

Basionym: *Nectria desmazieri* Becc. & De Not., Schem. di Classif. Sferiacei: 10. 1863.

≡ *Dialonectria desmazieri* (Becc. & De Not.) Petch, Naturalist (London): 281. 1937.

= *Nectria coccinea* var. *cicatricum* Desm., Ann. Sci. Nat., Bot. 10: 351. 1848 *fide* Wollenweber & Reinking 1935, Booth 1971. Type not seen.

= *Nectria gibbera* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23-24: 177. 1870.

= *Fusarium fuckelii* Sacc., Syll. Fung. 4: 695. 1886.

Stromata erumpent, prosenchymatous, cells 3.5–5.5(–6.5) µm wide, with at least some hypha-like cells, arranged in an irregular *textura porrecta*; hyphae continuous with cells of stroma clinging to wall of the perithecial base, either arranged like a network or as terminal hyphae 25–55 µm long, 5–8 µm wide, with walls 2–3 µm wide. *Perithecia* typically crowded in groups of 3 to > 50, sometimes solitary or gregarious, either formed superficially or with base somewhat immersed in stroma, smooth, broadly ampulliform with a short neck or broadly ellipsoidal, pale to brownish orange, reddish brown or brownish to greyish red, less often bright to dark red, frequently with a slightly darker ostiolar region when dry, brownish to deep violet in 2 % KOH, yellowish orange in lactic acid; in longitudinal section 200–300 µm high, 150–220 µm wide. *Perithecial wall* of a single region, 20–30 µm thick or, subapically 30–40 µm, consisting of 3–5 layers of cells; in face view, cell walls to 1.5 µm in outer layers thick, 0.5 µm thick or less in inner layers, in all layers with pores; cells in outer layers angular to somewhat lobed, (9.5–)13(–18.5) × (5.5–)9(–13.5) µm, arranged in a *textura epidermoidea* or *t. angularis*; cells of inner layers subglobose to angular, (10–)15(–23) × (8.5–)11.5(–16) µm, arranged in a *textura angularis*; in longitudinal sections, cells subglobose to angular, flatter towards centrum. *Asci* cylindrical or clavate, with a rounded or flattened apex, lacking or with an inconspicuous refractive ring, eight-spored, mostly overlapping uniseriate or biseriate above and uniseriate below, (75.5–)85(–100) × (8–)9(–11) µm. *Ascospores* equally 2-celled, broadly ellipsoidal with broadly rounded, rarely somewhat tapering ends, verruculose, hyaline or pale brown, (9.5–)11–12–12.5(–15) × (4.5–)5.5–5.5–6(–7) µm.

Colonies on PDA after 7 d at 20 °C 15 mm diam, 20 mm at 25 °C; optimum for growth 20–25 °C, maximum 30–34 °C, no growth at 35 °C. Colony reverse lacking red pigments, after 14–21 d on PDA at 15 °C without obvious pigment production, at 20–25 °C pale yellow, light yellow to greyish yellow (4A5–4B5), at 30 °C with a pale yellow soluble pigment. Colony surface on PDA with felt-like, white or somewhat greyish green aerial mycelium, smooth towards margin, wax-like or with sparse aerial mycelium; on SNA unpigmented or pale yellow, typically smooth or with scant cottony, white aerial mycelium near inoculum or CL or B plant material. Conidiation on SNA within 14 d or later inconspicuously submersed along hyphae or from sporodochia on surface or on CL or B; on PDA also sporulating in aerial mycelium. *Sporodochia* with a hymenium of branched conidiophores with single phialides, or whorls of 2–3 terminal monophialides; cells of stroma densely packed, arranged in an irregular *textura porrecta*. *Phialides* more or less cylindrical but tapering towards apex, on SNA (11–)18–21.5–24(–34) µm long, (2.5–)3–3–3.5(–4) µm wide at base, (2.5–)3–3.5–4(–4.5) µm in middle, (1.5–)2–2.5–2.5(–2.5) µm wide near the conidiogenous aperture. *Microconidia* not observed. *Macroconidia* formed in pale yellow to pale orange, slimy masses to 3 mm diam, gently curved throughout or with central part almost straight and cylindrical, with a pronounced pedicellate foot cell and an inequilaterally fusoid, hooked apical cell, (1–)3–5(–7) septate: 3-septate (41.5–)50–52.5–55.5(–63.5) × (4.5–)5–5–5(–5.5) µm; 4-septate (51–)57(–64.5) × (4.5–)5(–5.5) µm; 5-septate (55–)62(–72.5) × (4.5–)5(–5.5) µm; 6-septate 63–74 × 5.5–6 µm. *Chlamydospores* not observed.

Sporodochia on G 00110886, lectotype of *N. gibbera*, erumpent through bark, with pale yellow to off-white conidial masses. *Macroconidia* (1–)3–5 septate, when measured in water: 1-septate macroconidia 59–61 × 5–6 µm (n = 3); 3-septate 58–68.5 × 5–6.5 µm (n = 14); 4-septate 60.5 × 6 µm (n = 1); 5-septate 58–68 × 5.5–6.5 µm (n = 10); in lactic acid: 1-septate 61 × 5.5 µm (n = 1); 3-septate 53–61 × 5–6 µm (n = 3); 5-septate 59–66 × 5.5–6 µm (n = 5). *Macroconidia* on BPI 798402, isotype of *N. desmazieri*, measured in lactic acid/cotton blue, 3-septate 36.5–43.5 × 4.0–4.5 µm (n = 5).

Habitat: On decaying or small, dead branches or twigs of *Buxus balearica* and *B. sempervirens*, often on bark near or on scars of subterminal twigs or in axils of leaves and twigs, less frequently on dead buds.

Distribution: Europe (Belgium, France, Germany, Italy, Spain).

Typification: Lectotype of *Nectria desmazieri* designated here: **Italy**, Pisa, Botanical Gardens, on twig of *Buxus balearica*, 1862, O. Beccari, Erbar. Crittogam. Ital. Cent. X. n. 983, BPI 798402; ex herb. Bot. Gard. Pisa, a specimen from Shear Study Collection Types & Rarities where it was noted as an isotype, consisting of a single twig, *ca.* 4.5 cm long and 3–5 mm wide comprising several clustered perithecia and sporodochia with macroconidia. *Syntype*: K, a small fragment unsuitable for slide preparation. *Epitype* of *Nectria desmazieri* designated here: **Italy**, Latio, Bagnaia, Villa Lante, in park, on twig of *Buxus sempervirens*, Nov. 2007, W. Gams TG2007-87, CBS H-20372, ex-epitype strain, isolated from ascospores, CBS 125507; the specimen comprises several clustered perithecia but macroconidia and sporodochia were not seen. *Lectotype* of *Fusarium fuckelii* and *Nectria gibbera* designated here: **Germany**, Nassau (now Hesse), Oestrich, K.W.G.L. Fuckel Fungi rh. 2357, originally labelled "*Nectria desmazieri* + *F. integr.*; I. & II.", G 00110886, Herbier Fuckel 1894, Herbier Boissier. This is the specimen to which Fuckel added drawings showing (i) a *Fusarium* macroconidium 68 × 8 µm, (ii) an ascus 72 × 8 µm, (iii) an ascospore 11 × 5 µm, (iv) the habitat of a *Fusarium* sporodochium, and (v) the habitat of a "roth durchscheinend" perithecium. The lectotype consists of a twig *ca.* 5.5 cm long and *ca.* 4 mm thick with a few perithecia and sporodochia. *Isolectotypes* for *Nectria gibbera*: all labelled "Fungi rh. 2357" (see also lectotype of *Nectria gibbera*): Fuckel 852, as *Nectria gibbera,* G 00110885, Herbier Fuckel 1894, Herbier Barbey-Boissier; W 10342, Herbier Fuckel 1894, Herbier Barbey-Boissier. As *Nectria gibbera* II, G 00110888, G 00110887. As *Nectria desmazieri* det. Fuckel and *N. gibbera* (non *N. desmazieri*) det. J. Weese, 16 March 1910, W 2009-01115. As "*Nectria desmazieri* + *F. integr.*; I. & II.", M-0155489.

Additional specimens and strains examined: All from twigs of *Buxus sempervirens*. **Belgium**, as *Fusarium buxicola,* CBS 840.85 = BBA 64557. **France**, Jardin Public 64 Eaux Chaudes, 14 June 1992, F. Candoussau 4856-4, as *Nectria desmazieri,* BPI

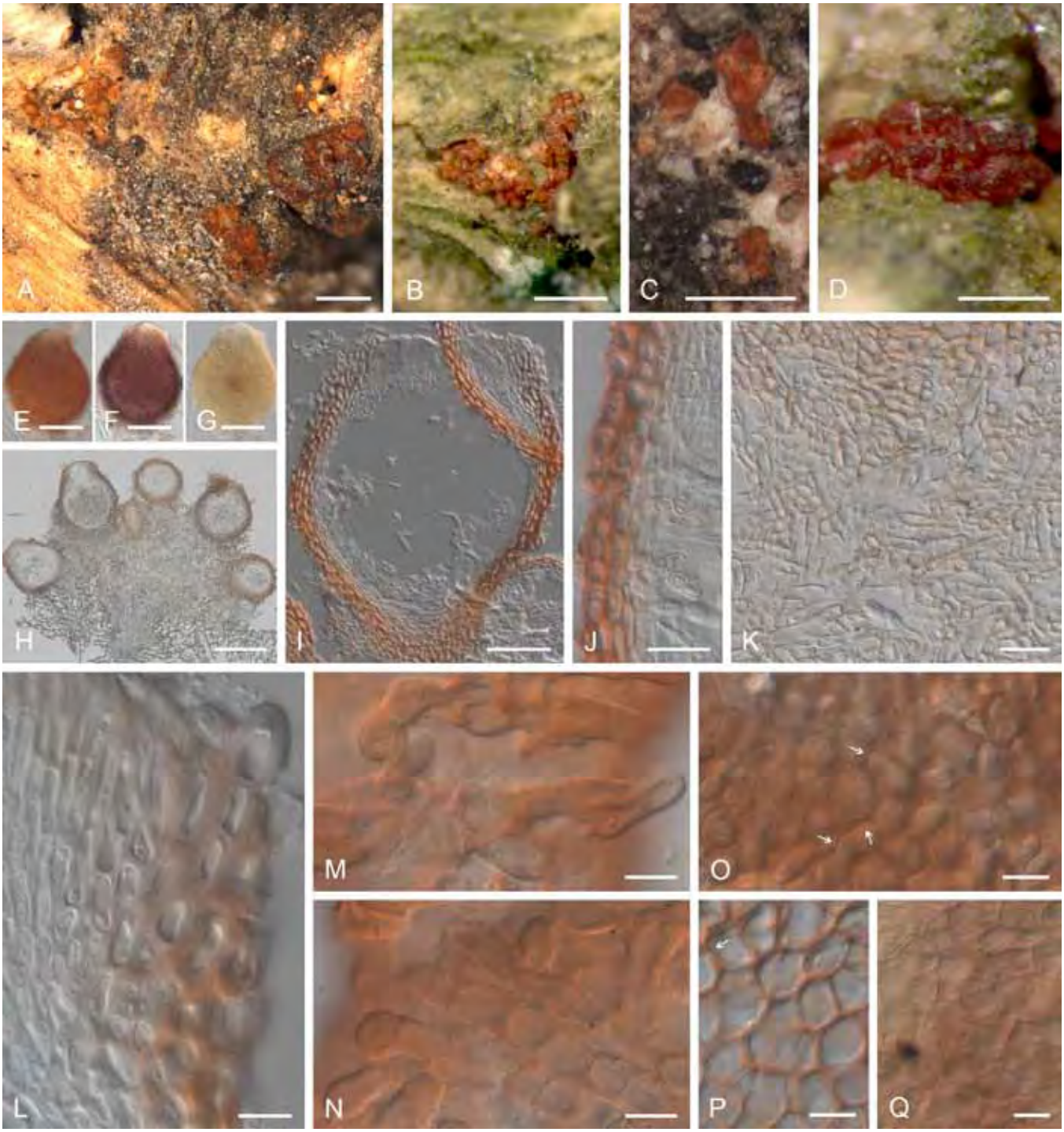

Fig. 10. *Geejayessia desmazieri*, perithecia on the natural substrate. A–D. Habit on twigs of *Buxus sempervirens*. E–G. Colour change in perithecium in water (E), replaced with 2 % KOH (F) and then lactic acid (G). H–L. Longitudinal section through perithecial stroma (H), single perithecium (I), lateral perithecial wall (J), stroma with hypha-like cells (K), perithecial wall near ostiole (L). M, N. Hyphal or setose cells on the surface of perithecial wall. O–Q. Face view of outermost (O), intermediate (P) and innermost (Q) cell layers of perithecial wall. Arrows in O, P indicate Samuels pores in cell walls. H–L in Shears; M–Q in water. A, BPI 798402, isotype of *N. desmazieri*; B, M–O CBS H-20373; C, Q W-10342, isotype of *N. gibbera*; D–L, P, CBS H-20372, epitype; Q, "Funghi. rh. 2357, Fuckel 852". Scale bars: A–D = 500 µm; E–G = 100 µm; H = 200 µm; I = 50 µm; J–L = 20 µm; M–Q = 10 µm.

747855; culture BBA 67515 = GJS 92-65; Cappenberg, G 00110881. **Italy**, Treviso, Selva, Saccardo Mycotheca Veneta 116, Sept. 1874, BPI 551667, annotated by G.J. Samuels, Nov. 1989: "This exsiccata was cited by Booth (1971: *Fusarium*) as *Nectria desmazier(es)i*. The perithecia here are immature and do not contain asci. Perithecia are orange-yellow, cells at the surface of the perithecial wall are angular. This is definitely not a member of the *Nectria episphaeria* group. *Fusarium* present". **Spain**, Montserrat, near Barcelona, Sept. 2007, W. Gams TG2007-69, CBS H-20373, culture CBS 125506. **UK**, England, Norfolk, Overstrand Woods near Norwich, as *Nectria desmazieri,* CBS 313.34.

DNA sequences generated: ITS rDNA (CBS 125507: HM626651, 840.85: HM626650, BBA 67515: HM626652). LSU rDNA (CBS 125507: HM626663, 840.85: HM626662, BBA 67515: HM626664). *acl1* (CBS 125506: HM626632, 125507: HM626633, 840.85: HM626634, BBA 67515: HM626631). *rpb2* (CBS 125506: HM626676, 125507: HM626675, 840.85: HM626678, BBA 67515: HM626677). *tef-1*α (CBS 125507: HQ728146, 840.85: HQ728147, BBA 67515: HM626641). See Gräfenhan *et al.* (2011) for other strains included in Fig. 1.

Notes: The syntype of *N. desmazieri* (K), possibly studied by Booth (1959, 1971), is in poor condition (B. Aguirre-Hudson, pers. comm.)

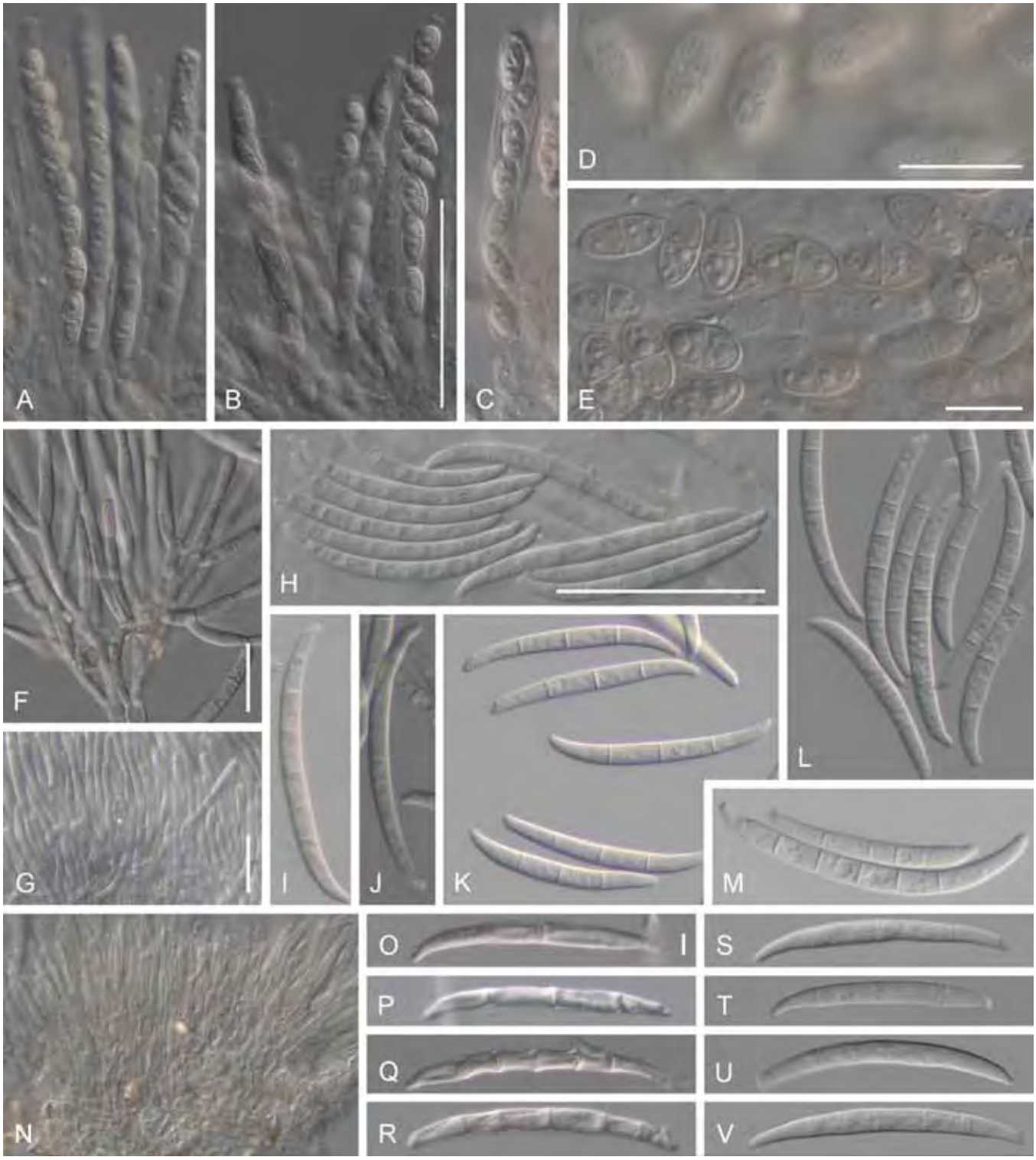

Fig. 11. *Geejayessia desmazieri*, spores and spore forming cells. A–C. Asci with broadly rounded or slightly flattened apex, lacking or with inconspicuous refractive rings. D. Ascospore surface. E. Ascospores. F. Branched conidiophores from sporodochia. G, N. Hymenium of monophialides from sporodochia. H–M, O–V. Macroconidia from sporodochia. A–E, N, O–V, from natural substrate. F–M, from SNA/B or SNA/CL. A–C, CBS H-20372, epitype of *G. desmazieri*; D, E, CBS H-20373; F, G, L, M, CBS 840.85; H–J, BBA 67515; K, CBS 125507, ex-epitype strain; N–V, G00110886, lectotype of *N. gibbera*. N, S–V, mounted in lactic acid, all others in water. Scale bars: B (also applies to A, C), H (I–M, O–V) = 50 µm; D, E = 10 µm; F, G (N) = 20 µm; O (H–M, P–V) = 5 µm.

and was unavailable. Booth (1959, 1971) reported perithecia and sporodochia on this specimen but it is unclear whether the microscopic details in his descriptions were based on original or secondary material. The label information on BPI 798402, "Erb. Critt. Ital. n. 983, ex Herb. Bot. Gard. Pisa" identifies this specimen as an isotype of *N. desmazieri* (De Notaris 1863).

Geejayessia desmazieri is characterised by pale orange to reddish brown, less typically reddish perithecia that turn brownish to deep violet in 2 % KOH. Perithecia on the isotype exhibit these colours, and are clustered in small or large groups, similar to what we observed on authentic material of *N. gibbera*. The perithecia of *G. desmazieri* are typically associated with scars on the bark of twigs or formed on the bark. By means of contrast, the perithecia of *G. cicraticum,* redescribed above, are bright red and associated with decaying buds.

The morphological characters of the anamorph support the distinction of *G. desmazieri* and *G. cicatricum*. These include sizes and shapes of macroconidia produced in culture and as observed on

the lectotype and additional specimens. Macroconidia or fragments of macroconidia encountered on reference specimens were compared with macroconidia from pure cultures of recently collected material. Measurements of the length and width of these macroconidia confirmed the identity of the recently collected specimens and the authentic material of *N. gibbera* as *G. desmazieri*. Sporodochial macroconidia on the lectotype of *N. gibbera* were used to recharacterise and lectotypify *Fusarium fuckelii,* which we consider a synonym of *G. desmazieri*. The macroconidia from these exsiccatae are typically less than 6.5 µm wide; on the isotype of *G. desmazieri*, they are 3-septate, while on the lectotype of *N. gibbera*, they are 3–5 septate (Fig. 11O–V) similar to macroconidia in recently isolated cultures (Fig. 11H–M). The few macroconidia encountered on the isotype of *G. cicatricum* were wider than those of *G. desmazieri*, 6.5–7.5 µm and at least one had 8 septa; similarly broad and septate macroconidia were produced by freshly collected strains of *G. cicraticum*.

De Notaris (1863) originally described *G. desmazieri* from *Buxus balearica*. The identification of the herbarium specimens noted above as *G. desmazieri*, all originating from *B. sempervirens*, is based on their morphological similarities to the lectotype of *N. desmazieri* designated above, and the concept is formalised by the designation of an ex-epitype strain tied to DNA sequences.

There has been confusion between *Fusarium fuckelii* (applicable to the anamorph of *G. desmazieri*) and *F. buxicola* (applicable to the anamorph of *Cyanonectria buxi,* see above), but the differences in macroconidial dimensions allow the relevant specimen to be reidentified and the names to be clarified. Saccardo (1886) copied Fuckel's description of the anamorph of *N. gibbera* for his diagnosis of *F. fuckelii* and explicitly referred to Fuckel (1870: 177) where the anamorph of *N. gibbera* is described. Therefore, *F. fuckelii* was unequivocally established as the anamorph of *N. gibbera,* and, following our concepts, is a synonym of *G. desmazieri*. Fuckel (1870) described the macroconidia of *Nectria gibbera*, which he later accepted as a synonym of *N. desmazieri* (Fuckel 1872), as "5–6-septatis, hyalinis, 68 × 8" µm. Our observations of Fuckel's original material of *N. gibbera* (G 00110886 and isotypes listed above) correct the width to 5– 6.5 µm, measurements that correspond to macroconidia of *G. desmazieri*. As discussed above, Wollenweber & Reinking (1935) and Booth (1959, 1971) followed Fuckel's synonymy of *N. gibbera* with *G. desmazieri*, but wrongly adopted Saccardo's *F. buxicola* for the anamorph. Booth (1959) reported 5–6 septate macroconidia measuring 30–55 × 4–5 µm, but later (Booth, 1971) reported 3–5 septate macroconidia measuring 56–73 × 6–7 µm. These macroconidial measurements correlate with our concept of *G. desmazieri*; macroconidia of *Cyanonectria buxi* and *G. cicatricum* are mostly longer, wider, and typically have more than 5 septa. His observation of "yellow to orange" perithecia suggests that Booth (1959, 1971) saw only specimens and strains of *G. desmazieri,* and did not see the species redescribed above as *C. buxi*.

Geejayessia zealandica (Cooke) Schroers, **comb. nov.** MycoBank MB519484.

Basionym: *Nectria zealandica* Cooke, Grevillea 8: 65. 1879.

≡ *Cosmospora zealandica* (Cooke) Samuels & Nirenberg, Canad. J. Bot. 78: 1483. 2000.

= *Fusarium zealandicum* Nirenberg & Samuels, Canad. J. Bot. 78: 1483. 2000.

Description and illustrations: Nirenberg & Samuels (2000).

Material studied: **New Zealand**, North Island, Auckland, Waitemata City, Waitakere Ranges, Cascades, on bark of *Hoheria populnea*, 3 June 1983, J.M. Dingley & A.Y. Rossman, CBS 111.93 = BBA 64792, GJS 83-235, ex holotypus anamorphicus; specimen PDD 46436 = BPI 802574; Canterbury, Christchurch, Riccarton, on bark of *Plagianthus* sp., J.M. Dingley, May 1986, BPI 802575, culture CBS 101913 = BBA 65034, GJS 86-509.

DNA sequences generated: ITS rDNA (CBS 111.93: HM626658). LSU rDNA (CBS 111.93: HM626670). *acl1* (CBS 111.93: HM626626). *tef-1*α (CBS 111.93: HQ728148, 101913: HM626640). *rpb2* (CBS 111.93: HM626684).

Notes: The perithecial wall anatomy, stromata development for perithecia and sporodochia, and overall morphological characters of the anamorph and teleomorph (Nirenberg & Samuels 2000) justify the classification of *N. zealandica* in *Geejayessia*. It differs from other members of the genus by relatively thick perithecial walls.

DISCUSSION

Supraspecific classification

Fusarium typified by *F. sambucinum* is firmly linked taxonomically to the teleomorphic genus *Gibberella* typified by *G. pulicaris*. Both names refer to the same genetic and phylogenetic species. *Fusarium sambucinum* is closely related to the *Fusarium fujikuroi*, *F. graminearum*, *F. incarnatum-equiseti, F. oxysporum* species groups and some others. Their close relationships are confirmed by studies using ribosomal DNA sequences or protein-encoding genes for phylogenetic analyses suggesting that these taxa form a monophyletic group (Summerbell & Schroers 2002, O'Donnell *et al.* 2007, Schroers *et al.* 2009, O'Donnell *et al.* 2010). The known teleomorphs of these species groups almost always correspond to the modern concept of *Gibberella;* they form homogeneously bluish black pigmented, KOH+, warted perithecia and mostly multiseptate ascospores (Rossman *et al.* 1999, Samuels *et al.* 2001). Therefore, the strongly supported phylogenetic clade accommodating *Fusarium sambucinum* and its closely related sister clades has been referred to as the "*Gibberella* clade" (O'Donnell *et al.* 2010). Applying the philosophy of Article 59 of the International Code of Botanical Nomenclature (McNeill 2006), *Gibberella* is the appropriate name for the holomorphs in this clade. However, following the logic argued in this volume by Gräfenhan *et al.* (2011) and earlier by Seifert & Samuels (2000), Cannon & Kirk (2000), Rossman & Samuels (2005), *Fusarium* Link (1809) has priority over *Gibberella* Sacc. (1877) and we prefer to use the earlier name for this clade.

Samuels *et al.* (2009) assigned the term "*Fusarium* group" to the moderately supported phylogenetic clade encompassing several statistically strongly supported subclades, whose relationships among each other remained unresolved. They accepted the subclades of the *Fusarium* group as genera, for example, *Albonectria*, *Cyanonectria*, *Gibberella*, *Neocosmospora*l *Haematonectria* (the latter to be replaced with an earlier, legitimate genus name), following the underlying principles applied to the generic concepts of nectriaceaous fungi presented by Rossman *et al.* (1999). Our phylogenetic studies based on protein-encoding genes (Fig. 1, Gräfenhan *et al.* 2011) extend the results shown by Samuels *et al.* (2009). They identify up to eight strongly supported clades with *Fusarium*-like anamorphs apart from *Dialonectria*, *Fusicolla*, *Macroconia Microcera,* and *Stylonectria* that comprise the distantly related, basal *Fusarium* clade.

Our recognition of the distinctiveness of *Cyanonectria, Geejayessia,* and other genera of the terminal *Fusarium* clade aims to encapsulate a similar degree of divergence at the generic

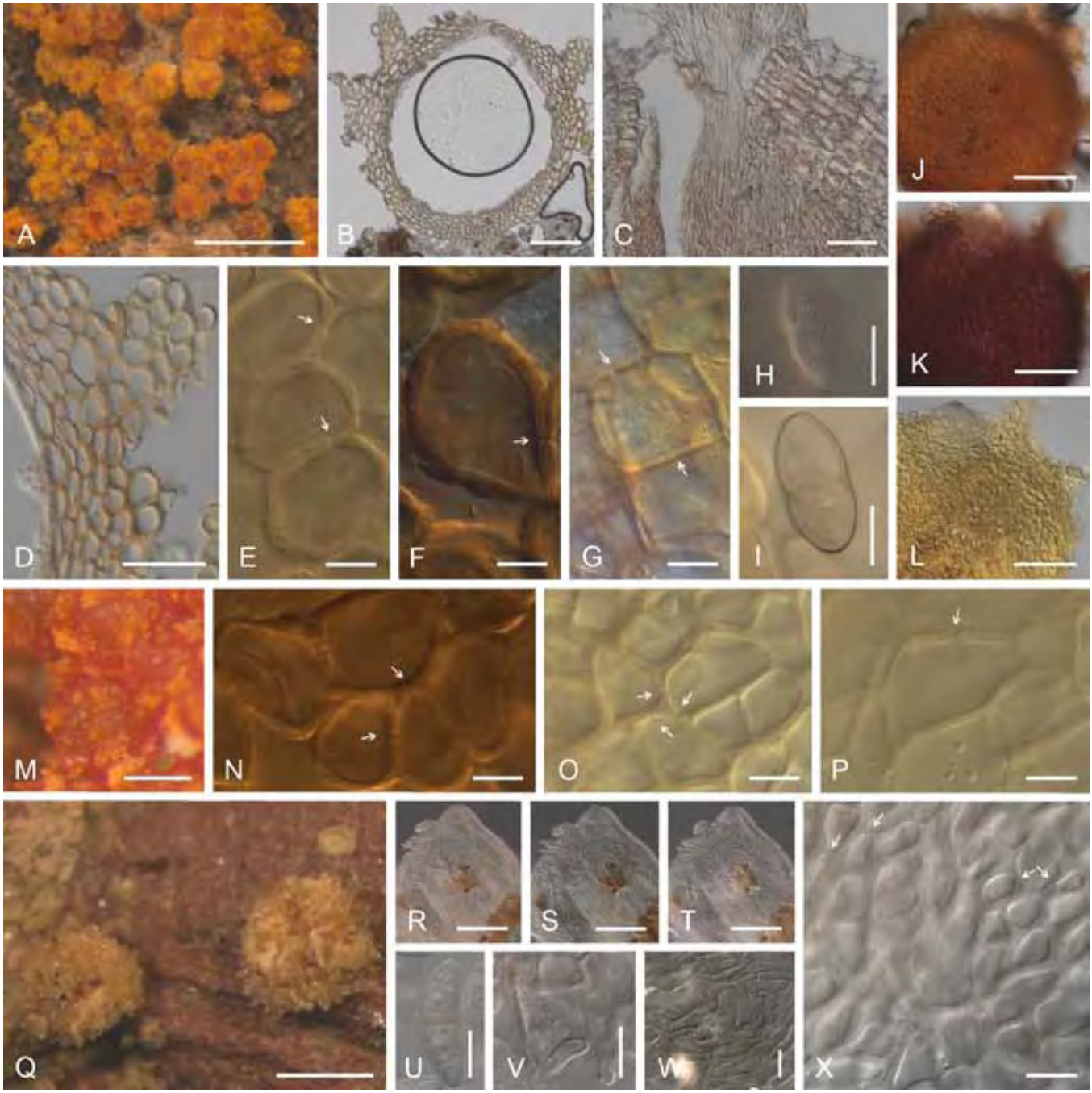

Fig. 12. Comparison of teleomorph characters of "*Haematonectria*" *illudens*, "*Haematonectria*" sp. and "*Nectria" albida*. A–I. "*Haematonectria*" *illudens* on the natural substrate. A. Habit of perithecia. B–D. Longitudinal sections of perithecia, erumpent stroma and lateral perithecial wall. E–G. Front view of cell layers of the perithecial wall, E, F showing cells of perithecial warts. H, I. Ascospore, H showing surface striations. J–P. "*Haematonectria*" sp. J–L. Colour changes in perithecium mounted in water (J), replaced with 2 % KOH (K) and then lactic acid (L). M. Habit of perithecia. N. Cells of perithecial warts. O, P. Intermediate cells of the perithecial wall. Q–X. "*Nectria" albida*. Q. Habit of perithecia. R–T. Colour changes in perithecium mounted in water (R), replaced with 2 % KOH (S) and then lactic acid (T). U. Ascospore. V. Short seta like cells emerging from perithecial wall. W. Hypha-like cells probably continuous with cells of the stroma covering base of perithecium. X. Outermost cell layer of perithecial wall. Arrows in E–G, N–P, X indicate Samuels pores in cell-walls. A–I BPI 802461; J–P BPI 745186; Q–X BPI 1108875. Scale bars: A, Q = 500 µm; B, J–L, R–T = 100 µm; C, D = 50 µm; E–I, N–P, U–X = 10 µm; M = 200 µm.

rank across the *Nectriaceae* (*cf.* Chaverri *et al.* 2011, Hirooka *et al.* 2011) and in other ascomycetous families or orders (*cf.* Crous *et al.* 2007, Tanaka *et al.* 2009). These conclusions also affirm the importance of applying monophyletic concepts to fungi at the generic level. As discussed by Gräfenhan *et al.* (2011), the falcate macroconidia of *Fusarium* and morphologically similar genera cannot be interpreted as a genus delineating structure, but are probably a plesiomorphic character present in unrelated taxa of the *Nectriaceae*. At the generic level, the recent name *Cyanonectria* is accepted here and the new genus *Geejayessia* is proposed because they have apparently evolved within the terminal *Fusarium* clade independently, and no other generic name is available.

Clarification of the concepts and nomenclature of the species of two of these genera, *Cyanonectria* and *Geejayessia*, is the main focus of this paper. Often misidentified as *Fusarium buxicola*, representatives of both genera were previously classified in *Fusarium* section *Macroconia* (Wollenweber & Reinking 1935, Gerlach & Nirenberg 1982).

Analysis of morphological characters

Delimitation of the genera *Cyanonectria* and *Geejayessia* using morphological characters requires reinterpretation of the shape, disposition, colour, and anatomical features of perithecia, ascal apex, stroma, and anamorphic characters.

Species of *Geejayessia* and *Cyanonectria buxi* form perithecia on a hyphal or byssoid tissue (Figs 3I; 5G–I; 7C, H; 8E, M; 10H, K) as observed in previous studies (Booth 1959, Samuels & Rogerson 1984, Nirenberg & Samuels 1990, Samuels *et al.* 1991). We interpret these cushions as stromata because they consist of densely aggregated, hypha-like cells that emerge through cracks of woody parts or plant hosts or through leaflets of decaying buds. Similar erumpent stromata were also seen in representatives of "*Haematonectria*" (Fig. 12C) and *Fusarium sensu stricto*, while well-developed stromatal structures are typically absent in genera such as *Cosmospora*, *Dialonectria*, *Macroconia*, and *Microcera* (Samuels *et al.* 1991, Gräfenhan *et al.* 2011). Booth (1971: 59) concluded that the presence or absence of stromata is "hardly worthy of generic rank", which explains why he placed *G. desmazieri* in the otherwise astromatic "*N.*" *episphaeria* group (*Dialonectria sensu* Gräfenhan *et al.* 2011). Phylogenetic analyses across the *Nectriaceae* and the phylogenetic distinction of stromata forming and astromatous taxa does not support Booth's view (Fig. 1, Samuels *et al.* 2009, Gräfenhan *et al.* 2011). Stromata erumpent through plant tissue and supporting sporodochia and perithecia occur in diverse groups of the *Hypocreales* (Samuels 1976, Rossman *et al.* 1999). However, they frequently occur in taxa of the terminal *Fusarium* clade, which is rich in plant parasitic species. In contrast, the nearly astromatous genera *Cosmospora*, *Dialonectria*, *Macroconia,* and *Microcera*, distantly related to the terminal *Fusarium* clade (Fig. 1, Gräfenhan *et al.* 2011), seem to be mostly associated with insects, lichens, and other fungi. In *Geejayessia* species with their frequent occurrence on dead branches of living trees, the stroma may be the interface between an endophytic or endoparasitc lifestyle and the exposed fruiting phase (Figs 7C, 8E, 10H for perithecia; Nirenberg & Samuels 2000, fig. 3 and Samuels & Rogerson 1984, fig. 5 for sporodochia). Even in species of the *Fusarium* clade associated with more ephemeral gramineous hosts, perithecia are typically firmly connected to the substrate by weakly developed stromata embedded in the plant tissue.

Perithecia of *C. buxi* and *Geejayessia* spp. can be at least partly covered by a network of hyphae that emerges from the byssoid stroma (Figs 3L, M; 5M; 7I) and terminal hyphae, apparently originating from this network, may appear as short setae (Figs 8F; 10M, N). A similar situation occurs in "*Nectria" albida,* where bases of the smooth perithecia seem to be covered by a hyphal network (Fig. 12W) from which some terminal hyphae emerge (Fig. 12V).

Perithecia of *Cyanonectria* and *Geejayessia* are obpyriform but those of the former have a somewhat widened, broadly rounded ostiolar neck, described by Samuels *et al.* (2009) as "knobby" for *C. cyanostoma* (Fig. 3B–D). On drying, the perithecia collapse laterally. In contrast, perithecia of *G. atrofusca* and *G. zealandica* are rather globose (Fig. 7B–D, Rogerson & Samuels 1984, fig. 1; Nirenberg & Samuels 2000, fig. 4).

Perithecial colour characters are often used to delineate teleomorphically typified genera with *Fusarium*-like anamorphs (Rossman *et al.* 1999). Although the *Nectriaceae* are reasonably well characterised by red or bluish black perithecia with positive colour changes in KOH and lactic acid, our phylogenetic results suggest independent, apomorphic losses or modifications of pigments. Red pigments have probably been lost independently in "*N.*" *albida* (Fig. 12Q–T), and *Albonectria* (Fig. 13K–O), and bluish black in "*Albonectria*" *verrucosa*, which has pale KOH– perithecia but is phylogenetically within *Fusarium sensu stricto* (Rossman *et al.* 1999, Gräfenhan *et al.* 2011). Colour changes of perithecia in *Cyanonectria* and *Geejayessia* correlate with the basic phenology of the *Nectriaceae*. However, *C. cyanostoma* has remarkable bicoloured perithecia (Samuels *et al.* 2009) having a bluish black apex that reacts in KOH in identical manner to the teleomorph of *F. sambucinum* (Fig. 13A–F) and other species of *Fusarium sensu stricto,* while the main part of the red perithecial body reacts identically to the red perithecia of other genera of the *Nectriaceae*. Although the perithecia of *C. buxi* lack red colours and thus do not obviously correspond to the generic concept of *Cyanonectria*, they are heterogeneously pigmented, intensely in their upper part and faintly in their lower part (Fig. 3C–G). The heterogeneous aspect of perithecial pigmentation supports segregation of *Cyanonectria* from other genera of the terminal *Fusarium* clade.

The spectrum of perithecial colours exhibited by *G. celtidicola* and *G. cicatricum* is also quite characteristic; their perithecia are bright or dark red on the natural substrate and become darker red or purple in KOH and pale yellowish in lactic acid (Figs 5A–F, 8A–D). In contrast, perithecia of *G. desmazieri* are mostly orange or brownish orange on the natural substrate (Fig. 10A–C, Samuels *et al.* 1991, Booth 1959). The perithecia of *G. atrofusca* are somewhat *Gibberella*-like because they appear black on the natural substrate. They seem not to change colour in KOH and only inconspicuously so in lactic acid (Fig. 7D–F; Samuels & Rogerson 1984). This behaviour differs not only from species of *Fusarium*, but also from its closely related, KOH+ sister species in *Geejayessia*.

Species of *Geejayessia* have outer perithecial wall layers differing from those of species of *Albonectria, Fusarium*, and "*Haematonectria*". Perithecial walls of these species are rather narrow, which led Booth (1959) to classify *N. desmazieri* in the *N. episphaeria* group. The wall consists of a single region, comprising several layers of morphologically similar cells that gradually change shape and size across the wall, but cannot be recognised as forming distinct regions. This pattern is also shared by species of *Cyanonectria* (Fig. 3H, K, N), "*N.*" *albida* (Fig. 12X), and the distantly related species of *Dialonectria*, *Cosmospora*, *Microcera,* and *Macroconia.* In contrast, *Albonectria*, *Fusarium,* and most species of "*Haematonectria*" have rather strongly warted perithecia and thicker perithecial walls.

In species of *Cyanonectria* and *Geejayessia*, the cell walls in all layers have locally and abruptly thinned areas *ca.* 1 µm diam or less, but which do not become complete pores (Figs 3N; 5N; 7J, K; 8G, H; 10O–P). We propose the name "Samuels pores" for these structures.They appear to differ from the so-called "Munk pores" in the *Nitschkiaceae* and other related *Sordariomycetes* (Carroll & Munk 1964), which are typically surrounded by a distinctly thickened and morphologically conspicuous rim (Samuels *et al.* 1993, figs 6, 12; Vasilyeva *et al.* 2010, fig. 7 j, k). In contrast, the cell wall surrounding Samuels pores in the *Hypocreales* is typically strongly and abruptly attenuated and is probably never completely perforated; no rim surrounds these pores. Samuels pores were seen in species of *Microcera* and, for example, *Cosmospora joca* (Samuels *et al.* 1991, fig. 23), *C. lasiodiplodiae* (*ibid*., fig. 25), *C. pseudepisphaeria* (Rossman *et al.* 1999, plate 28 i), *Chaetopsinectria chaetopsinae* (Samuels 1985, fig. 1B), *Ch. chaetopsinae-penicillatae* (*ibid*., fig. 4D), and *Ch. chaetopsinae-catenulatae* (*ibid*., fig. 5B). At least rarely, they occur in the outermost layers of perithecial cells or in the cells of perithecial warts of representatives also of "*Haematonectria*" (Fig. 12E–G, N–P), "*Nectria*" *albida* (Fig. 12X), *Fusarium sambucinum* (Fig. 13H, I), and *Albonectria rigidiuscula* (Fig. 13P–R).

Perithecial walls of species of *Cyanonectria* and *Geejayessia* are also similar to the innermost of the two or three regions observed in species of the distantly related genus *Bionectria* (*Bionectriaceae*). Samuels pores in *Bionectria* were only seen in the innermost

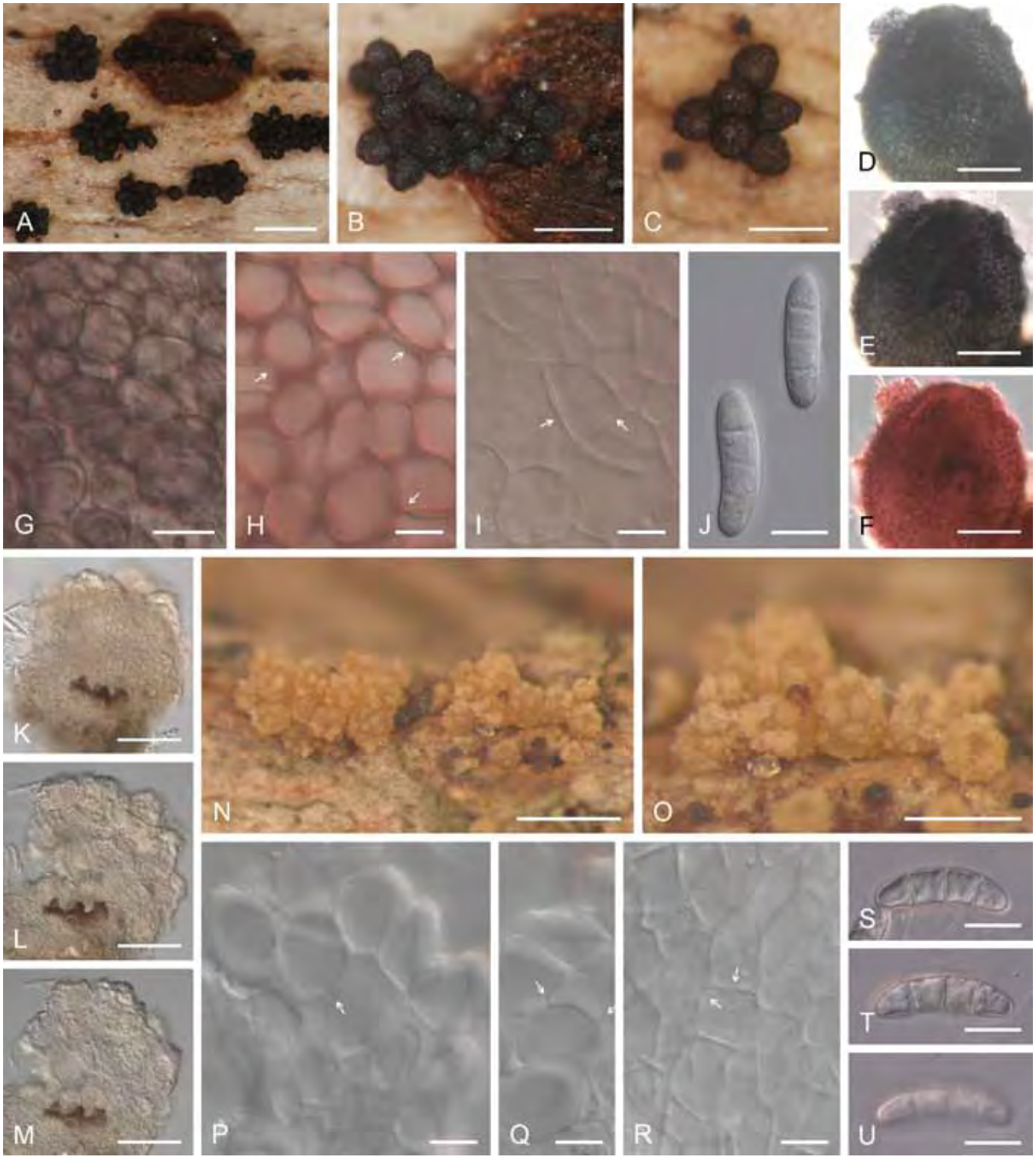

Fig. 13. Comparison of teleomorph characters of *Fusarium sambucinum* and *Albonectria rigidiuscula*. A–J. *Fusarium sambucinum* on the natural substrate. A–C. Habit of perithecia. D–F. Colour changes in perithecium mounted in water (D), replaced with 2 % KOH (E) and then with lactic acid (F). G–I. Face view of cell layers of the perithecial wall. G. Cells of perithecial warts. I. Innermost cells of the perithecial wall. K–U. *Albonectria rigidiuscula*. K–M. Colour changes in perithecium mounted in water (K), replaced with 2 % KOH (L) and then with lactic acid (M). N, O. Habit of perithecia. P, Q. Cells of perithecial warts. R. Cells of the main perithecial wall. S–U. Ascospores, U showing wall surface. Arrows in H, I, P–R indicate Samuels pores in cell walls. A, B, D–F HJS 1459; C, G–J BPI 1109327; K–U HJS 0109. Scale bars: A = 1 mm; B, C, N, O = 500 µm; D–F, K–M = 100 µm; G = 20 µm; H–J, P–U = 10 µm.

anatomical region of perithecial walls (Schroers 2001, figs 31i, 42k, 44h, 46k). Samuels pores may occur only in the inner region of perithecial walls that consist of multiple regions or throughout the entire perithecial wall when there is only a single wall region. Accordingly, the presence or absence of Samuels pores could be used as an additional criterion to identify homologous perithecial wall regions among hypocrealean taxa. Their observed presence in the innermost and also in the more or less outermost cell layers in "*Haematonectria*" (Fig. 12E–G, N–P), "*N." albida* (Fig. 12X) and *Albonectria* (Fig. 13P–R) suggests the perithecial walls may have been originally derived from, or consist of, only one wall region. This wall region may be homologous to the entire wall of *Geejayessia* species, but to the inner wall region only of *Bionectria* species. This interpretation is discordant with the prevailing view. For example, Rossman *et al.* (1999) distinguished three distinct perithecial wall regions in *Albonectria* and two in "*Haematonectria*", emphasising

characters seen in longitudinal sections such as shape of cells and thickness and pigmentation of cell-walls.

The asci of *Geejayessia* species are clavate and either lack or have an inconspicuous refractive ring (Figs 6A–C, 7L, 9A–C, 11A–C). In *Cyanonectria buxi* refractive rings were observed (Fig. 11A–D) comparable to those reported for *C. cyanostoma* (Samuels *et al.* 2009). The ascospores of all known *Cyanonectria* and *Geejayessia* species are 1-septate. They are initially more or less smooth, but, perhaps as a function of maturity, are sometimes finely warted in *Cyanonectria, G. atrofusca*, and *G. celtidicola* (Figs 4E–H, 7M, 9D, Samuels *et al.* 2009, fig. 2j), and clearly warted in *G. cicatricum* and *G. desmazieri* (Figs 6D–G; 11D, E). At maturity and when clearly warted, the ascospores were somewhat yellowish brown in *Geejayessia* but hyaline in *Cyanonectria*. Our generic concept emphasises the meaning of ascospore septation as a delimiting character. By means of contrast, "*N.*" *albida*, *Fusarium sensu stricto*, and *Albonectria* have multi-septate ascospores (Figs 12U; 13J, S, T).

The macroconidia in *Cyanonectria* and *Geejayessia* species correspond to *Nectria* section *Macroconia,* characterised by an almost cylindrical main body and relatively conspicuous or thick walls and septa (Wollenweber & Reinking 1935, Gerlach & Nirenberg 1982). They have moderately or well-developed, pedicellate basal cells and gently curved or clearly hooked and tapering apical cells. Most macroconidia are only gently curved (Figs 4U–Y; 7Q, R; 9L–P; 11H–M, O–V; Nirenberg & Samuels 2000, figs 8–10) but more arced macroconidia were seen in *G. cicatricum* (Fig. 6M–Q). Distal and proximal cells of macroconidia are usually longer than intercalary cells. A few macroconidia can be observed in squash mounts of perithecial stromata from herbarium specimens. Erumpent sporodochia sometimes occur, emerging through the outer cortex of the bark. Sporodochia of *C. buxi* were seen on specimens lacking perithecial stromata, *e.g.* CBS 125547. In culture, macroconidia are formed first on verticillately branched conidiophores that correspond to structures called macroconidial "sporodochia" by Wollenweber & Reinking (1935) and Gerlach & Nirenberg (1982) (Figs 6K, L; 9I, J; 11F). Conidiophore cells beneath the phialides in sporodochia of *Geejayessia* frequently have anastomosing bridges between neighbouring cells (Figs 6L; 9I, J). On SNA/CL or SNA/B, sporodochia with a well-developed subhymenium occur in *Cyanonectria* and *Geejayessia* (Figs 4T; 7N; 9G, H; 11G) similar to those observed in nature for *G. zealandica* (Nirenberg & Samuels 2000, fig. 3). In culture, species of *Cyanonectria* and *Geejayessia* are faster growing than the species originally included in *Nectria* section *Macroconia* (Wollenweber 1926), transferred to *Macroconia* or *Microcera* (Gräfenhan *et al.* 2011). The anamorph of *G. cicatricum* may have been confused with *C. buxi* or *G. desmazieri* in the past. It has similarly wide and long macroconidia as *C. buxi* and forms similarly pale colonies on SNA or PDA as *G. desmazieri*. *Geejayessia celtidicola* forms comparably little aerial mycelium on PDA and, at 30 °C, produces greyish colonies dissimilar to those of *G. atrofusca, G. desmazieri*, and *G. zealandica*. On PDA, *Cyanonectria buxi* forms a dark colony reverse and surface showing bluish hues (Fig. 4AA–AD). This combination of characters is not seen in other fusaria. A dark reverse is not produced in cultures of its closest relative, *C. cyanostoma*; Samuels *et al.* (2009) described its PDA cultures as white to cream. When describing *F. buxicola,* Gerlach & Nirenberg (1982) mentioned fawn to brown colours, rarely blue or verdigris spotted colonies. We encountered no such spotted colouration in *G. cicatricum* or *G. desmazieri*, which suggests that Gerlach & Nirenberg (1982) may have included *C. buxi* and *G. desmazieri* in their description of *F. buxicola*. No red pigments were observed in *Geejayessia*, while in *Albonectria*, *Fusarium sensu stricto*, and to some extent also "*Haematonectria*", red, violet, or purple pigments are commonly seen.

We did not see microconidia in our study of cultures of *C. buxi* and *G. desmazieri,* but Gerlach & Nirenberg (1982) reported "ellipsoid, spindle- or comma-shaped (according to Wollenweber & Reinking 1935 and J. Ehrlich, cited by Booth 1959)" macroconidia for *C. buxi*. Nirenberg & Samuels (2000) did not mention microconidia when describing *G. zealandica*. The microconidia we observed in *G. atrofusca* (Fig. 7S, T) largely confirm the observations made by Samuels & Rogerson (1984).

Life style and ecology

Cyanonectria and *Geejayessia* are associated only with woody hosts. Remarkably, we are not aware of any *Geejayessia* isolated from bulk soil, while representatives of several other taxa in the terminal *Fusarium* clade are well known as soil inhabitants or soil-borne plant pathogens. With the exception of *G. zealandica,* the species of *Geejayessia* and *Cyanonectria* have never been isolated from substrates other than *Buxus sempervirens, B. balearica* (*Buxales, Buxaceae*), *Celtis occidentalis* (*Rosales, Ulmaceae*), or *Staphylea trifolia* (*Crossosomatales, Staphyleaceae*).

ACKNOWLEDGEMENTS

We are grateful to the curators of the CBS and DAOM culture collections for providing and preserving cultures for our studies, and the herbaria BPI, DAOM, G, K, M, and W for loans of specimens. H.-J.S. extends his gratitude to Walter Gams (Baarn, the Netherlands) for assistance with the Latin diagnosis and Silvester Žgur (University of Ljubljana, Biotechnical Faculty, Institute for Animal Breeding) for kindly providing access to a microtome. We thank Amy Rossman (Systematic Mycology & Microbiology Laboratory (SMML), USDA, Beltsville, USA) and Brett Summerell (Royal Botanic Gardens, Sydney, Australia) for providing helpful comments on earlier versions of this text. The illustrations in Fig. 12B, C and D were made from longitudinal sections prepared by Gary J. Samuels (SMML).

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.06

Studies in Mycology 68: 139–162. 2011.

Acremonium phylogenetic overview and revision of *Gliomastix, Sarocladium,* and *Trichothecium*

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Abstract: Over 200 new sequences are generated for members of the genus *Acremonium* and related taxa including ribosomal small subunit sequences (SSU) for phylogenetic analysis and large subunit (LSU) sequences for phylogeny and DNA-based identification. Phylogenetic analysis reveals that within the *Hypocreales*, there are two major clusters containing multiple *Acremonium* species. One clade contains *Acremonium sclerotigenum,* the genus *Emericellopsis,* and the genus *Geosmithia* as prominent elements. The second clade contains the genera *Gliomastix sensu stricto* and *Bionectria*. In addition, there are numerous smaller clades plus two multi-species clades, one containing *Acremonium strictum* and the type species of the genus *Sarocladium*, and, as seen in the combined SSU/LSU analysis, one associated subclade containing *Acremonium breve* and related species plus *Acremonium curvulum* and related species. This sequence information allows the revision of three genera. *Gliomastix* is revived for five species, *G. murorum, G. polychroma, G. tumulicola, G. roseogrisea,* and *G. masseei*. *Sarocladium* is extended to include all members of the phylogenetically distinct *A. strictum* clade including the medically important *A. kiliense* and the protective maize endophyte *A. zeae*. Also included in *Sarocladium* are members of the phylogenetically delimited *Acremonium bacillisporum* clade, closely linked to the *A. strictum* clade. The genus *Trichothecium* is revised following the principles of unitary nomenclature based on the oldest valid anamorph or teleomorph name, and new combinations are made in *Trichothecium* for the tightly interrelated *Acremonium crotocinigenum*, *Spicellum roseum,* and teleomorph *Leucosphaerina indica*. Outside the *Hypocreales*, numerous *Acremonium*-like species fall into the *Plectosphaerellaceae*, and *A. atrogriseum* falls into the *Cephalothecaceae*.

Key words: *Acremonium, Cephalothecaceae*, *Gliomastix,* holomorph concept, *Leucosphaerina,* nomenclature, *Sarcopodium, Sarocladium, Trichothecium*.
Taxonomic novelties: *Trichothecium sympodiale* Summerbell, Seifert, & Schroers, nom. nov.; *Gliomastix roseogrisea* (S.B. Saksena) Summerbell, comb. nov., *Gliomastix tumulicola* (Kiyuna, An, Kigawa & Sugiy.) Summerbell, comb. nov., *Sarocladium bacillisporum* (Onions & Barron) Summerbell, comb. nov., *Sarocladium bactrocephalum* (W. Gams) Summerbell, comb. nov., *Sarocladium glaucum* (W. Gams) Summerbell, comb. nov., *Sarocladium kiliense* (Grütz) Summerbell, comb. nov., *Sarocladium ochraceum* (Onions & Barron) Summerbell, comb. nov., *Sarocladium strictum* (W. Gams) Summerbell, comb. nov., *Sarocladium zeae* (W. Gams & D.R. Sumner) Summerbell, comb. nov., *Trichothecium crotocinigenum* (Schol-Schwarz) Summerbell, Seifert, & Schroers, comb. nov., *Trichothecium indicum* (Arx, Mukerji & N. Singh) Summerbell, Seifert, & Schroers, comb. nov., *Trichothecium ovalisporum* (Seifert & Rehner) Seifert & Rehner, comb. nov.

INTRODUCTION

The genus *Acremonium* includes some of the most simply structured of all filamentous anamorphic fungi. The characteristic morphology consists of septate hyphae giving rise to thin, tapered, mostly lateral phialides produced singly or in small groups. Conidia tend to be unicellular, produced in mucoid heads or unconnected chains. They can be hyaline or melanised, but the hyphae are usually hyaline. A preliminary study of the phylogenetic diversity of *Acremonium* by Glenn *et al*. (1996), based on partial nuclear ribosomal small subunit (SSU) sequences, showed that recognised members belonged to at least three groups in distinct orders of fungi. Most species including the type, *A. alternatum*, belong to the order *Hypocreales*. A smaller group of species, *Acremonium* section *Chaetomioidea*, belongs to the *Sordariales*. This section, typified by the *Acremonium alabamense* anamorph of *Thielavia terrestris*, was conceived as including the *Acremonium*-like anamorphs of *Chaetomium* and *Thielavia* species (Morgan-Jones & Gams 1982). A recent study has placed several of these heretofore unnamed *Acremonium*-like anamorphs into the new genus *Taifanglania* (Liang *et al*. 2009), based on the type, *T. hechuanensis*. Another *Acremonium* species included by Glenn *et al.* (1996), *A. furcatum*, belongs to an order of uncertain identity. Subsequent publications have shown that *A. furcatum* is related to the well-known phytopathogen *Verticillium dahliae* and belongs to the recently established family *Plectosphaerellaceae* (Zare *et al*. 2007, Schoch *et al*. 2009), which groups together with the *Glomerellaceae* in a clade that forms a poorly defined, unnamed, ordinal-level sister-taxon to the *Microascales*. Several other *Acremonium* species such as the phytopathogen *A. cucurbitacearum* also have been shown to belong to the *Plectosphaerellaceae* (Zare *et al*. 2007). The simple structure of *Acremonium* has either convergently evolved in diverse fungal orders within the class *Sordariomycetes* or is symplesiomorphic at a very deep level.

The diversity of fungi throughout the *Ascomycota* that produce *Acremonium*-like anamorphs is high, including genera such as *Gabarnaudia* (*Microascales*), *Lecythophora* (*Coniochaetales*), and *Pseudogliomastix* (*Sordariales incertae sedis*). The present study does not review the vast range of fungi producing simple phialidic conidiophores, but instead, focuses specifically on: 1) anamorphs that have been formally placed into the genus *Acremonium*, and 2) species and genera phylogenetically related to the named *Acremonium* species.

The number of previously phylogenetically unstudied fungi is large. Currently, there are approximately 95 named *Acremonium* species with

traceable material (cultures or specimens in good condition), excluding endophyte species that were transferred to *Neotyphodium* by Glenn *et al*. (1996). In addition, there are an undetermined number of nectriaceous teleomorphs with unnamed *Acremonium*-like anamorphs plus about 15 named and unnamed *Emericellopsis* species with *Acremonium* anamorphs (Zuccaro *et al*. 2004). The preliminary phylogeny done by Glenn *et al*. (1996) includes only seven species that would currently be considered *Acremonium,* inclusive of the *Acremonium berkeleyanum,* anamorph of *Cosmospora berkeleyana*, formerly considered the anamorph of *Cosmospora vilior*, plus two *Emericellopsis* species. Clearly, further work is needed on the phylogeny of *Acremonium*.

Because of the high biodiversity within *Acremonium,* relatively evolutionarily labile, rapidly evolving genes like the ribosomal internal transcribed spacer (ITS) are not alignable across the genus (de Hoog *et al*. 2000) or even within some of the individual orders that the genus spans. Because many *Acremonium* species are derived from relatively closely related families in the *Sordariomycetes*, relatively slowly evolving genes that are alignable such as the ribosomal large subunit (LSU) may yield considerable ambiguity about relationships. To address this problem, we performed an analysis of LSU and whole SSU sequences for a larger number of *Acremonium* isolates than has been examined previously. Based on these results, we chose six of the most phylogenetically distinctive species and included them in the Ascomycetous Tree of Life project (Schoch *et al*. 2009). The elegant phylogenetic analysis in that project was based on two nuclear ribosomal genes, one mitochondrial ribosomal gene, and portions of three protein-coding genes. These results permitted us to gain a clearer picture of relationships among the *Acremonium* groups that were imperfectly resolved in LSU and SSU analysis.

In the present study we present the results of the LSU and small subunit (SSU) phylogenetic analyses for the majority of *Acremonium* species available in pure culture including described and undescribed species. This gives not only a phylogenetic overview of the genus, but also provides identification-enabling sequences for *Acremonium* species that have not been sequenced previously. Taken with the Tree of Life studies, these results shed new light on the biodiversity of these morphologically simple fungi that have long been profoundly problematical in terms of accurate classification and reliable species identification.

MATERIALS AND METHODS

Two separate sets of data matrices were assembled (Table 1). The first is a two-gene analysis that aims at investigating the phylogenetic position of *Acremonium* within the *Sordariomycetes.* The second is a one-gene analysis focusing on the *Acremonium* strains belonging to the order *Hypocreales*. The first set includes the large and small subunits of the nuclear ribosomal RNA gene (nucLSU and nucSSU, respectively) and 166 taxa, including 56 strains of *Acremonium*, 105 reference taxa of *Sordariomycetes,* and five species of *Leotiomycetes* as an outgroup (*Botryotinia fuckeliana*, *Chalara aurea*, *Leotia lubrica*, *Microglossum rufum*, and *Pseudeurotium zonatum*). The second set includes only the nucLSU for 331 taxa including 170 strains of *Acremonium*, 158 sequences of *Hypocreales,* and three outgroup species (*Ceratocystis fimbriata*, *Glomerella cingulata*, and *Ophiostoma piluliferum*).

DNA isolation and sequencing

DNA was extracted with a FastDNA kit (Qbiogene, Heidelberg, Germany) from mycelium grown for 5–14 d in liquid Complete Medium (Raper & Raper 1972). The LSU region of ribosomal DNA (rDNA) was amplified with primers V9G (de Hoog & Gerrits van den Ende 1998) and LR5 (Vilgalys & Hester 1990). The SSU region was amplified with primers NS1 and NS24 and sequenced using primers NS1–NS4, NS6, NS24 (White *et al*. 1990; Gargas *et al*. 1992). The components for the PCR were used as described by Schroers (2000). The PCR program was 60 s at 94 °C (initial denaturation); 35 cycles of 35 s at 94 °C (denaturation), 50 s at 55 °C (annealing), and 120 s at 72 °C (elongation); and 6 min at 72 °C (final elongation) followed by chilling to 4 °C. The PCR products were purified with a GFX purification kit (Amersham Pharmacia Biotech Inc., Roosendaal, The Netherlands) and visualised on an electrophoresis gel after ethidium bromide staining. The rDNA was sequenced with a BigDye terminator cycle sequencing kit (Applied Biosystems, Foster City, Calif.) and analysed on an ABI Prism 3700 instrument (Applied Biosystems) by using the standard conditions recommended by the vendor. The primers used in the sequence reaction were NL1 and NL4 (O'Donnell 1993), and LR5.

Alignments and phylogenetic analyses

Sequences were assembled and edited using SeqMan II software (DNAStar, Inc., Madison, Wis.). Manual alignments were performed using MacClade v. 4.08 (Maddison & Maddison 2003). Ambiguous regions (*sensu* Lutzoni *et al.* 2000) and introns were delimited manually and excluded from the alignments. Congruence was tested using a 70 % reciprocal bootstrap criterion (Mason-Gamer & Kellogg 1996, Reeb *et al.* 2004). Final phylogenetic analyses of the two-gene and one-gene datasets were performed using Stamatakis's "randomised axelerated (sic) maximum likelihood for high performance computing" (RAxML VI-HPC, Stamatakis *et al.* 2005, 2008) on the Cipres Web Portal (http://www.phylo.org/sub_sections/portal/). For the two-gene analysis, the maximum likelihood search followed a "GTRMIX" model of molecular evolution applied to two partitions, nucLSU and nucSSU. The same model was applied to the one-gene analysis without partition. Support values were obtained in RAxML with bootstrap analyses of 500 pseudoreplicates. The trees are labeled with the updated scientific names.

RESULTS

DNA sequence alignments

A total of 228 new sequences were generated for *Acremonium*, 192 nucLSU and 36 nucSSU (Table 1). For the two-gene dataset, one nucLSU and 41 nucSSU sequences were missing. After exclusion of ambiguous regions and introns, the two-gene dataset included 2 955 characters (1 250 nucLSU and 1 705 nucSSU). Among these, 1 739 were constant while 900 were parsimony-informative. After exclusion of ambiguous regions and introns, the one-gene dataset included 848 characters. Among these, 481 were constant while 260 were parsimony-informative.

Phylogenetic inference

As shown in Fig. 1, the species of *Acremonium* mostly fall into three groups, namely the *Hypocreales*, the *Plectosphaerellaceae,* and the *Sordariales*. The bulk of species fall into the *Hypocreales.*

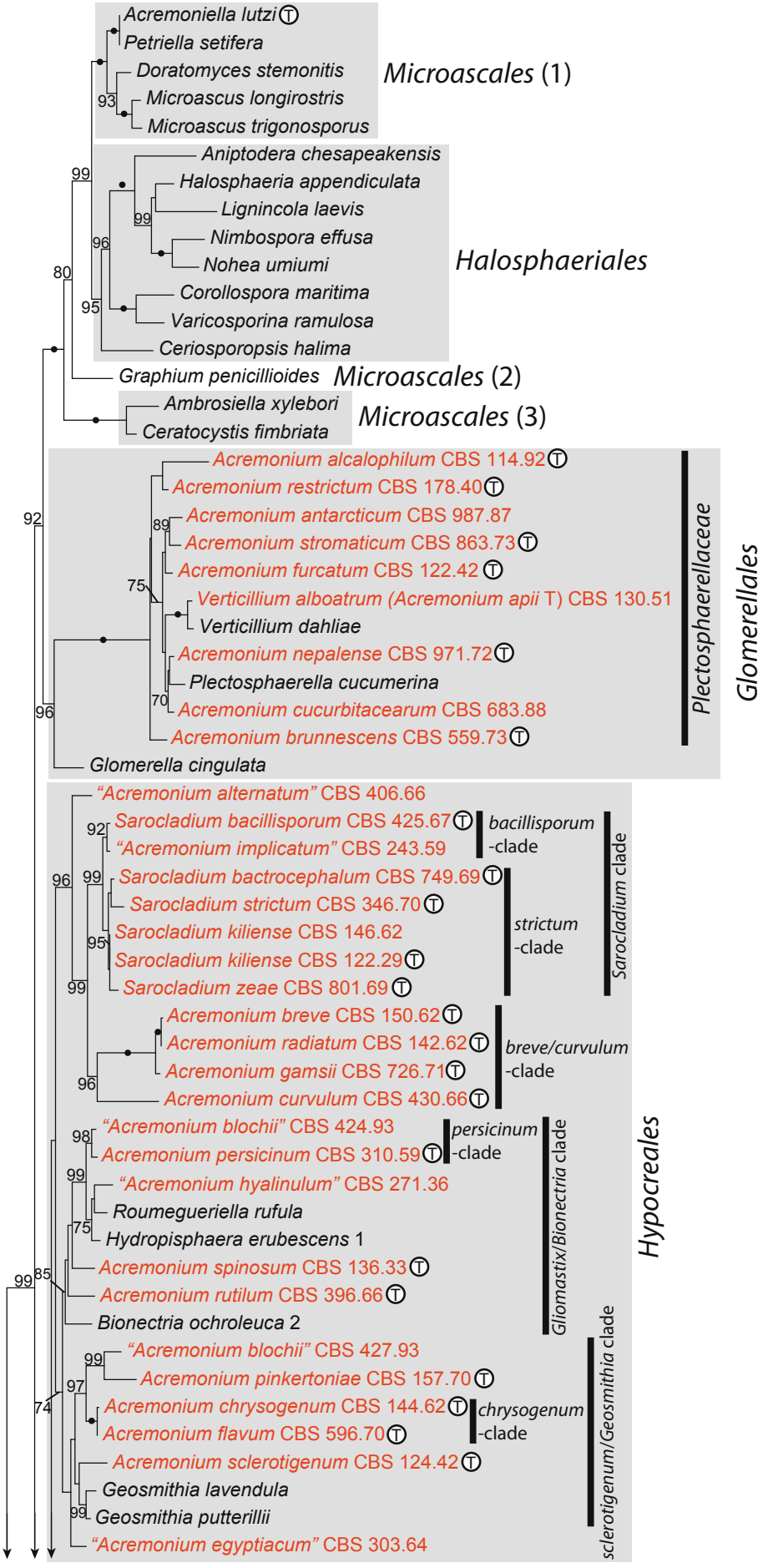

Fig. 1.A–C. The phylogenetic position of *Acremonium* and related fungi within the *Sordariomycetes*, as seen in combined analysis of the large and small subunits of the nuclear ribosomal RNA gene (LSU + SSU) analysed by maximum likelihood via RAxML VI-HPC following a GTRMIX model applied to two partitions. 100 % bootstrap values are indicated by a black dot on the relevant internode.

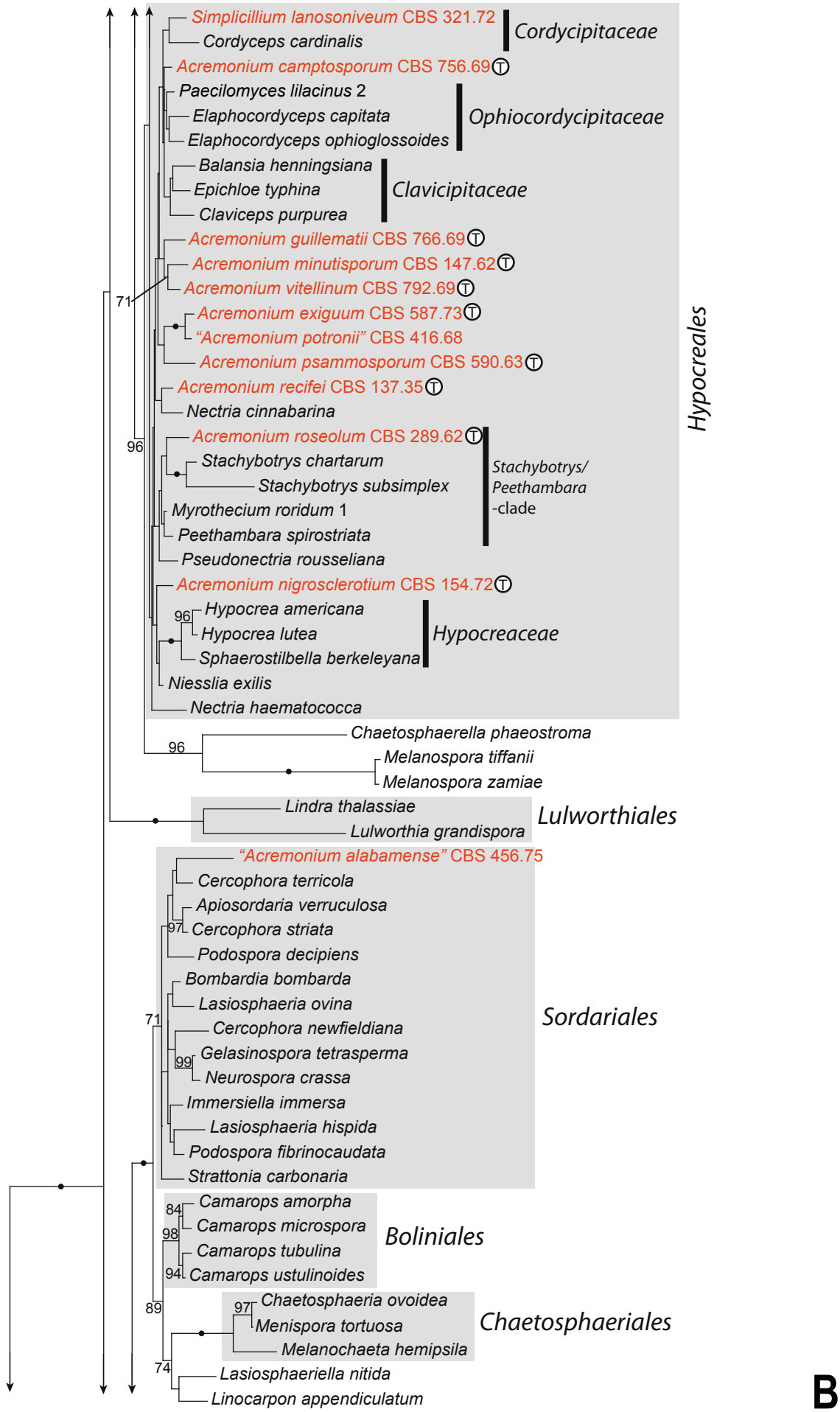

Fig. 1. (Continued).

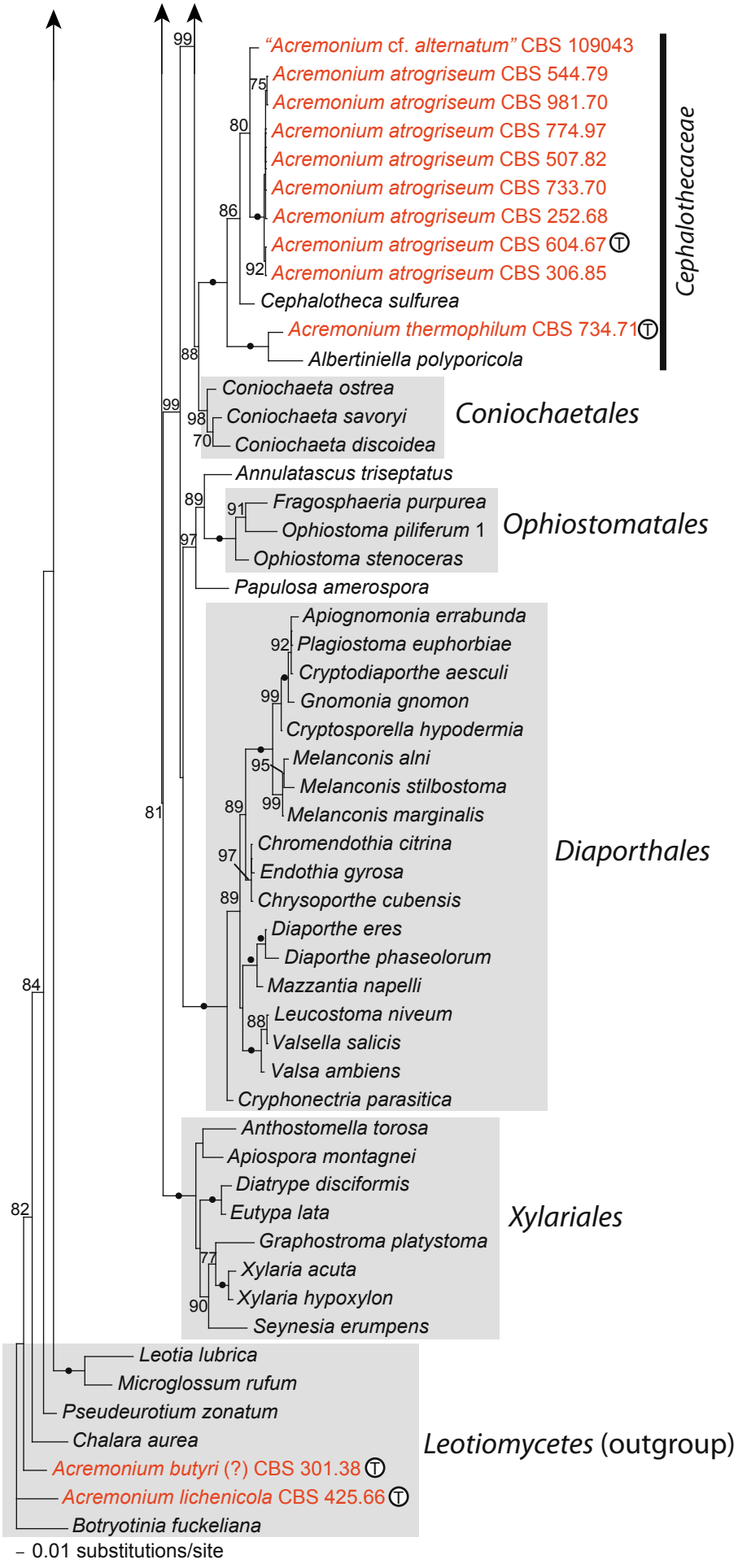

Fig. 1. (Continued).

Table 1. List of *Acremonium* species included in this study as well as other novel or independently redone sequences of related fungi used for comparison. Sequences from GenBank of other comparison taxa are listed in Supplemental Table 1a - see online Supplementary Information. Collection and GenBank numbers are indicated and type strains (T) are mentioned. Sequences generated in this study are shown in bold. Dashes indicate missing data in the two-gene analysis. Isolates that cannot be assigned a phylogenetically confirmed name are listed under the name under which they are currently held in the CBS collection.

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
Acremoniella lutzi T	CBS 103.48	**HQ231971**	–	Ex-type of *Acremoniella lutzi*
Acremonium acutatum T	CBS 682.71	**HQ231965**		
Acremonium alabamense	CBS 456.75	**HQ231972**	–	
Acremonium alcalophilum T	CBS 114.92	**HQ231973**	–	Ex-type of *Acremonium alcalophilum*
Acremonium alternatum T	CBS 407.66	**HQ231988**		
"Acremonium alternatum"	CBS 381.70A	**HQ231986**		
	CBS 406.66	**HQ231987**	**HQ232178**	
	CBS 831.97	**HQ231989**		
	CBS 114602	**HQ231990**		
"Acremonium cf. *alternatum"*	CBS 109043	**HQ231974**	–	
Acremonium antarcticum	CBS 987.87	**HQ231975**	–	
Acremonium atrogriseum T	CBS 604.67	**HQ231981**	–	Ex-type of *Phaeoscopulariopsis atrogrisea*
	CBS 252.68	**HQ231977**	–	
	CBS 306.85	**HQ231978**	–	
	CBS 507.82	**HQ231979**	–	
	CBS 544.79	**HQ231980**	–	
	CBS 733.70	**HQ231982**	–	
	CBS 774.97	**HQ231983**	–	
	CBS 981.70	**HQ231984**	–	
Acremonium biseptum T	CBS 750.69	**HQ231998**		Ex-type of *Acremonium biseptum*
"Acremonium blochii"	CBS 324.33	**HQ231999**		
	CBS 424.93	**HQ232000**	**HQ232181**	
	CBS 427.93	**HQ232001**	**HQ232182**	
	CBS 993.69	**HQ232002**		
Acremonium borodinense T	CBS 101148	**HQ232003**		Ex-type of *Acremonium borodinense*
*Acremonium brachypenium*T	CBS 866.73	**HQ232004**		
Acremonium breve T	CBS 150.62	**HQ232005**	**HQ232183**	Ex-type of *Cephalosporium roseum* var. *breve*
Acremonium brunnescens T	CBS 559.73	**HQ231966**	**HQ232184**	Ex-type of *Acremonium brunnescens*
Acremonium butyri T	CBS 301.38	**HQ231967**	–	Ex-type of *Tilachlidium butyri*; synonym of *Cadophora malorum*
Acremonium camptosporum T	CBS 756.69	**HQ232008**	**HQ232186**	Ex-type of *Acremonium camptosporum*
	CBS 677.74	**HQ232007**		
	CBS 757.69	**HQ232009**		
	CBS 835.91	**HQ232010**		
	CBS 890.85	**HQ232011**		
Acremonium cavaraeanum	CBS 758.69	**HQ232012**		
Acremonium cerealis	CBS 207.65	**HQ232013**		Ex-type of *Gliomastix guttuliformis*
	CBS 215.69	**HQ232014**		
Acremonium chrysogenum T	CBS 144.62	**HQ232017**	**HQ232187**	Ex-type of *Cephalosporium chrysogenum*
Acremonium cucurbitacearum	CBS 683.88	**HQ231968**	–	Previously identified as *Acremonium strictum*
Acremonium curvulum T	CBS 430.66	**HQ232026**	**HQ232188**	Ex-type of *Acremonium curvulum*
	CBS 104.78	**HQ232019**		
	CBS 214.70	**HQ232020**		
	CBS 229.75	**HQ232021**		
	CBS 333.92	**HQ232022**		
	CBS 384.70A	**HQ232023**		
	CBS 384.70C	**HQ232024**		
	CBS 523.72	**HQ232028**		
	CBS 761.69	**HQ232029**		
	CBS 898.85	**HQ232030**		
	CBS 110514	**HQ232032**		
"Acremonium aff. *curvulum"*	CBS 100551	**HQ232031**		
	CBS 113275	**HQ232033**		
Acremonium egyptiacum	CBS 303.64	**HQ232034**	**HQ232189**	
Acremonium exiguum T	CBS 587.73	**HQ232035**	**HQ232190**	Ex-type of *Acremonium exiguum*
Acremonium exuviarum T	UAMH 9995	**HQ232036**		
Acremonium flavum T	CBS 596.70	**HQ232037**	**HQ232191**	Ex-type of *Acremonium flavum*
Acremonium fuci	UAMH 6508	**HQ232038**		
Acremonium furcatum T	CBS 122.42	AY378154	**HQ232192**	Ex-type of *Acremonium furcatum*

Table 1. (Continued).

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
Acremonium fusidioides T	CBS 840.68	**HQ232039**		Ex-type of *Paecilomyces fusidioides*
Acremonium gamsii T	CBS 726.71	**HQ232040**	**HQ232193**	Ex-type of *Acremonium gamsii*
Acremonium guillematii T	CBS 766.69	**HQ232042**	**HQ232194**	Ex-type of *Acremonium guillematii*
Acremonium hansfordii	CBS 390.73	**HQ232043**		
Acremonium hennebertii T	CBS 768.69	**HQ232044**		Ex-type of *Acremonium hennebertii*
Acremonium hyalinulum	CBS 271.36	**HQ232045**	**HQ232195**	
"Acremonium implicatum"	CBS 243.59	**HQ232046**	**HQ232196**	Authentic strain of *Fusarium terricola*
	CBS 397.70B	**HQ232047**		
*Acremonium incrustatum*T	CBS 159.70	**HQ232049**		
Acremonium inflatum T	CBS 212.69	**HQ232050**		Ex-type of *Gliomastix inflata*
	CBS 439.70	**HQ232051**		
	CBS 403.70	**HQ231991**		In CBS as *Acremonium atrogriseum*
Acremonium lichenicola T	CBS 425.66	**HQ231969**	–	Ex-type of *Acremonium lichenicola*
Acremonium longisporum	CBS 113.69	**HQ232057**		
"Acremonium luzulae"	CBS 495.67	**HQ232058**		
	CBS 579.73	**HQ232059**		
Acremonium minutisporum T	CBS 147.62	**HQ232061**	**HQ232199**	Ex-type of *Cephalosporium minutisporum*
	det 267B	**HQ232062**		
Acremonium nepalense T	CBS 971.72	**HQ231970**	–	Ex-type of *Acremonium nepalense*
Acremonium nigrosclerotium T	CBS 154.72	**HQ232069**	**HQ232200**	Ex-type of *Acremonium nigrosclerotium*
Acremonium persicinum T	CBS 310.59	**HQ232077**	**HQ232201**	Ex-type of *Paecilomyces persicinus*
	CBS 169.65	**HQ232072**		
	CBS 295.70A	**HQ232075**		
	CBS 295.70M	**HQ232076**		
	CBS 330.80	**HQ232078**		
	CBS 378.70A	**HQ232079**		
	CBS 378.70D	**HQ232081**		
	CBS 378.70 E	**HQ232082**		
	CBS 439.66	**HQ232083**		
	CBS 469.67	**HQ232084**		
	CBS 101694	**HQ232085**		
	CBS 102349	**HQ232086**		
"Acremonium persicinum"	CBS 378.70C	**HQ232080**		
	CBS 110646	**HQ232088**		
"Acremonium aff. *persicinum"*	CBS 203.73	**HQ232073**		
	CBS 263.89	**HQ232074**		
"Acremonium cf. *persicinum"*	CBS 102877	**HQ232087**		
Acremonium pinkertoniae T	CBS 157.70	**HQ232089**	**HQ232202**	Ex-type of *Acremonium pinkertoniae*
"Acremonium potronii"	CBS 189.70	**HQ232094**		
	CBS 379.70F	**HQ232096**		
	CBS 416.68	**HQ232097**	**HQ232203**	
	CBS 433.88	**HQ232098**		
	CBS 781.69	**HQ232099**		
Acremonium psammosporum T	CBS 590.63	**HQ232100**	**HQ232204**	Ex-type of *Acremonium psammosporum*
Acremonium pseudozeylanicum T	CBS 560.73	**HQ232101**		Ex-type of *Acremonium pseudozeylanicum*
Acremonium pteridii T	CBS 782.69	**HQ232102**		Ex-type of *Acremonium pteridii*
	CBS 784.69	**HQ232103**		
Acremonium radiatum T	CBS 142.62	**HQ232104**	**HQ232205**	Ex-type of *Cephalosporium acremonium* var. *radiatum*
Acremonium recifei T	CBS 137.35	**HQ232106**	**HQ232206**	Ex-type of *Cephalosporium recifei*
	CBS 135.71	**HQ232105**		
	CBS 220.84	**HQ232107**		
	CBS 362.76	**HQ232108**		
	CBS 402.89	**HQ232109**		
	CBS 411.91	**HQ232110**		
	CBS 442.66	**HQ232111**		
	CBS 541.89	**HQ232114**		
	CBS 555.73	**HQ232115**		
	CBS 596.74	**HQ232116**		
	CBS 976.70	**HQ232117**		
	CBS 400.85	**HQ232025**		In CBS as *Acremonium curvulum*
	CBS 505.94	**HQ232027**		In CBS as *Acremonium cf. curvulum*
"Acremonium recifei"	CBS 485.77	**HQ232113**		
	CBS 482.78	**HQ232112**		

Table 1. (Continued).

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
	CBS 110348	**HQ232118**		
Acremonium restrictum T	CBS 178.40	**HQ232119**	–	Ex-type of *Verticillium dahliae* f. *restrictum*
Acremonium rhabdosporum T	CBS 438.66	**HQ232120**		Ex-type of *Acremonium rhabdosporum*
Acremonium roseolum T	CBS 289.62	**HQ232123**	**HQ232207**	Ex-type of *Paecilomyces roseolus*
Acremonium rutilum T	CBS 396.66	**HQ232124**	**HQ232208**	Ex-type of *Acremonium rutilum*
Acremonium salmoneum T	CBS 721.71	**HQ232125**		Ex-type of *Acremonium salmoneum*
Acremonium sclerotigenum T	CBS 124.42	**HQ232126**	**HQ232209**	Ex-type of *Cephalosporium sclerotigenum*
	CBS 270.86	**HQ232127**		
	CBS 281.80	**HQ232128**		
	CBS 384.65	**HQ232129**		
	CBS 786.69	**HQ232130**		
	CBS 100816	**HQ232131**		
	OMH F1648.97	**HQ232132**		
	OMH F2365.97	**HQ232133**		
	OMH F2969.97	**HQ232134**		
	OMH F3691.97	**HQ232135**		
	CBS 287.70O	**HQ232140**		In CBS as *Acremonium strictum*
	CBS 379.70D	**HQ232095**		In CBS as *Acremonium potronii*
	CBS 223.70	**HQ231985**		In CBS as *Acremonium alternatum*
Acremonium sordidulum T	CBS 385.73	**HQ232136**		Ex-type of *Acremonium sordidulum*
Acremonium sp.	CBS 314.72	**HQ232156**		
Acremonium spinosum T	CBS 136.33	**HQ232137**	**HQ232210**	Ex-type of *Cephalosporium spinosum*
"Acremonium strictum"	CBS 106.23	**HQ232138**		
	CBS 147.49	**HQ232139**		
Acremonium stromaticum T	CBS 863.73	**HQ232143**	–	Ex-type of *Acremonium stromaticum*
Acremonium tectonae T	CBS 725.87	**HQ232144**		Ex-type of *Acremonium tectonae*
Acremonium thermophilum T	CBS 734.71	**HQ232145**	–	Ex-type of *Acremonium thermophilum*
Acremonium tsugae T	CBS 788.69	**HQ232146**		Ex-type of *Acremonium tsugae*
Acremonium tubakii T	CBS 790.69	**HQ232148**		Ex-type of *Acremonium tubakii*
"Acremonium tubakii"	CBS 824.69	**HQ232149**		
Acremonium verruculosum T	CBS 989.69	**HQ232150**		Ex-type of *Acremonium verruculosum*
Acremonium vitellinum T	CBS 792.69	**HQ232151**	**HQ232212**	Ex-type of *Acremonium vitellinum*
Acremonium zeylanicum	CBS 746.73	**HQ232154**		
Acremonium zonatum	CBS 565.67	**HQ232155**		
"Cephalosporium acremonium var. cereum" T	CBS 140.62	**HQ232147**		Ex-type of *Cephalosporium acremonium* var. *cereum*. In CBS as *Acremonium tubakii*
"Cephalosporium acremonium var. funiculosum" T	CBS 141.62	**HQ232053**		Ex-type of *Cephalosporium acremonium* var. *funiculosum*. In CBS as *Acremonium kiliense*
"Cephalosporium ballagii" T	CBS 134.33	**HQ232016**		Ex-type of *Cephalosporium ballagii*. In CBS as *Acremonium charticola*
"Cephalosporium malorum" T	CBS 117.25	**HQ232015**		Ex-type of *Cephalosporium malorum*. In CBS as *Acremonium charticola*
"*Cephalosporium purpurascens*" T	CBS 149.62	**HQ232071**		Ex-type of *Cephalosporium purpurascens*. In CBS as *Acremonium persicinum*
Cosmospora khandalensis T	CBS 356.65	**HQ231996**		Ex-type of *Cephalosporium khandalense*. In CBS as *Acremonium berkeleyanum*
*Cosmospora lavitskiae*T	CBS 530.68	**HQ231997**		Ex-type of *Gliomastix lavitskiae*. In CBS as *Acremonium berkeleyanum*
Gliomastix masseei	CBS 794.69	**HQ232060**		In CBS as *Acremonium masseei*
Gliomastix murorum	CBS 154.25	**HQ232063**		Ex-type of *Graphium malorum*. In CBS as *Acremonium murorum* var. *felina*
	CBS 195.70	**HQ232064**		In CBS as *Acremonium murorum* var. *felina*
	CBS 119.67	**HQ232066**		In CBS as *Acremonium murorum* var. *murorum*
	CBS 157.72	**HQ232067**		In CBS as *Acremonium murorum* var. *murorum*
	CBS 378.36	**HQ232068**		Ex-type of *Torula cephalosporioides*. In CBS as *Acremonium murorum* var. *murorum*
Gliomastix polychroma T	CBS 181.27	**HQ232091**		Ex-type of *Oospora polychroma*. In CBS as *Acremonium polychromum*
	CBS 151.26	**HQ232090**		Ex-type of *Periconia tenuissima* var. *nigra*. In CBS as *Acremonium polychromum*
	CBS 617.94	**HQ232093**		In CBS as *Acremonium polychromum*
Gliomastix roseogrisea T	CBS 134.56	**HQ232121**		Ex-type of *Cephalosporium roseogriseum*. In CBS as *Acremonium roseogriseum*
	CBS 279.79	**HQ232122**		In CBS as *Acremonium roseogriseum*
	CBS 213.69	**HQ232092**		In CBS as *Acremonium polychromum*
	CCFC 226570	AY283559		Identified as *Acremonium murorum* var. *felina*
	CBS 211.69	**HQ232065**		In CBS as *Acremonium murorum* var. *felina*
Lanatonectria flavolanata	CBS 230.31	**HQ232157**		

Table 1. (Continued).

Currently assigned species name	Collection numbers	nucLSU	nucSSU	Notes
Lanatonectria flocculenta	CBS 113461	**HQ232158**		
Leucosphaerina arxii T	CBS 737.84	**HQ232159**		Ex-type of *Leucosphaerina arxii*
Nalanthamala diospyri T	CBS 560.89	**HQ232160**		Ex-type of *Cephalosporium diospyri* = *Acremonium diospyri*
Nectria rishbethii T	CBS 496.67	**HQ232162**		Ex-type of *Nectria rishbethii*
Neocosmospora endophytica	AR 2674	U17411		Anamorph is *Acremonium fungicola*
Paecilomyces lilacinus	CBS 101068	**HQ232163**	**HQ232214**	Atypical monophialidic isolate, *Acremonium+E402*-like
Pochonia bulbillosa	CBS 102853	**HQ232164**		Atypical isolate
Sarcopodium circinatum	CBS 376.81	**HQ232167**		
	CBS 587.92	**HQ232168**		
	CBS 114068	**HQ232169**		
Sarcopodium circinosetiferum	CBS 100251	**HQ232170**		
	CBS 100252	**HQ232171**		
	CBS 100998	**HQ232172**		
	CBS 101116	**HQ232173**		
Sarcopodium vanillae	CBS 100582	**HQ232174**		
Sarocladium attenuatum T	CBS 399.73	**HQ232165**		Ex-type of *Sarocladium attenuatum*
Sarocladium bacillisporum T	CBS 425.67	**HQ231992**	**HQ232179**	Ex-type of *Acremonium bacillisporum*
Sarocladium bactrocephalum T	CBS 749.69	**HQ231994**	**HQ232180**	Ex-type of *Acremonium bactrocephalum*
	NRRL 20583	**HQ231995**		
Sarocladium glaucum T	CBS 796.69	**HQ232041**		Ex-type of *Acremonium glaucum*
Sarocladium kiliense T	CBS 122.29	**HQ232052**	**HQ232198**	Ex-type of *Acremonium kiliense*
	CBS 146.62	**HQ232048**	**HQ232197**	Ex-type of *Cephalosporium incoloratum.* In CBS as *Acremonium incoloratum*
	CBS 155.61	**HQ232054**		Ex-type of *Cephalosporium incarnatum.* In CBS as *Acremonium kiliense*
	CBS 156.61	**HQ232055**		Ex-type of *Cephalosporium incarnatum* var. *macrospora.* In CBS as *Acremonium kiliense*
	CBS 157.61	**HQ232056**		Ex-type of *Cephalosporium infestans.*In CBS as *Acremonium kiliense*
Sarocladium ochraceum T	CBS 428.67	**HQ232070**		Ex-type of *Paecilomyces ochraceus.* In CBS as *Acremonium ochraceum*
Sarocladium oryzae	CBS 180.74	**HQ232166**		
Sarocladium strictum T	CBS 346.70	**HQ232141**	**HQ232211**	Ex-type of *Acremonium strictum*
"Sarocladium cf. strictum"	JY03-006	**HQ232142**		
Sarocladium zeae T	CBS 801.69	**HQ232152**	**HQ232213**	Ex-type of *Acremonium zeae*
	KAS 965	**HQ232153**		
Simplicillium lanosoniveum	CBS 321.72	**HQ232006**	**HQ232185**	Ex-type of *Acremonium byssoides*
Simplicillium obclavatum T	CBS 311.74	**HQ232175**		Ex-type of *Acremonium obclavatum*
Trichothecium crotocinigenum T	CBS 129.64	**HQ232018**		Ex-type of *Acremonium crotocinigenum*
*"Trichothecium indicum"/ Leucosphaerina indica*T	CBS 123.78	AF096194		Ex-type of *'Leucosphaera' indica*
Trichothecium roseum	DAOM 208997	U69891		
Trichothecium sympodiale	ATCC 36477	U69889		In CBS as *Spicellum roseum*
Verticillium alboatrum	CBS 130.51	**HQ231976**	–	Ex-type of *Cephalosporium apii,* in CBS as *Acremonium apii*
Verticillium insectorum	CBS 101239	**HQ248107**		
Verticillium leptobactrum	CBS 109351	**HQ231993**		In CBS as *Acremonium cf. bacillisporum*

Nine of the named *Acremonium* species in this analysis belong to the *Plectosphaerellaceae*. The *Sordariales* are represented in Fig. 1 only by *Acremonium alabamense*, the only named *Acremonium* species in *Acremonium* section *Chaetomioidea*. Outside these groups *Acremonium atrogriseum,* represented by numerous conspecific isolates, belongs to the family *Cephalothecaceae* (Fig. 1C), along with *Albertiniella polyporicola* and *Cephalotheca sulfurea*; this family is sister to the *Coniochaetales.* Another *Acremonium* species, *A. thermophilum*, falls into the *Cephalothecaceae* clade grouping with *Albertiniella polyporicola*. An isolate provisionally identified as *Acremonium alternatum*, CBS 109043 is a member of the *Cephalothecaceae*. The complex status of *A. alternatum* is discussed below.

The *Acremonium* species in the *Hypocreales* form an array of poorly to well distinguished clades, most of which do not correspond to previously recognised genera or suprageneric taxa. Included within the *Hypocreales* in the *Sarocladium* clade labeled the "*strictum*-clade" is the well known soil fungus long known as *Acremonium strictum* (Fig. 1A). The soil fungus and human opportunistic pathogen traditionally called *A. kiliense* is also included as is the maize corn endophyte known as *A. zeae.* The corresponding clade in Fig. 2C based on LSU reveals that this group of fungi includes the rice pathogen *Sarocladium oryzae* as a saltatory morphological apomorph. No teleomorphs are known to be associated with this group. This clade consists of fungi forming conidia in mucoid heads; it is closely related to a clade of species forming catenulate conidia, namely the *Acremonium bacillisporum* clade including *A. bacillisporum*, *A. glaucum*, *A. implicatum* pro parte, and, in a separate subclade, *A. ochraceum* (Figs 1A, 2C). The "bacillisporum-clade" and "strictum-clade" grouped together in an overall *Sarocladium* clade (Figs 1, 2). Two catenulate-conidial isolates labeled *A. alternatum* are also loosely associated with the *A. bacillisporum* clade in Fig. 2C. In Fig. 1A, one isolate CBS 406.66 is connected to the *Sarocladium* and *A. breve/curvulum* clades with a 96 % bootstrap value.

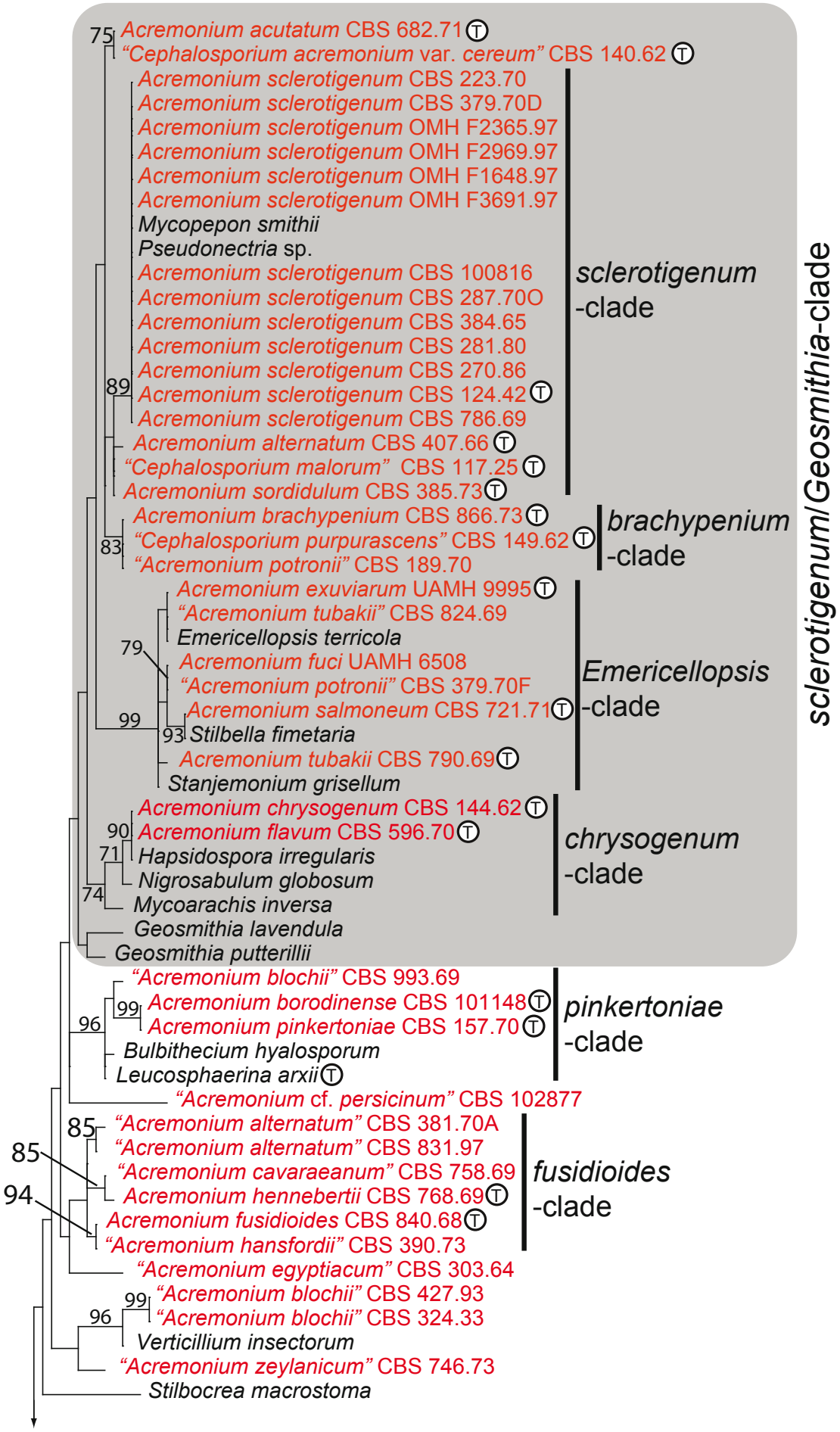

Fig. 2.A–E. The phylogenetic position of *Acremonium* and related fungi within the *Hypocreales*, as seen in nucLSU analysed by maximum likelihood via RAxML VI-HPC following a GTRMIX model applied to a single partition. 100 % bootstrap values are indicated by a black dot on the relevant internode.

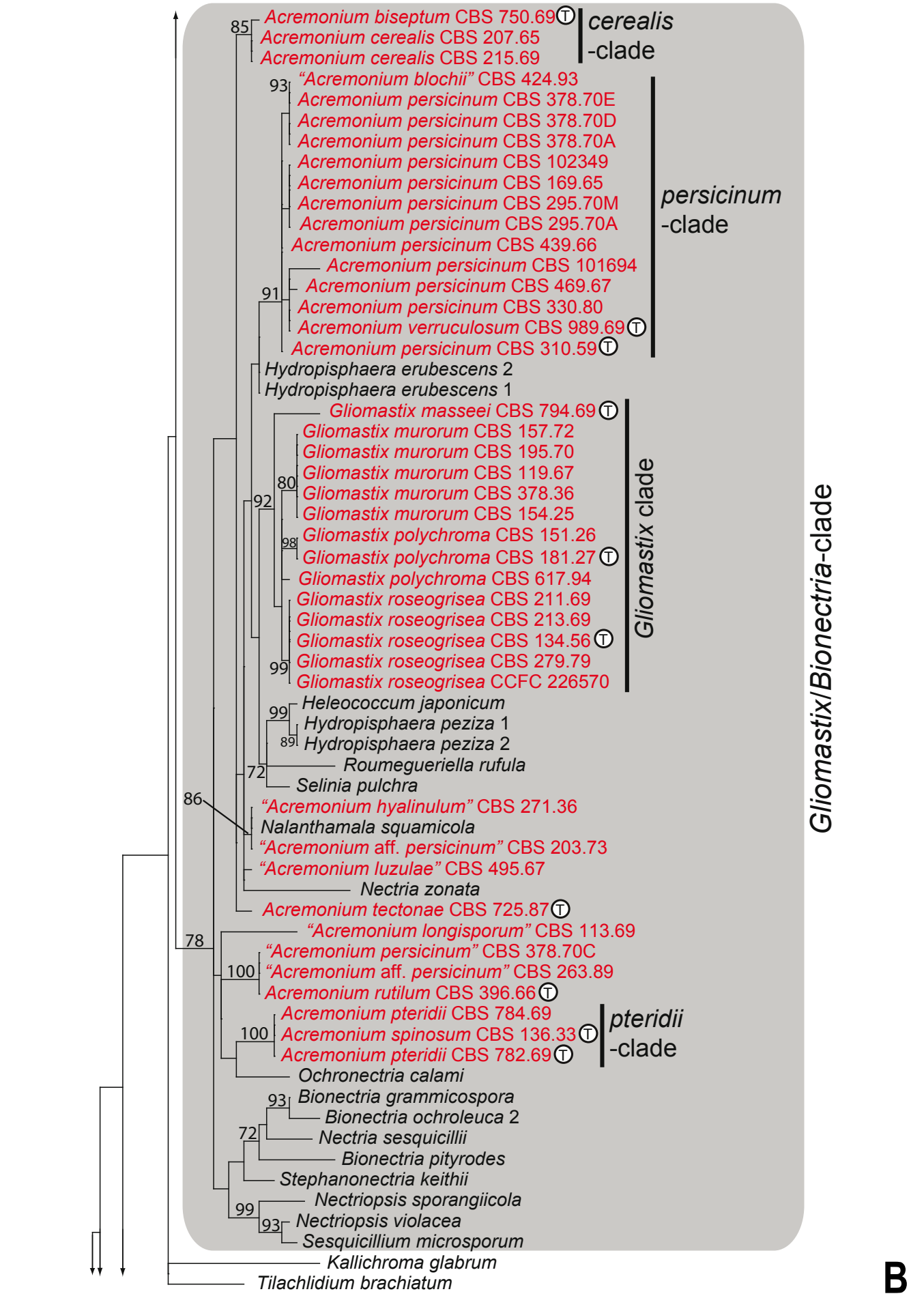

Fig. 2. (Continued).

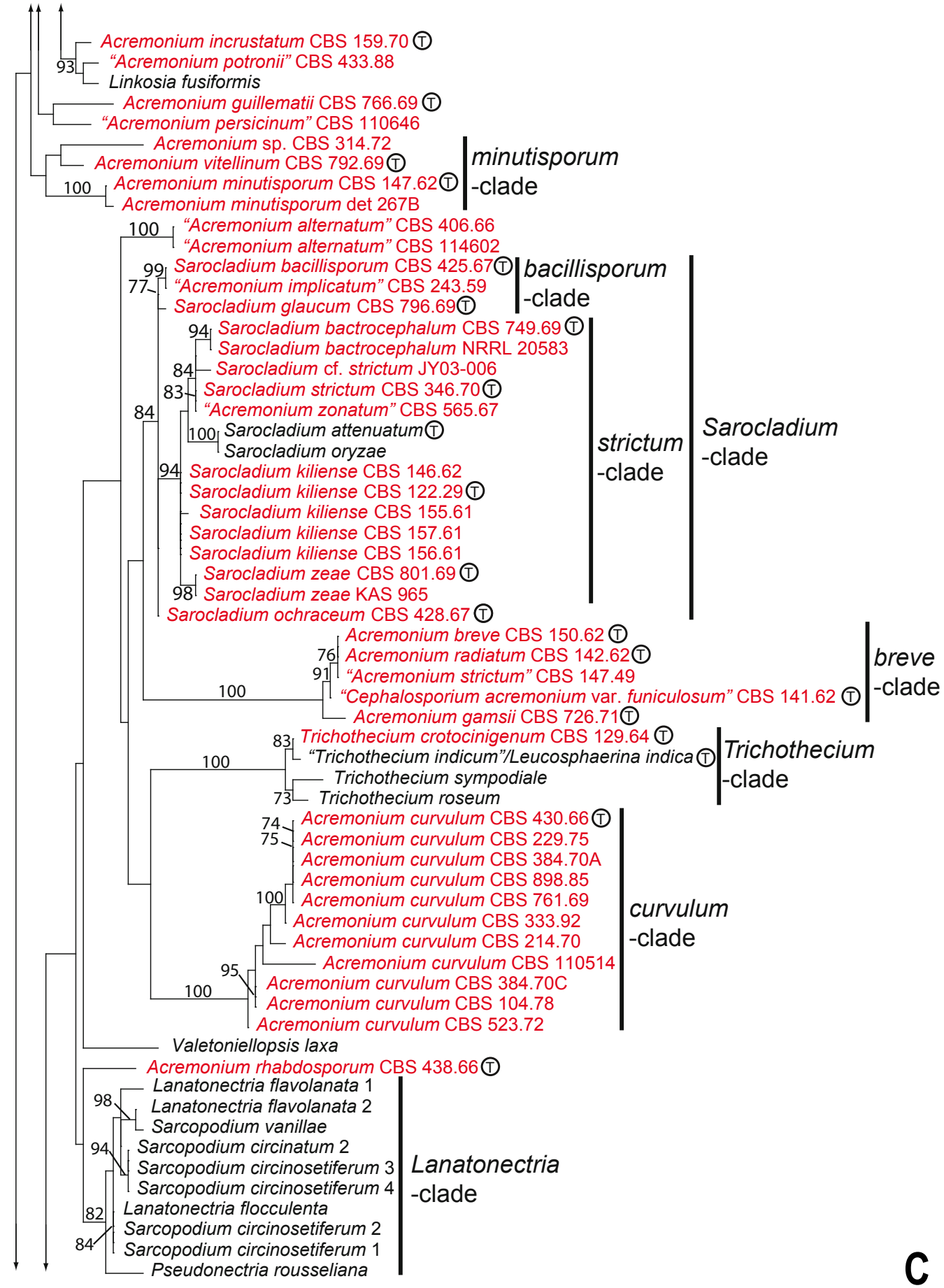

Fig. 2. (Continued).

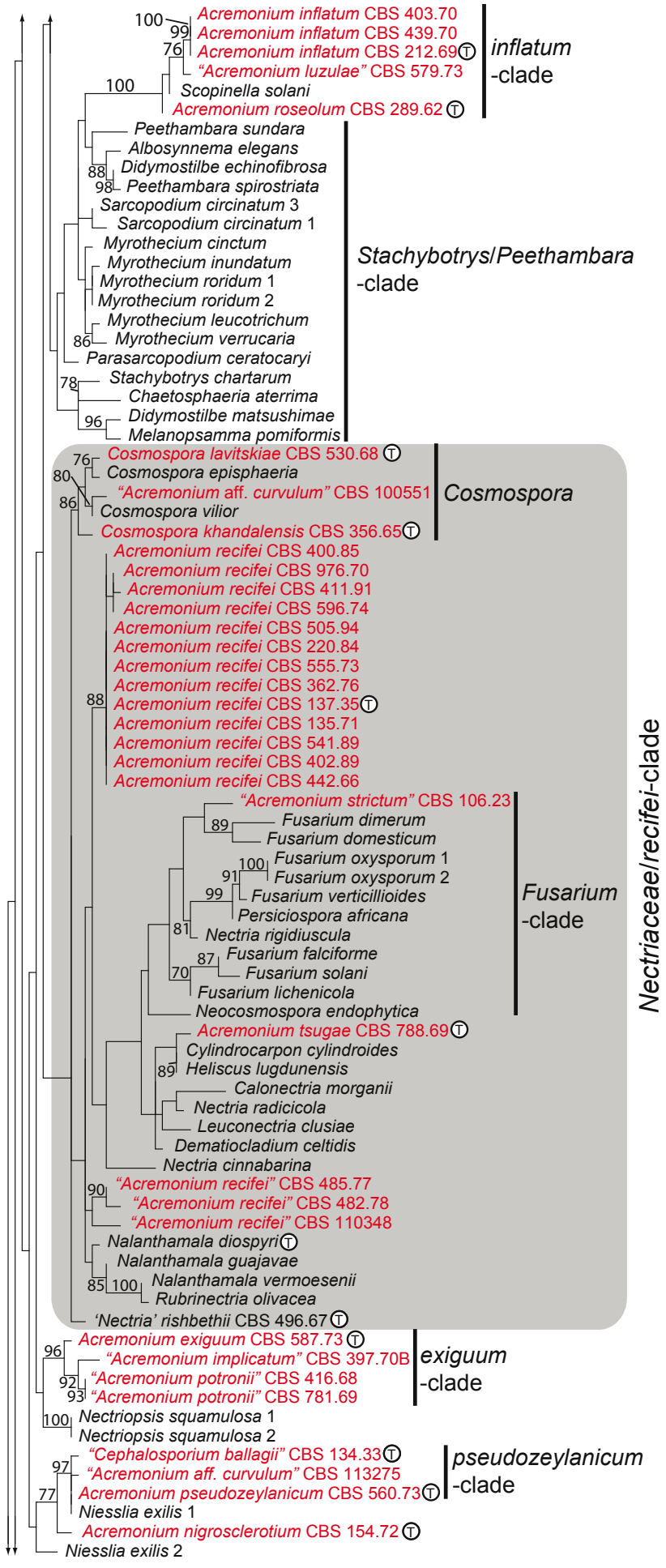

Fig. 2. (Continued).

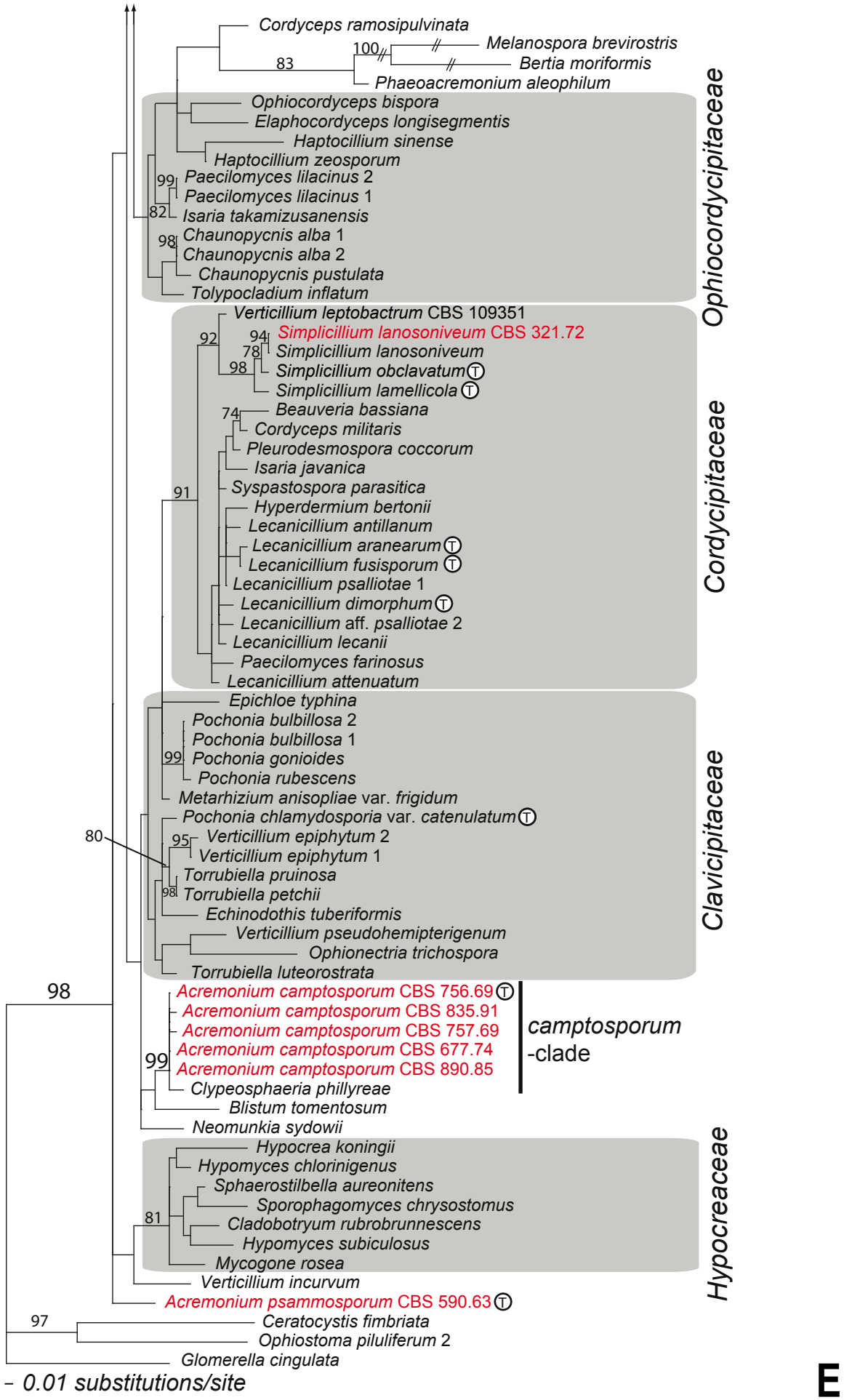

Fig. 2. (Continued).

Another major hypocrealean *Acremonium* clade in Fig. 1A contains *A. breve, A. radiatum, A. gamsii* and, more distantly, with 96 % bootstrap support, *A. curvulum*. In Fig. 2C where phylogenetic signal is lower, *A. curvulum* loses its tight association with *A. breve* and its relatives and appears in unsupported juxtaposition with the genus *Trichothecium* and the corresponding teleomorph genus, *Leucosphaerina*. The clade containing *Trichothecium roseum* and *Leucosphaerina indica* (see taxonomic comments below) also contains two anamorph species that were long placed in different genera based on conidiogenesis, namely, *Acremonium crotocinigenum* and *Spicellum roseum,* here recombined into *Trichothecium*.

The next clade in Fig. 1A is a loosely structured assemblage consisting of members of *Acremonium* subgenus *Gliomastix,* some of which are delineated below as members of a phylogenetically delineated genus *Gliomastix,* plus the teleomorphic genera *Bionectria,* linked to the well known penicillate hyphomycete anamorph genus *Clonostachys* (Schroers 2001), *Hydropisphaera,* and *Roumegueriella*. As Fig. 2B shows in more detail, the type species of the genus *Gliomastix*, originally named *Gliomastix chartarum* but currently called *G. murorum*, is in a relatively well supported clade (92 % bootstrap support) along with *G. masseei*, *G. polychroma,* and *G. roseogrisa,* three other species with melanised conidia that were placed in *Acremonium* subg. *Gliomastix* by Gams (1971). Related to *Gliomastix* are two clades of non-melanised *Acremonium* species placed in *A.* subg. *Gliomastix*, the *A. persicinum* clade, and *A. pteridii* clade. Smaller clades containing species in *A.* subg. *Gliomastix* such as *A. biseptum, A. cerealis, A. luzulae,* and *A. rutilum* (= *A. roseum*) are included in the large *Gliomastix/Bionectria* clade, which has 78 % bootstrap support. This clade includes additional teleomorphic fungi such as *Heleococcum, Hydropisphaera, Nectriopsis, Ochronectria, Selinia,* and *Stephanonectria*, along with the anamorph *Sesquicillium microsporum*.

The *Gliomastix/Bionectria* clade, the *sclerotigenum/Geosmithia* clade, and other members of the *Bionectriaceae* form a weakly supported clade with 74 % bootstrap value as shown in Fig. 1A. Included in the *sclerotigenum/Geosmithia* clade is the penicillate anamorph genus *Geosmithia sensu stricto* and the ex-type isolates of *Acremonium pinkertoniae* and *A. sclerotigenum* as well as the cephalosporin-producer *Acremonium chrysogenum* and its close relative, the thermophilic *A. flavum*. It also includes non-type isolates identified as *A. blochii* and *A. egyptiacum*. In the LSU-tree (Fig. 2A) the *sclerotigenum/Geosmithia* clade includes an extensive group of *Acremonium* species and cleistothecial *Bionectriaceae* with *Acremonium*-like anamorphs, namely, *Emericellopsis*, *Hapsidospora, Mycoarachis,* and *Nigrosabulum.* Among the anamorphic species in this group are most of the phylogenetically disparate isolates identified as the type species of *Acremonium*, *A. alternatum*. One of these, CBS 407.66, is designated below as epitype of *A. alternatum*. Prominent subclades include the *Acremonium sclerotigenum* clade containing the ex-type isolates of *A. sclerotigenum* and *A. sordidulum*.

Another major, well supported bionectriaceous subclade associated with the *sclerotigenum* clade is the *Emericellopsis* clade (Fig. 2A). It includes the type species of the synnematal hyphomycete genus *Stilbella*, *S. fimetaria* (Seifert 1985) as well as the type of *Stanjemonium* (Gams *et al*. 1998) and the marine *Acremonium tubakii sensu stricto* and *A. fuci* (Zuccaro *et al*. 2004). *Stilbella fimetaria* is closely related to the ex-type isolate of *Acremonium salmoneum* isolated from dung, also a typical habitat for *S. fimetaria* (Seifert 1985). An adjacent weakly supported clade includes *Hapsidospora, Mycoarachis,* and *Nigrosabulum,* and the two *Acremonium* species named for yellow pigmentation, *A. chrysogenum* and *A. flavum*. Although associated with *A. chrysogenum* and *A. flavum* in Fig. 1B, *A. pinkertoniae* and *A. borodinense* form a distinct clade in Fig. 2A along with an isolate included in the polyphyletic *A. blochii* (CBS 993.69), plus the cleistothecial teleomorphs *Bulbithecium hyalosporum* and *Leucosphaerina arxii,* both of which have unnamed *Acremonium* anamorphs. In Fig. 2A, the *A. chrysogenum* subclade appears to be distinct from the other clades containing *A. sclerotigenum, Emericellopsis,* and *Geosmithia*. The other clades within the overall *sclerotigenum/Geosmithia* clade include the *A. fusidioides* clade containing several acremonia forming similar conidial chains (*A. cavaraeanum, A. fusidioides, A. hansfordii, A. hennebertii,* one of the isolates labeled *A. alternatum*). A small *A. brachypenium* clade associated with the *A. sclerotigenum* clade includes *A. brachypenium* plus the ex-type strain of *Cephalosporium purpurascens* placed by Gams (1971) in *A. persicinum*. There is also an isolate of the polyphyletic, untypified species *A. potronii*. Basal to these clades is another small clade that links an entomogenous isolate identified as *Verticillium insectorum* with two isolates from human sources identified as *A. blochii*; these conidial chain-forming isolates are sister to an isolate of the chain-forming entomogenous species *Acremonium zeylanicum*. The "*A. blochii*" isolate CBS 427.93, linked with a 99 % bootstrap value to *A. pinkertoniae* in Fig. 1B, is one of the two isolates associated with *Acremonium zeylanicum* in Fig. 2A.

Adjacent and loosely linked to the bionectriaceous clades in Fig. 2B is a small clade in Fig. 2C containing the ex-type isolate of *Acremonium incrustatum* plus an isolate labeled *A. potronii*, and a sequence attributed to *Linkosia fusiformis*, although this sequence most likely represents a contaminant.

Below the *sclerotigenum/Geosmithia* clade in Fig. 1A and above the *Hypocreaceae* in Fig. 2E fall clades representing the *Clavicipitaceae sensu lato*. These clades include the families *Clavicipitaceae sensu stricto*, *Ophiocordycipitaceae*, and *Cordycipitaceae*. Although many species in this group of three families have *Acremonium*-like anamorphic states, only two described *Acremonium* species are associated here. In Fig. 2E *A. camptosporum* sits basally in a clade adjacent to the *Clavicipitaceae* and is close to the poorly understood teleomorphic species *Clypeosphaeria phillyreae*, assuming the latter is correctly associated with the sequence attributed to it. *Simplicillium obclavatum,* originally described as *Acremonium obclavatum,* provides the only other clavicipitaceous species in Fig. 2 representing a named species of *Acremonium*.

Below the *Clavicipitaceaceae* in Fig. 1B is a clade of ambiguous affinities containing *Acremonium guillematii, A. minutisporum* and *A. vitellinum*. This group also appears as two to three unaffiliated clades in Fig. 2C. An insignificant branch in Fig. 1B subtends *Acremonium exiguum, A. psammosporum,* and an isolate identified as *A. potronii*. In Fig. 2D, just *A. exiguum* and the *A. potronii* entity remain associated while *Acremonium psammosporum* segregates into a basal hypocrealean clade of its own in Fig. 2E.

The *Nectriaceae* is represented by *Nectria cinnabarina* in Fig. 1B along with the ex-type isolate of the tropical opportunistic pathogen of humans, *Acremonium recifei.* Fig. 2D shows *A. recifei* subtending multiple taxa with three non-type isolates splitting off as a separate clade. These clades have approximately the same status in the *Nectriaceae* as the genus *Nalanthamala*, including *N. diospyri*, the former *Acremonium diospyri.* Another nectriaceous *Acremonium* in Fig. 2D is *A. tsugae*, which is closely related

to *Cylindrocarpon cylindroides*. The broad morphotaxonomic concept of *Acremonium berkeleyanum* is polyphyletic consisting of isolates placed in the nectriaceous genus *Cosmospora* (Fig. 2D). *Acremonium berkeleyanum sensu lato* is represented in Fig. 2D by the newly recombined *Cosmospora* species, *C. lavitskiae* and *C. khandalensis* based on the ex-type isolates of *Gliomastix lavitskiae* and *Cephalosporium khandalense* (Gräfenhan *et al.* 2011). Another purported synonym of *A. berkeleyanum*, a *Cadophora* isolate received as *A. butyri* CBS 301.38, falls outside the *Hypocreales* (Fig. 1C).

Basally in the *Hypocreales* in Fig. 1B, *Acremonium roseolum* appears in loose association with *Stachybotrys* species. In Fig. 2D, it appears in a clade along with the teleomorph *Scopinella solani* and three *Acremonium inflatum* isolates, including CBS 403.70, an atypical, catenate-conidial isolate identified at CBS as *A. atrogriseum*. Nearby but statistically unlinked clades include *Stachybotrys* and allied fungi such as *Peethambara spirostriata* and *Didymostilbe echinofibrosa* (Castlebury *et al*. 2004).

Acremonium nigrosclerotium represents an isolated *Acremonium* near the families *Hypocreaceae* and *Niessliaceae* (Fig. 1B). In Fig. 2D, *A. nigrosclerotium* is intercalated among two genotypes ascribed to *N. exilis*, and loosely associated (77 % bootstrap) with *Acremonium pseudozeylanicum* and the type culture of *Cephalosporium ballagii*, currently in synonymy with *Acremonium charticola* (Gams 1971).

A distant outlier is *Acremonium lichenicola* at the bottom of Fig. 1C. This isolate, CBS 425.66, chosen to represent this species in lieu of ex-type material, blasts as a pezizalean fungus with affinities to another hyaline, phialidic fungus, *Phialophora alba*.

A number of genera in addition to *Acremonium* were investigated for possible affinity with *Acremonium* clades as shown in Fig. 2. The sporodochial genus *Sarcopodium* was investigated and found to split into two groups (Fig. 2C, D). One isolate identified as *S. circinatum* grouped with *Sarcopodium circinosetiferum* and *S. vanillae* in a widely separated clade along with *Lanatonectria* teleomorphs and a sequence identified as *Pseudonectria rousseliana* (Fig. 2C). This clade appeared in LSU sequencing to be independently situated within the *Hypocreales*. *Acremonium rhabdosporum* appeared as a statistically unsupported, possible distant relative. The other two isolates of *S. circinatum* formed a clade near *Myrothecium* in the *Stachybotrys/Peethambara* clade (Fig. 2D). Also appearing in this clade was *Parasarcopodium ceratocaryi*, a monotypic genus recently described by Mel'nik *et al*. (2004).

DISCUSSION

The main morphotaxonomic groundwork for *Acremonium* as conceived in the late 20th century was laid by Gams (1971) in his monograph *Cephalosporium-artige Schimmelpilze* (*Hyphomycetes*). This monograph was radically more comprehensive than previous treatments of the species and was followed by several key adjunct studies, including but not limited to Gams & Lacey (1972), Gams (1975), and Ito *et al*. (2000). Gams' studies were based on a meticulous morphological observation scheme that involved growing species on appropriate media, *e.g.*, oatmeal agar, and then making camera lucida drawings that could be directly compared with subsequent isolates. The comparison was done by superimposing the virtual image of the new isolate directly over the camera lucida drawings of previous isolates drawn at the same scale. This highly rigorous approach was necessary for a group of hyphomycetous fungi so morphologically simplified as *Acremonium*.

Gams (1971, 1975) also discovered a subtle character that allowed him to associate dark-conidial species, monographed by Dickinson (1968) as the genus *Gliomastix,* with numerous biologically related hyaline-conidial species. This character was "chondroid hyphae," which could be seen under the microscope as hyphae with wall thickenings, and which makes colonies somewhat resistant to being cut with a scalpel. The species Gams (1971) united using this character are, for the most part, grouped in the *Gliomastix/Bionectria* clade referred to earlier in this study.

Despite the rigorous approach and the discovery of new, useful characters, a number of the morphotaxonomic species names ultimately were applied in the CBS collection to phylogenetically divergent organisms. Six distinct taxa from CBS investigated in this study were identified as *A. persicinum*; three are now seen phylogenetically to fall within the *Gliomastix* clade and three sort elsewhere. These taxa are mostly directly visible as *A. persicinum* isolates in Fig. 2. Names without quotation marks are consistent with the type, while names in quotation marks sort into other phylogenetic groups. An exception is represented by CBS 149.62. This isolate, the ex-type of *Cephalosporium purpurascens*, was listed by Gams (1971) as a synonym of *A. persicinum*. Five taxa in Fig. 2 were labeled *A. potronii* in CBS, and four were called *A. strictum*. Within both *A. potronii* and *A. strictum*, as conceived morphologically, some isolates fall within *A. sclerotigenum*. The name *A. alternatum* was applied to four species, three of them visible in Fig. 2, plus isolates of *A. sclerotigenum* with catenulate conidia. "*Acremonium blochii*" was applied to three different species.

Phylogenetic analysis compared to the morphological treatment of *Acremonium*

Gams (1971, 1975) divided *Acremonium* into three major sections, *Simplex*, a name later updated as the type section *Acremonium*, *Gliomastix,* and *Nectrioidea*. Of these sections, only *Gliomastix* withstands phylogenetic scrutiny as a unit, albeit a loosely associated one.

The type section *Acremonium* contained four widely phylogenetically scattered major clades (Fig. 2), specifically the *A. sclerotigenum* clade, *Sarocladium* clade, *A. curvulum* clade, and *A. breve* clade. As seen best in Fig. 1, the *Sarocladium* clade and the *A. breve* and *A. curvulum* clades comprise a distinct group that falls within the *Hypocreales* but outside any currently recognised family. *Acremonium sclerotigenum* falls into a distinct clade within the *Bionectriaceae* that also contains *Emericellopsis* and *Geosmithia*. This clade also includes about half the investigated CBS isolates identified as the type species of *Acremonium*, *A. alternatum*, including CBS 407.66 as well as some isolates such as CBS 223.70 revealed as morphological variants of *A. sclerotigenum*. Despite the substantial phylogenetic distance between *A. sclerotigenum* and *A. strictum*, relatively glabrous, cylindrical-conidial isolates of *A. sclerotigenum* not producing sclerotia on special media (lupine stem agar according to Gams, 1971, later replaced at CBS by nettle stem agar) are essentially micromorphologically indistinguishable from *A. strictum*. Table 1 shows CBS 287.70 O as an *A. sclerotigenum* isolate identified in CBS as *A. strictum*; ITS sequencing studies of additional strains (data not shown) have found two more such isolates, CBS 319.70 D and CBS 474.67.

The convergence among isolates of phylogenetically remote species is remarkable. An unknown proportion of the literature on *A. strictum* is based on studies of *A. sclerotigenum*. For example, in a study influential in medical mycology, Novicki *et al*. (2003) labeled ITS-sequenced isolates of *A. sclerotigenum* in GenBank as "*Acremonium strictum* genogroup II." The complexity of *A. sclerotigenum,* not its earliest valid name, goes beyond the scope of this paper. Perdomo *et al*. (2010) have recently investigated the diversity of medically important isolates within this species.

Besides the four clades mentioned above, *Acremonium* sect. *Acremonium* species also make up the non-synnematal anamorphs of the *Emericellopsis* clade, most of the *A. fusidioides* clade, and most of the small *A. camptosporum, A. exiguum*, *A. minutisporum, A. pinkertoniae,* and *A. pseudozeylanicum* clades. Gams (1975) accommodated *A. byssoides*, now known to belong in *Simplicillium lanosoniveum* (Zare & Gams 2001), in *Acremonium* sect. *Acremonium*, while commenting that it was suggestive of *Verticillium* sect. *Prostrata*, later recognised as *Simplicillium* (Zare & Gams 2001). He withheld *A. byssoides* from *Verticillium* because the colony margin was relatively flat and slightly fasciculate, rather than cottony. To some extent *Acremonium* sect. *Acremonium* was based on keying out all the relatively flat or fasciculate *Acremonium*-like species together provided that they lacked the dark conidia or chondroid hyphae of *Gliomastix*.

Acremonium sect. *Nectrioidea* as delineated by Gams (1971) included many *Nectria sensu lato* anamorphs. Some of these species are now placed in the genus *Cosmospora* by Gräfenhan *et al.* (2011). These include members of the *A. berkeleyanum* complex as well as *A. arxii* and *A. cymosum*. *Acremonium falciforme* in *A.* sect. *Nectrioidea* had already been recognised as a member of the *Fusarium solani* complex (Summerbell & Schroers 2002) and *A. diospyri* had been transferred into *Nalanthamala* along with other nectriaceous species (Schroers *et al*. 2005). *Acremonium tsugae* appears to be a microconidial *Cylindrocarpon* species. The *Acremonium recifei* complex still remains as an undisposed major group of nectriaceous *Acremonium* species originally included in *A.* sect. *Nectrioidea*. The placement of *A.* sect. *Nectrioidea* species *A. alcalophilum*, *A. brunnescens*, *A. furcatum*, *A. nepalense*, *A. restrictum*, and *A. stromaticum* in the *Plectosphaerellaceae* has already been shown by Zare *et al.* (2007). *Acremonium apii* also has been shown to belong to this family as a synonym of *Verticillium alboatrum*, and its ex-type strain, CBS 130.51, was used as the representative isolate of that species by Zare *et al.* (2007).

Other anomalous elements of *A.* sect. *Nectrioidea* include *A. crotocinigenum* in the *Trichothecium* clade, *A. radiatum* in the phylogenetically isolated *A. breve* clade, *A. biseptum* in the *A. cerealis* clade near *Gliomastix*, *A. salmoneum* in the *Emericellopsis* clade near *Stilbella fimetaria*, *A. chrysogenum* in a bionectriaceous clade containing cleistothecial teleomorphs such as *Nigrosabulum*, *A. rutilum* in a clade otherwise containing isolates identified as *A. persicinum*, and a non-type *A. hyalinulum* isolate in another clade peripheral to *Gliomastix*. When *Sarocladium zeae* as *A. zeae* in *A.* sect. *Nectrioidea* was compared to the phylogenetically related *S. kiliense* as *A. kiliense* in *A.* sect. *Acremonium* by Gams (1971, p. 16), he noted that the latter species may sometimes also be strongly branched and thus resemble the former. The exigencies of dichotomous morphological keying tended to sort closely related species into widely separated Sections of the genus.

The main heterogeneous element included in Gams' (1971) original concept of sect. *Gliomastix* was the "*Striatisporum* series." These were later distinguished as the separate genus *Sagenomella* (Gams 1978). Both *Sagenomella* and the recently described genus *Phialosimplex* are members of the *Eurotiales* (Sigler *et al*. 2010). Another anomalous element in sect. *Gliomastix, Acremonium atrogriseum*, is here removed to the *Cephalothecaceae*.

Other species included by Gams (1971, 1975) in *A.* sect. *Gliomastix* that can now be seen to be separated from the *Gliomastix/Bionectria* clade include "*Cephalosporium purpurascens*," synonymised by Gams (1971) with *A. persicinum* as well as *A. brachypenium*, *A. hennebertii*, *A. incrustatum,* and *A. inflatum*. Species outside the *Gliomastix/Bionectria* clade that have well developed chondroid hyphae include *A. hennebertii* and *A. incrustatum*.

TAXONOMY

The main purpose of this study is to provide a phylogenetic overview of *Acremonium* plus distinctive LSU sequences to render the described species recognisable in molecular studies. In addition, some taxonomic changes are undertaken.

What is *Acremonium*?

The first task at hand is to establish what *Acremonium* is. The lectotype species of *Acremonium* is *A. alternatum* as designated by Gams (1968). Gams (1968) studied and illustrated the type material used by Link (1809) in describing *A. alternatum*. This material consists of a thin fungal mycelium colonising a birch leaf. In choosing living cultures that best approximated this specimen, Gams (1968) listed four isolates. From among these, one is chosen with a dried culture to be designated here as the epitype with an ex-epitype culture. This is CBS 407.66, which groups with the ex-type isolate of *Cephalosporium malorum*, synonymised by Gams (1971) with *A. charticola,* as well as with *A. sordidulum* and *A. charticola* in the poorly defined *A. sclerotigenum*/*Geosmithia* clade. Use of the corresponding dried culture CBS H-20525 as an epitype specimen serves nomenclatural stability because the genus name *Acremonium* is then used to designate a large group of species currently accepted in *Acremonium*.

Other candidate isolates included CBS 308.70 (called "Kultur 1127"), which died out and was replenished from its degenerated, nonsporulating subculture MUCL 8432, now also called CBS 114602. As a degenerated isolate, it makes poor potential epitype material. Another isolate mentioned by Gams (1968), CBS 406.66, is conspecific with CBS 114602 and in good condition. Both isolates are included in a clade relatively distant from any other *Acremonium* group but deeply basal to the *Sarocladium* and *A. breve* clades, as seen in Fig. 1A. If *Acremonium* were epitypified with one of these isolates, the generic name might be restricted to this single species. The final isolate is CBS 223.70, an isolate that, despite its catenate conidia, is conspecific with the type of *A. sclerotigenum* (100 % ITS sequence identity; GenBank AJ621772 for CBS 124.42 is essentially identical to *A. sclerotigenum*, U57674, CBS 223.70). Isolate CBS 223.70 strongly resembles pale greenish grey coloured, sclerotium-forming isolates identified as *A. egyptiacum* (*e.g.*, CBS 734.69), which are also conspecific with *A. sclerotigenum*. It differs by not forming sclerotia. Catenate conidia may or may not be produced in this group and the greenish grey colonies produced by chain-forming isolates have explicitly been connected with *A. egyptiacum*, not *A. alternatum*. One other taxon that Gams (1971, 1975) consistently identified as *A. alternatum*, a species in the *A. fusidioides* clade, is represented by CBS 831.97

and 381.70A. These isolates have the disadvantage of not having been explicitly compared with the type material. In addition, this clade is related to several clades with known teleomorphs, *e.g.*, *Emericellopsis* and *Nigrosabulum*, and anamorphs, *e.g.*, *Stilbella* and *Geosmithia*. In a revised nomenclatural system, it would root *Acremonium* as a broad unitary genus name encompassing the teleomorphs and complex anamorphs. Ultimately, it might epitypify *Acremonium* strictly as a genus name for the *A. fusidioides* clade.

Acremonium alternatum Link : Fr., Mag. Ges. naturf. Fr. Berlin 3: 15. 1809 : Fries, Syst. Mycol. 3: 425. 1832.

Holotype: **Germany**, Rostock, on leaf litter of *Betula*, collected by Ditmar, B-type specimen labeled in Link's handwriting.

Epitype designated here: Austria, Stangensteig near Innsbruck, ex *Ustulina deusta*, W. Gams, Dec. 1965, CBS-H 20525 dried culture of CBS 407.66, ex-epitype living culture CBS 407.66.

Additional genera recognised here

Based on these analyses, three genera are represented in sufficient detail and with high bootstrap support to be formally recognised here. In most cases, the genera and clades are not sufficiently populated with their constituent members without analysis of additional sequences. For example, the *Emericellopsis* clade is missing 12 of its 13 species including two identified as *E. minima* (Zuccaro *et al*. 2004) as well as one of its two *Stanjemonium* species.

Gliomastix

The core clade of *Gliomastix* including the type species is well delimited with a 92 % bootstrap value even in the very conservative LSU analysis. Although Gams (1971) placed this genus into *Acremonium*, several authors have recognised *Gliomastix.* Most notably, Matsushima (1975) placed *Acremonium masseei* and *A. polychromum* into *Gliomastix* and Lechat *et al.* (2010) linked *G. fusigera* with *Hydropisphaera bambusicola.* As circumscribed in this paper, the phylogenetically supported *Gliomastix* differs from previous morphological concepts by excluding several distantly related species such as *Acremonium cerealis* and *A. inflatum*. The closely related *A. persicinum* clade may also be included as suggested by Supplemental fig. 6E in Schoch *et al*. (2009) and discussed above. At the moment, we recognise only four species from the present study in *Gliomastix*. An additional species, published while the present manuscript was in preparation, *Acremonium tumulicola* (Kiyuna *et al.* 2010), should also be included in this concept of *Gliomastix*.

The generic characters do not differ significantly from those summarised in the generic diagnosis of Dickinson (1968).

1. Type species. ***Gliomastix murorum*** (Corda) S. Hughes, Canad. J. Bot. 36: 769. 1958.

Basionym: *Torula murorum* Corda, Icon. Fung. 2: 9. 1838.

≡ *Sagrahamala murorum* (Corda) Subram., Curr. Sci. 41: 49. 1972.

≡ *Acremonium murorum* (Corda) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 84. 1971.

= *Torula chartarum* Corda, Icon. Fung. 2: 9. 1839.

≡ *Gliomastix chartarum* (Corda) Guég, Bull. Soc. Mycol. France 21: 240. 1905.

For additional synonyms, see Gams (1971). The type species of *Gliomastix, G. chartarum*, is a synonym of *G. murorum* (Hughes 1958). The distinction between *G. murorum* var. *murorum* having conidia in chains and *G. murorum* var. *felina* having conidia in mucoid heads does not appear to be supported by phylogenetic analysis. *Gliomastix murorum* var. *felina* isolates originally described as *Graphium malorum* (ex-type CBS 154.25) and *Torula cephalosporioides* (ex-type CBS 378.36) are molecularly confirmed as synonyms of *G. murorum* (Fig. 2B). Recently, Kiyuna *et al.* (2010) neotypified *Gliomastix felina* (Marchal) Hammill, recombined as *Acremonium felinum* (Marchal) Kiyuna, An, Kigawa & Sugiy., with CBS 147.81. The sequences deposited in GenBank, *e.g.*, AB540562, suggest that this isolate represents *G. roseogrisea*. The new combination is reduced to synonymy with that species below.

2. ***Gliomastix masseei*** (Sacc.) Matsush., Icon. microfung. Matsush. lect. (Kobe): 76. 1975.

Basionym: *Trichosporium masseei* Sacc., Syll. Fung. 22: 1356. 1913

[= *Trichosporium aterrimum* Massee, Bull. Misc. Inform. 1899: 167 non (Corda) Sacc. 1886]

≡ *Acremonium masseei* (Sacc.) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 83. 1971.

The name lacks an ex-type isolate. Although the isolate (CBS 794.69) sequenced is basal to the *Gliomastix* clade (Fig. 2B), it appears to be a suitable to serve as the basis for epitypification.

Holotype of Trichosporium masseei: India, Punjab, Changa Manga, on *Morus indica*, Jan. 1898, J. Gleadow, ex Herb. Massee, K; isotypes IMI 49,214 = IMI 87,346.

Epitype designated here: **Italy**, Turin, isolated from rabbit dung, A. Fontana, CBS H-8244, ex-epitype culture CBS 794.69.

3. ***Gliomastix polychroma*** (J.F.H. Beyma) Matsush., Icon. microfung. Matsush. lect. (Kobe): 77. 1975.

Basionym: *Oospora polychroma* J.F.H. Beyma, Verh. K. Ned. Akad. Wetensch., Sect. 2, 26 (2): 5. 1928.

≡ *Sagrahamala polychroma* (J.F.H. Beyma) Subram., Curr. Sci. 41: 49. 1972.

≡ *Acremonium polychromum* (J.F.H. Beyma) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 81. 1971.

Additional synonyms are given by Gams (1971). This clade includes the ex-type isolate of *Oospora polychroma*, basionym of *G. polychroma*, CBS 181.27 (Fig. 2B). *Periconia tenuissima* var. *nigra* is confirmed as a synonym via inclusion of its ex-type isolate CBS 151.26 (Fig. 2B). The status of the different isolate, CBS 617.94, from banana, requires further clarification. This isolate may be related to *Acremonium musicola*, a species not represented in CBS.

4. ***Gliomastix roseogrisea*** (S.B. Saksena) Summerbell, **comb. nov.** MycoBank MB519588.

Basionym: *Cephalosporium roseogriseum* S.B. Saksena, Mycologia 47: 895. 1956 [1955].

≡ *Acremonium roseogriseum* (S.B. Saksena) W. Gams [as '*roseo-griseum*'], *Cephalosporium*-artige Schimmelpilze (Stuttgart): 87. 1971.

= *Acremonium felinum* (Marchal) Kiyuna, An, Kigawa & Sugiy., Mycoscience 52: 13. 2010.

Gliomastix roseogrisea, like *G. murorum*, has a variety of conidial forms including conidia in chains and conidia of various shapes in mucoid heads. This plasticity of form recalls the situation mentioned

above for *A. sclerotigenum* and may represent a relatively common situation in acremonioid species. As another example Gams (1971) lists "*Gliomastix murorum* var. *felina pro parte* in Dickinson *in* Mycol Pap. 115: 16, 1968" as an additional synonym of this taxon.

As mentioned above in the discussion of the genus, Kiyuna *et al.* (2010) recently neotypified *Gliomastix felina* (basionym *Periconia felina* Marchal, Bull. Soc. R. Bot. Belg. 34:141. 1895) with CBS 147.81, an isolate collected by Hammill (1981). This isolate is a typical *G. roseogrisea*, a taxon not studied by Kiyuna *et al.* (2010).

5. *Gliomastix tumulicola* (Kiyuna, An, Kigawa & Sugiy.) Summerbell, **comb. nov.** MycoBank MB519599.
Basionym: *Acremonium tumulicola* Kiyuna, An, Kigawa & Sugiy., Mycoscience 52: 13. 2010.

This newly described species is phylogenetically placed by its original authors (Kiyuna *et al.* 2010) in the *Gliomastix* clade and comparison of sequences confirms that placement. Although this information was received too late to include this species in our phylogenetic analyses, the species is placed in *Gliomastix*.

Sarocladium

The genus *Sarocladium* was described for two pinkish coloured fungal pathogens causing sheath blast of rice (Gams & Hawksworth 1976). The drawings in that paper and the photographs in Bills *et al.* (2004) show structures that overlap with those produced by the phylogenetically related *A. kiliense, A. strictum*, and *A. zeae*. As in *Fusarium*, plant pathogenic fungi that sporulate on above-ground plant parts are likely to produce upright, branching sporulating structures with mucoid conidia suggesting dispersal by insects that fly from plant to plant. Species with habitats where water flux or microarthropod movement may be important in dispersal, *e.g.*, various Acremonia occurring in soil or *Fusarium domesticum* growing on cheese, may have simplified conidiogenous structures. Bills *et al.* (2004) suggested that the generic placement of *Acremonium kiliense* and *A. strictum* should be re-examined in light of their close relationship with *Sarocladium oryzae*.

The genus *Sarocladium* is delineated here to include several species previously recognised in *Acremonium*, as seen in Figs 1 and 2. In Fig. 2, where phylogenetic signal is relatively low, *Sarocladium* tepidly (84 % bootstrap) links to the *A. bacillisporum* clade. In Fig. 1, it links with a 99 % bootstrap value. Phylogenetic clustering algorithms often insert the *A. bacillisporum* clade between *A. strictum* and *A. kiliense* due to certain apo- or plesiomorphies shared with one or the other of these two members of the *A. strictum* clade (data not shown). On the other hand, the next most closely related clade in Fig. 1, the *A. breve/A. curvulum* clade, has ITS sequences with substantial sections that are difficult to align with those of the *A. bacillisporum* and *A. strictum* clades, indicating considerable evolutionary distance.

The genus *Sarocladium* is emended here to include those species that belong to the *A. strictum* and *A. bacillisporum* clades. The generic name *Sagrahamala* is not a contender for this group because the type species is the unrelated *Acremonium luzulae*. In addition *Acremonium luzulae* is a species in need of epitypification, because, as shown in the present study, more than one phylogenetic species is encompassed under the name.

Sarocladium W. Gams & D. Hawksw., Kavaka 3: 57. 1976 [1975].

Colonies on 2 % malt extract agar slimy-glabrous to moderately floccose to deeply dusty, sometimes ropy; with, in Gams' terminology (Gams 1971), phalacrogenous, nematogenous, to plectonematogenous conidiation; growing 13–25 mm in 10 d at 20 °C, whitish to pinkish to salmonaceous or, when conidia are formed in chains, sometimes acquiring vivid conidial mass colouration such as ochraceous or greenish glaucous; reverse pale to pinkish orange to pale grey-brown, rarely greenish-blue. Conidiogenous apparatus ranging from adelophialides, solitary orthotropic phialides to conidiophore structures with one or a few branches, or with cymose branching or occasionally with one or two ranks of loosely structured verticils, sometimes with repeated branching extending to 90 µm long. Phialides subulate, aculeate to acerose, straight, slightly curved, or undulate, thin- and smooth-walled, 15–60(–75) µm long, tapering from a basal width of 1.2–2.5 µm, with minimal collarette; conidia borne in mucoid heads or dry chains, notably longer than broad, l/w mostly 2.2–7.0, cylindrical to fusiform to bacilliform, aseptate, smooth-walled, with rounded or tapered-truncate ends, 3.5–8(–14) × 0.5–2 µm. Chlamydospores present or absent, when present relatively thick-walled, smooth or slightly roughened, globose to ellipsoidal, intercalary or terminal, mostly solitary, occasionally in short chains, 4–8 µm. *Internal transcribed spacer sequence* mostly with distinctive CGGTCGCGCC motif in mid-ITS2 region.

Several species of *Sarocladium* are noted for melanogenesis yielding ochre-brown to dark grey-brown colony reverse colours on Sabouraud agar: *S. glaucum, S. kiliense,* and *S. zeae* (Gams 1971). In the case of *S. kiliense*, this melanogenesis has the result that most mycetoma cases feature black "grains" or sclerotium-like balls of compacted fungal hyphae (Summerbell 2003); melanogenesis is a well known pathogenicity factor in fungal diseases of humans and animals (Gómez & Nosanchuk 2003). As recognised here *Sarocladium* yields a remarkable unity of species with elongated conidia and phialides. Several species including *S. kiliense, S. oryzae,* and *S. strictum* form adelophialides prominently, at least in some isolates; acremonioid species outside *Sarocladium* usually lack this character.

The recognised species are given below. *Acremonium implicatum* may belong here, but the species lacks living ex-type or representative material. The "*A. implicatum*" isolate that grouped in *Sarocladium*, CBS 243.59, is noted by Gams (1971) as an authentic isolate of *Fusidium terricola* J.H. Mill., Giddens & A.A. Foster and this name could be used if *A. implicatum sensu* Gams is revealed as polyphyletic. The other "*A. implicatum*" isolate, CBS 397.70B, included in this study is not a *Sarocladium*; rather it is a member of the *A. exiguum* clade.

1. Type species. ***Sarocladium oryzae*** (Sawada) W. Gams & D. Hawksw., Kavaka 3: 58. 1976 [1975].

A description and synonymy are given by Gams & Hawksworth (1975). Bills *et al.* (2004) synonymised *Sarocladium attenuatum* with *S. oryzae* based on the reported identity of the ITS sequence of its ex-type isolate, CBS 399.73, with that of representative isolates of *S. oryzae*. We resequenced the ITS region of CBS 399.73 and obtained a sequence differing from Bills *et al.* (AY566995) by 6 base-pairs and 2 gaps. Some of the base pairs in our sequence appeared to be symplesiomorphies shared with *A. kiliense* or *A. strictum* but not *S. oryzae*, rather than random mutations or possible miscalls. Our resequencing of unequivocal *S. oryzae* isolates CBS 180.74 and CBS 361.75 yielded results consistent with those of Bills *et al.* (2004). The status of *S. attenuatum* thus requires further study.

2. *Sarocladium bacillisporum* (Onions & Barron) Summerbell, **comb. nov.** MycoBank MB519589.
Basionym: *Paecilomyces bacillisporus* Onions & G.L. Barron, Mycol. Pap. 107: 11. 1967.
≡ *Acremonium bacillisporum* (Onions & G.L. Barron) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 72. 1971.
≡ *Sagrahamala bacillispora* (Onions & G.L. Barron) Subram., Curr. Sci. 41: 49. 1972.

This species was described by Gams (1971). It is easily confused with *Verticillium leptobactrum*, which can be relatively floccose and loosely structured although some isolates are very dense and slow-growing (Gams, 1971). In addition colonies of *S. bacillisporum* at maturity have a pinkish colouration.

3. *Sarocladium bactrocephalum* (W. Gams) Summerbell, **comb. nov.** MycoBank MB519590.
Basionym: *Acremonium bactrocephalum* W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 44. 1971.

As indicated by Gams (1971) this uncommon species is closely related to *S. strictum*, but is distinguished morphologically by its long, narrow conidia. It is molecularly distinguishable by LSU sequences.

4. *Sarocladium glaucum* (W. Gams) Summerbell, **comb. nov.** MycoBank MB519591.
Basionym: *Acremonium glaucum* W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 68. 1971.

This species was described by Gams (1971). The ex-type culture CBS 796.69 indicates that this species belongs in *Sarocladium*.

5. *Sarocladium kiliense* (Grütz) Summerbell **comb. nov.** MycoBank MB519592.
Basionym: *Acremonium kiliense* Grütz, Dermatol. Wochenschr. 80: 774. 1925.
= *Cephalosporium incoloratum* Sukapure & Thirum., Sydowia 19: 171. 1966 [1965].
= *Acremonium incoloratum* (Sukapure & Thirum.) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 50. 1971.

Additional synonyms and a description of *S. kiliense* are given by Gams (1971) and Domsch *et al.* (2007); the species is also extensively illustrated by de Hoog *et al.* (2000). The ITS sequence of the ex-type strain of *Acremonium incoloratum*, CBS 146.62, is identical to that of the ex-type of *S. kiliense*, CBS 122.29 (data not shown). Though isolate CBS 146.62 is unusual in colour and lacks well differentiated chlamydospores that generally occur in *S. kiliense*, there is no phenetic difference profound enough to suggest that additional genes must be examined to be certain of their synonymy.

The sequences deposited in GenBank by Novicki *et al.* (2003) for their "*Acremonium strictum* genogroup III" (ITS: AY138846; LSU: AY138484) are actually of *S. kiliense*.

6. *Sarocladium ochraceum* (Onions & Barron) Summerbell, **comb. nov.** MycoBank MB519593.
Basionym: *Paecilomyces ochraceus* Onions & G.L. Barron, Mycol. Pap. 107: 15. 1967.
≡ *Acremonium ochraceum* (Onions & G.L. Barron) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 67. 1971.
≡ *Sagrahamala ochracea* (Onions & G.L. Barron) Subram. & Pushkaran, Kavaka 3: 89. 1975 [1976].

This species was described by Gams (1971). We analysed the ex-type culture, CBS 428.67.

7. *Sarocladium strictum* (W. Gams) Summerbell, **comb. nov.** MycoBank MB519594.
Basionym: *Acremonium strictum* W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 42. 1971.

Descriptions of *S. strictum* are given by Gams (1971) and Domsch *et al.* (2007). The type isolate of *S. strictum* was confirmed in this genus (Fig. 2C). Of the three isolates illustrated by Gams (1971) under *A. strictum,* CBS 287.70 D, is confirmed by sequencing as *S. strictum.* The only isolate of *Acremonium zonatum* in this study, CBS 565.67, turned out to have an ITS sequence identical to that of *S. strictum*. This is one of three isolates examined by Gams (1971) as *A. zonatum*. He stated that another isolate, CBS 145.62, appeared to be *A. kiliense*, but that examination of herbarium material suggested that this species had been growing on the natural substrate mixed with the real *A. zonatum* and had been isolated accidentally. One herbarium specimen examined by Gams (1971) showed septate conidia, something not otherwise seen in *Sarocladium*, so there may indeed be a real *A. zonatum*. It is not clear if *A. zonatum sensu* Gams is a unified concept or a designation of various acremonioid fungi forming leaf spots on tropical plants. In any case, the known connection of the genus *Sarocladium* with phytopathogenesis and endophytism as in *S. zeae* makes it plausible that species such as *S. strictum* and *S. kiliense* may play a role in plant disease.

8. *Sarocladium zeae* (W. Gams & D.R. Sumner) Summerbell, **comb. nov.** MycoBank MB519595.
Basionym: *Acremonium zeae* W. Gams & D.R. Sumner, in Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 121. 1971.

This economically important maize endophyte species fits the description given by Gams (1971) as a fungus with felty to shaggy colonies. Two *S. zeae* isolates with more flattened colonies were accessed in CBS as *A. strictum*. Both CBS 646.75 and 226.84 were from maize and found to be producers of pyrrocidine metabolites as well as dihydroresorcylide, characteristic of *S. zeae* (Wicklow *et al.* 2008). Pyrrocidines are antagonistic to *Aspergillus flavus* and *Fusarium verticillioides* in maize inflorescences and are thus important in the ecology and economic significance of *S. zeae*. An additional *A. strictum* isolate, CBS 310.85, is also *S. zeae* as evidenced by pyrrocidine production, but has not yet been sequenced (Wicklow *et al.* 2008).

Trichothecium

A significant theme of the current volume is the pioneering of a new approach to dikaryomycete nomenclature: the unitary naming of genus-level clades based on the oldest valid generic name, whether originally anamorphic or teleomorphic in nature (see discussion in Gräfenhan *et al.* 2011). Because the first named fungi were often species prominently in contact with humans and their environs and because the first names usually were attached to the most frequently seen reproductive state, there is considerable wisdom to using the oldest name applied to either aspect of the holomorph in constructing a unitary nomenclature.

The genus *Trichothecium* makes an excellent example, since the system used here preserves the best known species name in the group. A unitary system giving teleomorphs primacy

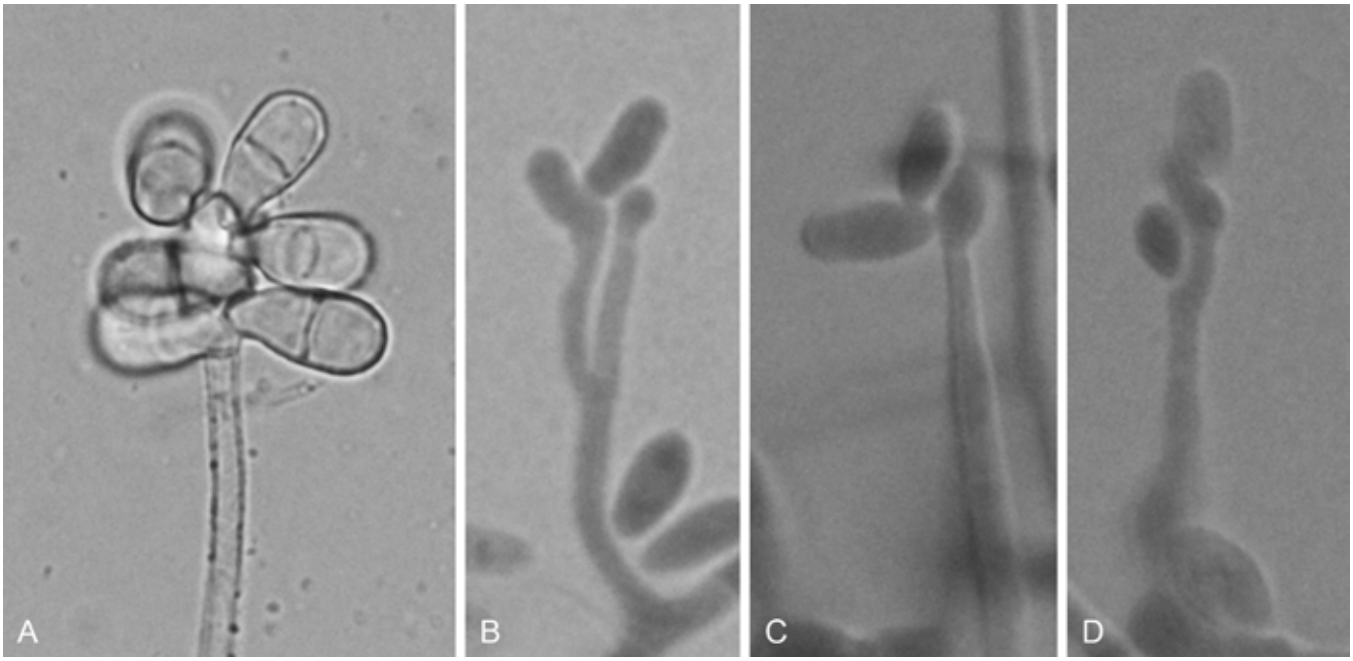

Fig. 3. A. *Trichothecium roseum* CBS 113334 showing retrogressive conidiation. B-D. conidiogenesis in "*Trichothecium indicum*"/ *Leucosphaerina indica* CBS 123.78 showing retrogressive development (B), phialidic development (B) and sympodial development (D).

would replace the familiar "*T. roseum*" with a *Leucosphaerina* name. A system that retains primacy for morphology, which is the only reasonable basis for dual nomenclature in the molecular era, would divide the *Trichothecium* clade into four genera, as is the case today. One of those genera, *Acremonium,* would be quintessentially artificial and almost completely divorced from evolutionary biological relationships. With increased emphasis on genomes, proteomes, and metabolomes, a focus on polyphyletic elements of microscopic shape seems counterproductive. Every new system of nomenclatural change will entail both fortunate and infelicitous changes and will receive some resistance in scientific communities. A nomenclatural system based on phylogeny will be considerably more stable than any previous system. The interests of all would be best served if it bridged gracefully out of pre-phylogenetic taxonomy, preserving as many familiar elements as possible. *Trichothecium roseum*, a constant from 1809 to today, is one of those elements that is worthy of being preserved.

The small, tightly unified clade of *Trichothecium* includes isolates with three different anamorphic forms, currently classified as *Acremonium* (phialoconidia), *Spicellum* (sympodial blastoconidia), and *Trichothecium* (retrogressive blastoconidia). The associated teleomorph, *Leucosphaerina indica*, produces anamorphic forms described as "*Acremonium* or *Sporothrix*" (Suh & Blackwell 1999). These morphs are illustrated by von Arx *et al.* (1978). The range of anamorphic forms produced by *L. indica* overlaps those produced by all the anamorphic species in the clade (Fig. 3).

The four species studied here, *Trichothecium roseum*, *Acremonium crotocinigenum*, *Leucosphaerina indica*, and *Spicellum roseum*, have recently been associated with a fifth, newly described species, *Spicellum ovalisporum*. The dendrogram produced by Seifert *et al.* (2008) makes it clear that *S. ovalisporum* is related to *S. roseum* and is certainly a member of the *Trichothecium* clade. In parallel with the revision of the genus *Microcera* by Gräfenhan *et al.* (2011), this clade is redefined here as a genus with the oldest valid generic name, *Trichothecium*.

As Fig. 2 shows, the second described *Leucosphaerina* species, *L. arxii*, is in the distant *Acremonium pinkertoniae* clade and is closely related to *Bulbithecium hyalosporum*. Malloch (1989) commented that it differed from *L. indica* by lacking sheathing gel around the ascospores and by having an *Acremonium* anamorph.

Trichothecium Link : Fr., Mag. Gesell. naturf. Freunde, Berlin 3: 18. 1809.

= *Spicellum* Nicot & Roquebert, Revue Mycol., Paris 39: 272. 1976 [1975].
= *Leucosphaerina* Arx, Persoonia 13: 294. 1987.

Older synonymy for the genus is given by Rifai & Cooke (1966).

Colonies on malt extract agar 20–40 µm after 7 d at 24 °C, white to salmon orange or salmon pink (Methuen 6-7A2, 4-5A2-3), felty, floccose or lanose, sometimes appearing powdery with heavy conidiation. Ascomatal initials, if present, produced on aerial mycelium, irregularly coiled. *Ascomata* spherical or nearly so, non-ostiolate, colourless or slightly pink, 150–300 µm; ascomatal wall persistent, nearly colourless, 10–13 µm thick, of indistinct hyphal cells; *asci* uniformly distributed in centrum, clavate to spherical, with thin, evanescent walls, 8-spored, 10–13 µm wide; ascospores ellipsoidal or reniform, with refractile walls and a 1–1.5 µm broad gelatinous sheath, smooth or finely striate, hyaline, yellow to pink *en masse*, without germ pore, 6–7 × 3–4 µm. *Conidiogenous apparatus* varying by species, featuring one or more of: conidiophores up to 125 µm long × 2–3.5 µm wide, septate, unbranched, with terminal phialides 10–65 µm long, producing unicellular, hyaline, smooth-walled phialoconidia, obovate, oblong or cylindrical 4.4–7.4 µm; or conidiophores up to 175 µm long, unbranched or uncommonly with one or more branches, retrogressive, shortening with production of each conidium, with each conidial base subsuming a portion of conidiophore apex; conidia 0–1-septate, ellipsoidal or ovate, with a decurved, abruptly narrowed basal hilum terminating in a distinct truncate end, 5–12 × 3–6.5 µm; or conidiophores ranging from unicellular conidiogenous cells to multicellular, multiply rebranched apparati extending indefinitely to beyond 200 µm long; terminal cells 9–37 µm long with a cylindrical basal part and a narrowing, apically extending conidiogenous rachis sympodially proliferating and producing oval to ellipsoidal to cylindrical or allantoid conidia 3.5–11 × 1.5–3.5 µm, with truncate bases. *Chlamydospores* absent

or present, when present mostly in intercalary chains, hyaline, smooth or finely warted, 5–8(–12) µm wide. *Internal transcribed spacer sequence* generally with distinct CACAAACCTCGCG motif in ITS2 region. The numerical position varies by species and isolate, cf. position 476 in GenBank record EU445372, ITS for *Spicellum ovalisporum* ex-type isolate DAOM 186447.

Various taxa described as *Trichothecium* need to be investigated to determine their relationship to this phylogenetic genus. For example, *Trichothecium luteum* and *T. parvum*, not represented by living cultures, should be investigated, as should *T. campaniforme* and *T. plasmoparae*, which are represented by one isolate each in CBS. *Trichothecium domesticum* was recently redisposed as *Fusarium domesticum* (Bachmann *et al.* 2005). Of teleomorphs reported to have *Trichothecium* anamorphs, *Heleococcum japonense* is unrelated to the *Trichothecium* clade (Fig. 2; the sequence is erroneously listed as *H. japonicum* in GenBank); rather it is related to *Gliomastix* and *Hydropisphaera.* A *Trichothecium* state of *Hypomyces subiculosus* (syn. *H. trichothecoides*) was described, but *Hypomyces*, a member of the *Hypocreaceae*, is a remote relative of the *Trichothecium* clade within the *Hypocreales* (Fig. 2).

1. Type species. ***Trichothecium roseum*** (Pers.) Link, Mag. Gesell. naturf. Freunde, Berlin 3: 18. 1809.
Synonymy is given in MycoBank record MB164181.

2. ***Trichothecium crotocinigenum*** (Schol-Schwarz) Summerbell, Seifert, & Schroers, **comb. nov.** MycoBank MB519596.
Basionym: *Cephalosporium crotocinigenum* Schol-Schwarz, Trans. Brit. Mycol. Soc. 48: 53. 1965.
≡ *Acremonium crotocinigenum* (Schol-Schwarz) W. Gams, *Cephalosporium*-artige Schimmelpilze (Stuttgart): 112. 1971.

As pointed out by Seifert *et al.* (2008, supplement), *T. crotocinigenum* has long been known to produce crotocin mycotoxins that are similar to the trichothecenes produced by *T. roseum* and *T. sympodiale*. The production of similar mycotoxins reinforces the argument for phylogenetic nomenclature such that scientific names reflect true relationships.

3. ***Trichothecium indicum*** (Arx, Mukerji & N. Singh) Summerbell, Seifert, & Schroers, **comb. nov.** MycoBank MB519597.
Basionym: *Leucosphaerina indica* (Arx, Mukerji & N. Singh) Arx, Persoonia 13: 294. 1987.

With phylogenetic hindsight, the photographs of this species' anamorph in the original description by von Arx *et al.* (1978) can be seen to suggest *Acremonium*, *Spicellum,* and *Trichothecium*.

4. ***Trichothecium ovalisporum*** (Seifert & Rehner) Seifert & Rehner, **comb. nov.** MycoBank MB519598.
Basionym: *Spicellum ovalisporum* Seifert & S.A. Rehner, Fungal Planet: no. 28. 2008.

The relationship of the recently described *Spicellum ovalisporum* to *T. sympodiale* is not clear. The ex-type of *T. sympodiale* (CBS 227.76) was resequenced for the ITS region; the resulting sequence differed from the GenBank record AB019365 by 7 gaps and one C ↔ T transition. The sequence had 100 % identity with ITS sequence record EU445372 for the ex-type isolate of *S. ovalisporum*, DAOM 186447. Two more CBS isolates accessed as *S. roseum*, CBS 119.77 and CBS 146.78, also gave ITS sequences identical to EU445372. A recent partial ITS sequence made by K.A. Seifert for CBS 227.76 agreed with our sequence (data not shown). No one has thus been able to replicate the sequence given for *S. roseum* in AB019365 and we are uncertain of its significance, even though a similar sequence (GenBank AB019364) has been attributed to two other *S. roseum* isolates in the JCM collection by the same depositor, G. Okada. If the fallibilities of earlier sequencing chemistries are involved in these discrepancies, *S. ovalisporum* may be more closely related to *T. sympodiale* than is evident in the literature. Preliminary results have shown at least one substitution distinguishing the translation elongation factor α sequence of *S. ovalisporum* from that of *T. sympodiale* (Rehner, data not shown). Based on comparative morphology and habitat, the authors of *S. ovalisporum* are confident that their species is distinct, and thus the new combination is included here with their sanction.

5. ***Trichothecium sympodiale*** Summerbell, Seifert, & Schroers, **nom. nov.** MycoBank MB 519600.
Basionym: *Spicellum roseum* Nicot & Roquebert, Revue Mycol., Paris 39: 272. 1976 [1975].

If recombined into *Trichothecium, Spicellum roseum* would result in a homonym of the type species, thus a new name is needed.

Acremonium atrogriseum and *Acremonium* cf. *alternatum* CBS 109043 in the *Cephalothecaceae*: a study in comparative morphology vs. phylogeny

Acremonium atrogriseum and an isolate identified as *Acremonium* cf. *alternatum* CBS 109043 belong in the *Cephalothecaceae* (Fig. 1C). This isolate is a white coloured acremonioid fungus forming fusoid conidia in long chains. It also forms small, dark structures that may be aborted ascomatal initials. Sequencing of the ITS region (data not shown) reveals it to be a representative of *Phialemonium obovatum*. It is identical in all bases but one to the ITS sequence of ex-type strain CBS 279.76 (AB278187) and in all but two bases to another isolate of this species, CBS 116.74. *Phialemonium obovatum* was described as having conidia in slimy heads (Gams & McGinnis 1983). CBS 109043 shows that either mucoid heads or chains may be formed in this species, as in *Acremonium persicinum*, *A. sclerotigenum,* and *Gliomastix murorum*. Gams (1971) mentions an isolate of *Sarocladium bacillisporum* that tends to produce mucoid heads. Colonies producing conidia in chains often have a different look from their head-forming conspecifics; the mass colour of the chains may give the colony colours not found in the species descriptions, such as the chalk white colour of CBS 109043 in contrast to the normally pale greenish brown of *P. obovatum* or the greenish grey of *A. sclerotigenum* isolate 223.70, in contrast to the normal pale salmon pink of non-catenate *A. sclerotigenum*.

Existing morphological keys and descriptions not just in *Acremonium* but in all the acremonioid fungi need to be cautiously and skeptically interpreted. At the very least, identifications for publication should be tested by sequencing. We hope that the LSU sequences in this paper will provide the foundation for a phylogenetically sound approach to the systematics and ecology of acremonioid fungi.

ACKNOWLEDGEMENTS

We greatly thank Arien van Iperen, Bert Gerrits-van den Ende, and Kasper Luijsterburg for essential technical support in this study, as well as Keith Seifert and Steve Rehner for scientific contributions. Key work was done by co-op students Salvatore Lopes, Saghal Ahmed-Suleyman, Arwin van der Rhee, and Nienke Lancee as well as visiting Canadian student Jonathan Shapero. For sending type cultures, we thank Akira Nakagiri of the NITE Biological Resource Centre Fungi collection and Françoise Symoens of the BCCM-IHEM collection. The staff of the CBS Collection deserve special thanks for strain cultivation and additional work. The encouragement and mentorship of Walter Gams is highly appreciated, and we hope our partial resolution of the dilemmas posed by phylogenetic systematics in *Acremonium* will be recognised as complementary to his invaluable work.

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.07

Studies in Mycology 68: 163–191. 2011.

Monilochaetes and allied genera of the *Glomerellales*, and a reconsideration of families in the *Microascales*

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Abstract: We examined the phylogenetic relationships of two species that mimic *Chaetosphaeria* in teleomorph and anamorph morphologies, *Chaetosphaeria tulasneorum* with a *Cylindrotrichum* anamorph and *Australiasca queenslandica* with a *Dischloridium* anamorph. Four data sets were analysed: a) the internal transcribed spacer region including ITS1, 5.8S rDNA and ITS2 (ITS), b) nc28S (ncLSU) rDNA, c) nc18S (ncSSU) rDNA, and d) a combined data set of ncLSU-ncSSU-RPB2 (ribosomal polymerase B2). The traditional placement of *Ch. tulasneorum* in the *Microascales* based on ncLSU sequences is unsupported and *Australiasca* does not belong to the *Chaetosphaeriaceae*. Both holomorph species are nested within the *Glomerellales.* A new genus, *Reticulascus*, is introduced for *Ch. tulasneorum* with associated *Cylindrotrichum* anamorph; another species of *Reticulascus* and its anamorph in *Cylindrotrichum* are described as new. The taxonomic structure of the *Glomerellales* is clarified and the name is validly published. As delimited here, it includes three families, the *Glomerellaceae* and the newly described *Australiascaceae* and *Reticulascaceae*. Based on ITS and ncLSU rDNA sequence analyses, we confirm the synonymy of the anamorph genera *Dischloridium* with *Monilochaetes*. Consequently *Dischloridium laeënse*, type species of the genus, and three related species are transferred to the older genus *Monilochaetes*. The teleomorph of *D. laeënse* is described in *Australiasca* as a new species. The *Plectosphaerellaceae,* to which the anamorph genus *Stachylidium* is added, is basal to the *Glomerellales* in the three-gene phylogeny. *Stilbella annulata* also belongs to this family and is newly combined in *Acrostalagmus.* Phylogenetic analyses based on ncLSU, ncSSU, and combined ncLSU-ncSSU-RPB2 sequences clarify family relationships within the *Microascales*. The family *Ceratocystidaceae* is validated as a strongly supported monophyletic group consisting of *Ceratocystis, Cornuvesica*, *Thielaviopsis,* and the type species of *Ambrosiella*. The new family *Gondwanamycetaceae*, a strongly supported sister clade to the *Ceratocystidaceae*, is introduced for the teleomorph genus *Gondwanamyces* and its *Custingophora* anamorphs. Four families are accepted in the *Microascales*, namely the *Ceratocystidaceae*, *Gondwanamycetaceae*, *Halosphaeriaceae,* and *Microascaceae*. Because of a suggested affinity of a *Faurelina indica* isolate to the *Microascales*, the phylogenetic position of the *Chadefaudiellaceae* is reevaluated. Based on the results from a separate ncLSU analysis of the *Dothideomycetes*, *Faurelina* is excluded from the *Microascales* and placed in the *Pleosporales*.

Key words: *Australiasca*, *Australiascaceae*, *Ceratocystidaceae, Cylindrotrichum*, *Dischloridium*, *Gondwanamycetaceae*, *Reticulascus*, *Reticulascaceae*, phylogeny, *Plectosphaerellaceae*.

Taxonomic novelties: New order: *Glomerellales* Chadef. ex Réblová, W. Gams & Seifert, ord. nov. **New families**: *Australiascaceae* Réblová & W. Gams, fam. nov., *Ceratocystidaceae* Locq. ex Réblová, W. Gams & Seifert, fam. nov., *Gondwanamycetaceae* Réblová, W. Gams & Seifert, fam. nov., *Reticulascaceae* Réblová & W. Gams, fam. nov. **New genera**: *Reticulascus* Réblová & W. Gams, gen. nov., **New species**: *Australiasca laeënsis* Réblová & W. Gams, sp. nov., *Cylindrotrichum setosum* Seifert, sp. nov., *Reticulascus clavatus* Réblová & Fournier, sp. nov. **New combinations:** *Acrostalagmus annulatus* (Berk. & Broome) Seifert, comb. nov., *Hyalocylindrophora rosea* (Petch) Réblová & W. Gams, comb. nov., *Monilochaetes basicurvata* (Matsush.) Réblová & Seifert, comb. nov., *Monilochaetes camelliae* (Alcorn & Sivan.) Réblová, W. Gams & Seifert, comb. nov., *Monilochaetes laeënsis* (Matsush.) Réblová, W. Gams & Seifert, comb. nov., *Monilochaetes regenerans* (Bhat & W.B. Kendr.) Réblová & Seifert, comb. nov., *Reticulascus tulasneorum* (Réblová & W. Gams) Réblová & W. Gams, comb. nov.

INTRODUCTION

The genus *Chaetosphaeria* (*Chaetosphaeriaceae*, *Chaetosphaeriales*) is a cosmopolitan genus of nonstromatic, perithecial ascomycetes (Réblová 2000, Réblová & Winka 2000, Fernández *et al.* 2006). It is characterised by dark, opaque, usually subglobose to conical perithecia. The asci are unitunicate, short-stipitate with a distinct, inamyloid apical ring. The ascospores are hyaline, rarely bicolorous, 1- to several-septate, ellipsoidal to fusoid, sometimes cylindrical, and rarely fragment into part-spores. Periphyses and paraphyses are persistent, cylindrical, seldom branching, septate, and longer than the asci. The genus has been linked to 13 anamorph genera of phialidic dematiaceous hyphomycetes (Réblová 2000, 2004).

Several distantly related fungi mimic *Chaetosphaeria* in the morphology of perithecia, asci, ascospores, and phialidic, dematiaceous, hyphomycetous anamorphs. Recognising these species as distinct from *Chaetosphaeria* is difficult based purely on morphology. In most cases, their systematic placement can be ascertained by DNA sequence data, which suggest that the morphological similarities are a result of convergent evolution.

Chaetosphaeria tulasneorum was experimentally linked to its anamorph *Cylindrotrichum oligospermum* by Réblová & Gams (1999). Based on ncLSU rDNA sequence data, *Ch. tulasneorum* was separated from the core species of *Chaetosphaeria* in the *Chaetosphaeriaceae* (Réblová & Winka 2000) and tentatively placed in the *Microascales,* along with *Cylindrotrichum hennebertii*, a non-setose counterpart of *C. oligospermum*. *Chaetosphaeria tulasneorum* colonises decaying wood and forms minute, black perithecia containing unitunicate, short-stipitate asci with an inamyloid apical ring, 2–4-celled ellipsoidal to ellipsoidal-fusoid ascospores, and branching and anastomosing filiform paraphyses forming a "network" within the centrum. The reticulate paraphyses and the 1-septate, cylindrical conidia of the *Cylindrotrichum* anamorph are the only deviating morphological characters between *Ch. tulasneorum* and other core *Chaetosphaeria* species.

The phialidic, dematiaceous hyphomycete *Dischloridium laeënse*, described originally from dead leaves of *Musa paradisiaca* in Papua New Guinea (Matsushima 1971), is common on dead palm spathes in Australia. In some respects it is similar to species of *Chloridium,* a well-established anamorph genus associated with *Chaetosphaeria,* but the microscopic structures are much larger. On material from Australia and England, perithecia of *Australiasca* (Sivanesan & Alcorn 2002) were associated with fertile conidiophores of *D. laeënse*. This teleomorph was first reported from England by Kirk (1986) on stems of *Dicksonia antarctica*, but never described or illustrated. Sivanesan & Alcorn (2002) erected the monotypic ascomycete genus *Australiasca* including the type species, *A. queenslandica,* and named its anamorph *Dischloridium camelliae.* The fungus was isolated from leaves, stems, and branches of *Camellia sinensis* and the connection between the morphs was proven experimentally *in vitro*. They distinguished *D. camelliae* from *D. laeënse* by longer conidia and larger conidiophores. Sivanesan & Alcorn (2002) compared *Australiasca* with genera in the morphologically similar families *Chaetosphaeriaceae* and *Lasiosphaeriaceae*. At that time, no molecular data were available to confirm placement in either family.

The *Australiasca* teleomorph of *D. laeënse* is morphologically similar to species of *Chaetosphaeria* in perithecial and anamorph characters. *Dischloridium laeënse,* the type of its genus, produces effuse colonies of single to fasciculate, macronematous conidiophores with a stromatic base. The conidiophores are dark brown but paler towards the apex. The phialidic conidiogenous cells are terminally integrated bearing an indistinct collarette producing basipetal, broadly ellipsoidal, hyaline, nonseptate conidia with a slightly obtuse base produced in slime. Several of the 15 species described in *Dischloridium* are remarkably similar to *Monilochaetes* (Halsted 1890), recently revised and delimited from *Exochalara* and *Dischloridium* by Rong & Gams (2000) based on detailed morphology and cultivation studies.

To assess the higher level phylogenetic relationships of *Ch. tulasneorum* and related species of *Cylindrotrichum, Australiasca*, *Dischloridium,* and *Monilochaetes*, we analysed members from 19 orders or families of perithecial ascomycetes. We used DNA sequence data from the nuclear large (ncLSU rDNA) and small (ncSSU rDNA) subunits in independent analyses and combined these with the second largest subunit of RNA polymerase (RPB2) for a multigene analysis.

Based on the phylogenies presented here, several new and strongly supported families and orders are proposed. The order *Glomerellales* is phylogenetically well-defined and validated to include three families, the *Glomerellaceae* and the newly described *Australiascaceae* and *Reticulascaceae*. The internal transcribed spacer region (ITS including ITS1, 5.8S and ITS2) was used to further analyse the phylogenetic relationships among species of *Dischloridium* and *Monilochaetes*. Within the *Microascales,* we accept four families, *i.e. Ceratocystidaceae*, which is validated here, and the newly described *Gondwanamycetaceae*, *Halosphaeriaceae,* and *Microascaceae*. We discuss the family and order affinities of *Faurelina* attributed to the *Chadefaudiellaceae* of the *Microascales* by von Arx (1978) and by Tang *et al.* (2007). We examined authentic material, specifically the *in vitro* ex-type and another strain of *F. indica,* and analysed ITS and ncLSU sequence data. Based on results from a ncLSU analysis of the *Dothideomycetes*, *Faurelina* (*Chadefaudiellaceae*) is excluded from the *Microascales* and placed in the *Pleosporales* (*Dothideomycetes*).

MATERIAL AND METHODS

Morphological observations

All herbarium specimens examined and cultures studied are listed under each treated species. Dried specimens were rehydrated in water; material was examined with an Olympus SZX12 dissecting microscope and centrum material including asci, ascospores, and paraphyses was mounted in Melzer's reagent or 90 % lactic acid. Hand sections of the perithecial wall were studied. When present, conidiophores, conidiogenous cells, and conidia were examined in water, Melzer's reagent, or 90 % lactic acid. All measurements were made in Melzer's reagent. Means ± standard errors (S.E.) based on 25 measurements are given for ascospore, ascal, and conidial dimensions. Images were captured using differential interference (DIC) or phase contrast (PC) microscopy using an Olympus DP70 Camera operated by Imaging Software Cell* on an Olympus BX51 compound microscope or an Evolution MP digital camera operated by ImagePro v. 6.0 on an Olympus BX50 compound microscope. Conidia and conidiogenous cells of *Australiasca queenslandica* were photographed in the living state using an FEI Quanta 200 Environmental Scanning Electron Microscope (ESEM). A *ca.* 2 × 2 mm cube of agar with mycelium was observed at 20kV after the sample chamber achieved local thermodynamic equilibrium: chamber pressure 200 Pa, sample temperature from -15 °C to -16 °C. A Gaseous Secondary Electron Detector (GSED) was used for signal detection. Cooling of the specimen in the chamber was achieved using a PC-controlled Peltier cooling stage with external water chiller (JT Manufacturing, Hudson, NH, USA). Images were processed with Adobe Photoshop CS4 Extended or Adobe Photoshop CS2.

Single-ascospore isolates were obtained from fresh material with the aid of a single-spore isolator (Meopta, Prague, Czech Republic). Isolates were grown on potato carrot agar (PCA), oatmeal agar (OA), and 2 % malt extract agar (MEA) (Gams *et al.* 1998). Colonies were examined after 7, 21, and 30 d at 25 °C in the dark and under near-UV light source (12 h light: 12 h dark). Two strains of *Faurelina indica* were grown on Blakeslee's malt extract agar (Gams *et al.* 1998) and OA and incubated under ambient room conditions for two mo to induce the arthroconidial anamorph. Cultures are maintained at BRIP (Plant Pathology Herbarium, Queensland, Australia), CBS (CBS Fungal Biodiversity Center, Utrecht, the Netherlands), DAOM (Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa, Canada), and the Institute of Botany, Academy of Sciences, Průhonice, Czech Republic.

DNA extraction, amplification and sequencing

DNA was isolated with an UltraClean Microbial DNA Kit (MoBio Laboratories, Inc., Canada) using mycelium removed from PCA or MEA cultures following the manufacturer's protocol for filamentous fungi. All PCR experiments were carried out using a PTC-200 thermal cycler (MJ Research Inc., Watertown, MA, USA). PCR reactions containing 2–4 mM $MgSO_4$ were performed using Platinum *Taq* DNA polymerase High Fidelity (Invitrogen, Carlsbad, CA, USA) in 25 mL volume reactions. PCR conditions were as follows: for ncSSU 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 55 °C and 150–300 s at 68 °C; for ITS and ncLSU 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 55–60 °C, and 165–270 s at 68 °C; and for RPB2 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 55–61

°C, and 90–180 s at 68 °C; all amplifications were concluded by incubation for 10 min at 68 °C. Amplicons were purified using the UltraClean PCR Clean-up Kit (MoBio Laboratories, Inc., Canada) following the manufacturer's directions. All nucleotide sequences were obtained by the dideoxy chain-terminating method using automated DNA sequencers ABI PRISM 3100 or ABI PRISM 3130xl (Applied Biosystems, Foster City, CA, USA). For PCR reactions, the following primers were used: ncSSU, NSSU131-NS24 (Kauff & Lutzoni 2002, White *et al*., 1990); ncLSU, ITS5/NS5/LR0R-LR8 (White *et al*., 1990, Vilgalys unpublished: www.botany.duke.edu / fungi/mycolab); ITS NS5/ITS5-ITS4 (White *et al*., 1990); RPB2 fRPB2-5F-fRPB2-7cR (Liu *et al*., 1999). For sequencing reactions, the following primers were used: ncSSU, NSSU131, SR11R, SR7, SR7R, NSSU897R, NSSU1088, NSSU1088R, NS6, NS24 (White *et al*., 1990, Gargas & Taylor 1992, Spatafora *et al*., 1995, Kauff & Lutzoni 2002, Vilgalys unpublished: www.botany.duke.edu/fungi/mycolab); ncLSU LR0R, LR3R, LR6, LR7, LR16, LR5 (Vilgalys & Hester 1990, Rehner & Samuels 1994, Vilgalys & Sun 1994), JS7 and JS8 (Landvik 1996); ITS, ITS5 and ITS4 (White *et al.* 1990); and RPB2 fRPB2-5F, fRPB2-7cR, RPB2-980R and RPB2-1014F (Reeb *et al*. 2004). Sequences were edited using Sequencher v. 4.9 software (Gene Codes Corp., Ann Arbor, MI, USA).

Phylogenetic analyses

Accession numbers and isolate information for new ITS, ncLSU, ncSSU rDNA and RPB2 sequences are listed in Table 1. The new sequences were aligned with data retrieved from GenBank, mostly from studies published by Wingfield *et al*. (1999), Réblová & Winka (2000), Spatafora *et al*. (2006), and Zhang *et al*. (2006).

All sequences were manually aligned in BioEdit v. 7.0.9.0 (Hall 1999). Predicted models of the secondary structure of the ncLSU and ncSSU molecules of *Saccharomyces cerevisiae* (Gutell 1993, Gutell *et al.* 1993) were used to improve decisions on homologous characters. To assist with decisions on homologous characters in the ITS alignment, we used the predicted models of the secondary structure designed for species of *Chaetosphaeria* (Réblová & Winka 2000). They included a model for the whole ITS2 region and a model for long duplex structures located in the middle of the ITS1 region. The long duplex represents the most variable part of the ITS1 alignment because of its variable lengths and irregular occurrence of internal asymmetrical loops.

Phylogenetic relationships were examined using ncLSU, ncSSU, ITS rDNA, and RPB2 sequences of species from 19 orders or families of the *Sordariomycetes*. For all analyses rooting was accomplished by the outgroup method (Nixon & Carpenter 1993). Two outgroup taxa, *Leotia lubrica* and *Microglossum rufum* (*Leotiaceae, Helotiales*, *Leotiomycetes*), were used in the ncLSU, ncSSU, and the three-gene (ncLSU-ncSSU-RPB2) analyses of the *Sordariomycetes*; two outgroup taxa, *Vanderwaltozyma polyspora* and *Saccharomyces cerevisiae* (*Saccharomycetaceae, Saccharomycetales*, *Saccharomycetes*), were used for the ncLSU phylogeny of *Faurelina* in the *Dothideomycetes*; two *Chaetosphaeria* species (*Chaetosphaeriaceae, Chaetosphaeriales*, *Sordariomycetes*) were used as outgroups for the ITS phylogeny.

Maximum parsimony and Bayesian analyses were used to estimate phylogenetic relationships. Four alignments for ITS, ncLSU, ncSSU, and the combined set were constructed. The lengths of the alignments were determined after introduction of gaps. All characters in the ITS alignment were included. Bases 1–75 were excluded from analyses of the ncLSU and ncSSU alignments and bases 1–59 were excluded from the analysis of the RPB2 alignment, because of the incompleteness of the 5'-end of the majority of the available sequences. An additional 69 bases in the RPB2 part of the alignment, which were difficult to identify as homologous, were also excluded. All alignments are deposited in TreeBase (10538).

The three genes for the combined analysis (ncLSU-ncSSU-RPB2) were tested for heterogeneity among data partitions before combining them for the total evidence analysis. We used the partition homogeneity/incongruence-length difference test implemented in PAUP (Swofford 2002) to determine if different partitions of the data gave significantly different signals. Because combining data with value P > 0.01 generally improves phylogenetic accuracy (Cunningham 1997) and our data did not show significant heterogeneity (P = 0.01), the sequences were combined for further analysis.

Maximum parsimony analyses were conducted with PAUP v. 4.0b10 (Swofford 2002). A heuristic search was performed with the stepwise-addition option with 1 000 random taxon addition replicates and TBR branch swapping. All characters were unordered and given equal weight. Gaps were treated as missing data. Branch support was estimated on the recovered topologies by performing a heuristic search of 1 000 bootstrap replicates consisting of ten random-addition replicates for each bootstrap replicate.

Bayesian analysis was performed in a likelihood framework, as implemented by the MrBayes v. 3.0b4 software package, to reconstruct phylogenetic trees (Huelsenbeck & Ronquist 2001). The program MrModeltest2 v. 2.3. (Nylander 2008) was used to infer the appropriate substitution model that would best fit the model of DNA evolution for our sequence data sets. Bayesian searches using Metropolis-coupled Markov chain Monte Carlo sampling were conducted. One cold and three heated Markov chains were used in the analysis. Bayesian analyses were run for 5 M generations with trees sampled every 1 000 generations. The first 20 000 trees representing the "burn-in" phase were discarded. To estimate posterior probabilities (PP) of recovered branches (Larget & Simon 1999), 50 % majority rule consensus trees were produced from the remaining trees using PAUP.

PHYLOGENETIC RESULTS

The first analysis was restricted to the ncLSU. The alignment consisted of the two first thirds of the ncLSU region for 99 sequences representing 91 species in 19 ascomycetous families and orders and 1 283 total characters: 615 constant, 140 not parsimony-informative, and 453 parsimony-informative. A maximum parsimony (MP) heuristic search produced 16 most parsimonious trees (MPTs) with a length of 3 303 steps (CI = 0.303, RI = 0.665, HI = 0.696). One of these trees is shown in Fig. 1. The GTR+I+G substitution model was selected for the Bayesian analysis. The order *Glomerellales* forms a monophyletic clade (82 % bootstrap support /0.7 posterior probability) with three families recognised, the *Australiascaceae* (90/1.0), *Glomerellaceae* (85/0.83), and *Reticulascaceae* (97/1.0). Within the *Reticulascaceae*, *Cylindrotrichum setosum* is sister to the *Reticulascus clavatus* clade (95/1.0), *R. tulasneorum* forms a well-supported clade (75/1.0), and *Kylindria peruamazonensis* and *Porosphaerellopsis* are nested at the base of the *Reticulascaceae* (97/1.0). The order *Microascales* as presently conceived appears to be polyphyletic. The monophyletic *Ceratocystidaceae* (100/1.0) and *Gondwanamycetaceae* (100/1.0) form a clade (92/1.0) as a

Table 1. Sources and accession numbers of isolates numbers of isolates analysed in this study. GU1806XX–GU1806YY are sequences newly generated in this study.

Teleomorph	Anamorph	M	Source*	Substrate and Locality	GenBank accession numbers **			
					ITS	LSU	SSU	RPB2
Australiasca laeënsis	*Monilochaetes laeënsis*	●	DAOM 226788	Australia, dead fronds of a tree fern	GU180623	GU180641	GU180610	–
	Monilochaetes laeënsis	●	PRM 915720	UK, stem of *Dicksonia antarctica*	GU180624	GU180642	–	–
Australiasca queenslandica	*Monilochaetes camelliae*	●	BRIP 24607a	Australia, branch of *Camellia sinensis*	HM237327	HM237324	–	–
	Monilochaetes camelliae	○	BRIP 24334c	Australia, branch of *Camellia sinensis*	HM237326	HM237323	–	–
Calosphaeria pulchella	*Calosphaeriophora pulchella*	●	CBS 115999	France, wood and bark of *Prunus avium*	–	AY761075**	AY761071**	GU180661
Ceratosphaeria lampadophora	*Harpophora*-like	●	CBS 117555	France, decayed wood	–	–	GU180618	–
Chaetosphaeria ciliata	*Menispora ciliata*	●	ICMP 18253	New Zealand, decayed wood	–	GU180637	GU180614	GU180659
Chaetosphaeria curvispora	*Chloridium*-like	●	ICMP 18255	New Zealand, decayed wood	–	GU180636	AY502933**	GU180655
Faurelina indica	*Arthrographis* sp.	●	CBS 126.78	India, dung of goat	GU291802	GU180653	–	–
	Arthrographis sp.	●	CBS 301.78	India, dung of cow	–	GU180654	–	–
Reticulascus clavatus	*Cylindrotrichum clavatum*	●	CBS 125296	France, submerged wood of *Alnus glutinosa*	GU180627	GU180643	GU180622	–
	Cylindrotrichum clavatum	○	CBS 125239	France, submerged wood of *Platanus* sp.	GU180633	GU180649	GU180615	–
	Cylindrotrichum clavatum	○	CBS 125297	France, submerged wood of *Fraxinus* sp.	GU180634	GU180650	–	–
	Cylindrotrichum clavatum	○	CBS 428.76	Sweden, decayed wood of *Ulmus scabra*	GU291799	–	–	–
Reticulascus tulasneorum	*Cylindrotrichum oligospermum*	○	CBS 561.77	Netherlands, twig of *Fraxinus excelsior*	GU291801	–	–	–
Reticulascus tulasneorum	*Cylindrotrichum oligospermum* (as *hennebertii*)	○	CBS 570.76	Germany, dead twig of *Symphoricarpos albus*	AF178560**	AF178560**	–	–
Reticulascus tulasneorum	*Cylindrotrichum oligospermum*	○	CBS 557.74	Czech Republic, wood of *Salix purpurea*	GU291798	–	–	–
	Cylindrotrichum oligospermum	●	CBS 101319	Czech Republic, wood of *Sambucus nigra*	AF178547**	AF178547 **	–	–
Togniniella acerosa	*Phaeocrella acerosa*	●	ICMP 18256 CBS 125298	New Zealand, decayed wood of *Nothofagus* sp.	–	AY761076**	AY761073**	GU180660
tu	*Acrostalagmus annulatus*	○	DAOM 212126	Germany, soil and roots	GU180632	GU180646	GU180611	GU180662
tu	*Cylindrotrichum gorii*	○	CBS 879.85	Sweden, dead stem of *Urtica dioica*	HM237328	HM237322	–	–
tu	*Cylindrotrichum setosum*	○	DAOM 229246	Australia, wood and bark mulch on the ground	GU180635	GU180652	GU180617	–
tu	*Custingophora olivacea*	○	CBS 335.68	Germany, compost	–	–	–	GU180665
tu	*Kylindria peruamazonensis*	○	CBS 838.91	Cuba, leaf litter of *Bucida palustris*	GU180628	GU180638	GU180609	GU180656
tu	*Kylindria peruamazonensis*	○	CBS 421.95	Cuba, leaf of *Bucida palustris*	GU291800	HM237325	–	–
tu	*Gibellulopsis nigrescens*	○	DAOM 226890	Canada, Ontario, soil	GU180631	GU180648	GU180613	GU180664
tu	*Monilochaetes guadalcanalensis*	○	CBS 346.76	Solomon Islands, leaf of *Musa*	GU180625	GU180640	–	–
tu	*Monilochaetes infuscans*	○	CBS 379.77	New Zealand, *Ipomoea batatas*	–	GU180645	GU180619	GU180658
tu	*Monilochaetes infuscans*	○	CBS 869.96	South Africa, *Ipomoea batatas*	GU180626	GU180639	GU180620	GU180657
tu	*Monilochaetes infuscans*	○	CBS 870.96	South Africa, *Ipomoea batatas*	–	GU180644	GU180621	–
tu	*Plectosporium tabacinum*	○	DAOM 229828	Canada, Ontario, soil	GU180630	GU180647	GU180612	GU180663
tu	*Stachylidium bicolor*	○	DAOM 226658	straw of *Oryza sativa* imported from India into Canada	–	GU180651	GU180616	–

* BRIP = Plant Pathology Herbarium, Queensland, Australia; CBS = Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; DAOM = Canadian Collection of Fungal Cultures, Agriculture and Agri-Food Canada, Ottawa.

** These sequences were published elsewhere (Réblová & Winka 1999, Réblová & Seifert 2004, Réblová *et al.* 2004).

M: morph of material available: • = teleomorph, ◦ = anamorph.

tu = teleomorph unknown

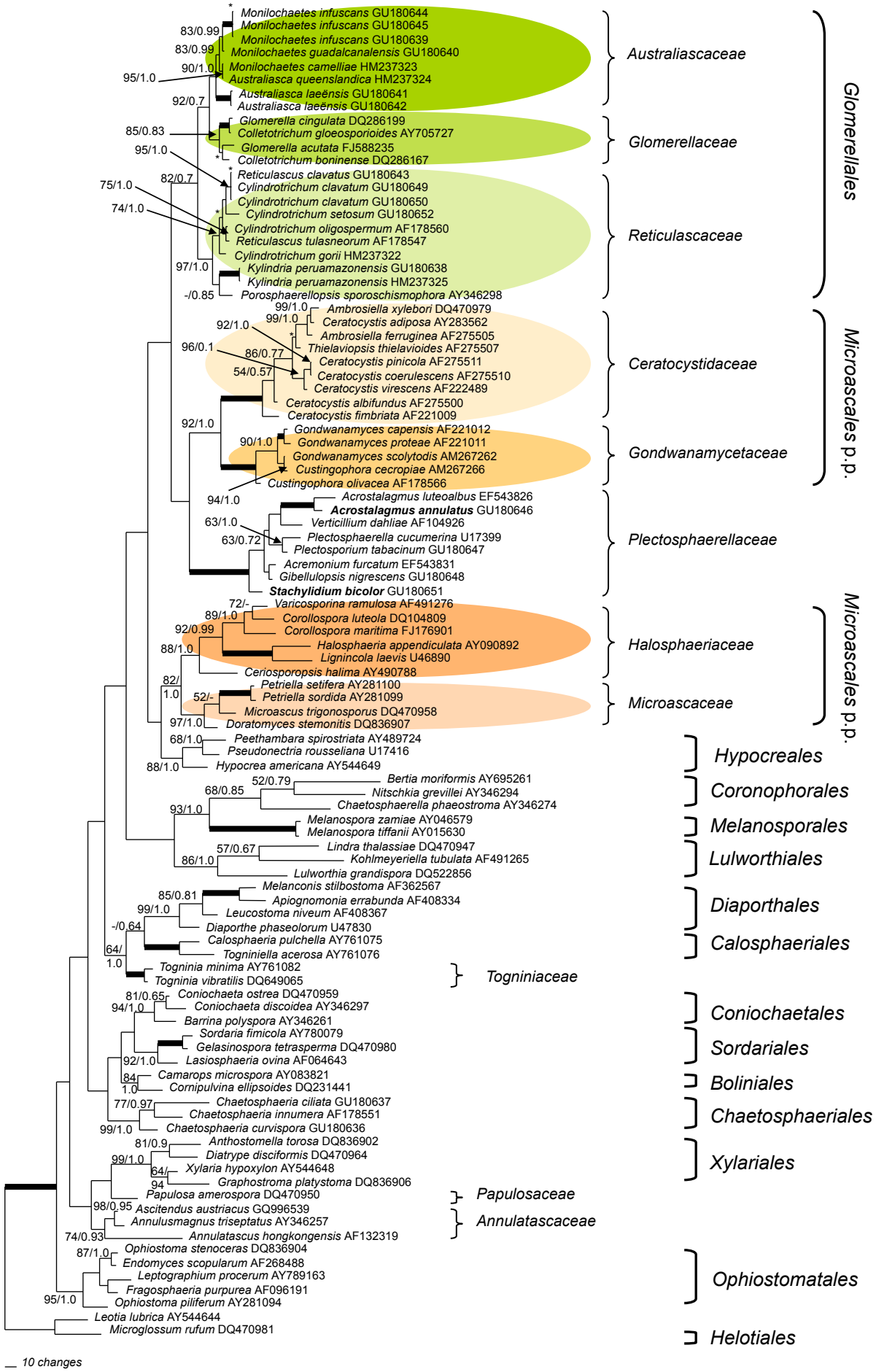

Fig. 1. One of 16 most parsimonious trees from a heuristic analysis of ncLSU rDNA sequences. Thickened branches indicate posterior probability values = 1.0 PP and 100 % bootstrap support. Bootstrap support values ≥ 50 % and Posterior probability values ≥ 0.5 are included at the nodes. Branch lengths are drawn to scale. An asterisk above or below a branch marks branches that collapse in the strict consensus tree.

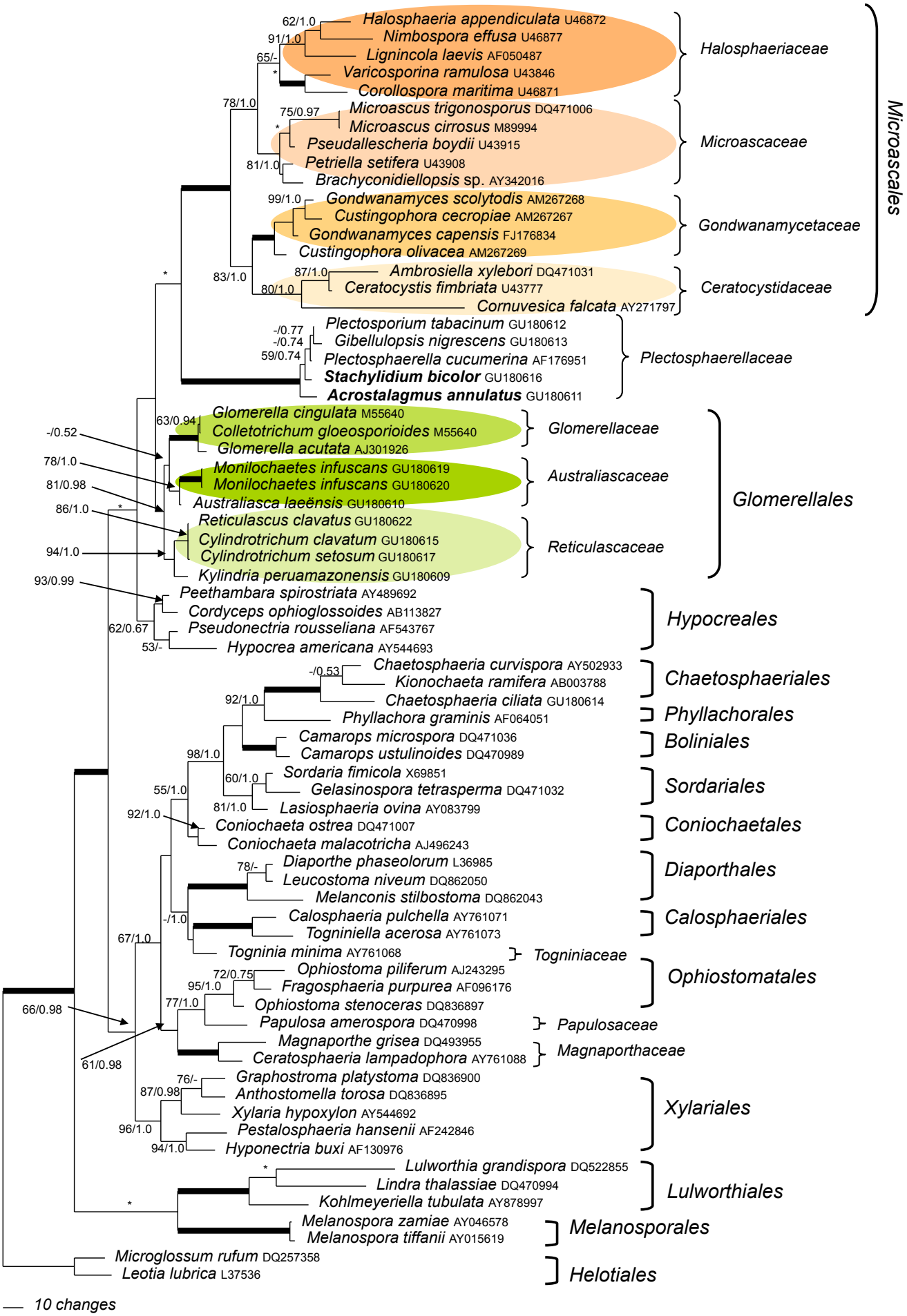

Fig. 2. One of the 14 most parsimonious trees from a heuristic analysis of ncSSU rDNA sequences. Details as in Fig. 1.

sister to the *Plectosphaerellaceae* (100/1.0). The other two families of the *Microascales* form a separate clade (82/1.0) containing the *Microascaceae* (97/1.0) and the *Halosphaeriaceae* (88/1.0). The second analysis was restricted to the ncSSU. The alignment consisted of the whole gene for ncSSU for 71 sequences representing 67 species in 19 ascomycetous orders and families and 1 777 total characters: 1 102 constant, 195 not parsimony-informative, and 405 parsimony-informative. A maximum parsimony heuristic search produced 14 MPTs with a length of 2 267 steps (CI = 0.390, RI = 0.697, HI = 0.609), one of which is shown in Fig. 2. For the Bayesian analysis, the GTR+I+G substitution model was inferred. The *Glomerellales* form a monophyletic, strongly supported clade (81/0.98) containing representatives of three families, the *Australiascaceae* (78/1.0), *Glomerellaceae* (100/1.0), and *Reticulascaceae* (94/1.0). The *Plectosphaerellaceae* form a separate, strongly supported clade (100/1.0) basal to the *Microascales*. The *Microascales* appear as a monophyletic clade (100/1.0) including two strongly supported subclades. The first subclade (78/1.0) contains the *Halosphaeriaceae* (65/-) and *Microascaceae* (81/1.0) and the second subclade (83/1.0) contains the *Ceratocystidaceae* (80/1.0) and *Gondwanamycetaceae* (100/1.0).

In the third analysis, a combination of the ncLSU and ncSSU data sets plus RPB2 sequences was assessed for 54 taxa representing 52 species in 18 ascomycetous orders and families. The alignment of the combined set of ncLSU-ncSSU-RPB2 DNA sequences consisted of 4 224 total characters: 2 148 constant, 314 not parsimony-informative, and 1 484 parsimony-informative. A maximum parsimony heuristic search produced two MPTs with a length of 11 688 steps (CI = 0.278, RI = 0.476, HI = 0.722); one is shown in Fig. 3. For the Bayesian analysis the GTR+I+G substitution model was selected. The *Glomerellales* are a monophyletic, well-supported clade (100/0.81) with the *Plectosphaerellaceae* as a sister group (100/1.0). The *Microascales* appear as a monophyletic, strongly supported clade (88/1.0), again with two subclades; the first (87/1.0) contains the *Halosphaeriaceae* (94/1.0) and *Microascaceae* (88/1.0) while the other (100/1.0) comprises the *Ceratocystidaceae* (100/1.0) and *Gondwanamycetaceae* (99/1.0).

The fourth analysis included ITS1, 5.8S, and ITS2 regions of species of the *Glomerellales* and *Plectosphaerellaceae*. The alignment consisted of 38 sequences representing 29 species in five families and 574 total characters: 277 constant, 75 not parsimony-informative, and 222 parsimony-informative. A maximum parsimony heuristic search produced nine MPTs with a length of 786 steps (CI = 0.592, RI = 0.821, HI = 0.407). One is shown in Fig. 4. The GTR+G substitution model was inferred for the Bayesian analysis. Following the results of our other analyses, two *Chaetosphaeria* species (*Chaetosphaeriales*) were used as outgroups. The order *Glomerellales* is a strongly supported monophylum (95/0.99) containing three strongly supported families, the *Australiascaceae* (99/1.0), *Glomerellaceae* (99/0.97), and *Reticulascaceae* (96/1.0). The *Plectosphaerellaceae* (100/1.0) appears as a strongly supported sister clade to the *Glomerellales*. Six strains represent the *Australiascaceae* in the analysis: two strains of *Australiasca queenslandica*, two strains of *A. laeënsis,* and one strain each of *Monilochaetes infuscans* and *M. guadalcanalensis*. The *Reticulascaceae* are represented by four strains of *Reticulascus clavatus* (anamorph *C. clavatum*), four strains of *R. tulasneorum* (anamorph *Cylindrotrichum oligospermum*), *C. setosum*, *C. gorii,* and two strains of *Kylindria peruamazonensis*. The two conidial (CBS 125239, CBS 125297) and single ascospore (ex-type strain CBS 125296) isolates of freshwater *R. clavatus* plus one terrestrial isolate (CBS 428.76) formed a strongly supported monophylum (100/1.0). Another strongly supported monophyletic clade (97/1.0) included one ascospore- (ex-type strain CBS 101319) and three conidial isolates of *R. tulasneorum* (CBS 557.74, CBS 561.77, ex-type strain of *C. hennebertii* CBS 570.76). The anamorphic *C. setosum* (ex-type strain DAOM 229246), *C. gorii* (CBS 879.85), and *K. peruamazonensis* (CBS 421.95, CBS 838.91) were basal to the rest of the clade on separate branches.

A fifth analysis of the ncLSU rDNA sequences was run to determine the relationship of two strains of *Faurelina indica* with members of the *Dothideomycetes* and *Eurotiomycetes*. The alignment consisted of the first two thirds of the ncLSU for 68 sequences representing 66 species in 11 orders and families and 1 229 total characters: 716 constant, 76 not parsimony-informative, and 362 parsimony-informative. A maximum parsimony heuristic search produced 66 MPTs with a length of 1 593 steps (CI = 0.433, RI = 0.760, HI = 0.567). One is shown in Fig. 5. The GTR+I+G substitution model was selected for the Bayesian analysis. The two strains of *Faurelina* form a monophyletic clade (88/0.9), which is a sister to the *Didymellaceae* (96/1.0). The suggested relationship of *Faurelina* with the *Eremomycetaceae* and *Testudinaceae* could not be confirmed; the families grouped on separate branches with no close relationship to each other. *Faurelina* appears to be a member of the *Pleosporales* within the *Dothideomycetes* unrelated to the *Microascales*.

TAXONOMY

Glomerellales

Chadefaud (1960) proposed the order "Glomérellales" for a group of endophytic fungi and parasites of living plants with ascomata varying from endostromatal to apostromatal and ascospores that are often unicellular and hyaline. No Latin diagnosis was provided for the order. Within the order he suggested an evolution of the apical apparatus from an initial condition of the periocular thickening of the apical dome lacking a pronounced chitinoid or amyloid ring to derived conditions of either the apical thickening converted into an apical cushion reduced to a simple lens-shaped disc or with the initial of a chitinoid ring developing in the periocular thickening. According to the texture and pigmentation of the ascomata, he further divided the order into two groups: a) "Eu-Glomérellales", which included genera with a non-fleshy black stroma *i.e. Gibellina*, *Glomerella*, *Phyllachora*, and *Physalospora;* and b) “Polystigmatales” as “Glomérellales nectrioïdes”, which comprised one genus, *Polystigma*, with a orange to red, fleshy stroma. After this invalid introduction of the name *Glomerellales*, the order was also cited by Lanier *et al.* (1978) and later by Locquin (1984), when he listed the *Glomerellales* and *Polystigmatales* as separate orders, again without a Latin diagnosis. After the validation of the *Glomerellaceae* in Zhang *et al.* (2006), we validate here the phylogenetically delimited order *Glomerellales*, excluding the earlier validated but unrelated *Phyllachorales.*

Three families are accepted in the *Glomerellales*, namely the *Glomerellaceae*, *Australiascaceae*, and *Reticulascaceae*. The latter two families are newly described below based on cultural studies, detailed morphological comparisons of the holomorphs, and newly generated ITS, ncLSU, ncSSU, and RPB2 sequences.

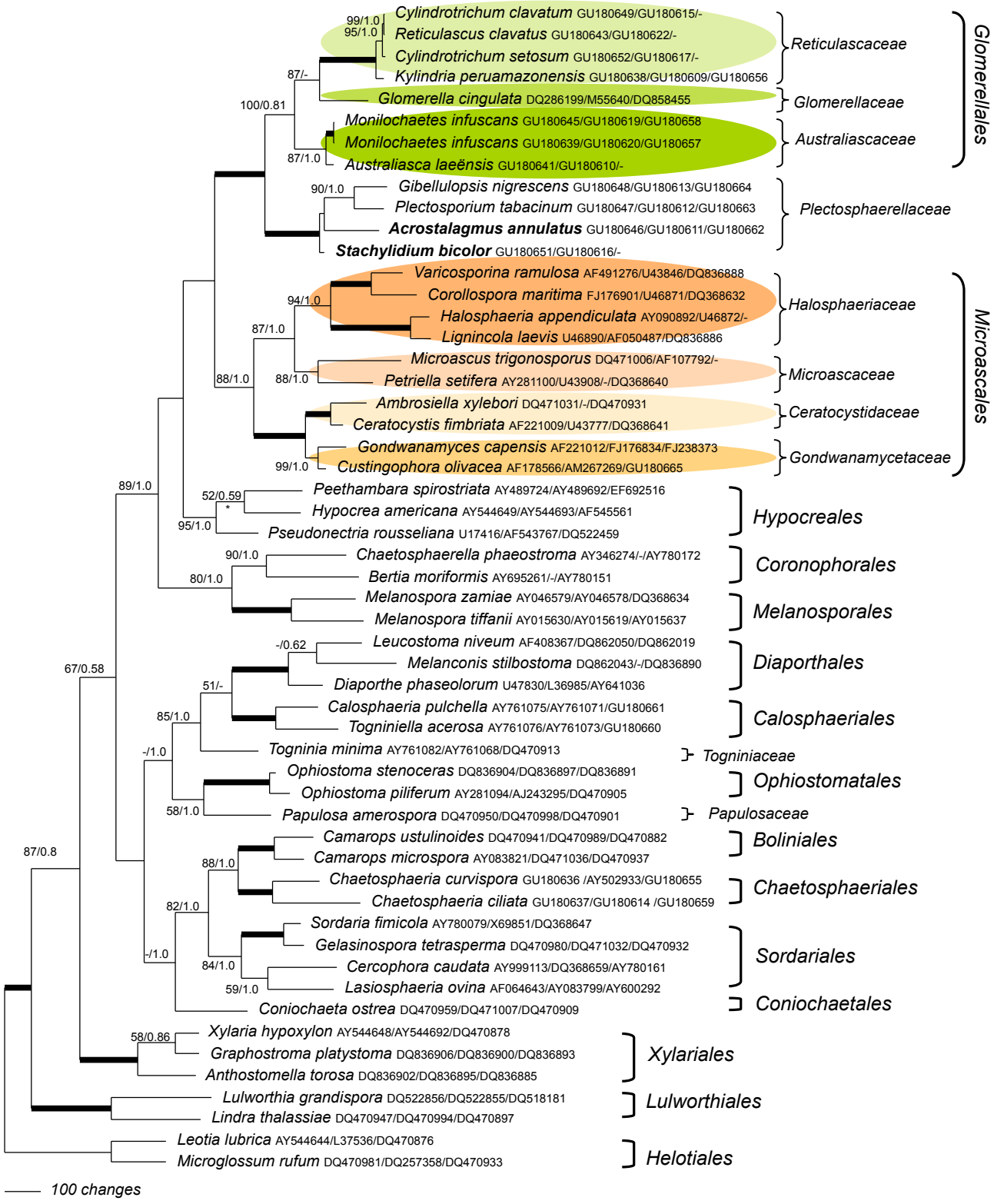

Fig. 3. One of the two most parsimonious trees from a heuristic analysis of the three-gene combined data set (ncLSU-ncSSU-RPB2). Details as in Fig. 1. The GenBank accession numbers given after the names are those of ncLSU/ncSSU/RPB2 genes. Missing sequences are indicated by "–".

Glomerellales Chadef. ex Réblová, W. Gams & Seifert, **ord. nov.** MycoBank MB515429.

Glomerellales Chadef., *Traité de botanique systématique*. Tome I, p. 613. 1960 (also in Lanier *et al.*, *Mycol. Pathol. Forest.* I: 292. 1978; Locquin, *Mycol. Gén. Struct.*, p. 170. 1984) nom. inval., Art. 36.

Ascomata perithecia, brunnea usque nigra, nonnumquam sclerotioidea, ostiolum periphysatum. Pariete ascomatum 2-3-stratoso. Hamathecium paraphyses verae. Asci unitunicati, brevi-stipitati, parte apicali iodo non reagente. Ascosporae hyalinae vel pallide pigmentatae, 0-pluri-cellulares. Anamorphe: conidia modo phialidico orientia.

Typus: *Glomerellaceae* Locq. ex Seifert & W. Gams, *Mycologia* 98: 1083. 2007 [2006].

Perithecia darkly pigmented, sometimes becoming ± sclerotial. *Perithecial wall* 2–3-layered, ostiolum periphysate. Interascal tissue of thin-walled, tapering paraphyses. *Asci* unitunicate, thin-

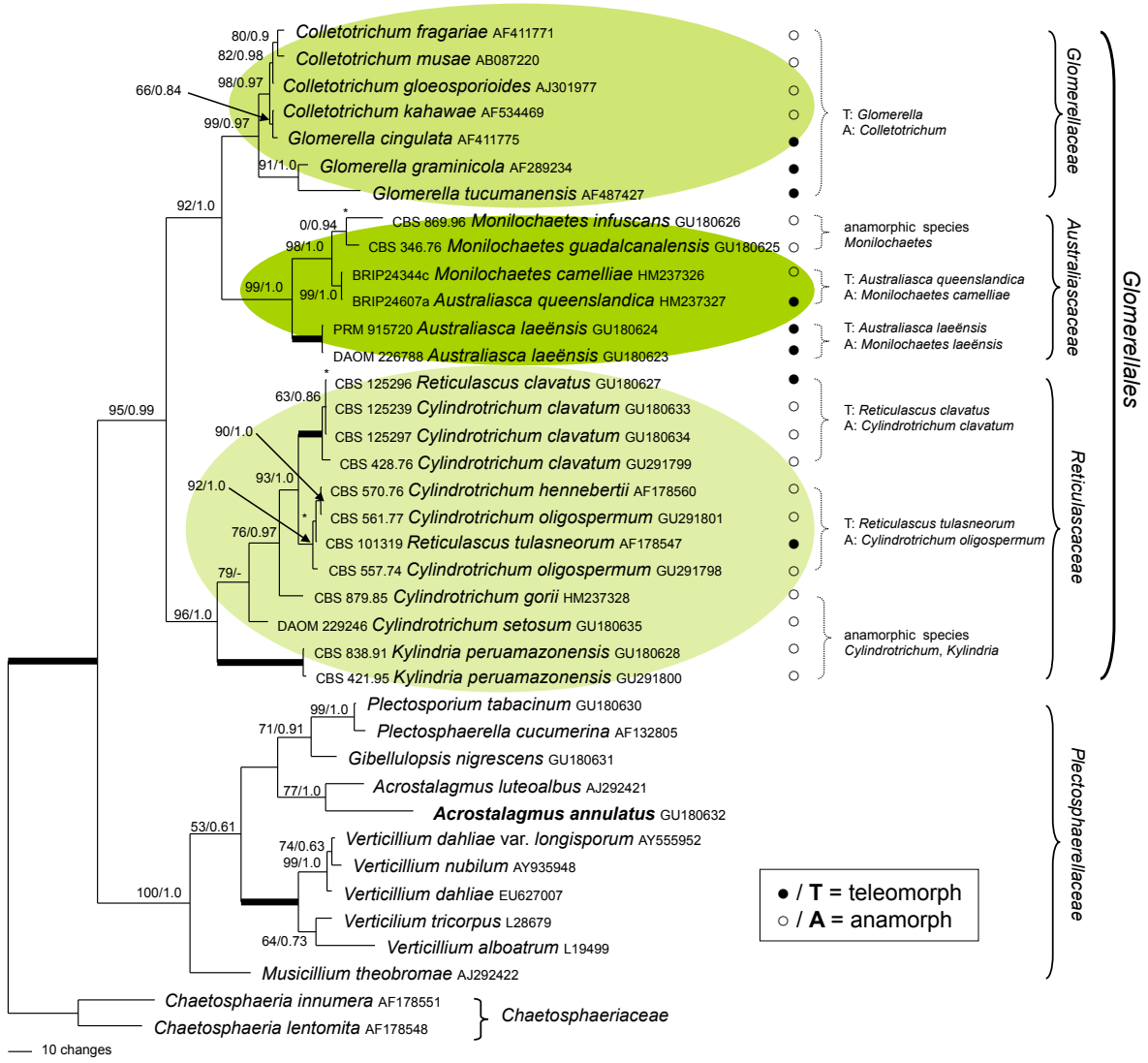

Fig. 4. One of the nine most parsimonious trees from a heuristic analysis of ITS rDNA operon of the *Glomerellales* and the *Plectosphaerellaceae*. The accession numbers of strains of the newly described *Australiascaceae* and *Reticulascaceae* are indicated. Details as in Fig. 1.

walled, ascal apex thickened without visible discharge mechanism or thin-walled with a distinct apical annulus, inamyloid, 8-spored. *Ascospores* hyaline or pigmented, 0–several-septate. Anamorphs with phialidic conidiogenesis.

Families: *Australiascaceae* Réblová & W. Gams, *Glomerellaceae* Locq. ex Seifert & W. Gams, and *Reticulascaceae* Réblová & W. Gams.

This order is phylogenetically distinct from the *Phyllachorales*, in which its members were formerly classified. The original classification proposed by Chadefaud (1960), who included *Phyllachora* in this order, is untenable based on our molecular data (Fig. 2). In the ncSSU phylogeny, the *Phyllachorales* represented by *Phyllachora graminis* (ncSSU rDNA sequence: AF064051, Winka & Eriksson 2000) are clearly separated from the *Glomerellales*; the former is nested within a clade (91/1.0) sister to the *Chaetosphaeriales* (100/1.0).

Glomerellaceae

This family accommodates the teleomorph genus *Glomerella* and its *Colletotrichum* anamorphs. For discussion and description refer to Zhang *et al.* (2006).

Glomerellaceae Locq. ex Seifert & W. Gams in Zhang *et al.*, Mycologia 98: 1083. 2007. [2006].

Australiascaceae Réblová & W. Gams, **fam. nov.** MycoBank MB515430.

Stromata absentia. Ascomata perithecia, brunnea usque nigra, ostiolum periphysatum. Pariete ascomatum fragili, 2-stratoso. Hamathecium paraphyses verae. Asci unitunicati, 8-spori, cylindraceo-clavati, annulo apicali iodo non reagente. Ascosporae hyalinae, septatae. Anamorphe *Monilochaetes*; conidiis 0(–3)-septatis, hyalinis modo phialidico orientibus.

Typus: *Australiasca* Sivan. & Alcorn, Aust. Syst. Bot. 15: 742. 2002.

Stroma absent. *Perithecia* brown to black, ostiolum periphysate. *Perithecial wall* 2-layered, fragile. *Interascal tissue* of thin-walled, tapering paraphyses. *Asci* unitunicate, 8-spored, cylindrical-clavate, apical ring distinct, inamyloid. *Ascospores* hyaline, septate. Anamorph: *Monilochaetes*; conidiogenesis phialidic, with hyaline 0(–3)-septate conidia, aggregated in slime or in chains.

The *Australiascaceae* accommodates the holomorphic genus *Australiasca* and anamorphic *Monilochaetes*. The molecular data for *Australiasca* (Figs 1–3) confirm that the genus is unrelated to the *Chaetosphaeriaceae* or *Lasiosphaeriaceae* as suggested by Sivanesan & Alcorn (2002). However, the *Australiascaceae*, like

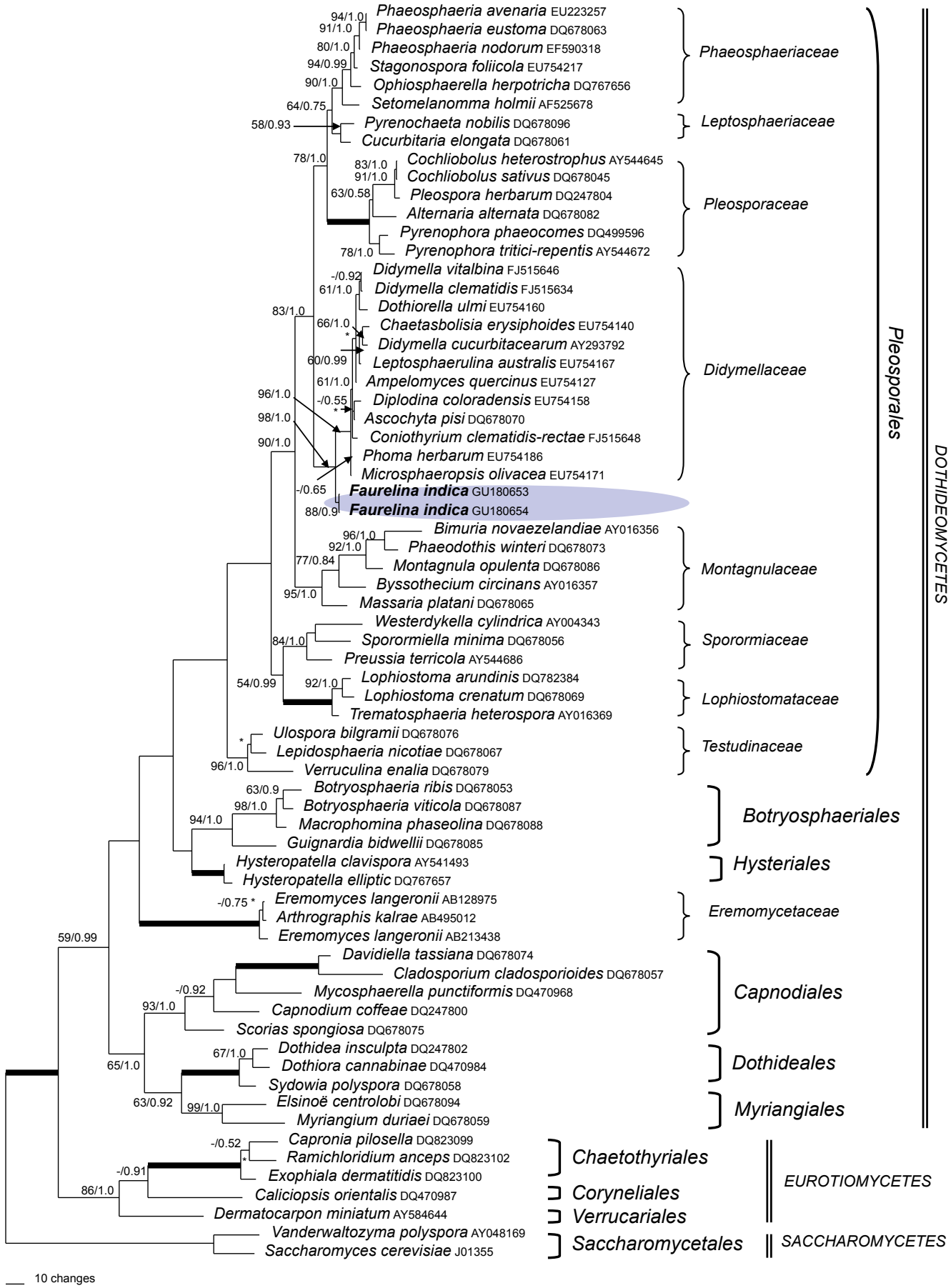

Fig. 5. One of 66 most parsimonious trees from a heuristic analysis of ncLSU rDNA of *Faurelina indica* and *Dothideomycetes*. Details as in Fig. 1.

the *Reticulascaceae*, accommodates teleomorphs that mimic *Chaetosphaeria* and which are almost indistinguishable from its perithecia on morphological grounds. The anamorphs are phialidic, dematiaceous hyphomycetes with hyaline, slimy conidia, which are also similar to anamorphs of *Chaetosphaeria*.

The dematiaceous hyphomycete genus *Monilochaetes* was described and illustrated for a single species, *M. infuscans* (Halsted 1890, Harter 1916), which causes scurf disease or soil stain of *Ipomoea batatas* (sweet-potato). Another saprobic species, *M. guadalcanalensis*, collected on leaves of *Musa* sp., originally described in *Catenularia,* was recently added (Rong & Gams 2000) and this classification is confirmed here by molecular data. *Monilochaetes* includes species with solitary, erect, sometimes curved or geniculate, macronematous conidiophores, darker near the base, becoming paler towards the apex, with prominently darkened septa, terminal, wide monophialides with a shallow collarette, and aseptate, rarely septate, hyaline conidia adhering in basipetal chains or heads. Rong & Gams (2000) distinguished *Monilochaetes* from the other two similar dematiaceous hyphomycete genera *Dischloridium* (Sutton 1976) and *Exochalara* (Gams & Holubová-Jechová 1976) by aspects of conidiophore branching and fasciculation and conidial shapes and dimensions. The present ITS and ncLSU phylogenies confirm that *Dischloridium* and the morphologically similar older genus *Monilochaetes*, which up to now was only known as asexual, are congeneric. Therefore, *Dischloridium laeënse*, type of the genus, is transferred to *Monilochaetes* and *Dischloridium* becomes a generic synonym of *Monilochaetes*.

The teleomorph-anamorph connections of *Australiasca queenslandica*, type species of the genus, with *M. camelliae* and of the newly described *A. laeënsis* with *M. laeënsis* were experimentally established (Sivanesan & Alcorn 2002, this study). The other four species accepted in *Monilochaetes* are presently only known to be anamorphic. A further species of *Monilochaetes* is described by Réblová *et al*. (2011)

KEY TO THE SPECIES OF *AUSTRALIASCA* AND *MONILOCHAETES* IN THE *AUSTRALIASCACEAE*

1. Conidia hyaline, ellipsoidal, aseptate, rarely 1–3-septate, longer than 26 µm 2
1. Conidia hyaline, ellipsoidal, aseptate, rarely 1-septate, shorter than 26 µm 3

2. Conidia ellipsoidal with an obtuse base, sometimes with laterally displaced hilum, aseptate, rarely 1–3-septate at maturity, 18–35 × 8–13 µm *in vitro*; 20.5–24(–26.5) × (10–)11–12(–13) µm on PCA; asci 65–140 × 12.5–17.5 µm; ascospores 18–31 × 7.5–10.5 µm ..... *A. camelliae* (anamorph *M. camelliae*)
2. Conidia cylindrical to ellipsoidal with an obtuse base, 25–38 × 12–16 µm *in vivo*; teleomorph unknown ..... *M. regenerans*

3. Conidia aseptate, ellipsoidal to oblong, usually in small clusters, aggregated in slimy droplets 4
3. Conidia 0–1-septate, rhomboid–ellipsoidal to obovoidal, usually forming chains 5

4. Conidia oblong, apically rounded, with an obtuse base, 9–25 × 3.5–6(–7) µm; teleomorph unknown ..... *M. basicurvata*
4. Conidia ellipsoidal to oblong with an obtuse base, 22–26 × 10–12 µm *in vivo*, (15.5–)18–22.5(–23.5) × 7.5–9(–10) µm *in vitro* (PCA); asci 130–148 × 12.5–17.5 µm; ascospores (20–)24.5–31.5(–33) × (7.5–)9–9.5 µm ..... *A. laeënsis* (anamorph *M. laeënsis*)

5. Conidia rhomboid–ellipsoidal to obovoidal on host, rarely 1-septate, ellipsoidal with an obtuse base in culture, 15–20 × 4–6 µm ..... *M. infuscans*
5. Conidia ellipsoidal with an obtuse base in culture, 18–21 × 6–9 µm ..... *M. guadalcanalensis*

Australiasca laeënsis Réblová & W. Gams, **sp. nov.** MycoBank MB518384, Fig. 6A–K.

Anamorph: ***Monilochaetes laeënsis*** (Matsush.) Réblová, W. Gams & Seifert, **comb. nov.** MycoBank MB515431.

Basionym: *Chloridium laeënse* Matsush., Bull. Natl. Sci. Mus. Tokyo 14: 462. 1971.

≡ *Dischloridium laeënse* (Matsush) B. Sutton, Kavaka 4: 47. 1976.

Etymology: Epithet from the anamorph species, originally derived from the type locality, Lae in Papua-New Guinea (Matsushima 1971).

Stromata absentia. Perithecia superficialia, gregaria vel solitaria, atra, conica usque obpyriformia, 200–320 µm diam, 340–450 µm alta, ostiolum periphysatum. Paries ascomatum fragilis, 2-stratosus. Paraphyses septatae, hyalinae, sursum angustatae, ascos superantes. Asci unitunicati, cylindraceo-clavati, 130–148 × 18–20 µm (in medio ± s.e. = 137.6 ± 5.3 × 19.3 ± 0.6 µm), 8-spori, brevi-stipitati, apice truncato. Ascosporae ellipsoideae usque ovoideae, 24.5–31.5(–33) × (8–)9–9.5 µm (in medio ± s.e. = 15.7 ± 0.2 × 4.4 ± 0.04 µm), hyalinae, 0–1-septatae. Anamorphe *Monilochaetes laeënsis*.

Perithecia 200–320 µm diam, 340–450 µm high, gregarious to solitary among conidiophores, superficial, base slightly immersed, conical to obpyriform, with a short beak, black, glabrous or with setae. Setae scanty, acute, thick-walled, septate, dark brown, paler to subhyaline towards apex, sometimes on upper half of perithecium, 90–155 × 5–7 µm; longer, thicker-walled setae, arising from base of perithecium, 300–420 × 10–11 µm. *Perithecial wall* 18–22 µm thick, becoming 45–54 µm thick towards base, fragile, 2-layered: outer layer of *textura prismatica* consisting of thick-walled, brick-like cells, cells becoming polyhedral towards base; inner layer of hyaline, compressed cells. *Paraphyses ca*. 2.5–3 µm wide, persistent, hyaline, septate, branching, longer than asci. *Asci* 130–148 × 18–20 µm (mean ± s.e. = 137.6 ± 5.3 × 19.3 ± 0.6 µm), unitunicate, cylindrical-clavate, short-stipitate, apex truncate, with a distinct, shallow annulus, *ca*. 6 µm wide, 1–1.5 µm high, 8-spored. *Ascospores* 24.5–31.5(–33) × (8–)9–9.5 µm (mean ± s.e. = 28.4 ± 0.6 × 8.9 ± 0.1 µm), ellipsoidal to oblong, apiculate at both ends, 1-celled, becoming transversely 1–3-septate after discharge, smooth, germinating with germ tubes at both ends, hyaline, irregularly 2-seriate in ascus.

Fig. 6.A–K. *Australiasca laeënsis*. A. Perithecium. B. Ascospores. C. Asci with ascospores, some ascospores with a developed median septum. D, E. Conidia and F–K. Conidiophores of the *Monilochaetes laeënsis* anamorph, in culture. A–C from PRM 915720; D–K DAOM 226788 (PCA, 14 d old). Scale bars: A = 100 µm; B, D–K = 10 µm; C = 50 µm. DIC: A, D, G–K; PC: B, C, E, F.

Colonies *in vivo* dark, hairy, effuse. *Conidiophores* 200–600 µm long, 6.5–9 µm wide, arising in small fascicles or small loose groups of 2–6 or solitary from a minute stromata, macronematous, percurrently proliferating, dark brown, 5–15-septate; base occasionally bulbous with smaller, thick-walled, adjacent pseudoparenchymatous cells forming stromatic tissue in substratum. *Conidiogenous cells* monophialidic, 50–70 × 4.5–8(–10) µm, terminal, cylindrical, hardly tapering at apex, subhyaline; collarette *ca.* 1–2 µm high, minute, conidiogenous locus located at base of collarette. *Conidia* 22–26 × 10–12 µm (mean ± S.E. = 23.2 ± 0.2 × 10.8 ± 0.2 µm), ellipsoidal to cylindrical-ellipsoidal, broadly rounded, sometimes obtuse at base, hyaline, basal scar 3.5–4 µm diam, smooth-walled.

Colonies *in vitro* after 14 d on PCA at 25 °C 15−20 mm diam, felty, stromatic tissue absent, aerial mycelium olive-brown, margin entire; reverse pale greyish-brown. Colonies readily sporulating, beginning

after 5 d on PCA at 25 °C under near-UV light (12 h light: 12 h dark). Conidiophores, phialides, and conidia morphologically identical to those on natural substratum. *Conidiophores* 40–160 × 7–8 µm, pale brown throughout, with none or 1 percurrent proliferation, 2–5-septate; in about 28 d, longer conidiophores developing, *ca.* 160-280 µm long, dark brown, subhyaline towards apex, with 1–4 percurrent proliferations, up to 2–15-septate. *Conidiogenous cells* monophialides 31–58 × (6–)7–9 µm, tapering to 4–6.5 µm just below collarette; collarette *ca*. 1.5 µm high and (5.5–)6–8 µm wide. *Conidia* (15.5–)18–22.5(–23.5) × 7.5–9(–10) µm (mean ± S.E. = 20.9 ± 1 × 8.2 ± 0.3 µm), ellipsoidal to cylindrical-ellipsoidal, broadly rounded, sometimes obtuse at base, hyaline, basal scar 2–3.5 µm diam, smooth-walled.

Specimens examined (anamorph and teleomorph): **Australia,** New South Wales, Blue Mountains, Mt. Tomah Botanical Garden, S 33 32.4, E 150 25.4, 1197 m alt., on dead stipes and spathes of a tree fern in a rain forest, 17 Aug. 1999, K.A. Seifert no. 884 and G.J. Samuels, DAOM 226788. **UK**, England, West Cornwall, Penjerrick House Gardens, 22 June 2000, dead stipes of *Dicksonia antarctica*, B. Candy, PRM 915720, **holotype** of *A. laeënsis*.

Notes: Based on the results from ITS and LSU rDNA phylogenies, *Australiasca laeënsis* and *A. queenslandica* are distinct species, although they are morphologically similar. *Australiasca queenslandica* and its *M. camelliae* anamorph were originally described and isolated into culture from leaves, stems and branches of *Camellia sinensis*; perithecia containing mature asci and ascospores formed *in vitro* (Sivanesan & Alcorn 2002). The ascospores released by *A. queenslandica* were often observed to be 1–3-septate, becoming dictyoseptate, and some produced phialides with hyaline microconidia *in vitro*. The recently collected material of *A. laeënsis* from England and Australia documents perithecia produced on the host associated with the conidiophores of its *M. laeënsis* anamorph. The ascospores were observed to be transversely 1–3-septate after discharge, but never became dictyoseptate or exhibited phialidic germination. *Australiasca laeënsis* is described here based on our observations on the host and the anamorph in culture.

The range of conidial lengths of *M. camelliae* and *M. laeënsis* overlap, but those of the former species are usually longer. *Monilochaetes camelliae* produces conidia 18–35 × 8–13 µm in culture on Sachs agar + maize leaves (Sivanesan & Alcorn 2002) or 20.5–24(–26.5) × (10–)11–12(–13) µm on PCA (this study). The conidia of *M. laeënsis* are 22–26 × 10–12 µm on the host and (15.5–)18–22.5(–23.5) × 7.5–9(–10) µm on PCA (this study). Therefore, the conidia of *M. camelliae* from Sachs agar overlap in length with conidia of *M. laeënsis*, but exceed its upper range by nearly 10 µm, while on PCA the conidia of *M. camelliae* are only slightly longer than those of *M. laeënsis*. The conidial dimensions for *M. laeënsis* from our collections correspond with measurements of the type and other specimens on host substrata from different localities, *e.g.* Sutton (1976, conidia 15–20 × 8–10 µm), Matsushima (1971, 17–26 × 8–12 µm), and Holubová-Jechová (1982, 14.5–24 × 6.5–10 µm). The conidia of *M. laeënsis* are hyaline, aseptate, and arise singly from the conidiogenous locus, usually in slimy heads. The conidia of *M. camelliae* were described as occasionally 1–3-septate, produced in heads or chains (Sivanesan & Alcorn 2002). The conidiophores of *M. camelliae* are also slightly longer, often swollen subapically (Sivanesan & Alcorn 2002).

Monilochaetes laeënsis has been collected on dead leaves in Papua New Guinea (Matsushima 1971), Sri Lanka (Sutton 1976, Bhat & Sutton 1985), and Cuba (Holubová-Jechová 1982), dead leaves or twigs and dead palm spathes in Australia, Ethiopia, India and Malaysia (Bhat & Sutton 1985), and dead fern stipes in the United Kingdom (Kirk 1986). Only the European and recent Australian material contained perithecia with mature asci and ascospores. Kirk (1986) noted that *Dischloridium* does not occur naturally in the British Isles but was probably introduced into gardens where it was found along with its host *Dicksonia antarctica*. He also suggested that the prevailing colder temperatures may have triggered sexual reproduction in nature; our own teleomorph specimen was collected in a cool, humid valley in the Australian winter.

Australiasca queenslandica Sivan. & Alcorn, Aust. Syst. Bot. 15: 742. 2002. Figs 7A–R, 8A–G.
Anamorph: ***Monilochaetes camelliae*** (Alcorn & Sivan.) Réblová, W. Gams & Seifert, **comb. nov.** MycoBank MB518385.
Basionym: *Dischloridium camelliae* Sivan. & Alcorn, Aust. Syst. Bot. 15: 743. 2002.

Colonies *in vitro* on MEA after 14 d at 25 °C with 22−25 mm radial growth, more or less planar, surface dark brown, covered with abundant, pale grey, lanose to cottony aerial mycelium, margin smooth and entire, reverse grey, sterile. Colonies on PCA after 14 d at 25 °C with 23–25 mm radial growth, planar, surface brown, covered with pale grey, lanose to cottony aerial mycelium, margin smooth and entire, reverse dark grey, sterile.

Colonies *in vitro* on PCA sporulating in 14 d at 25 °C in darkness. Setae absent. *Conidiophores* 200–720 µm long, 9–10(–10.5) µm wide near base and 6.5–7.5(–8.5) µm wide in middle, pale to dark brown, subhyaline towards apex, with none or 1 percurrent proliferation, up to 20-septate. *Conidiogenous cells* monophialidic, subhyaline, paler towards collarette, ampulliform to cylindrical, slightly swollen, 36–45(–60) µm long, 6.5–8(–9) µm wide at widest part, tapering to *ca*. 3–4 µm just below collarette; collarette 4.5–5.5 µm wide and *ca.* 1.5–2 µm high. *Conidia* 20.5–24(–26.5) × (10–)11–12 µm (mean ± S.E. 22.5 ± 0.3 × 11.8 ± 0.1), 0–1-septate, ellipsoidal to cylindrical-ellipsoidal, broadly rounded at end, obtuse at base, basal scar 3–3.5 µm diam, some conidia with a laterally displaced hilum, hyaline, smooth-walled.

After 6 mo on PCA at 25 °C in darkness, producing minute conidiophores with microconidia. Setae absent. *Conidiophores* more or less erect, arising from aerial mycelium, simple or sparingly branched, pale brown to subhyaline, 40–60 µm long and 2–2.5 µm wide, with terminally integrated or intercalary conidiogenous cells. *Conidiogenous cells* monophialidic, subhyaline to pale brown, usually paler towards apex, ampulliform to cylindrical, 8–20 µm long, 2.5–3.5 µm wide at widest part, tapering to *ca*. 1.5 µm just below collarette; collarette 2.5–3 wide, *ca*. 2 µm high. *Conidia* 4–5.5 × 3–3.5 µm (mean ± S.E. 4.5 ± 0.1 × 3.2 ± 0.1), aseptate, thick-walled, broadly ellipsoidal to subglobose, rounded at ends, base slightly tapering, obtuse with a minute abscission scar, accumulating in small, clear to whitish droplets, hyaline, smooth-walled. Chlamydospores not observed.

Specimens examined (anamorph only): **Australia,** Queensland, Malanda, isolated from branch of *Camellia sinensis*, 19 Feb. 1997, D. Steel M. 8982c, BRIP 24334c; Queensland, Brisbane, S 27 30, E 152 58, isolated from branch of *Camellia sinensis*, 10 July 1997, J.L. Alcorn, BRIP 24607a).

Notes: Two isolates of *M. camelliae* were examined and ITS and ncLSU sequences were generated (Table 1). One of these is an authentic, single-ascospore isolate listed among specimens examined in the protologue of *Dischloridium camelliae* (Sivanesan & Alcorn 2002).

The ESEM photographs of conidia of *M. camelliae* (Fig. 8A, B, F, G) demonstrate well that there is a continuum between conidial chains and slimy heads on the phialides. The osmolarity of the medium may influence the relative proportion of chains and slimy heads as seen particularly in *Chloridium,* where chains, cirrhi, and

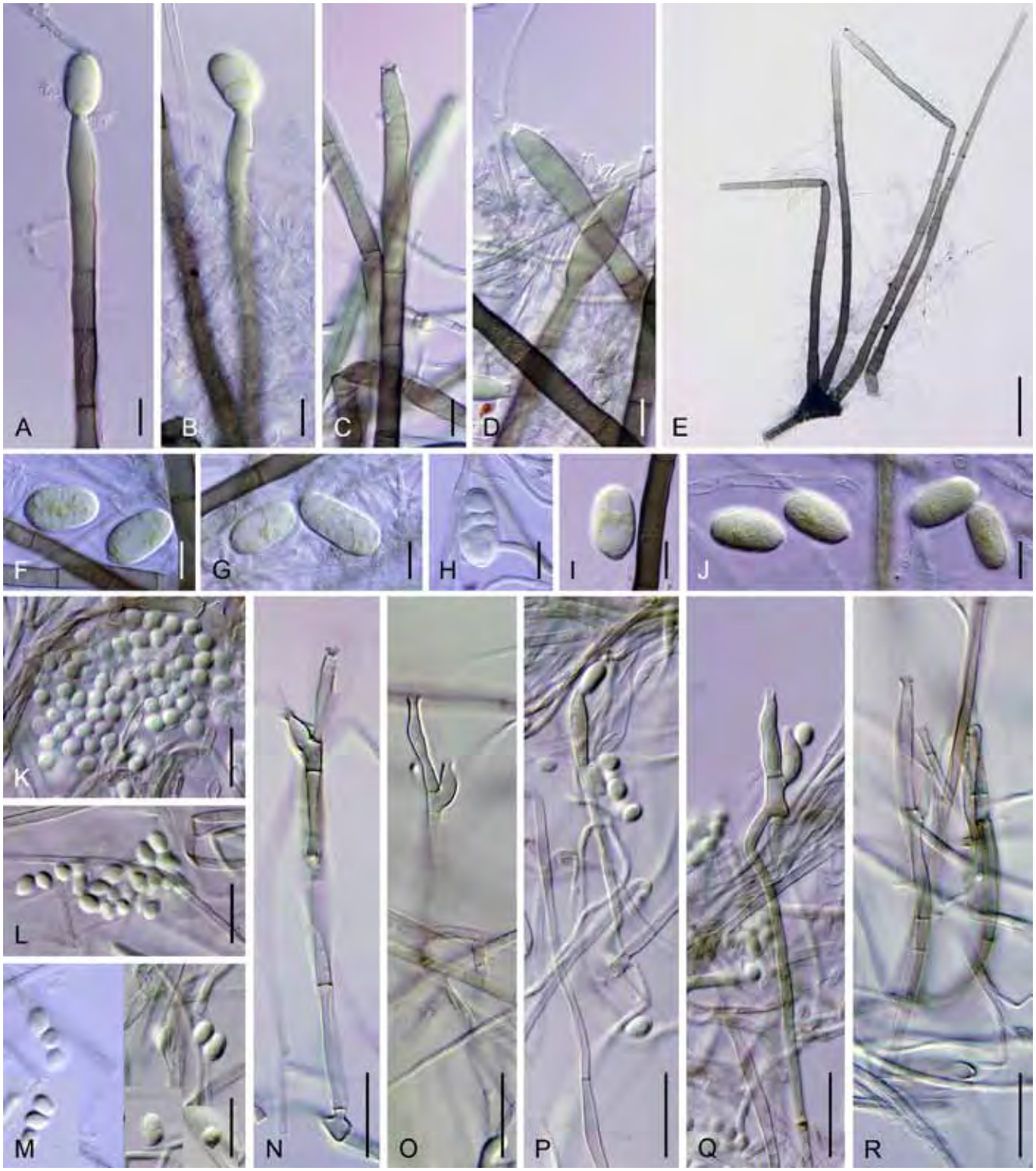

Fig. 7.A–R. *Monilochaetes camelliae* anamorph of *Australiasca queenslandica*. A–D. Conidiogenous cells. E. Conidiophores. F–J. Conidia. K–M. Microconidia. N–R. Minute conidiophores that produce microconidia. A–J from BRIP 24607 (PCA, 14 d old), K–R from BRIP 24334c (PCA, 6 mo old). Scale bars: A–D, F–J, K–R = 10 µm; E = 50 µm. A–R: DIC.

slimy heads are all observed in one genus or even one species (W. Gams, unpubl. data). The conidial chains of *M. camelliae* were difficult to observe in squash mounts from agar, but were visible directly in the Petri dish by light microscopy.

Additional species of *Monilochaetes*

Since its description the original generic concept of *Dischloridium* has been expanded with the addition of fifteen species having variable morphology of conidia and conidiophores including several species with brown, distoseptate conidia. To be consistent with the morphological delimitation of *Monilochaetes* indicated by phylogeny, we accept only two of the fourteen remaining species previously included in *Dischloridium* for transfer to *Monilochaetes,* namely *D. basicurvatum* and *D. regenerans.* Other species are newly transferred to or accepted in other hyphomycete genera, such as *Craspedodidymum*, *Hyalocylindrophora*, or *Paradischloridium*, and a few cannot presently be reassigned.

After revising type material, cultivation studies, and molecular data of *Exochalara longissima*, the type species of that genus, we

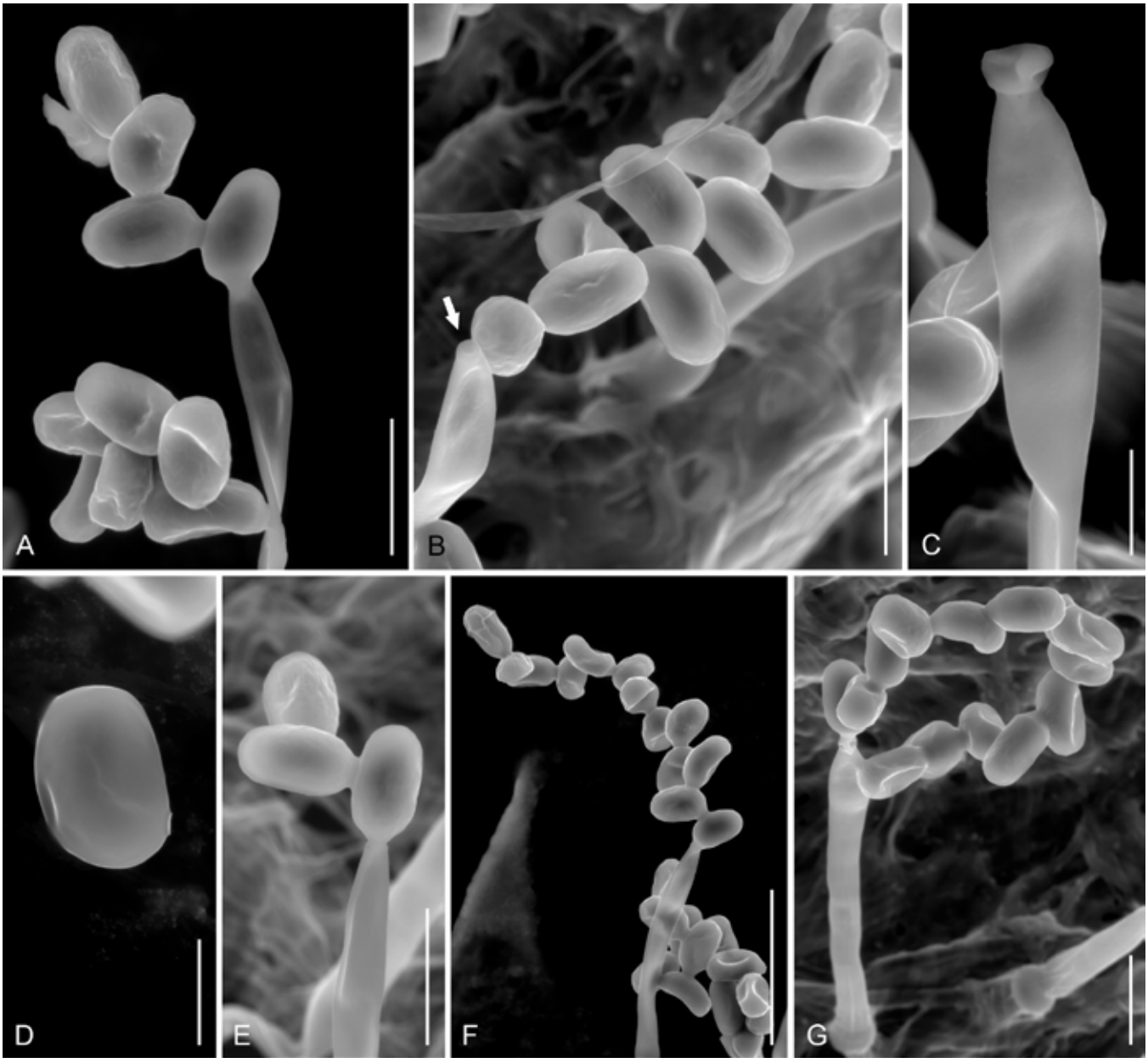

Fig. 8.A–G. Environmental Scanning Electron Microscopy photographs of *Monilochaetes camelliae* anamorph of *Australiasca queenslandica*. A, B, F, G. Chains of conidia; arrow indicates the tip with a porus of the conidiogenous cell after the liberation of the conidial chain. C. Conidiogenous cells with collarette. D. Conidium with laterally displaced hilum. E. Conidiogenous cell with conidia. A–G from BRIP 24607 (PCA, 14 d old). A, B, E, G = 20 µm; C, D = 10 µm; F = 50 µm.

confirm that the species is unrelated to *Monilochaetes* (material and isolates examined: IMI 18047 holotype of *Chalara longissima*; IMI 167413 holotype of *Catenularia piceae*; CBS 980.73, cited as the only strain in the description of *E. longissima* by Gams & Holubová-Jechová 1976, and CBS 393.82). The true relationship of the genus *Exochalara* lies with the *Helotiales* of the *Leotiomycetes* (Réblová *et al*. 2011). The strain studied by Rong & Gams (2000), CBS 662.82, with pronounced branching of the short conidiophores, is not conspecific with or related to *E. longissima.*

Monilochaetes Halst., New Jersey Agric. Exp. Stn. Bull. 76: 27. 1890.
= *Dischloridium* B. Sutton, Kavaka 4: 47. 1976.

Monilochaetes basicurvata (Matsush.) Réblová & Seifert, **comb. nov.** MycoBank MB515432.
Basionym: *Dischloridium basicurvatum* Matsush., Matsush. Mycol. Mem. 8: 18. 1995.

Monilochaetes guadalcanalensis (Matsush.) I.H. Rong & W. Gams, Mycotaxon 76: 455. 2000.
Basionym: *Catenularia guadalcanalensis* Matsush., Microfungi of the Salomon Islands and Papua New Guinea, Kobe, p. 10. 1971.
≡ *Exochalara guadalcanalensis* (Matsush.) W. Gams & Hol.-Jech., Stud. Mycol. 13: 58. 1976.

Monilochaetes infuscans Ellis & Halst., New Jersey Agric. Exp. Stn. Bull. 76: 27. 1890. Fig. 9A–I.
= *Dischloridium cylindrospermum* S.K. Srivast., Sydowia 39: 217. 1986.

Monilochaetes regenerans (Bhat & W.B. Kendr.) Réblová & Seifert, **comb. nov.** MycoBank MB515433.
Basionym: *Dischloridium regenerans* Bhat & W.B. Kendr., Mycotaxon 49: 48. 1993.

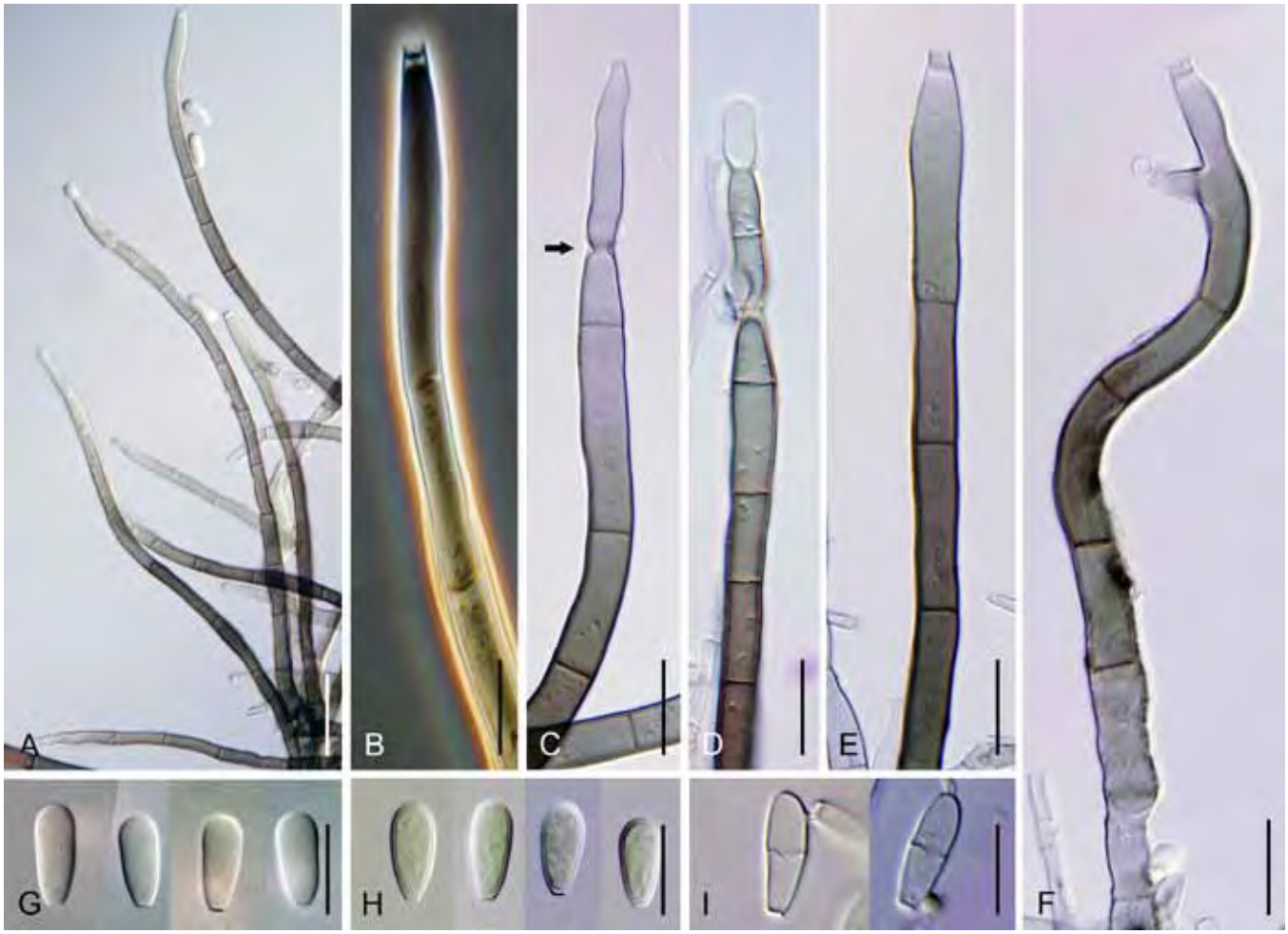

Fig. 9.A–I. *Monilochaetes infuscans*. A–F. Conidiophores; arrow indicates a percurrent regeneration of the conidiophore. G–I. Conidia. A–I from CBS 379.77 (PCA, 14 d old). Scale bars: A = 25 µm; B–I = 10 µm. DIC: A, C–I. PC: B.

Species excluded from *Dischloridium* and *Monilochaetes,* but not reclassified

Accepted names are printed in **bold**.

Dischloridium keniense P.M. Kirk, Mycotaxon 23: 30. 1985.
Basionym: *Craspedodidymum keniense* (P.M. Kirk) Bhat & W.B. Kendr., Mycotaxon 49: 37. 1993.

Dischloridium roseum (Petch) Seifert & W. Gams, Mycotaxon 24: 459. 1985.
Basionym: *Acremonium roseum* Petch, Ann. Royal Bot. Gard. Peradeniya 7: 317. 1922.
≡ ***Hyalocylindrophora rosea*** (Petch) Réblová & W. Gams, **comb. nov.** MycoBank MB515434
= *Hyalocylindrophora venezuelensis* J.L. Crane & Dumont, Canad. J. Bot. 56: 2616. 1978.
≡ *Dischloridium venezuelense* (J.L. Crane & Dumont) Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 725. 1985.

Notes: With this new combination the combining authors accept the argument by Holubová-Jechová (1990) that this hyaline species should not be considered congeneric with similar pigmented species. The species has not been cultured or sequenced.

Dischloridium triseptatum Hol.-Jech, Česká Mykol. 41: 110. 1987. Fig. 10A–J.
= ***Paradischloridium ychaffrei*** Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 723. 1985.

Specimens examined: **Cuba,** Oriente, Gran Piedra Mts., Nature Reserve Isabelica Norte, near Santiago de Cuba, on dead branches of an unidentified tree, 22 May 1985, V. Holubová-Jechová, PRM 842733, **holotype** of *D. triseptatum*.

Dischloridium venezuelense (J.L. Crane & Dumont) Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 725. 1985.
= ***Hyalocylindrophora rosea*** (Petch) Réblová & W. Gams (see above).

Dischloridium ychaffrei (Bhat & B. Sutton) Hol.-Jech., Česká Mykol. 42: 204. 1988.
Basionym: ***Paradischloridium ychaffrei*** Bhat & B. Sutton, Trans. Brit. Mycol. Soc. 84: 723. 1985. Fig. 10A–J.
= *Dischloridium triseptatum* Hol.-Jech, Česká Mykol. 41: 110. 1987.

Notes: *Paradischloridium* was erected for phialidic dematiaceous hyphomycetes reminiscent of *Dischloridium*, but with conidiophores that are not fasciculate and do not arise from stromatic tissue. The phialides lack even remnants of a collarette and conidia are brown with 3-distosepta (Bhat & Sutton 1985). The conidiogenesis of *P. ychaffrei* is particularly interesting. Fig. 10C–F show the conidiogenous locus sitting deeper in the venter of the cylindrical phialide than is typical for *M. laeënsis* or other *Monilochaetes* species; it is located more towards the bottom of the conidiogenous cells. Fig. 10C, D show young, hyaline conidia formed within the venter. In Fig. 10B, F, the top of a new phialide appears to be proliferating through the old phialide and collarette to form a new functional phialide. Similar phialidic structures and conidium ontogeny were described, for example, in species of *Catenularia*,

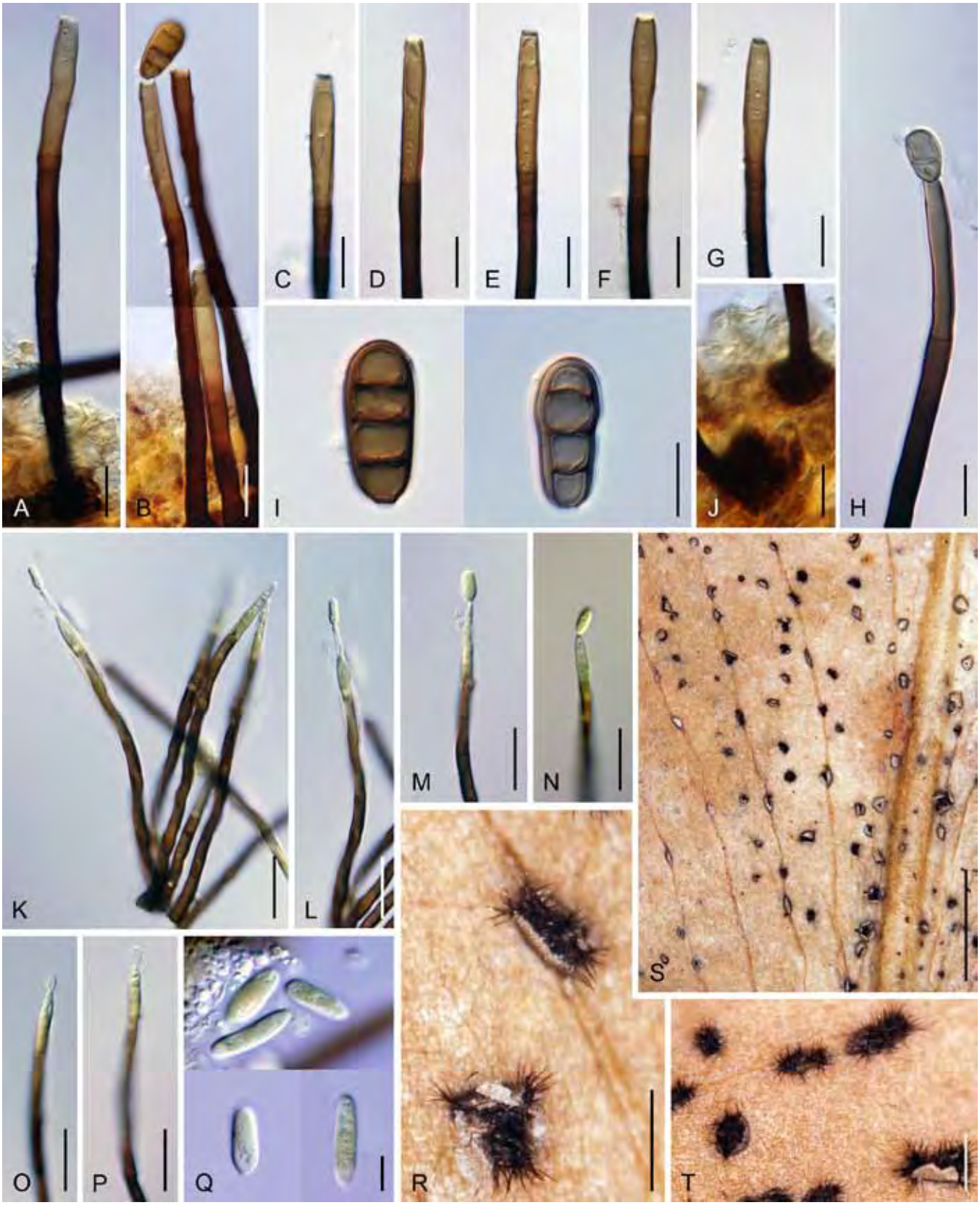

Fig. 10.A–J. *Paradischloridium ychaffrei*. A–H. Conidiophores. I. Conidia. J. Base of the conidiophore. K–T. *Dischloridium tenuisporum*. K–P. Conidiophores with conidia. Q. Conidia. R–T. Stromatic spots erumpent through the epidermis of the host bearing clusters of conidiophores. A–J from PRM 842733 (holotype of *Dischloridium triseptatum*), on the host; K–T from PRM 842727 (holotype), on the host. Scale bars: A–J, Q = 10 µm; K–P = 25 µm; R, T = 50 µm; S = 250 µm. DIC: A–J.

Chloridium, and *Sporoschismopsis* (Holubová-Jechová & Hennebert 1972). No living culture of *P. ychaffrei* was available to further assess the phylogenetic relationships of this genus.

Dischloridium species of uncertain status

A few *Dischloridium* species remain that cannot be transferred to *Monilochaetes* or other genera. Three of these form a group of morphologically similar taxa with features intermediate between *Monilochaetes* and *Colletotrichum*, *viz. Dischloridium*

gloeosporioides, *D. livistoniae,* and *D. tenuisporum.* The former two species were transferred into *Dischloridium* from *Cladosporium* and *Fusicladium* when Schubert & Braun (2005) observed terminal, monophialidic conidiogenous cells, stromata, and brown fasciculate conidiophores with paler tips. *Dischloridium gloeosporioides* was described from living stems and leaves, while the other two species were collected on dead leaves or petioles. All three produce well-delimited, subcircular to irregular spots, caused by emerging stromatic tissue that ruptures the epidermis (Fig. 10R–T), unlike the effuse colonies of *D. laeënse*. Conidia of *D. gloeosporioides* and *D. livistoniae* are obovoidal or ellipsoid-ovoidal, whereas conidia of *D. tenuisporum* are ellipsoidal to elongate-ellipsoidal, sometimes with a basal papilla. The single conidiogenous locus is at the base of the indistinct collarette. Although characters such as discrete stromatic tissue, fasciculate conidiophores, and terminal monophialides with hyaline conidia match the profile of dematiaceous hyphomycetes associated with the *Glomerellales*, transferring them to *Monilochaetes* or describing a new genus for them seems ill-advised until cultures and molecular data are available. Therefore, these species remain as *incertae sedis*.

Dischloridium gloeosporioides (G.F. Atk.) U. Braun & K. Schub., Fung. Diversity 20: 189. 2005.
Basionym: *Cladosporium gloeosporioides* G.F. Atk., Cornell Univ. Sci. Bull. 3: 39. 1897.

Dischloridium inaequiseptatum (Matsush.) Hol.-Jech., Česká Mykol. 41: 111. 1987.
Basionym: *Endophragmia inaequiseptata* Matsush., Icones Microfungorum a Matsushima lectorum, Kobe, p. 69. 1975.

Notes: This species is not accepted in *Monilochaetes* because of its 3-septate, cylindrical, slightly curved conidia with a subhyaline basal cell and the remainder of the conidial cells dark brown. Conidiophores are fasciculate without stromatic tissue; a collarette is absent or very indistinct.

Dischloridium livistoniae (P. Karst.) U. Braun & K. Schub., Fung. Diversity 20: 192. 2005.
Basionym: *Fusicladium livistoniae* P. Karst., Hedwigia 30: 302. 1891.

Dischloridium microsporum R.F. Castañeda & W.B. Kendr., Univ. Waterloo Biol. Ser. 35: 50 (fig. 29). 1991.

Specimen examined: **Cuba,** La Estrella, Buey Arriba, Granma, on dead leaves of *Trophis racemosa*, 14 Mar. 1991, R.F. Castañeda, INIFAT C91/98-2, **holotype**, ex-type strain CBS 498.92.

Notes: The ex-type strain (CBS 498.92) looks *Acremonium*-like; it formed a *Nectria*-like teleomorph *in vitro* (W. Gams, unpubl. data).

Dischloridium tenuisporum Hol.-Jech., Česká Mykol. 41: 31. 1987. Fig. 10K–T.

Specimen examined: **Cuba,** Habana province, Jaruco, Loma de la Coca, south from Campo Florido, 142 m a. s. l., on dead leaves of *Clusia rosea*, 13 Feb. 1981, V. Holubová-Jechová, PRM 842727, **holotype**.

Reticulascaceae

This family contains two holomorph genera, *Reticulascus* and *Porosphaerellopsis.* Although these genera differ morphologically, ontogeny and morphology of the centrum and interthecial filaments unite them and partially define the family. The interthecial tissue is formed of filiform branching and anastomosing filaments, forming a "network" among the asci. They are attached to the hymenium and to the top of the ascomatal wall. This structure was first described and illustrated by Samuels & Müller (1978) for *Porosphaerellopsis sporoschismophora* and is documented here for *Reticulascus tulasneorum* and *R. clavatus*. The second species in the genus *Porosphaerellopsis, P. bipolaris* (Ranghoo *et al*. 2001), collected on submerged wood in a stream in China, does not form this "network", and has paraphyses that are wider and simple. The link between *P. bipolaris* and a *Sporoschismopsis* anamorph suggested by Ranghoo *et al.* (2001) has not been established convincingly.

Reticulascaceae Réblová & W. Gams, **fam. nov.** MycoBank MB515435.

Stromata minuta nonnumquam formata. Ascomata perithecia, fusca usque nigra, ostiolum periphysatum. Pariete ascomatum 2-stratoso. Hamathecium paraphyses verae; paraphyses septatae, hyalinae, ramosae, anastomosantes, sursum angustatae, ascos superantes. Asci unitunicati, cylindraceo-clavati, 8-spori, annulo apicali iodo non reagente. Ascosporae hyalinae vel atrobrunneae, ellipsoideae usque fusiformes, septatae, nonnumquam utrinque poro praeditae. Anamorphae: *Cylindrotrichum*, *Sporoschismopsis*; conidia modo phialidico formata.

Typus: *Reticulascus* Réblová & W. Gams.

Stromata minute, sometimes present. *Perithecia* brown to black. Ostiolum periphysate. *Perithecial wall* 2-layered. Interascal tissue of thin-walled, tapering, branching and anastomosing paraphyses. *Asci* unitunicate, 8-spored, cylindrical-clavate, apical ring inamyloid. *Ascospores* hyaline or dark brown, ellipsoid to fusiform, sometimes with end pores. Anamorphs: *Cylindrotrichum*, *Sporoschismopsis*; conidiogenesis phialidic.

Reticulascus Réblová & W. Gams, **gen. nov.** MycoBank MB515436.

Etymology: from the Latin *ascus* and *reticulum*, referring to the network of interthecial filaments.

Stromata absentia. Perithecia superficialia, solitaria vel aggregata, fusca, venter subglobosus usque conicus, ostiolum periphysatum. Paries perithecii fragilis, bistratosus. Paraphyses septatae, hyalinae, filiformes, ramosae, anastomosantes, reticulum formantes, sursum angustatae, ascos superantes. Asci unitunicati, cylindraceo-clavati, 8-spori, brevi-stipitati. Ascosporae ellipsoideae usque fusiformes, hyalinae, septatae. Anamorphe *Cylindrotrichum*.

Typus: *Reticulascus tulasneorum* (Réblová & W. Gams) Réblová & W. Gams.

Stroma absent. *Perithecia* superficial, solitary, or gregarious, brown, venter subglobose to conical. Ostiolum periphysate. *Perithecial wall* fragile, 2-layered. *Paraphyses* septate, hyaline, filiform, forming a branching and anastomosing "network". *Asci* unitunicate, cylindrical-clavate, 8-spored, short-stipitate. *Ascospores* ellipsoidal to fusiform, hyaline, septate. Anamorph *Cylindrotrichum*.

Notes: Based on the results of our ITS, ncLSU, ncSSU analyses, and the combined three-gene phylogeny, the new holomorph genus *Reticulascus* is introduced below for two holomorph species. *Chaetosphaeria tulasneorum* with the anamorph *Cylindrotrichum oligospermum* including *C. hennebertii* as a synonym, is recombined as the type of *Reticulascus*; the second species, *R. clavatus,* is introduced as a new species with *C. clavatum* as its anamorph.

Several anamorphic species are related to this clade. The delimitation of *Cylindrotrichum,* typified by *C. oligosporum,* and morphologically similar genera of dematiaceous hyphomyces has been controversial, with varying concepts proposed by Gams & Holubová-Jechová (1976), DiCosmo *et al*. (1983), Rambelli & Onofri (1987), Arambarri & Cabello (1989), and Holubová-Jechová (1990). The *Cylindrotrichum* anamorphs of *Reticulascus* species generally resemble the dematiaceous, phialidic hyphomycetous anamorphs linked with *Chaetosphaeria* (Réblová 2000, 2004), but the presence of cylindrical, 1-septate conidia seems to be a deviating character. The conidia are formed from conspicuously sympodially proliferating, terminally integrated phialides within shallow collarettes (Gams & Holubová-Jechová 1976: 48, figs 23, 24; Réblová & Gams 1999: 34, fig. 16). Based on a ncLSU phylogeny, Réblová & Winka (2000) showed that several species included in *Cylindrotrichum* by Gams & Holubová-Jechová (1976) belong to the *Chaetosphaeriaceae* (*Chaetosphaeriales*), but others are phylogenetically unrelated with a possible affinity with the *Microascales*. Our molecular analyses of ITS, ncLSU, ncSSU, and the combined data set of three genes (Figs 1–4) confirm that *Reticulascus tulasneorum/C. oligospermum*, *R. clavatus/C. clavatum*, the newly described anamorphic *C. setosum,* previously known species *C. gorii*, *Kylindria peruamazonensis,* and *Porosphaerellopsis* (anamorph *Sporoschismopsis*) group outside the *Chaetosphaeriales* and *Microascales*. They form a monophyletic group that we recognise as a new family within the *Glomerellales*.

The dematiaceous hyphomycete genera *Cylindrotrichum*, *Kylindria,* and *Sporoschismopsis*, linked as anamorphs with the *Reticulascaceae*, possess conidia that vary in shape, colour, and size, and, although conidiogenesis is phialidic, the position of the conidiogenous locus within the collarette also varies. In *Sporoschismopsis,* the first and a few subsequent conidia arise endogenously and are formed in basipetal succession from the apical portion of the phialide from deep-set conidiogenous loci within a deep collarette. After formation of several conidia, the phialide proliferates through the collarette to form a new functional phialide (Holubová-Jechová & Hennebert 1972: 385, fig. 1). Similar conidium ontogeny also occurs in *Catenularia* and *Chloridium* anamorphs of *Chaetosphaeria* species and in species of *Cadophora* or *Phialophora*.

The remaining 18 species previously classified in *Cylindrotrichum*, including those transferred to *Kylindria* (13 species) and *Xenokylindria* (3 species) by DiCosmo *et al*. (1983), are putative members of the *Chaetosphaeriales* for which the name *Kylindria* was given preference by Réblová (2000). In fact, the *Cylindrotrichum*-like anamorphs linked with *Chaetosphaeria* are variations on the *Chloridium* theme and do not represent a unique or unusual pattern within the *Chaetosphaeriaceae*. If future analyses confirm the placement of *K. triseptata* in the *Reticulascaceae*, *Kylindria* will be excluded from the anamorphs linked with *Chaetosphaeria* and separated from *Xenokylindria*.

Kylindria peruamazonensis did not group in the same clade as the four *Cylindrotrichum* species, rather it formed a poorly supported branch with *Porosphaerellopsis* at the base of the *Reticulascus/ Cylindrotrichum* clade (Figs 1, 4). This species is discussed and illustrated below and is the only typical representative of the genus *Kylindria* included in our analysis. Unlike *Cylindrotrichum* species of *Kylindria* have oblong, longer, and wider, 1-several-septate, often asymmetrical conidia and wider and shorter conidiophores terminating with a monophialide swollen in its upper part with or without a collarette. The phialides occasionally elongate above the collarette with several percurrent extensions. These characters contrast with *Cylindrotrichum* having 1-septate, symmetrical, cylindrical conidia and narrower, longer, and often seta-like conidiophores with cylindrical mono- or polyphialides that never elongate above the collarette. Because of the morphological characters distinguishing *Kylindria* and *Cylindrotrichum* and results from the ITS and ncLSU phylogenetic analyses, we prefer to keep these anamorph genera separate.

Reticulascus tulasneorum (Réblová & W. Gams) Réblová & W. Gams, **comb. nov.** MycoBank MB515437. Fig. 11.

Basionym: *Chaetosphaeria tulasneorum* Réblová & W. Gams, Czech Mycol. 51: 32. 1999.

Anamorph: *Cylindrotrichum oligospermum* (Corda) Bonord., Handb. Allg. Mykol. p. 88. 1851.

= *Cylindrotrichum hennebertii* W. Gams & Hol.-Jech., Stud. Mycol. 13: 50. 1976.

For a full description and more information, refer to Réblová & Gams (1999).

Specimen examined: **Czech Republic**, South-western Bohemia, Javornická hornatina Mts., Strašín near Sušice, on dead branch of *Sambucus nigra*, 21 Oct. 1997, M. Svrček, PRM 842978, **holotype** of *Chaetosphaeria tulasneorum*, ex-type strain CBS 101319.

Notes: *Reticulascus tulasneorum* produces minute, black, nonstromatic ascomata growing on decaying wood. The ascospores are hyaline, narrowly ellipsoidal, 1- to rarely 3-septate, and glabrous at maturity, similar to those of *R. clavatus* having slightly verruculose ascospores. In the features of asci, interthecial filaments, and perithecial wall, these species are indistinguishable. The morphological characters of the associated anamorphs are diagnostic. The teleomorph is known from only one locality (Réblová & Gams 1999).

Cylindrotrichum hennebertii (ex-type strain CBS 570.76) groups with *R. tulasneorum* including its anamorph *C. oligospermum*. The former taxon was described for specimens with only a short layer of conidiophores (Gams & Holubová-Jechová 1976: 50, fig. 24), contrasting with the development of two strata of conidiophores for the latter species. The layering of the conidiophores described in the protologue of *C. hennebertii* seems to be quite variable depending on substrate and age of the material. With the further evidence of their identical ITS sequences, *C. hennebertii* is now regarded as a synonym of *C. oligospermum*, the anamorph of *Reticulascus tulasneorum*.

Reticulascus clavatus Réblová & Fournier, **sp. nov**. MycoBank MB515652. Figs 11F–M, 12A–F.

Anamorph: *Cylindrotrichum clavatum* W. Gams & Hol.-Jech., Stud. Mycol. 43: 54. 1976.

Etymology: Epithet taken from that of the anamorph species, derived from the shape of conidia.

Perithecia 150–170 µm alta, 120–200 µm diam, superficialia, solitaria, subglobosa vel conica, minute papillata, ostiolata, glabra. Canalis ostiolaris periphysatus. Paries perithecii fragilis, ad latus et apicem sclerotialis, deorsum attenuatus; paries lateralis 15 µm crassus, bistratosus. Paraphyses copiosae, filiformes, septatae, ramosae, anastomosantes, reticulum formantes, hyalinae, 1.5 µm latae, ultra ascorum apices protrudentes. Asci 87–108 × 7–8.5 µm (in medio ± s.e. = 95.5 ± 0.2 × 7.5 ± 0.2 µm), cylindrici vel clavati, breviter stipitati. Ascosporae 14–18(–19) × 4–4.5 µm (in medio ± s.e. = 15.7 ± 0.2 × 4.4 ± 0.04 µm), fusiformes, bi- vel quadri-cellulares, verruculosae, hyalinae, 1–2-seriatae in asco.

Perithecia 150–170 µm high, 120–200 µm diam, scattered among conidiophores, superficial, solitary, subglobose to conical, with

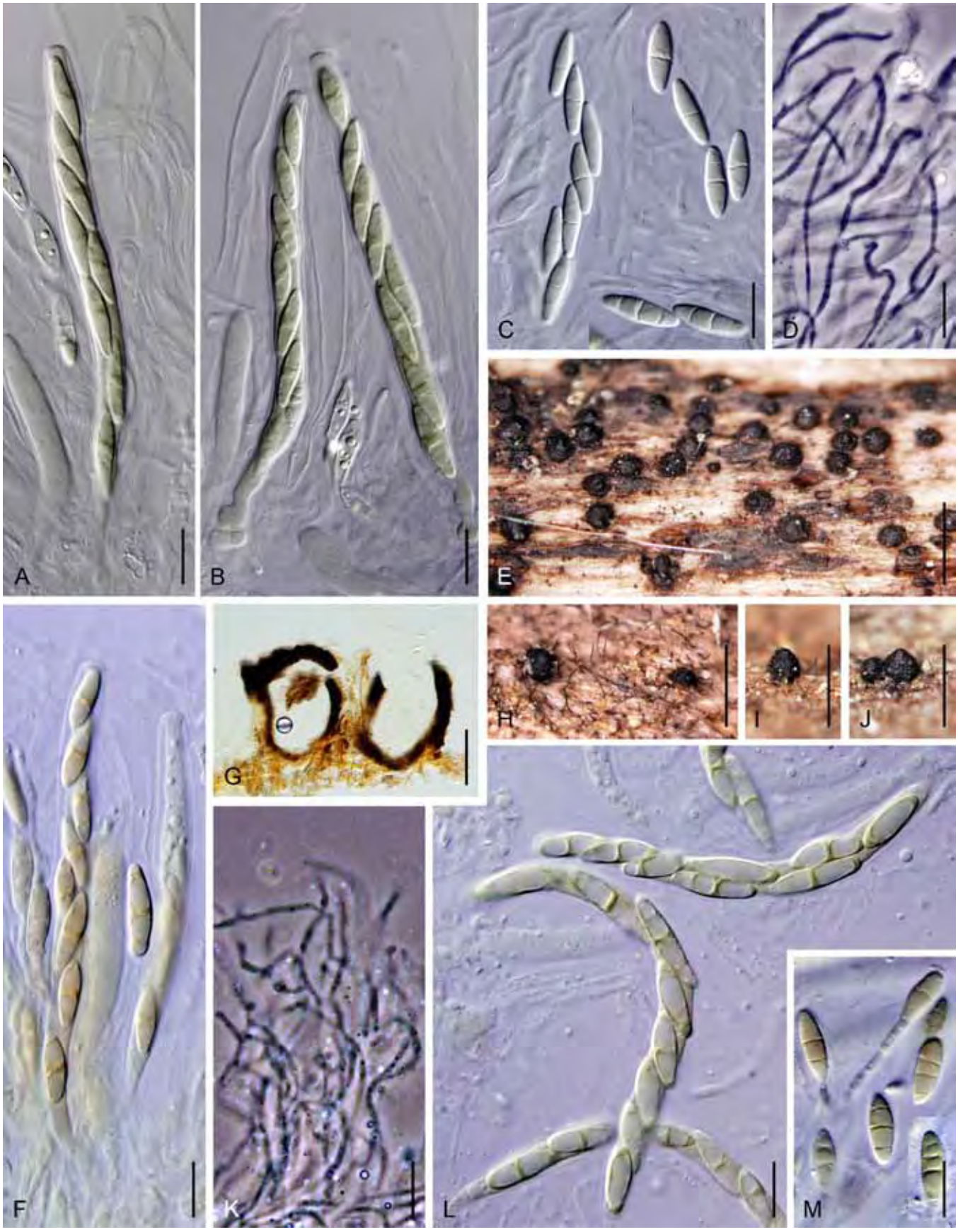

Fig. 11.A–E. *Reticulascus tulasneorum*. A, B. Asci containing ascospores. C. Ascospores. D. Interthecial filaments. E. Perithecia on the host. F–M. *Reticulascus clavatus*. F, L. Asci with ascospores. G. Vertical section of the perithecial wall. H–J. Perithecia with conidiophores of the anamorph on the host. K. Interthecial filaments. M. Ascospores. A–E from PRM 842978 (holotype); F–M from PRM 915717 (holotype). Scale bars: A = A–D, F, K–M = 10 µm; E, H–J = 250 µm; G = 50 µm. DIC: A–C, E–J, L, M; PC: D, K.

minute papilla, glabrous, ostiolum lined with periphyses. *Perithecial wall* brittle, heavily sclerotised in upper part, sclerotisation weakens towards base. Lateral wall *ca.* 15 µm thick, 2-layered: outer layer of thin-walled, dark brown, brick-like cells; inner layer of flattened, elongated hyaline cells. *Paraphyses ca.* 1.5 µm wide, copious, filiform, sparsely septate, not constricted at septa, forming a network, hyaline, longer than asci. *Asci* 87–108 × 7–8.5 µm (mean ± S.E. = 95.5 ± 0.2 × 7.5 ± 0.2 µm), cylindrical to clavate, slightly

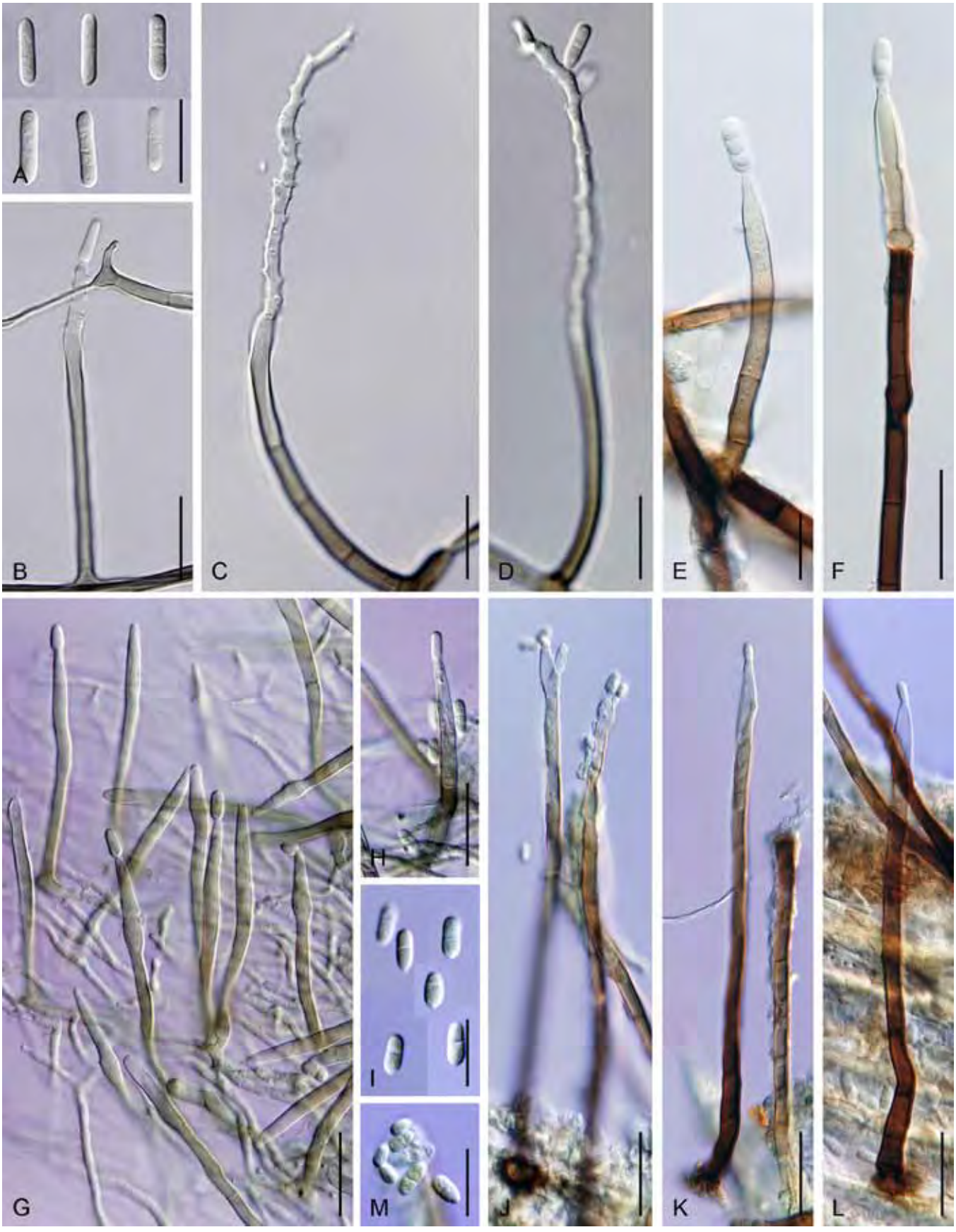

Fig. 12.A–F. *Cylindrotrichum clavatum* anamorph of *Reticulascus clavatus*. A. Conidia. B–D. Conidiophores of the lower layer (shorter conidiophores) with sympodially extending sporiferous apices, in culture. E–F. Conidiophores ending into a monophialide on the host. A–C from ex–type strain CBS 125296 (PCA, 14 d old), E–F from PRM 915717 (holotype). G–M. *Cylindrotrichum gorii*. G, H. Conidiophores, in culture. I. Conidia, in culture. J–L. Conidiophores, on the host. M. Conidia, on the host. G–M from CBS 879.85 (PCA, 14 d old). Scale bars: A = 10 µm; B–F = 20 µm; G, H, J–L = 20 µm; I, M = 10 µm. DIC: A–F, G–M.

truncate to broadly rounded at apex, short–stipitate, ascal apex with inamyloid apical annulus, 3–3.5 µm wide, 1–1.5 µm deep, 8-spored. *Ascospores* 14–18(–19) × 4–4.5 µm (mean ± S.E. = 15.7 ± 0.2 × 4.4 ± 0.04 µm), fusiform, 2–4-celled, with a delayed formation of second and third septa, slightly constricted at septa, mature ascospores finely verruculose, 1–2-seriate in ascus.

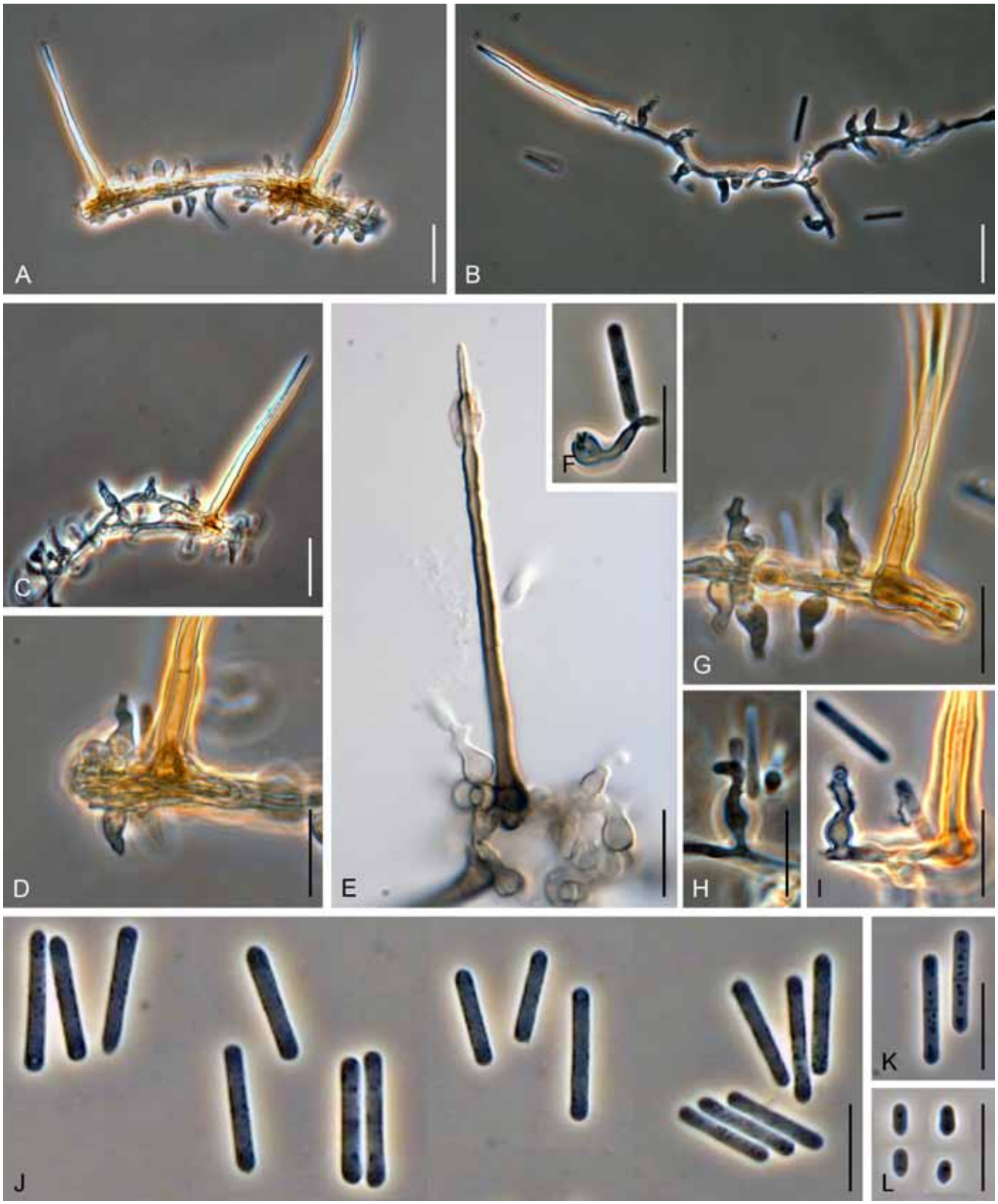

Fig. 13.A–L. *Cylindrotrichum setosum*. A–C. Conidiophores with setae and polyphialidic conidiogenous cells. D, F–I. Polyphialides. E. Seta with unbranched basal conidiogenous cells. J, K. Macroconidia. L. Microconidia. A–L from ex-type strain DAOM 229246 (OA, 3wk old). Scale bars: A–C = 20 µm; D–I = 10 µm. DIC: all PC except E, DIC.

Colonies *in vivo* brown to black, hairy, effuse. Setae absent. *Conidiophores* macronematous, mononematous, cylindrical, straight, forming two layers. *Conidiophores* of lower layer shorter, 60–135 × 4.5–5 µm, pale brown, subhyaline towards apex, 2–5-septate; longer conidiophores forming an upper layer, 200–360 × 5–5.5 µm, mid to dark brown, subhyaline towards apex, up to 10-septate; conidiophores of both layers ending in a monophialide or polyphialide. *Conidiogenous cells* 25–37 × 3.5–5 µm, usually monophialidic, rarely polyphialidic with up to two lateral openings; collarette hyaline to subhyaline, 1.5–2 µm wide, *ca.* 1.5 µm high. *Conidia* 10.5–11 × 4–4.5 µm (mean ± S.E. = 10.2 ± 0.2 × 4.2 ± 0.04 µm), cylindrical, rounded at apex, slightly tapering, obtuse at base, 1-septate, not constricted at septum, hyaline, smooth.

Colonies *in vitro* after 14 d on PCA at 25 °C 14–17 mm diam, cushion–like, aerial mycelium greyish brown, margin entire, reverse dark brown. Colonies sporulating after 7–10 d

on PCA at 25 °C in darkness. *Conidiophores* macronematous, mononematous, solitary, erect, forming two layers: conidiophores of lower layer 50–100 × 2.5–3 µm, cylindrical, straight or slightly flexuous, 2–10-septate, pale brown, subhyaline to hyaline towards apex; conidiophores of upper layer up to 260 µm long, 3.5–4 µm wide, mid brown, subhyaline towards apex. *Conidiogenous cells* integrated, terminal or intercalary, with up to 30 lateral phialidic openings arising from sympodial elongation, fertile apices 15–70 µm long; collarettes hyaline to subhyaline, 1–1.5 µm wide, *ca.* 1.5 µm high. *Conidia* 9–12.5(–13.5) × 2.5–3 µm (mean ± S.E. = 11.6 ± 0.3 × 2.7 ± 0.05 µm), cylindrical, rounded at apex, slightly tapering, obtuse at base, 1-septate, not constricted at septum, hyaline, smooth. In PDA culture, conidia slightly smaller, 8.5–10.5 × 2.5(–3) µm (mean ± S.E. = 9.3 ± 0.1 × 2.6 ± 0.03 µm).

Specimens examined: **France**, Haute Garonne, Mancioux, along road D635 on the way to Frechet, on submerged wood of *Alnus glutinosa*, 28 Feb. 2009, J. Fournier no. J.F. 09009, PRM 915717, **holotype**, ex-type strain CBS 125296; Rimont, Le Baup, on submerged wood of *Fraxinus* sp., 12 June 2009, J. Fournier no. J.F. 09154, PRM 915718, living culture CBS 125297; Ariège, Rimont, road D18, 1.5 km south of the village, Le Baup, 500 m a. s. l., on submerged wood of *Platanus* sp., associated with *Achroceratosphaeria potamia*, *Cosmospora* sp., *Savoryella limnetica*, 23 May 2008, J. Fournier & M. Delpont no. J.F. 08139, PRM 915719, living culture CBS 125239.

Notes: *Reticulascus clavatus* is a common dweller of submerged wood in lotic sites in France. The anamorph does not always occur on freshly collected material, although fertile conidiophores usually appear after incubation in a moist chamber for 1–2 wk (J. Fournier, unpubl. data).

Reticulascus clavatus differs from the closely related *R. tulasneorum* and its *C. oligospermum* anamorph by verruculose mature ascospores, absence of setae among the conidiophores, which terminate with a monophialide *in vivo* and only rarely a polyphialide. In axenic culture (PCA, PDA) of *R. clavatus,* the lower layer of conidiophores terminates in polyphialides with up to 30 lateral openings (Fig. 12C, D).

Cylindrotrichum setosum Seifert, **sp. nov.** MycoBank MB515589. Fig. 13A–L.

Coloniae in agaro farina avenae confecto post 20 dies radium 6–7 mm attingentes, in agaro maltoso 4–5 mm. Conidiophora simplicia vel raro ramosa, stipite subhyalino vel dilute brunneo ad 200 µm longo, 1.5–2.5 µm lato, vel cellulae conidiogenae ex hyphis fasciculatis dilute brunneis, 3.5–8.5 µm latis singulae vel acervatae oriundae; setae seu conidiophora superantes seu ex hyphis aggregatis perpendiculariter oriundae, 45–80 µm longae, simplices, brunneae vel fuscae, aciculares, in parte inferiore 3.5–4 µm latae, sursum acutatae. Cellulae conidiogenae mono- vel polyphialides, subhyalinae vel dilute brunneae, ampulliformes vel subulatae, 6–13 µm longae, parte inferiore ellipsoidea, 3.5–7 × 2–4 µm, rachide recta vel geniculata ad 7 × 1.5–2.5 µm, 1–6 foramina conidiogena sessilia vel < 3 µm longa ferente, collare inconspicuum, vix periclinaliter inspissatum. Conidia cylindrica, 1-septata, 12–16.5 × 1.5–2.5 µm; microconidia rara, continua, ellipsoidea vel oblonge ellipsoidea, 3.5–5 × 1.5–2.5 µm.

Colonies on OA after 3 wk about 6–7 mm radial growth, more or less planar, surface pale yellow, with little aerial mycelium but diffusely hirsute because of setae and conidiophores, margin smooth, entire, reverse unpigmented, lacking soluble pigments. Colonies on Blakeslee's malt-peptone agar after 3 wk 4–5 mm radial growth, convex, surface dark brown to black, covered with pale grey, lanose to cottony aerial mycelium that gives the central part of the colony a greyish aspect, with embedded small droplets of black exudates, with some sporulation but setae not seen, reverse grey, margin somewhat uneven.

Conidiophores on OA more or less erect, usually undulating, unbranched or sparingly branched, subhyaline to pale brown with stipes up to 200 µm long, 1.5–2.5 µm wide, or conidiogenous cells directly on erect or lax fascicles of pale brown hyphae 3.5–8.5 µm wide, more or less at right angles, single, in pairs or clusters, sometimes on a metula, with setae either terminating conidiophores or emerging from fascicles more or less at right angles. Setae 45–80 µm long, unbranched, brown to dark brown, acicular, 3.5–4 µm wide at base, slightly thick-walled, with 3–7 septa and acute apex, sometimes terminating with a monophialide. *Conidiogenous cells* monophialidic or polyphialidic, subhyaline to pale brown, concolourous with subtending hypha or conidiophore, usually ampulliform, sometimes subulate, 6–13 µm long, with an ellipsoidal base about 3.5–7 × 2–4 µm, slightly thick-walled, and then a narrower neck 1.5–2.5 µm wide, up to 7 µm long, straight or becoming geniculate with proliferation; lateral conidiogenous apertures usually sessile, but sometimes up to 3 µm long, with 1–6 conidiogenous openings about 1 µm wide with minute frills and inconspicuous periclinal thickening. *Conidia* 12–16.5 × 1.5–2.5 µm (mean ± S.E. 14.4 ± 0.2 × 2.1 ± 0.1), L/W 5.5–8, 1-septate, cylindrical, straight or rarely slightly bent, with rounded ends, base sometimes with an inconspicuous papilla-like abscission scar, accumulating in small, clear to whitish droplets. Microconidia rare, less than 1 % abundance, 3.5–5 × 1.5–2.5 µm, l/w ~1.7–3, aseptate, ellipsoidal to oblong-ellipsoidal, with a minute basal papilla, hyaline, with no obvious abscission scar.

Specimen examined: **Australia,** New South Wales, Mt. Annan Botanical Garden, S 34° 05.118', E 150° 45.438', 315 m alt., on wood and bark mulch on the ground, 26 Aug. 1999, K.A. Seifert no. 1228, DAOM 229246 **holotype**, ex-type strain in CCFC.

Notes: *Cylindrotrichum setosum* is unique in the genus because of the physical separation of the conidiogenous cells and the setae. In other species, the conidiophores are seta-like and have a terminal phialide or polyphialide at the apex. In *C. setosum*, the conidiogenous cells tend to be clustered at the base of the setae in a manner reminiscent of species of *Circinotrichum* or *Gyrothrix*. However, the proliferation of the conidiogenous cells and the morphology of the 1-septate conidia resemble other species of *Cylindrotrichum*. Unlike *C. setosum,* microconidia have not been reported in other *Cylindrotrichum* species.

KEY TO ACCEPTED SPECIES OF *CYLINDROTRICHUM*

1. Conidia cylindrical to slightly clavate, usually wider than 2.5 µm; conidiophores seta–like but sterile setae absent 2
1. Conidia cylindrical, not wider than 2.5 µm, usually 1.5–2.5 µm *in vivo*; setae present or absent 3

2. Conidia longer than 9 µm; 8.5–13 × 3–4 µm *in vivo* and 9–12.5(–13.5) × 2.5–3 µm *in vitro*; teleomorph *R. clavatus* ..... *C. clavatum*
2. Conidia shorter than 9 µm; (5–)5.5–7.5(–9) × 3–3.5 *in vivo* and 7–9(–9.5) × 3–3.5 µm *in vitro*; teleomorph unknown ..... *C. gorii* (Lunghini 1979)

3. Setae sterile, pointed, distinct from the ampulliform to subulate conidiogenous cells; teleomorph unknown ..... *C. setosum*
3. Conidiophores often seta-like, with a terminal mono- or polyphialide at the apex; teleomorph *R. tulasneorum* ..... *C. oligospermum*

Species phylogenetically related to *Cylindrotrichum*

Kylindria peruamazonensis Matsush., Matsush. Mycol. Mem. **7**: 56. 1993. Fig. 14.

Specimens examined: **Cuba**, Ciénaga de Zapata Matanzas, on leaf litter of *Bucida palustris*, Dec. 1991, R.F. Castañeda, INIFAT C91/111, living culture CBS 838.91; Sancti Spiritus. Las V, on leaf of *B. palustris*, 25 Aug. 1994, R.F. Castañeda, INIFAT C94/84R, living culture CBS 421.95.

Notes: Two strains identified as *Kylindria triseptata* were analysed (CBS 838.91, 421.95), but neither matches the fungus described by Matsushima (1975) as *Cylindrotrichum triseptatum* Matsush. in the morphology of conidiogenous cells and conidial dimensions. Our cultural observations suggest that the conidiophores, conidiogenous cells, and conidia of these strains match the description of *Kylindria peruamazonensis*. The apex of the phialide terminates with a funnel-shaped collarette unlike that of *C. triseptatum*, in which the monophialides lack a collarette and may elongate slightly and possess apical densely annellate proliferations. Previously such proliferations were observed in *Cacumisporium capitulatum*, the anamorph of *Chaetosphaeria decastyla*, and in the so-called *Cylindrotrichum* anamorph of *Ch. acutata* (Réblová & Gams 1999); these were considered a diagnostic character of *Xenokylindria* (DiCosmo *et al*. 1983). *Kylindria ellisii* also has 3-septate hyaline conidia, but differs from *K. peruamazonensis* by a hardly visible collarette and symmetrical, 3-septate conidia rounded at both ends, without an apiculus.

Unlike *K. peruamazonensis*, cylindrical to oblong, septate conidia with a tapering, obtuse to papillate base with a laterally displaced hilum are typical of several *Kylindria* species, namely *K. excentrica*, *K. pluriseptata,* and *K. triseptata*. *Kylindria excentrica* has 3-septate conidia, but differs from *K. peruamazonensis* in absence of a collarette and much larger conidia (27.5–35 × 7.5–8 µm; Bhat & Sutton 1985). *Kylindria peruamazonensis* is probably the species morphologically most similar to *K. triseptata*; it differs from the latter by the presence of a collarette, either lacking or with a very short elongation of the phialides above the collarette, with several percurrent proliferations, the unusual formation of imbricate conidial chains, and production of a microconidial form *in vitro* (macroconidia 12.5–23 × 4–7.5 µm; Matsushima 1993). Sympodial proliferation of the apex of the conidiogenous cell was not observed in cultures of *K. peruamazonensis* and *K. triseptata* (Matsushima 1975, 1993). Unlike *K. peruamazonensis, K. pluriseptata* has 6–8-septate and much longer conidia (35–40 × 5–6 µm; Castañeda 1987).

Additional anamorph species affiliated with the *Plectosphaerellaceae*

Our phylogenetic analyses place the anamorph species *Stachylidium bicolor* (DAOM 226658) in a basal position in the family *Plectosphaerellaceae* (Figs 1–3). Several anamorph genera in this family have verticillate conidiophores such as *Acrostalagmus* and *Verticillium*. *Stachylidium bicolor*, the type of its genus, produces erect, roughened, verticillate conidiophores, often with additional verticillate axes emerging from the main stipe; this results in a more complex conidiophore than in other similar genera. As with the species of the other genera, the conidiogenous cells are phialidic but taper strongly near the tip, and the conidia are oblong-ellipsoidal and accumulate in slime. We consider *S. bicolor* sufficiently distinct both morphologically and phylogenetically from *Acrostalagmus* and *Verticillium* to continue to be recognised as a distinct genus.

The phylogenetic analyses demonstrate that the common tropical hyphomycete described and illustrated by Seifert (1985) as *Stilbella annulata* is a member of the *Plectosphaerellaceae* and a sister species to *Acrostalagmus luteoalbus*, the type of the genus. Both *S. annulata* and *A. luteoalbus* produce ameroconidia in bright orange to reddish slimy masses; in both species the reddish pigmentation sometimes also colours the phialides. The conidiophore branching of *S. annulata* lacks the regular verticillate aspect of *A. luteoalbus*, being intermediate between verticillate and penicillate. The synnemata of *S. annulata* and their conspicuously lobed marginal hyphae are also deviating characters from the present generic concept of *Acrostalagmus*. Given the well-supported phylogenetic relationship between these two species, it seems preferable to focus on the similarities between these species rather than the differences and to transfer *S. annulata* to *Acrostalagmus* rather than propose a new genus. This modifies the generic concept of *Acrostalagmus* to include synnematous species:

Acrostalagmus annulatus (Berk. & Broome) Seifert, **comb. nov.** MycoBank MB518663.

Basionym: *Stilbum annulatum* Berk. & Broome, Grevillea 3: 63. 1874. (holotype: no. 6045, on Brassica sp., Car. Inf., herb. Berkeley, 1879, K.

≡ *Stilbella annulata* (Berk. & Broome) Seifert, Stud. Mycol. 27: 58. 1985

Note: For full synonymy and examined material, refer to Seifert (1985).

MICROASCALES

Kirk *et al*. (2008) and Cannon & Kirk (2007) included four families in the *Microascales*, *i.e. Ceratocystidaceae*, *Chadefaudiellaceae*, *Halosphaeriaceae,* and *Microascaceae*, although the *Ceratocystidaceae* is not validly published and was not listed among accepted fungal families by Hawksworth & David (1988). On the basis of our results from ncSSU rDNA and three-gene phylogenies (Figs 2, 3), the following families are accepted in the order, *Microascaceae*, *Halosphaeriaceae*, *Ceratocystidaceae*, which is validated here, and *Gondwanamycetaceae* fam. nov. We accept the *Halosphaeriaceae* as a family of the *Microascales* (Kirk *et al.* 2008), although they are often placed separately in their own order (Spatafora *et al.* 1998).

Recent studies by Spatafora *et al.* (1998), Kong *et al.* (2000), and Zhang *et al.* (2006) suggested that the *Microascales* may prove to be paraphyletic or polyphyletic. In our study, the cladogram based on ncLSU rDNA sequences (Fig. 1) provided no support for any of the backbone branches of the four families that we accept in the order. In the phylogenies based on ncSSU rDNA and the combined ncLSU-ncSSU-RPB2 data sets (Figs 2, 3), the *Microascales* appear as a monophyletic grouping of four families, all with high branch support. In both phylogenies the *Microascales* are divided into two major subclades, one containing the *Halosphaeriaceae* and *Microascaceae* and a second subclade with the *Ceratocystidaceae* and *Gondwanamycetaceae*. The ncSSU and the three-gene phylogeny did not support the putative para- or polyphyly of the *Microascales*.

The family *Microascaceae* and order *Microascales* were introduced by Luttrell (1951) and were later validated with Latin descriptions by Malloch (1970) and Benny & Kimbrough (1980),

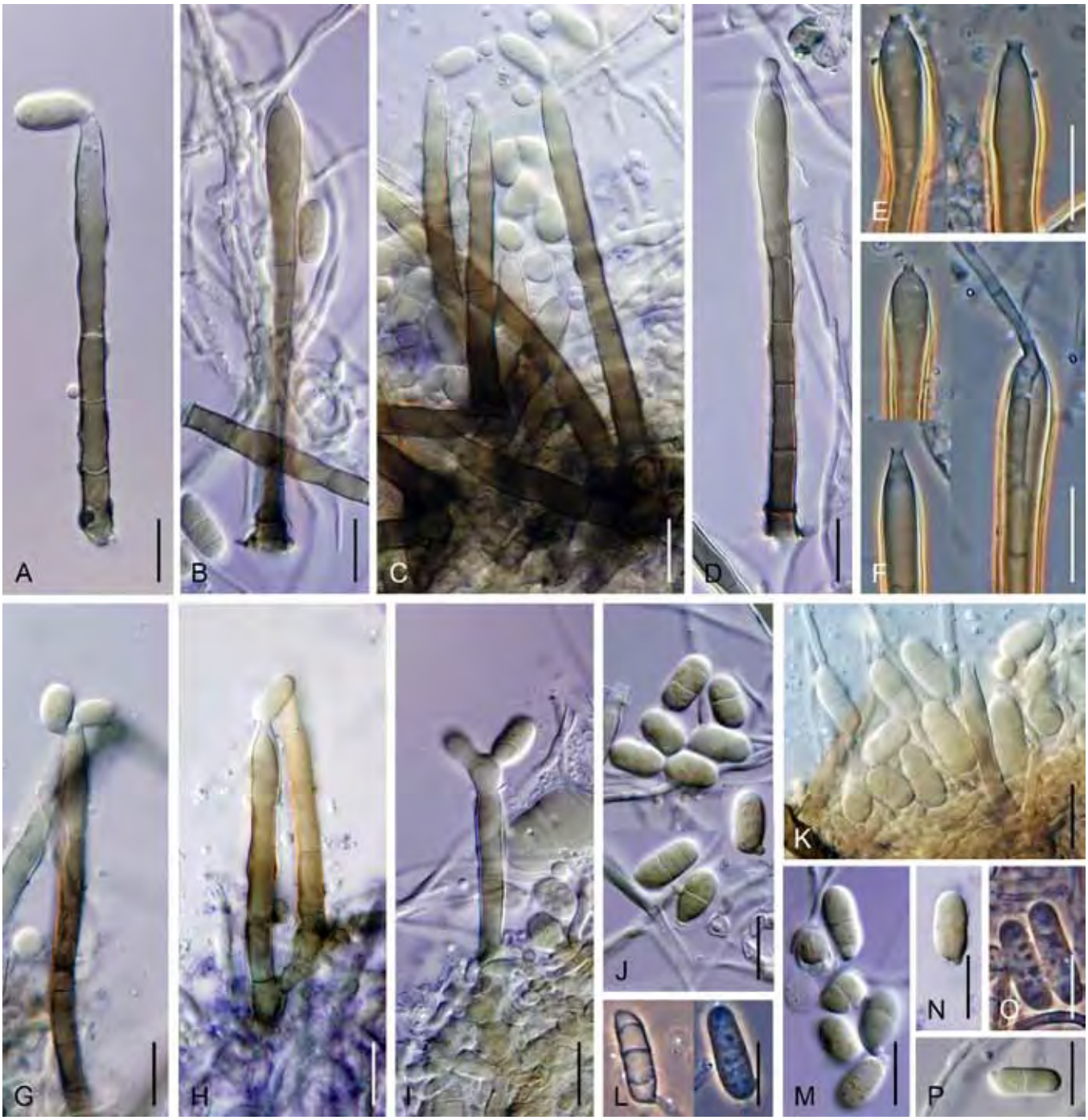

Fig. 14.A–P. *Kylindria peruamazonensis*. A–I. Conidiophores, in culture. J–P. Conidia, in culture. A–D, G–K, M, N, P from CBS 421.95 (PCA, 14 d old); E, F, L, O from CBS 838.91 (PCA, 3 wk old). Scale bars: A–D, G–K, M, N, P = 10 µm; E, F, L, O = 15 µm. DIC: A–D, G–K, M, N, P; PC: E, F, L, O.

respectively. Luttrell (1951) described the *Microascaceae* for taxa with beaked ascomata and evanescent, nonstipitate asci disposed irregularly throughout the filamentous centrum. Corlett (1963, 1966) confirmed the observations of Luttrell (1951) and described the asci of *Microascus* and *Petriella* as developing directly from the cells of the ascogenous hyphae and not from croziers. Members of the *Microascaceae* appear to have evolved away from a hymenial configuration; in the microascaceous centrum a peripheral layer of paraphysoidal elements develops that grows inward towards the ascogenous hyphae (Benny & Kimbrough 1980). Malloch (1970) redefined the *Microascaceae* to include both ostiolate and nonostiolate taxa; ascocarps are darkly pigmented, usually hairy, rarely glabrous; asci arise singly or in chains, without croziers, evanescent, irregularly disposed throughout the centrum; ascospores are reddish brown to copper-coloured with germ pores, dextrinoid when young and smooth. The genera of the *Microascaceae* differ in the manner of ramification of ascogenous hyphae and the formation of asci among the interthecial elements. The associated anamorphs are of the annellidic type, *e.g. Cephalotrichum* and *Scopulariopsis*. Aleurioconidia as in *Petriella* and arthroconidia as in *Kernia* also occur (Malloch 1970, 1971).

Ceratocystidaceae

The family level classification of *Ceratocystis* has been discussed since the genus was removed from the *Ophiostomatales* (Barr 1990, Samuels 1993). In recent literature the genus has sometimes been placed in the *Chadefaudiellaceae*, while other authors placed it in its own family, the *Ceratocystidaceae,* as proposed by Locquin (1972, as "*Ceratocystaceae*"). The name *Chadefaudiellaceae* predates

the *Ceratocystidaceae*, but these families are phylogenetically distinct (see below). The *Ceratocystis* clade is a monophyletic group centred on species of *Ceratocystis* or anamorphic species of the *Chalara*-like genus *Thielaviopsis*. *Ambrosiella xylebori*, type of this anamorph genus, occurs in a monophyletic clade together with *Ceratocystis,* now separated from similar anamorphs of the *Ophiostomatales* that are classified in *Raffaelea* (Cassar & Blackwell 1996, Jones & Blackwell 1998, Harrington *et al.* 2010).

The teleomorph genus *Cornuvesica* shares similar characters of centrum ontogeny, ascospore morphology, evanescent asci, and associated anamorphs with *Ceratocystis*, and may belong to the same clade. Because there are no available ncLSU sequences for *Cornuvesica*, its relationship to *Ceratocystis* and *A. xylebori* could only be explored with the ncSSU rDNA phylogeny (Fig. 2). *Cornuvesica falcata,* with a *Chalara*-like anamorph (Viljoen *et al.* 2000), falls in a basal position with these taxa in a monophyletic clade.

These four genera, *Ambrosiella, Ceratocystis*, *Cornuvesica,* and *Thielaviopsis*, constitute a family of their own, which has no valid name. The family name *Ceratocystidaceae* (as "*Ceratocystaceae*") proposed by Locquin (1972) was never validly published. It is phylogenetically well-established and is validated here.

Ceratocystidaceae Locq. ex Réblová, W. Gams & Seifert, **fam. nov.** MycoBank MB515438.

Ceratocystaceae Locq., Rev. Mycol., Supplément, 1 Table. 1972, *nom. inval.*, Art. 36.

Stromata absentia. Ascomata perithecia, fusca usque nigra, saepe aggregata, collo longo angustato et hyphis ostiolaribus protrudentibus, divergentibus praedita. Paries tenuis. Structura interascalis nulla. Asci unitunicati, catenati, saccati, evanescentes, 8-spori. Ascosporae hyalinae, forma variabiles, 0–1-septatae, saepe pariete partim inspissato vel lamina superficiali circumdatae. Anamorphe: aleurioconidia vel conidia modo phialidico orientia; *Thielaviopsis* vel *Chalara* similia.

Typus: *Ceratocystis* Ellis & Halst., New Jersey Agric. Coll. Exp. Sta. Bull. 76: 14. 1890.

Stromata absent. *Perithecia* dark brown to black, often aggregated, long-necked, usually with divergent ostiolar setae. *Perithecial wall* thin. *Interascal tissue* absent. *Asci* unitunicate, formed in chains, saccate, evanescent, 8-spored. *Ascospores* hyaline, varied in shape, 0–1-septate, often with eccentric wall thickening or sheaths. Anamorphs with phialidic conidiogenesis and aleurioconidia; *Thielaviopsis* and *Chalara*-like.

The holomorph taxa of the *Ceratocystidaceae* share common diagnostic characters of centrum ontogeny, evanescent catenate asci, ascospores, and associated anamorphs that are referred to *Thielaviopsis* (Fig. 1) or as *Chalara*-like, producing ameroconidia from phialides and in some cases also aleurioconidia. Ascospores are hyaline, often with eccentric wall thickening or sheaths, aseptate or 1-septate, hat-shaped in *Ceratocystis* or acicular in face view and falcate in side view with a hyaline sheath in *Cornuvesica*. Parguey-Leduc (1977) described the ontogeny of asci of this group with the examples of *Ceratocystis*, *Faurelina,* and *Sphaeronaemella,* Asci arise from the basal hymenium and, as the ascogenous hyphae ramify upward, asci differentiate, dissolve basally from the ascogenous hyphae, and become free within the centrum. Interascal tissue is lacking.

Faurelina and *Chadefaudiella* (*Chadefaudiellaceae*) are discussed below.

Gondwanamycetaceae

Species of *Gondwanamyces* and their *Custingophora* anamorphs form a strongly supported monophyletic clade (Figs 1–3) that is sister to the *Ceratocystidaceae*. The diagnostic characters of this clade include the apparent absence of interascal filaments in the ascomatal centrum and hyaline, allantoid ascospores with a hyaline sheath giving the spore a falcate to lunate appearance. The teleomorphs, described either from infructescences of *Protea* (Wingfield *et al.* 1988, Marais *et al.* 1998) or from sapwood associated with *Scolytidae* (bark beetles) (Bright & Torres 2006, Kolařík & Hulcr 2008), produce dark, globose perithecia with a long, filiform neck, evanescent asci, and hyaline, fusiform ascospores with or without a gelatinous sheath.

Detailed observations on the ontogeny of asci and centrum of *Gondwanamyces* are lacking. Based on the phylogenetic position of the genus, it is likely to be similar to that of the *Ceratocystidaceae*. The morphology of the anamorphs of *Gondwanamyces* is distinctive. The conidiophores are erect, darkly pigmented, paler towards the apex, and either monoverticillate, sometimes with a terminal vesicle or divergently penicillate with whorls of phialides producing hyaline conidia. The conidiogenous locus is located at the base of the shallow collarette. The terminal vesicle was not observed in the anamorph of *Gondwanamyces scolytodis* and *Custingophora cecropiae*, both associated with bark beetles in *Cecropia* (Kolařík & Hulcr 2008). The conidiogenesis of *Custingophora* (as *Knoxdaviesia proteae*), the anamorph of *Gondwanamyces proteae*, observed with fluorescence microscopy, TEM, and SEM, was illustrated by Mouton *et al.* (1993). After discharge, conidia adhere in slimy droplets on the phialide apices. In contrast, the phialidic conidia of species of the *Ceratocystidaceae* are formed in long chains deep within the venter of the cylindrical phialide.

The taxonomic relationships of the anamorph genera *Knoxdaviesia* and *Custingophora,* both phylogenetically related to this family, have been discussed by others, *e.g.* Viljoen *et al.* (1999), Kolařík & Hulcr (2008). Although the genera appear morphologically identical as originally described, they differ in their ecological behaviour. Species of *Custingophora* occur in compost, whereas species of *Knoxdaviesia* associated with *Gondwanamyces* were first observed in infructescences of *Protea* spp. infested by insects (Wingfield *et al.* 1988, Marais *et al.* 1998). The fact that some recently described species of *Gondwanamyces* and *Custingophora* are associated with *Scolytidae* (bark beetles) (Bright & Torres 2006, Kolařík & Hulcr 2008) raises the possibility that the originally reported ecological distinction might have been an artifact of intense sampling of *Protea* in a relatively narrow geographical area in the Western Cape Province of South Africa. Based on molecular and morphological features, Kolařík & Hulcr (2008) considered *Knoxdaviesia* and *Goidanichiella* to be synonyms of *Custingophora*. We prefer to recognise *Goidanichiella* as distinct because of the *Aspergillus*-like vesicles on the conidiophores of the only species, *G. barronii*.

We recognise this clade as a distinct family in the *Microascales*, proposed here as the *Gondwanamycetaceae*.

Gondwanamycetaceae Réblová, W. Gams & Seifert, **fam. nov.** MycoBank MB515439.

Stromata absentia. Ascomata perithecia, nigra, collo comparate longo praedita, apicem versus angustata, ostiolum hyphis divergentibus praeditum. Paries ascomatum fragilis. Filamenta interthecialia nulla. Asci unitunicati, evanescentes. Ascosporae hyalinae, aseptatae, fusiformes, lunatae vel falcatae, vagina gelatinosa

praesens vel absens. Anamorphe *Custingophora*; conidiophora monoverticillata vel penicillata, fusca, conidiis aseptatis modo phialidico orientibus, in massa mucida aggregatis.

Typus: *Gondwanamyces* G.J. Marais & M.J. Wingf., Mycologia 90: 139. 1998.

Stromata absent. *Ascomata* perithecioid, black, necks relatively long, tapered toward apex; ostiolar hyphae present. *Perithecial wall* fragile, thin-walled. *Interascal tissue* absent. *Asci* evanescent. *Ascospores* hyaline, aseptate, fusiform to lunate to falcate, with or without a gelatinous sheath. Anamorph: *Custingophora*; conidiophores monoverticillate or penicillate, brown, conidiogenesis phialidic, conidia aseptate, slimy.

Chadefaudiellaceae

Chadefaudiellaceae was described and validly published by Benny & Kimbrough (1980) for the coprophilous genus *Chadefaudiella*. Cannon & Kirk (2007) added a second genus to the family, *Faurelina* (Locquin-Linard 1975). Locquin-Linard (1973) and Parguey-Leduc (1977) placed the *Chadefaudiella* in the *Microascales* because of its perithecial acomata, catenate asci, and characteristic centrum structures, *i.e.* asci arising from a fertile layer lining the bottom of the cavity, ascogenous hyphae ramifying upwards, asci differentiated without croziers and liberated by basal dissolution to float free in the centrum (Benny & Kimbrough 1980). Ascospores are 1-celled, nondextrinoid, striate, and lack germ pores. No anamorph has been reported. *Faurelina* was described for coprophilous, cleistothecial fungi, otherwise reminiscent of *Chadefaudiella*, but differing by dextrinoid ascospores, and the absence of apical anastomosing setae on its ascomata. The ascomatal wall of *Faurelina* is cephalothecoid and the asci are catenate, irregularly disposed in the centrum at maturity, characters reminiscent of *Chadefaudiella* (Udagawa & Furuya 1973, Furuya 1978, von Arx *et al*. 1981). Von Arx (1978) and von Arx *et al*. (1981) regarded the anamorph of *Faurelina* as similar to the *Arthrographis* anamorph of *Pithoascus langeronii*, producing arthroconidia and secondary small blastoconidia in axenic culture (CBS 126.78).

The classification of *Faurelina* has been problematic. Despite the similarities with *Chadefaudiella* noted by Locquin-Linard (1975), Parguey-Leduc & Locquin-Linard (1976) concluded that *Faurelina* should be placed in the *Loculoascomycetes*. *Faurelina* was later transferred by von Arx (1978) to the *Microascaceae* because of its dextrinoid ascospores, which lack germ pores. He speculated on a relationship with *Neurospora* in the *Sordariaceae* (*Sordariomycetes*), which is characterised by elongate, striate ascospores with apical germ pores, and an anamorph with 1-celled, inflated arthroconidia or perhaps even with the *Testudinaceae* (*Dothideomycetes*). Benny & Kimbrough (1980) accepted *Faurelina* in the *Pithoascaceae* (= *Microascaceae fide* Kirk *et al*. 2008), a family erected for members of the *Microascales* with arthroconidial anamorphs and narrowly fusoid or naviculate ascospores. Recently both genera were placed in the *Chadefaudiellaceae, Microascales* (Cannon & Kirk 2007). This was in part based on the conclusions of Tang *et al.* (2007), who sequenced a single strain of *Faurelina indica* (CBS 126.78) and obtained ncLSU, ncSSU, and RPB2 sequences identical to those of *Ceratocystis fimbriata*, the type species of *Ceratocystis.*

We studied two authentic strains of *Faurelina indica,* the ex-type strain CBS 126.78 and CBS 301.78. They both grew slowly and mature ascomata did not develop on OA after 2 mo, but an arthroconidial anamorph with 0–1-septate conidia was observed similar to that illustrated by von Arx *et al.* (1981). No structures resembling phialides or *Ceratocystis*-type ascomata were produced. We generated new ITS and ncLSU sequences (ITS: GU291802; ncLSU: GU180653, GU180654) for these two strains. Phylogenetic analysis of ncLSU sequences (Fig. 5) suggests a relationship with the *Didymellaceae* (*Pleosporales, Dothideomycetes*). ITS sequences (phylogeny not shown) were similar to those of *Eremomyces* and *Arthrographis* species (90–91 % overall similarity), which also have arthroconidial anamorphs. We are confident that our sequences represent the fungus described by von Arx *et al*. (1981); those reported by Tang *et al*. (2007) were based on a different fungus. Our morphological and molecular studies fail to support the phylogenetic relationship of *Faurelina* with *Ceratocystis* suggested by Tang *et al*. (2007).

Based on these results, we confirm the hypothesis originally proposed by Parguey-Leduc & Locquin-Linard (1976) that *Faurelina* originated in the group of fungi with ascolocular development. Based on ncLSU sequences, we cannot confirm a close relationship of *Faurelina* with the *Testudinaceae* (von Arx 1978) or the *Eremomycetaceae*; the latter includes the morphologically similar *Arthrographis* (Fig. 5).

This phylogenetic reevaluation eliminates the *Chadefaudiellaceae* as an appropriate family name for the *Ceratocystis* clade. *Chadefaudiella* is morphologically slightly different from *Faurelina.* A further molecular analysis may lead to a re-establishment of the *Chadefaudiellaceae* in the *Microascales,* but with the exclusion of *Faurelina* from the family and distinct from the *Ceratocystidaceae*.

ACKNOWLEDGEMENTS

This study was supported by the Project of the National Foundation of the Czech Republic (GA206/09/0547) and Institutional Research Concept No. AV0Z60050516 (Institute of Botany of the ASCR). We would like to thank Jean Mouchacca and Johannes Groenewald for help with obtaining old French literature, Paul Kirk for providing fresh material of *Australiasca laeënsis* from England, Jacques Fournier for providing fresh material of *Cylindrotrichum clavatum* and *Reticulascus clavatus* from freshwater habitats in France, John L. Alcorn and B. McNeil for providing strains of *Australiasca queenslandica*, and Jan Holec from PRM herbarium in Prague for loans of type material. Brett Summerell arranged collecting expeditions to different campuses of the Australian Royal Botanic Gardens during a visit by KAS in 1999, which resulted in the collection of two of the taxa described here. We would like to thank the culture collections CBS (CBS Fungal Diversity Centre, Utrecht) and DAOM (Agriculture and Agri-Food Canada, Ottawa) for providing valuable strains. We are grateful for help of Václav Štěpánek and Gerry Louis-Seize who undertook the DNA sequencing of several members of the *Australiascaceae*, *Plectosphaerellaceae,* and *Reticulascaceae* and provided other sequences newly presented in this study.

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.08

Discovery of the teleomorph of the hyphomycete, *Sterigmatobotrys macrocarpa*, and epitypification of the genus to holomorphic status

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Abstract: *Sterigmatobotrys macrocarpa* is a conspicuous, lignicolous, dematiaceous hyphomycete with macronematous, penicillate conidiophores with branches or metulae arising from the apex of the stipe, terminating with cylindrical, elongated conidiogenous cells producing conidia in a holoblastic manner. The discovery of its teleomorph is documented here based on perithecial ascomata associated with fertile conidiophores of *S. macrocarpa* on a specimen collected in the Czech Republic; an identical anamorph developed from ascospores isolated in axenic culture. The teleomorph is morphologically similar to species of the genera *Carpoligna* and *Chaetosphaeria*, especially in its nonstromatic perithecia, hyaline, cylindrical to fusiform ascospores, unitunicate asci with a distinct apical annulus, and tapering paraphyses. Identical perithecia were later observed on a herbarium specimen of *S. macrocarpa* originating in New Zealand. *Sterigmatobotrys* includes two species, *S. macrocarpa*, a taxonomic synonym of the type species, *S. elata*, and *S. uniseptata*. Because no teleomorph was described in the protologue of *Sterigmatobotrys*, we apply Article 59.7 of the International Code of Botanical Nomenclature. We epitypify (teleotypify) both *Sterigmatobotrys elata* and *S. macrocarpa* to give the genus holomorphic status, and the name *S. macrocarpa* is adopted for the holomorph. To evaluate the ordinal and familial affinities of *Sterigmatobotrys* and its relationships with the morphologically similar genera *Carpoligna* and *Chaetosphaeria*, phylogenetic relationships were inferred based on aligned sequences of the large subunit nuclear ribosomal DNA (ncLSU rDNA).

Key words: Anamorph-teleomorph connection, *Carpoligna*, ncLSU rDNA, phylogeny, *Pleurothecium*, teleotypification.

INTRODUCTION

Sterigmatobotrys, which originally included *S. elata* and *S. papyrogena* (Oudemans 1886), is a conspicuous, cosmopolitan, dematiaceous hyphomycete genus with species occurring on decaying wood in both terrestrial (Sutton 1973, Hughes 1978, Thomas & Polwart 2003) and freshwater (Eaton & Jones 1971, Eaton 1972, Chang 1991, Hyde & Goh 1999, Kane *et al*. 2002) biotopes. It accommodates fungi with macronematous, irregularly biverticillate to terverticillate conidiophores with stout, septate, darkly pigmented stipes and a penicillus consisting of appressed branches and/or whorls of metulae, terminating in polyblastic conidiogenous cells with minute, sympodially arranged denticles, and hyaline, septate conidia that turn brown at maturity and are aggregated in slime.

Despite its distinctive differentiating characters, *Sterigmatobotrys* was transferred to *Stachybotrys* as a subgenus by Rabenhorst (1907). The transfer was apparently based on a portion of the original illustration of *S. elata* (Saccardo 1881: tab. 899), which depicts brown, globose structures that were possibly spores of a different fungus on the original specimen. Hughes (1958) equated *Graphium macrocarpum* (Corda 1839) with *S. elata* (Oudemans 1886) and re-established *Sterigmatobotrys* as a distinct genus, lectotypified by *S. elata,* with *S. macrocarpa* as the name for its type species. The revision of *Sterigmatobotrys* by Jong & Davis (1971) included a re-examination of Corda's type material of *G. macrocarpum* and a taxonomic review of *Sterigmatobotrys* that reconfirmed its status as a distinct genus.

Salonen & Ruokola (1969) introduced a new genus *Gliodendron*, based on *G. balnicola*, found on decaying wood in an old sauna in Finland. Although the conidia were illustrated as hyaline, they were probably immature. Jong & Davis (1971) and Sutton (1973) listed *Gliodendron* as a possible synonym of *Sterigmatobotrys* and *G. balnicola* is likely identical to *S. macrocarpa*, but type material could not be located.

Two species of *Sterigmatobotrys* are accepted in this study and differ in morphology of their conidia. Conidia of *S. macrocarpa* (= *S. elata*) are usually 2-septate, cylindrical to fusiform, hyaline with a truncate base, and there is a considerably protracted maturation of the middle cell, which turns brown. The other accepted species, *S. uniseptata* (Chang 1991), has 1-septate, hyaline conidia. Other species previously described or classified in the genus are discussed in the taxonomy section below.

Neither known *Sterigmatobotrys* species has a reported teleomorph. In a recent collection of *S. macrocarpa* from the Czech Republic, perithecia were found associated with fertile conidiophores. Identical conidiophores were obtained *in vitro* from single ascospore isolates. The teleomorph produces conical to subglobose, dark brown, opaque, nonstromatic perithecia. The asci are cylindrical, shortly stipitate, truncate at the apex with each ascus having a distinct, inamyloid apical annulus. Mature asci contain eight, hyaline, long-fusiform, 3-septate ascospores. Paraphyses are present but seem to disintegrate with age. Our examination of specimens collected in New Zealand and reported by Hughes (1978) uncovered a single specimen of the teleomorph from that country (DAOM 93821); no teleomorphic specimens were found among the abundant Canadian material accessioned in DAOM.

The teleomorph of *S. macrocarpa* morphologically resembles *Carpoligna pleurothecii* (Fernández *et al*. 1999), the teleomorph of the dematiaceous hyphomycete *Pleurothecium recurvatum*.

These fungi share characters such as macronematous, darkly pigmented conidiophores, cylindrical conidiogenous cells with holoblastic conidiogenesis, denticulate, sympodially arranged, broad and conspicuous denticles, and the morphology of asci and ascospores. The teleomorph of *S. macrocarpa* is also reminiscent of several species of *Chaetosphaeria* that have fusiform, hyaline ascospores, and cylindrical asci, *e.g. Chaet. acutata*, *Chaet. fennica* and *Chaet. ovoidea*. *Chaetosphaeria* is linked with 13 anamorphic genera of dematiaceous hyphomycetes producing phialidic conidia and is phylogenetically classified in the *Chaetosphaeriaceae, Chaetosphaeriales* (Réblová *et al*. 1999, Réblová 2000, Réblová & Winka 2000, Fernández *et al*. 2006). The systematic and phylogenetic position of *Carpoligna* is less certain. Based on the ITS rDNA and ncLSU rDNA sequence data, several hypothetical relationships were suggested and tested by Fernández *et al*. (1999), with discussion of possible relationships of *Carpoligna* with the *Microascales* and *Hypocreales*.

Because the teleomorph of *S. macrocarpa* is apparently undescribed and because no teleomorph was described in the protologue of *Sterigmatobotrys* (Oudemans 1886), we emend the generic name *Sterigmatobotrys* by the epitypification of both *S. elata* and *S. macrocarpa* with our teleomorphic specimen from the Czech Republic, applying ICBN Art. 59.7 (McNeill *et al.* 2006). The name *S. macrocarpa* is adopted for the holomorph and the recent herbarium material documenting both morphs designated as an epitype (teleotype) below. With our epitypification, the genus *Sterigmatobotrys* becomes holomorphic with one remaining anamorph-only species included, namely *S. uniseptata*.

The phylogenetic relationships of *Sterigmatobotrys* to other ascomycetes can only be vaguely inferred based on morphological characters of the anamorph, *e.g.* holoblastic conidiogenesis, in combination with the rather undiagnostic teleomorph. The aim of our phylogenetic study is to elucidate the relationship of *Sterigmatobotrys* with the morphologically similar *Carpoligna pleurothecii* and other representative taxa in relevant orders of *Ascomycota*. To evaluate such relationships, phylogenetic analyses were performed based on ncLSU rDNA sequences of ascospore and conidial isolates of terrestrial and freshwater strains of *S. macrocarpa*.

MATERIAL AND METHODS

Morphological observations

Dried herbarium specimens were rehydrated in water. Sections of perithecia, asci, ascospores, paraphyses, conidia, conidiophores, and conidiogenous cells were studied in microscope slide preparations mounted in water, Melzer's reagent, or 90 % lactic acid. Sections of the perithecial wall were made by hand. All measurements were made in Melzer's reagent. Means ± standard errors (s.e.) based on 25 measurements are given for dimensions of asci, ascospores, and conidia. Images were captured in Melzer's reagent using differential interference (DIC) or phase contrast (PC) microscopy using an Olympus DP70 camera operated by Imaging Software Cell* on an Olympus BX51 compound microscope and Olympus SZX12 stereomicroscope. Images were processed with Adobe Photoshop CS4 Extended.

Single ascospores were isolated from fresh material with the aid of a single-spore isolator (Meopta, Prague, Czech Republic). Isolates were grown on potato-carrot agar (PCA) and malt extract agar (2 % MEA) (Gams *et al*. 1998). Colonies were examined at 7, 21, and 30 d after incubation at 25 °C in the dark and under near UV/fluorescent light (12 h light/12 h dark). Cultures are maintained at CBS Fungal Biodiversity Centre, Utrecht, the Netherlands (CBS), and the Canadian Collection of Fungus Cultures, Agriculture and Agri-Food Canada, Ottawa, Canada (DAOM).

Table 1. Sources and accession numbers of isolates sequenced for this study.

Taxon	Source*	Substrate and Locality	GenBank accession numbers LSU
Sterigmatobotrys macrocarpa	DAOM 230059 CBS 113468	Canada, decayed wood in a stream	GU017316
Sterigmatobotrys macrocarpa	PRM 915682	Czech Republic, decayed wood of *Abies alba*	GU017317
Carpoligna pleurothecii	CBS 101581	Czech Republic, decayed wood of *Carpinus betulus*	AF261070
Carpoligna pleurothecii	CBS 101580	Czech Republic, decayed wood of *Carpinus betulus*	GU017318

*CBS = Centraalbureau voor Schimmelcultures, Utrecht, the Netherlands; DAOM = Agriculture and Agri-Food Canada Collection, Ottawa, Canada; PRM = Mycological Herbarium National Museum Prague, Czech Republic.

DNA extraction, amplification and sequencing

DNA was isolated with an UltraClean Microbial DNA Kit (MoBio Laboratories, Inc., Canada) using mycelium removed from PCA or MEA cultures following the manufacturer's protocol for filamentous fungi. All PCR experiments were carried out using a PTC-200 thermocycler (MJ Research). PCR reactions containing 2–4 mM $MgSO_4$ were performed using Platinum *Taq* DNA polymerase High Fidelity (Invitrogen) in 25.0 mL volumes. PCR conditions were as follows: 2 min at 94 °C; 35 cycles of 30 s at 94 °C, 30 s at 55–60 °C, and 165–270 s at 68 °C; 10 min at 68 °C. Amplicons were purified using UltraClean PCR Clean-up Kit (MoBio Laboratories, Inc., Canada) following the manufacturer's directions. All nucleotide sequences were obtained by the dideoxy chain-terminating method using ABI PRISM 3100 or ABI PRISM 3130xl automated DNA sequencers (Applied Biosystems). For PCR reactions the following primer pairs were used: ITS5 with LR0R or LR8 (Vilgalys unpubl. data: www.botany.duke.edu/fungi/mycolab, White *et al*. 1990). For sequencing reactions, the primers LR0R, LR3R, LR6, LR7, LR16, LR5 (Vilgalys & Hester 1990, Rehner & Samuels 1994, Vilgalys & Sun 1994), JS7 and JS8 (Landvik 1996) were used. Sequences were edited using Sequencher v. 4.9 software (Gene Codes Corporation, Ann Arbor, MI, USA).

Phylogenetic analyses

New ncLSU rDNA sequences of two strains of *S. macrocarpa* and two strains of *Carpoligna pleurothecii* were obtained from ascospore and conidial isolates. New sequences, their sources, and GenBank accession numbers are listed in Table 1; other homologous sequences retrieved from GenBank are given on Fig. 1, mostly from the studies of Huhndorf *et al.* (2004), Réblová & Seifert (2004), Spatafora *et al*. (2006), and Zhang *et al.* (2006).

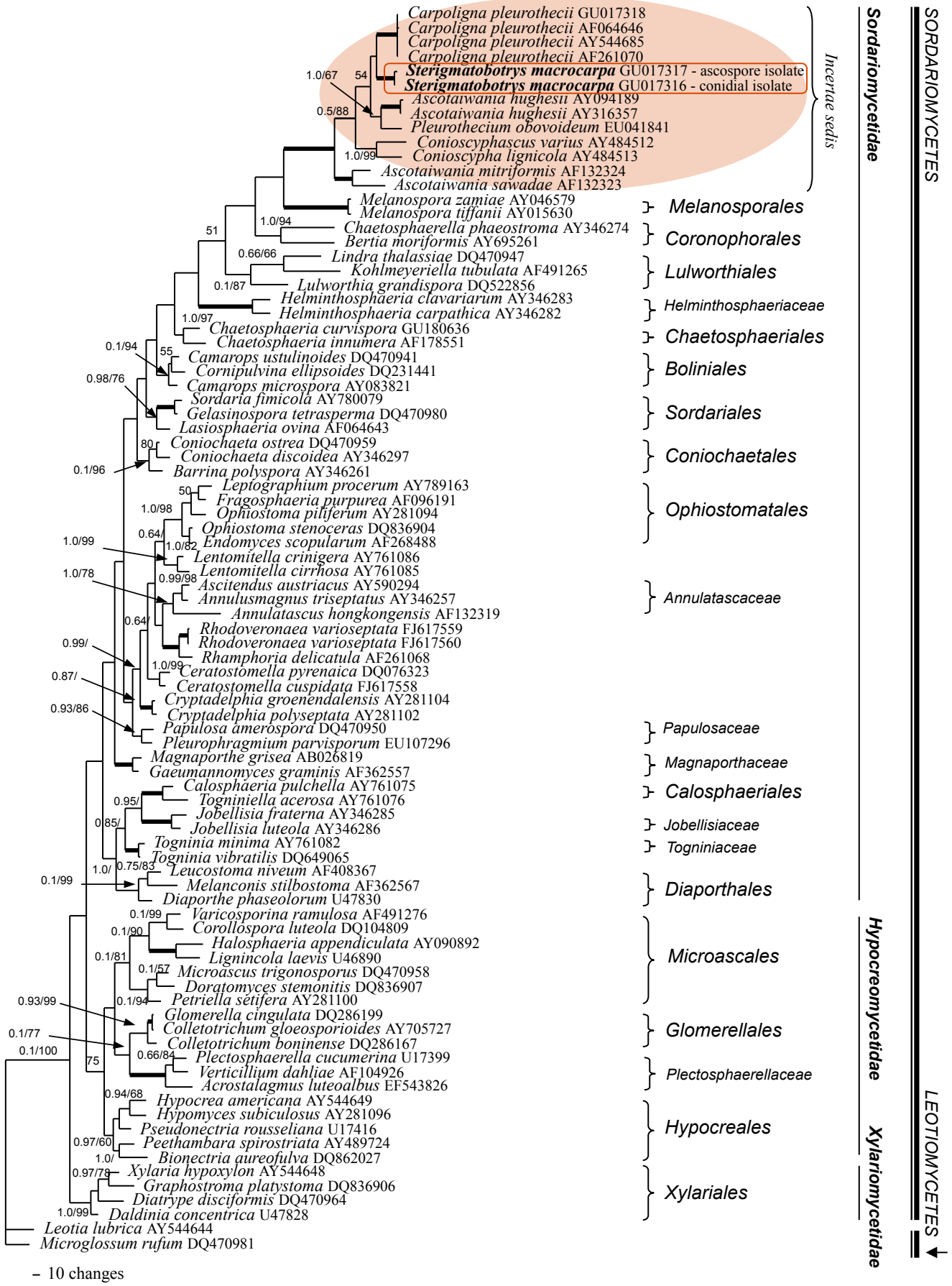

Fig. 1. One of the four most parsimonious trees from a heuristic analysis of ncLSU rDNA sequences from 21 ascomycetous orders and families. Bootstrap support values ≥ 50 % from 1000 replicates of full heuristic search are included at the nodes. Thickened branches indicate posterior probability values = 1.0 pP and 100 % bootstrap support. Posterior probability values < 0.95 pP are shown at the nodes. Branch lengths are drawn to scale.

All sequences were manually aligned in BioEdit v. 7.0.9.0 (Hall 1999). Predicted models of the secondary structure of the LSU rRNA molecules of *Saccharomyces cerevisiae* (Gutell *et al*. 1993) were used to improve decisions on homologous characters.

Phylogenetic relationships were examined using the ncLSU sequences of taxa from 21 orders or families of *Sordariomycetes,* using the outgroup method (Nixon & Carpenter 1993) with two outgroup species, *Leotia lubrica* and *Microglossum rufum* (*Leotiaceae*, *Helotiales*, *Leotiomycetes*). Bases 1–75 were excluded from the analysis because of incompleteness of the 5'-end of most available sequences. The final alignment is deposited in TreeBase (10527).

Maximum parsimony analyses were conducted with PAUP v. 4.0b10 (Swofford 2002). A heuristic search was performed with the stepwise-addition option with 1 000 random taxon addition replicates and TBR branch swapping. All characters were unordered and given equal weight. Gaps were treated as missing data. Branch support was estimated by performing 1 000 bootstrap resamplings using heuristic searches, each consisting of ten random-addition replicates.

Bayesian analysis was performed in a likelihood framework as implemented by MrBayes v. 3.0b4 (Huelsenbeck & Ronquist 2001). The program MrModeltest2 v. 2.3. (Nylander 2008) was used to infer the appropriate substitution model, which would best fit the model of DNA evolution for our sequence data set. Bayesian searches using Metropolis-coupled Markov chain Monte Carlo sampling were conducted. One cold and three heated Markov chains were used. Bayesian analyses were run for 5 million generations, with trees sampled every 1 000 generations. The first 20 000 trees, representing the burn-in phase, were discarded. To estimate posterior probabilities (PP) of recovered branches (Larget & Simon 1999), 50 % majority rule consensus trees were produced from the remaining trees using PAUP.

RESULTS

The phylogenetic analysis was performed on an alignment consisting of the first 2/3 of the ncLSU region for 87 isolates representing 81 species from 21 ascomycetous families or orders and 1299 total characters: 588 constant, 151 unique, and 485 parsimony informative. A maximum parsimony (MP) heuristic search produced four most parsimonious trees (MPTs) with a length of 3661 steps (CI = 0.297, RI = 0.639, HI = 0.703), one of which is shown in Fig. 1. For the Bayesian analysis, the GTR+I+G substitution model was inferred.

The ascospore (terrestrial) and conidial (freshwater) isolates of *Sterigmatobotrys macrocarpa* (1.0 posterior probabilities/100 % bootstrap support) are shown in a sister relationship to *Carpoligna* (1.0/100) (Fig. 1). Two other holomorphic genera, *Conioscyphascus* with its *Conioscypha* anamorphs (1.0/99) and the paraphyletic genus *Ascotaiwania,* group with the previously mentioned taxa in a robust clade (1.0/100) labeled as *incertae sedis* in the phylogram.

This robust clade is a sister group to the large group consisting of several well-defined orders or families, *viz. Melanosporales* (1.0/100), *Coronophorales* (1.0/94), *Lulworthiales* (0.1/87), *Helminthosphaeriaceae* (1.0/100), *Chaetosphaeriales* (1.0/97), *Coniochaetales* (1.0/96), *Boliniales* (1.0/94), and *Sordariales* (0.98/76).

TAXONOMY

Sterigmatobotrys Oudem., Nederl., Kruidk. Arch. Ser. II, 4: 548. 1886.

Type species: *Stachybotrys elata* Sacc., lectotype chosen by Hughes 1958, p. 814.

= *Stachybotrys* Corda subgenus *Sterigmatobotrys* Oudem., Krypt. Fl. Deutsch. Oesterr. Schweiz, Band I, Abt. 8: 631. 1907.

= *Gliodendron* Salonen & Rucuola, Mycopath. Mycol. Appl. 38: 332. 1969.

The following description of the teleomorph supplements the previous generic concept based on the anamorph (*cf.* Ellis 1971), to provide a holomorphic generic concept:

Perithecia nonstromatic, solitary, dark brown to black, papillate, venter conical to subglobose, superficial, ostiole periphysate. *Perithecial wall* leathery to fragile, two-layered. *Paraphyses* present, septate, hyaline, tapering towards apex, longer than asci. *Asci* unitunicate, cylindrical, 8-spored, truncate at apex, short-stipitate. *Ascospores* fusiform to cylindrical-fusiform, hyaline, 3-septate.

Sterigmatobotrys macrocarpa (Corda) S. Hughes, Canad. J. Bot. 36: 814. 1958. Figs 2, 3.

Basionym: *Graphium macrocarpum* Corda, Icon. Fung. 3: 13. 1839 (**holotype** PRM 155517; **epitype** PRM 915682 designated here).

[≡ *Graphium macrocarpum* Sacc., Mycol. Veneta, p. 187. 1873. *nom. illeg.*, *non G. macrocarpum* Corda 1839].

≡ *Harpographium macrocarpum* (Corda) Sacc., Syll. Fung. 4: 620. 1886.

= *Acrothecium bulbosum* Sacc., Michelia 1: 74. 1877 (**holotype** PAD, examined by us and Hughes 1958).

= *Stachybotrys elata* Sacc., Michelia 2: 560. 1882 (**lectotype** *Fungi Italici Autographice Delineati*, Fascs 17-28, Tab. 899. 1881, designated here and reproduced as Fig. 4, excluding the five dark globose spores in the centre of the figure; **epitype** PRM 915682 designated here).

≡ *Sterigmatobotrys elata* (Sacc.) Oudem., Nederl. Kruidk. Arch. Ser. II, 4: 548. 1886.

≡ *Phragmostachys elata* (Sacc.) Costantin, Les Mucédinées Simples: 97. 1888, as '*Phragmostachys atra*'. A *lapsus calami* for the species epithet *fide* Bisby (1943).

= *Atractina biseptata* Höhn., Hedwigia 43: 298. 1904 (holotype not examined by us or Hughes 1958).

= *Gliodendron balnicola* Salonen & Ruokola, Mycopath. Mycol. Appl. 38: 332. 1969. (holotype not traced).

Synonymy adapted from Hughes (1958) and Sutton (1973).

Perithecia 300–450 µm high, 380–500 µm diam, nonstromatic, solitary to gregarious, semi-immersed to superficial, dark brown to black, venter conical to subglobose, with a beak or short obtuse neck, with dark brown to black *ca.* 3–4 µm wide hairs at base, attached tightly to substratum. *Perithecial wall* 25–30 µm thick, leathery to fragile, two-layered, outer layer of *textura prismatica*, composed of dark brown cells, inner layer of *textura prismatica*; cells hyaline, thin-walled, flattened. Ostiole periphysate. *Paraphyses* septate, branched, slightly constricted at septa, *ca.* 4−5 µm wide tapering to *ca.* 2 µm, longer than asci, partially disintegrating with age. *Asci* 165–188 × 10–11 µm (mean ± S.E. = 176.9 ± 2.3 × 10.6 ± 0.1 µm), unitunicate, arising from croziers, cylindrical, ascal apex truncate with a distinct refractive, inamyloid apical annulus *ca.* 3 µm diam and 1.5 µm high. *Ascospores* 29–34.5(–36) × 4–5(–5.5) µm (mean ± S.E. = 32.6 ± 0.4 × 4. 7 ± 0.1 µm), fusiform to cylindrical-fusiform, narrowly rounded at ends, sometimes slightly flattened at one side, often curved, hyaline, smooth, 3-septate.

Colonies in vivo effuse, brown, hairy. *Conidiophores* up to 325 µm long, 10–13 µm wide, solitary, macronematous, mononematous, arising

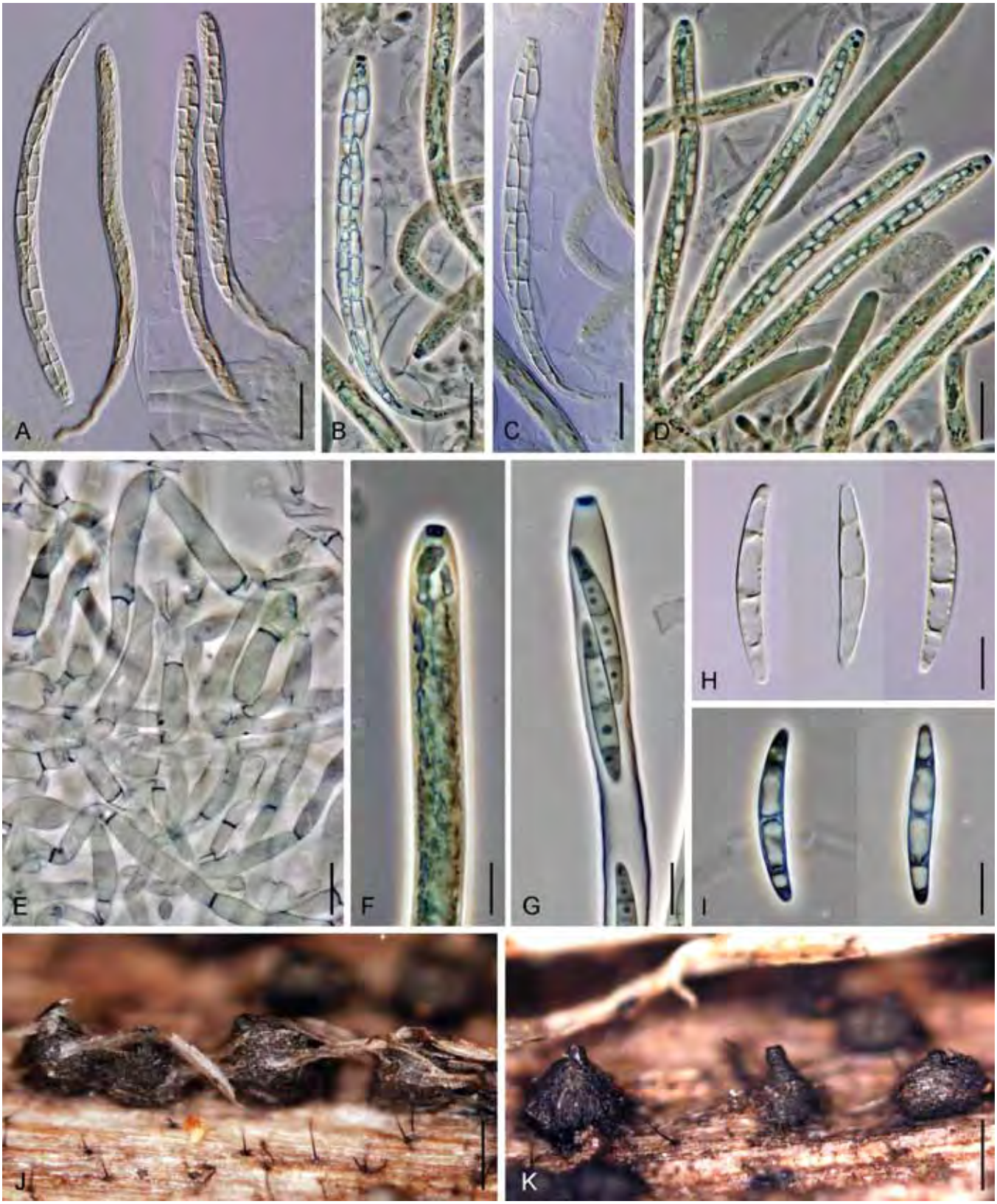

Fig. 2. *Sterigmatobotrys macrocarpa*. A–D. Asci with ascospores. E. Paraphyses. F, G. Asci with a distinct apical annulus. H, I. Ascospores. J, K. Perithecia of the teleomorph associated with conidiophores on the host. A–I from PRM 915682. Scale bars: A–D = 20 µm; E–I = 10 µm; J, K = 250 µm.

from stromatic cells, consisting of a well-defined stipe, terminating in an irregularly biverticillate to terverticillate head. Stipe straight, stout, septate, dark brown, slightly tapering and paler at apex. *Penicillate head* consisting of 2–4 brown branches, sometimes absent, then 2–4 brown to subhyaline metulae with terminally arranged conidiogenous cells. *Metulae* 6.5–13.5 × (2.5–) 3 µm. *Conidiogenous cells* 5–22 × 1.5–3.5 µm (mean ± S.E. = 12.3 ± 3.8 × 2.2 ± 0.6 µm), terminal, more or less parallel, polyblastic, smooth, cylindrical, hyaline, bearing 2–6 sympodially produced denticles from which conidia develop holoblastically. *Conidia* 17–20.5 × 4.5–5.5 µm (mean ± S.E. = 19.2 ± 0.2 × 5 ± 0.06 µm), ellipsoidal to ellipsoidal–fusoid to ellipsoidal–clavoid, apically rounded, with a flat basal scar, 2–3-septate, smooth, hyaline when young, at maturity the middle cell becomes larger and turns brown, often seen anastomosing; aggregated in a hyaline, slimy head.

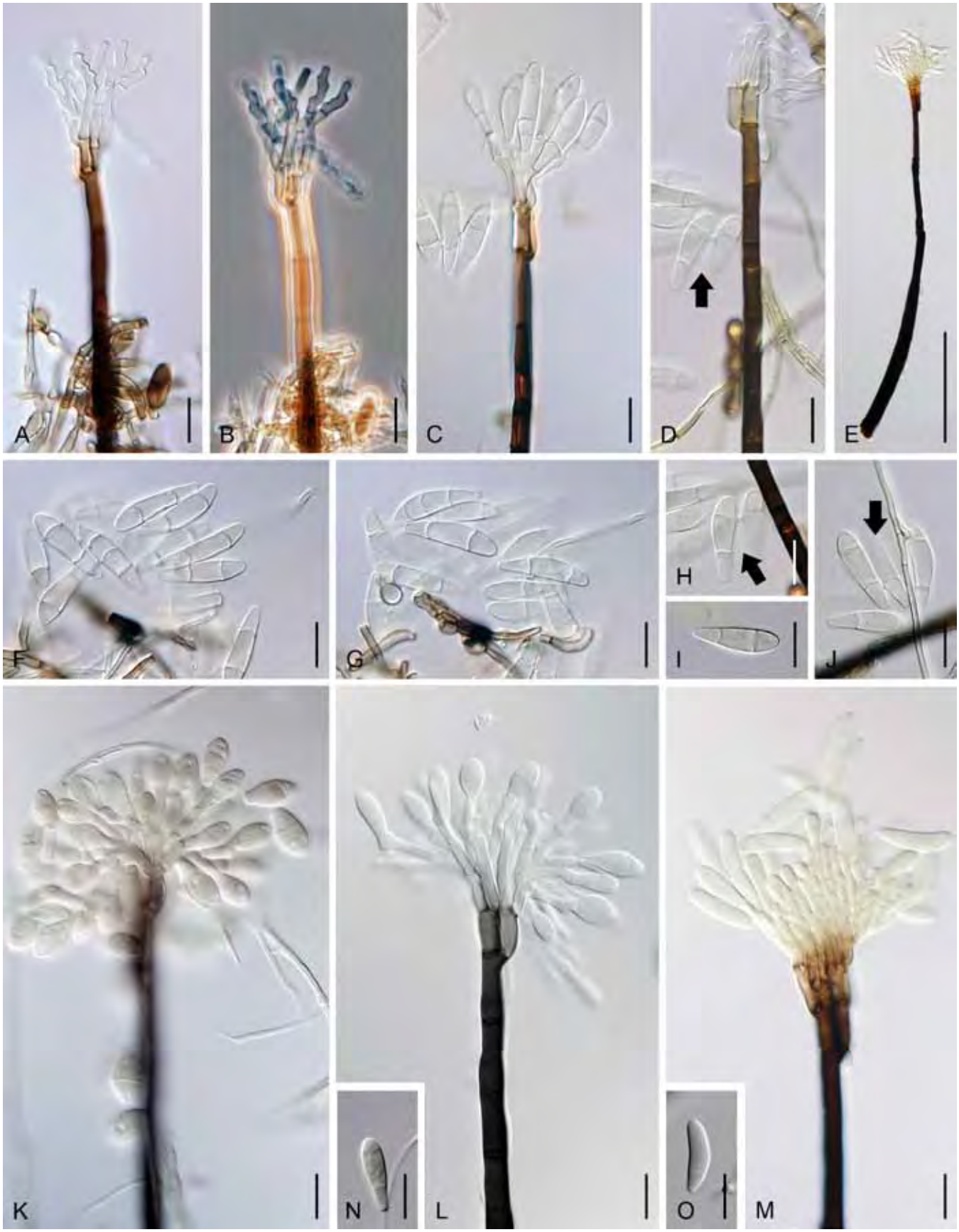

Fig. 3. *Sterigmatobotrys macrocarpa*. A–E, K–M. Conidiophores . F–J, N, O. Conidia. A–D, F–J from culture (PCA, 14 d old, DAOM 230059); E, M, O from the host *Abies alba* (PRM 915682); K, L, N from culture (MEA, 14 d old). Scale bars: A–D, F–O = 20 µm; E = 100 µm.

Colonies in vitro after 30 d on MEA at 25 °C 11–13 mm diam, convex in middle with abundant grayish-brown aerial mycelium, surrounded by a planar zone of sparse black aerial mycelium, margins subsurface; reverse black. Sporulating conidiophores develop throughout colony, more frequently at margins. *Conidiophores* 160–230 × 5.5–7 µm, morphologically identical to those *in vivo* but shorter and thinner. *Conidiogenous cells* 10–16(–25) × 2–3 µm (mean ± S.E. = 15.9 ± 1.5 × 2.7 ± 0.08 µm), identical in shape to those observed *in vivo*. *Metulae* 8–12(–14) × (2.5–)3–4 µm. *Conidia* 13–18 × 5.5–6(–7) µm (mean ± S.E. = 14.9 ± 0.6 × 6.4

Fig. 4. *Sterigmatobotrys macrocarpa*. Illustration of *Stachybotrys elata* (Saccardo, *Fungi Italici Autographice Delineati*, Fascs 17–28, Tab. 899. 1881); selected as a lectotype in this study.

± 0.2 µm), ellipsoidal to obovoidal, apically rounded, truncate at base with a flat basal scar, 1−2-septate, hyaline, smooth. On PCA *conidia* 19–23(–25) × 5–6 µm (mean ± S.E. = 22.2 ± 0.3 × 5.5 ± 0.07 µm), ellipsoidal, ellipsoidal-fusoid to ellipsoidal-clavoid, often slightly curved, apically rounded, truncate at base with a flat basal scar. *Chlamydospores* not observed.

Specimens examined: **Canada**, Ontario, Madawaska Highlands, Morrow Creek Trail, 9 May 2001, on submerged decayed wood in a stream (developing in a damp chamber), K.A. Seifert no. 1421, culture deposited as DAOM 230059, CBS 113468. **Czech Republic**, Šumava Mts. National park, Jilmová skála near Zátoň, 1 Oct. 2007, decaying wood of *Abies alba*, M. Réblová no. 2973, PRM 915682, **epitype designated here** of the holotype of *Graphium macrocarpum* Corda and **lectotype** of *Stachybotrys elata* Sacc.; Prague, Lobkowitz Garden, on a shingle made of pine wood, leg. A.C. Corda, PRM 155517, **holotype** of *Graphium macrocarpum*. **Italy**, Padova, on decaying wood of a trunk, PAD, **holotype** of *Acrothecium bulbosum*. **New Zealand**, North Island, North Auckland, Puketi Forest, 20 June 1963, on *Agathis australis*, leg. S.J. Hughes no. 898, DAOM 93821; Westland Province, Jackson River valley, a track to the Lake Ellery, 33 km SW of Haast, 11 Mar. 2003, on decayed wood, leg. M. Réblová, M.R. 2793, PDD 94360.

Notes: Fertile conidiophores of *Sterigmatobotrys macrocarpa* occur worldwide on wood of coniferous trees, *e.g. Abies*, *Picea,* and *Taxus* in Asia (Taiwan), Europe, North America, and New Zealand (Ellis 1971, Hughes 1978). Although the anamorph is reported from both terrestrial and freshwater biotopes, the teleomorph is known so far only from terrestrial material of *Abies alba* collected in the Czech Republic and *Agathis australis* from New Zealand.

Conidia of *S. macrocarpa* undergo a protracted maturation. The middle cell eventually turns brown, but often only hyaline conidia are observed on the substrate. Mature conidia were not seen either *in vitro* or on recently collected herbarium material. This aspect of conidial maturation was illustrated by Saccardo (1881: tab. 899) and Ellis (1971: 369; fig. 251). Conidia on PCA (Figs 3F–J, M, O) were identical to those found in nature, while conidia observed on MEA (Figs 3K, L, N) were rather obovoidal to obpyriform and significantly shorter, often slightly wider in the middle and usually with one septum; the second septum developed later. Conidia were observed to anastomose in culture (Fig. 3D, H, J, MEA and PCA, DAOM 230059). Conidiophores of *S. macrocarpa* produced in culture were shorter than those on the natural substrate.

No type material of *Stachybotrys elata* is available. The illustration (Saccardo 1881, tab. 899, reproduced here as Fig. 4) accompanying the original description of *S. elata* (Saccardo 1882: 560) is the only surviving original element. Therefore, the illustration of *S. elata* is designated as lectotype. Because the five globose brown structures in the centre of the figure are possibly spores of a different fungus on the original specimen, as noted in the Introduction, we explicitly exclude these from the lectotypification.

Unfortunately our culture of *S. macrocarpa* derived from ascospores (PRM 915682) is no longer viable.

Other species of *Sterigmatobotrys*

Sterigmatobotrys elongata (Peck) Pound & Clem., Minnesota Bot. Stud. 1: 667. 1896.
Basionym: *Stachybotrys elongata* Peck, Annual Rep. New York State Mus. 43: 29. 1890.

Notes: The protologue shows a macronematous, monoverticillate hyphomycete unlikely to be related to *Sterigmatobotrys;* it is perhaps better placed in *Aspergillus*, *Memnoniella,* or *Stachybotrys*.

Sterigmatobotrys papyrogena (Sacc.) Oudem., Ned. Kruidk. Arch., ser. 2, 4: 549. 1886.
Basionym: *Periconia papyrogena* Sacc. Michelia 1: 273. 1878.
≡ *Stachybotrys papyrogena* (Sacc.) Sacc., Syll. Fung. 4: 269. 1886.

Note: This species was considered a synonym of *Memnoniella echinata* by Smith (1962).

Sterigmatobotrys uniseptata H.S. Chang, Mycol. Res. 95: 1142. 1991.

Note: For a description and illustrations, see Chang (1991). The type is on an unidentified decaying twig submerged in a stream from Taiwan and is the only record of *S. uniseptata*.

KEY TO ACCEPTED SPECIES OF *STERIGMATOBOTRYS*

Conidia 2-septate at maturity, middle cell eventually turning brown, ellipsoidal, ellipsoidal-fusoid to ellipsoidal-clavoid, often gently curved, 17–20.5 × 4.5−5.5 µm *in vivo*, slightly smaller *in vitro* ..... *S. macrocarpa*
Conidia 1-septate, rarely 2-septate, at maturity, hyaline, cylindrical to subclavate, 13–17 × 4.5–5.5 µm ..... *S. uniseptata*

DISCUSSION

Although *Sterigmatobotrys macrocarpa* has rather nondescript teleomorphic characters such as dark, non-stromatic perithecia, unitunicate, short-stipitate asci with a distinct apical inamyloid annulus, septate, tapering paraphyses, and fusiform, hyaline, 3-septate ascospores, the experimentally proven connection with its distinctive anamorph makes the holomorph easily identifiable among other perithecial ascomycetes. If the morphologically poorly differentiated teleomorph of *Sterigmatobotrys* was found without its anamorph, it could be easily confused with species of *Carpoligna* or *Chaetosphaeria*. *Carpoligna pleurothecii*, the type and only species of its genus, differs from *S. macrocarpa* by setose papillate perithecia, shorter and wider asci, and shorter and slightly wider ascospores. Distinguishing *Chaetosphaeria* species from *S. macrocarpa* is more difficult, but generally the apical annulus of *Chaetosphaeria* is discoid and less conspicuous than the pronounced apical annulus of species of *Carpoligna* and *Sterigmatobotrys*.

Our ncLSU phylogeny confirms that *Sterigmatobotrys* is closely related to *Carpoligna* and its *Pleurothecium* anamorph and to the anamorphic species *Pleurothecium obovoideum*. *Pleurothecium recurvatum* (teleomorph *Carpoligna pleurothecii*) and *Sterigmatobotrys* share similar patterns of conidial ontogeny and conidiogenous cell morphology, but differ in conidiophore morphology. Cylindrical, prolonged, hyaline, polyblastic conidiogenous cells bearing several conspicuous denticles produced in a sympodial pattern, are typical of *P. recurvatum* (Fernández *et al.* 1999: 256; figs 15–23) and to some extent also *P. obovoideum* (Arzanlou *et al*. 2007: 83; fig. 28). The conidiophore apex of *Sterigmatobotrys* is more complex but could be interpreted as a branched, penicillate derivation of the basic pattern seen in *Pleurothecium*. *Sterigmatobotrys* species form several series of branches and metulae terminating in polyblastic conidiogenous cells that extend sympodially, resulting in a zig-pattern of opened conidiogenous loci. The denticles of *S. macrocarpa* are rather minute and rudimentary compared to those of *P. recurvatum*. In *P. recurvatum* and *S. macrocarpa*, macronematous, dematiaceous conidiophores regularly occur in axenic culture; however, the conidiophores of *P. obovoideum* are reduced to a conidiogenous cell bearing up to three denticles (CBS 209.95; Arzanlou *et al*. 2007).

Similarly complex apical conidiophore branching was reported for synanamorphs of the hyphomycetes *Taeniolella rudis* and *T. longissima* (Hughes 1980, Jones *et al.* 2002). In both species, thick-walled, dark brown, multiseptate macroconidia arise in acropetal chains and produce penicillate conidiophores on a hyaline extension of the apical cell of the terminal macroconidium; the head consists of several metulae with terminally arranged conidiogenous cells that produce hyaline 1- or 2-septate conidia. Preliminary ITS data (Seifert, unpubl. data) suggests that *T. rudis* is closely related phylogenetically to *S. macrocarpum*.

In the ncLSU phylogeny presented here, *Sterigmatobotrys* falls in a robust clade (1.0/100) as a sister to *Carpoligna pleurothecii* and its anamorph *Pleurothecium recurvatum* (1.0/100). Two other holomorphic genera, *Conioscyphascus* and its *Conioscypha* anamorphs (1.0/99) and the paraphyletic genus *Ascotaiwania*, group in this clade. *Ascotaiwania hughesii* with a helicosporous anamorph groups with the asexually reproducing *Pleurothecium obovoideum* (1.0/67), with a sister relationship to *Sterigmatobotrys*, while *Ascotaiwania mitriformis* and *A. sawadae* (1.0/100) with *Monotosporella*-like anamorphs (Ranghoo & Hyde 1998, Sivichai *et al*. 1998) occur at the basal position of the whole *incertae sedis* clade (1.0/100). *Pleurothecium obovoideum* was recently segregated from *Ramichloridium* by Arzanlou *et al.* (2007). In our ncLSU analysis *P. obovoideum* causes paraphyly of *Pleurothecium*; it is clearly segregated from the type species *P. recurvatum*.

The clade labeled *incertae sedis* (Fig. 1) includes four holomorphs described during the last two decades (Sivanesan & Chang 1992, Fernández *et al.* 1999, Réblová & Seifert 2004, Arzanlou *et al.* 2007). Part of this group was discussed by Réblová & Seifert (2004) when the genus *Conioscyphascus* was proposed. They performed a series of constraint analyses based on ncLSU and ncSSU rDNA sequences to test the monophyly of *Conioscyphascus* with the *Glomerellales*, *Hypocreales* and *Microascales,* which were indicated as possible alternative hypotheses. All four teleomorph genera of this clade share similar morphological characters such as nonstromatic perithecia, which are hyaline to pale orange in *Conioscyphascus* or darkly pigmented and opaque in other genera; similar anatomy of the perithecial wall, consisting of several layers of polyhedral cells; apically free, septate paraphyses; unitunicate asci with a distinct, inamyloid apical annulus; and symmetrical, transversely septate ascospores, which are hyaline in *Carpoligna*, *Conioscyphascus* and *Sterigmatobotrys* species but concolourous (pale brown) or bicolorous (brown middle cells, hyaline polar cells) in *Ascotaiwania* species.

The four holomorphic genera of this clade are experimentally linked with anamorphs, but with two different modes of conidiogenesis. The *Conioscypha* anamorphs of *Conioscyphascus* species have an unusual mode of conidiogenesis with multiple, conspicuous collarettes forming a multilamellar structure around a blastic conidiogenous locus producing ellipsoidal to ovoid dark pigmented conidia (Shearer 1973, Réblová & Seifert 2004). Conidiogenesis of the *Pleurothecium* anamorphs of *Carpoligna* and *Sterigmatobotrys* represents a variation of a holoblastic theme. *Pleurothecium recurvatum* and *S. macrocarpa* have rhexolytic conidial secession on polyblastic, denticulate, sympodially proliferating conidiogenous cells. The holoblastic conidiogenesis on wide, conspicuous denticles of *P. recurvatum* is reminiscent of several other hyphomycetes, such as species of *Brachysporium*, in which denticles often remain attached to the conidium, and the tiny denticles of, for example, species of *Dactylaria* or *Pleurophragmium*. *Cryptadelphia* with its *Brachysporium* anamorph and the anamorphic species *Pleurophragmium parvisporum*, recently reinstated and separated from *Dactylaria* by Réblová (2009), grouped near other perithecial ascomycetes that produce anamorphs with holoblastic-denticulate conidiogenesis of phaeoisaria-, ramichloridium- or sporothrix-type, *e.g.* species of *Lentomitella*, *Rhamphoria* or *Rhodoveronaea*. Although *P. parvisporum* can be placed in the family *Papulosaceae* (Réblová 2009) and *Rhodoveronaea* is sister to the *Annulatascaceae*, other morphologically similar anamorphs apparently do not belong in known families, as shown in Fig. 1.

Ascotaiwania hughesii was experimentally linked with a *Helicoön* anamorph identified as conspecific with *H. farinosum* (Fallah *et al*. 1999). The genus *Helicoön* includes about 17 species (Linder 1929, Goos *et al.* 1986, Zhao *et al*. 2007); based on a molecular analysis, it is polyphyletic (Tsui & Berbee 2006). The type species, *H. sessile*, was connected with *Orbilia* of the *Orbiliales* (*Orbiliomycetes*) (Pfister 1997). Other known phylogenetic affinities are with the *Tubeufiaceae* (*H. gigantisporum*), *Pleosporales* (*H. richonis*) or *Dothideomycetes s. lat*. (*H. fuscosporum*). Conidiogenesis in *Helicoön* species is generally monoblastic, but some have conidiogenous cells that extend sympodially once or twice, leaving broad conidiogenous denticles. Their conidium

development suggests that the coiled conidia may have been derived from structures that were originally chlamydospores or aleurioconidia. In this light, we could conclude that *Helicoön*, *Pleurothecium,* and *Sterigmatobotrys* are not homologous anamorphs and that taxonomic evaluations based on direct comparison of these characters may be inappropriate (Seifert & Samuels 2000). However, the connection between *A. hughesii* and *H. farinosum* needs to be reconfirmed.

By accepting *Sterigmatobotrys* as a separate genus morphologically and genetically closely related to *Pleurothecium obovoideum* and *P. recurvatum,* we acknowledge the existence of a characteristic pattern of conidium and conidiogenous cell development in this fungal clade.

ACKNOWLEDGEMENTS

This study was supported by the Project of the National Foundation of the Czech Republic (GA206/09/0547) and Institutional Research Concept No. AV0Z60050516 (Institute of Botany of the ASCR). We are grateful for the help of Dr Václav Štěpánek, who undertook the DNA sequencing of ascospore isolates of *Sterigmatobotrys macrocarpa* and other sequences newly presented in this study.

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.09

A molecular re-appraisal of taxa in the *Sordariomycetidae* and a new species of *Rimaconus* from New Zealand

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Abstract: Several taxa that share similar ascomatal and ascospore characters occur in monotypic or small genera throughout the *Sordariomycetidae* with uncertain relationships based on their morphology. Taxa in the genera *Duradens*, *Leptosporella, Linocarpon,* and *Rimaconus* share similar morphologies of conical ascomata, carbonised peridia and elongate ascospores, while taxa in the genera *Caudatispora, Erythromada* and *Lasiosphaeriella* possess clusters of superficial, obovoid ascomata with variable ascospores. Phylogenetic analyses of 28S large-subunit nrDNA sequences were used to test the monophyly of these genera and provide estimates of their relationships within the *Sordariomycetidae*. *Rimaconus coronatus* is described as a new species from New Zealand; it clusters with the type species, *R. jamaicensis*. *Leptosporella gregaria* is illustrated and a description is provided for this previously published taxon that is the type species and only sequenced representative of the genus. Both of these genera occur in separate, well-supported clades among taxa that form unsupported groups near the *Chaetosphaeriales* and *Helminthosphaeriaceae*. *Lasiosphaeriella* and *Linocarpon* appear to be polyphyletic with species occurring in several clades throughout the subclass. *Caudatispora* and *Erythromada* represented by single specimens and two putative *Duradens* spp. have unclear affinities in the *Sordariomycetidae*.

Key words: *Ascomycota*, *Caudatispora*, *Duradens*, *Erythromada*, *Lasiosphaeriella*, *Leptosporella, Linocarpon,* LSU, systematics.
Taxonomic novelties: *Rimaconus coronatus* Huhndorf & A.N. Mill., sp. nov.

INTRODUCTION

In recent years molecular data have helped to clarify relationships among the many taxa in the *Sordariomycetidae*. A number of taxonomic novelties have been described with sequence data useful in the placement of these new taxa. In our own phylogenetic studies of wood-inhabiting ascomycetes we have found species that consistently cluster around the *Chaetosphaeriales* but without the benefit of strongly supported branches. Some of these taxa share similar morphologies in possessing conical ascomata, carbonised peridia and elongate ascospores, while others possess clusters of superficial, obovoid ascomata with variable ascospores. *Caudatispora biapiculatis*, *Duradens* sp., *Erythromada lanciospora*, *Lasiosphaeriella nitida*, *Leptosporella gregaria*, *Linocarpon appendiculatum,* and *Rimaconus jamaicensis* were included in analyses of the 28S large-subunit (LSU) nrDNA and were consistently found to occur in the *Sordariomycetidae* on unsupported branches outside of the *Chaetosphaeriales* and *Helminthosphaeriaceae* (Huhndorf *et al.* 2004, Miller & Huhndorf 2004, Huhndorf *et al.* 2005, Miller & Huhndorf 2005). Ongoing surveys of wood-inhabiting ascomycetes have uncovered additional taxa with morphologies that suggest affinities to *Duradens*, *Leptosporella,* and *Rimaconus*. Sequence data from these taxa and *Lasiosphaeriella* and *Linocarpon* were assembled to further assess the phylogenetic relationships in this group of *Sordariomycetidae*. A new species of *Rimaconus* is described and illustrated from New Zealand.

Table 1. Taxa sequenced for this study. All specimens are deposited in F.

Taxon	Source	Origin	LSU GenBank Accession No.
Duradens sp. 2	SMH4427	Ecuador	HM171282
Lasiosphaeriella nitida	SMH1290	Puerto Rico	HM171283
Lasiosphaeriella noonae-daniae	SMH2818	Thailand	HM171284
Lasiosphaeriella pseudobombarda I	SMH4365	Ecuador	HM171285
Lasiosphaeriella pseudobombarda II	SMH4370	Ecuador	HM171286
Leptosporella gregaria II	SMH4673	Ecuador	HM171287
Leptosporella gregaria III	SMH4867	Costa Rica	HM171288
Leptosporella gregaria IV	SMH4700	Ecuador	HM171289
Linocarpon-like sp. 1	SMH3782	Puerto Rico	HM171290
Linocarpon-like sp. 2	SMH1600	Puerto Rico	HM171291
Rimaconus coronatus	SMH5212	New Zealand	HM171292
Rimaconus jamaicensis	SMH4782	Ecuador	HM171293

MATERIALS AND METHODS

Taxon sampling

Taxa sequenced in this study are listed in Table 1 with additional collection data provided under the examined specimens for selected taxa. Representatives from families and orders within

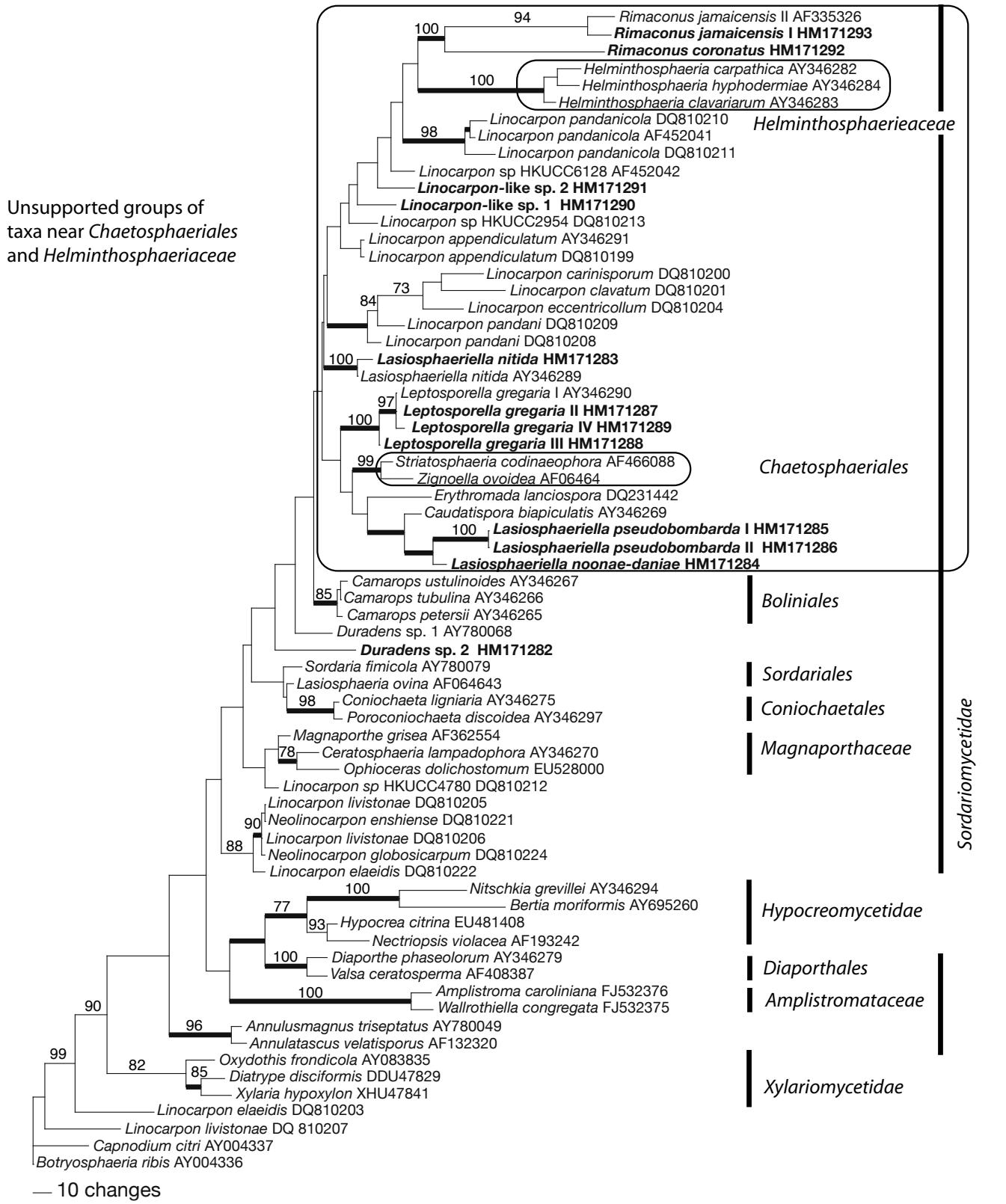

Fig. 1. Phylogeny of *Sordariomycetes.* One of eight most-parsimonious trees generated from a MP analysis of LSU sequence data for 68 taxa (L = 1690.65 steps, CI = 0.431, RI = 0.691, RC = 0.298). Taxa sequenced for this study are in bold. Thickened branches indicate Bayesian posterior probabilities ≥ 95 % while numbers above or below branches refer to MP bootstrap values ≥ 70 %. Two species in the *Dothideomycetes* are outgroups.

the *Sordariomycetes* were included to determine the phylogenetic position of the target taxa. Two members of the *Dothideomycetes* were used as outgroups. All voucher specimens are deposited in the Field Museum Mycology Herbarium (F). Ascomata were mounted in water and replaced with lactophenol containing azure A. Measurements were made and images were captured of material in both mounting fluids using photomacrography, bright field (BF), phase contrast (PH), and differential interference microscopy (DIC). Photographic plates were produced following the methods of Huhndorf & Fernández (1998). Format of the individual figures for the species follow those produced for the pyrenomycetes website (*Pyrenomycetes of the World*: www-s.life.illinois.edu/pyrenos/). The scale bars for the figures are as follows: ascomata bars = 500 µm; ascus bars = 10 µm; ascospore bars = 10 µm.

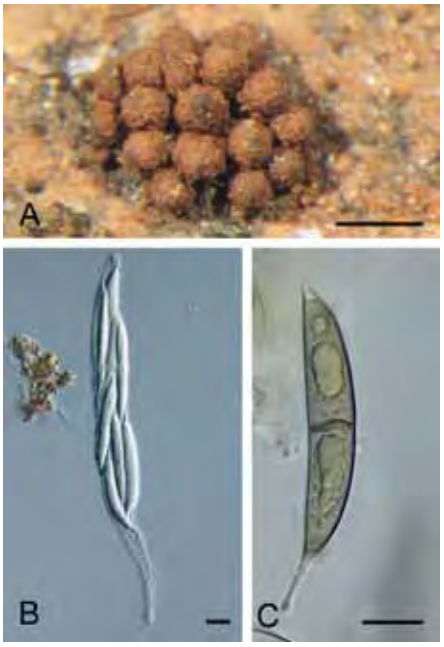

Fig. 2. *Caudatispora biapiculatis* (AY346269; *SMH1873*). A. Ascomata. B. Ascus. C. Ascospore.

Fig. 3. *Erythromada lanciospora* (DQ231442; *SMH1526*). A, B. Ascomata. C. Ascus. D. Ascospore.

Fig. 4. *Lasiosphaeriella nitida* (HM171283; *SMH1290*). A. Ascomata. B. Ascus. C, D. Ascospores.

DNA extraction, PCR amplification and sequencing

Detailed protocols for the extraction, amplification and sequencing of partial LSU are described in Huhndorf *et al.* (2004).

Sequence alignment and phylogenetic analyses

Sequences were assembled and aligned by eye using Sequencher v. 4.7 (Gene Codes Corp., Ann Arbor, Michigan). Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed using PAUP v. 4.0b10 (Swofford 2002). Fifty-nine and 210 bp of the 5' and 3' ends respectively were excluded from all analyses due to missing data in most taxa. Twelve ambiguously aligned regions totaling 340 bp were delimited and excluded from analyses along with two spliceosomal introns (Bhattacharya *et al.* 2000) with lengths of 67 bp and 75 bp. A portion of the phylogenetic signal was recovered from three of the ambiguously aligned regions by recoding them using the program INAASE (Lutzoni *et al.* 2000). The remaining nine ambiguously aligned regions could not be recoded due to their size so they were excluded from all analyses. The remaining unambiguously aligned characters were subjected to a symmetrical stepmatrix to differentially weight nucleotide transformations using STMatrix v. 2.2 (François Lutzoni & Stefan Zoller, Biology Dept., Duke University, Durham, North Carolina), which calculates the costs for changes among character states based on the negative natural logarithm of the percentages of reciprocal changes between any two character states. Unequally weighted MP analyses were performed with 1 000 stepwise random addition heuristic searches, TBR branch-swapping, MULTREES option in effect, zero-length branches collapsed, constant characters excluded and gaps treated as missing. Branch support was estimated by performing 100 bootstrap replicates (Felsenstein 1985) each consisting of 10 stepwise random addition heuristic searches as above. MODELTEST v. 3.7 (Posada & Crandall 1998) determined the best-fit model of evolution for LSU to be the GTR model (Rodríguez *et al.* 1990) with a proportion of invariable sites while the remaining sites were subjected to a gamma distribution shape parameter. ML analyses were performed using the above model with 100 stepwise random addition replicates and TBR branch-swapping with a reconnection limit of twelve. Constant characters were included and ambiguously aligned characters were excluded from the ML analyses. Bayesian analyses were performed using MrBayes v. 3.1 (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) as an additional means of assessing branch support. Constant characters were included, the above model of evolution was implemented, and 100 M generations were sampled every 1000th generation resulting in 100 000 total trees. The Markov chain always achieved stationarity after the first 100 000 generations, so the first 10 000 trees, which extended well beyond the burn-in phase of each analysis, were discarded. Posterior probabilities were determined from a 95 % consensus tree generated using the remaining 90 000 trees. This analysis was repeated twice starting from different random trees to ensure trees from the same tree space were ultimately being sampled during each analysis.

RESULTS

Sequence alignment and phylogenetic analyses

The LSU alignment contained 68 taxa and 1 338 characters of which 1 134 were excluded. Three ambiguously aligned regions were delimited and recoded resulting in 204 parsimony-informative characters. The MP analysis generated eight most-parsimonious trees, which did not differ significantly in topology. One of these most-parsimonious trees is shown in Fig. 1. The ML analysis generated two most likely trees, which did not differ significantly from one another or from the most-parsimonious trees (data not shown).

Species relationships

The LSU phylogeny contains a clade representing the proposed new species of *Rimaconus* supported by both bootstrap support

Fig. 5. *Lasiosphaeriella noonae-daniae* (HM171284; *SMH2818*). A, C. Ascomata. B. Ascus. D. Ascospores.

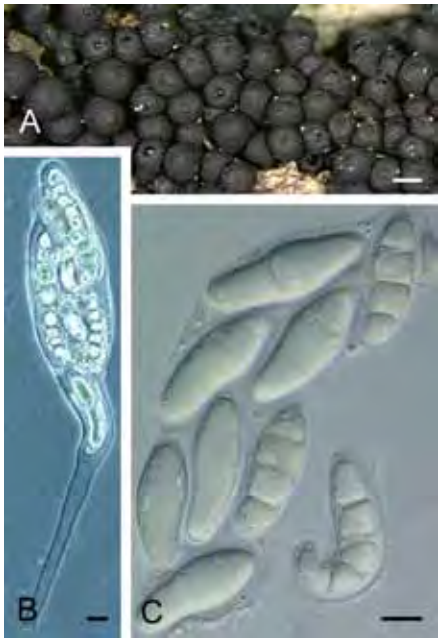

Fig. 6. *Lasiosphaeriella pseudobombarda* (HM171286; *SMH4370*). A. Ascomata. B. Ascus. C. Ascospores.

Fig. 7. *Duradens* sp. 1 (AY780068; *SMH1708*). A, B. Ascomata. C. Ascus. D. Ascospore.

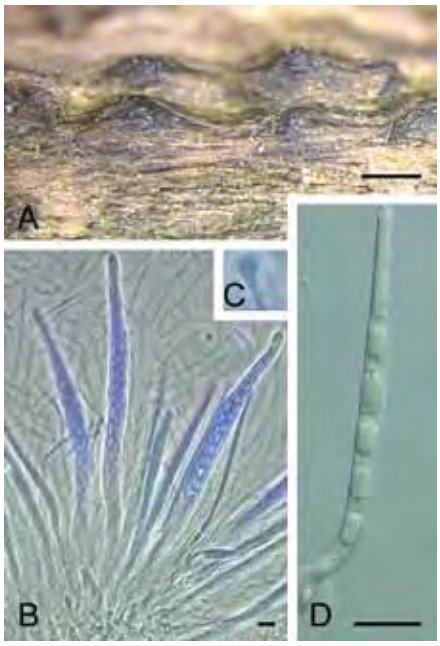

Fig. 8. *Duradens* sp. 2 (HM171282; *SMH4427*). A. Ascomata. B. Asci. C. Ascus ring. D. Ascospore.

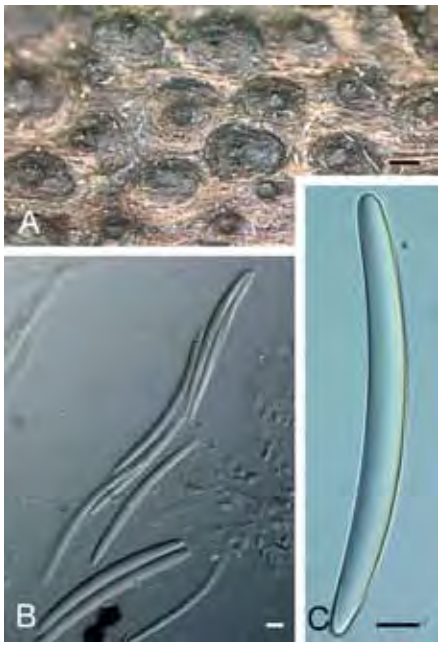

Fig. 9. *Linocarpon*-like sp. 2 (HM171291; *SMH1600*). A. Ascomata. B. Ascus. C. Ascospore.

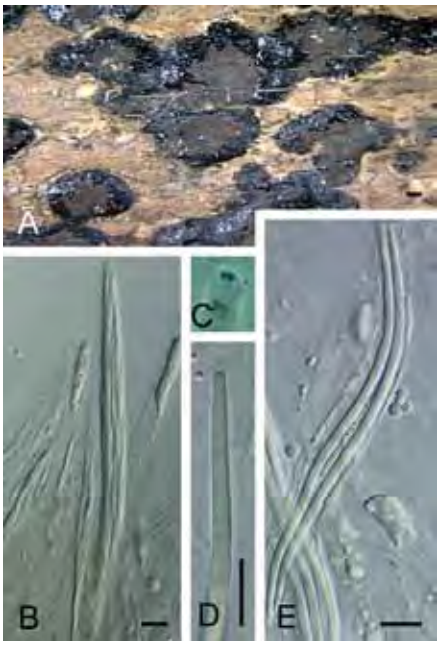

Fig. 10. *Linocarpon*-like sp. 1 (HM171290; *SMH3782*). A. Ascomata. B. Ascus. C. Ascus ring. D. Ascospore appendage. E. Ascospores.

(BS) and significant Bayesian posterior probability (PP). These data reveal a strongly supported clade containing all the collections of *Leptosporella gregaria*. The genus *Lasiosphaeriella* appears to be polyphyletic with the species clustering in two separate clades. The two collections of *Lasiosphaeriella nitida* group together with 100 % BS as do the two collections of *Lasiosphaeriella pseudobombarda*. In these analyses *L. pseudobombarda* groups with *L. noonae-daniae*, *Duradens* sp. 1, *Duradens* sp. 2, *Linocarpon*-like sp. 1, and *Linocarpon*-like sp. 2 occur on single unsupported branches in the *Sordariomycetidae*. The genus *Linocarpon* appears to be polyphyletic with species clustering in multiple separate clades scattered throughout the tree.

TAXONOMY

Images of sequenced taxa are included for comparison of morphological characteristics: *Caudatispora biapiculatis* (Fig. 2), *Erythromada lanciospora* (Fig. 3), *Lasiosphaeriella nitida* (Fig. 4), *L. noonae-daniae* (Fig. 5), *L. pseudobombarda* (Fig. 6), *Duradens* sp. 1 (Fig. 7), *Duradens* sp. 2 (Fig. 8), *Linocarpon*-like sp. 2 (Fig. 9), *Linocarpon*-like sp. 1 (Fig. 10), *Leptosporella gregaria* (Figs 11–15) and *Rimaconus jamaicensis* (Fig. 16). A description of *Leptosporella gregaria* is included here because it was not provided previously (Huhndorf & Fernández 2005).

Leptosporella gregaria Penz. & Sacc., Malpighia 11: 407. 1897. Figs 11–15.

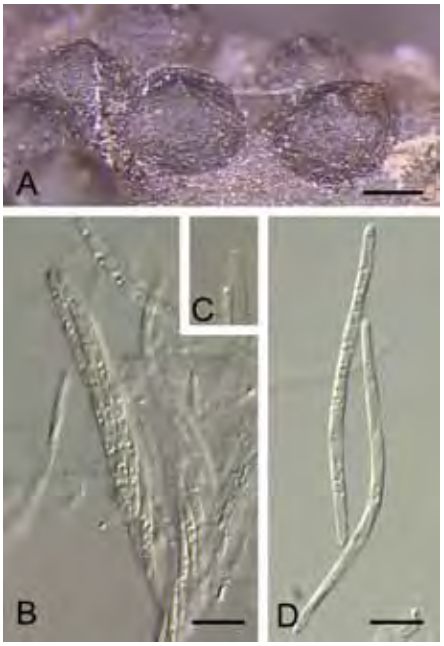

Fig. 11. *Leptosporella gregaria* (holotype; PAD). A. Ascomata. B. Ascus. C. Ascus ring. D. Ascospores.

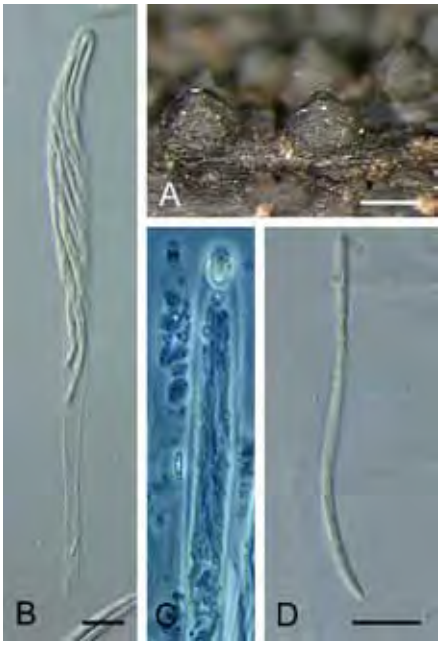

Fig. 12. *Leptosporella gregaria* I (AY346290; *SMH4290*). A. Ascomata. B. Ascus. C. Ascal rings. D. Ascospore.

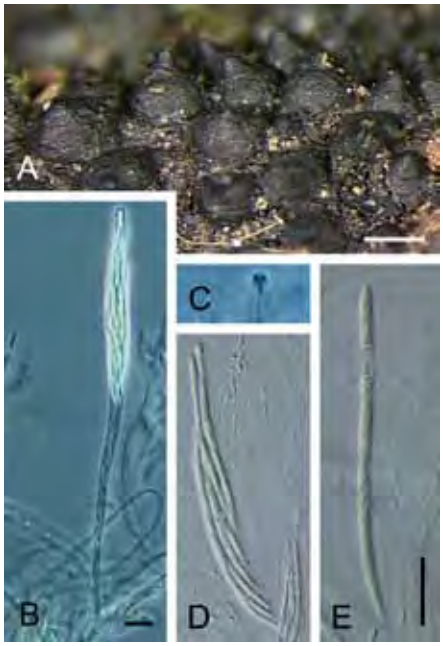

Fig. 13. *Leptosporella gregaria* II (HM171287; *SMH4673*). A. Ascomata. B, D. Asci. C. Ascus ring. E. Ascospore.

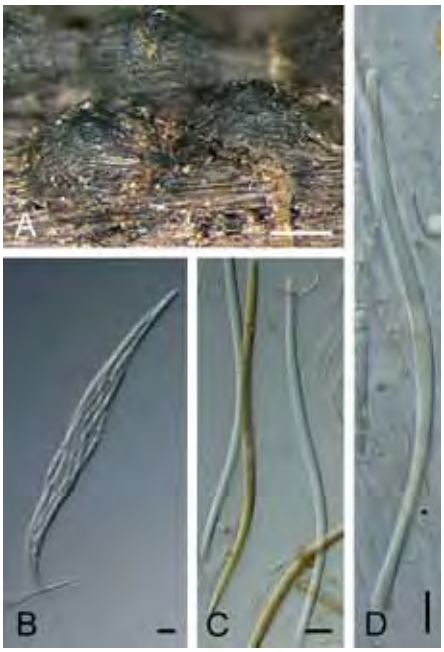

Fig. 14. *Leptosporella gregaria* III (HM171288; *SMH4867*). A. Ascomata. B. Ascus. C, D. Ascospores.

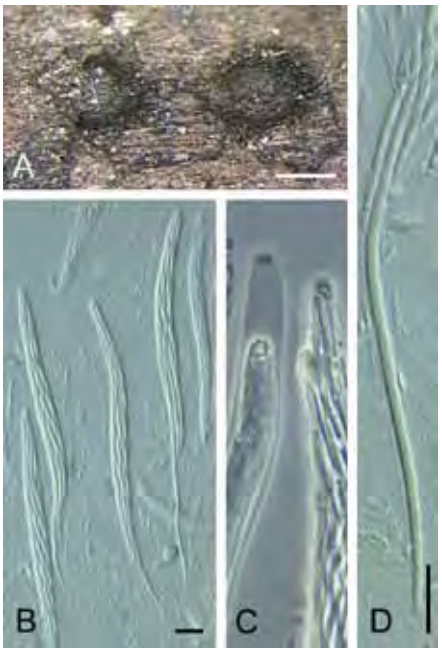

Fig. 15. *Leptosporella gregaria* IV (HM171289; *SMH4700*). A. Ascomata. B. Asci. C. Ascal rings. D. Ascospore.

Fig. 16. *Rimaconus jamaicensis* (HM171293; *SMH4782*). A. Ascomata. B. Ascus. C. Ascal rings. D. Ascospore.

Anamorph: None known.

Ascomata conical, hemispherical to mammiform, papillate, ostiolate, 600–1100 µm diam, 500–800 µm high, separate, gregarious often in large groups, immersed, becoming erumpent with or without fragments of host cells adherent to ascomal wall, surface roughened, dark brown appearing black. *Ascomal wall* in longitudinal section 40–60 µm thick, composed of polygonal, strongly melanised, pseudoparenchymatic cells, often mixed with host cells, very thin at base, mostly composed of fungal hyphae growing in host cells, a wedge of elongate, thinner-walled cells *ca.* 95 µm thick at periphery. *Ascomal apex* acute or rounded, ostiole circular, with indistinct periphyses. *Paraphyses* abundant, persistent, narrow, tapering towards apex, with gelatinous coating, centrum with distinct yellow pigment. *Asci* cylindrical, 90–110 × 8–10 µm, stalked, numerous, basal and lateral, partially lining the peripheral wall of centrum, unitunicate, apex tapered, with refractive ring, with 8 tri- to tetraseriate ascospores. *Ascospores* filiform, mostly 44–60 × 2–3 µm, long-spored collections 85–90 × 2–3 to 107–137 × 2.8–4 µm, curved, hyaline, at times staining yellow from centrum pigments, one-celled, without sheath or appendages.

Habitat: On decorticated wood.

Distribution: Costa Rica, Ecuador, Indonesia.

Specimens examined: **Costa Rica**, Puntarenas, Area de Conservacion Osa, Parque Nacional Corcovado, Sirena Station, Espaveles trail, elev. 5 m, 8.4814 N, 83.595 W, on wood fragment, 17 July 2000, F.A. Fernández SMH4290, F; Alajuela Prov., Alberto Manuel Brenes Biological Reserve, near San Ramón, elev. 1000 m, on branch, 2–5 Dec. 2002, S. M. Huhndorf, F.A. Fernández SMH4867, F. **Ecuador**,

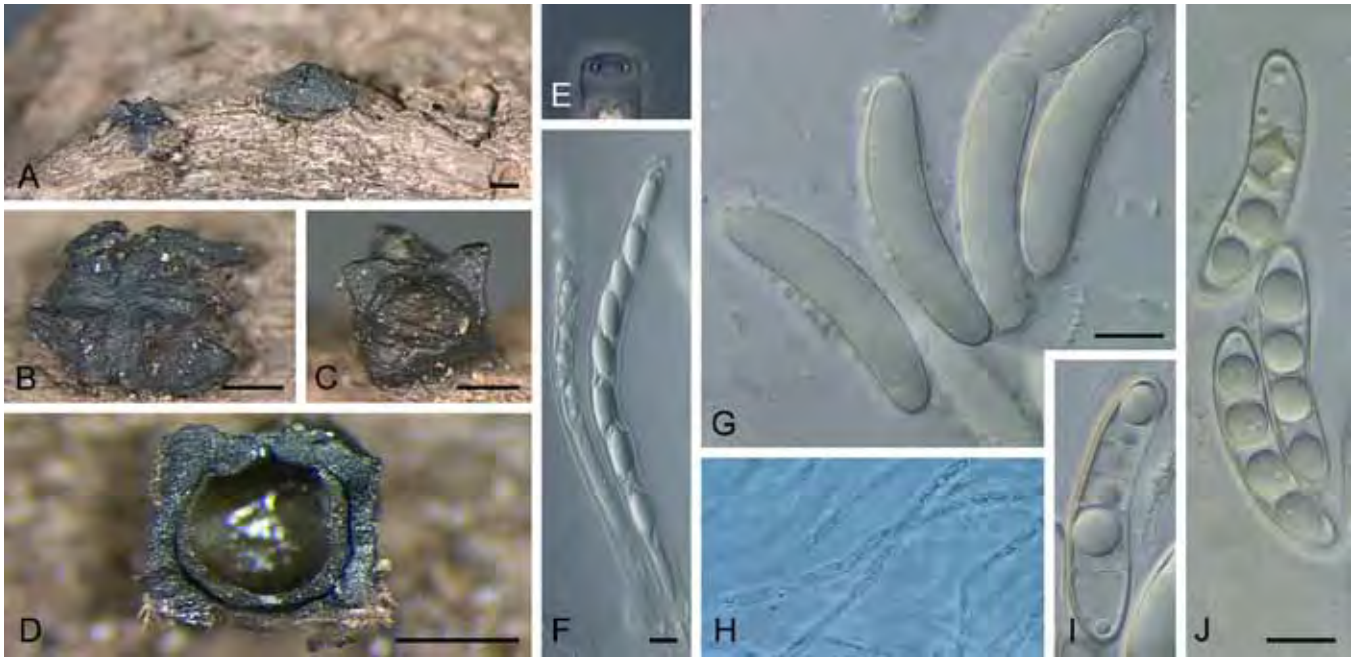

Fig. 17. *Rimaconus coronatus* (HM171292; *SMH5212*). A–D. Ascomata. E. Ascus ring. F. Ascus. G, I, J. Ascospores. H. Paraphyses.

Orellana Prov., Yasuni Biosphere Reserve, Tiputini Biological Station, Guacamayo trail, first 500 m, 0.6361 S, 76.1528 W, on log, 24 Mar. 2002, F. A. Fernández, A. N. Miller SMH4673, F; Matapalo trail, 0.6361 S, 76.1528 W, on palm petiole, 25 Mar. 2002, F. A. Fernández, A. N. Miller SMH4700, F. **Indonesia**, hab. in ligno putri, Tjibodas, 2 Feb. 1897, n. 135, **Holotype** PAD.

Notes: *Leptosporella* was described for two species, *L. gregaria* and *L. sparsa*; *L. gregaria* was selected as the type of the genus in Clements & Shear (1931). Currently 13 species are listed in *Index Fungorum* (www.indexfungorum.org). The type specimen of *L. gregaria* has abundant perithecia in marginal condition. Ascomatal contents are mostly agglutinated and distinct ascospores and asci are not abundant. Recent collections of this species from Costa Rica and Ecuador show unitunicate asci and hyaline scolecosporous ascospores. *Leptosporella sparsa* is probably a species of *Lasiosphaeria* based on the original drawings on the type specimen packet. The type specimen of *L. sparsa* no longer contains any perithecia, therefore, the name should be disregarded.

Rimaconus coronatus Huhndorf & A.N. Mill., **sp. nov**. MycoBank MB518333. Fig. 17.
Anamorph: None known.

Etymology: *coronatus* refers to the crown-shaped ascomatal apex.

Similis *R. jamaicensis* sed ascomata conica vel cylindrica, 900–1 500 µm diametro, 700–1 000 µm alta, apex planus ad depressus, coronatus. Asci cylindrici, pars sporiferi 190–250 × 13–15 µm, stipitati 18.5–51 × 2–5 µm. Ascosporae fusiformes vel cylindricae, 36–42 × 7.5–9 µm, hyalinae, triseptatae usque ad hexaseptatae.

Ascomata conical to applanate when young, becoming hemispherical or conical to cylindrical with coronate projections around apical rim, non-papillate, ostiolate, 900–1 500 µm diam, 700–1 000 µm high, separate to gregarious in small groups, immersed becoming erumpent, with fragments of host cells adherent to ascomal wall when young, surface roughened, dark brown appearing black. *Ascomal wall* in longitudinal section *ca.* 100–130 µm thick, composed of strongly melanised cells, thicker, *ca.* 250–400 µm, with coronate projections around periphery of apex, somewhat thinner at base. *Ascomal apex* flattened to sunken, crater-like, ostiole circular; periphyses not seen. *Paraphyses* 3–4 µm wide, abundant, persistent, narrow, tapering towards apex. *Asci* cylindrical, spore- bearing part 190–250 × 13–15 µm, stalk 36–50 µm long, numerous, basal and lateral, partially lining peripheral wall of centrum, unitunicate, apex tapered, with refractive ring 5 µm wide, with 8 overlapping uniseriate ascospores. *Ascospores* broadly fusiform to short cylindrical, broadly rounded at apex and base, 36–42 × 7.5–9 µm, curved symmetrical, hyaline, smooth, mostly 3-septate, a few up to 6-septate, without constrictions at septa, primary septum median, septa evenly distributed, without sheath or appendages.

Habitat: On decorticated wood.

Distribution: New Zealand.

Specimen examined: **New Zealand**, Auckland, Kawakawa Bay, Morehu Reserve, 36.9708 S, 175.1793 E, on large, decorticated log, 5 June 2008, S. M. Huhndorf, P. R. Johnston SMH5212, **holotype** PDD, **isotype** F.

DISCUSSION

A number of taxa in the *Sordariomycetidae* occur as unsupported, single lineages or appear to have uncertain relationships in their molecular phylogenies often grouping with other taxa in unsupported clades. This does not mean they have entirely unknown affinities since they often consistently cluster together or near certain well-supported taxa. The taxa that consistently cluster outside but near the well-supported clades of *Chaetosphaeriales* and *Helminthosphaeriaceae* are one such group that has a diverse mix of morphological characteristics.

Within this admixture, a few groups of taxa form well-supported clades. *Rimaconus coronatus* occurs in a clade with the type species, *R. jamaicensis.* Both taxa reside on long branches indicating that a significant amount of divergence has occurred between these species. The two species share morphological

similarities such as dark-coloured, strongly melanised ascomata that are erumpent through the woody substrate. *Rimaconus coronatus* differs by forming flaring, crown-shaped extensions of the ascomatal wall. Both species share a wide, flat, refractive ascus ring and hyaline, septate ascospores. However, the ascospores differ in their shape and septation. In *R. jamaicensis* the 7+ septate ascospores are long cylindrical with a distinct bend at the slightly submedian position. In *R. coronatus* the 3+ septate ascospores are shorter, wider, and more evenly curved. The highly supported clade containing these two species occurs as an unsupported sister group to the *Helminthosphaeriaceae*, but that relative placement is unstable.

Multiple specimens of *Leptosporella gregaria* form another well-supported clade within the pectinate topology of taxa clustering with the *Chaetosphaeriales* and *Helminthosphaeriaceae*. The species is distinguished by conical, erumpent ascomata and scolecosporous ascospores. The type specimen provides adequate morphological information to allow identification of fresh specimens. With ascospores measuring 60–67 × 2–3 µm, the type specimen from Indonesia fits in the middle of the range of measurements from the sequenced collections. Among the four specimens with sequence data, the morphology is not entirely uniform. *Leptosporella gregaria* I (*SMH4290*) and *L. gregaria* II (*SMH4673*) have ascomata and ascospores that are somewhat smaller in size (ascospores 37–56 × 2–3 µm) than those of the type specimen; *L. gregaria* IV (*SMH4700*) has smaller ascomata and spores longer than the type specimen (85–90 × 2–3 µm). *Leptosporella gregaria* III (*SMH4867*) has ascomata that are of a size close to the type specimen but the ascospores are almost twice as long (107–137 × 2.8–4 µm). All of them share a distinctive yellow colouration of the centrum that in some collections is often pronounced enough to stain some of the ascospores and asci yellow (Fig. 14). *Leptosporella gregaria* III (*SMH4867*) may represent a distinct species but given the mixture of collections in this overall group, sequences of additional specimens are necessary before another new species is described. In this analysis the clade containing these specimens occurs as an unsupported sister group to the *Chaetosphaeriales* and several other taxa, but their relative placement is not stable.

Other taxa clustering near the *Chaetosphaeriales* and *Helminthosphaeriaceae* possess conical, immersed to erumpent ascomata and scolecosporous ascospores. The numerous species of *Linocarpon* included in this analysis do not form a monophyletic group. Representatives of the type species, *L. pandani*, form a supported group with three other species, while three collections of *L. pandanicola* form the only well-supported clade in the genus. Additionally, several named species of *Linocarpon* occur well outside this group of taxa scattered among other *Sordariomycetidae* as well as outside the subclass. Our own collections of *Linocarpon*-like taxa do not provide any resolution to the question of what indicates relationships within the genus. *Linocarpon*-like sp. 1 (*SMH1600*) differs from the other described *Linocarpon* species in having erumpent ascomata, no clypeus and wide ascospores (Fig. 9). *Linocarpon*-like sp. 2 (*SMH3782*) appears to differ by having ascomata that are not separate but cluster together under a united clypeate covering. The ascomata have separate central ostioles thus precluding its placement in the genus *Palmicola*. Using molecular data their unsupported positions leave unclear the affinities of taxa within *Linocarpon*.

Near the *Chaetosphaeriales* and *Helminthosphaeriaceae* reside a number of taxa that have dense clusters of obovoid ascomata and occur superficially on the substrate. Species of *Lasiosphaeriella* have widely allantoid to ellipsoid ascospores that suggest morphological relatedness (Figs 4–6). However, these species do not form a single clade, but instead separate into two clades with *L. nitida* appearing to be distant from the other two species. In this analysis two additional unsupported taxa basal to *L. noonae-daniae* and *L. pseudobombarda* have clusters of superficial ascomata. *Caudatispora biapiculatis* has roughened ascomata as does *L. noonae-daniae*, but the ascospores have unique apical and basal wall extensions (Figs 2, 5). *Erythromada lanciospora* differs from the other gregarious taxa in having thin, elongate, lanceolate ascospores (Fig. 3). The presence of this scolecosporous ascospore type resembles those found in other species that are prevalent in this unsupported group. Lastly, two collections designated as *Duradens* spp. with morphology suggestive of inclusion in the unsupported group nest outside the group on branches between the *Boliniales* and *Sordariales*. *Duradens* was described as a monotypic genus for a single collection from Guyana (Samuels & Rogerson 1990). *Duradens lignicola* occurs as heavily carbonised, conical, erumpent ascomata on decorticated wood and has long, relatively wide ascospores. The generic description could match either unnamed species as well as the unnamed *Linocarpon*-like sp. 2. Describing these species in *Duradens* would create another polyphyletic genus. Choosing which species in the tree best fits the genus based on *D. lignicola* is problematic.

Where then is the predictability from the morphology in this group? Same-named species occur widely spaced in the tree suggesting difficulty in correctly identifying species and applying names. Beyond the molecular work, we find the same difficulty among our own collections when faced with only morphological data for identification. For the taxa remaining unnamed in this tree, there is no enthusiasm for erecting additional monotypic genera of uncertain affinities based on single collections. We choose to supply the sequences and illustrations in hopes that sister taxa may yet be uncovered that will allow for some confidence in applying names. The stability in classification surrounding the *Chaetosphaeriales* and *Helminthosphaeriaceae* will probably require extensive future sequencing of multiple genes.

ACKNOWLEDGEMENTS

This work was supported in part by NSF PEET Grant (Partnerships for Enhancing Expertise in Taxonomy) DEB-0118695 to SMH and NSF BS&I Grant (Biotic Surveys and Inventory) DEB-0515558 to ANM. The authors are grateful to P. Johnston for funding and fieldwork assistance in New Zealand. Sequences were generated in the Pritzker Laboratory for Molecular Systematics and Evolution at The Field Museum of Natural History.

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available online at www.studiesinmycology.org
doi:10.3114/sim.2011.68.10

Studies in Mycology 68: 211–235. 2011.

A systematic account of the genus *Plagiostoma* (*Gnomoniaceae*, *Diaporthales*) based on morphology, host-associations, and a four-gene phylogeny

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Abstract: Members of the genus *Plagiostoma* inhabit leaves, stems, twigs, and branches of woody and herbaceous plants predominantly in the temperate Northern Hemisphere. An account of all known species of *Plagiostoma* including *Cryptodiaporthe* is presented based on analyses of morphological, cultural, and DNA sequence data. Multigene phylogenetic analyses of DNA sequences from four genes (*β-tubulin*, ITS, *rpb2*, and *tef1-α*) revealed eight previously undescribed phylogenetic species and an association between a clade composed of 11 species of *Plagiostoma* and the host family *Salicaceae*. In this paper these eight new species of *Plagiostoma* are described, four species are redescribed, and four new combinations are proposed. A key to the 25 accepted species of *Plagiostoma* based on host, shape, and size of perithecia, perithecial arrangement in the host, and microscopic characteristics of the asci and ascospores is provided. Disposition of additional names in *Cryptodiaporthe* and *Plagiostoma* is also discussed.

Key words: *Ascomycota*, *Betulaceae*, epitypification, *Fraxinus*, new species, phylogeny, *Salicaceae*, *Sordariomycetidae*.
Taxonomic novelties: *Plagiostoma dilatatum* L.C. Mejía, sp. nov., *Plagiostoma exstocollum* L.C. Mejía, sp. nov., *Plagiostoma imperceptibile* L.C. Mejía, sp. nov., *Plagiostoma oregonense* L.C. Mejía, sp. nov., *Plagiostoma ovalisporum* L.C. Mejía, sp. nov., *Plagiostoma samuelsii* L.C. Mejía, sp. nov., *Plagiostoma versatile* L.C. Mejía & Sogonov, sp. nov., *Plagiostoma yunnanense* L.C. Mejía & Zhu L. Yang, sp. nov., *Plagiostoma apiculatum* (Wallr.) L.C. Mejía, comb. nov., *Plagiostoma convexum* (Preuss) L.C. Mejía, comb. nov., *Plagiostoma populinum* (Fuckel) L.C. Mejía, comb. nov., *Plagiostoma pulchellum* (Sacc. & Briard) L.C. Mejía, comb. nov.

INTRODUCTION

The genus *Plagiostoma* (*Gnomoniaceae, Diaporthales*) includes microscopic fungi that inhabit the leaves, stems, twigs, and branches of woody and herbaceous plants from a range of families including the *Betulaceae, Euphorbiaceae, Geraniaceae, Hippocastanaceae, Oleaceae, Polygonaceae, Salicaceae, Sapindaceae,* and *Staphylaceae* in temperate regions of the Northern Hemisphere (Sogonov *et al.* 2008). Although some species of *Plagiostoma* cause diseases, most do not show symptoms prior to production of perithecia on dead tissues. Described by Fuckel (1870), the morphological concept of *Plagiostoma* remained relatively unchanged (Barr 1978, Monod 1983) until recently. Multigene phylogenetic studies suggest that the genus *Plagiostoma* forms a highly supported monophyletic clade that includes the type species of *Plagiostoma*, *P. euphorbiae,* and the type species of *Cryptodiaporthe*, *C. aesculi,* among others (Mejía *et al.* 2008, Sogonov *et al.* 2008). Sogonov *et al.* (2008) included 13 species in the genus *Plagiostoma,* several of which were previously placed in *Cryptodiaporthe.*

A brief historical account of the major taxonomic treatments of *Plagiostoma* and *Cryptodiaporthe* illustrates the views of these genera through time. Fuckel (1870) proposed the genus *Plagiostoma* for sphaericeaous species characterised by flattened perithecia oriented horizontally having short, lateral, erumpent necks. Fuckel (1870) included the genera *Ceratostoma, Gnomonia*, *Linospora*, *Melanospora,* and *Rhaphidospora* together with *Plagiostoma* in the tribe *Ceratostomeae* of the *Sphaeriacei*. In his original description of *Plagiostoma*, Fuckel (1870) included four species, *P. euphorbiae*, *P. petiolicola*, *P devexum*, and *P. suspecta*. Fuckel's concept of *Plagiostoma* was followed by Höhnel (1917) and von Arx (1951) who, like Fuckel, considered *Plagiostoma* to be relatively closely related to *Gnomonia*, the name on which the *Gnomoniaceae* is based. These authors differentiated *Gnomonia* from *Plagiostoma* mainly by orientation of the perithecial neck. *Gnomonia* was characterised by having central, upright, perithecial necks in contrast to species of *Plagiostoma* with eccentric, laterally oriented, perithecial necks. In her treatment of the order *Diaporthales*, Barr (1978) followed Fuckel's concept of *Plagiostoma* and placed *Gnomonia* and *Plagiostoma* in the same suborder *Gnomoniineae* but in different families, *i.e. Gnomonia* in the *Gnomoniaceae* and *Plagiostoma* in the *Valsaceae*. The *Valsaceae* was defined based on having "beaks oblique or lateral, erumpent separately or converging through stromatic disc" (Barr, 1978 p. 15). Barr (1978) made nine new combinations in *Plagiostoma* expanding the number of species in the genus to 13.

In his monograph of the *Gnomoniaceae*, Monod (1983) accepted most species treated by Barr (1978). However, Monod considered that the typification of *Plagiostoma* as *P. euphorbiae* by Höhnel (1917) was not representative of *Plagiostoma* because the perithecial necks of this species are eccentric rather than lateral as stipulated by Fuckel (1870). Monod (1983) transferred *P. euphorbiae* to the genus *Gnomonia* and re-typified *Plagiostoma* with *P. devexum*. In agreement with Barr (1991) and Sogonov *et al.* (2008) the typification of the genus *Plagiostoma* with *P. euphorbiae* by Höhnel (1917) is accepted here because this typification predates Monod (1983) and is in accordance with Article 10 of the International Code of Botanical Nomenclature (McNeill *et al.* 2006).

Table 1. Isolates with sequences included in the phylogenetic analysis of *Plagiostoma*. Types and epitypes are indicated in bold.

Taxon	Specimen	Culture	Country	Host	Collector	*β-tubulin*	ITS	rpb2	tef1-α
Apiognomonia hystrix	CBS-H 11343	CBS 911.79	Switzerland	*Acer pseudoplatanus*	M. Monod	GU366973	DQ313549	EU219260	GU353957
Apiognomonia veneta	NA	CBS 897.79	Switzerland	*Platanus orientalis*	M. Monod	GU377974	DQ313532	EU219259	GU353958
Plagiostoma aesculi	BPI 748430	CBS 109765	Austria	*Aesculus hippocastaneum*	W. Jaklitsch	GU367021	DQ323530	EU199138	GU354004
	BPI 878950	CBS 126127 (= LCM 447.01)	Germany	*Aesculus hippocastaneum*	L.C. Mejía	GU367019	GU367076	GU367110	GU354002
	BPI 878950	LCM 447b.01	Germany	*Aesculus hippocastaneum*	L.C. Mejía	GU367020	GU367077	GU367111	GU354003
	BPI 840942	CBS 121905	Austria	*Aesculus hippocastaneum*	W. Jaklitsch	GU367022	EU254994	EU219269	GU354005
Plagiostoma amygdalinae	NA	CBS 791.79	Switzerland	*Euphorbia amygdaloides*	M. Monod	GU367030	EU254995	GU367113	GU354012
Plagiostoma apiculatum	BPI 747938	CBS 109775 (= AR 3455)	Austria	*Salix* sp.	W. Jaklitsch	GU367008	DQ323529	EU199141	GU353990
	BPI 878951	LCM 393.01	France	*Salix dasyclados*	L.C. Mejía	GU367010	GU367067	GU367101	GU353992
	BPI 878952	CBS 126126 (= LCM 436.01)	USA: WA	*Salix sitchensis*	L.C. Mejía	GU367009	GU367066	GU367100	GU353991
Plagiostoma barriae	BPI 878954	LCM 601.01	USA: WA	*Acer macrophyllum*	L.C. Mejía	GU366996	GU367054	GU367091	GU353980
Plagiostoma convexum	BPI 843490	CBS 123206	USA: NY	*Salix* sp.	L. Vasilyeva	GU367011	EU255047	-	GU353994
Plagiostoma devexum	BPI 843489	CBS 123201	USA: NY	*Polygonum* sp.	L. Vasilyeva	GU367027	EU255001	EU219258	GU354010
Plagiostoma dilatatum	BPI 878957	CBS 124976 (= LCM 402.02)	France	*Salix irrorata*	L.C. Mejía	GU367013	GU367070	GU367104	GU353996
	BPI 878958	LCM 403.02	France	*Salix caprea*	L.C. Mejía	GU367012	GU367069	GU367103	GU353995
Plagiostoma euphorbiaceum	NA	CBS 816.79	Switzerland	*Euphorbia palustris*	M. Monod	GU367031	EU255003	-	GU354013
Plagiostoma euphorbiae	NA	CBS 340.78	The Netherlands	*Euphorbia palustris*	W. Gams	GU367034	DQ323532	EU219292	GU354016
Plagiostoma exstocollum	BPI 878961	CBS 127662 (= LCM 468.01)	USA: OR	*Corylus californica*	L.C. Mejía	GU366988	GU367046	GU367086	GU353972
	BPI 878959	LCM 422.01	USA: OR	*Corylus californica*	L.C. Mejía	GU366985	GU367043	GU367085	GU353969
Plagiostoma fraxini	BPI 746412	CBS 109498	USA: MD	*Fraxinus pennsylvanica*	S. Redlin	GU367033	AY455810	EU219263	GU354015
Plagiostoma geranii	NA	CBS 824.79	Switzerland	*Geranium sylvaticum*	M. Monod	GU367032	EU255009	EU219273	GU354014
Plagiostoma imperceptibile	BPI 878967	LCM 456.01	USA: CA	*Salix* sp.	L.C. Mejía	GU367002	GU367059	GU367094	GU353984
Plagiostoma oregonense	BPI 878968	CBS 126124 (= LCM 597.01)	USA: OR	*Salix* sp.	L.C. Mejía	GU367016	GU367073	GU367107	GU353999
Plagiostoma ovalisporum	BPI 878969	CBS 124977 (= LCM 458.01)	USA: ID	*Salix* sp.	L.C. Mejía	GU367015	GU367072	GU367106	GU353998
Plagiostoma petiolophilum	BPI 878970	CBS 126123 (= LCM 181.01)	USA: NY	*Acer spicatum*	L.C. Mejía	GU367023	GU367078	GU367112	GU354006
	BPI 863769	AR 3821	USA: NY	Acer sp.	L. Vasilyeva	GU367025	EU255039	EU219257	GU354008
Plagiostoma populinum	NA	CBS 144.57	The Netherlands	*Populus trichocarpa*	B. Gerrits van den Ende	GU367018	GU367075	GU367109	GU354001
	NA	CBS 174.58	The Netherlands	*Populus canadensis*	B. Gerrits van den Ende	GU367017	GU367074	GU367108	GU354000
Plagiostoma pulchellum	BPI 878971	CBS 126653 (= LCM 365.04)	USA: MD	*Salix babylonica*	L.C. Mejía	GU367006	GU367063	GU367098	GU353987
	BPI 878972	LCM 371.02	USA: MD	*Salix babylonica*	L.C. Mejía	GU367007	GU367064	GU367099	GU353988
	BPI 878973	LCM 438.04	USA: WA	*Salix lucida*	L.C. Mejía	GU366004	GU367061	GU367096	GU353985
	BPI 878974	LCM 623.01	Argentina	*Salix humboldtiana*	L.C. Mejía	GU367005	GU367062	GU367097	GU353986
	NA	CBS 170.69	The Netherlands	*Populus balsamifera*	Unknown	-	EU255043	-	GU353989
Plagiostoma rhododendri	NA	CBS 847.79	Switzerland	*Rhododendron hirsutum*	M. Monod	GU367026	EU255044	EU2192578	GU354009
Plagiostoma robergeanum	BPI 843593	CBS 121472	Austria	*Staphylea pinnata*	W. Jaklitsch	GU367029	EU255046	EU219262	GU354011
Plagiostoma salicellum	BPI 843527	CBS 121466 (= AR 3828)	Austria	*Salix alba*	W. Jaklitsch	GU366978	EU254996	EU219278	GU353962
	BPI 878975	CBS 126121 (= LCM 449.01)	Germany	*Salix repens*	L.C. Mejía	GU366977	GU367037	GU367081	GU353961
Plagiostoma samuelsii	BPI 878977	CBS 125668 (= LCM 454.04)	USA: CA	*Alnus tenuifolia*	L.C. Mejía	GU366993	GU367051	GU367089	GU353977
	BPI 878979	LCM 596.01	USA: WA	*Alnus* sp.	L.C. Mejía	GU366994	GU367052	GU367090	GU353978
Plagiostoma versatile	BPI 878980	CBS 124978 (= LCM 594.01)	USA: WA	*Salix scouleriana*	L.C. Mejía	GU366979	GU367038	GU367082	GU393963
	BPI 878981	LCM 595.01	USA: WA	*Salix scouleriana*	L.C. Mejía	GU366980	GU367039	GU367083	GU393964
	BPI 878982	LCM 598.01	USA: OR	*Salix* sp.	L.C. Mejía	GU366981	GU367040	GU367084	GU393965
	BPI 877702	CBS 121251	Canada	*Salix* sp.	M.V. Sogonov	GU366982	EU255059	EU219268	GU393966

Table 1. (Continued).

Taxon	Specimen	Culture	Country	Host	Collector	*β-tubulin*	ITS	rpb2	tef1-α
Plagiostoma yunnanense	BPI 878983	CBS 124979 (= LCM 513.03)	China	*Salix* sp.	L.C. Mejía	GU366975	GU367035	GU367079	GU353959
Plagiostoma yunnanense	BPI 878983	LCM 513.02	China	*Salix* sp.	L.C. Mejía	GU366976	GU367036	GU367080	GU353960

In addition, the character of perithecial neck orientation has been found not to be phylogenetically informative (Sogonov *et al.* 2008).

Cryptodiaporthe was described by Petrak (1921) for species with euvalsoid arrangement of perithecia and, in contrast to *Diaporth*e, lacks a blackened margin in the substratum surrounding the perithecia. In describing *Cryptodiaporthe,* Petrak (1921) designated *C. aesculi* as type and included *C. hystrix* and *C. populina*. Later, Wehmeyer (1933) recircumscribed *Cryptodiaporthe* emphasising the lack of a blackened margin within the substratum and made 17 new combinations in this genus for species previously included in *Diaporthe* expanding the genus to 19 species.

In this study, specimens of *Plagiostoma* were collected primarily from North America but also from South America, Europe, and China. Among these recent collections eight new species were discovered and a number of described species were recollected, cultured, and sequenced. A multigene phylogenetic analysis is provided of 24 of the 25 species of *Plagiostoma* accepted here. Eight new species are described and illustrated, four species are redescribed, and four new combinations are proposed. A key to the 25 accepted species of *Plagiostoma* is provided along with the disposition of additional species names in *Cryptodiaporthe* and *Plagiostoma*.

MATERIAL AND METHODS

Collection of specimens, culture preparation, and morphological observations

Collections were made as listed in Table 1 from the following countries mainly during the spring and summers of 2007 and 2008: Argentina (Tucumán), China (Yunnan), France (Deux-Sèvres Département), Germany (Frankfurt), and the United States of America (California, Maryland, New York, Oregon, Washington). Specimens consisting of overwintered, dead, attached, or fallen twigs and branches with perithecia were placed in paper bags, air-dried, and stored at 8–10 °C in sealed plastic bags for a period of 1 wk to 6 mo before processing. All specimens are deposited in the U.S. National Fungus Collections (BPI).

Observations, measurements, and digital imaging of morphological characters and isolation of cultures were performed using the same equipment and procedures as in Mejía *et al.* (2008). AxioVision v. 4.7.2.0 (Carl Zeiss Image Solutions, Carl Zeiss, New York, NY, USA) was used in conjunction with those methods to measure structures. Fresh specimens were mounted in water for microscopic observations; dried specimens were mounted in 3 % potassium hydroxide. Cultural characteristics were observed on Potato Dextrose Agar (PDA, Difco™, Becton, Dickinson & Co., Sparks, MD, USA) 7 d after plating as described in Mejía *et al.* (2008). Colony diameters were measured twice perpendicularly and averaged and thus are listed as average colony diameter (a.c.d.). Representative cultures of species considered in this study were deposited at the Centraalbureau voor Schimmelcultures (CBS, The Netherlands) as listed in Table 1.

DNA extraction and PCR amplification

DNA extractions were done as described by Mejía *et al.* (2008) using a Fast Prep FP 120 with Lysing Matrix "A" (MP Biomedicals, Solon, OH, USA) for mechanical lysis. Four gene fragments were amplified and sequenced for the phylogenetic analyses: the complete nuclear ribosomal internal transcribed spacer regions 1 and 2 including 5.8 S rDNA (ITS), regions of the RNA polymerase second largest subunit (*rpb2*), beta-tubulin (β-*tubulin*), and translation elongation factor 1-alpha (*tef1*-α) genes. The ITS and *rpb2* genes were amplified and sequenced as described in Mejía *et al.* (2008) in 25 µL reactions with two internal sequencing primers designed specifically for species of *Plagiostoma*: *rpb2* Plag-F (5' CGT CGC TGC ATY ATC TCR CA 3') and *rpb2* Plag-R (5' TGY GAG ATR ATG CAG CGA CG 3'). β-*tubulin* was amplified using primers T1 and T22 and sequenced with the PCR primers and the internal primers T2 and T12 from O'Donnell & Cigelnik (1997). For some isolates it was necessary to amplify the *tef1*-α region in two fragments using the following primer combinations: EF1-728F /EF1-1199R and EF1-983F/ EF1-1567R (Carbone & Kohn 1999, Castlebury, unpubl. data, for primer 1199R 5' GGG AAG TAC CMG TGA TCA TGT 3', Rehner 2001). The *rpb2* gene could not be amplified for *P. convexum, P. euphorbiaceum*, and *P. pulchellum* CBS 170.69. In addition, β-*tubulin* could not be amplified for *P. pulchellum* CBS 170.69. For the purpose of determining taxonomic affinities of species previously described as *Cryptodiaporthe* or *Plagiostoma* but not congeneric with *P. euphorbiae* (type species), a region of the nuclear ribosomal large subunit (LSU) was amplified as described in Castlebury *et al.* (2002).

Phylogenetic analyses

Editing and alignment of DNA sequences were performed as described in Mejía *et al.* (2008). Individual genes were aligned separately and subsequently concatenated into a single alignment. Table 1 includes detailed information about the gene sequences including GenBank numbers. The concatenated sequence alignment includes β-*tubulin* (1584 bp), ITS (625 bp), *rpb2* (1212 bp), and *tef1*-α (1149 bp) for a total of 4570 bp and 45 isolates. The taxa included in this alignment represent 24 of the 25 accepted species of *Plagiostoma* with *Apiognomonia hystrix* and *A. veneta* as outgroup taxa. Outgroup selection was based on the sister relationship of the genus *Apiognomonia* with *Plagiostoma* as inferred by a three-gene phylogeny of the family *Gnomoniaceae* (Sogonov *et al.* 2008). Positions with ambiguous alignment were excluded from the analyses.

The concatenated alignment was partitioned by gene and codon position for β-*tubulin*, *rpb2*, and *tef1*-α using PAUP (Swofford 2002). The gene partitions were analysed for conflict with the partition homogeneity test (PHT) as implemented in PAUP (Swofford 2002) using the following settings: 100 homogeneity replicates, 10 random sequence addition replicates, and MULTREES off. Conflict among gene partitions was assessed by reciprocal bootstrap analyses (Reeb *et al.* 2004) using distance settings for each partition as

determined by Modeltest v. 3.7 (Posada & Crandall 1998) following the Bayesian Information Criterion (BIC).

Genes were first analysed individually and then as a combined alignment using maximum parsimony, Bayesian, and maximum likelihood analyses. Trees and bootstrap support of branches were estimated by MP analysis as in Sogonov *et al.* (2008) with all characters considered unordered with equal weight and an additional analysis with unordered characters weighted as follows: weight = 3 for first and second codon positions and weight = 1 for third codon position. Additionally, trees were estimated using Bayesian analysis with the program MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001) as described in Sogonov *et al.* (2008) with sampling every 500 generations. Model settings for each gene were determined using the program MrModeltest v. 2 (Nylander 2004) and selected based on the Akaike Information Criterion (AIC). The first 50 000 generations were discarded (burn-in period) based on comparison of tree likelihood scores. A 50 % majority rule consensus tree and a consensus phylogram were constructed from the trees saved after the burn-in period. The Bayesian posterior probabilities (PP) of nodes of the consensus trees are presented in Fig. 1. Trees were also estimated by Maximum Likelihood (ML) analysis using the program PAUP (Swofford 2002) as described in Sogonov *et al.* (2008) with Modeltest v. 3.7 (Posada & Crandall 1998) used to estimate the best model for the concatenated alignment. Maximum likelihood bootstrap analysis was not conducted.

RESULTS

Collection of specimens

The following plant species are reported as new hosts for species of *Plagiostoma*: *Alnus tenuifolia, Salix dasyclados*, *S. humboldtiana, S. irrorata, S. lucida*, and *S. sitchensis* (Table 1). *Plagiostoma pulchellum* from Argentina and *P. yunnanense* from southwestern China were collected in regions where no species of *Plagiostoma* had been previously reported.

Phylogenetic analyses

The partition homogeneity test suggested conflict among the four genes (ITS, *rpb2*, *β-tubulin*, and *tef1-α*) sequenced for this study (P = 0.01) with *rpb2 as* the source of this conflict. For combinations of the remaining three genes (ITS, *β-tubulin*, and *tef1-α*), no incongruence among gene trees was detected when all three were analysed (P = 0.09), with P = 0.07 for ITS and *β-tubulin* and P = 0.24 for ITS and *tef1-α*. The following are the likelihood settings estimated for each gene for the reciprocal NJ bootstrap analyses: ITS: Base = equal Nst = 2 TRatio = 2.5434 Rates = equal Pinvar = 0.8337; *rpb2*: Base = equal Nst = 6 Rmat = (1.0000 4.6961 1.0000 1.0000 13.3827) Rates = gamma Shape = 0.2029 Pinvar = 0; *β-tubulin*: Base = (0.2006 0.3249 0.2505) Nst = 2 TRatio = 2.1757 Rates = gamma Shape = 0.5017 Pinvar = 0; and *tef1-α*: Base = (0.1918 0.3110 0.2229) Nst = 2 TRatio = 1.8586 Rates = gamma Shape = 0.6109 Pinvar = 0.

The ITS, *β-tubulin*, and *tef1-α* trees individually resolved terminal clades for most of the species analysed. Trees for each gene are provided - see online Supplementary Information. No single gene analysis resolved all the species of *Plagiostoma* with bootstrap support higher than 70 %. The following numbers of species were resolved by genes with bootstrap > 70 %: ITS = 11, *rpb2* = 9, *β-tubulin* = 12, and *tef1-α* = 11. In general, *rpb2* was not as useful for resolving clades of closely related species as the other three genes. The ITS gene resolved and supported all terminal clades except *P. amygdalinae* and *P. euphorbiaceae* for which the sequences were nearly identical. However, it did not support backbone nodes at levels greater than 70 %. In contrast, bootstrap support greater than 90 % for all backbone nodes containing two or more species was obtained in the *β-tubulin*, *rpb2*, and *tef1-α* gene trees. The topology of the individual gene trees differed only slightly. One topological conflict supported by bootstrap values greater than 70 % was observed between the *β-tubulin* analysis resulting in a clade (97 %) that included all species of *Plagiostoma* on *Salicaceae* and the *rpb2* analysis resulting in a clade (72 %) that included some but not all the species on *Salicaceae* with some species on other hosts.

Phylogenetic trees resulting from the combined four-gene dataset (ITS, *β-tubulin*, *rpb2*, and *tef1-α*) were compared with those resulting from the ITS, *β-tubulin*, *tef1-α* dataset found to be conflict-free by the PHT. Maximum parsimony analyses of the four-gene combination resulted in 114 equally parsimonious trees (length = 1713, CI = 0.689, RI = 0.809) for the unweighted analysis and 42 equally parsimonious trees (length = 2062, CI = 0.689, RI = 0.807) for the weighted analysis. Fifty percent majority rule consensus trees computed for each analysis did not differ in the terminal species clades but higher bootstrap support was obtained for several clades in the weighted analysis. Maximum parsimony analysis of the three-gene combination composed of ITS, *β-tubulin*, and *tef-α* resulted in eight equally parsimonious trees (length = 1275, CI = 0.707, RI = 0.817). The tree topologies obtained by MP analyses of the two alignments did not contradict each other; however, bootstrap support for several nodes increased in analyses of the four-gene combination. Therefore, subsequent analyses were performed on the four-gene combination.

The following models were the best estimates for each gene and were applied during the Bayesian analyses: HKY + I + G for ITS and *tef1*-α, SYM + G for *rpb2*, and HKY + G for β-*tubulin.* The model TrN+G was estimated to be the best for the entire alignment by both hLRT and BIC and those settings were applied to the maximum likelihood analysis: Base = (0.2245 0.2859 0.2454) Nst = 6 Rmat = (1.0000 3.5234 1.0000 1.0000 5.8336) Rates = gamma Shape = 0.2849 Pinvar = 0. Bayesian, ML, MP, and weighted parsimony (WP) analyses of the four-gene alignment all resulted in the same topology. Maximum likelihood analysis of the concatenated alignment of four genes resulted in one tree –lnL score of 13921.12887 and is presented as the inferred phylogeny of *Plagiostoma* (Fig. 1). Bayesian PP and MP bootstraps are shown above and below the branches. This phylogeny of *Plagiostoma* supports the recognition of eight new species, which are described in the taxonomic section of this work. Bayesian PP and MP bootstrap supports greater than 90 % were obtained for all the species of *Plagiostoma* in this multigene phylogeny. *Plagiostoma euphorbiae-verrucosae* is not included in the multigene phylogeny as only the ITS was available for this species. This species was confirmed as belonging in *Plagiostoma* by analysis of ITS sequences (tree not shown).

Evaluation of clades and species

Both Bayesian analysis and MP bootstrapping support a clade containing 11 species that occurs exclusively on hosts of the family *Salicaceae*. All of these species occur on the bark of twigs and branches with one species, *Plagiostoma versatile*, also occurring in the leaf midvein and petioles. Within the species on *Salicaceae*,

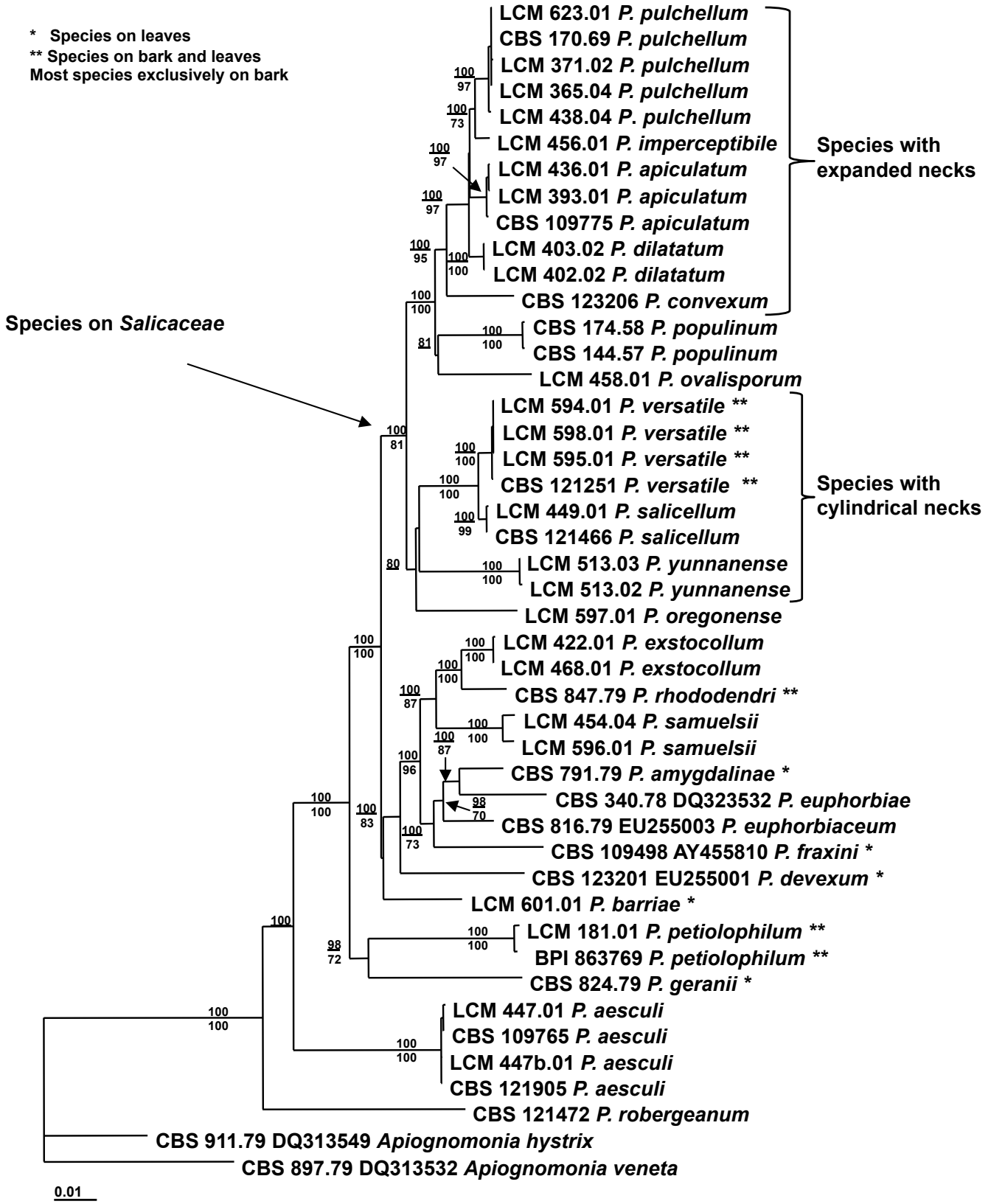

Fig. 1. Maximum likelihood phylogenetic tree (ML score = - lnL 13921.12887) estimated from sequences of the *β-tubulin*, ITS, *rpb2*, and *tef1-α* genes for 24 species of *Plagiostoma* and two species of *Apiognomonia*. Bayesian posterior probabilities greater than 80 % are shown above each branch and maximum parsimony bootstrap values greater than 70 % are shown below branches. Trees for each gene were also generated; see online Supplementary Information.

one clade consists of four closely related species characterised by having an expanded perithecial neck: *P. apiculatum*, *P. dilatatum*, *P. imperceptibile*, and *P. pulchellum*. These species are distinguished by morphological features such as perithecium size, ascospore size and length-to-width (l : w) ratio, and hyphal colour in culture. *Plagiostoma imperceptibile* is characterised by having ascospores longer than 18 µm but with a length-width ratio (l : w) less than five. *Plagiostoma pulchellum* is characterised by having ascospores with a l : w greater than five and by producing rosy-coloured hyphae that become dark green on PDA. *Plagiostoma apiculatum* and *P. dilatatum* are similar to one another but the perithecia and ascospores of *P. dilatatum* are larger than those of *P. apiculatum*. *Plagiostoma convexum* with a moderately expanded perithecial neck is highly supported (> 95 % MP, PP) as basal to these four species.

Plagiostoma ovalisporum and the pathogenic species *P. populinum* are closely related and contained within a larger clade including the five species previously mentioned (100 % MP, PP). The remaining species of *Plagiostoma* on *Salicaceae* form a weakly supported clade sister to the species on *Salicaceae* with expanded necks mentioned above. This clade contains three species having cylindrical, usually elongated, perithecial necks, and elongated ascospores: *P. salicellum*, *P. versatile*, and *P. yunnanense*. The remaining member of this clade, *P. oregonense,* is characterised by short, expanded perithecial necks and short ascospores.

Bayesian PP and MP bootstrapping also support a clade (83 % MP, 100 % PP) of eight species with hosts representing a range of woody and herbaceous plant families. One of the subclades in this group is composed of three species that grow on *Euphorbiaceae*: *P. amygdalinae*, *P. euphorbiaceum,* and *P. euphorbiae,* type species of the genus. Basal to these species is *P. fraxinum* on *Fraxinus pennsylvanica*. A second subclade contains *P. exstocollum* and *P. samuelsii* both on betulaceous hosts and *P. rhododendri* on *Rhododendron*. The rest of the species included in the tree, namely *P. aesculi*, *P. barriae*, *P. geranii*, *P. petiolophilum,* and *P. robergeanum,* are relatively distant from one another and the species previously mentioned. *Plagiostoma robergeanum,* a species that grows on *Staphylea (Staphyleaceae)* in Europe*,* was basal to the other species of *Plagiostoma*.

Specimens of *P. pulchellum* were collected in Europe, North America (USA), and South America (Argentina). This species is recognised as the most widely distributed species of *Plagiostoma* included in this study and is presented here as the first report of *Gnomoniaceae* for South America. *Plagiostoma yunnanense* is the first report of *Plagiostoma* for China.

DISCUSSION

Due to the morphological diversity in species of *Plagiostoma*, as illustrated in Figs 2–6, no single morphological character is unique or diagnostic for this genus. The following morphological characters differentiate *Plagiostoma* from other genera of the *Gnomoniaceae* as defined by Sogonov *et al.* (2008, table 2). Unlike *Gnomonia,* species of *Plagiostoma* have perithecia that often collapse from the base when dry as illustrated in Sogonov et al. (2008, fig. 43 B–C). In *Plagiostoma* the neck length is short to long about equal or less than the diameter of perithecia, while in *Ophiognomonia* the perithecial neck length is usually very long, often pointed, and 2.5–5 times the perithecial diameter. Species of *Ophiognomonia* occur only on leaves while those of *Plagiostoma* are found on leaves as well as woody tissues. Except for *P. rhododendri,* the ascospores of *Plagiostoma* are not broader at the upper part as in *Gnomoniopsis.* Ascospores of *Plagiostoma* are never cylindrical or femuroid as in *Cryptosporella*. Species of *Plagiostoma* with ellipsoid, aseptate ascospores similar to those of *C. hypodermia* do not have a valsoid arrangement of perithecia as do species of *Cryptosporella*.

Species of *Plagiostoma,* except for *P. rhododendri*, are not apiosporous, differentiating them from species of *Apiognomonia* except *A. hystrix*, which possesses flattened perithecial necks. Species of *Pleuroceras* have elongated ascospores that are quite distinct from those of *Plagiostoma*. The type and only species of *Ditopella, D. ditopa,* is characterised by having polysporic asci. *Phragmoporthe conformis,* a species closely related to *Ditopella ditopa,* is characterised by phragmosporic ascospores, a character not present in *Plagiostoma*. The perithecia of *Amphiporthe hranicensis*, the type species of *Amphiporthe,* are grouped near the base of the entostroma and, thus, are different from those found in *Plagiostoma*. In addition, *Amphiporthe hranicensis* produces perithecia in clusters of up to 20, with perithecial necks protruding as a group from the host periderm and surrounded by gray stromatic tissue.

Perithecial neck characters and ascospore morphology are the most important characters for differentiating *Plagiostoma* from other genera in the *Gnomoniaceae*. Host identity, geographic locality, and presence or absence of stroma are secondary characters for the identification of species. For example, the presence of white stromatic tissues surrounding the emerging perithecial necks is diagnostic in species such as *P. aesculi*, *P. salicellum*, and *P. samuelsii*. Within *Plagiostoma* perithecial neck shape ranges from very short, cylindrical to expanded and thick or thin, cylindrical and elongated with various shapes in the opening area, *e.g.* conic, flared, or rounded. In one species, *P. versatile*, the perithecial neck can be both very short when on twigs or elongated when on a leaf midvein suggesting that this structure varies with substrate. Four species, *P. apiculatum, P. convexum*, *P. dilatatum*, and *P. imperceptibile,* are characterised by having an apically expanded perithecial neck. The expanded neck was noticed by Wallroth (1833, as *coronatum dilatatis*) and Butin (1958, as cushion- or pad-like structure) but neither of these authors used this character to differentiate species. This structure may be involved in rupture of host periderm and release of the ascospores.

The asci of *Plagiostoma* are clavate, obclavate, ovoidal, cylindrical, or cylindric-fusoid, generally with a short stalk but with a long stalk in *P. imperceptibile.* Ascospores of *Plagiostoma* are ellipsoid, ellipsoid-fusoid, oblong-ellipsoid, or ovoid usually with one median septum, although three species, *P. euphorbiae-verrucosae*, *P. fraxini*, and *P. ovalisporum,* have non-septate ascospores and one species, *P. rhododendri*, is apiosporous. Ascospores vary in size from short, 7.7–13.8 × 2.2–6.6 µm in *P. fraxini,* to relatively long, 18–27 × 3–4 µm in *P. versatile* and *P. yunnanense*. Most species lack appendages although *P. salicellum* has short, thick, evanescent appendages and *P. devexum* and *P. samuelsii* may have long, thin appendages. Morphological characters that are phylogenetically informative for subclades of *Plagiostoma* include the expanded neck characteristic of species with broadly ellipsoid ascospores versus the cylindrical neck characteristic of species with narrowly ellipsoidal ascospores.

In traditional classification schemes of the *Diaporthales*, *Cryptodiaporthe* and *Plagiostoma* were considered distinct and not closely related genera, each with a specific morphology and arrangement of perithecia (Barr 1978, Kobayashi 1970, Monod 1983). Species of *Plagiostoma* were characterised by the lack of a stroma and production of a single perithecium, primarily on leaves. Species of *Cryptodiaporthe* were characterised by production of a rudimentary stroma and grouped perithecia, primarily in the bark of their host branches. The differences between *Cryptodiaporthe* and *Plagiostoma* have been emphasised such that some authors placed them in different families or subfamilies (Barr 1978, Wehmeyer 1975).

Monod's (1983) concept of *Plagiostoma* differed significantly from the concept presented here. Of the 13 species treated by Monod (1983) as *Plagiostoma*, only *Plagiostoma devexum* is accepted here in that genus. Of the 13 species of *Plagiostoma* accepted by Sogonov *et al.* (2008), only *P. euphorbiae* and *P. devexum* were originally described as *Plagiostoma* with *Plagiostoma barriae* newly described in that work. *Plagiostoma aesculi* and *P. salicellum* were previously regarded by Wehmeyer (1933) as *Cryptodiaporthe*. Four

additional species of *Cryptodiaporthe* are here formally combined in *Plagiostoma*, namely *P. apiculatum, P. convexum, P. populinum*, and *P. pulchellum.* The recognition of these four species formerly classified as *Cryptodiaporthe salicina* broadens the range of morphological and ecological traits of the genus *Plagiostoma*. The pathogenic species, *P. apiculatum*, *P. fraxini*, and *P. populinum,* contrasts with the concept of *Plagiostoma* as primarily saprobic.

The economically important species of *Plagiostoma* are pathogens that cause cankers on willows and poplars. *Plagiostoma apiculatum* (synonym *Cryptodiaporthe salicella*) is here determined to be the correct name for the fungus causing a canker disease of willow (Sinclair & Lyon 2005). This species, referred to by the anamorph *Diplodina microsperma,* has been reported as the most abundant endophyte in healthy twigs of *Salix fragilis* in England (Petrini & Fisher 1990) and is thus an important component of the host microbiota. Similarly, the closely related species *P. dilatatum, P. imperceptibile,* and *P. pulchellum* form a black halo or spot on the host surface, a feature that may be associated with the early stages of canker development. Whether or not these species are primarily pathogenic or establish an asymptomatic infection that later develops into cankers needs to be determined. These species form a highly supported monophyletic group (Fig. 1) characterised by having an expanded perithecial neck and broad ellipsoid to renoid ascospores. This group of species is part of a larger, highly supported clade that also includes *P. convexum*, *P. ovalisporum,* and *P. populinum* (synonym *Cryptodiaporthe populea*), the pathogen causing a canker of poplars. *Plagiostoma fraxini* causes anthracnose on ash (*Fraxinus pennsylvanica*) and fringetree (*Chionanthus retusis*) (Gregory *et al.* 2004, Sinclair & Lyon 2005), and is sister to the clade containing three species on *Euphorbiaceae.*

Species of *Plagiostoma* occur on a broad range of host plant families within the Eudicots, although most species are associated with Rosids. This study shows an association between a clade composed of 11 species of *Plagiostoma* and the host family *Salicaceae* (Fig. 1) especially on the genus *Salix*. Most of the species of *Plagiostoma* on *Salix* have expanded necks. These findings agree with those for other genera within the *Gnomoniaceae* that are associated primarily with specific host genera in the *Betulaceae* such as *Cryptosporella* on *Alnus* and *Betula* (Mejía *et al*. 2008) and *Gnomonia* on the *Coryloideae* (Sogonov *et al.* 2008).

TAXONOMY

KEY TO SPECIES OF *PLAGIOSTOMA*

1. Ascospores non-septate 2
1'. Ascospores 1-septate 4

2. Ascospores ovoid, (12–)14–16(–17) × 7–8(–9) µm. On twigs of *Salix* sp., in North America (USA: ID) ..... *P. ovalisporum*
2'. Ascospores ellipsoid-fusoid. Not on *Salix,* in Europe and North America 3

3. Ascospores 20–25.5 × 5.3–6 µm *fide* Monod (1983), with pointed ends. On *Euphorbia,* in Europe ..... *P. euphorbiae-verrucosae*
3'. Ascospores (7.7–)8.6–12.7(–13.8) × (2.2)2.8–5.9(–6.6) µm *fide* Redlin & Stack (1988). On *Chionanthus* and *Fraxinus* (*Oleaceae*), in Canada and USA ..... *P. fraxini*

4. On *Salicaceae* 5
4'. On hosts other than the *Salicaceae* 14

5. Perithecia neck cylindric. On woody substrates except *P. versatile,* which occurs on both leafy and woody substrates 6
5'. Perithecial neck dilated *i.e.* with an expanded or thickened area that appears disk-like when seen from above, like a thick collar in section, usually appearing with a black halo or black spot in host surface where perithecial necks protrude. On woody substrates 10

6. Perithecial neck surrounded by a whitish stroma. On *Salix,* in Europe ..... *P. salicellum*
6'. Perithecial neck without a whitish stroma. On *Salix* or *Populus,* in Europe and elsewhere 7

7. On twigs and branches of *Populus,* in Europe and North America (USA). Ascospores 14–16 × 6–9 µm *fide* Butin (1958) ..... *P. populinum*
7'. On twigs and branches of *Salix,* in China, Europe, and North America. Ascospores greater than 16 µm long 8

8. Ascospores ellipsoid-fusoid, constricted, curved, tapering to acute ends, (16–)18–20 (–22) × 4–5 µm. In Europe and North America (USA: NY) ..... *P. convexum*
8'. Ascospores ellipsoid-elongated, slightly constricted, straight to slightly curved, rounded ends, generally longer than 20 µm. In China or North America 9

9. Perithecial neck slightly twisted in upper half, of constant length. Ascospores (19–)23–26(–27) × 3–4 µm. On *Salix* sp., in China (Yunnan) ..... *P. yunnanense*
9'. Perithecial neck straight, of variable length, very short in twigs, longer in leaves. Ascospores (18–)20–23(–25) × 3–4 µm. On *Salix* spp., in North America (Pacific Northwest region). ..... *P. versatile*

10. Ascospores ellipsoid to broadly ellipsoid, constricted, tapering to narrowly rounded ends, (16–)17–19(–22) × (4–)6(–7) µm. On *Salix*, in North America (USA: OR) ..... *P. oregonense*
10'. Ascospores oblong-ellipsoid to renoid, not or slightly constricted, rounded ends, size different than above. On *Populus* and *Salix*, in North America and elsewhere 11

11. Ascospores usually straight, sometimes slightly curved, l : w > 5, (17–)18–22(–27) × (5–)6–7(–7.5) µm. On *Populus* and *Salix*, in Europe, North and South America (Argentina) ..... *P. pulchellum*
11'. Ascospores slightly curved, l : w < 5. On *Salix* spp., in Europe and North America 12

12. Asci ovoid elongated, with long, usually persistent stalk. Ascospores (18–)19–20(–21) × (5–)6–7(–8) µm, l : w (2.5–)2.9–3.1(–3.8). On *Salix* sp., in North America (USA: CA) ..... *P. imperceptibile*
12'. Asci cylindric, often with long but not persistent stalk. Ascospores averaging < 18 µm long. In Europe and North America 13

13. Ascospores (12–)13–15(–22) × 4–5(–7) µm, mean = 15 × 5 µm, l : w (2.6–)3.0–3.3(–3.8). On *Salix*, in Europe (France) ..... *P. dilatatum*
13'. Ascospores (12–)16–18.5(–21) × (3–)5–6(–7) µm, mean = 17 × 6 µm, l : w (2.4–)2.9–3.2(–4.0). On *Salix*, in Europe and North America ..... *P. apiculatum*

14. On hosts in the *Euphorbiaceae* 15
14'. On hosts other than *Euphorbiaceae* 17

15. On leaves of *Euphorbiaceae*, specifically *Euphorbia amygdaloides* and *E. stepposa*. Ascospores 13–15.5 × 2.3–3 µm *fide* Monod (1983 as *Gnomonia amygdalinae*), with a thin appendage at each end ..... *P. amygdalinae*
15'. On twigs, branches, or stems of the *Euphorbiaceae*. Ascospores without appendages 16

16. Perithecial neck less than 100 µm. Ascospores (12–)13–13.5(–15.5) × (3–)3.5(–4) µm *fide* Sogonov *et al.* (2008) ..... *P. euphorbiae*
16'. Perithecial neck 100–150 µm. Ascospores 14–17.5 × 3.5–4.5 µm *fide* Monod (1983 as *Gnomonia euphorbiacea*) ..... *P. euphorbiaceum*

17. On *Acer* 18
17'. On hosts other than *Acer* 19

18. On leaves, twigs, and branches of *Acer* spp., in the Pacific Northwest region of USA. Ascospores (11.5–)14–15.5(–17.5) × (2.5–)3.5–4(–4.5) µm *fide* Sogonov *et al.* (2008) ..... *P. barriae*
18'. On leaves, twigs, and branches of *Acer saccharum* and *A. spicatum*, in eastern USA and Canada. Ascospores 7–12 × 1–2.5 µm *fide* Barr (1978) ..... *P. petiolophilum*

19. Ascospores with thin, deliquescent appendages 20
19'. Ascospores without appendages 21

20. Necks eccentric, stout, cone-shaped, surrounded by a whitish stroma. Ascospores (10–)11–12(–19) × 3–4 µm. On *Alnus* spp., in the Pacific Northwest region of USA ..... *P. samuelsii*
20'. Necks marginal, cylindrical, without whitish stroma. Ascospores 8–10 × 2–3 µm *fide* Monod (1983). On *Persicaria* and *Polygonum,* rarely on *Rumex* and *Vitis*, in Europe and USA (NY) ..... *P. devexum*

21. Ascospore upper cell rounded, basal cell short-conic, 13–16 × 4–5 µm/12–16 × 5–7 µm *fide* Monod 1983 & Remler 1979 as *Apiognomonia rhododendri*. In pedicels and branches of *Rhododendron* spp., in Europe ..... *P. rhododendri*
21'. Ascospores not as above 22

22. In dead stems of herbaceous plants, specifically *Geranium* spp., in Europe. Ascospores 13–18 × 1.8–2.5 µm *fide* Monod (1983) ..... *P. geranii*
22'. In twigs and branches of woody plants, in Europe or North America 23

23. Perithecia in groups, with necks closely appressed as a mass emerging together or in a row, surrounded by a white stroma. On *Aesculus hippocastanum,* in Europe ..... *P. aesculi*
23'. Perithecia in groups or solitary, with necks emerging together or not, surrounded or not by a brownish stroma. On hosts other than *Aesculus hippocastanum,* in Europe or North America 24

24. Stroma brownish, covering perithecia but not surrounding necks. Perithecia arranged in groups, with necks emerging together but oriented in different directions where they protrude through host epidermis. On *Corylus californica,* in the Pacific Northwest region of USA ..... *P. exstocollum*
24'. Stroma absent. Perithecia solitary or in groups with convergent, protruding necks. On *Staphylea*, in Europe ..... *P. robergeanum*

DESCRIPTIONS

Plagiostoma Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 118. 1870.

Lectotype designated by Höhnel (1917): *Plagiostoma euphorbiae* (Fuckel) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 118. 1870.

= *Cryptodiaporthe* Petr., Ann. Mycol. 19: 118. 1921. Lectotype designated by Clements and Shear (1931): *Cryptodiaporthe aesculi* (Fuckel) Petr., now *Plagiostoma aesculi* (Fuckel) Sogonov, Stud. Mycol. 62: 69. 2008.

= *Rostrocoronophora* Munk, Dansk Bot. Arkiv 15: 98. 1953. Type: *R. geranii* (Hollós) Munk, now *Plagiostoma geranii* (Hollós) Sogonov, Stud. Mycol. 62: 72. 2008.

Anamorph: *Diplodina* Westend., Bull. Acad. Roy. Sci. Belgique, sér. 2, 2: 562. 1857.

Anamorph type species: *Diplodina salicis* Westend., *Bull. Acad. R. Sci. Belg.*, Cl. Sci., sér. 2 **12**(7) (1857), now recognised as *Diplodina microsperma* (Johnst.) B. Sutton, Mycol. Pap. 141: 69. 1977 *fide* Sutton (1980).

Perithecia produced in dead, fallen or still attached host organs, immersed in bark of stems, branches, and twigs, in midvein or petiole of leaves (*P. fraxini* on leaf lamina), on stalks of herbaceous plants, and on peduncles (*P. rhododendri*). Most species initially appearing as conic-shaped or rounded elevations, usually 0.2–0.5 mm high × 1–2 mm diam, produced where a single perithecium or group of perithecia push up host surface from below. Perithecial necks protrude through epidermis or periderm making a small hole or slit, with perithecia partially or completely exposed by peeling host periderm. In bark, perithecia arranged in groups or solitary, scattered, numerous; in leaves, perithecia discrete, but growing close together. *Stroma* scanty, flocculose, gray, brownish, cream, yellowish white, or whitish. *Perithecia* black, globose, slightly flattened or suboblate, usually collapsed from base when dry, with or without stromatic tissue surrounding neck. *Neck* central to marginal, mostly cylindrical, also flattened, short and stout, upright, straight or contorted, or slanted and straight; 30–150 µm diam not including expanded area, with or without a disk-like expansion, up to 450 µm diam; apex rounded, acute, flared, cupulate, papillate, or conic, black, brown, yellow or hyaline, with or without furrows. *Asci* clavate, obclavate, ovoidal to cylindrical and cylindric-fusoid, usually with a short stalk, with a long stalk in *P. imperceptibile*, with a conspicuous apical ring that may appear single and thick or as two refractive bodies, eight ascospores arranged obliquely parallel, biseriate, multiseriate, or twisted. *Ascospores* ellipsoid, ellipsoid-fusoid, oblong-ellipsoid, ovoid, hyaline, non- or 1-septate, constricted or not at median to submedian septum, apiosporous in *P. rhododendri*, often with four or more rounded guttules, or appearing granulated, with or without an appendage at each end. Cultures of *Plagiostoma* generally grow moderately (4 cm) to fast (5–6 cm) diam after 7 d on PDA, velvety, granular, with concentric halo, with scant aerial mycelium, translucent, white, pale to very dark gray, hazel, dark green, olive or with various dark yellow to orange pigmentation, margins fringed, stringed, or root-like.

Species of *Plagiostoma*

Plagiostoma aesculi (Fuckel) Sogonov, Stud. Mycol. 62: 69. 2008.

Basionym: *Cryptospora aesculi* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 193. 1870.

≡ *Cryptosporella aesculi* (Fuckel) Sacc., Michelia 1: 30. 1877.

[≡ *Diaporthe aesculi* (Fuckel) Höhn., Ann. Mycol. 16: 116. 1918, nom. illeg. non Cooke & Harkn. 1881]

≡ *Cryptodiaporthe aesculi* (Fuckel) Petr., Ann. Mycol. 19:119. 1921.

Note: Sogonov *et al.* (2008) provided a description and illustrations of this species. Cultures are illustrated here in Fig. 7A–B.

Specimen examined: **Germany**, Langen, on branches of *Aesculus hippocastaneum*, L.C. Mejía, BPI 878950, culture LCM 447.01 = CBS 126127.

Plagiostoma amygdalinae (Fuckel) Sogonov, Stud. Mycol. 62: 70. 2008.

Basionym: *Gnomonia amygdalinae* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 121. 1870.

≡ *Gnomoniella amygdalinae* (Fuckel) Sacc., Syll. Fung. 1: 418. 1882.

= *Gnomoniella amygdalinae* f. *euphorbiae-stepposae* Sandu, Stud. Cercet. Biol., Bot. 18: 18. 1966 *fide* Monod (1983).

Note: Monod (1983) provided a detailed description of this species as *Gnomonia amygdalinae*. Although ITS sequences of *P. amygdalinae* (Monod 207 = CBS 791.79) and *P. euphorbiaceum* (MS196 = CBS 121241, Monod 465 = CBS 816.79) suggest that these taxa are the same, the multigene phylogeny obtained here reveals that *P. amygdalinae* and *P. euphorbiaceum* are distinct species. *Plagiostoma amygdalinae* occurs on leaves and has a longer and thinner perithecial neck, shorter asci, thinner apical ring, and ascospores not constricted at septum and thinner than *P. euphorbiaceum* that occurs on twigs, stems, and branches (also see Monod 1983).

Plagiostoma apiculatum (Wallr.) L.C. Mejía, **comb. nov.** MycoBank MB515689. Figs 2A–J, 7C–F

Basionym: *Sphaeria apiculata* Wallr., Fl. Crypt. Germ. 2: 778. 1833.

≡ *Metasphaeria apiculata* (Wallr.) Sacc., Syll. Fung. 2: 166. 1883.

≡ *Gnomonia apiculata* (Wallr.) G. Winter, Rabenh., Kryptog.- Fl., ed. 2, vol. 1(2): 589. 1887.

≡ *Diaporthe spina* Fuckel var. *apiculata* (Wallr.) Rehm, Ann. Mycol. 7: 404. 1909.

≡ *Cryptodiaporthe apiculata* (Wallr.) Petr., Ann. Mycol. 19: 177. 1921.

Anamorph: *Diplodina microsperma* (Johnst.) B. Sutton, Mycol. Pap. 141: 69. 1977.

Perithecia immersed in bark, solitary, scattered, appearing initially as slight punctiform elevations of periderm surrounded by a black halo with tip of neck protruding through slit, usually with three short radiating slits, halo paler in some collections, later becoming completely black, globose, (223–)252–364(–440) µm high × (349–)370–476(–477) µm diam (mean = 314 × 429 µm, SD 59, 77, n = 8), each with one neck. *Neck* central to eccentric, straight to oblique, with a pale brown papilla, with an expanded area that appears disk-like, sometimes evident only as a thick neck, initially below epidermis, becoming exposed, producing a black halo at surface, (115–)159–256(–351) µm long (mean = 208, SD 78, n = 8), expanded area (187–)224–340(–389) µm diam (mean = 284, SD 74, n = 8), (62.5–)81–128(–134) µm diam at apex (mean = 104, SD 29, n = 7). *Asci* cylindrical, (45–)51–80(–86) × 10–16(–18) µm (mean = 68 × 13, SD 15, 4, n = 19), apical ring 2.5–5.0 µm diam, variable in shape *e.g.* elongated as two bodies or hexagonal, with eight ascospores arranged biseriate to multiseriate. *Ascospores* oblong-ellipsoid, slightly tapering to rounded ends, straight to slightly curved, one median to submedian septum, not constricted, (12–)16–18.5(–21) × (3–)5–6(–7) µm (mean = 16.5 × 5.5, SD 2.5, 1.0, n = 106), l : w (2.4–)2.9–3.2(–4) (mean = 3.0, SD 0.3, n = 106), with granular cytoplasm.

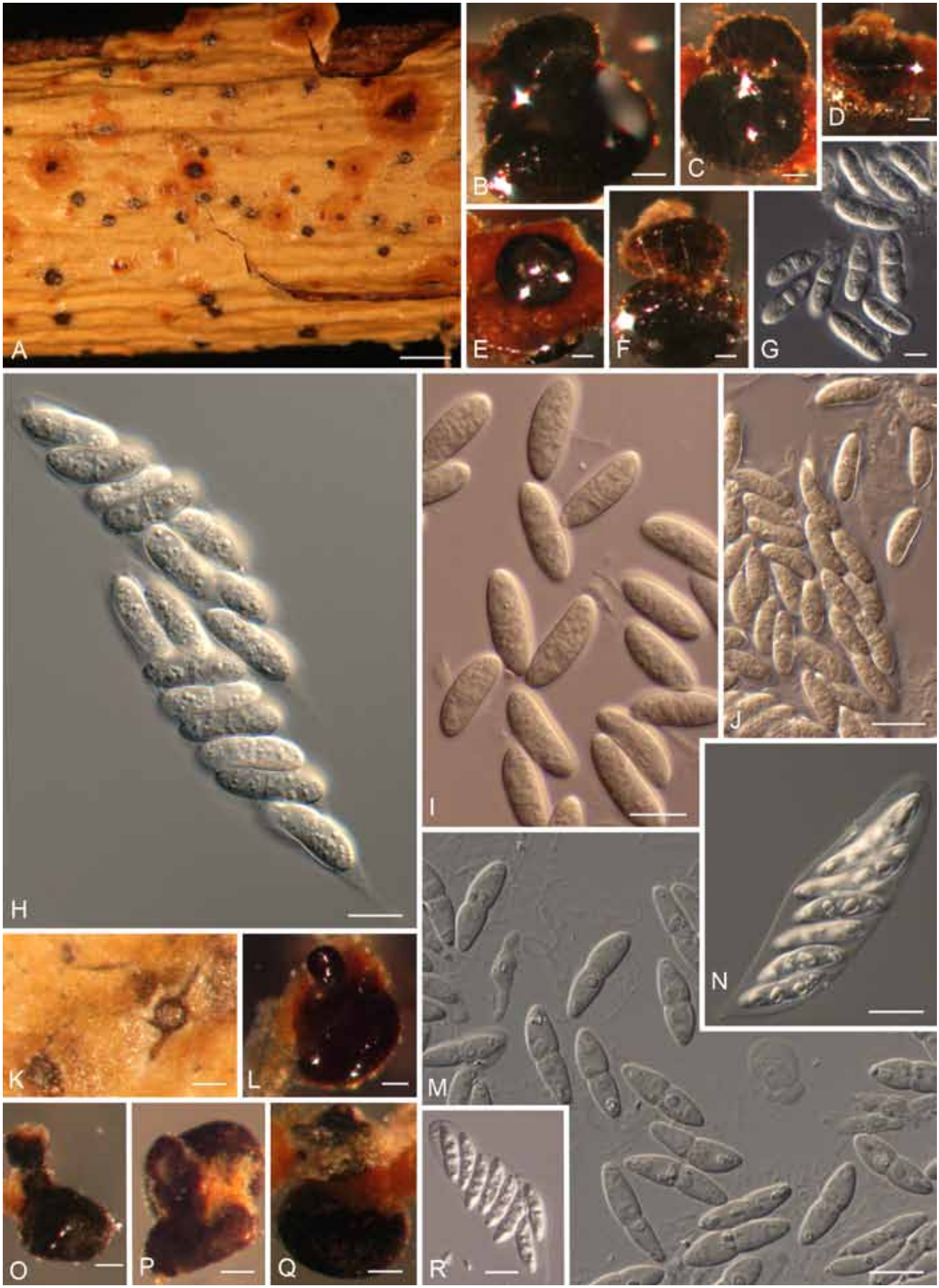

Fig. 2. Morphology on natural substrate. A–J: *Plagiostoma apiculatum*: A,B,I,J = BPI 799002 (lectotype), C–G = BPI 747938 (epitype), H = BPI 878952. K–R. *P. convexum*: K–M = BPI 799418 (lectotype), L–R = BPI 843490 (epitype). Bars = (A, K) 1 mm; (B–F, L, O–Q) 100 µm; (G–J, M–N, R) 10 µm.

Cultures: Moderate to fast growth on PDA after 7 d a.c.d. 5 cm (SD 0.4, n = 4), thin aerial mycelium of velvety granular texture, central area vinaceous buff 45, with scattered black mycelial clumps of 0.5 mm diam in central area, margin white, stringy; reverse similar but slightly darker.

Habitat and host: On dead twigs and branches of *Salix* spp., *Salix alba, S. alba* subsp. *vitellina*, *S. dasyclados,* and *S. sitchensis* (*Salicaceae*).

Distribution: Europe and North America.

Lectotype of Sphaeria apiculata designated here: BPI 799092, labelled *Sphaeria apiculata* Wallr., ex. Herb. Strasbourg.

Epitype of Sphaeria apiculata designated here: **Austria**, Vienna, 21st district, Marchfeldkanalweg, MTB 7764/1, on *Salix* sp., 20 May 2000, W. Jaklitsch 1463, BPI 747938, derived culture CBS 109775 = AR3455.

Exsiccatus examined: Fungi Rhenani 918, as *Sphaeria apiculata*, from *Salix vitellina*, BPI bound.

Additional specimens examined: **Austria**, Vienna, St. Margareten im Rosental, Kaernten, Drau-Auen, 9452/1, on *Salix alba*, 2 May 2002, W. Jaklitsch 1890, BPI 843511, derived culture AR 3826; St. Margareten im Rosental, Drau-Auen, Kaernten. 9452/2, on *Salix alba*, 14 Apr. 2001, W. Jaklitsch 1741, BPI 872037. **France**, Deux-Sèvres Département, Melle, Melle Arboretum, 15 Apr. 2008, on twigs of *Salix dasyclados*, L.C. Mejía 393, BPI 878951, derived cultures L.C. Mejía 393.01 and CBS 124974 = LCM393.03. **USA**, Washington, Kitsap County, Kitsap Memorial State Park, on twigs of *Salix sitchensis*, 28 May 2008, L.C. Mejía 436, BPI 878952, derived culture CBS 126126 = LCM436.01.

Notes: The specimen designated here as lectotype is part of the collection of *Sphaeria apiculata* referred to in the protologue. It agrees with Wallroth's description of *S. apiculata.* Fuckel (1870) recircumscribed *Sphaeria apiculata* Wallr. based on Fungi Rhenani 918. The original Latin description of *Sphaeria apiculata* includes morphological characters of the perithecia such as an apiculate papilla, *i.e.* "*coronatum dilatatis*", here interpreted as the disk-shaped expansion of the perithecial neck, and "*nucleo atro*" at the apex. These morphological characters are present in the type specimen BPI 799092 of *S. apiculata* designated here as the lectotype. The protologue of *S. apiculata* by Wallroth (1833) does not include a description of the ascospores, however, the fungus on this specimen contains broadly ellipsoid ascospores. This specimen and thus *Plagiostoma apiculatum* is distinctive and differs from *Plagiostoma salicellum* as discussed under that species.

The concept of the name *Sphaeria apiculata* has been confused. The following is an account of this species and its various synonyms based on the results of our study of the original description, type specimens, and relevant later specimens. Höhnel (1917), Petrak (1921), and later authors considered *Sphaeria apiculata* to have narrowly elongated ascospores while Wehmeyer (1933) recognised this species as having broadly ellipsoid ascospores and considered *Cryptodiaporthe salicina* to be a synonym. Höhnel (1917) examined specimens made by Rehm, Krieger, and his own of *Diaporthe spina* and considered this name to be a synonym of *Sphaeria apiculata.* He acknowledged differences in perithecial neck length among collections of these two species. To determine the synonymy of these two species we compared the original description of *D. spina* with the original description of *S. apiculata* by Wallroth (1833) as well as the recircumscription by Fuckel (1870). In his original description of *D. spina* Fuckel (1870) provided a drawing that is quite unlike the original description of *S. apiculata*. Based on the comparison of descriptions and the specimens observed, we do not consider *S. apiculata* and *D. spina* to be synonyms. The synonymy of these two species proposed by Höhnel (1917) and accepted by Petrak's (1921) who provided a description of *Cryptodiaporthe apiculata* (≡ *Sphaeria apiculata*) may be the reason that later authors considered *S. apiculata* to be characterised by narrow, elongated ascospores as described and observed for *D. spina*.

Plagiostoma barriae Sogonov, Stud. Mycol. 62: 69. 2008.

Note: Sogonov *et al.* (2008) provided a description and illustrations of this species. Cultures of isolates used in this study are illustrated in Fig. 7G–H. Originally described from the state of Washington (USA), this species is here reported from Oregon.

Specimens examined: **USA**, Oregon, on *Acer* sp., coll. L.C. Mejía LCM 484.01, BPI 878953, derived culture CBS 126125 = LCM 484.01; Washington, on *Acer macrophyllum*, L.C. Mejía 601, BPI 87895, derived culture LCM 601.01.

Plagiostoma convexum (Preuss) L.C. Mejía, **comb. nov.** MycoBank MB515690. Fig. 2K–R.

Basionym: *Sphaeria convexa* Preuss, Linnea 26: 714. 1853.

≡ *Diaporthe convexa* (Preuss) Sacc., Syll. Fung. 1: 630. 1882.

= *Cryptodiaporthe salicina* Wehm. as (Curr.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates p. 194. 1933.

[≡ *Sphaeria salicina* Curr., Trans. Linn. Soc. Lond., 22: 279, 1858 non *Sphaeria salicina* Pers., 1796]

≡ *Diaporthe punctata* (Cooke) Berl. & Voglino, Syll. Fung., Add. 108. 1886.

Perithecia immersed in bark, solitary or in groups of up to four, appearing initially as slight conic elevation of periderm with apex protruding through a small hole, black, globose, (180–)213–258(–326) µm high × (282–)303–352(–415) µm diam (mean = 238 × 329, SD 38, 44, n = 13), each with one neck. *Neck* central to eccentric, cylindrical, thick, usually thicker toward apex, some thicker elsewhere on neck, upright, diagonally straight, or curved, closely appressed when in groups, (82–)161–204(–222) µm long (mean = 176, SD 36, n = 13), (71–)82–104(–121) µm diam at base (mean = 95, SD 16, n = 13), (64–)78–108(–128) µm diam at apex (mean = 93, SD 21, n = 13), apex usually paler. *Asci* clavate, (54–)60–63(–69) × (14–)15–18(–20) µm (mean = 61 × 17, SD 4.5, 2.2, n = 8) apical ring 3.0–4.0 µm diam, with eight ascospores arranged obliquely parallel to multiseriate. *Ascospores* ellipsoid-fusoid, tapering toward rounded ends, curved or straight, one median to submedian septum, constricted, (16–)18–20(–22) × 4–5 µm (mean = 18.5 × 4.5, SD 1.0, 0.4, n = 51), l : w (3.2–)3.9–4.5(–4.9) (mean = 4.2, SD 0.4, n = 51), with four refractive bodies of various shapes, often globose.

Habitat and host: On twigs of *Salix* spp.

Distribution: Germany, USA (New York).

Lectotype specimen of Sphaeria convexa *designated here*: *Sphaeria convexa* Preuss, without other data, ex. Herb. Brussels in Shear study collection types and rarities, BPI 799418.

Epitype specimen of Sphaeria convexa designated here: **USA**, New York, Tompkins Co., near Ithaca, Arnot Forest, on *Salix* sp., 12 Jul 2002, L. Vasilyeva, BPI 843490, derived culture CBS 123206.

Notes: *Plagiostoma convexum* as *Sphaeria convexa* was considered a synonym of *Cryptodiaporthe salicina* by Wehmeyer (1933). *Plagiostoma convexum* has ascospores that agree with those drawn by Wehmeyer (1933 as *C. salicina,* plate XIII, figs 3–5). In his description of *S. salicina*, Currey (1858) mentions that the septum in the sporidia (ascospores) is "often very difficult to make out", but the ascospores in his drawing have a septum. The rest of his description agrees with the description of *S. convexa*. It also agrees with the lectotype specimen of *S. convexa*, BPI 799418 ex. Herb. Brussels with a note on the label saying apparently from Preuss). This evidence suggests that *S. salicina* Curr. 1858 and *S. convexa* Preuss 1852 represent the same species. Because *S. salicina* Curr. is a later homonym of *Sphaeria salicina* Pers. 1796, this basionym cannot be used and the next available epithet is *S. convexa;* hence the correct name for this taxon is *Plagiostoma convexum*. The specimen BPI 799418 is here designated the lectotype and the specimen BPI 843490 with the ex-epitype culture CBS 123206 is designated the epitype of *Sphaeria convexa*.

Wehmeyer (1933) listed 28 synonyms of *Cryptodiaporthe salicina*. Among specimens that Wehmeyer (1933) recognised under that name, Butin (1958) elaborated differences in ascospore morphology, conidial state, host, and ecological characteristics and distinguished three species: *C. apiculata* (Wallr.) Petr., *C. populea* (Sacc.) Butin, and *C. pulchella* (Sacc.) Butin, here accepted as *Plagiostoma apiculatum*, *P. populinum,* and *P. pulchellum.* Butin (1958) did not consider any of these species to be conspecific with *Sphaeria salicina* Curr. On the contrary he listed *Cryptodiaporthe salicina* based on *Sphaeria salicina* Curr. as a synonym of *Cryptodiaporthe salicella*, here recognised as *Plagiostoma salicellum*. Although Wehmeyer (1933) listed *Sphaeria sphingiophora* Oudem. 1873 [≡ *Diaporthe sphingiophora* (Oudem.) Sacc.] as a synonym of *C. salicella*, *S. sphingiophora* occurs on *Cornus.* It is unlikely to be the same species as *P. convexum*. *Diaporthe cupulata* Berl. & Destrée was considered a synonym of *Sphaeria convexa* by Wehmeyer (1933), however, the ascospore sizes of these species are different. We do not consider them to be synonymous. The specimen at BPI of *Sphaeria salicina* Pers., Scleromyceti Sueciae 10, was examined and determined to be a species of *Valsa*.

Plagiostoma devexum (Desm.) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 119. 1870.

Basionym: *Sphaeria devexa* Desm., Pl. Cryptog. Nord. de France, Edit. II, Ser. II, No. 367. 1856.

≡ *Gnomonia devexa* (Desm.) Auersw. in Gonn. & Rabenh., Mycol. Europ. 5/6: 23. 1869.

≡ *Gnomoniella devexa* (Desm.) Sacc., Syll. Fung. 1: 417. 1881.

≡ *Gnomoniopsis devexa* (Desm.) Moesz & Smarods, Bot. Közlem. 38: 68. 1941.

= *Sphaeria excentrica* Cooke & Peck, Annual Rep. New York State Mus. 25: 105. 1873 *fide* Monod (1983).

≡ *Gnomoniella excentrica* (Cooke & Peck) Sacc., Syll. Fung. 1: 418. 1882.

= *Diaporthe sechalinensis* Sacc., Atti Del Congr. Bot. Di Palermo 1902: 52. 1902 *fide* Monod (1983).

= *Ceriosporella polygoni* A. L. Sm. & Ramsb., Trans. Brit. Mycol. Soc. 4: 325. 1914 *fide* Monod (1983).

Note: Barr (1978) and Monod (1983) provided detailed descriptions of this species.

Plagiostoma dilatatum L.C. Mejía, **sp. nov.** MycoBank MB515700. Figs 3A–D, 7I–L.

Etymology: *dilatatum* - dilate; referring to the dilated or expanded area of the perithecial neck that appears disk-like when seen from above, and like a thick collar in section.

Perithecia globosa, (277–)320–442(–502) µm elata, (382–)475–572(–642) µm diametro; rostrum breve, apice punctatum, (152–)257–308(–327) µm longum, cum expansa area disciformi vertice visu, simili collo in sectione, (217–)352–401(–452) µm diametro ubi latissima, (92–)95–108(–122) µm diametro apice. Ascosporae reniformes vel oblongo-ellipticae, uni-septatae, constrictae ubi medianae vel submedianae septatae, (12–)13–15(–22) × (4–)4–5(–7) µm, L:l (2.6–)3.0–3.3(–3.8).

Perithecia immersed in bark, solitary or aggregated, appearing initially as slight elevation of periderm surrounded by a black halo, later developing into a black circular spot, apex protruding through a tiny slit, globose, (277–)320–442(–502) µm high × (382–)475–572(–642) µm diam (mean = 383 × 515, SD 78, 79, n1 = 11, n2 = 10), each with one neck. *Neck* central to eccentric, relatively short, with punctate ostiolar opening, expanded, initially below epidermis, appearing disk-like when seen from above, like a thick collar in section, becoming exposed, with black halo or circular area below epidermis, when epidermis removed, exposing expanded neck and apex, sometimes two necks joined at expanded area; sometimes black mycelium of developing conidioma above perithecia; neck (152–)257–308(–327) µm long (mean = 263, SD 61, n = 10), (217–)352–401(–452) µm diam at base (mean = 367, SD 67, n = 10), (92–)95–108(–122) µm diam at apex (mean = 103, SD 10, n = 9). *Asci* cylindric, (48–)54–62(–77) × (8–)12–14(–18) µm (mean = 58 × 13, SD 7.2, 2.5, n = 15), long stalked, apical ring 2.1–4.3 µm diam, appearing rectangular, with eight ascospores arranged obliquely parallel to multiseriate. *Ascospores* renoid to oblong-ellipsoid, slightly tapering to rounded ends, slightly curved, one, median to submedian septum, slightly constricted, (12–)13–15(–22) × 4–5(–7) µm (mean = 15 × 5, SD 2.5, 1.0, n = 48), l : w (2.6–)3.0–3.3(–3.8) (mean = 3.2, SD 0.3, n = 48), with granular cytoplasm.

Cultures: Moderate to fast growth on PDA after 7 d a.c.d. 5.2 cm (SD 0.2, n = 8), thin aerial mycelium of velvety to granular texture, whitish to vinaceous buff 86, becoming olivaceous 48 toward margin; fasiculate mycelium buff 45 developing from concave central area; reverse same; 7 d a.c.d. denser mycelium hazel 88 in centre, with vinaceous 86, black droplets on surface, with immersed mycelium dark, reverse dark, with a lighter halo and whitish to translucent margin.

Habitat and host: On dead, still attached twigs of *Salix caprea* and *S. irrorata* (*Salicaceae*).

Distribution: France (Melle).

Holotype: **France**, Deux-Sèvres Département, Melle, Melle Arboretum, on *Salix irrorata*, 15 Apr 2008, L.C. Mejía 402, BPI 878959, derived cultures CBS 124976 = LCM 402.02, = LCM402.01.

Additional specimens examined: **France**, Deux-Sèvres Département, Foret del' Hermitain, on *Salix caprea*, 17 Apr. 2008, L.C. Mejía 403, BPI 878958, derived cultures LCM403.01, LCM403.02.

Notes: The intricate mycelium that develops above the body of the perithecia in some pustules resembles the conidioma of *Diplodina*, the anamorph of *Plagiostoma*.

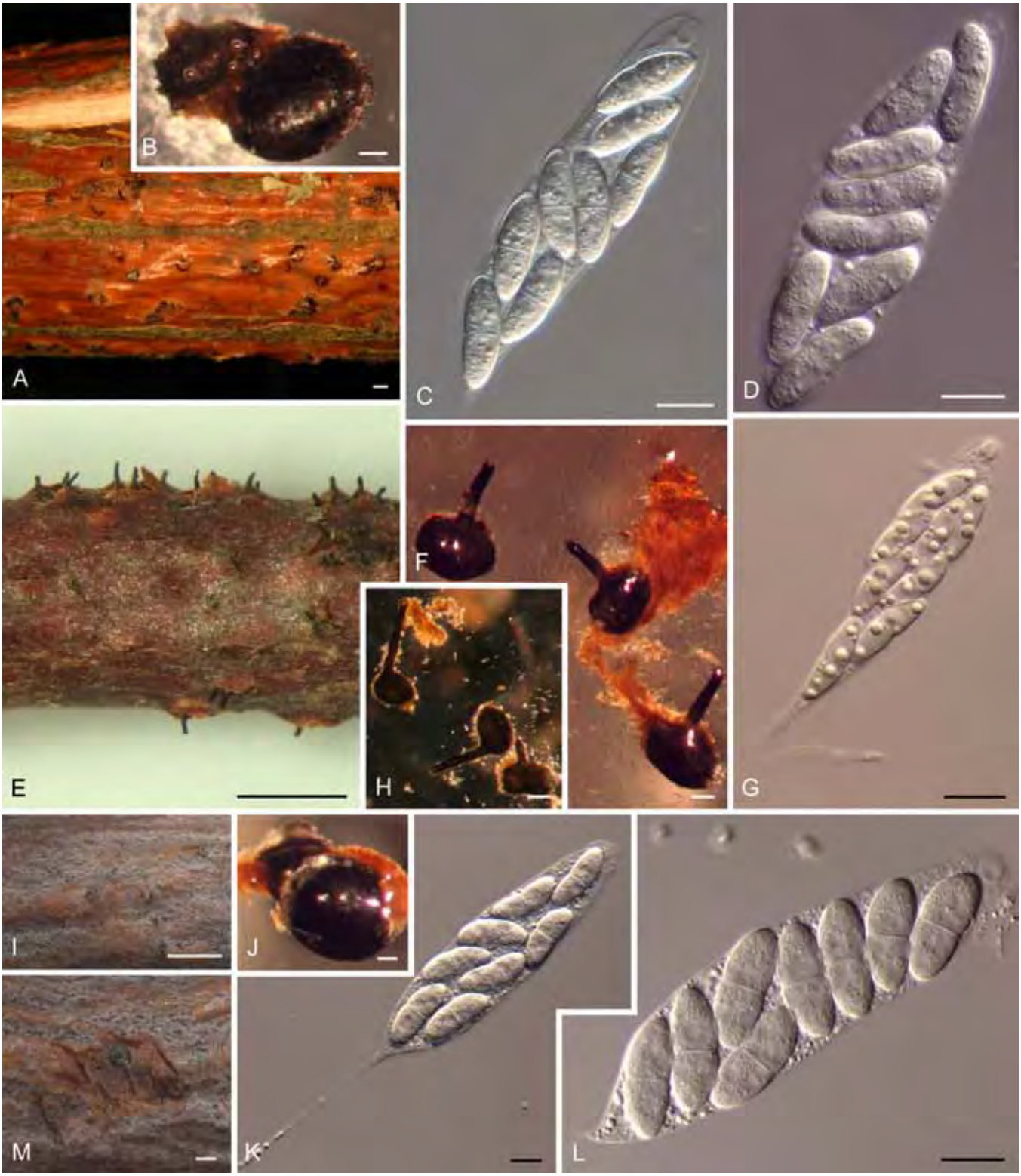

Fig. 3. Morphology on natural substrate. A–D: *Plagiostoma dilatatum*: A–C = BPI 878959 (holotype), D = BPI 878958. E–H: *P. exstocollum*: E–G = BPI 878961 (holotype), H = BPI 878964. I–M: *P. imperceptibile* BPI 878967 (holotype). Bars = (A, E, I) 1mm; (M) 200 µm; (B, F, H, J) 100 µm; (C–D) 20 µm; (G, K–L) 10 µm.

Plagiostoma euphorbiae (Fuckel) Fuckel, Jahrb. Nassauischen Vereins Naturk. 23–24: 118. 1870.

Basionym: *Sphaeria euphorbiae* Fuckel, Enumeratio Fung. Nassoviae p. 69. 1860.

≡ *Gnomonia euphorbiae* (Fuckel) Sacc., Michelia 2: 312. 1881.

≡ *Gnomoniella euphorbiae* (Fuckel) Sacc., Syll. Fung. 1: 418. 1882.

= *Gnomoniella tithymalina* Sacc. & Briard, Rev. Mycol. (Toulouse) 7: 209. 1885 *fide* Monod (1983).

Note: This species was fully described and illustrated by Fröhlich & Hyde (1995) and Sogonov *et al.* (2008).

Plagiostoma euphorbiaceum (Sacc. & Briard) Sogonov, Stud. Mycol. 62: 72. 2008.

Basionym: *Gnomonia euphorbiacea* Sacc. & Briard, Rev. Mycol. (Toulouse) 7: 208. 1885.

Note: Monod (1983) provided a detailed description of this species. *Plagiostoma euphorbiaceum* is phylogenetically related to *P. amygdalinae* as discussed under that species.

Plagiostoma euphorbiae-verrucosae (M. Monod) Sogonov, Stud. Mycol. 62: 72. 2008
Basionym: *Gnomoniella euphorbiae-verrucosae* M. Monod, Beih. Sydowia 9: 42. 1983.

Note: Monod (1983) provided a detailed description of this species.

Plagiostoma exstocollum L.C. Mejía, **sp. nov.** MycoBank MB515701. Figs 3E–H, 7M–P.

Etymology: *exsto* – standing out; *collus* – neck, referring to the perithecial neck that emerges from the host periderm.

Perithecia suboblata, (186–)194–227(–278) µm etata, (219–)269–336(–341) µm diámetro, rostrum (197–)247–281(–382) µm longum, (50–)53–63(–67) µm diamwtro basi, (39–)44–49(–50) µm diametro apice. Ascosporae ellipsoideae, uni-septatae, constrictae ubi submedianae septatae, (9–)10–15(–16) × (2–)2–3(–4) µm, L:l (3–)4–4.5(–6).

Perithecia immersed in bark, aggregated in groups up to 12, joined by a scanty, brownish to cream stroma, occasionally solitary, appearing as elevations in bark where perithecial necks emerge through slit or crack in periderm, usually ellipsoid in shape when seen from top, black, suboblate, (186–)194–227(–278) µm high × (219–)269–336(–341) µm diam (mean = 216 × 293, SD 31, 49, n = 9), each with one neck. *Neck* marginal, slightly sulcate, long, (197–)247–281(–382) µm long (mean = 270, SD 54, n = 9), (50–)53–63(–67) µm diam at base (mean = 59, SD 6.1, n = 9), (39–)44–49(–50) µm diam at apex (mean = 46, SD 3.7, n = 9). *Asci* cylindric to clavate, (15–)39–57(–76) × (3.5–)6.5–11(–13) µm (mean = 49.5 × 8.5, SD 15.1, 2.6, n = 26), apical ring 1.5–3.5 µm diam, with eight ascospores arranged biseriate. *Ascospores* ellipsoid, tapering to rounded ends, 1-septate, constricted at submedian septum, (9–)10–15(–16) × 2–3(–4) µm (mean = 12.5 × 3.0, SD 2.4, 0.7, n = 49), l : w (3–)4–4.5(–6) (mean = 4.3, SD 0.4, n = 49), usually with at least four refractive circular bodies in each ascospore, two large ones on each side of septum, one smaller one at end of each cell.

Cultures: Moderate to fast growth on PDA after 7 d a.c.d. 4.3 cm (SD 1, n = 16), thin aerial mycelium appearing velvety, margin fringed, stringy, whitish to buff 45 or vinaceous buff 86 from top, with a slightly to pronounced halo of thick, white mycelium extending about 2 cm from centre, reverse whitish to buff 45.

Habitat and host: On dead, still attached, overwintered twigs of *Corylus californica* (*Betulaceae*).

Distribution: **USA** (Oregon).

Holotype: **USA**, Oregon, Jackson Co., Upper Rogue River, River Bridge Campground, on *Corylus californica*, 20 May 2008, L.C. Mejía 468, BPI 878961, derived culture CBS 127663 = LCM468.01.

Specimens examined: **USA**, Oregon, Jackson Co., River Bridge Campground, Upper Rogue River, on *Corylus californica*, 20 May 2008, L.C. Mejía 469, BPI 878962; on *Corylus californica*, 21 May 2008, L.C. Mejía 422, BPI 878959, derived culture LCM422.02; on *Corylus californica*, 21 May 2008, L.C. Mejía 472, BPI 878963, derived culture LCM472.01; Upper Rogue River trail, on *Corylus californica*, 21 May 2008, L.C. Mejía 473, BPI 878964, derived culture LCM473.01; Oregon, Lane Co., Willamette National Forest, Salmon Creek, 22 May 2008. L.C. Mejía 483, BPI 878965, derived culture LCM483.01; on *Corylus californica*, 23 May 2008, L.C. Mejía 464, BPI 878960, derived culture LCM464.

Plagiostoma fraxini (Redlin & Stack) Sogonov, Stud. Mycol. 62: 72. 2008.

Basionym: *Gnomoniella fraxini* Redlin & Stack, Mycotaxon 32:185. 1988.

Note: This species, often as its anamorph referred to as *Discula fraxinea* (Peck) Redlin & Stack, causes an anthracnose disease of ash and fringetree (*Oleaceae*) known most commonly in the eastern and midwestern United States, rarely from Oregon (Gregory *et al.* 2004, Rossman *et al.* 2004). Redlin & Stack (1988) provided a detailed description of this species as *Gnomoniella fraxini*.

Plagiostoma geranii (Hollós) Sogonov, Stud. Mycol. 62: 72. 2008.
Basionym: *Gnomonia geranii* Hollós, Annls. Mus. Nat. Hung. 7: 52. 1909.
≡ *Rostrocoronophora geranii* (Hollós) Munk, Dansk Bot. Arkiv 15: 98. 1953.

Note: Müller & Arx (1962) and Monod (1983) provided detailed descriptions of this species as *Gnomonia geranii*.

Plagiostoma imperceptibile L.C. Mejía, **sp. nov.** MycoBank MB515702. Figs 3I–M, 7Q–R.

Etymology: *imperceptibile* referring to the very short, non-protruding neck, thus the species is difficult to see in nature.

Perithecia globosa, (289–)309–356(–414) µm elata, (385–)412–462(–504) µm diametro, rostrum breve, (136–)175–211(–225) µm longum, cum expansa area, disciformi vertice visu, simili collo in sectione, (251–)301–318(–351) µm diametro ubi latissima, (87–)89–100(–113) µm diametro apice. Ascosporae reniformes vel oblongo-ellipticae, uniseptatae, constrictae ubi septatae, (18–)19–20(–21) × (5–)6–7(–8) µm, L:l (2.5–)2.9–3.1(–3.8).

Perithecia immersed in bark, solitary, appearing as slight elevations of periderm, central area pale, delimited by black halo from which apex of neck protrudes, black, globose, (289–)309–356(–414) µm high × (385–)412–462(–504) µm diam (mean = 338 × 437, SD 44, 41, n = 7), each with one neck. *Neck* central to eccentric, short, with apex scarcely protruding through a tiny slit, with neck expanded below epidermis, disk-like when seen from above, like a thick collar in section, with black halo or circular black spot through epidermis or black when exposed, (136–)175–211(–225) µm long (mean = 189, SD 38, n = 4), (251–)301–318(–351) µm diam at widest point (mean = 307, SD 36.3, n = 5), (87–)89–100(–113) µm diam at apex (mean = 97.5, SD 10.5, n = 5). *Asci* ovoid elongate, often with long, slender, persistent stalk, (67–)76–80(–87) × (13–)18–21(–24) µm (mean = 77.5 × 19.5, SD 4.9, 3.1, n = 11), apical ring 3.0–4.5 µm diam, with eight ascospores arranged obliquely parallel to multiseriate. *Ascospores* renoid to oblong-ellipsoid, slightly tapering to broadly rounded ends, slightly curved, one median septum, slightly constricted, (18–)19–20(–21) × (5–)6–7(–8) µm (mean = 19.5 × 6.5, SD 0.9, 0.6, n = 45), l : w (2.5–)3(–4) (mean = 3, SD 0.3, n = 45), with granular cytoplasm.

Cultures: Moderate growth on PDA after 7 d a.c.d. 4 cm (SD 0.4, n = 4), thin aerial mycelium of velvety, powdery texture, margin stringy, colour grey becoming vinaceous buff 86 from the top, reverse isabelline 65.

Habitat and host: On twigs of *Salix* sp. (*Salicaeae*).

Distribution: **USA** (California).

Holotype: **USA**, California, Shasta Co., Cow Creek, close to Old Station, on *Salix* sp., 18 May 2008, L.C. Mejía 456, BPI 878967, derived cultures LCM456.01 and LCM456.02 = CBS 127495.

Note: *Plagiostoma imperceptibile* has an expanded neck similar to other species in the clade, specifically *P. apiculatum, P. convexum*, *P. dilatatum*, and *P. pulchellum* (Fig. 1).

Plagiostoma oregonense L.C. Mejía, **sp. nov.** MycoBank MB515703. Figs 4A–C, 7S–T.

Etymology: *oregonense* – from Oregon, referring to the only state in the USA where it was collected.

Perithecia subglobosa, (261–)270–326(–373) µm elata, (369–)381–400(–407) µm diametro; rostrum breve, (156–)168–182(–185) µm longum, cum expansa area, disciformi vertice visu, simili collo in sectione, (176–)182–204(–221) µm diametro ubi latissima, 119–120(–121) µm diametro apice. Ascosporae latoellipticae vel ellipticae, uni-septatae, constrictae medianae vel submedianae septatae, (16–)17–19(–22)×(4–)6(–7) µm, L:l (2.6–)2.9–3.2(–4.0).

Perithecia immersed in bark, solitary, evident as conic-shaped elevation of periderm with neck protruding, black, globose to subglobose, (261–)270–326(–373) µm high × (369–)381–400(–407) µm diam (mean = 304 × 389, SD 60, 19, n = 3), each with one neck. *Neck* eccentric or lateral, expanded, usually attached to periderm, (156–)168–182(–185) µm long (mean = 173, SD 16, n = 3), (176–)182–204(–221) µm diam at base (mean = 195, SD 23, n = 3), (119–)119–120(–121) µm diam at apex (mean = 120, SD 1.0, n = 3). *Asci* cylindric, (74–)78–92(–95) × (12–)15–17(–19) µm (mean = 86 × 16, SD 8, 2, n = 10), apical ring 2.8–4.0 µm diam, looks like a stretched hexagon, with eight ascospores arranged obliquely parallel or biseriate. *Ascospores* broadly ellipsoid to ellipsoid, with rounded ends, 1-septate, constricted at median to submedian septum, (16–)17–19(–22) × (4.5–)5.5–6(–7) µm (mean = 18.0 × 6.0, SD 1.5, 0.5, n = 36), l : w (2.6–)2.9–3.2(–4.0) (mean = 3.1, SD 0.3, n = 36), with granular cytoplasm.

Cultures: Moderate growth on PDA after 7 d a.c.d. 4.6 cm (SD 0.1, n = 2), thin aerial mycelium of felty texture, margin fringed, stringy, central area white, with a halo of aerial mycelium 1.5 cm from centre, marginal area buff 45m, reverse with a central circular area of 2 cm diam fawn 87.

Habitat and host: On overwintered branches of *Salix* sp. (*Salicaceae*).

Distribution: **USA** (Oregon).

Holotype: **USA**, Oregon, Lincoln Co., Fogarty Creek, on *Salix* sp., 24 May 2008, L.C. Mejía 597, BPI 878968, derived culture LCM597.01 = CBS 126124.

Plagiostoma ovalisporum L.C. Mejía, **sp. nov.** Figs 4D–H, 7U–V.

Etymology: *ovalis* - ovoid; *sporum* - spore, referring to the ovoid shape of the ascospores.

Perithecia globosa, (246–)277–363(–385) µm elata, (394–)403–414(–427) µm diametro; rostrum breve, (131–)146–159(–162) µm longum, apice cupulatum, (125–)136–153(–194) µm basi, (113–)117–160(–168) µm diametro apice. Ascosporae ovoideae, non-septatae, (12–)14–16(–17) × (7–)7–8(–9) µm, L:l (1.6–) 1.8–2.0(–2.2).

Perithecia immersed in bark, solitary, or in groups up to five, usually in a row, scattered, erumpent, appearing as raised, conical area of bark periderm, with neck protruding through slit or hole, black, globose, (246–)277–363(–385) µm high × (394–)403–414(–427) µm diam (mean = 322 × 409, SD 57, 11, n = 6), each with one neck. *Neck* lateral, short and thick, apex cupulate, (131–)146–159(–162) µm long (mean = 151, SD 12, n = 6), (125–)136–153(–194) µm diam at base (mean = 150, SD 24, n = 6), (113–)117–160(–168) µm diam at apex (mean = 139, SD 24, n = 6). *Asci* cylindric to obclavate, (63.5–) 68.5–75.5(–87.5) × (12.5–)14.5–17(–18) µm (mean = 72 × 15.5, SD 6.5, 1.5, n = 19), apical ring 3.5–4.5 µm diam, with eight ascospores arranged obliquely parallel to biseriate. *Ascospores* ovoid, non-septate, appearing double-walled, more evident when stained with cotton blue lactophenol or Melzer's reagent, (12–)14–16(–17) × 7–8(–9) µm (mean = 15 × 7.5, SD 1.2, 0.5, n = 35), l : w (1.6–)1.8–2(–2.2) (mean = 1.9, SD 0.1, n = 35).

Cultures: Moderate growth on PDA after 7 d a.c.d. 4.2 cm (SD 0.1, n = 2), thin aerial mycelium of felty texture, margin fringed, like roots, whitish, with denser mycelium in centre within a radius of 1 cm, reverse buff 45 becoming dark grey, whitish in the margin.

Habitat and host: On dead twigs of *Salix* sp. (*Salicaceae*).

Holotype: **USA**, Idaho, Idaho Co., near Burgdorf, Burgdorf Rd. FR246, parking area at camping site at Three Mile Creek, approx. GPS: N45º 18.139 W 115º 55.782, elevation 6309 ft, on dead twigs of *Salix* sp., 5 Sep. 2008 (NAMA Annual Foray, Orson K. Miller Jr. Memorial Foray), A.M. Minnis *s.n.*, BPI 878969, derived culture CBS 124977 = LCM458.01.

Notes: This species differs from other species of *Plagiostoma* by having ovoid, non-septate ascospores. The other two known species of *Plagiostoma* with non-septate ascospores, *P. euphorbiae-verrucosae* and *P. fraxini,* occur on hosts other than *Salix* and their ascospores are ellipsoid-fusoid. Unlike *P. dilatatum*, *P. ovalisporum* does not have a circular black halo or spot at the point where the perithecial necks emerge through the periderm.

Plagiostoma petiolophilum (Peck) Sogonov, Stud. Mycol. 62: 72. 2008.

Basionym: *Sphaeria petiolophila* Peck, Annual Rep. New York State Mus. 35: 144. 1884.

≡ *Gnomonia petiolophila* (Peck) Berl. & Voglino, Syll. Fung. Addit. 1–4: 90. 1886.

≡ *Cryptodiaporthe petiolophila* (Peck) M.E. Barr, Mycol. Mem. 7: 136. 1978.

Notes: Barr (1978) provided a detailed description of this species as *Cryptodiaporthe petiolophila*.

Plagiostoma populinum (Fuckel) L.C. Mejía, **comb. nov.** MycoBank MB515705.

Basionym: *Cryptospora populina* Fuckel, Jahrb. Nassauischen Vereins Naturk. 23/24: 193. 1870.

= *Diaporthe populea* Sacc. in Mouton, Bull. Soc. Roy. Bot. Belgique 26: 174. 1887 *fide* Butin (1958).

≡ *Cryptodiaporthe populea* (Sacc.) Butin, Sydowia 11: 31. 1958 [1957].

Moderate to fast growth on PDA after 7 d a.c.d. 3.3 cm (SD 1.2, n = 8), thin aerial mycelium of velvety or felty texture, whitish to buff 45 or rosy buff 6 in central area and isabeline 65 in the margin, with some droplets (honey 64) in the centre, with fringed margin appearing like roots, reverse whitish to fawn 87 or honey 64, in

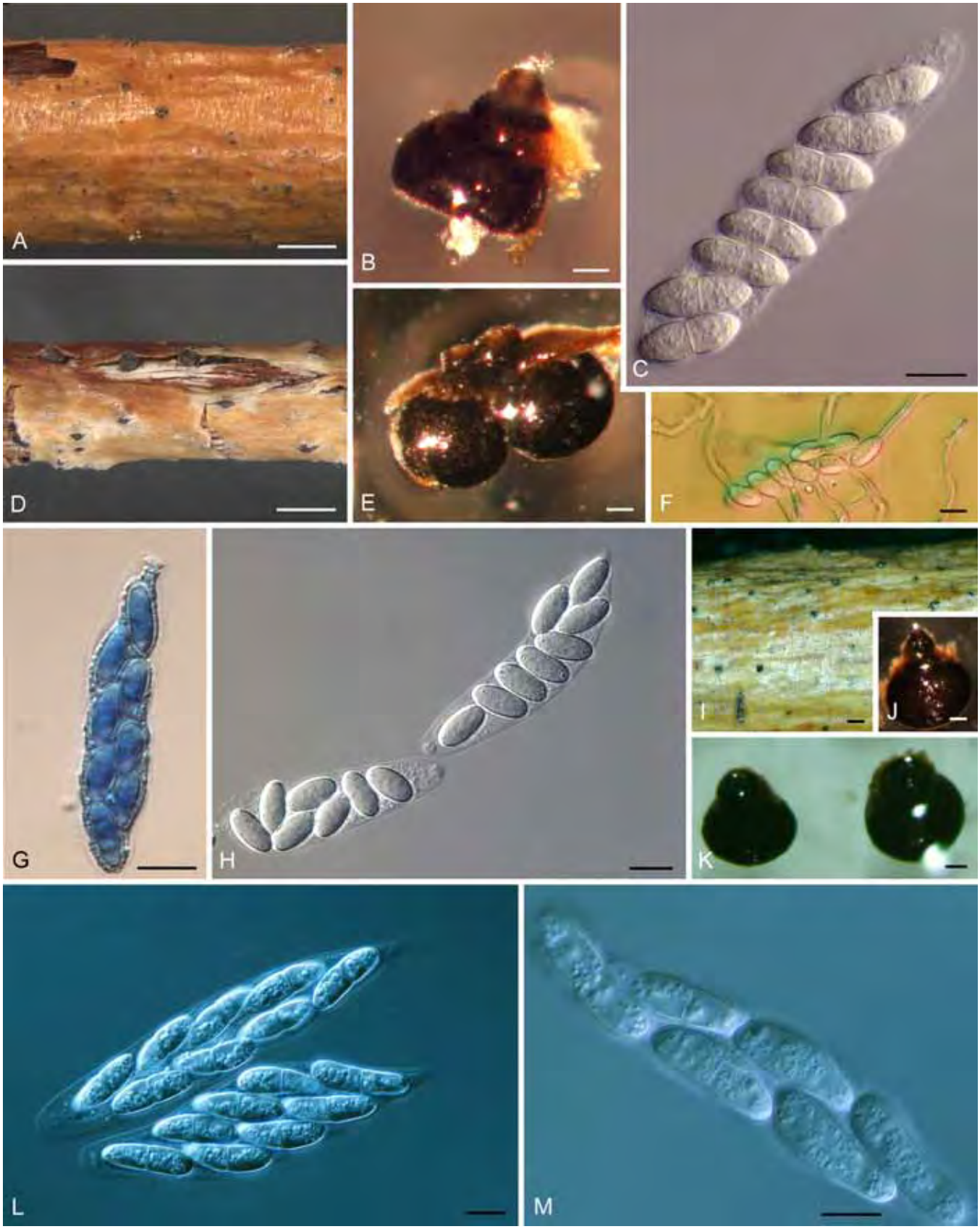

Fig. 4. Morphology on natural substrate. A–C: *Plagiostoma oregonense* BPI 878968 (holotype). D–H. *P. ovalisporum*: BPI 878969 (holotype). I–M. *P. pulchellum*: I, M = BPI 878971, J = BPI 878974, K–L = BPI 878972. Bars = (A, D, I) 1 mm; (K) 300 µm; (B, E, J) 100 µm; (H, L–M) 20 µm; (C, F–G) 10 µm.

some cultures becoming dark and with a concentric halo light. Cultures are illustrated in Fig. 8A–D.

Notes: Butin (1958) presented a full description with illustrations of this species as *Cryptodiaporthe populea.* Because the name *Cryptodiaporthe populina* (Fuckel)Petr. based on *Valsa populina* Fuckel was already occupied in *Cryptodiaporthe*, Butin (1958) based his new combination on *Diaporthe populea* Sacc. When placed in *Plagiostoma* the basionym *Cryptospora populina* Fuckel provides the oldest epithet for this species.

Plagiostoma pulchellum (Sacc. & Briard) L.C. Mejía, **comb. nov.** MycoBank MB515706. Figs 4I–M, 8E–J.

Basionym: *Diaporthe pulchella* Sacc. & Briard in Sacc., Atti Ist. Veneto Sci. 2, Ser. 6, 437. 1884.

≡ *Cryptodiaporthe pulchella* (Sacc. & Briard) Butin, Phytopathol. Z. 32: 407. 1958.

= *Diaporthe recedens* Sacc., Ann. Mycol. 12: 290 1914 *fide* Butin (1958).

Perithecia immersed in bark, solitary, often growing close together, appearing initially as slight elevation of periderm, with black halo or black spot where apex protrudes through a small hole, black, globose, (311–)371–473(–613) µm high × (467–)483–642(–660) µm diam (mean = 435 × 563, SD 128, 99, n = 4), each with one neck. *Neck* central to eccentric, straight to oblique, with an expanded disk-like area, initially below epidermis, becoming exposed with time, producing black halo or spot at surface, (169–)173–319(–388) µm long (mean = 257, SD 105, n = 4), (153–)209–256(–306) µm diam at widest point (mean = 231, SD 62.5, n = 4), (93–)99–160(–212) µm diam at apex (mean = 137, SD 54, n = 4). *Asci* ovoid elongated, (75–)85–107(–117) × (15–)17–21(–24) µm (mean = 95 × 19, SD 13.5, 3.0, n = 15), apical ring 4–4.8 µm diam, very thick, with eight ascospores arranged obliquely parallel to multiseriate. *Ascospores* oblong ellipsoid-elongated, slightly tapering, with rounded ends, straight to slightly curved, one median to submedian septum, not constricted, (17–)18–22(–27) × (5–)6–7(–7.5) µm (mean = 20.3 × 6.3, SD 2.9, 0.6, n = 39), l : w (2.5–)2.9–3.4(–4.4) (mean = 3.2, SD 0.4, n = 39), with granular cytoplasm.

Cultures: Moderate growth on PDA after 7 d a.c.d. 3.9 cm (0.8 n = 6), thin aerial mycelium whitish to rosy vinaceous 58 colour, of velvety, granular texture due to mycelial clumps *ca.* 500 um diam, isabeline 65, produced in central area of 2.4 cm diam, central area appearing often moist, margin translucent to buff 45, with hyphae extending radially, stringy, becoming fringed toward margin; reverse whitish to rosy vinaceous 58 or olivaceous. At 14 d small black and dark green slimy droplet surrounded by a second halo rosy vinaceous 58 with white greyish margin, reverse same colour pattern.

Habitat and host: On dead, still attached branches of *Populus balsamifera*, *Populus* sp., *Salix babylonica*, *S. humboldtiana* and *S. lucida* (*Salicaceae*).

Distribution: North America, South America (Argentina), and Europe.

Type specimen: **France**, Troyes, on branch of *Populus alba* cv. *pyramidalis*, Briard n. 5, PAD-not available.

Specimens examined: **Argentina**, Tucumán, vicinity of Villa Nougués, on twigs of *Salix humboldtiana*, 16 Nov 2008, L.C. Mejía 623, BPI 878974, derived cultures LCM623.01 and LCM623.03. **Netherlands**, ex leaf of *Populus balsamifera*, (CBS 170.69 as *Cryptodiaporthe pulchella*. **USA**, Maryland, Prince George's Co., Beltsville, USDA-BARC, outside of B011A, on twigs of *Salix babylonica*, 3 Mar 2008, Amy Y. Rossman & L.C. Mejía 365, BPI 878971, derived culture LCM365.04 = CBS 126653; Maryland, Prince George's Co., Greenbelt, Lake Artemisia, on twigs of *Salix babylonica,* 15 Mar 2008, L.C. Mejía 371, BPI 878972, derived culture LCM371.02; Washington, Kitsap Co., Kitsap Memorial State Park, on twigs of *Salix lucida*, 28 May 2008, L.C. Mejía 438, BPI 878973, derived cultures LCM438.03 (= CBS 126122) and LCM438.04.

Notes: Butin (1958) refers to this species as saprobic on *Populus* spp. The evidence presented in this study shows that this species also infects *Salix* spp. and has a more extensive geographic distribution than previously reported.

Plagiostoma rhododendri (Auersw.) Sogonov, Stud. Mycol. 62: 72. 2008.

Basionym: *Gnomonia rhododendri* Auersw. in Gonn. & Rabenh., Mycol. Europ. 5/6: 26. 1869.

≡ *Apiognomonia rhododendri* (Auersw.) Remler, Bibliotheca Mycologica 68: 74. 1979.

Note: Remler (1979 as *A. rhododendri*) and Monod (1983 as *G. rhododendri*) presented descriptions of this species.

Plagiostoma robergeanum (Desm.) Sogonov, Stud. Mycol. 62: 73. 2008.

Basionym: *Sphaeria robergeana* Desm., Ann. Sci. Nat. Bot. ser. 3, 16: 306. 1851.

≡ *Diaporthe robergeana* (Desm.) Niessl. in Rabenh., Fungi Europ. 2222. 1882.

≡ *Cryptodiaporthe robergeana* (Desm.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates p. 200. 1933.

Note: Wehmeyer (1933) provided a description of this species as *Cryptodiaporthe robergeana.*

Plagiostoma salicellum (Fr.) Sogonov, Stud. Mycol. 62: 73. 2008. Fig. 5A–H.

Basionym: *Sphaeria salicella* Fr., Syst. Mycol. 2: 377. 1823.

≡ *Diaporthe salicella* (Fr.) Sacc., Mycotheca Venet. 135. 1873.

≡ *Gnomonia salicella* (Fr.) J. Schröt., Pilze Schles. 3, 2: 392.1897.

≡ *Chorostate salicella* (Fr.) Traverso, Fl. Ital. Crypt. 2: 203. 1906.

≡ *Cryptodiaporthe salicella* (Fr.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates p. 193. 1933.

Perithecia immersed in bark, solitary or in groups up to five, scattered, evident as slight elevation of periderm, black, subglobose, (157–)208–308(–331) µm high × (339–)372–410(–507) µm diam (mean = 257 × 397, SD 60, 43, n = 11), each with one neck. *Neck* cylindrical, eccentric to lateral, surrounded by a whitish stroma, (96–)147–202(–308) µm long (mean = 177, SD 67, n = 11), (61–)80–84(–95) µm diam at base (mean = 81, SD 8.8, n = 11), (54–)74–85(–91) µm diam at apex (mean = 79, SD 10, n = 11). *Asci* cylindric to clavate, (40–)51.5–59(–63) × (11–)13–14(–15) µm (mean = 55 × 13, SD 5.8, 1.4, n = 15), with apical ring 2.0–3.5 µm diam, with eight ascospores arranged obliquely parallel or irregularly seriate. *Ascospores* ellipsoid-elongated, slightly tapering toward rounded ends, 1-septate, often with short appendages 1.5–2 µm, slightly constricted at median to submedian septum, (14–)17–20(–27) × 3–4(–5) µm (mean = 18.5 × 3.5, SD 2.3, 0.5, n = 57), l : w (3.2–)5.2–6.6(–8.7) (mean = 5.9, SD 1.1, n = 57), with granular cytoplasm.

Habitat and host: On dead, still attached branches of *Salix alba, S. repens,* and *Salix* sp. (*Salicaceae*).

Distribution: Europe.

Lectotype of Sphaeria salicella designated here: Scleromyceti Sueciae 188 issued 1821, Sbarbaro Collection, BPI exsiccati).

Epitype of Sphaeria salicella designated here: **Austria**, St. Margareten im Rosental, Kaernten, Drau-Auen. 9452/1, as *Cryptodiaporthe apiculata* on *Salix alba*, 2 May 2002, W. Jaklitsch 1889, BPI 843527, derived culture CBS 121466.

Additional specimen examined: **Germany**, Langen, on *Salix repens*, L.C. Mejía , **BPI** 878975, derived culture CBS 126121 = LCM 449.01.

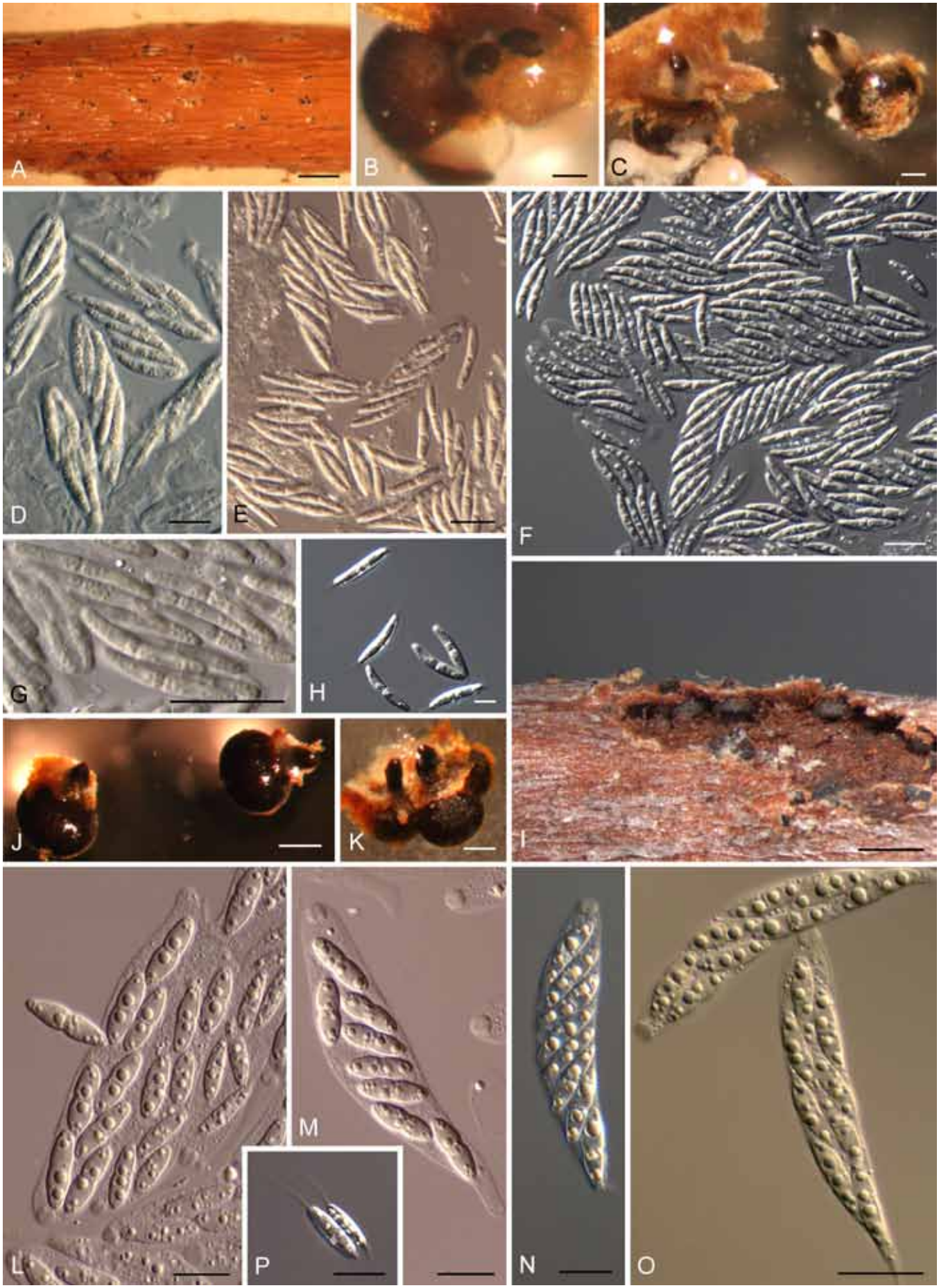

Fig. 5. Morphology on natural substrate. A–H: *Plagiostoma salicellum*: A, B, D, G = Scleromyceti Sueciae 188 (lectotype), C, E, F, H = BPI 843527 (epitype); note whitish stromatic tissue surrounding perithecial neck in Figs 5.5 B and C. I–O: *P. samuelsii*: I, M, P = BPI 878977 (holotype), N–O = BPI 878979. Bars = (A) 1 mm; (I) 500 µm; (C, J) 200 µm; (B, K) 100 µm; (D–G) 20 µm; (H, L–P) 10 µm.

Notes: The application of the name *Sphaeria salicella* Fr. has been the source of confusion and the subject of taxonomic studies since the 1800's. It was clearly specified by Fries (1823) that this name is typified by Fries : Scleromyceti Sueciae 188 issued in 1821. According to Wehmeyer (1933) and Butin (1958) confusion about this name was in part due to the fact that different parts of exsiccati Scleromyceti Sueciae 188 contain different species. One of the two species has the narrowly ellipsoid, elongated ascospores of *P. salicellum* while the other has the broadly ellipsoid ascospores of *P. apiculatum*. Not recognising the confusion regarding Scleromyceti Sueciae 188, Petrak (1921) wrongly suggested that *S. salicella* was characterised by having broadly ellipsoid ascospores and made a new combination *Cryptodiaporthe salicella* (Fr.) Petr. in addition to the new combination *C. apiculata* (Wallr.) Petr. based on *S. apiculata* Wallr. The latter species was wrongly considered to have narrowly ellipsoid, elongated ascospores. It is not clear if Petrak (1921) looked at the type specimen of *S. apiculata* or if he based his conclusions solely on the description of *S. apiculata* by Wallroth (1833).

Wehmeyer (1933) arrived at a conclusion different from that of Petrak (1921). Wehmeyer (1933) studied the exsiccati Scleromyceti Sueciae 188 at the Farlow Herbarium and determined that this number and hence *S. salicella* Fr. were characterised by having narrowly ellipsoid, elongated ascospores. To use his words, *S. salicella* represents "the narrow-spored species". He synonymised *S. salicella* Fr. with *C. apiculata* (Wallr.) Petr. and published the combination *C. salicella* (Fr.) Wehm. (1933) non Petrak (1921). In addition, Wehmeyer (1933) made the new combination *C. salicina* (Curr.) Wehm. based on *S. salicina* Curr. for species having broadly ellipsoid ascospores (see notes under *P. convexum*). Later Butin (1958) studied species of *Cryptodiaporthe* on *Populus* and *Salix,* examined Scleromyceti Sueciae 188 at Uppsala Herbarium, and suggested that *S. salicella* should be understood as the species with broadly ellipsoid ascospores and followed Petrak's concept of *S. salicella*.

We studied the Scleromyceti Sueciae 188 (Sbarbaro collection) available at the BPI Herbarium as well as other exsiccati of taxa that have been synonymised with *S. salicella* and *C. salicina* including *S. apiculata*. In doing so we paid close attention to the original descriptions of *S. apiculata* Wallr. and *S. salicella* Fr. In referring to Scleromyceti Sueciae 188 Fries (1823) described *S. salicella* as having a powdery "albicant" (whitish) stroma and that the multiple ostioles are "erumpent simultaneously". The specimen of Scleromyceti Sueciae 188 at BPI includes all of these morphological characters and has ascospores that are ellipsoid elongated (see Fig. 5A, B, D, and G).

In their treatment of *Plagiostoma*, Sogonov *et al.* (2008) made the combination *Plagiostoma salicellum* (Fr.) Sogonov. In our study of *P. salicellum* we noticed that ascospore length and width can be quite variable, even within an ascus, but with a prevalence of elongated ascospores (Fig. 5A–H). A second specimen, BPI 878975 from Germany on *Salix repens*, was sequenced and determined to be conspecific with the epitype of *P. salicellum* within a major clade containing two other species having cylindrical ostioles and ellipsoid elongated ascospores. Unlike the lectotype and epitype of *P. salicellium*, the ascospores of BPI 878975 are ellipsoid but not elongated. In spite of this difference in ascospore morphology, BPI 878975 is *P. salicellum* based on the cylindrical perithecial neck surrounded by a whitish stroma as well as DNA sequence data.

In summary *Plagiostoma salicellum* is characterised by having cylindrical perithecial necks surrounded by a whitish stroma and ascospores predominantly ellipsoid-elongated, less commonly ellipsoid, tapering to slightly acute, rounded ends (Fig. 5D–G), unlike *P. apiculatum* that has oblong ellipsoid to renoid, broadly rounded ascospores (Fig. 2H–J).

Plagiostoma samuelsii L.C. Mejía, **sp. nov.** MycoBank MB515707. Figs 5I–O, 8M–P.

Etymology: Named in honour of distinguished mycologist Gary J. Samuels for his outstanding contributions to the systematics of Pyrenomycetes.

Perithecia subglobosa, (192–)204–258(–305) µm elata, (295–)302–327(–334) µm diametro, rostrum conicum, (114–)128–161(–170) µm longum, (69–)72–74(–81) µm diametro basi, (58–)62–73(–78) µm diametro apice. Ascosporae ellipticae, uniseptatae, constrictae ubi medianae vel submedianae septatae, (10–)11–12(–19) × 3–4 µm, appendiculatae duabus extremitatibus, anguste filiformes, ascosporis vulgo 2-plo longiores, appendices deliquescentes.

Perithecia immersed in bark, solitary or in groups up to five, scattered on substrate, evident as conical shaped elevations of host periderm with necks protruding through small holes in periderm, black, subglobose, (192–)204–258(–305) µm high × (295–)302–327(–334) µm diam (mean = 239 × 313, SD 43, 16, n = 6), each with one neck. *Neck* eccentric to lateral, surrounded by a whitish stroma, cone-shaped with rounded apex, (114–)128–161(–170) µm long (mean = 145, SD 23, n = 6), (69–)72–74(–81) µm at base (mean = 73.8, SD 3.9, n = 6), (58–)62–73(–78) µm at apex (mean = 67.5, SD 8.0, n = 6). *Asci* cylindric to clavate, (32–)42–62(–79) × (6–)7–11(–12) µm (mean = 53 × 9, SD 13, 2.1, n = 24), apical ring 1.8–3.6 µm diam, with eight ascospores arranged obliquely parallel or biseriate. *Ascospores* ellipsoid, 1-septate, constricted at median to submedian septum, with two deliquescent appendages, one at end of each cell, narrowly filiform, usually twice the length of ascospores, (10–)11–12(–19) × 3–4 µm (mean = 12 × 3.5, SD 1.4, 0.2, n = 48), l : w (2.8–)3.2–3.5(–4.8) (mean = 3.4, SD 0.4, n = 48), with four refractive bodies in each cell, two big ones near septum, one smaller one at end of each cell.

Cultures: Fast growth on PDA after 7 d reaching edge of petri plates of 6 cm diam (n = 8), thin aerial mycelium of felty to granular texture, fringed, stringy margin, with concentric halo of dense mycelium 1.4 cm from centre, buff 45 inside halo or central region, white toward margin, some cultures with depression at concentric halo, reverse honey 64 developing a halo fawn 87 near margin**.**

Habitat and host: On dead, still attached twigs and branches of *Alnus incana* var. *tenuifolia*, *A. rubra*, and *Alnus* spp. (*Betulaceae*).

Distribution: **USA** (California, Oregon, Washington).

Holotype: **USA**, California, Plumas Co., Little Last Chance Creek, Chilcook Campground, on *Alnus incana* var. *tenuifolia*, 17 May 2008, L.C. Mejía 454, BPI 878977, derived CBS 125668 = LCM454.04.

Specimens examined: **USA**, Oregon, Jackson Co., Upper Rogue River, on *Alnus* (*tenuifolia*?), 21 May 2008, L.C. Mejía 419, BPI 878976, derived culture LCM419.01 and LCM419.02; Upper Rogue River trail on *Alnus* sp. 21 May 2008, L.C. Mejía 474, BPI 878978, derived culture LCM474.01; Washington, Clallam Co., Crescent Lake, on *Alnus rubra* (branch on soil), 27 May 2008, L.C. Mejía 596, BPI 878979, derived culture LCM596.01.

Notes: *Plagiostoma samuelsii* is the only species of *Plagiostoma* on leaves of *Alnus* except for *P. jensenii* M.E. Barr. Unlike *P. samuelsii*,

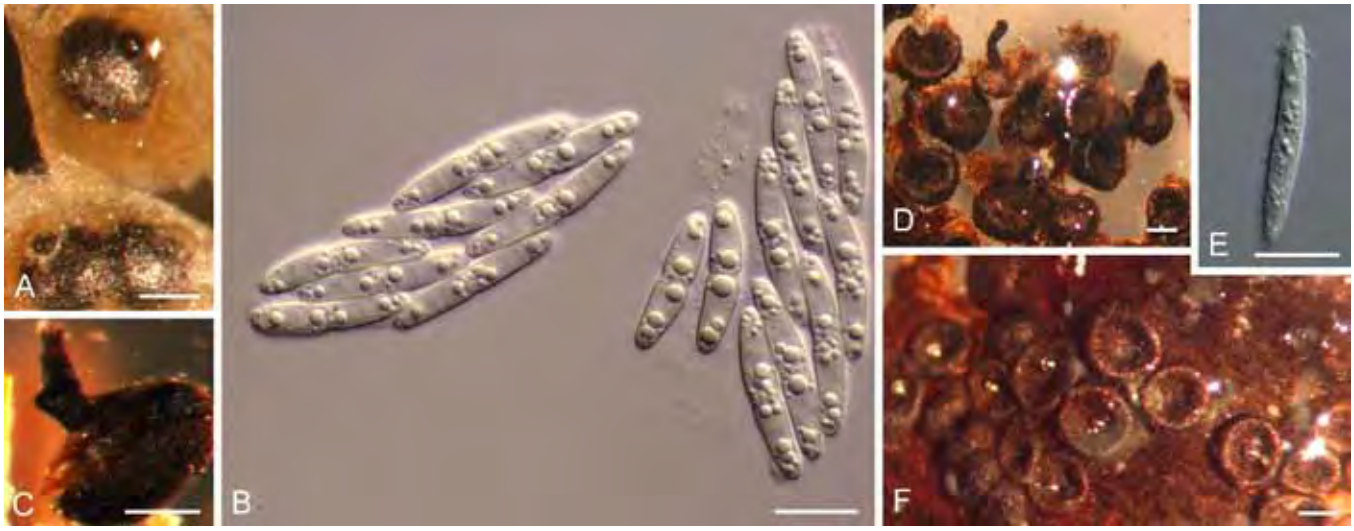

Fig. 6. Morphology on natural substrate. A–C. *Plagiostoma versatile*: A–B = BPI 878980 (holotype), C = BPI 877702. D–F. *P. yunnanense* BPI 878983 (holotype). Bars = (A, C–D, F) 200 µm; (B, E) 10 µm.

P. jensenii lacks a stroma and perithecial neck and has longer and wider ascospores (20–30 × 4–6 µm) with very short pulvinate appendages (Barr 1991). Most likely *P. jensenii* does not belong in *Plagiostoma*.

Plagiostoma versatile L.C. Mejía & Sogonov, **sp. nov.** MycoBank MB515708. Figs 6A–C, 8Q–V.

Etymology: *versatile* – versatile, referring to the occurrence of this species on different plant organs, twigs, branches, and leaves; and to the variable nature of the perithecia that grow with short necks on twigs and branches and with medium to long necks on leaves.

Perithecia subglobosa, (178–)194–317(–345) µm elata, (232–)264–378(–444) µm diametro; rostrum cylindricum, (60–)77–137(–226) µm longum, (51–)56–80(–87) µm diamtro basi, (37–)49–60(–76) µm apice. Ascosporae elliptico-elongatae, uni-septatae, constrictae ubi medianae vel submedianae septatae, (18–)20–23(–25) × 3–4 µm, L:l (4.9–)5.6–6.8(–8.6).

Perithecia immersed in bark of twigs or in midvein and petioles of adaxial and abaxial side of leaves, solitary or in pairs, scattered, on twigs evident as slight elevations of periderm that appear black, upper part of perithecia showing a few cell layers below epidermis, on leaves producing swollen, raised areas on midvein, becoming highly erumpent, cracking periderm and leaving an ellipsoidal cavity, with longer neck on leaves than on twigs, black, subglobose, (178–)194–317(–345) µm high × (232–)264–378(–444) µm diam (mean = 248 × 323, SD 68.5, 78, n = 8), each with one neck. *Neck* eccentric to lateral, short, ostiolar opening sulcate with four grooves, (60–)77–137(–226) µm long (mean = 115, SD 59.7, n = 8), (51–)56–80(–87) µm diam at base (mean = 68.5, SD 13.4, n = 8), (37–)49–60(–76) µm diam at apex (mean = 55, SD 11.8, n = 8). *Asci* cylindric to clavate, (49–)54–66(–71) × (11–)13–16(–20) µm (mean = 60 × 15, SD 7.5, 2.5, n = 15), apical ring 2.0–3.5 µm diam, with eight ascospores arranged biseriate. *Ascospores* ellipsoid elongated, slightly tapering toward rounded ends, 1-septate, constricted at median to submedian septum, (18–)20–23(–25) × 3–4 µm (mean = 21.5 × 3.5, SD 2.0, 0.4, n = 36), l : w (4.9–)5.6–6.8(–8.6) (mean = 6.2, SD 1.0, n = 36), usually with four large refractive bodies, two near septum, one in each end of cells.

Cultures: Fast growth on PDA after 7 d reaching the edge of petri plates of 6 cm diam (n = 12), thin aerial mycelium of felty to granular texture, margin fringed, like roots, buff 45 with clumps of white mycelium, with a halo of elevated mycelium at 1.5 cm from centre, reverse buff 45 becoming dark, with halo visible from reverse.

Habitat and hosts: On dead twigs of *Salix scouleriana* and *Salix* sp., on overwintered leaves of *Salix* sp. (*Salicaceae*).

Distribution: **USA** (Oregon, Washington); **Canada** (British Columbia).

Holotype: **USA**, Washington, Jefferson Co., intersection of Upper Hoh River Road & Route 101, on *Salix scouleriana*, 27 May 2008, L.C. Mejía 594, BPI 878980, derived culture CBS 124978 = LCM594.01.

Additional specimens examined: **Canada**, British Columbia, Vancouver, on overwintered dead leaves of *Salix* sp., 12 May 2006, M. V. Sogonov 379, BPI 877702, derived culture CBS 121251 = AR4294. **USA**, Oregon, Lane Co., Willamette Pass, on *Salix* sp., 22 May 2008, L.C. Mejía 598, BPI 878982, derived culture LCM598.01; Washington, Jefferson Co., Hoh River Campground, on *Salix scouleriana*, 27 May 2008, L.C. Mejía 595, BPI 878981, derived culture LCM595.01.

Notes: The ascospores of this species are similar to those of *Plagiostoma salicellum,* however, the perithecial necks of *P. versatile* lack the whitish stroma characteristic of *P. salicellum.*

Plagiostoma yunnanense L.C. Mejía & Zhu L. Yang, **sp. nov.** MycoBank MB515709. Figs 6D–F, 8W–X.

Etymology: referring to the place where this species was collected: Yunnan, China.

Perithecia globosa, (231–)267–311(–318) µm elata, (282–)312–352(–362) µm diametro, rostrum cylindricum, contortum, (315–)318–321(–322) µm longum, (77–)78–81(–82) µm diametro basi, (57–)59–63(–66) µm diametro apice. Ascosporae elliptico-elongatae, uni-septatae, leviter vel non constrictum ubi septatae, (19–)23–26(–27) × 3–4, L:l (6. 6–)6.8–7.9(–8.2).

Perithecia immersed, solitary or in groups, numerous, appearing as conical elevations of periderm where necks protrude, black, globose, (231–)267–311(–318) µm high × (282–)312–352(–362) µm diam (mean = 284 × 328, SD 48, 42, n = 3), each with one neck. *Neck* eccentric, contorted, (315–)318–321(–322) µm long (mean = 319, SD 3.8, n = 3), (77–)78–81(–82) µm diam at base (mean = 79,

SD 2.4, n = 3), (57–)59–63(–66) µm diam at apex (mean = 61, SD 4.8, n = 3). *Asci* not observed. *Ascospores* ellipsoid-elongate, with rounded ends, 1-septate, slightly or not constricted at median to submedian septum, (19–)23–26(–27) × 3–4 µm (mean = 24 × 3.3, SD 2.7, 0.4, n = 6), l : w (6.6–)6.8–7.9(–8.2) (mean = 7.3, SD 0.7, n = 6), with granular cytoplasm.

Cultures: Moderate growth on PDA after 7 d a.c.d. 3.4 cm (SD 0.2, n = 4). Mycelium of granular texture, margin stringy, whitish with granules, becoming grey or vinaceous buff, reverse with dark inclusions near centre, most of colony whitish.

Habitat and host: On dead, still attached branches of *Salix* sp. (*Salicaceae*).

Distribution: China (Yunnan).

Holotype: **China**, Yunnan, Ailoshan, on *Salix* sp., 14 Jul. 2008, L.C. Mejía 513, BPI 878983, derived cultures CBS 124979 = LCM513.03 and LCM513.02.

Additional names in *Cryptodiaporthe* and *Plagiostoma*

Cryptodiaporthe acerinum J. Reid & Cain, Canad. J. Bot. 40: 839. 1962.

Notes: A fresh specimen determined to be this species was cultured and sequenced. Analyses of LSU and RPB2 sequences place this species in a basal branch of the *Gnomoniaceae*.

Specimen examined: **USA**, New York, Adirondacks, Cranberry Lake, on dead branch of *Acer* sp., 13 Jun. 2002, L. Vasilyeva, BPI 870989, culture CBS 121465 = AR 3822.

Cryptodiaporthe aculeans (Schwein.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates p. 212. 1933.
Basionym: *Sphaeria aculeans* Schwein., Trans. Am. Phil. Soc., New Series 4(2): 204. 1834,. [1832].

Notes: The only available culture of this species was sequenced. Analyses of LSU sequences place this species in a clade sister to the *Melanconidaceae*.

Culture sequenced: **Japan**, on branch of *Rhus javanica*, isol. G. Okada, CBS 525.85.

Cryptodiaporthe aubertii (Westend.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates 202. 1933.
Basionym: *Sphaeria aubertii* Westend., Bull. Acad. R. Sci. Belg., Cl. Sci., sér. 2: tab. 7, no. 5. 1859.

Notes: A culture of this species was sequenced. Analyses of this LSU sequence suggests that this species is related to the genus *Cryptosporella* within the *Gnomoniaceae*.

Culture sequenced: **Sweden**, Småland, on *Myrica gale*, 14 Apr. 1989, K. & L. Holm, isol. O. Constantinescu 89–53, CBS 114196.

Cryptodiaporthe galericulata (Tul. & C. Tul.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates p. 211. 1933.
Basionym: *Valsa galericulata* Tul. & C. Tul., Select. Fung. Carpol. (Paris) 2: 203. 1863.

Notes: A fresh specimen determined to be this species was cultured and sequenced. Analyses of LSU sequences suggest this species belongs in the *Sydowiellaceae*.

Specimen examined: **USA**, Tennessee, Great Smoky Mts. National Park, near Cosby, Horse Trail, on *Fagus grandifolia*, 25 Mar. 2002, L. Vasilyeva, BPI 863767 ex culture AR 3811.

Cryptodiaporthe liquidambaris Petr., Sydowia 5: 236. 1951.

Notes: A fresh specimen determined to be this species was cultured and sequenced. Analyses of LSU sequences place this species within the *Diaporthales* but not within any described family.

Specimen examined: **USA**, Maryland, Beltsville, on overwintered twig of *Liquidambar styraciflua*, 15 May 2001, M. Barr, isol. A. Rossman, BPI 749123 culture AR 3648 (now dead).

Cryptodiaporthe macounii (Dearn.) Wehm., The Genus *Diaporthe* Nitschke and its Segregates p. 191. 1933.
Basionym: *Diaporthe macounii* Dearn., Mycologia 8: 100. 1916.

Note: This species was included in the genus *Gnomoniopsis* (*Gnomoniaceae*) by Sogonov *et al.* (2008).

Cryptodiaporthe vepris (Delacr.) Petr., Ann. Mycol. 32: 445. 1934.
Basionym: *Sphaeria vepris* Delacr., Fungi europ. 443. 1862.

Notes: A fresh specimen determined to be this species was cultured and sequenced. Analyses of LSU sequences place this species within the *Diaporthales* but not in any described family.

Specimen examined: **Austria,** Wograda, St. Margareten, Kaernten, on *Rubus idaeus*, 27 Oct. 2000, W. Jaklitsch 1661, isol. A. Rossman, BPI 749132, culture AR 3559.

Plagiostoma acerophilum (Dearn. & House) M.E. Barr, Mycol. Mem. 7: 113. 1978.
Basionym: *Gnomoniopsis acerophila* Dearn. & House, Bull. New York State Mus. 233–234: 36. 1921.

Notes: A fresh specimen determined to be this species was cultured and sequenced. This species falls within the *Gnomoniaceae* according to analyses of ITS sequences but not within any known genus. The perithecial neck of this species is lateral, upright, and slightly curved at the apex.

Specimens examined: **USA**, New York, Sullivan Co., Roscoe, on overwintered leaves of *Acer pensylvanicum*, Jul. 2005, M.V. Sogonov MS 0302, BPI 877681; Tennessee, Blount Co., Great Smoky Mountains National Park, Cades Cove, on overwintered petioles of *Acer pensylvanicum*, 24 May 2006, M.V. Sogonov MS 0467, BPI 877679; Sevier Co., Great Smoky Mountains National Park, on overwintered leaves and petioles of *Acer pensylvanicum*, 22 May 2006, M.V. Sogonov MS 0473, BPI 877682.

Plagiostoma alneum (Fr.) Arx, Antonie van Leeuwenhoek 17: 264. 1951.
= *Sphaeria alnea* Fr. : Fr., Observ. mycol. 1: 185. 1815 : Syst. Mycol. 2: 520. 1823.

Notes: This species is now regarded as *Gnomonia alnea* (Fr.) Sogonov and was described and illustrated in Sogonov *et al.* (2008).

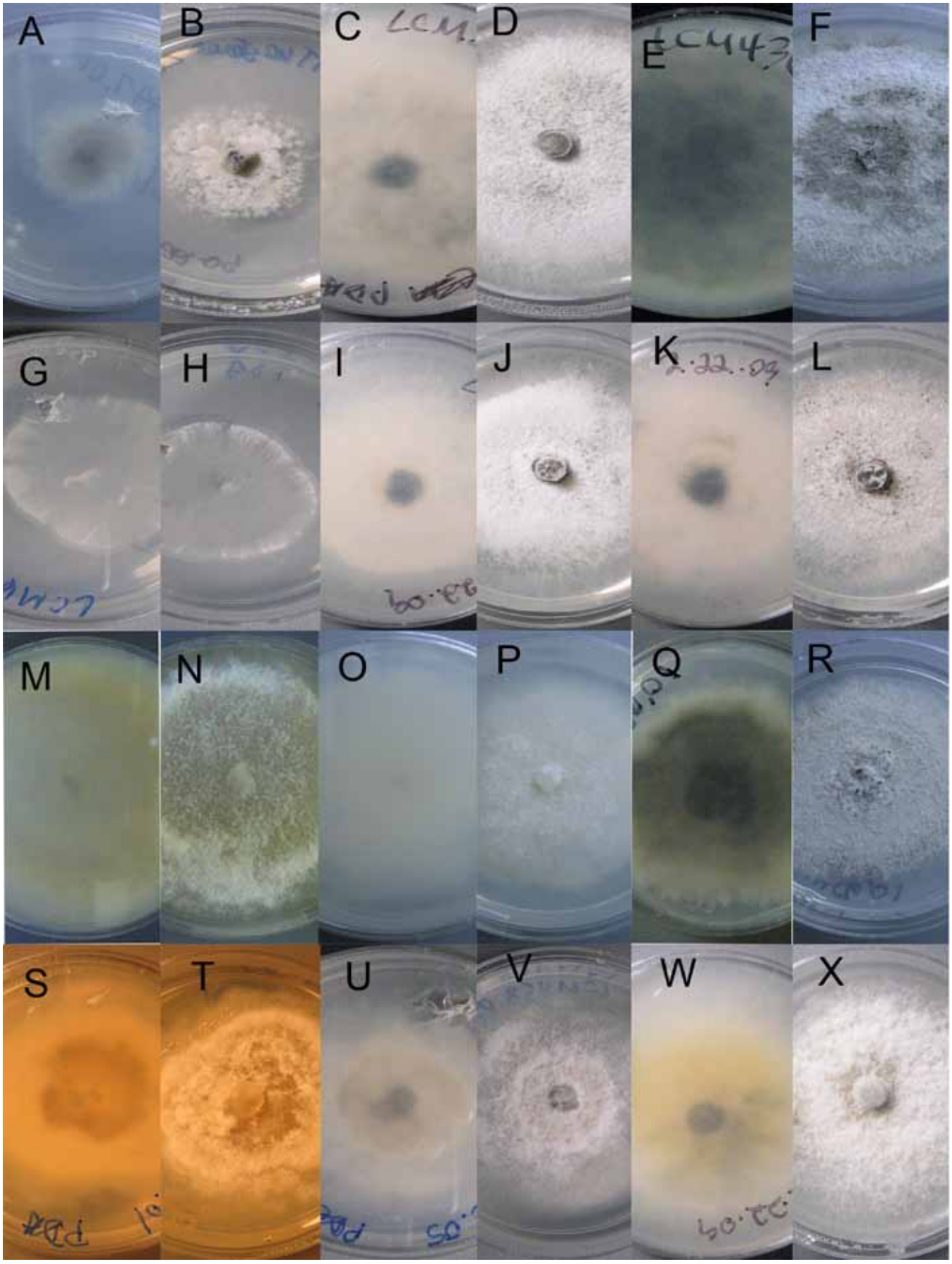

Fig. 7. Culture morphology. A–B. *Plagiostoma aesculi*. CBS 126127 = LCM447.01. C–F. *P. apiculatum*. C–D. LCM 393.01. E–F. CBS 126126 = LCM436.01. G–H. *P. barriae*. LCM 601.02. I–L. *P. dilatatum*. I–J. LCM 402.01. K–L. LCM 403.01. M–P. *P. exstocollum*. M–N. LCM 422.02. O–P. LCM 468.02. Q–R. P. *imperceptibile*. LCM 456.01. S–T. *P. oregonense*. Ex-type CBS 126124 = LCM 597.01. U–V. *P. ovalisporum*.LCM 458.05. W–X. *P. petiolophilum*. CBS 126123 = LCM 181.01. A–D, I–L, W–X. Colony habit, 10 d, 23 °C. E–H, M–R, U–V. Colony habit, 9 d, 23 °C. S–T. Colony habit, 7 d, 23 °C. A, C, E, G, I, K, M, O, Q, S, U, W. Reverse. B, D, F, H, J, L, N, P, R, T, V, X. Surface.

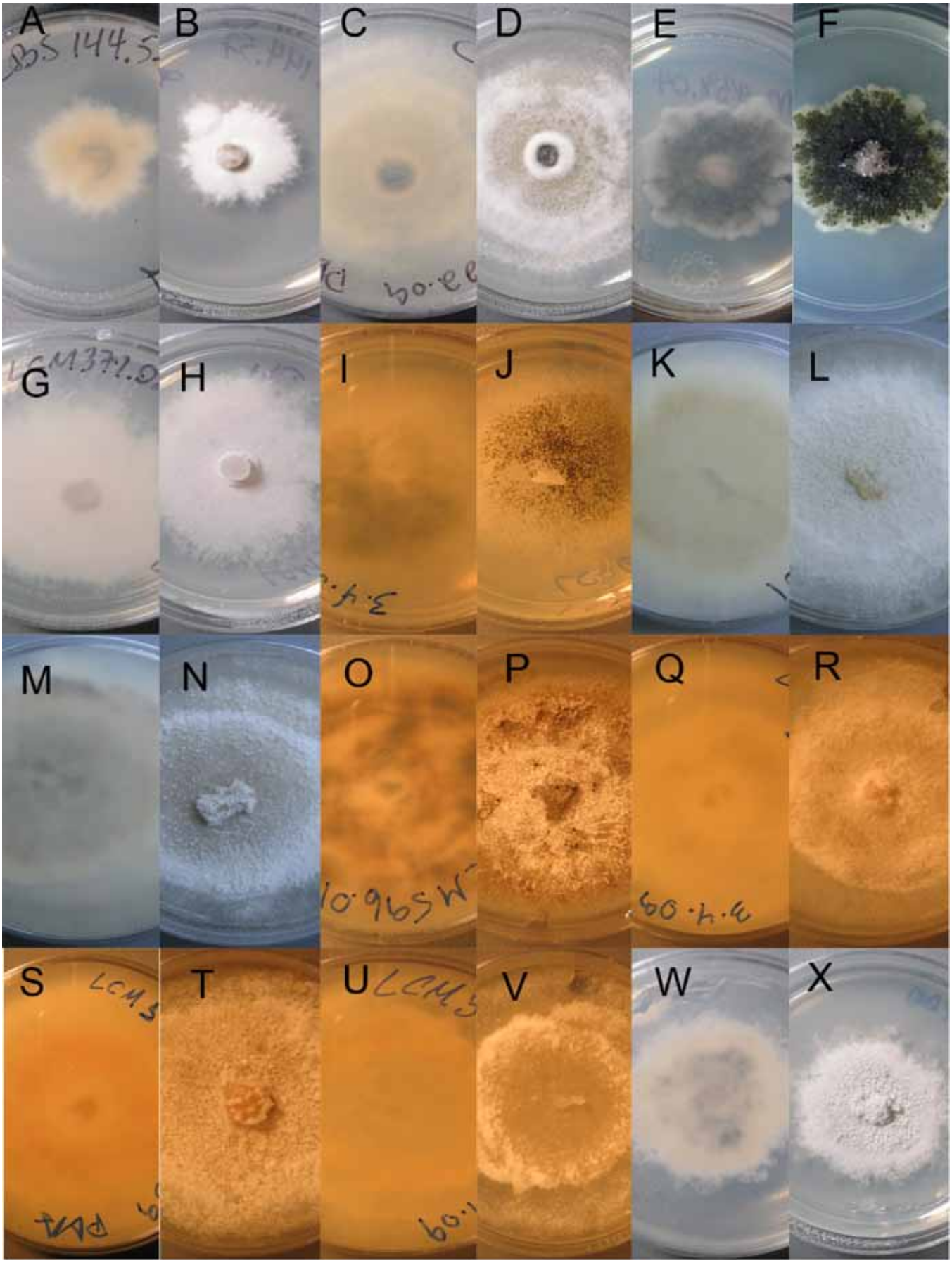

Fig. 8. Culture morphology. A–D. *Plagiostoma populinum*. A–B. CBS 144.57. C–D. CBS 174.58. E–J. *P. pulchellum*. E–F. LCM 438.04. G–H. LCM 371.02. I–J. LCM 623.01. K–L. *P. salicellum*. CBS 126121 = LCM449.01. M–P. *P. samuelsii*. M–N. Ex-type CBS 125668 = LCM 454.04. O–P. LCM 596.01. Q–V. *P. versatile*. Q–R. Ex-type CBS 124978 = LCM 594.01. S–T. LCM 595.01. U–V. LCM 598.01. W–X. *P. yunnanense*. Ex-type CBS 124979 = LCM 513.03. A–D, G–H, W–X. Colony habit, 10 d, 23 °C. E–F, K–N. Colony habit, 9 d, 23 °C. I–J, O–V. Colony habit, 7 d, 23 °C. A, C, E, G, I, K, M, O, Q, S, U, W. Reverse. B, D, F, H, J, L, N, P, R, T, V, X. Surface.

Plagiostoma arnstadtiense (Auersw.) M. Monod, Beihefte Sydowia 9: 143. 1983.
Basionym: *Gnomonia arnstadtiensis* Auersw. in Gonnerm. & Robenh., Mycol. Europ. 5/6: 22. 1869.

Notes: This species is now accepted in *Gnomonia* according to Sogonov *et al*. (2008).

Plagiostoma bavaricum (Rehm) M.E. Barr, Mycol. Mem. 7: 112. 1978.
Basionym: *Hypospila bavarica* Rehm, Ann. Mycol. 6:322. 1908.

Note: Based on an LSU sequence, this species belongs in the *Gnomoniaceae* but it cannot be placed in a genus.

Culture sequenced: **Switzerland**, on *Acer opalus*, M. Monod, CBS 772.79.

Plagiostoma conradii (Ellis) M.E. Barr, Mycol. Mem. 7: 107. 1978.
Basionym: *Diaporthe conradii* Ellis, Am. Nat. 17: 316. 1883.

Notes: A fresh specimen determined to be this species was cultured and sequenced. Analysis of the LSU sequence suggests this species is closely related to *Cryptodiaporthe aubertii* and *Cryptosporella* but not within any known genus in the *Gnomoniaceae*. The perithecial neck of this species is lateral and upright.

Specimen examined: **USA**, New Jersey, on living stems of *Hudsonia tomentosa*, G. Bills, BPI 746482, culture CBS 109761 = AR 3488.

Plagiostoma inclinatum (Auersw.) M.E. Barr, Mycol. Mem. 7: 115. 1978.
Basionym: *Gnomonia inclinata* Auersw. in Rabenh., Mycol. Europ. 5/6: 27. 1869.
[≡ *Sphaeria inclinata* Desm., Ann. Sci. Nat. Bot. III, 16: 315. 1851 non Schwein. 1832]

Notes: Two isolates of this species were sequenced. This species apparently belongs in the *Gnomoniaceae* but it cannot be placed in a genus.

Cultures sequenced: **The Netherlands**, on dead leaf of *Acer pseudoplatanus*, CBS 209.67. **Switzerland**, on *Acer platanoides*, M. Monod, CBS 830.79.

Plagiostoma jensenii M.E. Barr, Mycotaxon 41: 298. 1991.

Note: Based on the lack of a perithecial neck and the pulvinate appendages on the ascospores, *P. jensenii* most likely does not belong in *Plagiostoma*.

Plagiostoma lugubre (P. Karst.) Bolay, Ber. Schweiz. Bot. Ges. 81: 436. 1972.
Basionym: *Gnomonia lugubris* P. Karst., Bidr. Känn. Finl. Nat. Folk 23: 121. 1873.

Note: The disposition of this species was not investigated in this study.

Plagiostoma magnoliae (Ellis) M.E. Barr, Mycol. Mem. 7: 117. 1978.
Basionym: *Gnomonia magnoliae* Ellis, Amer. Nat. 17: 318. 1883.

Notes: This species has been reported in leaves of *Magnolia virginiana* in North America. The perithecial neck of this species is lateral and obliquely upright as drawn by Barr (1978). The disposition of this species was not investigated in this study.

Plagiostoma micromegalum (Ellis & Everh.) M.E. Barr, Mycol. Mem. 7: 112. 1978.
Basionym: *Diaporthe micromegala* Ellis & Everh., Proc. Acad. Nat. Sci. Philadelphia 1893: 449. 1894.

Notes: This species is now placed in *Ophiognomonia* as *O. micromegala* (Ellis & Everh.) Sogonov according to Sogonov *et al.* (2008).

Plagiostoma petrakii (E. Müll.) M. Monod, Beihefte Sydowia 9: 146. 1983.
Basionym: *Plagiostigme petrakii* E. Müll., Sydowia 18:90. 1965.

Note: No material of this species was located.

Plagiostoma pseudobavaricum M. Monod, Beihefte Sydowia 9: 151. 1983.

Notes: ITS sequences of this species were included in a phylogenetic analysis. Although closely related to *Apiognomonia* and *Plagiostoma,* the results suggest that this species may represent an undescribed genus within the *Gnomoniaceae*.

Specimens examined: **USA**, New York, Adirondack Mts., Cranberry Lake, on petioles of *Acer* sp., 22 Jun. 2002, L. Vasilyeva, BPI 843494, ex culture AR 3819; *ibid*., 23 Jun. 2002, L. Vasilyeva, BPI 843495, ex culture AR 3894; Tennessee, Sevier Co., Great Smokey Mountains National Park, on overwintered petioles of *Acer saccharum*, 22 May 2006, M.V. Sogonov MS 0483, BPI 877700.

Plagiostoma robertiani (Petr.) M.E. Barr, Mycol. Mem. 7: 113. 1978.
Basionym: *Gnomonia robertiani* Petr., Ann. Mycol. 23: 122. 1925.

Note: No material of this species was located.

Plagiostoma tormentillae (Lind) Bolay, Ber. Schwiz. Bot. Ges. 81: 436. 1971.
Basionym: *Gnomoniella tormentillae* Lind, Bot. Tidsskr. 41: 217. 1931.

Note: This species is now recognised as *Gnomoniopsis tormentillae* (Lind) Sogonov according to Sogonov *et al.* (2008).

ACKNOWLEDGEMENTS

This work was funded by the National Science Foundation Partnerships for Enhancing Expertise in Taxonomy (NSF 03-28364). Additional funding for field work by LCM was received through Rutgers University, New Brunswick, NJ, from the Neyra Fund, the Spencer Davis Research Award from the Department of Plant Biology and Pathology, a Special Study Support Award, and a Graduate School Travel Award and through the Backus Award from the Mycological Society of America. Much appreciation is extended to Lena Struwe for her valuable comments and insights during the course of this work. We acknowledge and appreciate

Andrew Minnis for providing a specimen from which the new species *Plagiostoma ovalisporum* was described and for nomenclatural advice. Christian Feuillet kindly provided translations of the diagnoses into Latin. Tunesha Phipps and Sasha Allen are sincerely acknowledged for their technical expertise in the molecular laboratory. LCM appreciates the following people for graciously hosting visits for collecting and facilitating the shipment of specimens: Michael Giraurd, Adriana Hladki, Tina Hoffman, Christian Lechat, Christophe Lecuru, and Ralph Mangelsdorff. Special thanks to Zhu LiangYang for hosting LCM and providing superb logistical support during his collecting trip in China.

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SUPPLEMENTARY INFORMATION

Table 1a. Reference taxa with sequences obtained from GenBank used in phylogenetic analysis of *Acremonium* and related organisms. Collection and GenBank numbers are indicated. Dashes indicate missing data in the two-gene analysis.

Spieces name	Collection#	nuLSU	nuSSU	Notes
Albertiniella polyporicola	CBS 457.88	AF096185	AF096170	
Albosynnema elegans	GB3101	AF193226		
Ambrosiella xylebori	CBS 110.61	DQ470979	DQ471031	
Aniptodera chesapeakensis	ATCC 32818	U46882	U46870	
Annulatascus triseptatus	SMH 2359	AY346257	–	
Anthostomella torosa	JK 5678E	DQ836902	DQ836895	
Apiognomonia errabunda	AR 2813, CBS 109747	AF408334	DQ862045	
Apiosordaria verruculosa	F-152365	AY346258	–	
Apiospora montagnei	CBS 212.30	DQ471018	–	
Balansia henningsiana	GAM 16112	AY489715	AY489683	
Beauveria bassiana	IFO4848	AB027382		
Bertia moriformis	SMH 4320	AY695260		
Bionectria grammicospora	GJS 85-218	AF193238		
Bionectria ochroleuca 1	CBS 193.74	U00750		
Bionectria ochroleuca 2	AFTOL 187	DQ862027	DQ862044	
Bionectria pityrodes	ATCC 208842	AF193239		
Blistum tomentosum	Arsef 5353	AY259545		
Bombardia bombarda	AFTOL 967	DQ470970	DQ471021	
Botryotinia fuckeliana	OSC 100012	AY544651	AY544695	
Bulbithecium hyalosporum	CBS 318.91	AF096187		
Calonectria morganii	ATCC 11614	U17409		
Camarops amorpha	SHM 1450	AY780054	–	
Camarops microspora	CBS 649.92	AY083821	DQ471036	
Camarops tubulina	SMH 4614	AY346266	–	
Camarops ustulinoides	DEH 2164	DQ470941	DQ470989	
Cephalotheca sulfurea	CBS 135.34	AF096188	AF096176	
Ceratocystis fimbriata	TCH C89	U17401	U32418	
Cercophora newfieldiana	SMH 2622	AF064642	–	
Cercophora striata	SMH 4036	AY780066	–	
Cercophora terricola	ATCC 200395	AY780067	–	
Ceriosporopsis halima	JK 5473F	U47844	U47843	
Chaetosphaerella phaeostroma	SMH 4585 (a)	AY346274	–	
Chaetosphaeria aterrima	MR 871	AF178565		
Chaetosphaeria ovoidea	SMH 2605	AF064641	–	
Chalara aurea	CBS 729.69	AF222449	AF222503	
Chaunopycnis alba 1	G. Bills 5123	AF245296		
Chaunopycnis alba 2	Merck GB5123	AF245296		
Chaunopycnis pustulata	MF5368LR	AF373282		
Chromendothia citrina	AR 3445	AF408335	DQ862046	
Chrysoporthe cubensis	CBS 101281	AF408338	DQ862047	
Cladobotryum rubrobrunnescens	CBS 176.92	AF160228		
Claviceps purpurea	GAM 12885	AF543789	AF543765	
Clypeosphaeria phillyreae	–	AF452043		
Coniochaeta discoidea	SANK 12878	AY346297	–	
Coniochaeta ostrea	CBS 507.70	DQ470959	DQ471007	
Coniochaeta savoryi	TRTC 51980	AY346276	–	

Table 1. (Continued).

Spieces name	Collection#	nuLSU	nuSSU	Notes
Cordyceps cardinalis	OSC 93609	AY184962	AY184973	
Cordyceps militaris	NRRL 28021	AF049166		
Cordyceps ramosopulvinata	–	AB027372		
Corollospora maritima	JK 4834	U46884	U46871	
Cosmospora episphaeria	GJS 88-29	AY015625		
Cosmospora vilior	ATCC 16217	U57348		
Cryphonectria parasitica	ATCC 38755	–	DQ862048	
Cryptodiaporthe aesculi	CBS 109765	DQ836905	DQ836899	
Cryptosporella hypodermia	CBS 171.69	DQ862028	DQ862049	
Cylindrocarpon cylindroides	CCFC 226722	AY283551		
Dematiocladium celtidis	CBS 115994	AY793438		
Diaporthe eres	CBS 109767	AF408350	DQ471015	
Diaporthe phaseolorum	NRRL 13736	U47830	L36985	
Diatrype disciformis	CBS 197.49	DQ470964	DQ471012	
Didymostilbe echinofibrosa	AR 2824	AY489706		
Didymostilbe matsushimae	CCFC 54984	AY283545		
Doratomyces stemonitis	CBS 127.22	DQ836907	DQ836901	
Echinodothis tuberiformis	JF. White s.n.	U57083		
Elaphocordyceps capitata	OSC 71233	AY489721	AY489689	
Elaphocordyceps longisegmentis	OSC 110992	EF468816		
Elaphocordyceps ophioglossoides	OSC 106405	AY489723	AY489691	
Emericellopsis terricola	CBS 120.40 T	U57082		
Endothia gyrosa	CBS 112915	DQ470972	DQ836898	
Epichloe typhina	KCetCV188-1	U17396	U32405	
Eutypa lata	CBS 208.87	DQ836903	DQ836896	
Fragosphaeria purpurea	CBS 133.34	AF096191	AF096176	
Fusarium dimerum	IP 1516	AF130378		
Fusarium domesticum	CBS 434.43	AY230194		
Fusarium falciforme	CBS 475.67	AY097319		
Fusarium lichenicola	CBS 109048	AY097324		
Fusarium oxysporum 1	NRRL 13307	U34542		
Fusarium oxysporum 2	NRRL 22902	U34537		
Fusarium solani	CBS 102556	AY097317		
Fusarium verticillioides	NRRL 22172	U34526		
Gelasinospora tetrasperma	CBS 178.33	DQ470980	DQ471032	
Geosmithia lavendula	IFO 7729	D88325	D14405	
Geosmithia putterillii	IFO 31131	AB047215	AB031390	
Glomerella cingulata	HKUCC 9036	AY083820	AF543762	
Gnomonia gnomon	CBS 199.53	AF408361	DQ471019	
Graphium penicillioides	CBS 506.86	AF027384	DQ471038	
Graphostroma platystoma	CBS 270.87	DQ836906	DQ836900	
Halosphaeria appendiculata	CBS 197.60	U46885	U46872	
Hapsidospora irregularis	ATCC 22087	AF096192		
Haptocillium sinense	CBS 131.95	AF339546		
Haptocillium zeosporum	CBS 335.80	AF339540		
Heleococcum japonicum	ATCC 18157	U17429		
Heliscus lugdunensis	NRRL 20592	U88128		
Hydropisphaera erubescens 1	ATCC 36092	AF193229	AY545722	

Table 1. (Continued).

Spieces name	Collection#	nuLSU	nuSSU	Notes
Hydropisphaera erubescens 2	ATCC 36093	AY545722		
Hydropisphaera peziza 1	GJS 92-101, CBS 102038	AF193232		
Hydropisphaera peziza 2	BPI 802846	AY489730		
Hyperdermium bertonii	–	AF242354		
Hypocrea americana	OSC 100005	AY544649	NG016487	
Hypocrea koningii	ATCC 64262	AF127149		
Hypocrea lutea	ATCC 208838	AF543791	AF543768	
Hypomyces chlorinigenus	G. Arnold i43	AF213027		
Hypomyces subiculosus	GJS 83-288, CBS 123056	AJ459309		
Immersiella immersa	SMH 4104	AY436409	–	
Isaria javanica	Arsef 322	AF339533		
Isaria takamizusanensis	NHJ 3582	EU369034		
Kallichroma glabrum	JK 5123	AF193233		
Lanatonectria flavolanata 1	CCFC 216608	AY281098		
Lasiosphaeria hispida	SHM 3336	AY436419	–	
Lasiosphaeria ovina	SMH 4605	AY436413	DQ836894	
Lasiosphaeriella nitida	SMH 1664	AY346289	–	
Lecanicillium antillanum	CBS 350.85	AF339536		
Lecanicillium aranearum T	CBS 726.73a	AF339537		Type of *Cephalosporium aranearum*
Lecanicillium attenuatum	CBS 402.78	AF339565		
Lecanicillium dimorphum T	CBS 363.86	AF339559		Type of *Aphanocladium dimorphum*
Lecanicillium fusisporum T	CBS 164.70	AF339549		Type of *Verticillium fusisporum*
Lecanicillium lecanii	CBS 101247	AF339555		
Lecanicillium psalliotae 1	IMI 163640	AF339557		
Lecanicillium aff. *psalliotae* 2	CBS 639.85	AF339561		
Leotia lubrica	OSC 100001	AY544644	AY544687	
Leuconectria clusiae	AR 2706	U17412		
Leucostoma niveum	AR 3413, CBS 109489	AF362558	DQ862050	
Lignincola laevis	JK 5180A	U46890	U46873	
Lindra thalassiae	JK 5090A	DQ470947	DQ470994	
Linkosia fusiformis	HKUCC 10824	DQ408571		
Linocarpon appendiculatum	ATCC 90499	AY346291	–	
Lulworthia grandispora	JK 4686	DQ522856	DQ522855	
Mazzantia napelli	AR 3498, CBS 109769	AF408368	DQ862051	
Melanconis alni	AR 3500, CBS 109773	AF408371	DQ862052	
Melanconis marginalis	AR 3442, CBS 109744	AF408373	DQ862053	
Melanconis stilbostoma	AR 3501, CBS 109778	AF408374	DQ862054	
Melanochaeta hemipsila	SMH 2125	AY346292	–	
Melanopsamma pomiformis	ATCC 18873	AY489709		
Melanospora brevirostris	ATCC 42427	AY015627		
Melanospora tiffanii	ATCC 15515	AY015630	AY015619	
Melanospora zamiae	ATCC 12340	AY046579	AY046578	
Menispora tortuosa	DAOM 231154	AY544682	AY544723	
Metarhizium anisopliae var. *frigidum*	Arsef 4606	AF339529		
Microascus longirostris	CBS 267.49	AF400865	DQ471026	
Microascus trigonosporus	CBS 218.31	DQ470958	DQ471006	
Microglossum rufum	OSC 100641	DQ470981	DQ471033	
Mycoarachis inversa	ATCC 22107	U00745		

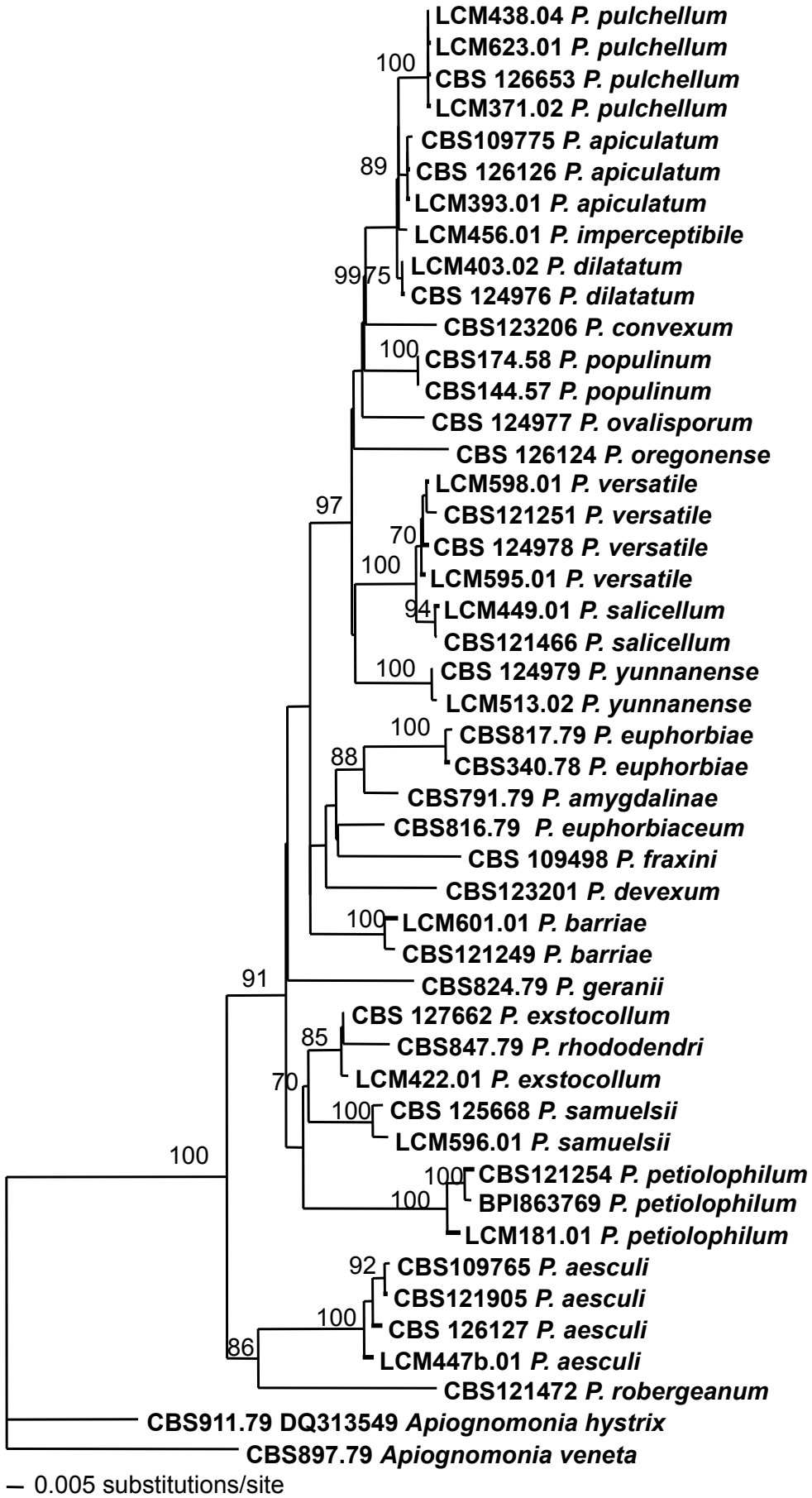
Table 1. (Continued).

Spieces name	Collection#	nuLSU	nuSSU	Notes
Mycogone rosea	TFC 96-62	AF213031		
Mycopepon smithii	SMH 1609	AF279400		
Myrothecium cinctum	ATCC 22270	AY489710		
Myrothecium inundatum	IMI 158855	AY489731		
Myrothecium leucotrichum	AR 3506, CBS 114052	AY489707		
Myrothecium roridum 1	ATCC 16297	AY489708	AY489676	
Myrothecium roridum 2	BBA 67679	AJ301995		
Myrothecium verrucaria	BBA 70749	AJ301999		
Nalanthamala psidii	CBS 912.85	HQ232161		
Nalanthamala squamicola	–	AF373281		
Nalanthamala vermoesenii	CBS 137.24	AY554260		
Nectria cinnabarina	GJS 89-107	U00748	U32412	
Nectria haematococca	GJS 89-70, CBS 114067	AY489729	AY489697	
Nectria radicicola	AR 2553	U17415		
Nectria rigidiuscula	IFO 30918	AB084302		
Nectria sesquicillii	ATCC 66880	AF193241		
Nectria zonata	AR 1612	U17424		
Nectriopsis sporangiicola	ATCC 26542	U00753		
Nectriopsis squamulosa 1	AR 1464	U17423		
Nectriopsis squamulosa 2	AR 1464	U17423		
Nectriopsis violacea	MUCL 40056	AF193242		
Neomunkia sydowii	–	AY327047		
Neurospora crassa	MUCL 19026	AF286411	X04971	
Niesslia exilis 1	CBS 560.74	AY489720	AY489688	
Niesslia exilis 2	CBS 357.70	AY489718		
Nigrosabulum globosum	ATCC 22102	AF096195		
Nimbospora effusa	JK 5104A	U46892	U46877	
Nohea umiumi	JK 5103F	U46893	U46878	
Ochronectria calami	ATCC 46694	AF193244		
Ophiocordyceps bispora	KVL 606	AF009654		
Ophionectria trichospora	CBS 109876	AF543790		
Ophiostoma piliferum 1	CBS 158.74	DQ470955	DQ471003	
Ophiostoma piliferum 2	–	AF221010		
Ophiostoma stenoceras	CBS 139.51	DQ836904	DQ836897	
Paecilomyces farinosus	PFA 2169	AF172341		
Paecilomyces lilacinus 1	Arsef 2181	AF339534		
Papulosa amerospora	JK 5547F	DQ470950	DQ470998	
Parasarcopodium ceratocaryi	CBS 110664	AY425026		
Peethambara spirostriata	CBS 110115	AY489724	AY489692	
Peethambara sundara	CBS 646.77	AF193245		
Petriella setifera	ATCC 26490	U48421	DQ471020	
Persiciospora africana	ATCC 64691	AY015631		
Phaeoacremonium aleophilum	Harrington A207	AY249088		
Plagiostoma euphorbiae	CBS 340.78	AF408382	DQ862055	
Plectosphaerella cucumerina	FAU508/NRRL20430	U17399	AF176951	
Pleurodesmospora coccorum	CBS 101284	AF339564		
Pochonia bulbillosa 1	CBS 145.70	AF339542		
Pochonia chlamydosporia var. *catenulatum* T	CBS 504.66	AF339544		Type of *Diheterospora catenulata*

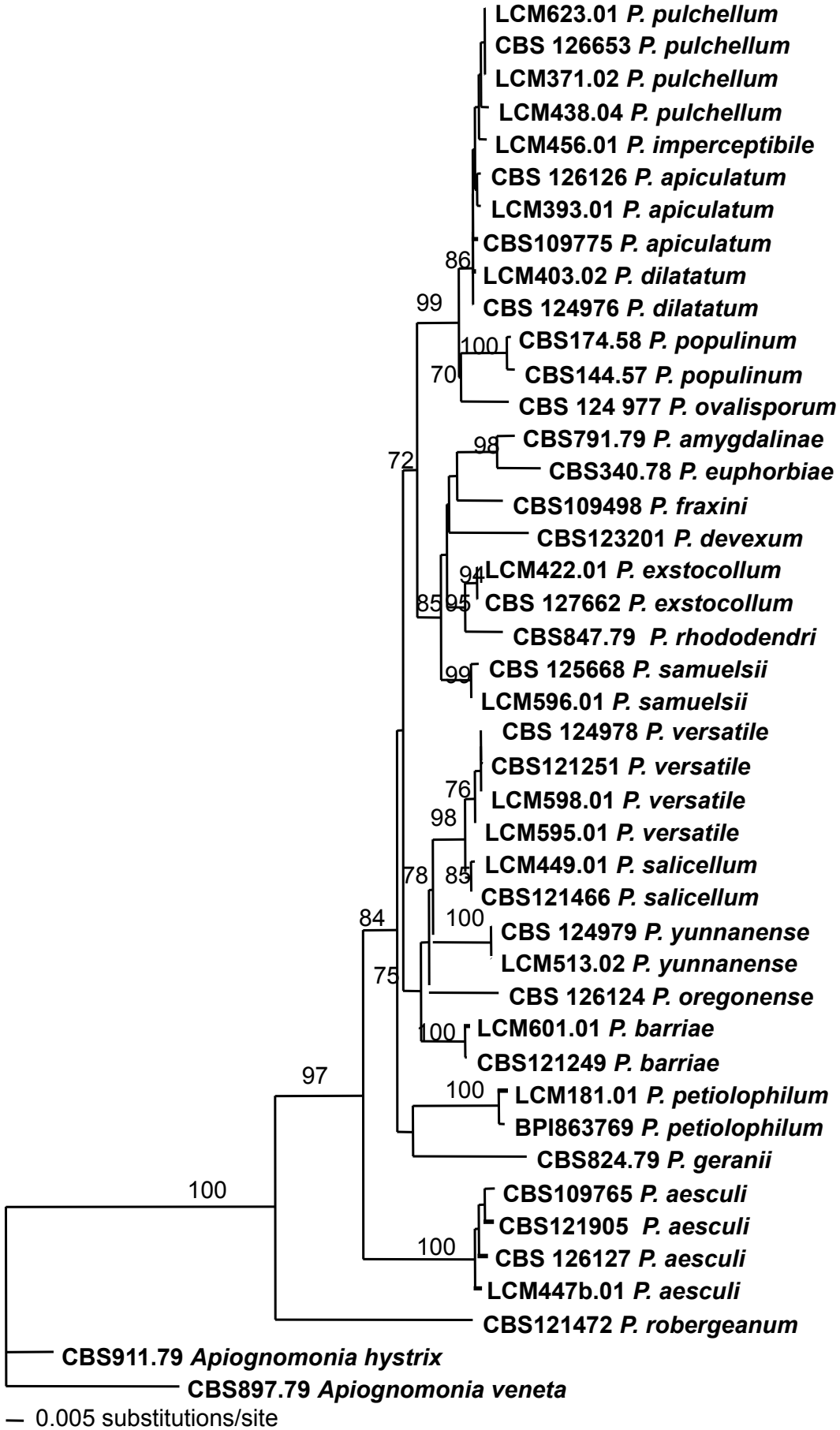
Table 1. (Continued).

Spieces name	Collection#	nuLSU	nuSSU	Notes
Pochonia gonioides	CBS 891.72	AF339550		
Pochonia rubescens	CBS 464.88	AF339566		
Podospora decipiens	CBS 258.64	AY780073	–	
Podospora fibrinocaudata	TRTC 48343	AY780074	–	
Pseudeurotium zonatum	CBS 329.36	AF096198	DQ471040	
Pseudonectria rousseliana	AR 2716, CBS 114049	U17416	AF543767	
Pseudonectria sp.	AR 2721	U17420		
Roumegueriella rufula	CBS 346.85	U00754	DQ522561	
Rubrinectria olivacea	CBS 102268	AY554244		
Scopinella solani	CBS 770.84	AY015632		
Selinia pulchra	AR 2750	AF193246		
Sesquicillium microsporum	G. Bills 5311	AF245298		
Seynesia erumpens	SMH 1291	AF279410	AF279409	
Simplicillium lamellicola T	CBS 116.25	AF339552		Type of *Cephalosporium lamellicola*
Simplicillium lanosoniveum	CBS 704.86	AF339553		
Sphaerostilbella aureonitens	Poldmaa TFC 96-77	AF160246		
Sphaerostilbella berkeleyana	CBS 102308	U00756	AF543770	
Sporophagomyces chrysostomus	TFC 96-193	AF160235		
Stachybotrys chartarum	ATCC 9182/UAMH 6417	AF081468	AY489680	
Stachybotrys subsimplex	ATCC 32888	AY489711	AY489679	
Stephanonectria keithii	GJS 92-133, CBS 100005	AY89727		
Stilbella fimetaria	DAOM 229279	**HQ232176**		
Stilbocrea macrostoma	GJS 73-26, CBS 114375	AY489725		
Stanjemonium grisellum	NRRL 26548	AF049171		
Strattonia carbonaria	ATCC 34567	AY346302	–	
Syspastospora parasitica	IMI 255607	AY015634		
Tilachlidium brachiatum	CBS 506.67	**HQ232177**		
Tolypocladium inflatum	IFO 31669	AB044645		
Torrubiella luteorostrata	NHJ 12516	EF468849		
Torrubiella petchii	NHJ 6240	EU369038		
Torrubiella pruinosa	NHJ 12994	EU369041		
Valetoniellopsis laxa	GJS 96-174, CBS 191.97	AY015635		
Valsa ambiens	AR 3516, CBS 109491	AF362564	DQ862056	
Valsella salicis	AR 3514, CBS 109754	AF408389	DQ862057	
Varicosporina ramulosa	RVG-113	U44092	U43846	
Verticillium dahliae	Typas 76/ATCC 16535	AF104926	AY489705	
Verticillium epiphytum 1	CBS 154.61	AF339548		
Verticillium epiphytum 2	CBS 384.81	AF339547		
Verticillium incurvum	CBS 460.88	AF339551		
Verticillium pseudohemipterigenum	Arsef 5687	AF339562		
Xylaria acuta	ATCC 56487	AY544676	AY544719	
Xylaria hypoxylon	OSC 100004	AY544648	AY544692	

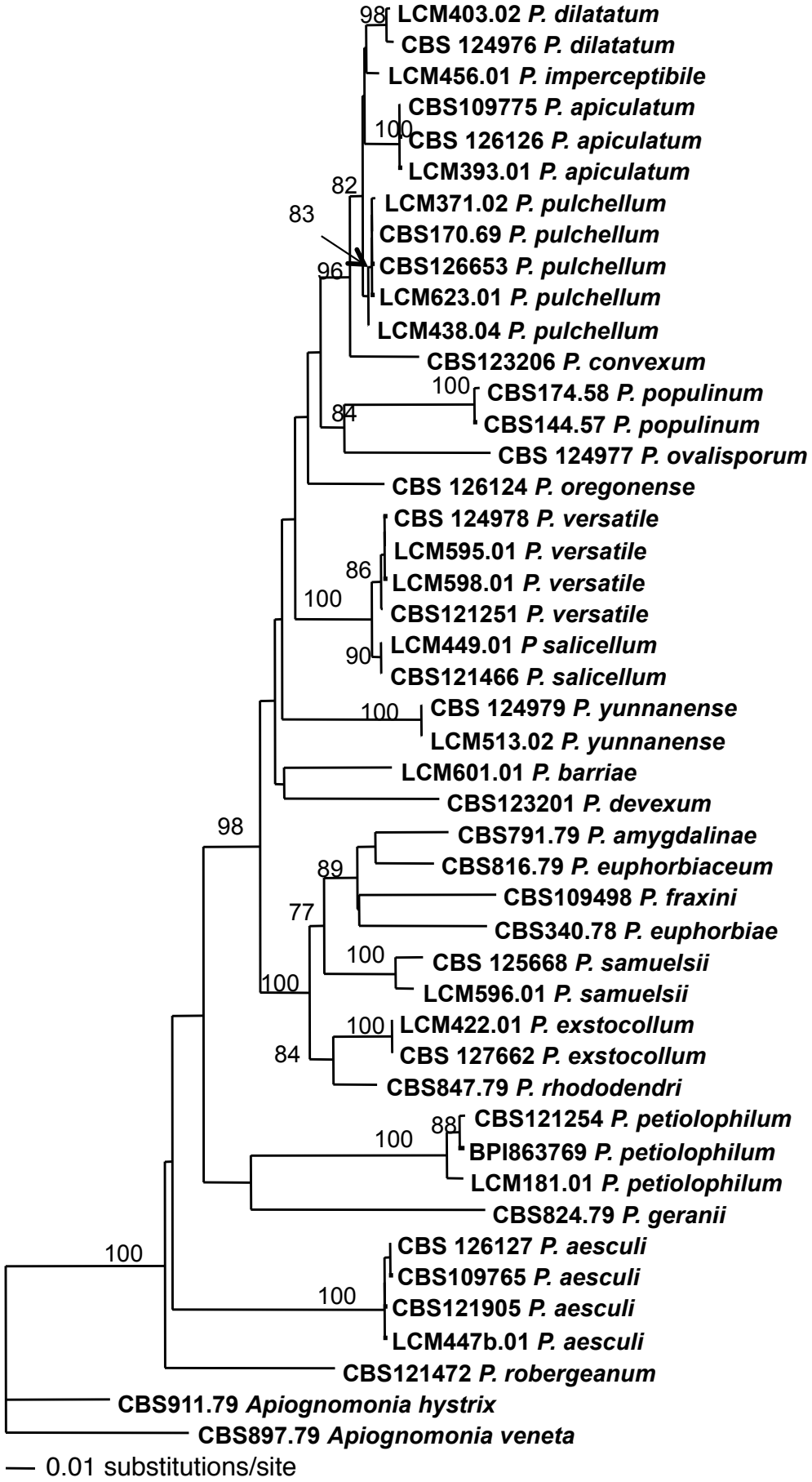
SUPPLEMENTARY INFORMATION



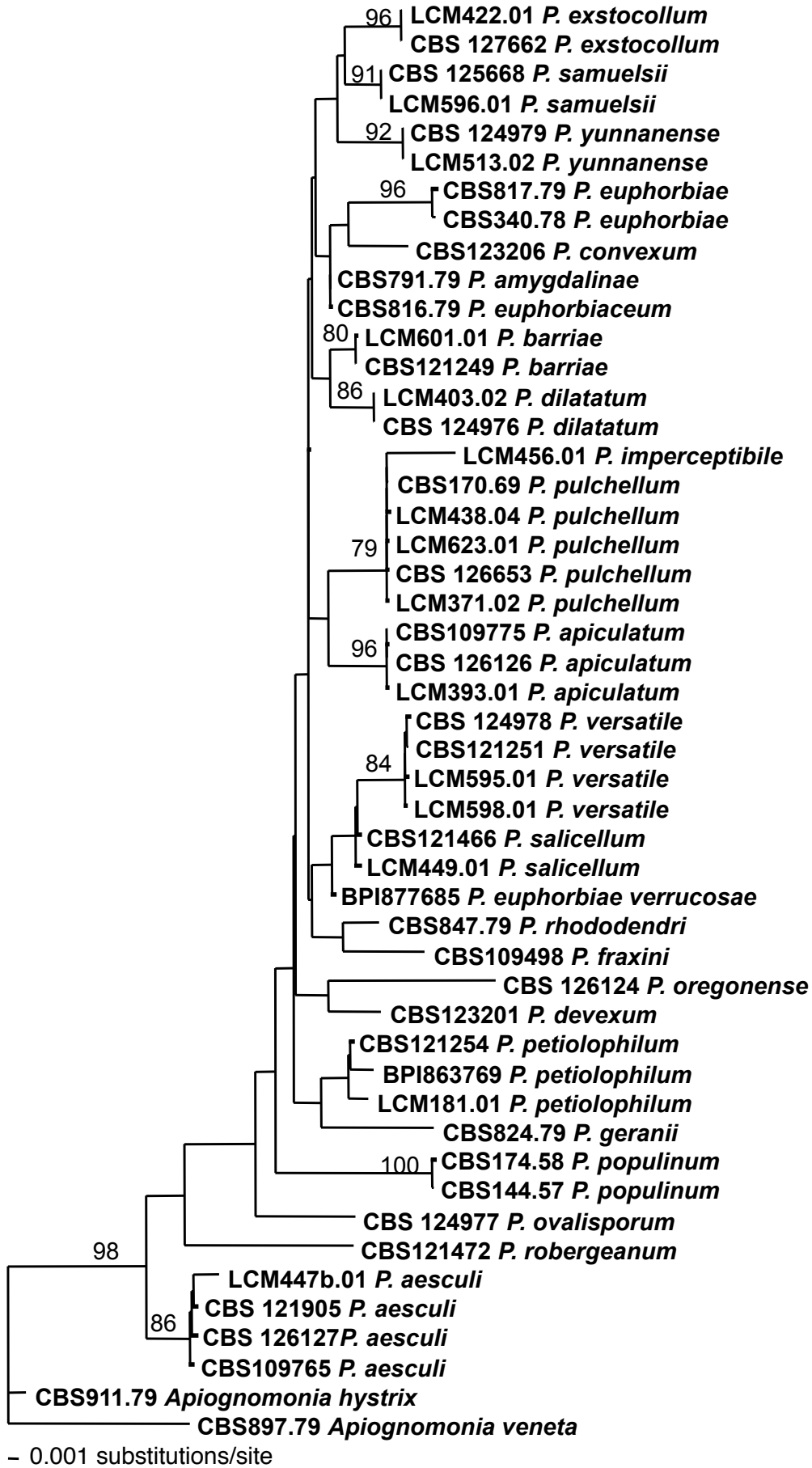
S.Fig. 1. *β-tubulin* tree for 24 species of *Plagiostoma* and two species of *Apiognomonia* generated using Neighbor Joining method with distance settings estimated by Modeltest v. 3.7 (Posada & Crandall 1998). Bootstrap values equal or greater than 70% are shown on top or to the left of branches.



S.Fig. 2. *rpb2* tree for 22 species of *Plagiostoma* and two species of *Apiognomonia* generated using Neighbor Joining method with distance settings estimated by Modeltest v. 3.7 (Posada & Crandall 1998). Bootstrap values equal or greater than 70% are shown on top or to the left of branches.



S.Fig. 3. *tef1-α* tree for 24 species of *Plagiostoma* and two species of *Apiognomonia* generated using Neighbor Joining method with distance settings estimated by Modeltest v. 3.7 (Posada & Crandall 1998). Bootstrap values equal or greater than 70% are shown on top or to the left of branches.



S.Fig. 4. ITS tree for 25 species of *Plagiostoma* and two species of *Apiognomonia* generated using Neighbor Joining method with distance settings estimated by Modeltest v. 3.7 (Posada & Crandall 1998). Bootstrap values equal or greater than 70% are shown on top or to the left of branches.

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Page numbers in **bold** represent pages with a more detailed treatment of the taxonomic entity.

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SIM68 Reference for Citations

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