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# Classification of the guava wilt fungus *Myxosporium psidii,* the palm pathogen *Gliocladium vermoesenii* and the persimmon wilt fungus *Acremonium diospyri* in *Nalanthamala*

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***Abstract:*** *Psidium guajava* wilt is known from South Africa, Malaysia and Taiwan. The fungus causing this disease, *Myxosporium psidii,* forms dry chains of conidia on surfaces of pseudoparenchymatous sporodochia, which develop in blisters on bark. Similar sporodochia are characteristic of *Nalanthamala madreeya,* the type species of *Nalanthamala. Nalanthamala,* therefore, is the appropriate anamorph genus for *Myxosporium psidii,* while *Myxosporium* is a nomen nudum (based on *M. croceum*). For *M. psidii* the combination *Nalanthamala psidii* is proposed. *Nalanthamala psidii,* the palm pathogen *Gliocladium* (*Penicillium*) *vermoesenii,* another undescribed anamorphic species from palm, two species of *Rubrinectria* and the persimmon pathogen *Acremonium diospyri* are monophyletic and belong to the Nectriaceae (Hypocreales) based on partial nuclear large subunit ribosomal DNA (LSU rDNA) analyses. *Rubrinectria,* therefore, is the teleomorph of *Nalanthamala,* in which the anamorphs are classified as *N. vermoesenii, N. diospyri* or *Nalanthamala* sp. *Nalanthamala squamicola,* the only other *Nalanthamala* species, has affinities with the Bionectriaceae and is excluded from this group. *Rubrinectria/Nalanthamala* species form dimorphic conidiophores and conidia in culture. Fusiform, cylindrical, or allantoid conidia arise in colorless liquid heads on acremonium-like conidiophores; ovoidal conidia with somewhat truncated ends arise in long, persistent, dry chains on penicillate conidiophores. No penicillate but irregularly branched conidiophores were observed in *N. diospyri*. Conidia of *N. psidii* that are held in chains are shorter than those of *N. madreeya,* of which no living material is available. *Nalanthamala psidii* and *N. diospyri* are pathogenic specifically to their hosts. They form pale yellow to pale orange or brownish orange colonies, respectively, and more or less white conidial masses. Most strains of *Rubrinectria* sp., *Nalanthamala* sp. and *N. vermoesenii* originate from palm hosts, form mostly greenish or olive-brown colonies and white-to-salmon conidial masses. They form a monophyletic clade to which *Nalanthamala psidii* and *N. diospyri* are related based on analyses of the internal transcribed spacer regions and 5.8S rDNA (ITS rDNA), LSU rDNA, and partial β-tubulin gene. Few polymorphic sites in the ITS rDNA and β-tubulin gene indicate that *Nalanthamala psidii* comprises two lineages, one of which has been detected only in South Africa.

***Key words:*** β-tubulin gene, internal transcribed spacer, *Nalanthamala madreeya, Nalanthamala squamicola,* Nectriaceae, nuclear large subunit ribosomal DNA, phylogeny, systematics, wilt disease

## INTRODUCTION

*Psidium guajava* (guava) wilt is a serious disease in Taiwan (Kurosawa 1926, Leu et al 1979), South Africa (Grech 1985, Anonymous 1987, Grech 1990, Schoeman et al 1997) and Malaysia (Schoeman unpubl). The disease is characterized by a rapid or a slow decline of trees and the development of red-brown blisters on trunks and branches consisting of sporodochia and conidial masses of the pathogen and the outer cortex of the host (Schoeman et al 1997).

The guava wilt fungus was described as *Myxosporium psidii* Sawada & Kurosawa (Kurosawa 1926) based on acervuli-like conidiomata, penicillate and simple branched conidiophores, as well as two dis-

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tinct types of conidia, one of which is formed in linear chains. The generic classification of *M. psidii* is unsettled. The genus *Myxosporium* Link based on *M. croceum* (Pers. : Fr.) Link (= *Naemaspora crocea* Pers.) was rejected by von Höhnel (1915) and regarded as a nomen nudum by Sutton (1977). Independently of Kurosawa (1926), the guava wilt fungus has been linked with *Septofusidium* W. Gams (Grech 1985) but *S. elegantulum* (Pidopl.) W. Gams, the type species of *Septofusidium,* hardly grows in culture (Gams 1971) and no living strain of the type species is available. The guava wilt fungus was also compared with *Gliocladium* (*Penicillium*) *vermoesenii* (Biourge) Thom (Schoeman et al 1997) and *Clonostachys* (as "*Gliocladium roseum* Bainier series") (Thom 1930). According to current concepts, however, neither *Gliocladium* nor *Clonostachys* could accommodate the guava wilt fungus or *G. vermoesenii* (Seifert 1985, Schroers et al 1999). *Penicillium vermoesenii* Biourge was described as forming salmon-colored coremia, penicillate conidiophores and ellipsoidal conidia of 5–7.5 × 3–4 μm arranged in chains and as being pathogenic to *Areca* L. (Biourge 1923). Its identity is supported by an ex-type strain (Thom 1930, Raper and Thom 1949). Thom (1930) mentioned an additional conidial form produced by *P. vermoesenii* and transferred it to *Gliocladium* Corda. As a cause of necrosis and blight of palms, it is known from the United States (Bliss 1938, Reynolds 1964), Europe (López-Llorca and Orts 1994), and Australia (Anonymous 2001) and was described as occurring worldwide (Aragaki et al 1991) or as widespread (Farr et al 1989).

Phylogenetic analyses of various other fungi suggested that linear, persistent or caducous chains of conidia or heads of liquid to slimy conidial masses formed on penicillate conidiophores (penicillium-like or gliocladium-like conidiophores, respectively) have evolved in unrelated groups of fungi (Berbee et al 1995, Ogawa et al 1997, Rehner and Samuels 1994) and that both forms even can occur in the same monophyletic group (Haugland et al 2001).

*Nalanthamala* was introduced for *N. madreeya* Subramanian. It was characterized by pseudoparenchymatous sporodochia formed on an unidentified dead stem, phialides formed at the surface of these sporodochia and elliptical to oval or lenticular conidia arranged in chains (Subramanian 1956). *Nalanthamala madreeya* apparently has not been cultured and *Nalanthamala* is reported rarely in literature. *Fusidium squamicola* Berk. & Broome was placed in *Nalanthamala* because a strain resembling the type of *F. squamicola* formed sporodochia and chains of conidia in culture (Gams 1975). No teleomorph is known for *N. madreeya, M. psidii, G. vermoesenii* and *N. squamicola* (Berk. & Broome) W. Gams, but the ex-ascospore isolate of *Macbridella olivacea* Seaver, now *Rubrinectria olivacea* (Seaver) Rossman & Samuels (Rossman et al 1999), produced conidia in dry chains similar to those formed by *G. vermoesenii* (Seaver 1910, Samuels 1973).

*Acremonium diospyri* (Crandall) W. Gams forms masses of conidia beneath the bark of its host *Diospyros virginiana,* on which it causes a serious wilt (Crandall and Baker 1950). Durrell (1963) observed chains of conidia, and Gams (1971) described two different kinds of conidia formed by *A. diospyri*. Benade et al (1991) observed morphological similarities between *A. diospyri* and the guava pathogen and distinguished both species based on their cellular long-chain fatty acid composition and growth rate in culture.

In this study, morphological characters and DNA sequences of the partial β-tubulin gene exons and introns and the ribosomal gene cluster were used to characterize, both taxonomically and phylogenetically, *M. psidii, G. vermoesenii, A. diospyri* and ascospore isolates of *Rubrinectria.* To infer their higher-rank phylogeny, sequences of the LSU rDNA of these taxa were compared with those of other, mainly hypocrealean taxa forming conidial chains and penicillate conidiophores (TABLE I).

## MATERIALS AND METHODS

*Fungal strains and herbarium specimens.*—Strains of *M. psidii* were isolated from diseased trees in South Africa and Malaysia (TABLE II); a strain from Taiwan was collected and isolated by Y.-F. Yen (National Taiwan University, Taipei, Taiwan) and Yu-ming Ju (Institute of Botany, Academia Sinica, Taipei, Taiwan), respectively. Twig fragments of dead *Psidium guajava* trees containing sporodochia of *M. psidii* were obtained from Barry Manicom (ARC-ITSC, Nelspruit, South Africa); the type specimen of *M. psidii* was obtained from the herbarium of the National Taiwan University. Additional strains of *M. psidii* or strains and herbarium specimens of other included species were obtained from the CBS Fungal Biodiversity Centre (CBS, Utrecht, Netherlands), Agro-industrial Fungi & Yeasts Collection (MUCL, Louvain-la-Neuve, Belgium) and Systematic Botany and Mycology Laboratory (BPI, Beltsville, Maryland). The strains were maintained at CBS and the Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, South Africa (CMW).

*Morphological examinations.*—Bark from 3–5 cm thick dead guava twigs was placed in moist chamber. After 3 d, portions of developing conidial chains were removed and streaked on oatmeal agar (OA), containing streptomycin and penicillin (Gams et al 1998a), with a sterile glass needle. Longitudinal sections of sporodochia formed beneath blisters were prepared as described elsewhere (Schroers 2001). Synthetic nutrient-poor agar (SNA) with 1 × 3 cm pieces of filter-paper (Nirenberg 1976), potato-dextrose agar (PDA,

TABLE I. Selected hypocrealean taxa forming linear, persistent, but disconnected or imbricate condidial chains

| Genus | Family | Type of conidiophore | Shape of catenate conidia | Synanamorph with conidial heads | References |
|---|---|---|---|---|---|
| | | | Taxa forming linear, persistent conidial chains | | |
| *Acremonium* "sect. *Simplex*" W. Gams, "*Terricola series*", teleomorph unknown | partly Bionectriaceae or unknown | acremonium-like | ± fusiform | not known | Gams (1971) |
| *Geosmithia* J. Pitt, teleomorph unknown | Bionectriaceae | penicillium-like | ellipsoidal | not known | Pitt (1979), Ogawa et al (1997) |
| *Cordyceps* (Fr.) Link, anamorph *Isaria* Fr. | Clavicipitaceae | penicillium-like | ellipsoid, subglobose, fusiform | not known | Samson (1974) |
| *Torrubiella luteorostrata* Zimm., anamorph *Paecilomyces cinnamomeus* (Petch) Samson & W. Gams | Clavicipitaceae | penicillium-like | fusiform | not known | Hywel-Jones (1993) |
| *Albonectria* Rossman & Samuels; anamorph *Fusarium* Link | Nectriaceae | typically verticillate | ovoidal | generally present, sporodochial | Rossman et al (1999), Gerlach and Nirenberg (1982) |
| *Gibberella fujikuroi* species complex, anamorph *Fusarium* Link | Nectriceae | acremonium-like or irregularly branched | clavate–fusiform | generally present | Nirenberg and O'Donnell (1998) |
| *Rubrinectria* Rossman & Samuels, anamorph *Nalanthamala* Subramanian | Nectriaceae | penicillium-like | ovoidal | generally present | this paper |
| *Viridispora* Samuels & Rossman, anamorph *Penicillifer* Emden | Nectriaceae | acremonium-like | ellipsoid to subfusiform, typically 1-septate | not known | Samuels (1989) |
| | | | Taxa forming imbricate conidial chains | | |
| *Bionectria* Speg., anamorph *Clonostachys* Corda | Bionectriaceae | gliocladium-like | ovoidal, slightly curved, hilum laterally displaced | generally present | Schroers (2001) |
| "*Nectria*", anamorph *Mariannaea* Arnaud ex Samson | Nectriaceae | verticillium to gliocladium-like | ovoidal, slightly curved, hilum laterally displaced | present in some of the species | Samson (1974), Samuels and Seifert (1981) |

Difco, Sparks, Nevada) and OA in 9 cm diam Petri dishes were used. Growth was measured from 5 d old PDA cultures incubated in the dark at 20, 25, 30 and 33 C using blocks of 3 mm$^2$ excised from young parts of OA colonies as inocula. Measurements of microscopic characters, obtained from lactic acid mounts, were made from 5–12 d old SNA or OA colonies incubated at 20 C in the dark. Ranges of measurements are reported as described elsewhere (Schroers 2001). Macroscopic characters and colony colors were described from 14 d or 3–4 wk old PDA or OA cultures incubated at 20 C in the dark or under continuous near-UV light (400–315 nm) (Sylvania blacklight-blue). Color names are from Kornerup and Wanscher (1978). Low temperature scanning electron microscopy (SEM) was done as described by Dijksterhuis et al (1991) using sporulating material on squares smaller than 0.5 cm$^2$ excised from OA cultures.

*DNA isolation, amplification and sequencing.*—Mycelium for DNA extraction was grown and harvested as described by Rehner and Samuels (1994). DNA was extracted using the FastDNA®Kit (BIO 101 Inc., Carlsbad, California). These primer pairs were used for PCR amplifications: T1/T22 (O'Donnell and Cigelnik 1997) for the partial β-tubulin gene, V9G/LR5 (de Hoog and Gerrits van den Ende 1998, Vilgalys and Hester 1990) for the partial LSU rDNA, V9G/LR5 or ITS1/ITS4 (White et al 1990) for the ITS rDNA. A PCR System 9700 (PE Applied Biosystems) using ramp speeds of the PCR System 9600 was used for amplification using these programs: an initial denaturation step at 94 C

TABLE II. Strains studied and GenBank accession numbers of newly generated sequences

| | | | | | GenBank accession numbers | | |
|---|---|---|---|---|---|---|---|
| Source[a] | Identity | Host | Origin | Collector, isolated by, depositor | β-tubulin | ITS rDNA | LSU rDNA |
| CBS 110507 | *Nalanthamala psidii* | *Psidium guajava* L. | South Africa, Nelspruit | B.Q. Manicom | AY554223 | AY554204 | AY554243 |
| CBS 912.85 | *N. psidii* | *P. guajava* | South Africa, Nelspruit | N. Grech | AY554222 | AY554203 | AY554258 |
| CBS 110187 (= CMW 8607) | *N. psidii* | *P. guajava* | South Africa, Nelspruit | M. Schoeman | AY554220 | AY554201 | AY554253 |
| CBS 110185 (= CMW 8605) | *N. psidii* | *P. guajava* | South Africa, Nelspruit | M. Schoeman | — | — | — |
| CBS 110186 (= CMW 8606) | *N. psidii* | *P. guajava* | South Africa, Nelspruit | M. Schoeman | — | — | — |
| CMW 8608 | *N. psidii* | *P. guajava* | South Africa, Levubu | M. Schoeman | — | — | — |
| CBS 590.96 (= CMW 3771) | *N. psidii* | *P. guajava* | South Africa | M.J. Wingfield | AY554224 | AY554205 | AY554259 |
| CBS 591.96 (= CMW 3779) | *N. psidii* | *P. guajava* | South Africa | M.J. Wingfield | AY554221 | AY554202 | AY554254 |
| CBS 110184 (= CMW 4168) | *N. psidii* | *P. guajava* | Malaysia | M. Schoeman | AY554226 | AY554207 | AY554257 |
| CBS 110188 (= CMW 4204) | *N. psidii* | *P. guajava* | Malaysia | M. Schoeman | AY554225 | AY554206 | AY554256 |
| CBS 110183 (= CMW 4177) | *N. psidii* | *P. guajava* | Malaysia | M. Schoeman | — | — | — |
| CBS 110182 (= CMW 4213) | *N. psidii* | *P. guajava* | Malaysia | M. Schoeman | — | — | — |
| CBS 687.97 | *N. psidii* | *P. guajava*, Beaumont cultivar | Malaysia | H.C. Tuck | AY554227 | AY554208 | AY554255 |
| CBS 116952 | *N. psidii* | *P. guajava* | Taiwan | Y.-F. Yen, Yu-ming Ju | AY864838 | AY864836 | AY864837 |
| CBS 110893 (= MUCL 9504, Biourge 415, ex-type) | *Nalanthamala vermoesenii* | *Areca* sp. | | | AY554233 | AY554214 | AY554246 |
| CBS 137.24 (= MUCL 7994, Biourge 416) | *N. vermoesenii* | palm | | A. van Luijk | AY554236 | AY554217 | AT554260 |
| CBS 356.87 (= FRR 3073, CMW 3919) | *N. vermoesenii* | leaf of Palmae | Australia, Victoria, Burnley Gardens | I. Pascoe | AY554234 | AY554215 | AY554261 |
| CBS 222.36 (= CMW 3918) | *N. vermoesenii* | *Phoenix canariensis* Hort. ex Chabaud | California, USA, South Pasadena | D.E. Bliss | AY554232 | AY554213 | AY554262 |
| CBS 669.74 (= IMI 160990) | *N. vermoesenii* | *Latania* sp., decayed basal part of petiole | Czech Republic, Southern Moravia, Palm house | V. Holubová-Jechová | AY554235 | AY554216 | — |
| CBS 230.48 (= ATCC 10522, DSMZ 3709, IMI 040231, MUCL 7584, NRRL 1752) | *N. vermoesenii* | *Citrus medica* L. | Spain | K.B. Raper | AY554231 | AY554212 | AY554263 |
| CBS 357.87 (= PD 86/1179) | *Nalanthamala* sp. | *Areca catechu* L., showing foot rot | The Netherlands, Naaldwijk | PD | AY554230 | AY554211 | — |

TABLE II. Continued

| Source[a] | Identity | Host | Origin | Collector, isolated by, depositor | GenBank accession numbers | | |
|---|---|---|---|---|---|---|---|
| | | | | | β-tubulin | ITS rDNA | LSU rDNA |
| CBS 456.92 | *Nalanthamala* sp. | leaf of *Areca* sp., possibly causing brown spots | The Netherlands, Maasdijk, greenhouse | J.W. Vennbaas-Rijks | AY554229 | AY554210 | AY554247 |
| CBS 102268 (= G.J.S. 99-72) | *Rubrinectria olivacea* | bark | Costa Rica | G.J. Samuels | AY554238 | AY554219 | AY554244 |
| CBS 101648 | *Rubrinectria* sp. | *Prestoea* litter | USA, Puerto Rico | W. Gams | AY554237 | AY554218 | AY554245 |
| CBS 560.89 (= CMW 1707) | *Nalanthamala diospyri* | wood of *Diospyros virginiana* L. | USA, Tennessee, Readyville | B.C. Crandall | AY554239 | — | — |
| CBS 430.89 (= CMW 1709) | *N. diospyri* | *Diospyros virginiana* | USA, Mississippi | B.C. Crandall | AY554228 | AY554209 | AY554248 |
| CBS 745.88 (= C.T.R. 71-199) | "*Nectria*" *mariannaeae* Samuels & Seifert | *Pinus* sp. | Venezuela | K.P. Dumont, G.J. Samuels and Borjas | — | — | AY554242 |
| CBS 101067 | *Geosmithia* sp. | starch | The Netherlands | P. Willemse | — | — | AY554251 |
| CBS 209.73 (= IMI 186965) | *Mariannaea camptospora* Samson | forest soil | The Netherlands | E. Jansen | — | — | AY554241 |
| CBS 308.59 (= CCFC 55208) | *Mariannaea elegans* (Corda) Samson var. *elegans* | *Pseudotsuga menziesii* (Mirb.) Franco | Canada, British Columbia, Kamloops | — | — | — | AY554240 |
| CBS 398.86 (= INIFAT C86/45) | *Paecilomyces cinnamomeus* (Petch) Samson & W. Gams | living leaf of *Syzygium jambos* (L.) Alston | Cuba, Soroa, Pinar del Rio | R.F. Castañeda and G. Arnold | — | — | AY554252 |
| CBS 363.58 (= ATCC 22172) | *Stachybotrys bisbyi* (Srinivasan) Barron | soil from mangrove swamp | Mozambique, Inhaca Island | H.J. Swart | — | — | AY554250 |
| CBS 363.49 | *Stachybotrys chartarum* (Ehrenberg) S. Hughes | wilting *Clematis* sp. | The Netherlands | I. de Boer | — | — | AY554249 |

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[a] Cultures are deposited/were obtained from the following collections: ATCC, American Type Culture collection, Manassas, Virginia, USA; CBS, Centraalbureau voor Schimmelcultures, Utrecht, The Netherlands; CMW, culture collection, Forestry and Agricultural Biotechnology Institute, FABI, Pretoria, South Africa; C.T.R., C.T. Rogerson culture collection, United States Department of Agriculture, Beltsville, Maryland, USA; CCFC, Canadian Collection of Fungal Cultures; DSMZ, Deutsche Sammlung von Mikrorrganismen und Zellkulturen GmbH, Braunschweig, Germany; FRR, Division of Food Research, CSIRO, North Ryde, Sydney, Australia; G.J.S., culture collection G.J. Samuels, United States Department of Agriculture, Beltsville, Maryland, USA; IMI, CABI Bioscience, Egham, UK; INIFAT, Instituto Nacional de Investigaciones Fundamentales de Agricultura Tropical, Havana, Cuba; MUCL, (Agro)industrial fungi & yeasts collection, Mycothèque de l'Université Catholique de Louvain, Louvain-la-Neuve, Belgium; NRRL, Agricultural Research Service Culture Collection, National Center for Agricultural Utilization Research, Peoria, Illinois, USA; PD, Plant Protection Service, Wageningen, The Netherlands.

for 2 min, 35 cycles of 94 C for 35 s, 58 (for T1/T22) or 55 C (for V9G/LR5 and ITS1/ITS4) for 50 s, 72 C for 2 min, and a final extension at 72 C for 6 min. The vials of 50 μL contained 1 μL genomic DNA extract, 25 pmol of each of the primers, 200 μmol of each of the dNTPs (Amersham Biosciences), 1 U of Taq polymerase (Super Taq, HT Biotechnology, UK), and 1 × standard PCR buffer supplied with the Taq polymerase. PCR fragments were purified using the GFX® purification kit (Amersham Pharmacia Biotech Inc., Roosendaal, Netherlands). The amplicons were sequenced with the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems, Foster City, California) and analyzed on an ABI Prism 3700 (Applied Biosystems) by using the standard conditions recommended by the vendor. The primers used in the sequence reactions were ITS1, ITS4, LR5, NL1 or NL4 (O'Donnell 1993) for the rDNA and T1 or T2 (O'Donnell and Cigelnik 1997) for the partial β-tubulin gene.

*Sequence analyses.*—Newly generated (TABLE II) and published sequences were aligned using Clustal X 1.81 (Jeannmougin et al 1998). The alignments were adjusted manually. An LSU rDNA dataset comprised hypocrealean taxa, including members of the Clavicipitaceae, *Penicillium expansum* Link, the type species of the genus *Penicillium* Link (Eurotiales), and *Verticillium dahliae* Kleb. (Phyllachorales), of which the latter was used as outgroup. A region containing multiple gaps and its flanking sides (bp 50–60 of the alignment) was excluded from the analyses of this dataset. Another dataset comprising partial LSU rDNA, complete ITS rDNA and partial β-tubulin gene intron and exon sequences was used to analyze the relationship of strains of the guava pathogen and its close relatives using *Bionectria/Clonostachys* (Bionectriaceae) as outgroup and *Gibberella* Sacc./*Fusarium* (Nectriaceae) as sister group. Incomplete 3′- and 5′-parts of sequences were coded as missing characters. Phylogenetic relationships were estimated from the aligned sequences by the maximum parsimony criterion as implemented in PAUP 4.0b10 (Swofford 2002). Heuristic searches were performed using parsimony informative, unordered and equally weighted characters; branch robustness was tested by 1000 search replications, each on bootstrapped datasets. Gaps were treated as missing characters. Starting tree(s) were obtained via stepwise, random, 100× (10× in bootstrap analyses) repeated sequence addition. A maximum number of 1000 trees were allowed.

*Sequence data.*—Newly generated sequences (TABLE II) and the alignments were deposited in GenBank (www.ncbi.nlm.nih.gov) and TreeBase (www.treebase.org), respectively. These taxa and published sequences were included in the analyses: *Acremonium alternatum* Link per S.F. Gray, U57349 (Glenn and Bacon unpubl); *Albonectria albosuccinea* (Pat.) Rossman & Samuels, U34554 (O'Donnell and Cigelnik 1997); *A. rigidiuscula* (Berk. & Broome) Rossman & Samuels, U88104 (O'Donnell 1993); *Bionectria ochroleuca* (Schw.) Schroers & Samuels, U00750 (Rehner and Samuels 1994), AF210686, AF358159 (Schroers 2001); *B. ralfsii* (Berk. & Broome) Schroers & Samuels, AF210676 (Schroers 2001); *B. zelandiaenovae* Schroers, AF210684 (Schroers 2001); *Calonectria morganii* Crous et al, U17409 (Rehner and Samuels 1995); *C. pyrochroa* (Desm.) Sacc., U88097 (O'Donnell 1993); *Clonostachys miodochialis* Schroers, AF358210, AF210674 (Schroers 2001); *Epichloë typhina* (Pers. : Fr.) Tulasne & C. Tulasne, U17396 (Rehner and Samuels 1995); *Fusarium fujikuroi* Nirenberg, U34415, U34528, U34557 (O'Donnell and Cigelnik 1997, O'Donnell et al 1998); *F. verticillioides* (Sacc.) Nirenberg, U34526 (O'Donnell and Cigelnik 1997); *Geosmithia lavendula* (Raper & Fennell) Pitt, D88325 (Ogawa et al 1997); *G. putterillii* (Thom) Pitt, D88326 (Ogawa et al 1997); *Gibberella zeae* (Schw.) Petch, U34436, U34549, U34578 (O'Donnell and Cigelnik 1997); *Haematonectria haematococca* (Berk. & Broome) Samuels & Nirenberg, L36623 (O'Donnell and Gray 1995); *Hydropisphaera arenula* (Berk. & Broome) Rossman & Samuels, U88121 (O'Donnell 1993); *H. erubescens* (Desm.) Rossman & Samuels, AF193228 (Rossman et al 2001); *H. peziza* (Tode : Fr.) Dumort., U88131 (O'Donnell 1993); *Hypocrea lutea* (Tode) Petch, U00739 (Rehner and Samuels 1994); *H. schweinitzii* (Fr.) Sacc., U47833 (Spatafora unpubl); *Hypomyces odoratus* G. Arnold, AF160240 (Põldmaa et al 1999); *Lecanicillium lecanii* (Zimm.) Zare & W. Gams, U17421 (Rehner and Samuels 1995); *Metarhizium anisopliae* (Metschn.) Sorok., AF339529 (Sung et al 2001); *Myrothecium inundatum* Tode : Fr., AF193236 (Rossman et al 2001); ''*Nalanthamala*'' *squamicola,* AF373281 (Bills et al 2002); *Nectria cinnabarina* (Tode : Fr.) Fr., U00749 (Rehner and Samuels 1994); *N. pseudotrichia* Berk. & M.A. Curtis, U17410 (Rehner and Samuels 1995); *Nectriopsis sporangiicola* (Samuels) Samuels, U00753 (Rehner and Samuels 1994); *N. violacea* (Schmidt : Fr.) Maire, AF193242 (Rossman et al 2001); *Neocosmospora vasinfecta* E.F. Smith, U47836 (Spatafora unpubl); *Neonectria radicicola* (Gerlach & L. Nilsson) Mantiri & Samuels, U17415 (Rehner and Samuels 1995); *Neotyphodium coenophialum* (Morgan-Jones & W. Gams) Glenn et al, U57681 (Glenn and Bacon unpubl); *Peethambara sundara* Subramanian & D.J. Bhat, AF193245 (Rossman et al 2001); *Penicillium expansum,* AF003359 (Seifert and Louis-Seize unpubl); *Roumegueriella rufula* (Berk. & Broome) Malloch & Cain, U00754 (Rehner and Samuels 1994); *Sphaerostilbella aureonitens* (Tulasne) Seifert et al, AF160246 (Põldmaa et al 1999); *Stachybotrys echinata* (Rivolta) G. Smith, AF081470 (Haugland et al 2001); *Stanjemonium grisellum* W. Gams et al, AF049171 (Gams et al 1998b); *Torrubiella luteorostrata,* AF327380 (Artjariyasripong et al 2001); *Verticillium dahliae,* U17425 (Rehner and Samuels 1995); *Viridispora diparietispora* (J.H. Miller et al) Samuels & Rossman, U17411 (Rehner and Samuels 1995).

## RESULTS

*Myxosporium psidii, G. vermoesenii, A. diospyri,* for which the combinations *Nalanthamala psidii, N. vermoesenii* and *N. diospyri* are proposed in this paper, as well as a *Nalanthamala* sp. and two *Rubrinectria* species are closely related and present distinct phylogenetic taxa (FIGS. 1, 2). Sporodochia and conidia formed by *N. psidii* from Taiwan and South Africa are indistinguishable (Kurosawa 1926; FIGS. 3–28). Similar characters but longer conidia are also formed

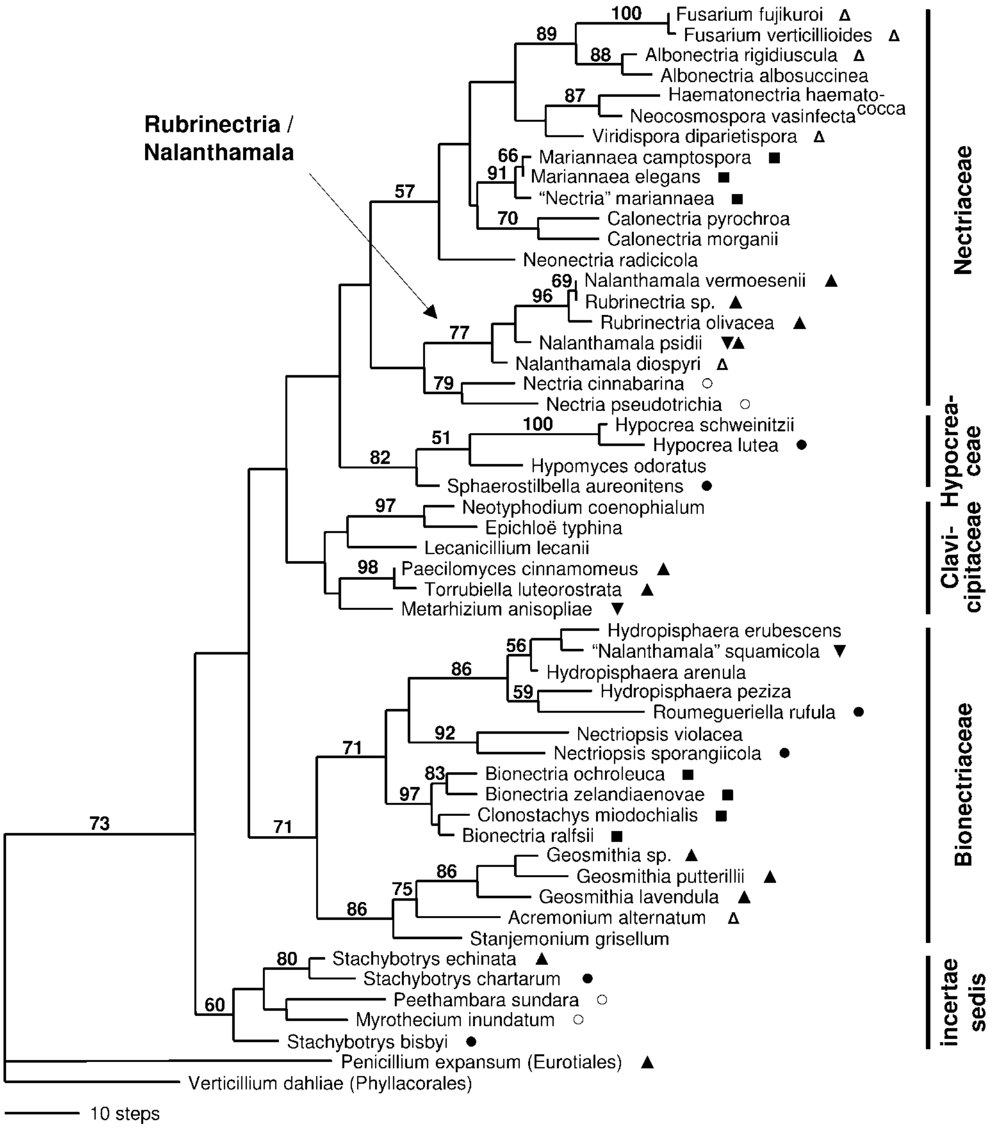


FIG. 1. One of seven equally parsimonious phylograms inferred from partial LSU rDNA sequences. Bootstrap intervals from 1000 replicates are indicated above nodes. Symbols (right of the tree) indicate taxa forming linear chains of conidia on acremonium-like or branched but not penicillately branched conidiophores (△), penicillately branched conidiophores (▲) or conidiomata (▼); mucous heads or slimy masses of conidia on penicillately branched conidiophores (●) or conidiomata (○); imbricate chains of conidia on penicillately branched conidiophores or conidiomata (■). The *Rubrinectria/ Nalanthamala* clade forms a moderately supported monophyletic clade among other genera of the Nectriaceae. CI = 0.319; RI = 0.641.

by *N. madreeya,* the type of *Nalanthamala* (Subramanian 1956). In pure cultures, *N. psidii* (FIGS. 11–28), *N. vermoesenii* (FIGS. 29–43), the two *Rubrinectria* species, the undescribed anamorphic *Nalanthamala* sp. and *N. diospyri* (FIGS. 44–59) form similar dimorphic conidia, observed in all species, and dimorphic conidiophores, formed in all species except *N. diospyri. Nalanthamala psidii* differs from *N. vermoesenii, N. diospyri, Nalanthamala* sp. and *Rubrinectria* sp. mainly in macroscopic characters such as growth rates of colonies, pigmentation of conidial masses and pigmentation of colonies as well as in pathogenicity and host spectrum (TABLE III).

*Sequence data analyses.*—Heuristic parsimony analyses of LSU rDNA aligned sequences (536 bp alignment positions containing 126 parsimony informative characters, PIC) resulted in seven equally most-parsimonious trees 645 steps in length, with a consistency index (CI) of 0.319 and a retention index (RI) of 0.641. The seven equally parsimonious trees showed the same overall branching topology. *Penicillium ex-*

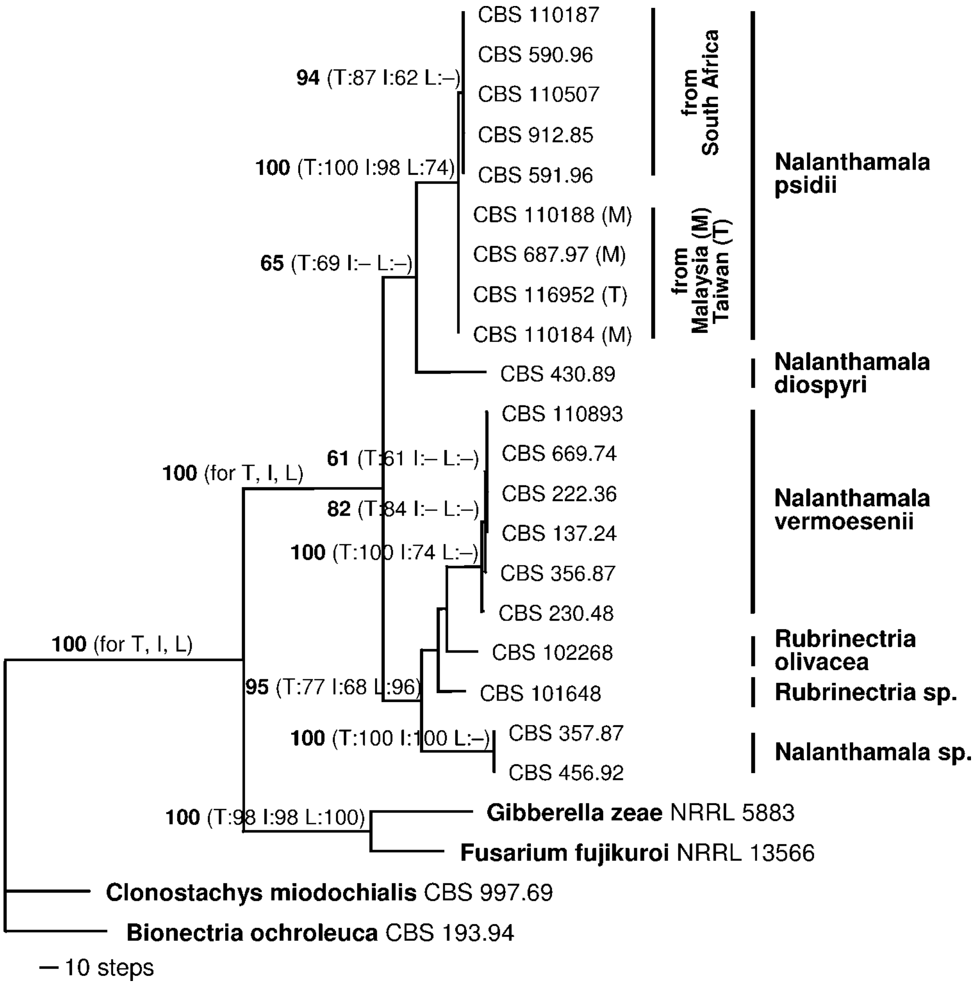
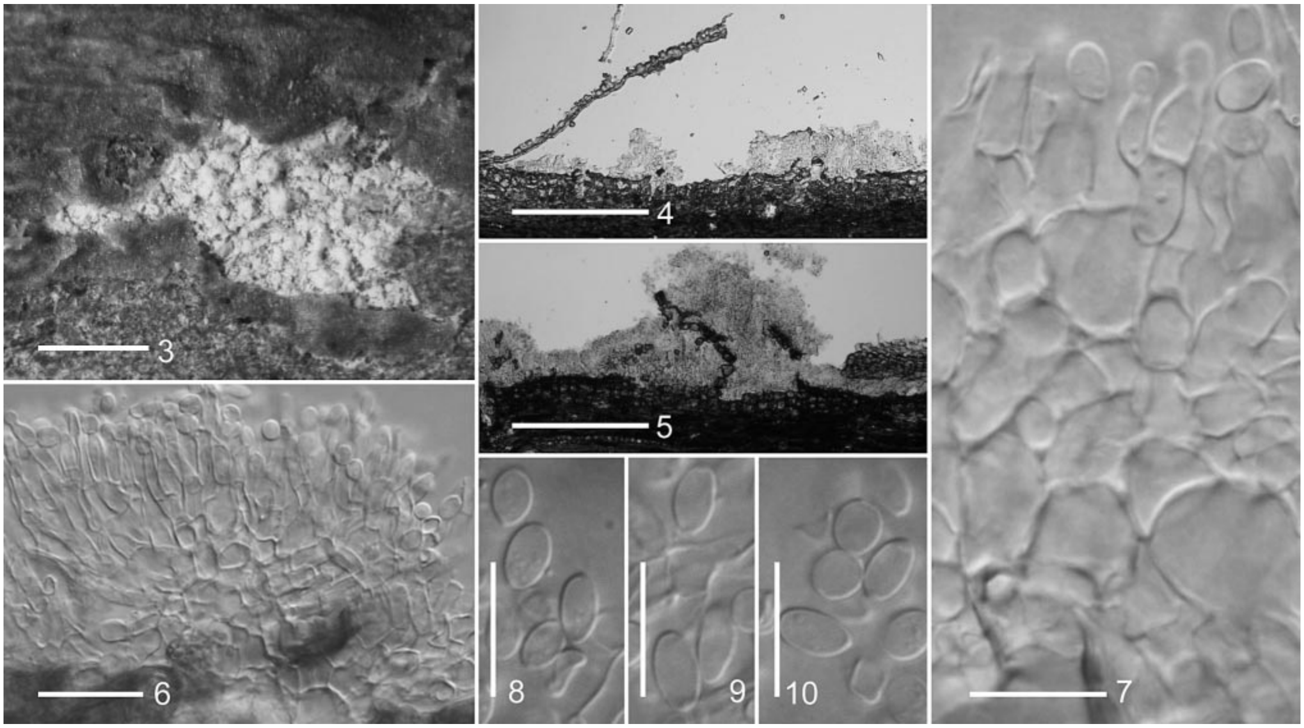


FIG. 2. One of three equally parsimonious phylograms inferred from the combined ITS1, 5.8S, ITS2 ribosomal DNA (ITS rDNA), partial LSU of the rDNA and partial β-tubulin dataset. Bootstrap intervals from 1000 replicates of the combined data are indicated above nodes, followed in brackets by intervals from 1000 replicates of the individual partitions β-tubulin (T), ITS rDNA (I) and LSU rDNA (L). The *Nalanthamala* sp., *N. vermoesenii* and the *N. psidii* clades are strongly supported (bootstraps = 100%) as is the *Rubrinectria/Nalanthamala* clade (bootstrap = 100%). Sister group relationship of *N. diospyri* and *N. psidii* is supported weakly (bootstrap = 65%). The two ascospore isolates (*Rubrinectria* sp.) are more closely related to *N. vermoesenii* and *Nalanthamala* sp. CI = 0.743; RI = 0.844.

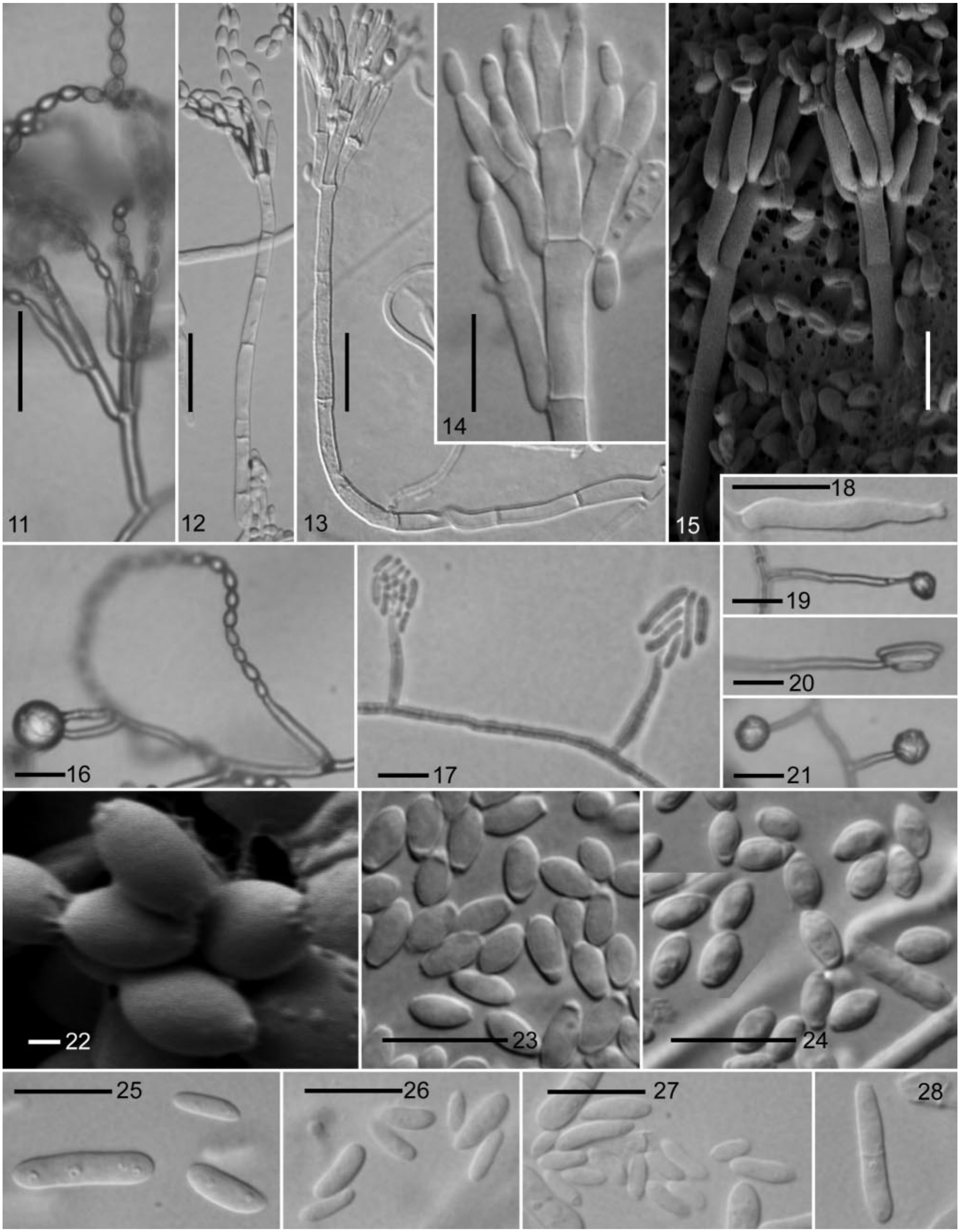
*pansum* was placed next to the root and outside of a moderately supported hypocrealean clade (bootstrap = 73%). *Myrothecium inundatum, Peethambara sundara, Stachybotrys chartarum, S. echinata* and *S. bisbyi* either formed an unresolved (encountered in five trees) or a monophyletic group (encountered in two trees, of which one is shown) (FIG. 1) at the base of the hypocrealean clade. The Bionectriaceae and the Hypocreaceae received moderate support (bootstrap = 71 or 82%, respectively). The Clavicipitaceae and the Nectriaceae formed monophyletic but not supported groups. Most of the included genera formed moderately to strongly supported clades. Ex-ascospore isolates of *Rubrinectria* specimens and conidial isolates of *N. psidii, N. vermoesenii, Nalanthamala* sp., isolated from palm, and *N. diospyri* form a moderately supported monophyletic group (bootstrap = 77%), which is placed among taxa of the Nectriaceae. The *Rubrinectria* clade appears closely related to *Nectria cinnabarina* and *N. pseudotrichia,* which belong to the type genus of the Nectriaceae. Other genera of the Nectriaceae, such as *Mariannaea, Albonectria* and the *Gibberella fujikuroi* species complex, which in part form conidia arranged in linear or imbricate chains, are related more distantly to *Rubrinectria/Nalanthamala. Gliocladium penicillioides* Corda, type species of *Gliocladium* and anamorph of *Sphaerostilbella aureonitens* (Hypocreaceae) phylogenetically is unrelated to *Rubrinectria,* as are gliocladium-like taxa such as *Roumegueriella rufula, Nectriopsis sporangiicola,* and species of *Bionectria* (all Bionectriaceae). Taxa forming conidial chains such as *Geosmithia* species on



FIGS. 3–10. *Nalanthamala psidii* on twig of diseased *Psidium guajava*. 3. Sporodochia pictured from above (whitish region) partly covered by outermost cortex of host. 4–7. Longitudinal sections through sporodochia. 8–10. Conidia. All from CBS, H-13961. Scale bars: 3 = 1 mm; 4, 5 = 100 μm; 6 = 20 μm; 7–10 = 10 μm.

penicillium-like conidiophores, *Acremonium alternatum,* the sporodochial "*Nalanthamala*" *squamicola* (all Bionectriaceae) also are unrelated phylogenetically to *Rubrinectria. Stachybotrys chartarum,* which forms slimy conidial heads, and *S. echinata,* which forms dry chains of conidia, are closely related and monophyletic.

Strains of *N. psidii* isolated from Malaysia and the single strain isolated from Taiwan had identical sequences. They differed from strains of *N. psidii* isolated from South Africa in two substitutions and one indel (a C2 instead of a C4 group) of the partial β-tubulin gene. Strains of *N. vermoesenii* contained five polymorphic intron sites, all of which were found in CBS 230.48, one of which was found in CBS 356.87. No variation was found within the partial β-tubulin gene of strains CBS 222.36, 110893, 669.74 and 137.24 (*N. vermoesenii*), two strains of *Nalanthamala* sp. and two strains of *N. diospyri,* respectively. The ITS rDNA of *N. vermoesenii* strains was identical. The ITS rDNA of strains of *N. psidii* isolated from South Africa differed from strains isolated from Malaysia/Taiwan in one substitution and one indel. Heuristic parsimony analyses of the combined partial LSU rDNA (525 bp alignment positions containing 63 PIC); ITS rDNA (505 bp alignment positions containing 103 PIC); and partial β-tubulin gene (662 bp alignment positions containing 207 PIC) resulted in three equally most parsimonious trees 740 steps in length with a CI of 0.743 and a RI of 0.844, of which one is shown (FIG. 2). Monophyly of the *Rubrinectria/Nalanthamala* clade as well as the species clades of *Nalanthamala* sp., *N. vermoesenii,* and *N. psidii* were strongly supported (bootstrap = 100%). Sister group relationship of *N. psidii* and *N. diospyri* was supported weakly (bootstrap = 65%). Relatedness of the two ex-ascospore isolates of *Rubrinectria, N. vermoesenii* and *Nalanthamala* sp. was supported highly (bootstrap = 95%); within this clade, the phylogenetic position of these species remained unresolved. The three trees and the bootstrap consensus tree suggested paraphyly of the strains from Asia (Malaysia and Taiwan) and South Africa, respectively. Partitioned parsimony and bootstrap analyses of the ITS rDNA (resulting in two equally parsimonious, 178-steps-long trees having a CI of 0.781 and RI of 0.869) and the partial β-tubulin gene (resulting in ten equally parsimonious, 469-steps-long trees having a CI of 0.719 and RI of 0.819) also supported the *Rubrinectria/Nalanthamala, N. vermoesenii, N. psidii* and *Nalanthamala* sp. clades (ITS rDNA: 100, 74, 98, 100% bootstrap support; β-tubulin: 100% for all taxa). Partitioned analysis of the LSU rDNA (resulting in four equally parsimonious, 90-steps-long trees having a CI of 0.822 and RI of 0.915) supported the



FIGS. 11–28. *Nalanthamala psidii* in pure culture. 11–15. Penicillate conidiophores forming chains of ovoidal conidia. 16. Acremonium-like conidiophore forming chains of ovoidal conidia. 17–21. Acremonium-like conidiophores arising from aerial mycelium forming heads of ellipsoidal to fusiform, straight to slightly curved conidia. 22–24. Ovoidal conidia from linear

*Rubrinectria/Nalanthamala* and the *N. psidii* clades (bootstrap = 100 and 74%).

## TAXONOMY

*Nalanthamala* Subramanian, J. Indian Bot. Soc. 35: 478. 1956.

TYPE SPECIES: *N. madreeya* Subramanian.

*Sporulation* on natural substratum by sporodochia or penicillate, stalked, mononematous or aggregated conidiophores. *Sporodochia* unpigmented, erumpent through outer cortex of substratum or formed in blisters below outermost host cortex, hemispherical or flat; cells of well-developed sporodochia angular to globose, forming a pseudoparenchymatous tissue (textura angularis), evenly thin-walled, hyaline. *Phialides* formed singly or in whorls on cylindrical cells that arise from pseudoparenchymatous tissue of sporodochia or in whorls on penicillately branched conidiophores, elongate, widest at the base or in the lower third, narrowing toward the apex or more or less cylindrical and narrowing below the apex. *Conidia* formed on sporodochia ovoidal, frequently with somewhat truncated ends, hyaline, 1-celled, smooth, held in dry chains.

*Colonies* yellowish, orange, brownish orange, or in light green, dark green, or olive-brown hues. *Aerial mycelium* sparsely to moderately developed, hyaline or greenish. *Conidiophores* in culture mostly dimorphic, penicillium-like or acremonium-like. Penicillium-like conidiophores short- or long-stalked, once or several times branched, with terminal whorls of phialides. Acremonium-like conidiophores of a single phialide or sparsely and sometimes irregularly branched, formed on submerged or aerial mycelium. *Conidia* generally dimorphic, either ovoidal or fusiform, cylindrical to allantoid, straight to slightly curved; ovoidal conidia mostly held in long chains, fusiform conidia held in heads. *Conidial masses* white or in pale yellowish, orange or salmon hues.

*Teleomorph. Rubrinectria* Rossman & Samuels, Stud. Mycol. 42:164. 1999.

*Descriptions*. For the holomorph/teleomorph: Seaver (1910), Samuels (1973), Samuels and Brayford (1994), Rossman et al (1999); for the anamorph: Subramanian (1956, 1971).

*Notes.* The original description provided by Subramanian is expanded based on the observation of mononematous conidiophores on guava twigs and pure culture characters of species here included in *Nalanthamala.*

*Nalanthamala madreeya* Subramanian, J. Indian Bot. Soc. 35:478. 1956.

*Diagnostic characters from original description.* Sporodochia pseudoparenchymatous consisting of angular to globose, up to 28 μm wide cells; phialides formed at the surface of sporodochia; conidia produced in linear, basipetal chains, elliptical-oval or lenticular, hyaline, 1-celled, smooth, mostly 7 × 2.8 μm.

HOLOTYPE. INDIA. Madras, University Botany Laboratory campus. On dead stem, 3 Dec 1955, *K. Ramakrishnan* (Madras, University Botany Laboratory Madras, No. 1466).

*Teleomorph.* Unknown.

*Habitat.* On dead stem.

*Distribution.* India, only known from the type location.

*Descriptions.* Subramanian (1956, 1971).

*Notes. Nalanthamala madreeya* has not been described from pure culture. To our knowledge, the species has not been recollected. We could not locate the type specimen in the herbaria MUBL (now at the CAS in Botany, University of Madras, Guinday Campus, India) and IMI (CABI, Egham, Surrey, UK). The description provided by Subramanian (1956) allows the conclusion that *Nalanthamala psidii* is closely related to *N. madreeya* and that it is well accommodated in the genus *Nalanthamala.*

**Nalanthamala psidii** (Sawada & Kurosawa) Schroers & M.J. Wingf., comb. nov. FIGS. 3–28.

≡ *Myxosporium psidii* Sawada & Kurosawa, Rep. Taiwan Museum 83:59. 1926.

*Sporulation* on dead twigs as sporodochia and mononematous, penicillate conidiophores, covered by outermost cortex of host or exposed. *Sporodochia* unpigmented, up to 400 μm diam, hemispherical, or flat, covering areas of up to 1 $cm^2$, 100–250 μm high, white; cells of sporodochia angular to globose, 5–15 μm diam, forming a pseudoparenchymatous tissue (textura angularis), evenly thin-walled, hyaline, supporting phialides or phialides forming cylindrical cells. *Conidiophores* penicillate, solitary or formed in aggregates, mono- to quaterverticillate, forming

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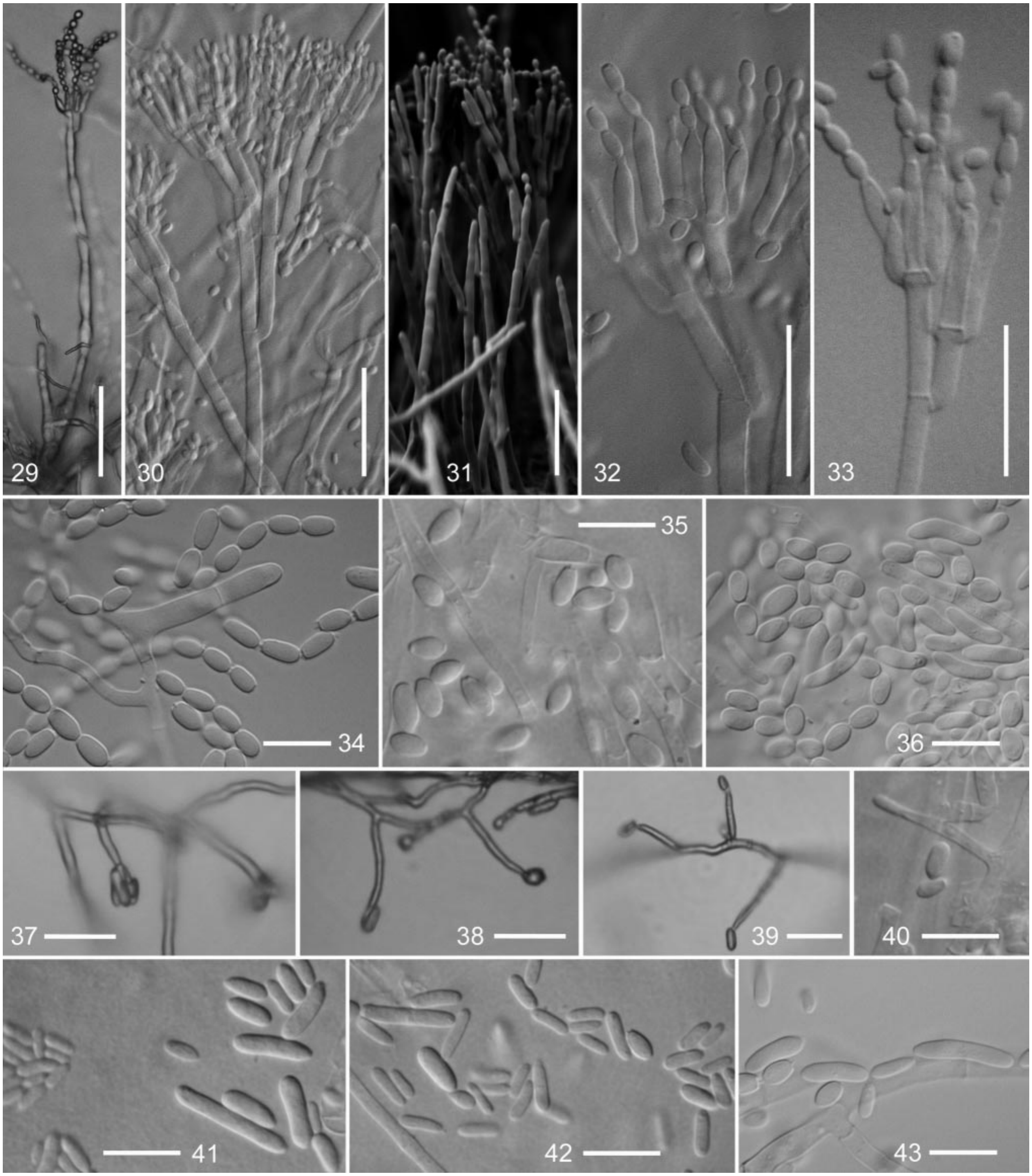
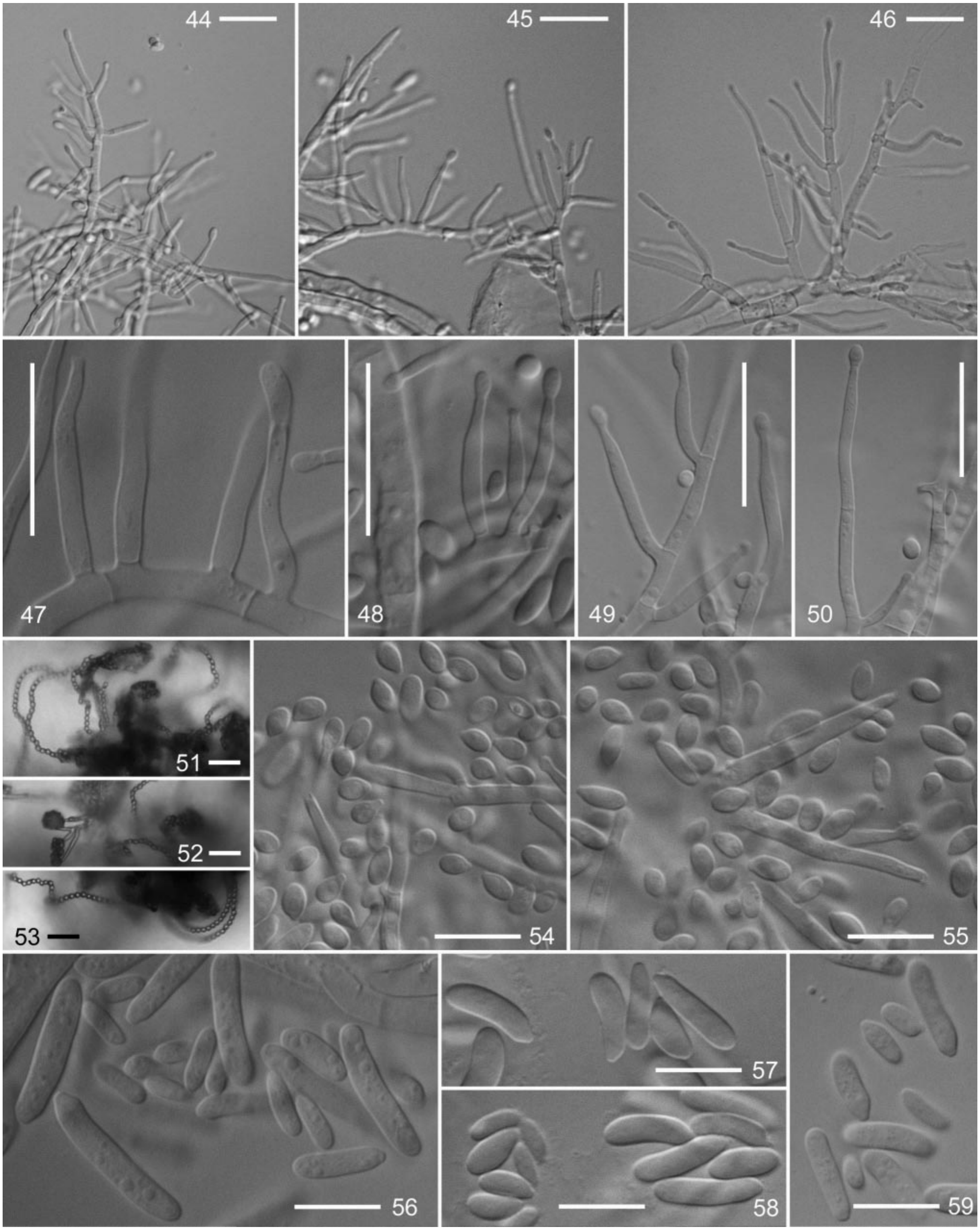
chains formed by penicillate conidiophores. 25–28. Ellipsoidal to fusiform, typically 1-celled, rarely 1-septate conidia from simple, acremonium-like conidiophores. 15, 22 from 10 d old OA culture (SEM); all others from 7–14 d old SNA cultures. 11, 16, 17, 19, 20, 21 from CBS 912.85; 12, 13, 24, 26 from CBS 110507; 14, 18, 23, 25, 27, 28 from CBS 110188; 15, 22 from CBS 591.96. Scale bars: 11–13 = 20 μm; 14–21, 23–27 = 10 μm; 22 = 1 μm; bar in 27 also applies to 28.



FIGS. 29–43. *Nalanthamala vermoesenii* in pure culture. 29–33. Penicillate conidiophores forming chains of ovoidal conidia. 34, 35, partly 36. Ovoidal conidia from linear chains formed by penicillate conidiophores. 37–40. Acremonium-like conidiophores arising from aerial mycelium forming heads of ellipsoidal to fusiform conidia. 41–43, partly 36. Ellipsoidal to fusiform, straight to slightly curved conidia formed by simple, acremonium-like conidiophores. 31 from 4 d old OA culture (SEM), 37–39 from 4–7 d old OA cultures; all others from 10–14 d old OA cultures. 29, 30, 32, 34, 36, 37, 43 from CBS 110893; 31, 38 from 356.87; 33, 39 from CBS 669.74; 35, 40–42 from CBS 222.36. Scale bars: 29, 31 = 30 μm; 30 = 50 μm; 32, 33, 37–39 = 20 μm; 34–36, 40–43 = 10 μm.



Figs. 44–59. *Nalanthamala diospyri* in pure culture. 44–50. Irregularly branched or simple, acremonium-like conidiophores. 51–53. Conidia arranged in chains. 54, 55. Ovoidal conidia with a truncated base and a rounded tip. 56–59. Ellipsoidal to fusiform, straight to slightly curved conidia with or without a visible, slightly laterally displaced hilum. All from 14 d old OA cultures of CBS 560.89. Scale bars: 44–53 = 20 μm; 54–59 = 10 μm.

TABLE III. Synopsis of characters that distinguish species of *Rubrinectria* and *Nalanthamala*

| Characters | *N. psidii* | *N. diospyri* | *N. vermoesenii* | *Nalanthamala* sp. | *Rubrinectria olivacea*, CBS 102268 | *Rubrinectria* sp., CBS 101648 |
|---|---|---|---|---|---|---|
| Colony radius (mm)[a] | | | | | | |
| 20 C | 3.5–8 | 8.5/9 | (9–)24–28(–47)[b] | 15/25 | 19.5 | 5 |
| 25 C | 8–11 | 13/15 | (10–)31–38(–58)[b] | 23/30 | 30 | 6.5 |
| 30 C | 12–17 | 18/23.5 | 3–12.5(–25)[c] | 23/40 | 19.5 | 25 |
| 33 C | 11–14 | 14/22 | 0(0.5)[c] | 2.5/6 | 1 | 0 |
| 36 C[d] | 0–<1 | 2–3 | 0 | 0 | 1 | 0 |
| Color of conidial masses | white, pale yellow (4A3), pale orange (5A3) | unpigmented or pale to light to brownish orange (5A3–5A4, 5C4) | salmon to greyish red (6A4–7B4) | salmon to greyish red (6A4–7B4) | off-white, orange white (5A2), or pale orange (5A3) | off-white to orange white (5A2) |
| Color of colony reverse[e] | pale yellow (3A3–4A3) to maize yellow (4A6), greenish hues absent | pale orange (5A3), brownish orange (5C4–5C5, 7C4) to brown (7D4); dirty orange (Gams 1971) | flesh (6B3), light orange (5A4), greyish orange (5B4), olive (3F6), olive brown (4F6), mustard brown (5E6) | dark green (28F6) to olive (1E5–1F5) | unpigmented, off-white, pale yellow (4A3), chamois (4C5), or lime green (2C5) | unpigmented, off-white, olive to mustard brown (4F6–5E6) |
| Plant host | *Pisidium guajava* | *Diospyros virginiana* | various Arecaceae, one strain from *Citrus medica* | *Areca* sp. | deciduous tree (bark) | *Prestoea* sp. (Arecaceae) (dead litter) |
| Disease observed on the host | destructive, rapid wilt | destructive, rapid wilt | necrosis, blight on Arecaceae | foot rot | unknown | unknown |

[a] Measured after 5 d incubated on PDA in the dark.

[b] Low value given in brackets applies to strain CBS 222.36 and 110893; high value to CBS 356.87.

[c] High value given in brackets applies to strains CBS 356.87.

[d] Measured after 4 d.

[e] Measured after 14 d incubated on PDA or OA in the dark at 20 C.

phialides in whorls. *Phialides* 5–12 μm long, 2–3.5 μm wide at base, 1–2 μm wide near apex. *Conidia* formed by sporodochia or penicillate conidiophores 1-celled, ovoidal, with somewhat truncated ends, held in dry chains, 4–5–6.7 × 2.5–3–3.5 μm (n = 79).

*Colonies* reaching a radius of 8–11 mm at 25 C when incubated 5 d on PDA in the dark. *Reverse* on OA and PDA pale yellow (3A2–3A3) after 14 d incubation in the dark, later or after incubation under near-UV, becoming light yellow (4A5), maize yellow (4A7), light orange (5A5) or chrome yellow (5A8), particularly in the colony center; greenish hues absent; on SNA unpigmented. *Colony surface* on OA and PDA cottony, in pale yellowish hues or appearing white due to moderately developed aerial mycelium and conidial masses. *Conidiophores* dimorphic, penicillate and acremonium-like. Penicillate conidiophores arising from hyphae growing near the agar surface or from aerial hyphae; stipe consisting of one or several cells, 20–200 μm long or longer, up to 7 μm wide at the base; penicillus consisting of a single whorl of phialides (monoverticillate) or several times branched (bi- to quaterverticillate), 15–50 μm high, typically adpressed or with slightly diverging primary branches; metulae 6–14 × 2–3 μm (n = 20); phialides in whorls of usually 4, narrowly bottle-shaped, widest in the lower third and slightly narrowing toward the tip, or more or less cylindrical and narrowing below the apex, (7.5–)11.5–13–15(–20) μm long, 1.5–3.2 μm wide at base, 2.1–3.1 μm wide in the lower third, and 1–2 μm wide at the tip (n = 99). Acremonium-like conidiophores formed submerged or by aerial hyphae, unbranched; phialides cylindrical or slightly tapering toward the tip, frequently somewhat bent, 10–30 μm long, 2–3 μm wide at base, and 1.2–1.4 μm wide at tip. *Conidia* dimorphic: on penicillate conidiophores (rarely also on simple or sparsely branched conidiophores) ovoidal, typically with somewhat truncated ends, (3.3–)4.5–4.8–5.1(–6.5) × (1.9–)2.4–2.6–2.7(–3.4) μm (n = 450), 1-celled, typically held in long, dry, persisting chains, slightly hydrophobic, in masses white or pale yellow to pale orange (4A3–5A3); on acremonium-like conidiophores ellipsoidal, cylindrical, or fusiform, with obtuse ends, or with an obtuse tip and a visible, slightly laterally displaced hilum, (3.5–)6–8.5–11(–20) × (1.2–)1.7–2.5–2.8(–5) μm (n = 150), typically 1-celled, rarely 2-celled because of a transverse septum, held in liquid drops at the tip of the phialides. *Chlamydospores* not observed.

HOLOTYPE. TAIWAN. Figure in Rep. Taiwan Museum 83:50. 1926. SYNTYPES. Chang-hua Co., on wood of *Psidium guajava,* 10 Aug 1923, *E. Kurosawa.* Chia-yi Co., on wood of *Psidium* sp., 8 Sep 1923, *K. Sawada* (both herb. Universitatis Taiwanensis). EPITYPE of *Myxosporium psidii,* designated herewith: Dried culture of CBS 116952 (BPI), filed together with BPI 863661 from which CBS 116952 was isolated. TAIWAN: Tainan Co., Ho-pi, on wood of *Psidium guajava,* 7 Sep 2004, coll. by *Y.-F. Yen,* isol. by *Yuming Ju* (BPI 863661, AR 4095; CBS 116952).

*Teleomorph.* Unknown.

*Habitat.* Decaying twigs or trunks of *Psidium guajava* trees in guava plantations, causing a destructive wilt disease.

*Distribution.* Guava orchards in Malaysia, South Africa and Taiwan, possibly restricted to subtropical or tropical regions.

*Description.* Kurosawa (1926) (in Japanese), Leu et al (1979).

*Additional strains and specimens examined.* All from *Psidium guajava.* MALAYSIA. M. Schoeman (CBS 110182, 110183, 110184). Beaumont cultivar, *H.C. Tuck* (CBS 687.97). SOUTH AFRICA. LIMPOPO: Levubu. *M. Schoeman* (CMW 8608). MPUMALANGA: Nelspruit. *M. Schoeman* (CBS 110185, 110186, 110187). *N. Grech* (CBS 912.85). *M.J. Wingfield* (CBS 590.96, 591.96). Twigs of dead *Psidium guajava* trees that were removed from the plantation and kept drying for several months, Mar 2002, *B.Q. Manicom* (herb. CBS, H-13961; CBS 110507).

*Notes.* Two syntypes of *M. psidii* are deposited at the herbarium of the Taiwan National University of which the specimen from Chia-yi County collected by E. Kurosawa is in good condition. Structures illustrated here from the natural substratum of a specimen from South Africa (FIGS. 3–10) match those encountered on both syntypes and in the illustration provided by Kurosawa (1926). On their natural substrata, *Nalanthamala psidii* (FIGS. 3–10) and *N. madreeya* (Subramanian 1956, FIGS. 1–8) form morphologically similar conidia, conidial chains and sporodochia. Conidia of chains of *N. psidii* mostly are shorter than 6 μm, while those of *N. madreeya* were described as mostly 7 μm long (Subramanian 1956). In culture, *N. psidii* typically forms penicillate (FIGS. 11–15) and acremonium-like (FIGS. 16–21) conidiophores simultaneously. Most of the strains studied, however, showed tendencies to form sectors, in which acremonium-like conidiophores dominated and penicillate conidiophores with conidial chains were sparsely formed or inconspicuous. No morphological discontinuity was observed by which strains from South Africa and Asia (Malaysia and Taiwan) might be distinguished. Strains from South Africa and Malaysia showed similar disease symptoms. Growth rates for *N. psidii* strains varied somewhat at 20 C but were less variable at 25, 30 and 33 C. Pale yellowish to pale orange colony pigments on OA and PDA and relatively well growing colonies at 33 C distinguish *N. psidii* from mostly greenish pigmented *Nalanthamala* taxa, frequently associated with palm hosts and generally not or hardly growing at 33 C (TABLE III).

**Nalanthamala vermoesenii** (Biourge) Schroers, comb. nov. FIGS. 29–43.

≡ *Penicillium vermoesenii* Biourge, La Cellule 33:230. 1923.

≡ *Gliocladium vermoesenii* (Biourge) Thom, The Penicillia, p. 502. 1930.

*Colonies* typically reaching a radius of 31–38 mm at 25 C when incubated 5 d on PDA in the dark. *Reverse* on OA and PDA flesh (6B3), light orange (5A4), grayish orange (5B4), yellowish green (3C3–3C7, 30A8), olive (3F6), olive brown (4F6), or mustard brown (5E6); on SNA unpigmented or with a faint of green. *Colony surface* on OA and PDA dusty to fine powdery, salmon to grayish red (6A4–7B4) due to occurrence and color of conidial masses; aerial mycelium sparsely developed. *Conidiophores* dimorphic, penicillate and acremonium-like. Penicillate conidiophores arising from agar surface or hyphae growing near the agar, in young colonies also from the weakly produced aerial mycelium; stipe consisting of one or several cells, up to 200 μm long or longer, up to 7 μm wide at the base; penicillus monoverticillate to quaterverticillate, 15–70 μm high, typically adpressed or with slightly diverging primary branches; metulae 7.5–16.5 × 2.5–3.5 μm (n = 20); phialides narrowly bottle-shaped, widest in the lower third and slightly narrowing toward the tip, or more or less cylindrical and narrowing below the apex, (8.5–)11–12.5–14(–19) μm long, 2–3 μm wide at base, 2.5–3 μm wide in the lower third, and 1–1.5 μm wide at the tip (n = 42). Acremonium-like conidiophores submerged or formed by aerial hyphae, unbranched, sometimes sparsely branched; phialides cylindrical or slightly tapering toward the tip, sometimes somewhat bent, 10–30 μm long, 2–2.5 μm wide at base, 1–1.5 μm wide at tip (n = 10); submerged conidiogenous cells also shorter, up to 5 μm long. *Conidia* dimorphic: on penicillate conidiophores ovoidal, typically with somewhat truncated ends, (3–)4–4.5–5(–7.5) × (1.5–)2.5–2.5–3(–4.5) μm (n = 162), 1-celled, typically held in long, dry, persisting chains, somewhat hydrophobic, in masses appearing salmon (6A4); on acremonium-like conidiophores ellipsoidal, cylindrical, or fusiform, straight or slightly curved, with obtuse ends, or with an obtuse tip and a visible, slightly laterally displaced hilum, (4–)5–7–8(–17) × (1.5–)1.5–2–3(–4.5) μm (n = 89), 1-celled, held in liquid drops at the tip of phialides. *Chlamydospores* not observed.

NEOTYPE for *Penicillium vermoesenii,* designated herewith: Location unknown. From *Areca* sp. Dried OA culture of CBS 110893 (= MUCL 9504, Biourge 415, ex-type strain of *Penicillium vermoesenii*) (herbarium CBS, H-13962).

*Teleomorph.* Unknown.

*Habitat.* Various Arecaceae, causing necrosis and blight; also reported once from *Citrus medica.*

*Distribution.* Particularly known from warm temperate, Mediterranean, or (sub)tropical climates; also known from hosts kept in glasshouses of other climatic regions.

*Description.* Biourge (1923).

*Strains examined.* Location unknown, from palm, *A. van Luijk, No. 7* (CBS 137.24, MUCL 7994, Biourge 416). USA. CALIFORNIA: South Pasadena, from *Phoenix canariensis* Hort. ex Chabaud, pathogenic to *Syagrus romanzoffiana* (Cham.) Glassm., *Phoenix canariensis, Washingtonia filifera* H. Wendl., Nov 1931, *D.E. Bliss* (CBS 222.36). AUSTRALIA. VICTORIA: Burnley Gardens, leaf of palm, *I. Pascoe* (CBS 356.87, FRR 3073). CZECH REPUBLIC. SOUTHERN MORAVIA: Palm house at Lednice village, decayed basal part of petiole of *Latania* sp., Dec 1971, *V. Holubová-Jechová* (CBS 669.74, IMI 160990). SPAIN. From *Citrus medica* (CBS 230.48, ATCC 10522, DSM 3709, IMI 040231, MUCL 7584, NRRL 1752).

*Notes. Nalanthamala vermoesenii* and *N. psidii* differ in colony growth rates (TABLE III). *Nalanthamala psidii* has a temperature optimum of around 30 C and continues to grow at 33 C, while *N. vermoesenii* grows most rapidly at approximately 25 C and does not grow at 33 C. Both species differ in the pigmentation of the conidial chains or masses, in the pigmentation of colonies on OA and PDA, and in their plant hosts (TABLES II, III).

**Nalanthamala diospyri** (Crandall) Schroers & M.J. Wingf., comb. nov. FIGS. 44–59.

≡ *Cephalosporium diospyri* Crandall, Mycologia 37:495. 1945.

≡ *Acremonium diospyri* (Crandall) W. Gams, Cephalosporium-artige Schimmelpilze (Hyphomycetes). Gustav Fischer. Stuttgart. p. 122. 1971.

*Colonies* reaching a radius of ca. 15 mm at 25 C when incubated 5 d on PDA in the dark. *Reverse* on OA and PDA pale orange (5A3), brownish orange (5C4–5C5, 7C4) to brown (7D4). *Colony surface* on OA and PDA dusty and white due to sporulation from sparsely formed aerial mycelium or slimy and brownish orange (5C4–5C5, 7C4) due to sporulation on agar surface. *Conidiophores* irregularly branched or acremonium-like as single phialides; phialides mostly cylindrical, narrowing slightly in the upper third, somewhat bent, (12.5–)16–21–25(–35.5) μm long, 1.5–3 μm wide at base, 1–2 wide at tip (n = 30). *Conidia* either obovate, with an obtuse tip and a truncated base, 1-celled, formed in chains or heads, (3.5–)4–4.5–4.5(–6) × (2–)2.5–2.5–2.5(–4) μm (n =

95) or ellipsoidal, cylindrical, or fusiform, straight or slightly curved, with obtuse ends or with an obtuse tip and a visible, slightly laterally displaced hilum, 1-celled, formed in heads, (4.5–)8–10.5–12(–20) × (2–)2.5–3–3.5(–4.5) μm (n = 107). *Chlamydospores* not observed.

*Teleomorph.* Unknown.

*Habitat.* Bark of *Diospyros virginiana,* American persimmon, causing a destructive wilt.

*Distribution.* Southeastern USA.

*Descriptions.* Crandall (1945), Durrell (1963), Gams (1971).

*Strains examined.* USA. TENNESSEE: Readyville, from wood of *Diospyros virginiana, B.C. Crandall* (CBS 560.89 = CBS 131.51, ATCC 9066, DSM 2939, IFO 6118, MUCL 9732). MISSISSIPPI: From *Diospyros virginiana, B.C. Crandall BC-1* (CBS 430.89 = ATCC 22202).

*Notes.* In young colonies, *Nalanthamala diospyri* forms conidial chains only sparsely but more abundantly in colonies older than 14 d, particularly on OA and PDA. The lack of penicillate conidiophores, shape of conidia that are arranged in chains, colony pigmentation, and host spectrum distinguish it from other *Nalanthamala* species (TABLE III). Chain formation of the obovate conidia and the two types of conidia encountered links *N. diospyri* morphologically to the other *Nalanthamala* species.

*Nalanthamala* sp.

*Habitat.* On diseased *Areca* sp.

*Distribution.* Netherlands.

*Strains examined.* NETHERLANDS. Maasdijk, greenhouse, from leaf of *Areca* sp. *J.W. Veenbaas-Rijks* (CBS 456.92). Naaldwijk, from *Areca catechu,* causing foot rot (CBS 357.87, PD 86/1179).

*Notes.* Two conidial isolates of this *Nalanthamala* species are available. They are similar to *N. vermoesenii* in micro- and macromorphological features and both species inhabit Arecaceae (TABLES II, III). *Nalanthamala* sp. is distinguished weakly from *N. vermoesenii* by faster colony growth rates, particularly at 30 C, and by darker, greenish colony pigmentation (TABLE III).

*Rubrinectria olivacea* (Seaver) Rossman & Samuels, Stud. Mycol. 42:164. 1999.

≡ *Macbridella olivacea* Seaver, Mycologia 2:178. 1910.

*Synonymy.* Samuels (1973), Rossman et al (1999).

HOLOTYPE (NY). MEXICO. Motzorongo, near Córdoba, in moist forest, on stem of unidentified palm, 15 Jan 1910, *Murrill & Murrill 911.*

*Anamorph. Nalanthamala* sp.

*Habitat.* Known from palm and bark.

*Distribution.* Mexico, Costa Rica, ?Philippines, possibly restricted to tropical regions.

*Additional specimens examined.* COSTA RICA. Limon, Puerto Viejo, Refugio Nacional Mendoza-Manzanilla, 0–50 m elevation, on bark, 8 Jul 1999, *G.J. Samuels 8532, P. Chaverri, S. Salas et al* (BPI 746597; culture G.J.S. 99-72/99-178, CBS 102268). PHILIPPINES. Luzon, Mount Maquiling, on bark, 23–28 Feb 1912, *P.W. Graff, Lloyd 11408* (BPI 801936).

*Descriptions.* Seaver (1910), Samuels (1973), Samuels and Brayford (1994), Rossman et al (1999).

*Notes.* The two examined specimens form perithecia on well-developed erumpent stromata. The same kind of stroma was described for the type of *R. olivacea* (illustrated by Samuels and Brayford 1994). However, they originate from bark of deciduous trees, while the type specimen was described from a palm host. Strain CBS 102268 is characterized mainly by off-white, pale yellow or chamois colony pigments and white conidial masses, however, in older OA and PDA colonies yellowish green or lime green (2C5) pigments also developed, similar to those formed by *N. vermoesenii* and *Nalanthamala* sp.

*Rubrinectria* sp.

*Anamorph. Nalanthamala* sp.

*Habitat.* Known from dead parts of palm.

*Distribution.* USA, Puerto Rico.

*Specimen examined.* USA. PUERTO RICO: Caribbean National Forest, Luquillo Mountains, Big Tree Trail, on litter of *Prestoea* sp. (Arecaceae), 19 Jun 1998, *W. Gams, H.-J. Schroers 278* (CBS 101648).

*Notes.* This *Rubrinectria* sp. is characterized by small, poorly developed, erumpent perithecial stromata and differs by that from the well-developed stromata found in *R. olivacea.* Additional specimens would need to be examined to determine whether the stromatal morphology has significance in distinguishing it from *R. olivacea. Rubrinectria* sp. (CBS 101648) forms perithecia homothallically in cultures. Perithecia are initially dull orange to dull red but become greenish-black because of olivaceous granules on the perithecial wall. Ascospores are brownish, coarsely striate and appear in olivaceous-black cirri. The pigmentation of the perithecia as well as the ornamentation and pigmentation of the ascospores are diagnostic of the genus (Seaver 1910, Samuels 1973, Samuels and Brayford 1994, Rossman et al 1999).

## DISCUSSION

Nalanthamala *is the appropriate genus for the guava pathogen.*—*Nalanthamala psidii* was described originally in *Myxosporium* (Kurosawa 1926), but this genus was rejected by von Höhnel (1915) and regarded as nomen nudum by Sutton (1977) because its type species, *M. croceum,* is based on a mixture of different fungi. Similarities of conidiomata, conidia and conidial chains formed by *Nalanthamala madreeya* and *N. psidii* on their natural substrata led us to conclude that both species are congeneric. Similar conidiomata are formed also by *Nectria cinnabarina* (Seifert 1985), however, conidia of *N. cinnabarina* are formed in slimy masses but not in chains. Sporodochia of *Dendrodochium* Bonorden and other sporodochial genera listed as synonyms under *Clonostachys* (Schroers 2001) have a hyphal subhymenium and dry, linear chains of conidia have been described for none of these genera. *Volutella* Fr. and *Myrothecium* Tode are characterized by setae (Domsch et al 1980), which were not described for *N. madreeya* nor observed in *N. psidii. Nalanthamala madreeya* was not described from pure cultures (Subramanian 1956) and could not be compared with *N. psidii* in vitro.

Rubrinectria, *teleomorph of* Nalanthamala, *belongs to the Nectriaceae.*—Based on LSU rDNA sequence analyses, *N. psidii, N. vermoesenii, N. diospyri* and two ex-ascospore isolates of *Rubrinectria* form a monophyletic group among taxa of the Nectriaceae (Hypocreales), which is particularly rich in plant-pathogenic or plant-invading taxa (Gerlach and Nirenberg 1982, Rossman et al 1999). One of the ex-ascospore isolates was identified as *R. olivacea* based on morphological characters of the teleomorph. This phylogeny supports classification of *Rubrinectria* in the Nectriaceae based on morphological characters (Rossman et al 1999) and links *Rubrinectria* with the anamorphic genus *Nalanthamala.* The connection is supported by the similar dimorphism of conidiophores and conidia in *N. vermoesenii, N. psidii, Nalanthamala* sp., and the ex-ascospore isolates of *Rubrinectria.*

Classification of *Rubrinectria/Nalanthamala* in the Nectriaceae is in agreement with results of chemotaxonomic studies that suggested close relationship of *N. vermoesenii* with *Fusarium* sp. and *Nectria cinnabarina* rather than species of *Penicillium* and *Clonostachys* (cited as *Gliocladium roseum, Nectria* sp. or *Sesquicillium* sp.) (Ahrazem et al 1999, 2001).

Nalanthamala *and phenotypically similar taxa.*—*Rubrinectria/Nalanthamala* is unrelated to eurotialean or hypocrealean taxa characterized by penicillate conidiophores either forming conidial chains or heads (FIG. 1). "*Nalanthamala*" *squamicola* (Gams 1975) the only other species ever classified in *Nalanthamala,* is excluded from the *Nalanthamala/Rubrinectria* clade, clustering instead with members of the Bionectriaceae. It forms sporodochia abundantly in pure culture, while well-developed sporodochia have not been observed in cultures of taxa classified here in *Nalanthamala.*

In *N. psidii,* stability of conidial chains is achieved apparently by wall material connecting subterminal parts of adjacent conidia (FIG. 22), while, in *Penicillium,* chain stability is achieved by connectives that attach central terminal points of two adjacent conidial apices (Gams 1978, Cole and Samson 1979). In other genera of the Hypocreales forming conidial chains, conidia also can be connected to each other through an amorphous mucous matrix (Gams 1978).

The polyphyletic distribution of taxa with penicillate conidiophores forming either linear chains or mucous heads of conidia has been discussed for several cases (Berbee et al 1995, Ogawa et al 1997, Rehner and Samuels 1994) and might suggest that overall morphological characters of these anamorphs are inconclusive for classification schemes. Our morphological analysis, however, indicates that a more sound generic delimitation can be achieved when various characters from culture, in addition to those from the natural substratum, are considered jointly. The close relationship of *Stachybotrys chartarum,* which forms slimy masses of conidia, and *S. echinata,* which forms linear chains of conidia, previously postulated based on morphological observations (Smith 1962) and confirmed by sequence data (Haugland et al 2001, this paper) is consistent with this view.

*Distinction and phylogeny of* Nalanthamala *species.*—*Nalanthamala diospyri* is characterized by ovoidal conidia showing truncation only at the base, while truncation is shown at both conidial ends in other *Nalanthamala* species, and by irregularly branched conidiophores. Penicillate conidiophores were not observed. Absence of penicillate conidiophores also was observed sometimes in colony sectors of *N. psidii,* and the lack of this feature could be explained by degeneration in vitro. Conidial chains and the two kinds of conidia formed by *N. diospyri* also were described in earlier studies (Durrell 1963, Gams 1971). They support classification of *N. diospyri* in *Nalanthamala.* All other *Nalanthamala* species showed similar conidiophores and conidia. *Nalanthamala vermoesenii, N. psidii* and *N. diospyri* are distinguished from each other by macroscopical characters such as pigmentation of colonies and conidial masses and growth rates (TABLE III). *Nalanthamala vermoesenii, Nalanthamala* sp. and *Rubrinectria* sp. form a supported monophyletic group, of which *N. diospyri* and *N. psidii* are sister taxa (FIG. 2). Most strains of this monophyletic group are pathogenic to or originating from palm hosts and are characterized by greenish colony pigments ranging from yellowish green to dark olive as well as salmon or white conidial masses. *Nalanthamala vermoesenii* strain CBS 230.48 and *R. olivacea* strain CBS 102268 were isolated from *Citrus medica* or bark of a deciduous tree, respectively, however, the type of *R. olivacea,* which could not be included in the molecular analysis, originated from palm.

*Infraspecific variation within* N. psidii *and* N. vermoesenii.—Two polymorphic sites in the ITS rDNA and three in the partial β-tubulin gene consistently distinguished morphologically identical *N. psidii* strains from South Africa and Malaysia/Taiwan. DNA sequence data therefore support occurrence of distinct lineages within *N. psidii.* Because monophyly of the two lineages was not supported by sequence data and paraphyly was seen instead (FIG. 2), subspecific phylogenetic taxa were not distinguished.

Five strains of *N. vermoesenii* including the ex-type strain (CBS 110893) originate from palm species on three continents (TABLE II). With the exception of one nucleotide change in the partial β-tubulin gene of strain CBS 356.87, sequences thus far examined are identical for these strains. Molecular data, therefore, support earlier assumptions concerning distribution and host specificity of *N. vermoesenii* (Aragaki et al 1991, Farr et al 1989, Raper and Thom 1949). The strains are homogeneous in overall morphological characters but show variable growth rates at 20, 25 and 30 C. Slow growth was observed in two strains (CBS 222.36 and CBS 110893) that have been maintained in culture collections for many years, while more recently isolated strains grew more rapidly in culture. Relatedness of CBS 230.48 to the core group of *N. vermoesenii* is supported by sequence data (bootstrap value for the species clade of *N. vermoesenii* = 100%) (FIG. 2) and by overall micro- and macroscopical characters. It differed from the core group of *N. vermoesenii* in several nucleotides of the partial β-tubulin gene sequences and in its occurrence on *Citrus medica.* No additional data regarding its ecology and pathogenicity on *Citrus medica* are available.

*Pathogenicity and ecology.*—Crandall and Baker (1950) characterized the persimmon wilt caused by *N. diospyri* as abrupt, rapidly spreading throughout the tree and causing discoloration of leaves at the tops of trees, followed by general wilting, rapid defoliation and death within a few months; conidia of *N. diospyri* form in orange masses below the bark resulting in red erumpent blisters. These symptoms are comparable to those caused by *N. psidii* on *Psidium guajava* (Leu et al 1979, Schoeman et al 1997).

Wounds are required for infection of persimmon trees by *N. diospyri* (Crandall and Baker 1950) and of palms by *N. vermoesenii* (López-Llorca and Orts 1994). Crandall and Baker (1950) demonstrated that *N. diospyri* infects persimmon trees by airborne conidia. Conidia of *N. psidii* held in long, dry chains are well adapted for wind dispersal and, like *N. diospyri* and *N. vermoesenii,* infect guava trees through naturally and artificially inflicted wounds (Leu et al 1979).

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