The polyphyletic nature of *Paecilomyces sensu lato* based on 18S-generated rDNA phylogeny

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**Abstract:** Nuclear-encoded small-subunit ribosomal DNA was used to examine phylogenetic relationships in *Paecilomyces sensu lato*. Phylogenetic analysis of the 18S nr DNA demonstrates that *Paecilomyces* is polyphyletic across two subclasses, Sordariomycetidae and Eurotiomycetidae. The type species, *Paecilomyces variotii*, and thermophilic relatives belong in the order Eurotiales (Trichocomaceae), while mesophilic species related to *Paecilomyces variotii*, and thermophilic relatives belong in the order Eurotiales (Trichocomaceae), while mesophilic species related to *Paecilomyces farinosus* are in the order Hypocreales (Clavicipitaceae and Hypocreaceae). One species, *Paecilomyces inflatus*, had affinities for the order Sordariales. Within the Eurotiales, *Paecilomyces* is monophyletic. Within the Hypocreales, species of *Paecilomyces* are polyphyletic, although the data failed to fully resolve these relationships.

**Key words:** 18S rDNA, anamorph-teleomorph connections, Clavicipitaceae, Hypocreaceae, *Paecilomyces*, phylogenetics, Trichocomaceae

**INTRODUCTION**

The hyphomycete genus *Paecilomyces* was established by Bainier (1907) for *Paecilomyces variotii* characterized by verticillate conidiophores with divergent whorls of phialides, which have a cylindrical or inflated base tapering to a long and distinct neck. The conidia are typically hyaline, one-celled, smooth-walled and are produced in basipetal chains. The genus was revised by Brown and Smith (1957) and modified by Samson (1974), who accepted 31 species. There has been no comprehensive review of the genus since, but more than forty species now have been recognized in the genus *Paecilomyces*.

Brown and Smith (1957) significantly transferred the insect-pathogenic *Isaria farinosa* (Holm ex S.F. Gray) Fr. to *Paecilomyces* and with it other entomogenous species previously classified in *Isaria* or *Spiralectra*. Samson (1974) considered all entomogenous *Isaria* with flask-shaped phialides tapering abruptly to long thin necks and catenate conidia as *Paecilomyces* and proposed several further combinations that generally have been accepted.

The cleistothecial ascomycete *Bysschlamys* Westling (Eurotiales: Trichocomaceae) was first described by Westling (1909) and the connection of a *Paecilomyces* anamorph with *Bysschlamys* was made by Stolk and Samson (1972). *P. fulvus* Stolk & Samson was found to be the anamorph of *B. fulva* Oliver & G. Smith. Other links include: *B. zolleriae* Ram with *P. zolleriae* Stolk & Samson and *B. nivea* Westling with *P. niveus* Stolk & Samson. Within the Trichocomaceae, *Paecilomyces* also is linked with the gymnothecial *Talaromyces* (*T. byssochlamydioides* Stolk & Samson; *P. byssochlamydioides* Stolk & Samson and *T. leycettanii* Evans & Stolk; *P. leycettanii* [Evans & Stolk] Stolk, Samson & Evans). In addition, Samson (1974) recognized *P. crustaceus* Apinis & Chesters as the anamorph of the cleistothecial *Thermoascus crustaceus* (Apinis & Chesters) Stolk.

With the inclusion of mesophilic, entomogenous *Paecilomyces*, further teleomorph connections were added. For these species teleomorph associations were assumed to be clavicipitaceous and within the Hypocreales (Samson 1974) with *Cordyceps* and *Torrubiella* as purported teleomorph connections. While the clear connection with a teleomorph was established for the thermophilic *Paecilomyces* spp., the insect taxa were not so clear with many purported connections regularly being disproved. In particular, Petch (1936) refuted the connection between *Cordyceps militaris* (L. : Fr.) Link and *P. farinosus* (Holm ex S.F. Gray) Brown & Smith while that between *P. tenuipes* (Peck) Samson and *C. takaomontana* Yakusuiji & Kumazawa became accepted. Hywel-Jones (1993) confirmed a link between *P. cinnamonmeus* (Petch) Samson & W. Gams and *Torrubiella luteostrata* Zimm.

Thus, *Paecilomyces* in this broad sense can be considered polyphyletic across two ascomycete orders, the Eurotiales and the Hypocreales. To investigate...
the order relationships of mesophilic and thermo-
philic isolates of Paecilomyces with teleomorph gen-
era, the 18S region of rDNA was sequenced. A single
hypothesis was advanced for testing: The genus Paeci-
ломыces is polyphyletic at the order level.

MATERIALS AND METHODS

Fungi used.—Paecilomyces species and strains were selected
from material collected in Thailand and from the CBS col-
lection (Table I). Representatives of known or purported
teleomorphs of Paecilomyces also were used where available.
Isolates were grown on malt-peptone broth and incubated
at optimum temperature (25, 30 or 40 C, depending on
species) for 3–4 d.

DNA extraction.—Mycelia were harvested, and a Fast DNA
Kit (BIO 101, Systems, Vista, California) isolated genomic
dNA. CSL-Y buffer was used and extractions were processed
in a FastPrep machine (FastPrep FP 120, BIO 101, Savant)
for 30 s at speed 4.5.

DNA amplification.—Amplification of the 18S rDNA was
done using universal primers NS1-NS24 (White et al 1990,
Gargas and Taylor 1992). PCR reactions were performed in
50 µL volume comprising 1 unit SuperTaq (HT Technolo-
gies), 2.5 mM MgCl2, 200 µM dNTP, 0.2 µM primer, 1×
buffer and 10–50 ng DNA template. The PCR was per-
fomed using GeneAmp PCR System 9700 (Applied Biosys-
tems) programmed as: 4 min denaturation step at 94 C,
followed by 35 cycles of 1 min at 94 C, 1 min at 52–55 C
and 1.5 min at 72 C, with a final extension of 7 min.

Table I. Cultures used in this study (CBS = Centraalbureau voor Schimmelcultures, The Netherlands; BCC = BIOTEC,
Thailand)

<table>
<thead>
<tr>
<th>Species</th>
<th>Strain number</th>
<th>Remarks</th>
<th>Host</th>
<th>GenBank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aphanoascus cinnabarinus</td>
<td>CBS 267.72</td>
<td>NT</td>
<td>Soil</td>
<td>AY526483</td>
</tr>
<tr>
<td>Bysochlamys fulva</td>
<td>CBS 132.33</td>
<td>T</td>
<td>Bottled fruit</td>
<td>AY526482</td>
</tr>
<tr>
<td>Bysochlamys zollerniae</td>
<td>CBS 374.70</td>
<td>T</td>
<td>Wood of Zollernia ilicifolia</td>
<td>AY526485</td>
</tr>
<tr>
<td>Mariannaea elegans var punicea</td>
<td>CBS 239.56</td>
<td>T</td>
<td>Soil, Zaire</td>
<td>AY526489</td>
</tr>
<tr>
<td>Mariannaea atypica</td>
<td>CBS 744.73</td>
<td>T</td>
<td>Spider, Japan</td>
<td>AY526490</td>
</tr>
<tr>
<td>Nomuraea rileyi</td>
<td>CBS 867.71</td>
<td>T</td>
<td>Trichoplusia ni, USA</td>
<td>AY526491</td>
</tr>
<tr>
<td>Paecilomyces aeruginus</td>
<td>CBS 350.66</td>
<td>T</td>
<td>Debris of Glyceria maxima</td>
<td>AY526484</td>
</tr>
<tr>
<td>Paecilomyces amoeneroseus</td>
<td>CBS 107.73</td>
<td>T</td>
<td>Coleopteran pupa</td>
<td>AY526464</td>
</tr>
<tr>
<td>Paecilomyces carneus</td>
<td>CBS 399.59</td>
<td>T</td>
<td>Forest soil</td>
<td>AY526481</td>
</tr>
<tr>
<td>Paecilomyces cateniannulatus</td>
<td>CBS 152.83</td>
<td>T</td>
<td>Coleopteran adult</td>
<td>AY526465</td>
</tr>
<tr>
<td>Paecilomyces catenobiliquus</td>
<td>CBS 153.83</td>
<td>T</td>
<td>Adoxophyes privatana</td>
<td>AY526466</td>
</tr>
<tr>
<td>Paecilomyces cinnamomeus</td>
<td>CBS 398.86</td>
<td>T</td>
<td>Living leaf of Syzygium jambos</td>
<td>AY526468</td>
</tr>
<tr>
<td>Paecilomyces farinosus</td>
<td>CBS 111113</td>
<td>T</td>
<td>Derived from epitype from type</td>
<td>Denmark</td>
</tr>
<tr>
<td>Paecilomyces ghanensis</td>
<td>CBS 105.73</td>
<td>T</td>
<td>Lepidopteran pupa</td>
<td>AY526490</td>
</tr>
<tr>
<td>Paecilomyces inflatus</td>
<td>CBS 259.39</td>
<td>T</td>
<td>Abdomen of adult Apis mellifera</td>
<td>AY526479</td>
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<tr>
<td>Paecilomyces javanicus</td>
<td>CBS 263.58</td>
<td>T</td>
<td>Soil</td>
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</tr>
<tr>
<td>Paecilomyces lilacinus</td>
<td>CBS 994.73</td>
<td>T</td>
<td>Coleopteran pupa</td>
<td>AY526463</td>
</tr>
<tr>
<td>Paecilomyces marquandii</td>
<td>CBS 182.27</td>
<td>T</td>
<td>Soil</td>
<td>AY526475</td>
</tr>
<tr>
<td>Paecilomyces niphetodes</td>
<td>CBS 364.76</td>
<td>T</td>
<td>Soil, on a rock</td>
<td>AY526472</td>
</tr>
<tr>
<td>Paecilomyces penicillatus</td>
<td>CBS 448.69</td>
<td>T</td>
<td>Rotting mushroom</td>
<td>AY526493</td>
</tr>
<tr>
<td>Paecilomyces tenuipes</td>
<td>ARSEF 5135</td>
<td>T</td>
<td>Lepidoptera pupa</td>
<td>AY526492</td>
</tr>
<tr>
<td>Paecilomyces variotii</td>
<td>CBS 102.74</td>
<td>T</td>
<td>Urtica dioica, UK</td>
<td>AY526480</td>
</tr>
<tr>
<td>Septofusidium herbarum</td>
<td>CBS 265.58</td>
<td>T</td>
<td>Dry soil</td>
<td>AY526476</td>
</tr>
<tr>
<td>Thermoascus crustaceus</td>
<td>CBS 398.68</td>
<td>T</td>
<td>Coal spoil tip soil</td>
<td>AY526487</td>
</tr>
<tr>
<td>Talaromyces bysochlamydoides</td>
<td>CBS 413.71</td>
<td>T</td>
<td>Fruit drink</td>
<td>AY526473</td>
</tr>
</tbody>
</table>
| Talaromyces lycettanus      | CBS 101075    | T                         | Decaying Parthenium argenta-
tum                                      | AY526486        |
| Talaromyces spectabilis     | CBS 181.67    | T                         | Homoptera—scale insect        | AY526469        |
| Torubiella luteorostrata    | BCC 7627      | T                         | Soil Thailand                 | AY526488        |
| Warcipliella spinulosa      | BCC 13745     | T                         | Neotype.                      |                 |

T = Type, NT = Neotype.
DNA visualization, quantification and purification.—Success of PCR reaction was confirmed by ultraviolet fluorescence after agarose gel electrophoresis and ethidium bromide staining of 5 μL of the reaction mix. Single-band PCR products were purified using GFX Purification Kit (Amersham Pharmacia 27-9602-01) and quantified for sequencing using DNA Smart Ladder on a 1% agarose gel (Gibco BRL, ultrapure) stained with 0.5 μg mL⁻¹ ethidium bromide.

DNA sequencing.—DNA sequence reactions were performed using a BigDye Terminator Sequencing Kit. Additional internal primers used for sequencing were NS3, NS5, NS23UBCR and NS20 UCB (Gargas et al. 1992). The SeqMan software program was used to compile and edit multiple sequences generated from each template.

Sequence alignment and phylogenetic analyses.—A preliminary alignment of the sequences obtained from this study and GenBank was performed with ClustalW incorporated in BioEdit version 5.06 (Tom Hall, Department of Microbiology, North Carolina State University, Raleigh) using default parameters. The positions of some gaps in the output of this program were adjusted manually with BioEdit to maximize for homology. Alignment gaps were treated as missing data. Eight hundred seventy-four uninformative and ambiguous characters in the alignment were excluded. Maximum-parsimony analysis was done in PAUP version 4 b10, using heuristic methods with characters first defined as unordered and having equal weights. Successive weighting was done to select for more consistent characters. Relative support for resulting trees was obtained from bootstrap analyses (Felsenstein 1985) using 500 heuristic searches with groups occurring at 50% or greater frequencies being retained in the consensus trees. All heuristic searches were performed by tree-bisection-reconstruction branch swapping with 100 random sequence addition and MULTIPARS option in effect. To test the robustness of the branches of the tree consistency index (CI), homoplasy index (HI), retention index (RI) and rescaled consistency index (RC) were calculated. The trees were rooted with Cookeina spp. (Pezizales: Sarcoscyphaceae) as outgroup.

RESULTS
An initial dataset of 14 18S sequences was obtained by sequencing isolates of thermophilic fungi made from soil samples and other substrates in Thailand plus CBS (type) isolates. In the mesophilic section Isariaoidae the BIOTEC culture collection contained ninety Paecilomyces isolates from insects; these isolates were augmented with mesophilic Paecilomyces isolates made available from CBS. Of these, 31 isolates representing 22 species of Paecilomyces sensu lato were sequenced for the 18S region. These Paecilomyces isolates and an in-house database of 18S sequences of other members of the Clavicipitaceae was augmented with sequences of comparable length from GenBank. The data presented here is derived from preliminary analyses (data not shown) and is a subset selected to present the maximum information with the minimum of ambiguity. This dataset contains 70 taxa, including 26 taxa of thermophilic and mesophilic Paecilomyces or their teleomorphs. The sequences represent members of two Ascomycete subclasses, the Sordariomycetidae and the Eurotiomycetidae (Kirk et al. 2001).

Initial analysis of this dataset yielded 1394 trees with a tree length of 762 (CI = 0.423; RI = 0.823; RC = 0.348; HI = 0.577). Successive reweighting based on the RC value yielded six equally parsimonious trees with a tree length of 224.39 (CI = 0.671; RI = 0.936; RC = 0.628; HI = 0.329). A consensus tree of these MPTs was used to generate bootstrap values. These values then were superimposed upon a cladogram of the best tree as determined by the Kishino-Hasagawa test (Fig. 1). A bootstrap analysis was generated by a full heuristic search of the six most-parsimonious trees of 70 taxa, taking 500 replications with 10 random sequence additions at a time.

The data shows Paecilomyces sensu lato to be split across two subclasses of the Ascomycetes, Eurotiomycetidae and Sordariomycetidae. The type species P. variotii was placed in the Euriotymycetidae within the order Eurotiales with 100% support (Fig. 2 Clade E) and shared a close affinity for the ascomycete Talaryomyces spectabilis (93%). Within the Eurotiomycetidae the genus Paecilomyces was represented by two Paecilomyces species plus five teleomorphs known to produce Paecilomyces anamorphs in the order Eurotiales (Fig. 2). In the Eurotiomycetidae, Paecilomyces formed an ill-defined clade within the Eurotiales. Clade B had 80% support and consisted of the type P. variotii and Byssochondys teleomorphs.

The type species of Paecilomyces section Isarioidea (P. farinosus) similarly was placed in the subclass Sordariomycetidae in the order Hypocreales with 100% support for a clade based on the orders Hypocreales (Clade H, Fig. 2) and Glomerellaceae/Colletotrichaceae (Fig. 2). Furthermore, P. farinosus exhibited a 79% homology with a sister clade that supported C. takaomontana (Fig. 2 Clade I).

Within the Hypocreales, three significant clades (Fig. 2) were identified based on the families Clavicipitaceae, Hypocreaceae and Nectriaceae. Paecilomyces (11 species) were predominant in the Clavicipitaceae with two species—P. niphedodes and P. penicillatus—present in the Hypocreaceae. With the current dataset no Paecilomyces were associated with the Nectriaceae. Also within the Sordariomycetidae, P. inflatus was sister to a clade of the Sordariales with 97% support (Fig. 2).

Within the Hypocreales clade were species of Paecilomyces with known affinities for insects. A major subclade (Clade I) with a bootstrap support of 79%
FIG. 1. Phylogenetic relationships of Paecilomyces species with selected anamorphs and teleomorphs of ascomycete genera based on 18S rDNA sequences. The cladogram represented was the best tree obtained from Kishino-Hasegawa Test in PAUP* version 4b10. The percentages above the branches are the frequencies with which a given branch appeared in 1000 bootstrap replications. Bootstrap values less than 50% are not displayed. The letters in bold above the branches represent these splits: H: Hypocreales split; E: Eurotiales split.

included a recent Danish isolate of *P. farinosus* that Samson (1974) recognized as the type species for Section *Isarioidea*. This isolate (CBS 111113), derived from a specimen of a Lepidoptera pupa (CBS 6856) collected close to the type locality of *Isaria farinose*, now serves as the epitype (K.T. Hodge, personal communication). From our analysis the sister clade containing *P. amoeneroseus* and *P. cateniobliquus* (clade I) needs further comparison with *P. farinosus* because these also might be part of a larger *Isarioidea* clade. Clade P was another well-defined (although poorly supported) sister clade of *Paecilomyces* species.
Within the Ascomycetes, *Paecilomyces* appears to be polyphyletic at the subclass and ordinal level. While Oborník, Jirku and Dolezel (2001) recognized that

and allies. Two species—*P. carneus* and *P. marquandi*—had uncertain affinities within the Clavicipitaceae. Finally, within the family Hypocreaceae were two further *Paecilomyces* species from which appear to be derived *Hypocrea.*

**Figure 2.** Phylogenetic relationships of *Paecilomyces* species with selected anamorphs and teleomorphs of ascomycete genera based on 18S rDNA sequences. The phylogram represented was the resulting best tree from Kishino-Hasegawa Test. The letters in bold above the branches represent these splits: H: Hypocreales split; E: Eurotiales split. The vertical lines on the far right show the division of *Paecilomyces* into three major clades spreading over two subclasses, Sordariomycetidae and Eurotiomycetidae. The tree was rooted with * Cookeina sulcipes* and * Cookeina tricholoma* as outgroup.
Paecilomyces is polyphyletic at the ordinal level, these authors included only species of the section Isarioidea. Thermophilic species based on the type of Paecilomyces belong with gymnothecial teleomorphs in the Eurotiales, while most mesophilic Paecilomyces and Paecilomyces-like genera belong in the Hypocreales.

Samson (1974) represents the most recent monographic treatment of Paecilomyces and related genera. This work was significant for its recognition that within Paecilomyces there are two distinct groups, placed in two sections; the thermophilic section Paecilomyces, based on the type species P. variotii, while section Isarioidea was reserved for mesophilic, generally entomogenous species but also nonentomogenous taxa. Our work confirms that Samson’s section Paecilomyces belongs with the Eurotiales while section Isarioidea is either poly- or paraphyletic at the order level within the Sordariomycetidae.

While many species of Paecilomyces are known, definite teleomorph connections have been established for a few. And yet six teleomorphs have been accepted for Paecilomyces indicating a polyphyletic nature. The genus Paecilomyces sensu lato thus presents problems similar to those previously considered for Penicillium (Berbee et al 1995) and Geosmithia (Ogawa et al 1997). Ogawa et al (1997) noted that “Penicillium never appears outside Trichocomaceae.” This is in contrast to Geosmithia (Ogawa et al 1997) and now Paecilomyces (in this study). While Berbee et al (1995) demonstrated that Penicillium was polyphyletic; it nevertheless was polyphyletic only within the Trichocomaceae. Geosmithia (Ogawa et al 1997) and Paecilomyces (in this study) appear to be polyphyletic within and without the Trichocomaceae (Geosmithia) and within and without the subclass Eurotiomycetidae (Paecilomyces).

Within the Eurotiomycetidae, Paecilomyces has been associated with four ascomycete genera, Aphanoascus, Byssochlamys, Talaromyces and Thermoascus. Samson (1974) described Paecilomyces aeruginus based on material isolated by Apinis (1962). Our phylogeny places this close to Aphanoascus cinnabarinus (Fig. 2), which was reported to have a Paecilomyces anamorph (Jong and Davis 1975). Zukal (1890) described A. cinnabarinus from alligator dung. However, Apinis (1968) proposed A. fulvoscent (Cooke) Apinis as the type of the genus, accepting A. cinnabarinus as a synonym. Later, Udagawa and Takada (1973) re-introduced by neotypification of A. cinnabarinus with the Paecilomyces anamorph described by Jong and Davis (1975). Currah (1985) considered the description of Udagawa and Takada (1973) and Jong and Davis (1975) of dagger-like spines on the ascospores and a Paecilomyces anamorph, but he did not accept the neotypification “since these features differ from Zukal’s protologue, and since Zukal’s type is available.” Aphanoascus was recognized by Currah (1985) to have a Chrysosporium anamorph, and he placed this genus in the Onygenaceae. Yaguchi et al (1993) erected a new genus Chromocleista for the new species C. malachita and combined A. cinnabarinus as a second species. The type species of Chromocleista is a typical Eutypenillium (Frisvad and Samson, unpublished), and therefore the taxonomic status of A. cinnabarinus remains unsolved. P. aeruginus differs significantly from other Paecilomyces in having conidia surrounded by a mucilaginous layer. Based on its Aphanoascus affinities and the presence of mucoid conidia we do not consider this species to fit with Paecilomyces sensu stricto.

Udagawa and Suzuki (1994) described Talaromyces spectabilis with a Paecilomyces anamorph. However, the morphology and molecular data suggest that T. spectabilis is better placed in Byssochlamys (RA Samson, unpublished data). Accepting this we then have Clade B as a Paecilomyces clade with Byssochlamys as the exclusive teleomorph.

While the thermophilic Section Paecilomyces was confined to the Eurotiales, we found that section Isarioidea was present in two orders of the Sordariomycetidae. P. inflatus was grouped with the Sordariales, although we could not place it in this order with confidence. Samson (1974) accepted this species as “the only monophiliadic species of Paecilomyces.” Isolate CBS 259.39 is the type culture of Myceliophthora inflata and was isolated from the abdomen of a honeybee (Samson 1974). The genus Myceliophthora has been associated with the teleomorphs Arthrodema and Ctenomyces (both Onygenales) and with Corynascus (Chaetomiaceae; Sordariales). P. inflatus needs to be compared, therefore, with Myceliophthora and Corynascus.

With the exception of P. inflatus, all other Paecilomyces of section Isarioidea (after Samson 1974) were within the Hypocreales. Most of these could be placed within the family Clavicipitaceae with two species placed in the Hypocreaceae. Both P. penicillatus and P. niphetodes were basal in the Hypocreaceae clade, which had 100% support. Our isolate of P. penicillatus significantly was from a mushroom, but the type specimen was found on dead moss and rotting wood and it grouped into a clade of fungicolous genera/species. P. niphetodes is known from decaying wood of Fagus sp. and Mercurialis perennis. Further work is needed to determine the teleomorph associations of these two species within the Hypocreaceae.

Within the Clavicipitaceae, Paecilomyces section Isarioidea also appeared to be polyphyletic as concluded by Obornik et al (2001). However, the genus Cor-
**dyceps** is large and several phylogenies (Nikoh and Fukatsu 2000, Artjariyasripong et al 2001, Oborník et al 2001) suggest that it too is polyphyletic within the order Clavicipitaceae. We included two species of Cordyceps in our dataset. *C. militaris* (the type species) was sister to the *Isaria* clade (Clade I), while *C. takamontana* was placed well within Clade I with a bootstrap support of 79% and sister to *P. farinosus* (CBS 111113). We recognize Clade I as an *Isaria* clade based on the epitype *P. farinosus* (CBS 111113). Support for the *C. militaris* sister clade of Clade I, which contained *P. amoeneroseus* and *P. cateniobliquus*, was not strong at 58%. Other topologies (not shown) suggest also that *P. amoeneroseus* and *P. cateniobliquus* probably belong in an *Isaria* clade.

Another major clade (Clade P) that we identify in the Clavicipitaceae is based on pinkish or purple colonies or spores. In the phylogeny presented here, there is no support while other phylogenies (not shown) indicate a weak support of just over 50%. Within this clade *P. cinnamomeus* groups with a *Torrubiaella* teleomorph as reported by Hywel-Jones (1993) and confirmed by phylogenetic analysis using the 28S region of the rRNA (Artjariyasripong et al 2001). Sister to this was a clade that included *Nomuraea atypicola* from spiders and *P. lilacinus*. A Cordyceps teleomorph is known for *N. atypicola* although no teleomorph has been reported for *P. lilacinus*. Although *P. marquandii* and *P. carneus* both are placed in the Clavicipitaceae, it was not possible to determine their relationships further based on the dataset available.

Our work clearly shows *Paecilomyces* to be polyphyletic at the order level. The genus *Paecilomyces* therefore should be retained only for eurotiaceous species with affinities for *P. variotii* and with a *Byssochlamys* teleomorph. Those within the Hypocreales fall in section Isarioidea of Samson (1974), but there is evidence that this section also is not monophyletic (Oborník et al 2001, this study).

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**LITERATURE CITED**


Stolk AC, Samson RA 1972. Studies on *Talaromyces* and re-


