Taxonomy of *Dactylella* complex and *Vermispora*. I. Generic concepts based on morphology and ITS sequences data

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Chen, J., Xu, L.L., Liu, B. and Liu, X.Z. (2007). Taxonomy of *Dactylella* complex and *Vermispora*. I. Generic concepts based on morphology and ITS sequences data. Fungal Diversity: 26: 73-83.

Dactylella, anamorphic *Orbiliaceae* (Ascomycetes) and related genus *Vermispora* are systematically studied and are revised according to morphology and phylogenetic analyses of ITS1-5.8S-ITS2 rDNA sequences. Thirty-nine isolates formerly assigned to *Dactylella* and *Vermispora*, including 28 from the Centraalbureau voor Schimmelcultures and 11 from our laboratory were studied. Based on ITS sequence alignment, all the tested strains cluster into three monophylogenic clades corresponding to three genera, e.g. *Dactylella*, *Vermispora* and a distinct group comprising species with very short conidiophores. The circumscription of *Dactylella* and *Vermispora* are emended and a new genus *Brachyphoris* is introduced.

Key words: *Brachyphoris* gen. nov., classification, *Dactylella*, phylogeny, teleomorph-anamorph connection, *Vermispora*

Introduction

Dactylella was established by Grove (1884) on the basis of one species, *D. minuta* Grove. The genus was characterized as "Saprophytic. Vegetative hyphae creeping, sparse. Conidiophores erect, simple, septate or non-septate, smooth, hyaline. Conidia borne singly at the apex of conidiophores, ellipsoidal or fusoid or cylindrical, one-celled at first, later 2- to many-septate, hyaline". According to Grove's initial description, *D. minuta* was incapable of preying on nematodes, however, this genus had been emended several times in subsequent years and both non-predacious and predacious fungi had been included in the genus (Subrammanian, 1963; Schenck *et al*., 1977; Hoog and Oorschot, 1985; Zhang *et al*., 1994). Rubner (1996) revised the generic concept

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of *Dactylella* and excluded the nematode-trapping species. However, the classification has not commonly been accepted and several predacious species had been described under *Dactylella* (Liu *et al*., 2003; Zhang *et al*., 2005). *Dactylella* includes diverse taxa in morphology and behaviour. There are considerable differences in conidiophore length and conidial size among species. Some species are saprotrophic, while others are oospore or nematode-egg parasites (Zhang *et al*., 1994).

Vermispora was introduced by Deighton and Pirozynski (1972) with the type species *V. grandispora*, a parasite of the leaf-inhabiting *Irenopsis aciculosae* (*Meliolaceae*) in Sierra Leone. Species in *Vermispora* were defined as having hyaline conidiophores which proliferate in a sympodial manner and terminate with slightly curved fusiform conidia. Burghouts and Gams (1989) compared *Vermispora fusarina* Burghouts & W. Gams with *Dactylella oviparasitica* G.R. Stirling & R. Mankau. Liu *et al*. (2005) discussed the relationship of *Vermispora fusarina*, *Dactylella oviparasitica* and *D. brevistipitata* B. Liu, Xing Z. Liu & W.Y. Zhuang according to phylogenetic analysis of ITS sequences, however a thorough revision involving more species in *Dactylella* and *Vermispora* is still needed.

In view of vast biological differences in species of *Dactylella* and the complicated relationship between *Dactylella* and *Vermispora*, a systematic study dealing with these fungi has been conducted.

Materials and methods

Fungal isolates

Thirty-two isolates of available strains representing 22 worldwide species were sequenced in this study (Table 1). Generally, cultures grew on PDA plates at 25ºC or were stored in glycerol at –80ºC.

Extraction of genomic DNA

DNA was extracted from pure cultures following the method of Liu *et al*. (2005) with modification. The isolates were inoculated on a disc of cellophane (5 cm diam.) which was placed on the surface of a PDA plate and incubated at 25ºC for 10 days. Ten - 50 mg of fresh mycelium were scraped from the cellophane and placed in a 1.5 ml eppendorf tube containing 1 mg sterile siliceous sand, 1 mg polyvinylpyrrolidone (PVP) and 150 µl CTAB buffer (100 mM Tris, pH 8.5; 1.4 M NaCl; 20 mM EDTA; 2% CTAB), the mixture was crushed with a glass pestle and then supplemented with 450 µl CTAB buffer,

incubated at 65°C for 60 minutes. This was followed by mixing with equal volume of phenol:chloroform:isoamyl alcohol at the ratio of 25:24:1 and centrifuging at 12000 rpm for 10 minutes. The DNA in supernatant was then precipitated by isopropanol at –20°C for 30 minutes, washed with 70% ethanol, and resuspended into 50 µl sterile distilled water.

PCR amplification and DNA sequencing

Ribosomal DNA from the 5' end of ITS1 to the 3' end of ITS2 region was defined by primers ITS1 and ITS4 (White *et al*., 1990) and amplified by polymerase chain reaction (PCR) with the procedure of denaturing at 95°C for 3 minutes, followed by 34 cycles at 94°C for 1 minute, 54°C for 40 seconds and 72°C for 1 minute, then a final extension at 72°C for 10 minutes after cycling. A portion (2 µl) of the amplified product was electrophoresed in 0.5% TAE buffer (40 mM Tris-acetate, 1 mM EDTA, pH 8.0) at 120 V for 30 minutes. The gel was stained with ethidium bromide (0.5 g/mL), examined under a UV light and photographed. The PCR product was purified by Go3S PCR Product Purification Kit (Shenergy Biocolor BioScience and Technology Company, Shanghai, China), and sequenced on an automated ABI 377 sequencer (Perkin Elmer) by the same company.

Phylogenetic analysis

Sequences for each strain together with reference sequences obtained from GenBank (Table 1) were aligned using Clustal X (Thomson *et al*., 1997). Alignment was manually adjusted where necessary with MEGA version 3.0 (Kumar *et al*., 2004). Cladistic analyses using the neighbor-joining method (Saitou and Nei, 1987) was performed with the same program. The neighbor-joining tree was constructed with Kimura 2-parameter model, including transitions and transversions and with pairwise deletion of gaps. Clade stability was assessed in a bootstrap analysis with 1000 replicates.

Results

A phylogenetic analysis using ITS1-5.8S-ITS2 rDNA sequences of *Datylella* and *Vermispora* species was conducted. The matrix contained 38 sequences including 7 from GenBank. There are 3 main clades in the phylogenetic tree with rather high bootstrap value (Fig. 1). One clade (*Dactylella* group) is well in accordance with *Dactylella* with the exception of *Dactylella spermatophaga* Drechsler, *D. oviparasitica*, *D. brevistipitata* and *D.*

Table 1. List of taxa used in this study.

Specimen voucher	Taxon	Substrates	Location	GeneBank accession number
CBS 109506	*D. intermedia* T.F. Lei & X.Z. Liu	Litter	Oman	DQ494359
CBS 102487	*D. oxyspora* Sacc. & Marchal	Leaf litter	Spain	DQ494356
CBS 129.83	*D. arnaudii* Yadav	Dead stems	UK	DQ494353
CBS 157.89	*D. oxyspora* Sacc. & Marchal	Root	Netherlands	DQ494352
CBS 167.95	*D. clavata* Gao, Sun & Liu	Soil of Cocos nucifera	China, Hainan	AY515568
CBS 257.70	*D. oxyspora* Sacc. & Marchal	Agricultural soil	Netherlands	DQ494351
CBS 255.76	*D. spermatophaga* Drechsler	Oospore	USA	DQ494374
CBS 280.70	*D. oxyspora* Sacc. & Marchal	Old stem	Germany	AY902793
CBS 291.84	*D. oxyspora* Sacc. & Marchal	Rabbit pellet	Netherlands	DQ494348
CBS 310.84	*D. atractoides* Drechsler	Dead stem	Netherlands	DQ494349
CBS325.70	*D. cylindrospora* R.C. Cooke	Soil	Western Samoa	AF106538
CBS 347.85	*D. oviparasitica* Stirling & Mankau	Nematode eggs	Netherlands	AY514637
CBS 348.85	*D. oviparasitica* Stirling & Mankau	Nematode eggs	Netherlands	DQ494372
CBS 349.85	*D. oviparasitica* Stirling & Mankau	Nematode eggs	Netherlands	DQ494373
CBS 379.84	*D. oviparasitica* Stirling & Mankau	Nematode eggs	USA	AY776168
CBS 478.93	*D. ramosa* Matsushima	Leaf	Cuba	DQ494361
CBS 382.84	*V. fusarina* Burghouts & W. Gams	Egg of *Globodera pallida*	Netherlands	DQ494377
CBS 383.84A	*V. fusarina* Burghouts & W. Gams	Egg of *Globodera pallida*	Netherlands	DQ494378
CBS 383.84B	*V. fusarina* Burghouts & W. Gams	Egg of *Globodera pallida*	Netherlands	DQ494379
CBS 493.67	*D. rhopalota* Drechsler	Wood	Netherlands	DQ494369
CBS 497.92	*D. oxyspora* Matsushima	Soil	USA	DQ494350
CBS 615.92	*D. rhopalota* Drechsler	Decaying wood	Netherlands	DQ494367
CBS 616.92	*D. rhopalota* Drechsler	Needle of *Pinus* sp.	Netherlands	DQ494368
CBS 617.92	*D. rhopalota* Drechsler		Sweden	DQ494366
CBS 617.95	*D. tenuifusaria* Liu, Gao, Zhang & Cao	Forest soil	China, Guizhou	DQ494371
CBS 844.70	*D. clavispora* chen, Xu, Liu & Liu	Living leaf	UK	DQ494355
CBS 845.70	*D. rhopalota* Drechsler	Living leaf	UK	DQ494370
CBS 916.72	*Orbilia coccinella* Fries			AY515567

Table 1. List of taxa used in this study.

Specimen voucher	Taxon	Substrates	Location	GeneBank accession number
YMF1.00568	*D. zhongdianensis* Zhang *et al*.	Soil	China, Yunnan	DQ494365
YMF1.00128	*D. panlongna* Liu & Zhang	Soil	China, Yunnan	DQ494362
YMF1.01447	*D. yunnanensis* Zhang, Liu & Cao	Soil	China, Yunnan	DQ494354
SDT-2-34	*D. clavata* Gao, Sun & Liu	Soil	China, Yunnan	
AS 6.0287	*D. tenuis* Drechsler	Soil	China, Xinjiang	DQ494360
AS 6.0288	*D. xinjiangensis* chen, Xu, Liu & Liu	Soil	China, Xinjiang	DQ494363
AS 6.0297	*D. heptameres* Drechsler	Soil	China, Beijing	DQ494358
AS 6.0298	*D. heptameres* Drechsler	Soil	China, Beijing	DQ494357
AS 6.0286	*D. brevistipitata* Liu, Liu & Zhuang	Soil	China, Beijing	AY514636
AS 6.0291	*V. leguminacea* chen, Xu, Liu & Liu	Soil	China, Fujian	DQ494376
AS 6.0290	*V. leguminacea* chen, Xu, Liu & Liu	Soil	China, Fujian	DQ494375

tenuifusaria Xing Z. Liu, R.H. Gao, K.Q. Zhang & L. Cao. One clade (*Vermispora* group) includes species of *Vermispora* plus *Dactylella spermatophaga*. The third clade (*Brachyphoris* group) comprises *Dactylella oviparasitica*, *D. brevistipitata* and *D. tenuifusaria*, three species which obviously differ morphologically from the type species *D. minuta*. According to the molecular and morphological analysis, circumscriptions of *Dactylella* and *Vermispora* are emended and the new genus *Brachyphoris* with type species *Brachyphoris oviparasitica* is proposed.

Anamorphic genera of Orbiliaceae

Dactylella Grove, Journal of Botany 22: 195, 1884.

= *Drechslermyces* Subrammanian, Kavaka 5: 93-97, 1977.
= *Gangliophragma* Subrammanian, Kavaka 5: 93-97, 1977.
= *Lactydina* Subrammanian, Kavaka 5: 93-97, 1977.
= *Kafiaddinia* Mekhtieva, Khishchnye nematofagovye Griby-Gi-fomitsety: 123, 1979.

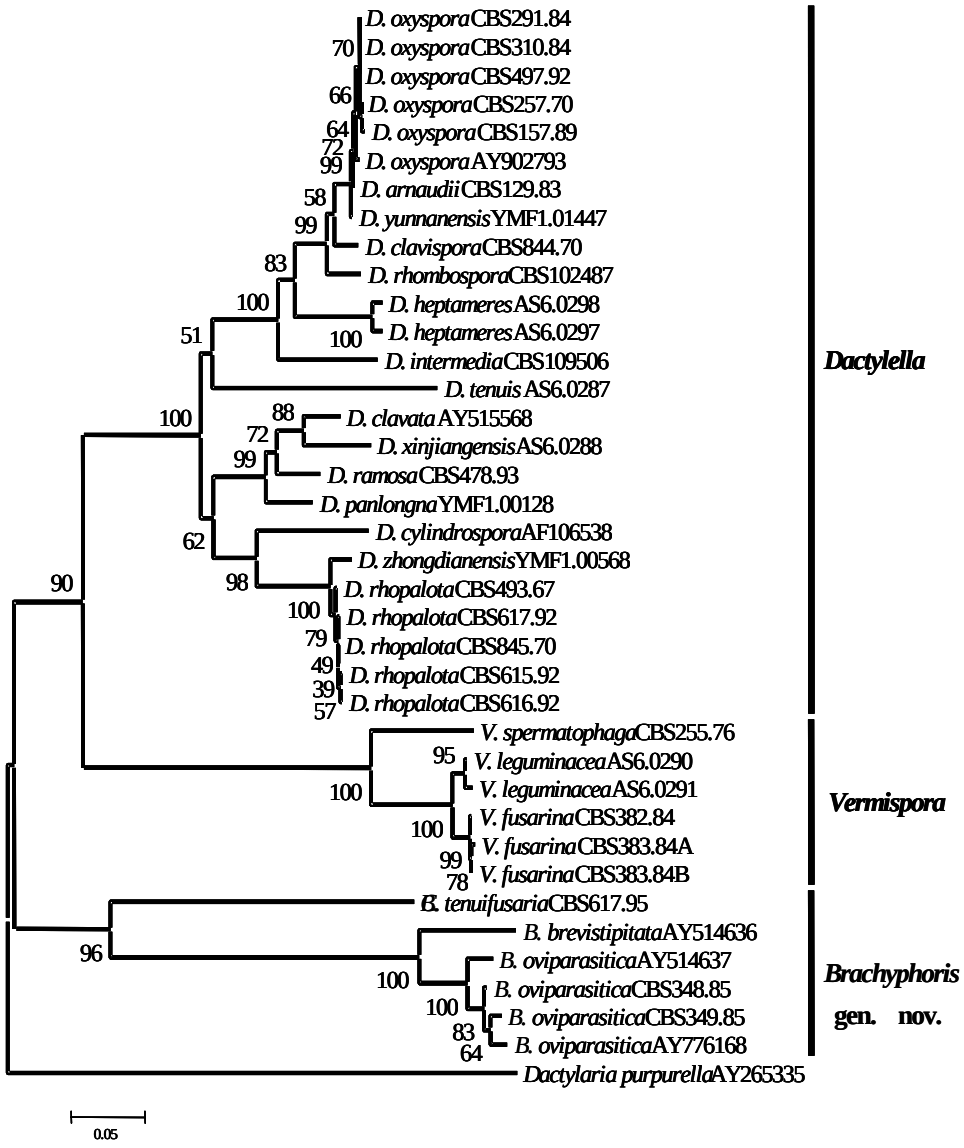

Fig. 1. Neighbor-joining tree inferred from the ITS1-5.8S-ITS2 rDNA.

Colonies white. *Vegetative hyphae* hyaline, thin-walled, septate. *Conidiophores* long, hyaline, simple, septate, solitary, erect or branched. *Conidia* hyaline, thin-walled, fusiform, clavate or ellipsoidal, borne singly at the apex of the conidiophores and on short branches.

Type species: *Dactylella minuta* Grove

Brachyphoris J. Chen, L.L. Xu, B. Liu & Xing Z. Liu, **gen. nov.**
MycoBank: 510641

Etymology: The epithet refers to the very short conidiophores.

Conidiophora inconspicua, conidio vix longiora, simplicia vel interdum ramosa, vulgo solitaria vel pauce aggregata. Conidium unum vel interdum duo gerentia. *Conidia* hyalina, fusiformia vel filiformia, recta vel leviter curvata.

Conidiophores simple or occasionally branched, hyaline, very short, scarcely longer than conidia. Conidiophore mostly produces a single conidium, sometimes two conidia. *Conidia* hyaline, smooth-walled, spindle-shaped, filiform or elongate fusoid, straight or slightly curved.

Type species: ***Brachyphoris oviparasitica*** (G.R. Stirling & R. Mankau) J. Chen, L.L. Xu, B. Liu & Xing Z. Liu, **comb. nov.**
MycoBank: 510644

= *Dactylella oviparasitica* G.R. Stirling & R. Mankau, Mycologia 70: 777, 1978.

Vermispora Deighton & Pirozynski, Mycological Papers 128: 87, 1972.

Colonies white to salmon. *Hyphae* colourless, septate, branched. *Conidiophores* borne as lateral branches of the mycelial hyphae, colorless, simple, smooth, thin-walled, slightly geniculate above the old conidial scars. Conidial scars inconspicuous, truncate, unthickened. *Conidia* colourless, long cylindric to fusiform, obclavate or elongate fusoid, smooth, thin-walled, slightly curved and usually slightly sigmoid.

Type species: *Vermispora grandispora* Deighton & Pirozynski

Key to anamorphic genera of *Orbiliaceae*

1. Trapping nematodes with trapping devices 2
1. No trapping devices formed 4

2. Trapping nematodes with adhesive networks ..... ***Arthrobotrys***
2. Trapping nematodes with other devices 3

3. Trapping nematodes with constricting rings ..... ***Drechslerella***
3. Trapping nematodes with adhesive knobs or non-constricting rings ..... ***Dactylellina***

4. Conidia forked 5
4. Conidia not forked 8
5. Conidia with a main axis bearing two divergent radiate arms 6
5. Conidia branched dichotomously twice at the apex, with a cylindric-ellipsoidal main axis and four curved and tapering side arms ..... ***Dwayaangam***

6. Conidia bilobate, lobes parallel, U-shaped or Y-shaped ..... ***Dicranidion***
6. Conidia triradiate, Y-shaped or T-shaped ..... ***Trinacrium***

7. Conidia sigmoid to coiled 10
7 Conidia not sigmoid 8

8. Conidia falcate ..... ***Idriella***
8. Conidia straight, fusiform or cylindrical or clavate 9

9. Conidiophores long, straight or occasionally branched ..... ***Dactylella***
9. Conidiophores scarcely longer than conidia ..... ***Brachyphoris***

10. Conidia coiled in three dimensions ..... ***Helicoon***
10. Conidia vermiform to sigmoid ..... ***Anguillospora***

Discussion

Species in *Dactylella* form a polyphyletic group and disperse into three clades, indicating that *Dactylella* is a phylogenetically heterogeneous group. Molecular phylogeny has demonstrated that the morphological criteria formerly considered important in defining *Dactylella* and related genera could be inadequate. The *Dactylella* clade includes the type species and is characterized by erect, long conidiophores producing multiseptate, clavate, fusiform or cylindrical conidia. Interestingly, *Dactylella spermatophaga*, *D. oviparasitica*, *D. brevistipitata* and *D. tenuifusaria* previously assigned to *Dactylella* are excluded by the molecular data. Our subsequent morphological analysis is in full agreement with the molecular analysis. The living culture of *D. spermatophaga* (CBS 255.76) is characterized by elongate spindle-shaped, curved conidia, borne successively on procumbent conidiophores. Both the morphology of conidia and conidiophores indicate its taxon should be accommodated in *Vermispora*. *Dactylella oviparasitica*, *D. brevistipitata* and *D. tenuifusaria* produce very short conidiophores (no longer than the conidia), and the colony configuration differs considerably from other species in *Dactylella*. Considering the great discrepancy in morphology as well as molecular evidence, we consider that the feature of short conidiophores represents an important characteristic to delimit these taxa into a new genus *Brachyphoris*.

The Vermispora clade comprises species of *Vermispora* and *Dactylella spermatophaga*. Since being established in 1972, only 4 species have been reported in *Vermispora*, all of which bear elongate-fusoid conidia on procumbent conidiophores. *Dactylella spermatophaga* was described as conidia elongate spindle-shaped, slightly curved; conidiophores repeatedly elongated, give rise at successive intervals to 10 or 15 additional conidia (Drechsler, 1938). According to this description and our detailed observation

of the living culture (CBS 255.76), we reclassify *D. spermatophaga* in *Vermispora* under the new name *Vermispora spermatophaga*.

Dactylella oviparasitica, *D. brevistipitata* and *D. tenuifusaria* formed a monophyletic group adjacent to the Dactylella and Vermispora clades. Since this group differs from *Dactylella* in morphology and molecular data, we proposed a new genus for this clade. *Brachyphoris* gen. nov. is characterized by very short conidiophores and *Dactylella oviparasitica*, *D. brevistipitata*, *D. tenuifusaria*, *D. helminthodes* Drechsler and *D. stenomeces* Drechsler are transferred.

The connection between anamorphs and teleomorphs has been reported in taxonomy of filamentous fungi (Pfister, 1997; Kohlmeyer *et al*., 1998; Liu *et al*., 2005). Mo *et al*. (2005) listed the anamorphs of *Orbilia* and concluded three connections between *Orbilia* and *Dactylella*. Yang and Liu (2005) reported *Dactylella coccinella* Y. Yang & Xing Z. Liu as anamorph of *Orbilia coccinella*. Since then 4 species of *Dactylella* have been connected with *Orbilia* (Zachariah, 1989; Pfister, 1997; Webster *et al*., 1998; Yang and Liu, 2005). One *Brachyphoris* species has been connected to *Hyalorbilia* (Liu *et al*, 2005) (Table 2). From the phylogenetic tree, the teleomorphs of the three anamorph genera should be orbiliacous fungi. Although some more new species of *Orbilia* and *Hyalorbilia* have been reported recently (Liu *et al*., 2006; Wu *et al*., 2007), no teleomorph is yet known for *Vermispora*. *Orbilia* (Fr.) Fr. and *Hyalorbilia* Baral & G. Marson are the only two genera of *Orbiliaceae* recognized, which differ considerably in morphological and molecular characteristics (Baral, 2001; Liu *et al*., 2005). The relationship between *Orbilia* and *Dactylella*, *Hyalorbilia* and *Brachyphoris* may partly indicate their diverse taxonomic positions.

Table 2. Anamorph-teleomorph connection.

Anamorph		Teleomorph	Reference and author
Dactylella			
	D. rhopalota	*O.* sp.	Zachariah (1989)
	D. sp.	*O. alnea*	Pfister (1997)
	D. cf. *oxyspora*	*O. fimicoloides*	Webster *et al*. (1998)
	D. coccinella	*O. coccinella*	Yang *et al*. (2005)
Brachyphoris			
	B. brevistipitata	*H. brevistipitata*	Liu *et al*. (2005)

Acknowledgements

We thank K.Q. Zhang for kindly providing fungal material and J.Y. Zhuang for correcting the Latin diagnoses. This project is supported by the National Natural Science Foundations of China (nos. 30270007).

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(Received 24 June 2006; accepted 17 April 2007)