

The philosophy and practicalities of amalgamating anamorph and teleomorph concepts

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Abstract: The separate naming of fungal anamorphs (those producing spores through mitosis) and teleomorphs (with spores formed after a meiotic event) has until now been an unavoidable complication for many fungal groups, due to the rarity with which multiple morphs are encountered, and technical difficulties in linking stages of life cycles. This arrangement has great practical value for identification, but is massively confusing to non-taxonomists who cannot understand why a single organism can have more than one correct name. It is also a major barrier to information flow. The rapidly increasing amounts of data available from molecular phylogenetic studies, as well as from traditional culture-based connection work, mean that the integration of the two classification systems is becoming more feasible, at least for many economically important fungal groups. The need to prepare for this event is stressed, and options are considered for managing the change with minimum disruption to working scientists.

Key words: International Code of Botanical Nomenclature, Article 59, botanical classification, pleomorphic fungi.

Introduction

“The taxonomic and nomenclatural separation of sexual and asexual expressions ... is against the laws of nature.” — The Tulasne brothers, quoted by Weresub & Pirozynski, 1979.

Pleomorphism is one of the great challenges of systematic mycology. Holomorphic fungi that are known to produce both sexual and asexual spores have caused difficulties for taxonomists attempting to place them within classifications, ever since their nature was discerned by Berkeley and the Tulasnes in the mid nineteenth century, and the recognition of the sexual nature of ascospore and basidiospore production (Weresub & Pirozynski, 1979). The existence of holomorphs that consist of anamorphs only was predicted as far back as Berkeley (1857), and has been widely accepted in recent years (e.g. Hennebert, 1993). Addressing the theory and practicalities of integrating classification and naming systems for anamorphs and teleomorphs has become more and more important.

The nomenclature of pleomorphic fungi (and

their non-pleomorphic relatives) has proved controversial from the earliest days of recognition of the dual ontogeny of fungal spores. Polarized views (strongly influenced by pervading religious influences on scientific thought) were expressed on the acceptability of ‘incomplete’ fungal species that formed conidia but not sexual spores (Weresub & Pirozynski, 1979), and differences of opinion emerged as to whether apparently mitotic species should be integrated into mainstream fungal classification. The separation of the ‘Fungi Imperfecti’ from the ‘Fungi Perfecti’ became established with publication of Fuckel’s *Symbolae Mycologicae* (Fuckel, 1870) and was cemented by the third and subsequent volumes of Saccardo’s *Sylloge Fungorum* (Saccardo, 1884). This unfolding history, along with complex discussions on the nature of anamorphic taxa, has been described on a number of occasions (e.g. Hennebert, 1971, 1987), and will not be repeated here in detail. The practical utility of a dual classification and nomenclature system has rarely been questioned even in recent years. However, there is now a groundswell of opinion from two separate sources, molecular phylogeneticists on one hand and applied biologists on the other, who

question the advisability of maintaining this state of affairs. Modern biosystematic tools, especially nucleic acid analysis, but also techniques such as serology and study of hyphal anastomosis and vegetative compatibility, now offer robust mechanisms for the integration of anamorph and teleomorph classifications. The value of a combined system is clear, but its nomenclatural implications are profound.

Anamorph taxa are currently used in two distinct manners, as systematic taxa with phylogenetic relevance, and as morphological formulae within an artificial framework. Because taxonomists almost never state what they mean when they use anamorph names (cf. Seifert & Samuels, this volume), it is not surprising that other biologists are confused. An avowedly artificial classification is a strange chimera, and perhaps a contradiction in terms. Anamorph classifications are in effect considered to be artificial in the *International Code of Botanical Nomenclature* and by many of the most prominent and well-respected anamorph taxonomists, but in reality they are rarely treated purely as mechanistic creations. Even their inclusion within the structure of the *Code* itself might be regarded as controversial. Requirements for valid publication are similar to those for teleomorph taxa, such as the stipulations concerning Latin descriptions and typification. The whole concept of an anamorph-teleomorph connection is hard to interpret unless the taxa are considered to be comparable in status.

Anamorph taxa cannot continue to be treated as morphological formulae divorced from phylogenetic systematics. Their use in this fashion has done great damage to fungal taxonomy, and is one of the main reasons why anamorph and teleomorph classification systems are proving difficult to integrate. The artificial classifications of mitospore-producing fungi, first those of Saccardo (first employed in the third volume of the *Sylloge*; Saccardo, 1884) based on conidial morphology and then those of Hughes (1953) based on developmental features, were heroic attempts to provide an overall framework for classification of anamorphic fungi, which were great advances in their time and greatly facilitated identification. However, neither system can provide an acceptable overall systematic structure, with clearly related genera placed in completely different parts of the classification. In addition, a plethora of taxa has been described to accommodate anamorphs within clearly closely related groups with different means of conidial production, such as those within *Ophiostoma* Syd. & P. Syd. (Wingfield *et al.*, 1993, 1994) and *Hypomyces* (Rogerson & Samuels, 1993), or where the extent of morphological variation of anamorphs

greatly exceeds that of the teleomorph, as with *Chaetosphaeria* Tul. & C. Tul. (Réblová, this volume), *Mycosphaerella* Johans. (Crous *et al.*, this volume) and *Capronia* Sacc. (Untereiner, this volume).

If anamorph names are considered to have phylogenetic value, the case for maintaining a dual nomenclatural system rapidly becomes weaker. The time-honoured practice of studying type species combined with modern DNA-based phylogenetic analysis is providing unambiguous placements for important anamorph taxa within the overall classification structure of the *Fungi*. For example, recent work by Glenn *et al.* (1996) and others on one of the most morphologically intractable form-genera, *Acremonium* Link, has placed the type species *A. alternatum* Link squarely as a member of the *Hypocreales*, within the *Bionectriaceae* as circumscribed by Rossman *et al.* (1999) and closely linked to the teleomorph genus *Emericloopsis* J.F.H. Beyma. Other well-known species groups that were referred to *Acremonium* have been recognized as independent phylogenetic units for some time, such as the grass endophytes placed firstly in section *Albolanosa* Morgan-Jones & Gams (Morgan-Jones & Gams, 1982), and subsequently in a new form-genus *Neotyphodium* Glenn, C.W. Bacon & Hanlin by Glenn *et al.* (1996).

There is no reason why anamorph genera should not be placed provisionally within higher holomorph taxa based on morphological evidence alone. In an ideal world, all links between fungal morphs should be supported by molecular and/or cultural evidence, but we are happy both to place teleomorph genera within families based on morphological criteria, and also in many cases anamorph species within genera. Why not anamorph genera within holomorph families? Fungal taxa are frequently moved from one higher taxon to another as new evidence is presented that alters their perceived relationships. This process has been accepted by practicing systematists for years, but Article 59 has been a major nomenclatural stumbling block to formalizing these links, even when overwhelming evidence is presented. The *Dictionary of the Fungi* is considered by some to be a bastion of conservatism (and by others to be too 'creative!'), but in the latest edition (Hawksworth *et al.*, 1995) anamorph genera were stated as belonging to holomorph higher taxa (families and orders) where the links were perceived by the editors to be unambiguous. This is not as dramatic a step as might be imagined; nearly thirty years ago Weresub & LeClair (1971) advocated classification of the hyphomycete genus *Papulaspora* in the '*Melanosporaceae Imper-*

fectae'. The assignment of anamorph genera to teleomorph families is an essential first step to integration of the two classification systems, which will lead to a gradual reduction of taxa formally considered to belong to the '*Fungi Imperfecti*'. The degree of proof necessary for assignment of anamorph taxa to holomorph parents will inevitably vary according to the opinions, systematic expertise (and willingness to take risks!) of the practitioners. However, there are arguments for suggesting provisional placements based on morphological similarity alone in order to stimulate debate, and to form systematic hypotheses that can be tested by others.

Once anamorph taxa are accepted as members of holomorphic parent taxa, opportunities are presented for further integration. In some circumstances, there is a one-to-one correlation between anamorph and teleomorph taxa, which makes merging of the two taxonomies simple. For example, *Colletotrichum* Corda and *Glomerella* Spauld. & H. Schrenk are considered to be effective synonyms in biological terms, although not all currently accepted species of *Colletotrichum* are known to reproduce sexually (Sutton, 1992). There is, therefore, no philosophical barrier to uniting the two groups of species under one generic name, although (as with many other plant pathogens) species concepts are poorly understood (Brasier, 1997; Cannon *et al.*, 2000). There is ample molecular and morphological evidence to link *Colletotrichum* species that do not produce ascospores with their meiotically reproducing relatives (e.g. Sreenivasaprasad *et al.*, 1996; Johnston & Jones, 1997). There is no reason why these orphan taxa should not be considered as belonging to the relevant ascomycete clade along with their holomorphic partners.

Other orphan taxa have less clearly established relationships. The assignment of *Acremonium* to the *Bionectriaceae* based on molecular analysis of the type species potentially leaves hundreds of other *Acremonium* species in limbo, even when phylogenetically meaningful groups such as *Neotyphodium* are removed. It will clearly be impractical in the foreseeable future to generate sequences for all *Acremonium* taxa, because many are poorly defined and have type material that is inadequate or completely lacking. But it does no-one any harm to consider these as provisional members of the *Bionectriaceae*, as most will continue to be ignored by all but the most masochistic of systematists, and redispositions will occur where appropriate as new data are acquired.

The inclusion of anamorphic taxa within holomorphic parent groups immediately raises issues of competition among synonyms. As the nomenclatural

rules currently stand, teleomorph names automatically take precedence over anamorph names when referred to as holomorphic taxa. This is not necessarily the best solution when the needs of the users of classifications are taken into account. For many fungal genera of economic importance, the asexual forms are more prominent and frequently encountered than the teleomorphs. This is the case for the vast majority of plant pathogens, food spoilage fungi, industrial metabolite producers etc. But it is also true that the asexual taxa have date priority in most cases over their sexual partners. In these circumstances, one could argue that removal of priority for teleomorph names would actually increase rather than reduce nomenclatural stability. Clearly it will be necessary to investigate this in more detail before proposing a change of the nomenclatural rules, but our counterparts in applied biology frequently use anamorph names with little or no appreciation that other names exist for different morphs that systematists consider intrinsically preferable. Do we consider the needs of our users, or maintain a system that has glorified a reproductive method analagous to our own since Linnaean times?

There is some evidence that the disruption to nomenclatural stability caused by integration of anamorph and teleomorph nomenclature accompanied by abolition of the priority rules for sexually reproducing morph names would actually be less than integration while keeping the current priority rule. Seifert (pers. comm.; see Table 1) analyzed 223 names in the *Penicillium* Link complex accepted by Pitt & Samson (1993). Under the scenario with teleomorph priority, 164 new combinations or new names (73% of the total number of species) would be required in *Eupenicillium* F. Ludw. or *Talaromyces* C.R. Benj. in order to provide acceptable holomorph names for the species currently accepted. If anamorph and teleomorph names competed equally, just four new names (2% of taxa) would be needed. It is clear that the *Penicillium* case lies at one end of the spectrum because the anamorphs of most species of this genus are much more prominent than their sexual morphs. Maintaining a priority system through the integration process, which might cause so much disruption to the names of familiar species, should surely be questioned carefully.

The real level of disruption is very difficult to estimate, for two principal reasons. Firstly, the classifications and species concepts of so many groups need major surgery. Secondly, connections in the literature need individual assessment because the proportion of dubious links is high, especially in the older literature. The only practical strategy is to consider groups on a

Table 1. Nomenclatural status of 223 species of *Penicillium* accepted by Pitt and Samson (1993).

If one name per species was adopted, different numbers of new names would be required if (a) teleomorph generic names automatically retained priority over anamorph generic names (and *Penicillium* became a facultative synonym of *Eupenicillium*, irrespective of dates of publication), or (b) if teleomorph and anamorph names competed equally for priority (and *Penicillium* 1809 assumed priority over *Eupenicillium* 1892 and *Talaromyces* 1955). See text for discussion. From Seifert (*in litt.*, during a discussion on Art. 59 on the Internet, 1996).

	number of species	coincident epithets ¹	teleomorph priority ²	anamorph priority ²	teleomorph assumed anamorph basionym ³
<i>Penicillium</i> (no teleomorph)	164	—	—	—	—
<i>Eupenicillium</i> (with named <i>Penicillium</i> anamorphs)	42	28	2	6	7
<i>Talaromyces</i> (with named <i>Penicillium</i> anamorphs)	17	10	2	2	7
Totals	223	38	4	8	14

¹The anamorph and teleomorph were described at the same time, with the same species epithet. Either binomial could assume priority for the holomorph.

²Either the anamorph or teleomorph was discovered and named before the other morph. The epithet of the first named morph would have priority for the holomorph.

³New anamorph epithets were proposed when the original epithet was co-opted for the holomorph. The original anamorph epithets would still be available in a unified system.

case-by-case basis, in conjunction with monographic revision and preferably also molecular phylogenetic analysis. In cases where well-known taxon names are threatened by the removal of teleomorph priority, the option should be made available to propose conservation, preferably before publication of the monograph. There is a possibility that the Special Committee for Fungi (perhaps augmented for the purpose) will be overstretched, but considering the significant reduction in taxonomic activity in recent years caused by funding difficulties, it is difficult to imagine that this will be a major problem.

Holomorphs do not necessarily differ morphologically in both their teleomorph and anamorph stages. In some circumstances major differences in morphology appear to be the result of minor genetic divergence. The distinctive ascospore features of *Neocosmospora* may be less significant systematically than was previously believed (Spatafora & Blackwell, 1994; O'Donnell, 1996) and the morphological groups of *Colletotrichum* species with falcate conidia seem not to be reflected in the phylogeny reconstructed using molecular data (Sreenivasaprasad *et al.*, 1996). Classifications of many groups remain grossly artificial. The most intractable problems lie where anamorph and teleomorph taxon concepts do not coincide. This is not surprising because in many

cases their classifications have been developed over the years by independent groups of taxonomists, often with little or no contact with their counterparts studying other morphs. In these circumstances, a simple one-to-one taxon relationship may not occur, either with a single teleomorph taxon linked to several anamorphic ones (whether or not synanamorphs are concerned), or where a single anamorph taxon is linked to multiple teleomorphs. In the case of *Verticillium* Nees previously described by Gams (1995), the entomogenous and fungicolous species of *Verticillium* are firmly linked to the *Hypocreales*, with a range of genera including *Cordyceps* Link and *Hypomyces* (Fr.) Tul. In contrast, the well-known plant pathogenic species *V. albo-atrum* Reinke & Berthold and *V. dahliae* Kleb. are apparently related to the teleomorph genus *Plectosphaerella* Kleb. (Messner *et al.*, 1996; Rehner & Samuels, 1995; R. Zare, *pers. comm.*), at one time placed in the *Hypocreales* but now regarded as completely separate and possibly related to *Glomerella* and *Colletotrichum*. The separation of the plant pathogenic species was recognized much earlier, when they were placed in a morphologically distinct section *Nigrescentia* by Gams & van Zaayen (1982). The continuing use of the generic name *Verticillium* for both major assemblages cannot be justified. The type of *Verticillium* is cur-

rently considered to belong to the plant pathogen group (although some recent evidence suggests that it is distinct generically; Gams, pers. comm.). The name *Verticillium* will continue for the moment to be available for the important plant pathogens, as the phylogenetic link to *Plectosphaerella* is weak enough to justify separation at generic level, and there is no obvious competing teleomorph generic name. *Nectria inventa* Pethybr. has been reported as being connected with the type species of *Verticillium*, although the teleomorph is clearly not correctly placed at generic rank (Rossman *et al.*, 1999) and the connection appears doubtful (R. Zare, pers. comm.). There does not therefore seem to be an obstacle (other than the current Article 59) to use the name *Verticillium* in a holomorphic sense as a constituent of the (currently uncertain) ascomycete family to which *Plectosphaerella* belongs. It must be regarded as a sterile and counter-productive occupation to introduce a new teleomorph genus name into the literature, and expect users to cease referring to *Verticillium* plant pathogens in favour of the new name. If the type *V. luteoalbum* is found after further research to be distinct from *V. dahliae* and *V. albo-atrum* at generic level, the option for conservation of the generic name with a conserved type can still be exercised. Conversely, as anamorphs of well-known teleomorph taxa are reassessed in the light of molecular data and critical morphological study, describing supposedly new taxa to accommodate the conidium-producing morph alone adds further layers of confusion rather than introducing new taxonomic precision – a practice to be discouraged by inclusion of a recommendation in the forthcoming St Louis Code (Gams, pers. comm.). A good example of this is the recent introduction of the genus *Plectosporium* M.E. Palm, W. Gams & Nirenberg for the *Fusarium*-like anamorph of *Plectosphaerella cucumerina* (Lindf.) W. Gams (Palm *et al.*, 1995). Use of the name *Fusarium tabacinum* (J.F.H. Beyma) W. Gams for the anamorph is obviously not advisable, but why not accept the holomorphic nature of the species as currently circumscribed, and adopt the original teleomorph genus name for all morphs?

The converse of the practice of introducing unnecessary new anamorph generic names is equally unfortunate for nomenclatural stability, and is actually enshrined in the Code. Where teleomorphs are discovered for well-known anamorph taxa, or where type material of species which are well-known as teleomorphs is re-examined and found to be anamorphic, a new name must be published for the teleomorph, which automatically takes precedence over the anamorph name as the Code is currently desig-

ned. For example, Groves & Wilson (1967) were forced to introduce the generic name *Ascocoryne* J.W. Groves & D.E. Wilson for species that had been known since 1816 as *Coryne* Nees (Nees von Esenbeck, 1816), after concluding that the material on which the name had originally been based did not include asci and ascospores. Technically, the same fate should probably befall the well-known tar spot genus *Rhytisma* Fr.; we hope that this paper is not read by too many nomenclatural fanatics. We also have the situation where anamorph and teleomorph taxon names are actually derived from the same basionym, as with *Omphalospora* Fr.; *O. melaena* (Fr.) Höhn. and its anamorph *Podoplaconema melaenum* (Fr.) Petrak are both based on *Sphaeria melaena* Fr. A further example is *Diachora* Jul. Müller, the type species of which is *D. onobrychidis* (DC.) Jul. Müller with its anamorph *Diachorella onobrychidis* (DC.) Höhn., both based on *Xyloma onobrychidis* DC. In all of these cases, anamorph and teleomorph are formed in or on the same long-lived stroma, and the connection is undisputed. The need to introduce new generic names for either morph should be resisted, and it seems pointless to jump through nomenclatural hoops to identify spurious alternative basionyms which could never have been intended by their original authors.

The requirement for maintaining a dual nomenclatural system for practical identification reasons has been promulgated repeatedly, by Gams (1993, 1995) among many others. However, there is a significant problem in distinguishing between anamorph names denoting traditional morphological formulae and those representing phylogenetic units. There must indeed be a continuum between these two extremes. There may be a case for using a limited number of anamorph generic names as short-hand for morphological character combinations. For example, *Acremonium* is a generalized concept for fungi producing a succession of simple slimy conidia from hyaline hyphal tips. It may be more convenient to use the generic name rather than describe the morphology, but it must be recognized that in these circumstances 'Acremonium' means little more than 'fungus with probable ascomycetous affinities'. If it is necessary to use the name in this fashion, then it might be presented as 'acremonium' in Roman letters and without a capital letter, or less radically as 'Acremonium-like'. This would distinguish the morphological concept from the genus as typified by *Acremonium alternatum*.

Deletion of Article 59 is inevitable in the long term, and it will be in the interests of nomenclatural stability (and therefore of all systematics prac-

tioners) to prepare for this event. Predicting the consequences of this deletion is difficult, and it might be impossible to avoid retroactive name changes completely. Whatever strategies are agreed upon to implement a change, conservation procedures will have to be resorted to in many instances. Article 59 currently serves three purposes; the definition of anamorph and teleomorph in nomenclatural terms, restrictions on exchanging and combining epithets between morphs, and priority of teleomorph names over competing anamorph ones. One option might be to deal with these separately, but the definitions would become redundant in the *Code* on removal of the other two clauses, and a two-stage removal of the second and third sections might well cause further (and temporary) name changes and an extended period of confusion for taxonomist and non-taxonomist alike. Perhaps a more logical first step would be to extend the rules on conservation to allow names currently considered as applying to anamorphs to become acceptable as names for holomorph taxa. This would allow the integration of the dual system on a case-by-case basis, and avoid the need to (attempt to) manage simultaneous change throughout the fungal kingdom.

These are issues that must be resolved, but most of the problems lie with taxonomy rather than nomenclature. We cannot continue to sit on the fence. Either we accept that *Eupenicillium* and *Talaromyces* are separate genera and by implication that *Penicillium* should be split, or that *Penicillium* is acceptable as a generic concept, and therefore *Eupenicillium* and *Talaromyces* should be considered as infrageneric taxa. Once we are happy with genus and species concepts on a holomorphic basis, it is time to consider what the most appropriate names should be for the fungi in all their guises. It should be emphasized that harmonization of taxonomic concepts must occur at least on an individual holomorph group basis before the application of any proposed changes in Article 59. Wholesale enforcement of the removal of these provisions without a full understanding of its effects in specific cases would in all probability lead to complete chaos. Changes must be made with users' interests at the fore, but without impeding systematic progress. The one group of people above all who can adapt to name changes best are systematists and nomenclaturalists themselves.

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Literature cited

- BERKELEY, M.J., 1857 — Introduction to cryptogamic botany. — Baillière, London etc. 604 pp.
- BRASIER, C.M., 1997 — Fungal species in practice: Identifying species units in fungi. — In CLARIDGE, M.F., DAWAH, H.A. & WILSON, M.R. (eds): *Species: The units of biodiversity*. Pp. 135–170. — Chapman & Hall, London etc.
- CANNON, P.F., BRIDGE, P.D. & MONTE, E., 2000 — Linking the past, present, and future of *Colletotrichum* systematics. — In: PRUSKY, D., FREEMAN, S. & DICKMAN, M.B. (eds): *Colletotrichum: Host Specificity, pathology and host-pathogen interaction*, in press.
- FUCKEL, L., 1870 — *Symbolae Mycologicae*. Beiträge zur Kenntniss der Rheinischen Pilze. — Jahrb. Nassauischen Ver. Naturk. 23/24: 1–459.
- GAMS, W., 1993 — Anamorphic species and nomenclature. — In: REYNOLDS, D.R. & TAYLOR, J.W. (eds): *The fungal holomorph: Mitotic, meiotic and pleomorphic speciation in fungal systematics*. Pp. 295–304. — CAB International, Wallingford, UK.
- GAMS, W., 1995 — How natural should anamorph genera be? — *Canad. J. Bot.* 73 (Suppl. 1): S747–S753.
- GAMS, W. & VAN ZAAAYEN, A., 1982 — Contribution to the taxonomy and pathogenicity of fungicolous *Verticillium* species. I. Taxonomy. — *Netherl. J. Pl. Pathol.* 88: 57–78.
- GLENN, A.E., BACON, C.W., PRICE, R. & HANLIN, R.T., 1996. — Molecular phylogeny of *Acremonium* and its taxonomic implications. — *Mycologia* 88: 369–383.
- GROVES, J.W. & WILSON, D.E., 1967 — The nomenclatural status of *Coryne*. — *Taxon* 16: 35–41.
- HAWKSWORTH, D.L., KIRK, P.M., SUTTON, B.C. & PEGLER, D.N. (eds), 1995 — *Ainsworth & Bisby's Dictionary of the Fungi*, 8th edition. — CAB International, Wallingford, UK. 616 pp.
- HENNEBERT, G.L., 1971 — Pleomorphism in Fungi Imperfecti. — In: KENDRICK, B. (ed.): *Taxonomy of Fungi Imperfecti*. Pp. 202–223. — University of Toronto Press, Toronto, Canada.
- HENNEBERT, G.L., 1987 — Pleoanamorphy and its nomenclatural problem. — In: SUGIYAMA, J. (ed.): *Pleomorphic Fungi: The Diversity and its Taxonomic Implications*. Pp. 263–290. — Kodansha, Tokyo.
- HENNEBERT, G.L., 1993 — Towards a natural classification of the fungi. — In: REYNOLDS, D.R. & TAYLOR, J.W. (eds): *The fungal holomorph: Mitotic, meiotic and pleomorphic speciation in fungal systematics*. Pp. 283–294. — CAB International, Wallingford, UK.
- HUGHES, S.J. 1953 — Conidiophores, conidia, and classification. — *Canad. J. Bot.* 31: 577–659.
- JOHNSTON, P.R. & JONES, D., 1997 — Relationships among *Colletotrichum* isolates from fruit-rots assessed using rDNA sequences. — *Mycologia* 89: 420–430.
- MESSNER, R., SCHWEIGKOFER, W., IBL, M., BERG, G. & PRILLINGER, H., 1996. — Molecular characterization of the plant pathogen *Verticillium dahliae* Kleb. using

- RAPD-PCR and sequencing of the 18S rRNA gene. — *J. Phytopathol.* **144**: 346–354.
- MORGAN-JONES, G. & GAMS, W., 1982 — Notes on hyphomycetes. XLI. An endophyte of *Festuca arundinacea* and the anamorph of *Epichloë typhina*, new taxa in one of two new sections of *Acremonium*. — *Mycotaxon* **15**: 311–318.
- NEES VON ESENBECK, C.F.G., 1817 ('1817') — *Das System der Pilze und Schwämme*. — Stahelsche Buchhandlung, Würzburg, Germany.
- O'DONNELL, K., 1996 — Progress towards a phylogenetic classification of *Fusarium*. — *Sydowia* **48**: 57–70.
- PALM, M.E., GAMS, W. & NIRENBERG, H.I., 1995 — *Plectosporium*, a new genus for *Fusarium tabacinum*, the anamorph of *Plectosphaerella cucumerina*. — *Mycologia* **87**: 397–406.
- PITT, J.I. & SAMSON, R.A., 1993 — Species names in current use in the *Trichocomaceae* (Fungi, *Eurotiales*). — *Regnum Veget.* **128**: 13–57.
- REHNER, S.A. & SAMUELS, G.J., 1995. — Molecular systematics of the *Hypocreales*: a teleomorph gene phylogeny and the status of their anamorphs. — *Canad. J. Bot.* **73** (Suppl. 1): S816–S823.
- ROGERSON, C.T. & SAMUELS, G.J. 1993 — Polyporiculous species of *Hypomyces*. — *Mycologia* **85**: 231–272.
- ROSSMAN, A.Y., SAMUELS, G.J., ROGERSON, C.T. & LOWEN, R., 1999 — Genera of *Bionectriaceae*, *Hypocreaceae* and *Nectriaceae* (*Hypocreales*, *Ascomycetes*). — *Stud. Mycol.* **42**: 1–248.
- SACCARDO, P.A., 1884 — *Sylloge Fungorum omnium hucusque cognitorum*. Vol. 3. — Padova.
- SPATAFORA, J.W. & BLACKWELL, M., 1993 — Molecular systematics of unitunicate perithecial ascomycetes. I. The *Clavicipitales*–*Hypocreales* connection. — *Mycologia* **85**: 912–922.
- SREENIVASAPRASAD, S., MILLS, P.R., MEEHAN, B.M., & BROWN, A.E., 1996. — Phylogeny and systematics of 18 *Colletotrichum* species based on ribosomal DNA spacer sequences. — *Genome* **39**: 499–512.
- SUTTON, B.C., 1992 — The genus *Glomerella* and its anamorph *Colletotrichum*. — In: BAILEY, J.A. & JEGER, M.J. (eds): *Colletotrichum*. Biology, pathology and control. pp. 1–26. — CAB International, Wallingford, UK.
- WERESUB, L.K. & LECLAIR, P.M., 1971. — On *Papulaspora* and bulbiferous basidiomycetes *Burgoa* and *Minimedusa*. — *Canad. J. Bot.* **49**: 2203–2213.
- WERESUB, L.K. & PIROZYNSKI, K.A., 1979. — Pleomorphism of fungi as treated in the history of mycology and nomenclature. — In: KENDRICK, B. (ed.): *The whole fungus*, vol. 1: 17–25. — National Museums of Canada, Ottawa.
- WINGFIELD, M.J., SEIFERT, K.A. & WEBBER, J.F. (eds), 1993. — *Ceratocystis* and *Ophiostoma*. Taxonomy, ecology and pathogenicity. — American Phytopathological Society, St Paul, MN.
- WINGFIELD, M.J., WINGFIELD, B.D. & KENDRICK, W.B., 1994 — The development of holomorphic concepts in ophiostomatalean ascomycetes. — In: HAWKSWORTH, D.L. (ed.): *Ascomycete systematics. Problems and perspectives in the nineties*. Pp. 333–340. — Plenum, NATO ASI Series A: Life Sciences vol. 269. New York & London.