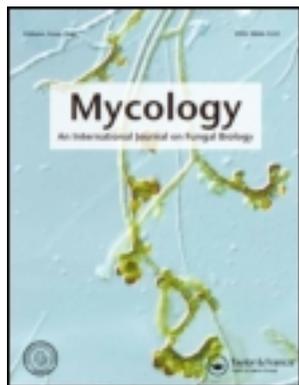


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The Xylariaceae as model example for a unified nomenclature following the "One Fungus-One Name" (1F1N) concept

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The Xylariaceae as model example for a unified nomenclature following the “One Fungus-One Name” (1F1N) concept

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The introduction of a One Fungus-One Name (1F1N) concept has led to intensive discussions among taxonomists. Based on the Xylariaceae, a hyperdiverse family of Ascomycota with over 1300 species, the advantages and pitfalls of these nomenclatural changes and their consequences for taxonomy and applied mycology are discussed. Historically, in the Xylariaceae, an 1F1N concept had already been realised: the types of all important genera are conserved. Most teleomorphs were discovered long before the anamorphic states and the latter did not receive separate names, hence no drastic taxonomic changes are expected. The new nomenclature calls for abandonment of some ill-defined anamorph genera, such as *Muscodor*. Other anamorph genera will be retained because their names refer to morphological symplesiomorphies that occur in several teleomorph genera. Various important taxa are only known from ancient specimens, and no DNA-based data are available. Much work still remains to be done to recollect these fungi, select epitypes, and settle their phylogenetic relationships. Until then, we recommend that taxonomic changes be applied at the suprageneric ranks whenever possible to maintain nomenclatural stability.

Keywords: ascomycetes; endophytes; *Geniculosporium*; *Libertella*; *Muscodor Nodulisporium*; nomenclature; phylogeny; taxonomy; *Virgaria*; Xylariales

Introduction

The last International Botanical Congress (IBC) in Melbourne has brought about some drastic changes in fungal nomenclature (Hawksworth 2011; Norvell 2011). Out of those, especially the introduction of a unified nomenclature for pleomorphic fungi, has been discussed intensively. The pros and cons of the new nomenclature have been outlined in some opinion papers that were published before or after the IBC decision (Gams et al. 2011, 2012b; Hawksworth et al. 2011) and are not commented on in detail here. After several international workshops that were held on this topic in 2012, the mycological community is now about to find a way to develop workable concepts, in order to implement these changes on a rather short notice. Hawksworth (2012) outlined a very optimistic option to cope with the numerous changes in nomenclature of pleomorphic fungi that are to be expected in a transitional period. This was generally accepted, and expert committees have been installed to deal with many of the important taxonomic groups and establish “list-accepted and list-demoted” names (Gams et al. 2012a). Notably, Hawksworth (2012a) admitted that “some cryptic dual nomenclature” was bound to persist. A much clearer

picture on the current situation that certainly has reassured many morphologists was drawn by Braun (2012). He clarified that most of the problems associated with acceptance of the new *Code* are not actually related to the nomenclatural rules themselves. According to Braun (2012), the widespread concerns and anxieties that the new nomenclatural rules *could negatively influence taxonomic work on pleomorphic fungi* are *groundless*. Braun emphasised that the new rules primarily apply to those fungal taxa that will be newly described in the future. He further stated that *with pleomorphic fungi, taxonomists will in future have to answer the question whether different morphs can represent one taxon, but this remains a taxonomic decision and has nothing to do with nomenclature*. Indeed, the controversial discussions have been due to a great extent to the incongruent genus and species concepts that are still being applied by experts on different groups of fungi.

There are still various important practical questions to consider, such as those recently addressed by Gams et al. (2012a) on prioritisation of list-accepted and list-demoted names. However, we are confident that it will be possible to find a workable solution towards a universal One Fungus-One Name (1F1N) concept in all groups of

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pleomorphic fungi, based on a team effort of all experts in the mycological community.

This article is intended to demonstrate, based on an important family of pleomorphic fungi, that the few really existing problems in nomenclature can easily be overcome. However, we will also address some problems associated with the lack of information on the phylogeny of these fungi, which will in all likelihood prevent the full implementation of the new Article 9 of the “International Code of Nomenclature for algae, fungi, and plants” (ICN), i.e. a 1F1N concept, for many years to come.

The Xylariaceae is one of the largest and most diverse families of Ascomycota, currently comprising over 1300 accepted species, and many more remain to be discovered. They are cosmopolitan, ubiquitous wood-degraders, but some genera are typically encountered on dung or associated with insect nests (see overviews by Rogers 2000; Stadler 2011). They clearly exhibit their highest diversity in the tropics, but even in the temperate climate zones, new species are continuously being discovered. The teleomorphs of the Xylariaceae are often formed on conspicuous stromata, hence certain genera such as *Xylaria*, *Daldinia*, and *Hypoxylon* have been known for a long time and were first described by botanists, including Dillenius and Linnaeus, prior to the eighteenth century. Only in the past decades, however, have mycologists started to realise that the Xylariaceae are among the predominant fungal endophytes of plants (Carroll 1988; Petrini et al. 1995; Whalley 1996). Thousands of orphan DNA sequences that can be assigned to this family or the order Xylariales are deposited in GenBank and other public repositories. The corresponding teleomorphs are as yet unknown, and often the respective fungal strains were not even cultured and preserved. The diversity of Xylariaceae and their ubiquitous occurrence may also relate to their being associated with insect vectors, which have mediated adaptive radiation (Guidot et al. 2003; Pažoutová et al. 2010). This may be the reason why these fungi are highly interesting objects of studies by molecular ecologists. Furthermore, Xylariaceae belong to the most prolific producers of bioactive secondary metabolites within the fungal kingdom (Stadler & Hellwig 2005). Only from the Trichocomaceae and Hypocreaceae have more such compounds been described.

As will be outlined herein, the Xylariaceae also represent a good model on how a unified fungal nomenclature can be established. This is owing to the fact that

- (1) Traditionally, xylariaceous anamorphs were rarely named when encountered together with the corresponding teleomorphs
- (2) Although their taxonomy is certainly not trivial, there are relatively few “problem taxa” in this family where name changes will be unavoidable
- (3) The problem of prioritisation of older synonyms will affect the Xylariaceae less than most

other families of the Ascomycota because several generic types are already conserved against earlier homonyms

- (4) The potential drawbacks associated with “molecular” fungal taxonomy in lack of adequate reference data derived from a concise genetic barcoding approach relying on phenotypically well-defined materials can easily be demonstrated in the Xylariaceae

Inventory of the Xylariaceae genera and consequences for the adaptation to the new nomenclature rules

For the current outline of the status of Xylariaceae genera, the following publications have been most helpful: Læssøe (1994) has compiled a list of acceptable genera based on his own meticulous studies of the types and the historical literature. He connected various anamorph names with the corresponding teleomorphs and also clarified some other taxonomic problems relating to old names in the Xylariaceae. Lumbsch and Huhndorf (2010) have continued the important work initiated by Ove Eriksson (“Myconet”) to keep track of the numerous newly erected genera and provide regular updates. The papers by Hyde et al. (2011) and Wijayawardene et al. (2012), who attempted to provide a general overview on the current status of anamorph–teleomorph relationships in the Ascomycota and Basidiomycota, were also consulted. In addition, the information provided on the Internet in Index Fungorum¹ and Mycobank,² as well as the original taxonomic literature, was taken into account.

Anamorph types and nomenclature in the Xylariales

Ju and Rogers (1996) have subdivided the Xylariaceae into two groups according to anamorph types as inferred from extensive studies of their conidial states that had given rise to segregate *Hypoxylon* sensu Miller (1961). This grouping in taxa with geniculosporium-like and nodulisporium-like conidiophores, respectively, has been strongly supported by all subsequent studies on the molecular phylogeny of the Xylariaceae and Xylariales. This approach can be regarded as pioneer work in scope of a unified nomenclature of pleomorphic fungi, as the authors have avoided giving separate names to the conidial states and always referred to the holomorphs.

The major groups and the respective genera of the Xylariaceae (cf. Figures 2 and 3) are listed in different columns in Table 1, providing an update of the subdivision proposed by Ju and Rogers (1996), also including more recently erected and nonstromatic genera.

The concept by Dennis (1961), who proposed that *Hypoxylon* and *Xylaria* and their respective allies should be recognised as separate subfamilies, now appears workable, even though the subfamilies (Hypoxylloideae and

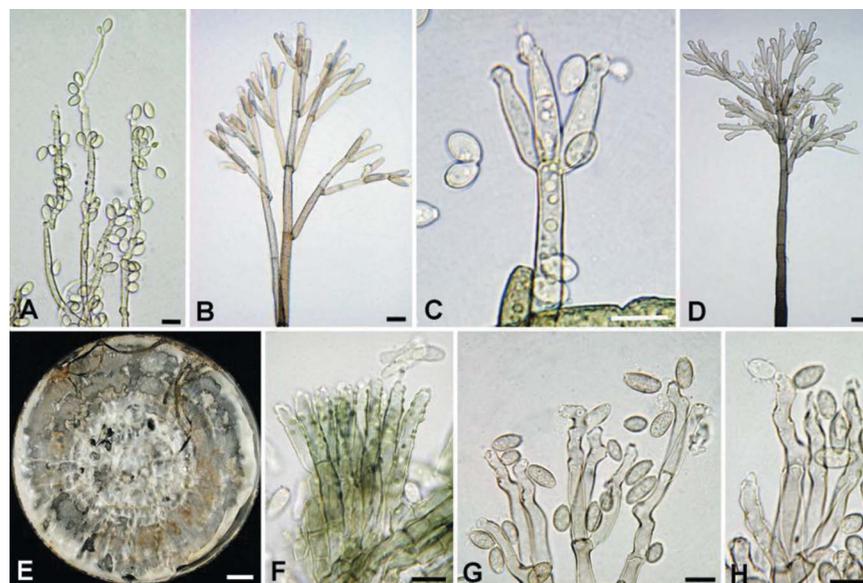


Figure 1. Anamorphic structures of Hypoxyloideae (A-D) and Xylarioideae (E-G) observed in 1% SDS. A: sporothrix- to virgariella-like branching pattern (*Hypoxylon* sp., JF 11167, anamorph from culture on OA); B: nodulisporium-like branching pattern (*Annulohypoxylon* sp., KP-JF 010, from anamorph on natural substrate); C: nodulisporium-like branching pattern (*H. rubiginosum*, JF 11181, from anamorph on natural substrate); D: periconiella-like branching pattern (*Annulohypoxylon* sp., KP-JF 037, from anamorph on natural substrate); E: culture of *Xylaria polymorpha* on OA after 45 days (JF 09311); F: palisadic geniculosporium-like anamorph of *X. polymorpha* on anamorphic stromata on natural substrate (JF 11063), in 3% KOH; G, H: typical geniculosporium-like anamorph of *Rosellinia corticium* (JF 11065) on natural substrate. Scale bars: E: 1 cm; A-D, F-H: 10 μ m.

Xylarioideae, respectively) were not validly erected by the latter author. Moreover, a third “subfamily” proposed by Dennis (1961), i.e. the Thamnomycetoideae, was rejected. Stadler et al. (2010b) demonstrated that the core group of *Thamnomycetes* is clearly closely related to the genus *Daldinia* in the hypoxyloid Xylariaceae. Some other species that were eventually included in the genus *Thamnomycetes* are now considered to be members of xylarioid genera (i.e. *Leprieuria* and *Xylaria*, respectively). A case could be made to emend and officially circumscribe the two remaining subfamilies, but for reasons given below, this seems to be rather premature in lack of evidence on the boundaries within the major lineages of the Xylariales.

Xylariaceae incertae sedis: interfaces to Diatrypaceae

Historically, the Xylariaceae have been defined by their ascospore and ascal morphology. The family still predominantly comprises pyrenomycetes that have brown to dark brown, ellipsoid ascospores, cylindrical stipitate asci and an amyloid apical ring. Anamorphic structures were recently included as further informative characters in the past decades and have still not yet been studied for far over 50% of the accepted species. As shown in Table 1, there are various further genera presently included in the Xylariaceae that either have anamorph types different from both the geniculosporium-like and the nodulisporium-like type or that have not been studied yet on their conidiophore

morphology. Some of these genera have libertella-like conidiogeneous structures; characterised by long slender falcate conidia (scoleospores), rather than the globose to ellipsoid ones of the typical Xylariaceae. Such features are characteristic of the anamorphic states of the Diatrypaceae, which have always been regarded as sister family to the Xylariaceae.

Interestingly, the genus *Libertella* comprises coelomycetes, which form the scoleospores in pycnidia and are commonly encountered as asexual states of several genera in the Diatrypaceae and other families of the Xylariales. The type species of *Libertella*, *L. betulina* Desm. 1830, has not been epi- or neotypified, and no viable cultures are apparently extant in public collections.

However, the few DNA sequence data available in the public domain of strains of this genus indeed show strong homologies of *Libertella* to the Diatrypaceae. The anamorph of the important grape pathogen, *Eutypa lata* Tul. & C. Tul. 1863, has been described as *Libertella blepharis* A.L. Sm. 1900. *Eutypa lata* is also the type species of the genus *Eutypa* Tul. & C. Tul. 1863, which was erected 33 years later than *Libertella*. This could accordingly pose a problem, in view of the application of the new Art. 59 ICN to *Libertella* and their xylarialean teleomorphs. Nevertheless, the corresponding teleomorph of *Libertella betulina* is said to be *Diatrype stigma* (Hoffm.) Fr. 1849, a species sanctioned by Fries that goes back to the basionym, *Sphaeria stigma* Hoffm. 1787. Rappaz (1987), however,

Table 1. Accepted genera of the Xylariaceae and their synonyms, divided into three major groups, according to anamorph types as defined by Ju and Rogers (1996). **Bold** typeset indicates that molecular phylogenetic data are available from authentic (but not necessarily holo-, neo- or epitype) material of the type species and/or cultures are deposited in public collections. The names that will probably be list-accepted have been underlined. **A** indicates anamorph and **T** teleomorph names (mostly given in those cases where nomenclature of pleomorphic fungi needs to be unified). Arrows indicate that the respective younger name is automatically replaced by the respective older name of the corresponding morph upon application of a IFIN concept. In case no homotypic synonyms exist at genus rank, as no anamorph–teleomorph connection of the respective type species has so far been established, the respective corresponding teleomorph genera are indicated.

Subfamily Xylarioideae; geniculosporium-like anamorphs s. Ju and Rogers (1996)	Subfamily Hypoxyloideae; nodulisporium-like anamorphs s. Ju and Rogers (1996)	Genera Incertae sedis (libertella-like anamorphs or unknown conidiogenic structures)
<i>Acanthodochium</i> Samuels, J.D. Rogers & Nagas 1987 ⇒ <i>Collodiscula</i> ^a	<i>Annellosporium</i> M.L. Davey (A) ⇒ <i>Daldinia</i>	<i>Anthostomella</i> Sacc. 1875
<i>Amphiroseellinia</i> Y.M. Ju, J.D. Rogers, H.M. Hsieh & Lar. N. Vassiljeva 2004	<i>Annulohypoxylon</i> Y.M. Ju, J.D. Rogers & H.M. Hsieh 2005	<i>Appendixia</i> B.S. Lu & K.D. Hyde 2000
<i>Arthroxyllaria</i> Seifert & W. Gams 2002	<i>Basidiobotrys</i> Höhn. 1909 (A) = <i>Xylocladium</i> (A)	<i>Ascovirgaria</i> J.D. Rogers & Y.M. Ju 2002 (T) ⇒ <i>Virgaria</i>
<i>Ascotricha</i> Berk. 1838	<i>Biscogniauxia</i> Kuntze 1891	<i>Barrmaelia</i> Rappaz 1995b
<i>Astrocystis</i> Berk. & Broome 1873	<i>Calceomyces</i> Udagawa & S. Ueda 1988	<i>Biporispora</i> J.D. Rogers, Y.M. Ju & Cand. 1999
<i>Collodiscula</i> I. Hino & Katum. 1955	<i>Camillea</i> Fr. 1849	<i>Cannonia</i> Joanne E. Taylor & K.D. Hyde 1999
<i>Conitolaritella</i> Dania Garcia, Stichel & Guarro 2006 (A)	<i>Daldinia</i> Ces. & De Not. 1863	<i>Chaenocarpus</i> Rebert. 1804
<i>Dematophora</i> R. Hartig 1883 ⇒ <i>Rosellinia</i>	<i>Entonaema</i> Möller 1901	<i>Chlorostroma</i> A.N. Mill., Lar.N. Vassiljeva & J.D. Rogers 2007
<i>Dicyma</i> Boulanger 1897 (A) ⇒ <i>Ascotricha</i>	<i>Hypoxylon</i> Bull. 1791	<i>Colletomanginia</i> Har. & Pat. 1906
<i>Discoxyllaria</i> J.C. Lindq. & J.E. Wright 1964 (T) ⇒ <i>Hypocreodendron</i>	<i>Induratia</i> Samuels, E. Müll. & O. Pettrini 1987	<i>Creosphaeria</i> Theiss. 1910 ^b
<i>Emarcea</i> Duong, Jeewon & K.D. Hyde 2004	<i>Masoniomyces</i> J.L. Crane & Dumont 1975 (A) ⇒ <i>Camillea</i>	<i>Cyanopulvis</i> J. Fröhl. & K.D. Hyde 2000
<i>Entoleuca</i> Syd. 1922	<i>Nodulisporium</i> Preuss 1849	<i>Diamantina</i> A.N. Mill., Læssøe & Huhndorf 2003
<i>Eupixylon</i> Füsting 1867	<i>Obolarina</i> Pouzar 1986	<i>Engleromyces</i> Henn. 1900 ^e
<i>Geniculisyminema</i> Okane & Nakagiri 2007 (A) ⇒ <i>Nemania</i>	<i>Phylacia</i> Lév. 1845	<i>Gigantiospora</i> B.S. Lu & K.D. Hyde 2003
<i>Geniculosporium</i> Chesters & Greenh. 1964 (A) ⇒ <i>Nemania</i>	<i>Pleurographium</i> (A) = <i>Nodulisporium</i>	<i>Guestia</i> G.J.D. Sm. & K.D. Hyde 2001
<i>Halorosellinia</i> Whalley, E.B.G. Jones, K.D. Hyde & Læssøe 2000	<i>Pyrenomyxa</i> Morgan 1895	<i>Junillera</i> J.D. Rogers, Y.M. Ju & San Martín 1997 ^{b,c}
<i>Helicogermislita</i> Lodha & D. Hawksw. 1983	<i>Pyrenopolyporus</i> Lloyd 1917 = <i>Hypoxylon</i>	<i>Libertella</i> Desm. 1830

(Continued)

Table 1. (Continued).

Subfamily Xylarioideae; geniculosporium like anamorphs s. Ju and Rogers (1996)	Subfamily Hypoxyloideae; nodulisporium like anamorphs s. Ju and Rogers (1996)	Genera Incertae sedis (libertella-like anamorphs or unknown conidiogenic structures)
<i>Holtmania</i> Lloyd 1924 = <i>Kretzschmaria</i> <i>Hypocopa</i> (Fr.) J. Kieck f. 1867 Hypocreodendron Henn. 1897	Rhopalostroma D. Hawksw. 1977 Rostrophoxylon J. Fourn. & M. Stadler 2010 Ruvenzoria J. Fournier, M. Stadler, Læssøe & C. Decock 2010 Thannomyces Ehrenb. 1820 Theissenia Maubl. 1914 Thuemenella Penz. & Sacc. 1898	<i>Lopodostoma</i> (Nitschke) Traverso 1906 ^b <i>Myconeesia</i> Kirschst. 1936 <i>Occultitheca</i> J.D. Rogers & Y.M. Ju 2003 <i>Padixonia</i> Subram. 1972 <i>Paramphisphaeria</i> F.A. Fernández, J.D. Rogers, Y.M. Ju, Huhndorf & Umaña 2004 <i>Paucithecium</i> Lloyd 1923
Kretzschmaria Viégas 1944 <i>Leptreuria</i> Læssøe, J.D. Rogers & Whalley 1989	Tripllicaria P. Karst. 1889 (A) ⇒ Hypoxylon <i>Iersiomyces</i> Whalley & Watling 1989 = <i>Daldinia</i> <i>Vivantia</i> J.D. Rogers, Y.M. Ju & Cand. 1996 <i>Xylocladium</i> P. Syd. ex Lindau 1900 (A) ⇒ Camillea ^f	<i>Sabalicola</i> K.D. Hyde 1995 <i>Sarcoxyton</i> Cooke 1883 <i>Spirodecospora</i> B.S. Lu, K.D. Hyde & W.H. Ho 1998 <i>Squamotubera</i> Henn. 1903 ^d
Lindquistia Subram. & Chandrash. 1977 (a) ⇒ Poronia		<i>Streblema</i> Chevall. 1826 <i>Striatodecospora</i> D.Q. Zhou, K.D. Hyde & B.S. Lu 2000 <i>Vingaria</i> Nees 1816 (A)
Moelleroclavus Henn. 1902 (A) ⇒ Xylaria Muscodor (A) ⇒ (?) Xylaria Nemania S.F. Gray 1821 <i>Ophiorosellinia</i> J.D. Rogers, A. Hidalgo, F.A. Fernández & Huhndorf 2004		<i>Wawelia</i> Namysl. 1908, <i>Whalleya</i> J.D. Rogers, Y.M. Ju & F. San Martín 1997 ^b <i>Xylocrea</i> Möller 1901 ^d
Padixonia Subram. 1972 (A) ⇒ Xylaria Podosordaria Ellis & Holw. 1897 <i>Poroleptreuria</i> M.C. González, Hanlin, Ulloa & Elv. Aguirre 2004		
Poronia Willd. 1787 Pseudoxylaria Boedijn 1959 = Xylaria <i>Pucicola</i> De Bert. 1976 = <i>Dicyma</i> ⇒ Ascotricha Rosellinia De Not. 1844		
Stilbohypoxyton Henn. 1902 <i>Vriksopama</i> D. Rao & P. Rag. Rao 1964 (A) = <i>Dematophora</i> ⇒ Rosellinia Xylocoremium J.D. Rogers 1984 (A) ⇒ Xylaria <i>Xyloatumulus</i> J.D. Rogers, Y.M. Ju & Hemmes 2006		

^aDespite acanthodochium-like anamorphic states are also known from *Astrocystis*, the genus name *Acanthodochium* is a straightforward synonym of *Collidiscala* (cf. Jaklitsch & Voglmayr 2012).

^bThese genera are characterised by libertella-like conidiogenous structures.

^cThis genus is characterised by libertella-like conidiogenous structures and a nodulisporium-like synanamorph.

^dThese genera are currently synonymised with *Sarcoxyton* in Index Fungorum, but there does not seem to be any conclusive evidence, based on type studies, and the holotype specimens are believed to have been lost.

^e*Xylocladium* is the anamorph of several *Camillea* spp., including the widespread neotropical species *C. tinctor*. However, some *Biscogniauxia* spp. also have a xylocladium-like anamorph, and for the type species of *Xylocladium*, *Xylocladium claurivarii* (Pat.) P. Syd. ex Lindau 1900, no straightforward anamorph–teleomorph relationship has so far been established.

^fThis genus is currently regarded as a synonym of *Engleromyces* in Index Fungorum, but this was never confirmed based on type studies.

segregated the European *Diatrype* sp. that is typically associated with *Betula* and proposed the name *D. undulata*. The Diatrypaceae obviously deserve more attention, and some important teleomorph species will need to be re-examined and re-classified based on morphological and ecological evidence. In addition, the results of the few hitherto published molecular phylogenetic studies of the Diatrypaceae (e.g. Acero et al. 2004; Carmaran et al. 2006) suggest that a re-organisation of the family at generic rank will be unavoidable in the near future.

Unfortunately, the hitherto published papers did not include many DNA sequences derived from type material or at least material from the original geographic regions and hosts where the respective taxa had originally been collected. As in other families comprising plant pathogens of global importance, it will be very important to include such material after employing concise epi- and neotypification procedures, in order to avoid chaos in their nomenclature, due to the use of parallel taxonomic systems.

In this context, it is important to note that libertella-like anamorphs have also been found in a range of genera that are presently included in the Xylariaceae. Examples are *Barrmaelia*, *Creosphaeria*, *Lopadostoma*, *Whalleya*, and, above all, the large, heterogeneous genus *Anthostomella* and its segregates. The prototype of *Anthostomella* is characterised by having uniperitheciate ascomata immersed under a stroma reduced to a black clypeus with “xylariaceous” eight-celled brown ellipsoid ascospores. Such a combination of features may be interpreted as basal, i.e. the respective species may be a primitive taxon that has not yet developed stromata. On the other hand, it cannot be excluded that certain *Anthostomella* species are derived from the stromatic genera of the Xylariaceae, through secondary reduction that may have arisen in the course of their co-evolution with plant hosts. In addition, there are *Anthostomella* species that have been reported to have nodulisporium-like anamorphs as well as others that have “diatrypaceous” libertella-like scoleococonidia. In the stromatic genus *Jumillera*, libertella-like conidiogenous structures are even accompanied by geniculosporium-like synanamorphs (Rogers et al. 1997). In *Graphostroma*, the presence of a nodulisporium-like conidial state besides a *Diatrype*-like teleomorph featuring allantoid ascospores (Pirozynski 1974), has given rise to the erection of a separate monotypic family (Graphostromataceae).

Other genera in the Xylariaceae, such as *Chlorostroma*, *Engleromyces*, *Sarcoxydon*, and *Squamotubera*, are so far only known from their stromatic teleomorphs, often just from drawings made in the nineteenth century. Even though some of them are characterised by production of conspicuous stromata, they seem to be rare and are primarily known from remote places in the tropics. These fungi have never been cultured and studied for their molecular phylogenetic

affinities to one of the major lineages in the Xylariaceae (i.e. Xylarioideae and Hypoxyloideae). Rogers (1981) used characters such as the morphology of the ascus apical apparatus to link some of these genera to either the xylarioid or the hypoxyloid Xylariaceae. However, neither this author nor others who treated the tropical Xylariaceae could get hold of the type material of certain species. The holotype material of *Engleromyces goetzii* (Rogers 1981) and *Xylocrea piriformis* (Fournier & Stadler unpublished³) is highly depauperate and not suitable for a straightforward assessment of typical morphological features. These fungi will also need to be collected in fresh state in order to assess their affinities to one of the large subfamilies of the Xylariaceae.

The same is true for most of the aforementioned genera: only a few morphologically validated strains and even fewer DNA sequence data derived from type material are deposited in public domain databases. It will be prudent to refrain from application of premature name changes until the majority of taxa listed in the *Incertae sedis* column in Table 1 have been studied for their molecular phylogeny and for the morphology of their conidiogenous apparatus.

The only genus in this group where anamorph–teleomorph connections have already been safely established and the anamorph has been described much earlier is *Virgaria*. The corresponding teleomorph, *Ascovirgaria*, will therefore be suppressed in future. Notably, the *Virgaria* anamorph is quite distinctive as compared to other conidiogenous structures associated with the Xylariales. The asexual state of this fungus is also certainly more frequent in nature than its corresponding teleomorph. Therefore, it is unlikely that a proposal will be made to retain *Ascovirgaria*. The affinities of (*Asco*-)*Virgaria* to either of the large xylariaceous subfamilies, however, remain to be established by molecular phylogenetic methods.

Xylarioideae

The xylarioid Xylariaceae, or Xylarioideae, are thought to be closely related to the genus *Xylaria*, owing to the fact that their conidiogenous structures resemble those of *Geniculosporium*. The genus *Geniculosporium* was erected by Chesters and Greenhalgh (1964) and typified by the anamorph of *Hypoxydon* (= *Nemania*) *serpens*, which is also the type species of the teleomorph genus *Nemania* S.F. Gray 1821. *Geniculosporium* can in future be suppressed in favour of *Nemania*. Other named xylarioid anamorphs, such as *Arthroxydon*, *Moelleroclavus*, and *Xylocoremium*, have been connected convincingly to certain lineages in *Xylaria*. Those names would be available in the future to accommodate some species of *Xylaria*, if this large and diverse genus will eventually be further split up. Recent molecular phylogenetic work has already suggested that this may become necessary very soon. For instance, the study by Hsieh et al. (2010) has clearly shown that *Xylaria*

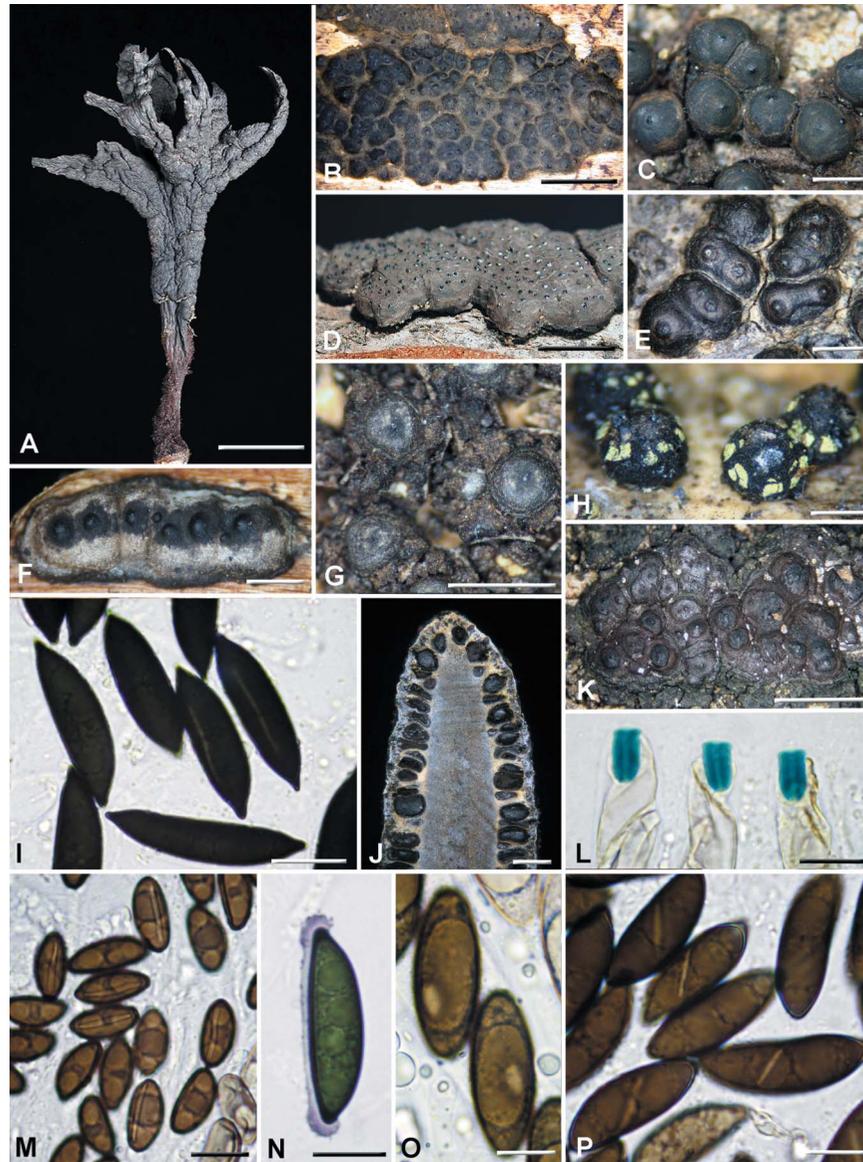


Figure 2. Teleomorphic structures of Xylarioideae. **Type species are in bold** A: Stroma of *Xylaria hypoxylon* (L.) Grev. (JF 05066, France); B: Stroma of *Nemania serpens* (Pers.) Gray (JF 12014, France); C: Stromata of *Rosellinia aquila* (Fr.) Ces. & De Not. (JF 10091, France); D: Stroma of *Kretzschmaria deusta* (Hoffm.) P.M.D. Martin (JF 02131, France); E: Stromata of *Halorosellinia oceanica* (S. Schatz) Whalley, E.B.G. Jones, K.D. Hyde & Læssøe (CLL 8038B, French Guiana); F: Stroma of *Euepixylon udum* (Pers.) Læssøe & Spooner (JF 11195, France); G: Stromata of *Astrocystis mirabilis* Berk. & Broome (CLL 5395, Martinique); H: Stromata of *Stilbohypoxyton elaeicola* (Henn.) L.E. Petrini (CLL 1010, Martinique); I: Ascospores of *Xylaria fockei* (Miq.) Cooke (X-581, Gabon); J: Stroma of *Xylaria escharoidea* (Berk.) Sacc. in vertical section (ZY-070730, Hainan, P.R.C.); K: Stroma of *Entoleuca mammata* (Wahlenb.) J.D. Rogers & Y.M. Ju (CWU-AS 2045, Ukraine); L: Ascospore of *Xylaria anisopleura* (Mont.) Fr. in Melzer's reagent (CLL 8268, Martinique); M: Ascospores of *Xylaria hypoxylon* (L.) Grev. (JF 04258, France); N: Ascospore of *Rosellinia britannica* L.E. Petrini, Petrini & S.M. Francis in aqueous nigrosin showing slimy appendages (JF 02044, France); O: Ascospores of *Euepixylon udum* (cf. F) showing germ pores; P: Ascospores of *X. anisopleura* (cf. L) showing oblique germ slits. Scale bars: A = 1 cm; B, D, K: 5 mm; C, E-G, J: 1 mm; H: 0,5 mm; I, L-P: 10 μ m

is divided into several clades and appears paraphyletic with respect to other xylarioid genera, including *Kretzschmaria*, *Nemania*, and *Rosellinia*. Also supported by a molecular ecology study by Visser et al. (2009), *Pseudoxylaria*, which had eventually been erected for the termite-associated species and is currently regarded as a subgenus of *Xylaria*,

represents a monophyletic lineage within the Xylarioideae. It might well deserve to be recognised as a genus of its own, whose evolution seems to have occurred in convergence to certain plant-inhabiting Xylariaceae.

The recent study by Hsieh et al. (2010) and concurrent work by Peršoh et al. (2009) and Fournier et al. (2011)

on the molecular phylogeny and polyphasic taxonomy of *Xylaria* can only be seen as the first step towards a modern taxonomy of this hyperdiverse genus and the associated subfamily. It is very important to note that even the concept of the type species, *Xylaria hypoxylon*, has only recently been clarified by concise molecular phylogenetic studies in conjunction with extensive morphological work. Peršoh et al. (2009) revealed that most DNA sequence data in GenBank and the majority of cultures assigned to *Xylaria hypoxylon* in public domain collections corresponded to different species of *Xylaria*. These misleading data have still not been corrected at the time this article was submitted, and unfortunately “molecular taxonomists” are still committing errors in falsely assuming that all names on sequence data in GenBank are genuine.

Unfortunately, this also concerned a mislabelled strain in ATCC, whose sequence data have been used as reference in hundreds of molecular phylogenetic studies. This strain (ATCC 42768) actually corresponds to *Xylaria longiana*, rather than to *X. hypoxylon*. Peršoh et al. (2009) have provided a detailed description of *X. hypoxylon* and allied species and deposited several strains of this taxon from Sweden, i.e. the country where the fungus has probably been found and studied by mycologists such as Linnaeus and Fries. One of these specimens would serve very well as epitype. Even from other important Xylariaceae, well-characterised material and corresponding DNA sequences are now readily available. However, hundreds of further names in *Xylaria* remain to be studied and connected to fresh material that can be used in modern monographic and phylogenetic studies. We think that, until this task has been accomplished, it will be prudent to maintain the current generic concept of *Xylaria* as a heterogeneous mega-genus, thus avoiding excessive changes in taxonomy and nomenclature.

The name of the teleomorph of another insect-associated xylarioid taxon, *Discoxylaria*, will in future be suppressed, since its anamorph *Hypocreodendron* has been described much earlier. The Xylarioideae also comprises *Ascotricha* and its associated anamorph names *Dicyma* and *Puciola*, which will both remain subordinate to their corresponding teleomorph as *Ascotricha* is the older name. The recently erected *Geniculisyneema* also appears to be a straightforward younger synonym of *Nemania*. The same is true for *Dematophora*, the asexual state of many *Rosellinia* species.

Hypoxyloideae

Within the hypoxyloid Xylariaceae, only a few nomenclatural changes are foreseen with respect to the application of a 1FIN concept. The generic names *Hadrotrichum*, *Periconiella*, *Virgariella*, and *Sporothrix* have occasionally been used in the past to characterise the anamorphs of hypoxyloid Xylariaceae, but this is of no consequence. Ju

and Rogers (1996) and most other authors who treated the family after their monograph on *Hypoxylon* was published refrained from giving the anamorphs separate names. They referred to the asexual states by using terms such as “nodulisporium-like, virgariella-like,” etc., conidiogenous structures. The genus *Nodulisporium*, which was erected by Preuss (1849), is typified by *Nodulisporium ochraceum*, an acervuli-forming hyphomycete that was found on birch wood in Saxony Province, Germany. The description by Preuss (1849) is not very clear and could in principle refer to many different xylariaceous anamorphs that spread on wood. Important details that could nowadays be diagnostically helpful, such as the dimensions of conidiogenous structures, the type of conidiogenesis, and the branching patterns, were not mentioned by Preuss (1849). It might be feasible to associate *N. ochraceum* with the conspicuous anamorph of *Hypoxylon howeanum*, which can be frequently encountered on dead wood of *Betula* in Germany (in which case it would be feasible to regard *Nodulisporium* as a straightforward synonym of *Hypoxylon*). However, even type studies of *N. ochraceum* might not allow to prove this presumption conclusively.⁴

Various additional *Nodulisporium* species have been described in the literature. However, in most cases, no type strains are extant, precluding the possibility to link them to any teleomorphic names by comparative studies of the cultures using molecular and morphological methods. In principle, they could belong to any of the Hypoxyloideae genera, and even to other species in the Xylariaceae such as *Graphostroma* and *Anthostomella*, which are known to have nodulisporium-like anamorphs as well.

To further complicate the situation, Rodrigues and Samuels (1989) have assigned the anamorph of *Phylacia* to the genus *Geniculosporium*, even though there can be no doubt, from the original publication and recent work by Bitzer et al. (2008) on *Phylacia*, that the conidiogenous structures of these fungi are rather assignable to a nodulisporium-like anamorph sensu Ju and Rogers (1996). Several of the previously described *Nodulisporium* species will therefore in all likelihood have to join the “dustbin” of old fungal names that cannot be safely connected to a certain teleomorph genus. In consequence, the name *Nodulisporium* will not disappear even when following Art. 59 ICN.

The genus *Annellosporium*, which has recently been erected for a species of hyphomycetes with clear phylogenetic affinities to *Daldinia*, will need to be abandoned because the salient features of *Annellosporium* are also encountered in the conidial states of some *Daldinia* spp. Even though these species (i.e. *Daldinia petriniae*, *D. decipiens*, and their allies) seem to be phylogenetically distinct from *Annellosporium nemorosum*, the latter species will be recognised as an anamorphic *Daldinia* sp. This has already been accomplished in the new world monograph of *Daldinia* (Stadler et al. Forthcoming 2013).

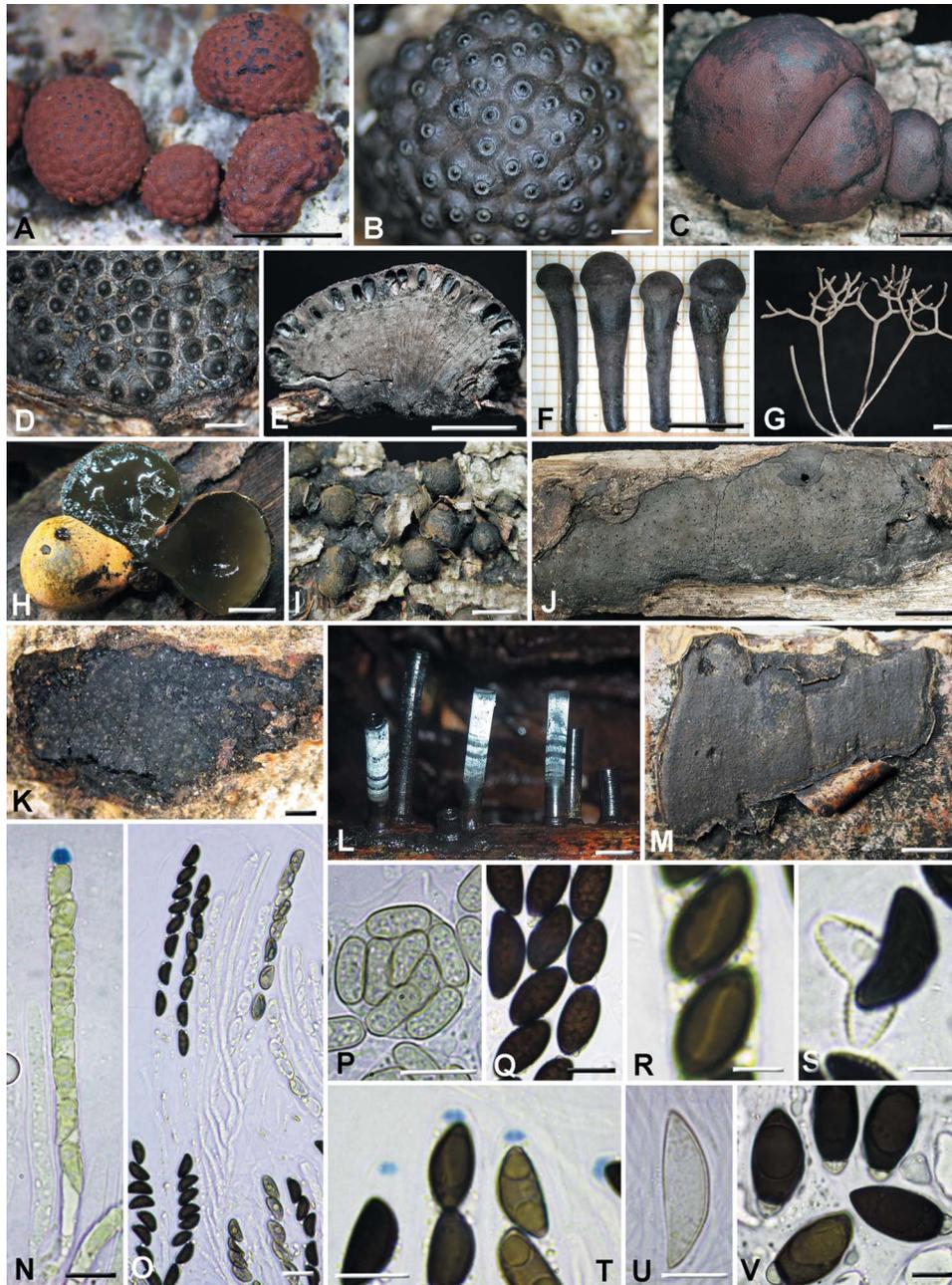


Figure 3. Teleomorphic structures of Hypoxyloideae. **Type species are in bold** A: Stromata of *Hypoxylon fragiforme* (Pers.: Fr.) J. Kickx fil. (JF 04245, France); B: Stroma of *Annulohypoxylon truncatum* (Schwein.) Y.M. Ju, J.D. Rogers & H.M. Hsieh (MP 3889, Panama); C: Stromata of *Daldinia concentrica* (Bolton) Ces. & De Not. (JF 09129, France); D: Stroma of *Rostrohypoxylon terebratum* J. Fourn. & M. Stadler (JF-TH 06-04, Thailand, holotype); E: stroma of *Ruwenzoria pseudoannulata* J. Fourn., M. Stadler, Læssøe & C. Decock in vertical section (MUCL 51394, Democratic Republic of the Congo, holotype); F: Stromata of *Rhopalostroma angolense* (Welw. & Curr.) D. Hawksw. (SG 284, Côte d'Ivoire); G: Stroma of *Thamnomyces camerunensis* (P. Henn.) P. Henn. (KRAM-56276, Cameroon); H: Stromata of *Entonaema liquescens* Möller in vertical section showing liquid-filled interior (MP 4332, Panama); I: Stromata of *Phylacia bomba* (Mont.) Pat. (GYJF 12009, French Guiana); J: Stroma of *Theissenia pyrenocrata* (Theiss.) Maubl. (GYJF 12221, French Guiana); K: Stroma of *Obolarina dryophila* (Tul. & C. Tul.) Pouzar (JF 08193, France); L: Stromata of *Camillea lepreurii* Mont. (GYJF 12145, French Guiana); M: Stroma of *Biscogniauxia nummularia* (Bull.) Kuntze (JF 99047, France); N: Ascus of *Camillea fossulata* (Mont.) Læssøe, J.D. Rogers & Whalley in Melzer's reagent (GYJF 12078, French Guiana); O: Asci of *Hypoxylon trugodes* Berk. & Broome (GYJF 12043, French Guiana); P: Ascus and ascospores of *Phylacia bomba* (cf. I); Q: Ascospores of *Hypoxylon haematostroma* Mont. (MJF 07262, Martinique); R: Ascospores of *Hypoxylon lenormandii* Berk. & M.A. Curtis showing sigmoid germ slits (MJF 07128, Martinique); S: Ascospore of *Hypoxylon duranii* J.D. Rogers with ornamented perispore dehiscing in 10% KOH (WSP 67597, Mexico, holotype); T: Ascus apical apparatus of *H. lenormandii* in Melzer's reagent (cf. R); U: Ascospore of *Camillea* sp. (GYJF 12223, French Guiana); V: Ascospores of *Biscogniauxia philippinensis* (Ricker) Whalley & Læssøe, provided with a cellular appendage (MJF 10187, Martinique). Scale bars: C, H, J: 1 cm; A, E-G, I, L, M: 5 mm; B, D, K: 1 mm; N-Q, T-V: 10 μ m; R, S: 5 μ m.

In this article, one salient problem of current “molecular taxonomy” has been addressed: inadequateness of ITS rRNA gene sequences for species discrimination. The type species of *Daldinia*, *D. concentrica* sensu Rogers et al. (1999) was found to have 100% homology of its ITS rRNA gene sequence as *Daldinia steglichii*, a taxon known from Papua New Guinea, India, and Réunion Island (and may actually be more widely distributed in tropical Asia). *Daldinia concentrica* (which has still not been discovered outside Europe even after studies of hundreds of fresh collections and revision of several thousands of herbarium specimens) and *D. steglichii* drastically differ in their morphology, host range, secondary metabolite production, and geographic distribution. The only features they seem to have in common are their ascospore dimensions and their ITS rRNA genes. Similar discrepancies have also been noted in our ongoing work on polyphasic taxonomy of various other species in the Xylariaceae. Whereas some species seem to have fairly specific “signature ITS sequences,” it appears hardly possible to discriminate others from taxa that are fairly distantly related with respect to their phenotypes. Nevertheless, molecular ecologists who seek to “identify” ITS-based “operational taxonomic units” (OTU) by mere sequence comparison are very likely to create confusions. A different gene seems to be needed for the purpose of concise genetic barcoding of the Xylariaceae.

It is well known that *Daldinia* spp. are among the predominant fungal endophytes and many species are apparently rare because they only produce their stromata on damaged and stressed hosts (Stadler 2011). Sequence data from inventories of fungal endophytes that are regularly being accepted in leading “high impact” scientific journals are therefore very likely to be misleading. As of recently, the number of such studies is steadily increasing. At the same time, the number of capable well-trained mycologists, especially in those countries that are believed to harbour the bulk of the untapped fungal biodiversity, is steadily diminishing. Even in the Northern hemisphere countries, next generation mycologists may no longer be able to receive training in the classical mycological core disciplines. When advertising the Amsterdam Declaration (Hawksworth et al. 2011), which ultimately gave rise to the new rules in fungal nomenclature, the authors emphasised the advantages associated with the availability of molecular phylogenetic techniques in establishing teleomorph–anamorph relationships. Their rationale was that it should be possible to concisely link different morphs of pleomorphic fungi by molecular phylogenetic studies. However, this evidently can only work if the type material of both morphs is represented by viable cultures or freshly collected specimens. Old herbarium material will often not yield any DNA suitable for PCR, and evidently it is not possible to sequence those taxa that are only known from their iconotypes. In case there will be some need to establish the identity of certain taxa based on comparisons of

loci other than rRNA genes, it may even be mandatory to obtain cultures, as housekeeping genes can often not be sequenced from dried specimens or even from fresh material of microfungi.

We therefore think that, in the scope of attaining a unified fungal nomenclature, it will be more important than ever to train mycologists to acquire high skills in classical field work and microscopy, as well as advanced microbiological techniques. Only under these circumstances can the badly needed epitypification campaigns succeed.

Disposition of *Muscodor* and impetus of “molecular taxonomy”

The genus *Muscodor* was erected by Worapong et al. (2001) for an endophytic fungus that produces volatile antibiotics. This discovery gave rise to substantial research on so-called “biofumigants,” and other authors have since then also described a number of different species based on differences in their profile of volatiles as assessed by gas chromatography coupled to mass spectrometry (GC-MS) and, above all, molecular phylogenetic data. Nevertheless, the quality of the phylogenetic data that were also used to erect *Muscodor* in the first place may be illustrated by the fact that only a few reference DNA sequences have been used for comparison. Worapong et al. (2001) compared only ribosomal RNA gene sequences out of nine species taken from four genera among the manifold taxa of the Xylariaceae to their “new taxon.” They did not actually study the respective strains for comparison, and those certainly did not represent type or epitype strains. Some of these reference sequences, including those derived from “*X. hypoxylon*,” have meanwhile turned out to be derived from mislabelled or misidentified material. In addition, much of the argumentation was based on 18S rRNA data, which has not been proven up to date to contain any valid information to determine a xylarialean taxon beyond the family and higher taxonomic ranks.

For this lack of taxon sampling and reference material, the rationale the authors used to erect a new genus appears highly questionable. Furthermore, they used SEM to characterise the hyphae, but once again did not study any other Xylariaceae species for comparison. One of the salient features used to erect the new genus was the profile of volatile metabolites as assessed by gas chromatography coupled to mass spectrometry (GC-MS), which would appear adequate as means of chemotaxonomic characterisation. However, up to date, over 10 years after the first report of *Muscodor*, no other xylariaceous fungus has been compared on its volatile profile in any of the studies dealing with *Muscodor* spp. The reported volatile profiles always relied on a single cultivation experiment per strain or “species”, and apparently the authors did not check whether the GC-MS profiles are reproducible for a given “taxon.”

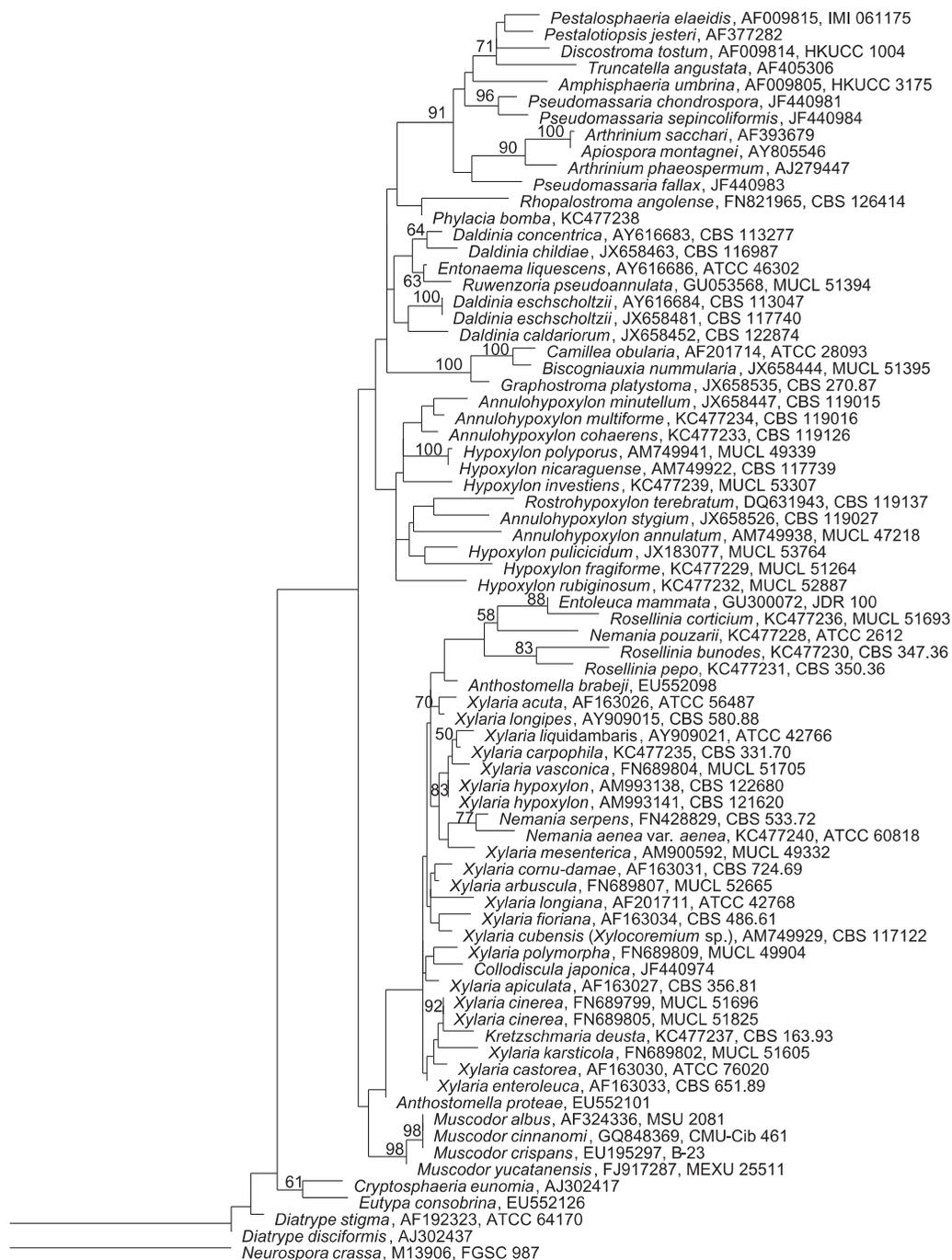


Figure 4. Phylogenetic relationships among Xylariaceae and selected representatives of other families of the Xylariales (material listed in Table 2). Tree found by RAxML to most likely explain the ITS data set. Bootstrap support values (500 replicates) above 50% are indicated. Species names are followed by the GenBank accession number and number of the deposited voucher (if available).

Later on, as additional DNA sequences of other Xylariaceae were made available, due to the work by other authors on well-characterised genuine material, it became fairly evident that the *Muscodora* spp. are nested in the xylarioid Xylariaceae. Thus they represent an ingroup in the heterogeneous clade that comprises members of the genus *Xylaria* itself. Interestingly, many known species of *Xylaria* (and other xylariales fungi which include an

endophytic state in their life cycle) are known to lack differentiated mycelia in culture.

Xylaria is one of the frequently reported genera among the inventories of endophytes inhabiting seed plants. Still, we are not aware of any study that used those *Xylaria* spp. for comparison with *Muscodora* or – for that measure, of any comprehensive study on the production of volatiles in the Xylariales. As antibiosis is a widespread phenomenon

among the filamentous ascomycetes, it cannot be taken for granted that *Muscodor* “species” represent not merely the anamorphs of known teleomorphic *Xylaria* species or another yet unknown xylariaceous or xylarialean genus.

The current status of Xylariaceae phylogeny is exemplified by the phylogenetic tree in Figure 4 containing the DNA sequences of *Muscodor* spp. in comparison to other Xylariaceae. The data were taken from previous studies using morphologically and chemotaxonomically well-characterised materials that are all deposited in public domain collections. Nevertheless, only a few of them constitute ex-type materials, even though it might be feasible to eventually use some of these strains and the corresponding vouchers as epitype or neotype material.

The monophyletic clade in Figure 4 comprising sequences derived from *Muscodor* does not appear related to any teleomorph-typified taxon. According to these preliminary results, its closest phylogenetic affinities are with *Anthostomella proteae* and the Xylarioideae, but there are not enough validated DNA sequence data in the basal Xylariales to further speculate about this matter. The phylogenetic tree clearly demonstrates the limitations of ITS rRNA gene sequences for reconstruction of the phylogenetic relationships within the Xylariales: the major nodes obtained only negligible statistical support and the Xylariaceae appear paraphyletic, due to representatives of other families of the Xylariales being nested within the Hypoxyloideae. The topology of the latter, again, reflects the current limitations. The Hypoxyloideae are split into four clades. The *Hypoxylo*/*Annulohypoxylo* clade (including *Rostrohyoxylo terebratum*) comprises genera featuring stromatal pigments and unipartite stromata, which is in accordance with their relationship within the tree. However, as on all other studies on rDNA so far published, the genera *Hypoxylo* and *Annulohypoxylo* were not fairly separated. The second subclade consists of *Daldinia* and closely related genera like *Entonaema* and *Ruwenzoria*. *Rhopalostroma* and *Phylacia* cluster separately in the poorly supported tree, in contrast to earlier studies (e.g. Stadler et al. 2010a). The most basal lineage of the Hypoxyloideae, which comprises of the genera *Camillea* and *Biscogniauxia*, is also present in the phylogeny as a non-supported third subclade. Both have bipartite stromata, lacking apparent KOH extractable pigments. Notably, *Graphostroma* appeared more closely related to *Biscogniauxia* and *Camillea* than to *Diatrype*.

In summary, a multi-gene genealogy of all important crucial morphological lineages of Xylariaceae and associated Xylariales, which should best be obtained after all crucial taxa have been recollected and epitypified, appears necessary before a conclusive picture on the evolutionary relationships of this diverse fungal family can be drawn.

The point of this study is that, even though quite a large a number of ITS sequences of well-characterised Xylariaceae taxa have meanwhile become available, it does

not appear practical to integrate *Muscodor* into *Xylaria* (to which close affinities were proposed by the authors of several *Muscodor* species). The integration of the younger anamorph genus *Muscodor* into any of the older genera is not quite advisable because

- (1) For reasons mentioned above, not even the taxonomic interfaces between the basal xylarialean lineages have been settled, and some sequence data derived from *Anthostomella* strains also show suspiciously high homologies to those of *Muscodor*.
- (2) The species concepts within *Muscodor* seems to be ill-defined; for instance, the “interspecific” variability within ITS sequences of strains designated as *M. albus* in GenBank is almost as high as that of the genus itself. Furthermore, no chemotaxonomic physiological marker compounds among the volatiles detected in the various strains have as yet been defined to segregate certain species. This concept is quite incongruent to all other concepts that have hitherto been used in the taxonomy of the Xylariales and other ascomycetes. It is therefore actually rejected by most experts that are nowadays familiar with these fungi. *Muscodor* is, for instance, not listed among the valid genera of Xylariaceae compiled by Lumbsch and Huhndorf (2010), even though it was included in the *Genera of Hyphomycetes* by Seifert et al. (2011).
- (3) Most importantly, as convincingly argued by Braun (2012), the new rules of nomenclature do not call for immediate implementation of a unified nomenclature in all fungal taxa, but it will only be mandatory not to propose different names for different morphs in case of future new species discoveries.

Even if someone now attempted to integrate *Muscodor* in a holomorphic genus of the Xylariales, the names in *Muscodor* as well as the genus would still remain validly described. They could be resurrected at any time, once a thorough revision of the genus *Xylaria* and the xylarioid Xylariaceae has been carried out. By then, it might become feasible to assign the “*Muscodor* clade” to a xylariaceous teleomorph (of which several names are available). On the other hand, once a significant percentage of the species of *Xylaria* has been studied by both their molecular phylogeny and their production of volatile compounds, it could eventually be confirmed that *Muscodor* really represents an isolated evolutionary lineage that has sufficiently diverged from *Xylaria* to justify the status of an own genus.

We have to realise that taxonomy has always been a subjective matter, and this will in all likelihood not change in the future. For this reason, nomenclatural changes proposed for *Muscodor* would also not affect trademarks or commercialisation of novel “biofumigants” based on

Muscodor strains. However, we strongly feel that taxonomy and nomenclature should not be used for advertising or commercialisation purposes, but rather follow stringent rules, as outlined by Seifert and Rossman (2010). Editors and reviewers of taxonomic journals are strongly encouraged to maintain such standards in the future. In addition, we propose that it should be mandatory for all authors of taxonomic and non-taxonomic papers that deal with characterisation of fungi based on DNA-based data to cite the original work from which reference sequence data have been derived, rather than just cite the GenBank accession numbers. Such a procedure would (a) help the capable taxonomists to increase their citation indices and thereby their chances to obtain funding to continue their taxonomic studies, (b) encourage morphologists and molecular phylogeneticists/ecologists to join forces and (c) allow the reviewers of submitted manuscripts to evaluate more easily whether the reference DNA data come from a reliable source or from an unpublished study conducted by non-taxonomists.

Exceptions could be made, e.g. in large molecular ecological studies where thousands of sequence data are being retrieved, and it would not appear practical to cite all original sources. Nevertheless, even the authors of those studies should not take it for granted that all published DNA sequences with taxonomic labels have undergone a stringent quality control prior to their release to the public domain.

A recent paper by Bills et al. (2012) may provide a suitable alternative on how to cope with the diversity of xylariaceous and other biotechnologically important endophytes in a taxonomic and nomenclatural context. The teleomorph of an endophytic *Nodulisporium* sp. that had been originally discovered in the 1990s as producer organisms of a series of highly potent and selective insecticidal alkaloids named nodulisporic acids (NAs) was encountered in two different localities on Martinique Island. Interestingly, several years of natural product screening for novel insecticides at Merck & Co., paired with molecular phylogenetic and morphological work, had revealed multiple NA production isolates that were all endophytes derived from throughout the tropics. Their DNA sequences formed a monophyletic clade and they showed a similar morphology and physiology. Nevertheless, no new species were erected for these *Nodulisporium* isolates, as the DNA sequences suggested it to be a member of the genus *Hypoxylon*, which is known to harbour many species with endophytic states (cf. Whalley 1996; Rogers 2000).

The discovery of the corresponding teleomorph of the NA-producing endophytes (Bills et al. 2012) also relied on the study of ca. 4000 specimens of *Hypoxylon*, including most of the relevant type specimens that are extant in public herbaria. These specimens had been checked by meticulous morphological studies and HPLC profiling

of their stromata to evaluate chemotaxonomically important secondary metabolites. Fresh material that was in full accordance with the type specimens was cultured and studied for morphological and chemotaxonomic characteristics as well. Representative strains had been deposited in public collections to make them available to others for comparison. These studies also relied heavily on the work by Ju and Rogers (1996), and intensive collaborations with the authors of this article, in the course of a global research network. The description of the new teleomorph associated to the NA-producing endophytes was based on a comparison of teleomorphic and anamorphic morphology. HPLC profiling of stromata and corresponding cultures (the latter of which were grown under standardised conditions that are favourable for the production of NAs) and molecular phylogenies relying on three different gene loci were conducted in addition. Multiple isolates from different geographic regions of *Hypoxylon investiens*, i.e. the most closely related species as inferred from genotype- and phenotype-based evidence, were studied for comparison, and none was able to produce the NA insecticides.

Interestingly, mining in GenBank using BLAST searches revealed that the characteristic ITS sequences of the new species, *Hypoxylon pulicicidum*, had already been recovered repeatedly by molecular ecologists in plant and even air samples from various different localities, which provided additional information on the biogeography of the new fungal taxon. In addition, knowledge on the teleomorph of the NA-producing endophytes now allows for concise studies on the role of these potent compounds in the course of the life cycle of their producer, and to verify the hypothesis of their potential benefit for the host plants as deterrent or means of protection against insect pests.

So far, concise anamorph–teleomorph relationships based on the availability of cultures and supported by morphological and molecular phylogenetic studies have been established for less than 10% of the known species of Xylariaceae, and most of those are distributed in the temperate and subtropical zones of the Northern hemisphere. We likewise propose that extensive sampling of teleomorphic material of further Xylariaceae, especially in the tropical regions of the world and the Southern hemisphere, be carried out, in parallel to assessing the diversity of the endophytes. Teleomorphic material is badly needed to create epitype or neotype specimens, in order to establish further teleomorph–anamorph relationships, and ultimately apply a unified nomenclature for the Xylariaceae in general, using a polyphasic taxonomic approach. Only if and when the majority of species have been treated in this manner will it be possible to assess whether *Muscodor* and many other “apparently unique” endophytes truly constitute endophytes that never complete their life cycles.

Table 2. Overview of the origin of the DNA sequences used for the phylogenetic tree in Figure 4.

Species	GB acc no.	Strain no	Origin	Status	Reference
<i>Amphisphaeria umbrina</i>	AF009805	HKUCC 3175			Jaklitsch and Voglmayr (2012)
<i>Annulohypoxyton annulatum</i>	AM749938	MUCL 47218	P.R. China		Bitzer et al. (2008)
<i>Annulohypoxyton cohaerens</i>	KC477233	CBS 119126	Austria		Bitzer et al. (2008), sequenced in this study
<i>Annulohypoxyton minutellum</i>	JX658447	CBS 119015	Portugal		Bitzer et al. (2008), sequenced in this study
<i>Annulohypoxyton multifforme</i>	KC477234	CBS 119016	Germany		Bitzer et al. (2008), sequenced in this study
<i>Annulohypoxyton stygium</i>	JX658526	CBS 119027	Malaysia		This study
<i>Anthostomella brabeji</i>	EU552098				Jaklitsch and Voglmayr (2012)
<i>Anthostomella proteae</i>	EU552101				Jaklitsch and Voglmayr (2012)
<i>Apiospora montagnei</i>	AY805546				Jaklitsch and Voglmayr (2012)
<i>Arthrinium phaeospermum</i>	AJ279447				Jaklitsch and Voglmayr (2012)
<i>Arthrinium sacchari</i>	AF393679				Jaklitsch and Voglmayr (2012)
<i>Biscogniauxia nummularia</i>	JX658444	MUCL 51395	France		Stadler et al. (Forthcoming 2013)
<i>Camillea obularia</i>	AF201714	ATCC 28093	Puerto Rico		Rogers et al. (1991), sequence derived from unpublished study (GenBank data verified by us)
<i>Collodiscula japonica</i>	JF440974				Jaklitsch and Voglmayr (2012)
<i>Cryptosphaeria eunomia</i>	AJ302417				Jaklitsch and Voglmayr (2012)
<i>Daldinia concentrica</i>	AY616683	CBS 113277	Germany		Triebel et al. (2005)
<i>Daldinia caldariorum</i>	JX658452	CBS 122874	Mexico		This study
<i>Daldinia childiae</i>	JX658463	CBS 116987	Japan		This study
<i>Daldinia eschscholtzii</i>	AY616684	CBS 113047	Thailand		Triebel et al. (2005)
<i>Daldinia eschscholtzii</i>	JX658481	CBS 117740	Burkina Faso		This study
<i>Diatrype disciformis</i>	AJ302437				Jaklitsch and Voglmayr (2012)
<i>Diatrype stigma</i>	AF192323	ATCC 64170	Sweden		Adams et al. (2005)
<i>Discostroma tostum</i>	AF009814	HKUCC 1004			Jaklitsch and Voglmayr (2012)
<i>Entoleuca mammata</i>	GU300072	JDR 100	France		Hsieh et al. (2010)
<i>Entonaema liquescens</i>	AY616686	ATCC 46302	USA		Triebel et al. (2005)
<i>Eutypa consobrina</i>	EU522126				Jaklitsch and Voglmayr (2012)
<i>Graphostroma platystoma</i>	JX658535	CBS 270.87	France	Ex-type strain	Pirozynski (1974); sequence obtained in this study
<i>Hypoxyton fragiforme</i>	KC477229	MUCL 51264	Germany		This study
<i>Hypoxyton investiens</i>	KC477239	MUCL 53307	Martinique		This study (ex MJF10083)
<i>Hypoxyton nicaraguense</i>	AM749922	CBS 117739	Burkina Faso		Bitzer et al. (2008)
<i>Hypoxyton polyporus</i>	AM749941	MUCL 49339	Ivory Coast		Bitzer et al. (2008)
<i>Hypoxyton pulicicidum</i>	JX183077	MUCL 53764	Martinique		Bills et al. (2012)
<i>Hypoxyton rubiginosum</i>	KC477232	MUCL 52887	Germany		This study
<i>Kretzschmaria deusta</i>	KC477237	CBS 163.93	Germany		This study
<i>Muscodor albus</i>	AF324336	MSU 2081	Honduras	Type strain	Worapong et al. (2001)
<i>Muscodor cinnamomi</i>	GQ848369	CMU-Cib 461	Thailand	Type strain	Suwanarach et al. (2010)
<i>Muscodor crispans</i>	EU195297	B-23	Bolivia	Type strain	Mitchell et al. (2008)
<i>Muscodor yucatanensis</i>	FJ917287	MEXU 25511	Mexico	Type strain	Gonzalez et al. (2009)
<i>Nemania aenea</i> var. <i>aenea</i>	KC477240	ATCC 60818	Czech Republic		This study
<i>Nemania pouzarii</i>	KC477228	ATCC 2612	Hawaii		This study
<i>Nemania serpens</i>	FN428829	CBS 533.72	United Kingdom		Stadler et al. (2010b)
<i>Neurospora crassa</i>	M13906	FGSC 987	USA		Chambers et al. (1986)
<i>Pestalospaeria elaeidis</i>	AF009815	IMI 061175			Jaklitsch and Voglmayr (2012)
<i>Pestalotiopsis jester</i>	AF377282				Jaklitsch and Voglmayr (2012)
<i>Phylacia bomba</i>	KC477238	(GYJF12009)	French Guiana		This study
<i>Pseudomassaria chondrospora</i>	JF440981				Jaklitsch and Voglmayr (2012)
<i>Pseudomassaria fallax</i>	JF440983				Jaklitsch and Voglmayr (2012)
<i>Pseudomassaria sepincoliformis</i>	JF440984				Jaklitsch and Voglmayr (2012)

(Continued)

Table 2. (Continued).

Species	GB acc no.	Strain no	Origin	Status	Reference
<i>Rhopalostroma angolense</i>	FN821965	CBS 126414	Ivory Coast		Stadler et al. (2010b)
<i>Rosellinia bunodes</i>	KC477230	CBS 347.36	Bahamas		This study
<i>Rosellinia corticium</i>	KC477236	MUCL 51693	France		This study
<i>Rosellinia pepo</i>	KC477231	CBS 350.36	Trinidad and Tobago		This study
<i>Rostrohypoxylon terebratum</i>	DQ631943	CBS 119137	Thailand	Ex-type strain	Fournier et al. (2010), originally sequenced by Tang et al. (2009)
<i>Ruwenzoria pseudoannulata</i>	GU053568	MUCL 51394	D.R. Congo	Ex-type strain	Stadler et al. (2010b)
<i>Truncatella angustata</i>	AF405306				Jaklitsch and Voglmayr (2012)
<i>Xylaria acuta</i>	AF163026	ATCC 56487	USA		Fournier et al. (2011); originally sequenced by Lee et al. (2000)
<i>Xylaria apiculata</i>	AF163027	CBS 356.81	Colombia		Fournier et al. (2011); originally sequenced by Lee et al. (2000)
<i>Xylaria arbuscula</i>	FN689807	MUCL 52665	Germany		Fournier et al. (2011)
<i>Xylaria carpophila</i>	KC477235	CBS 331.70	United Kingdom		This study
<i>Xylaria castorea</i>	AF163030	ATCC 76020	New Zealand		Peršoh et al. (2009); originally sequenced by Lee et al. (2000)
<i>Xylaria cinerea</i>	FN689799	MUCL 51696	France	Ex-paratype strain	Fournier et al. (2011)
<i>Xylaria cinerea</i>	FN689805	MUCL 51825	Spain, Canary Islands	Ex-paratype strain	Fournier et al. (2011)
<i>Xylaria cornu-damae</i>	AF163031	CBS 724.69	Canada		Fournier et al. (2011); originally sequenced by Lee et al. (2000)
<i>Xylaria cubensis</i> anamorph (<i>Xylocoremium</i> sp.)	AM749929	CBS 117122	Panama		Bitzer et al. (2008)
<i>Xylaria enteroleuca</i>	AF163033	CBS 651.89	USA, Hawaii		Fournier et al. (2011); originally sequenced by Lee et al. (2000)
<i>Xylaria fioriana</i>	AF163034	CBS 486.61	South Africa		Fournier et al. (2011); originally sequenced by Lee et al. (2000)
<i>Xylaria hypoxylon</i>	AM993138	CBS 121680	Germany		Persoh et al. (2009)
<i>Xylaria hypoxylon</i>	AM993141	CBS 122620	Sweden		Persoh et al. (2009)
<i>Xylaria karsticola</i>	FN689802	MUCL 51605	France	Ex-type strain	Fournier et al. (2011)
<i>Xylaria liquidambaris</i>	AY909021	ATCC 42766	USA		Pelaéz et al. (2008)
<i>Xylaria longiana</i>	AF201711	ATCC 42768	USA		Persoh et al. (2009); original sequence from GenBank unpublished but verified by us. Wrongly assigned to <i>Xylaria hypoxylon</i> in many phylogenetic studies
<i>Xylaria longipes</i>	AY909015	CBS 580.88	Germany		Pelaéz et al. (2008); Fournier et al. (2011)
<i>Xylaria mesenterica</i>	AM900592	MUCL 49332	Panama		Stadler et al. (2008)
<i>Xylaria polymorpha</i>	FN689809	MUCL 49904	France		Fournier et al. (2011)
<i>Xylaria vasconica</i>	FN689804	MUCL 51705	France	Ex-type strain	Fournier et al. (2011)

Experimental

No extensive experimental data were obtained for this article. The images in Figures 1–3 and the phylogenetic tree in Figure 4 were obtained in a similar manner as described in Fournier et al. (2011) and Stadler et al. (Forthcoming 2013), preferentially using vouchers that

have been identified by experts and used in previous studies. Information on all investigated vouchers is compiled in Table 2. The most likely molecular phylogenetic tree was reconstructed using RAxML v7.0.3 (Stamatakis 2006), as implemented in ARB (Ludwig et al. 2004). The program was also used to test the robustness of the tree topology by calculating 500 bootstrap replicates. Default parameters

and the GTRCAT approximation of nucleotide substitution were applied for both analyses, with all free model parameters having been estimated by RAxML.

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Notes

1. <http://www.indexfungorum.org>
2. <http://www.mycobank.org>
3. Part of the type material of *X. piriformis* has been encountered in 2007 in the herbarium B (Berlin) by M.S. and Harry Sipman, but it had been soaked in alcohol for over 100 years and is now highly depauperate. A duplicate extant at S represents a fragmentary, immature stroma. None of the specimens yielded DNA suitable for PCR.
4. A type specimen of *N. ochraceum* is present in the herbarium B, fide a list published by Jülich W (1974) Liste der im mykologischen Herbar von C.G.T. Preuss († 1855) vorhandenen Arten, Willdenowia 7: 261–332, but has apparently never been re-studied.

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