The application of the name *Xylaria hypoxylon*, based on *Clavaria hypoxylon* of Linnaeus *

Marc Stadler1, David L. Hawksworth2, and Jacques Fournier3

Helmholtz Centre for Infection Research, Department Microbial Drugs, Inhoffenstrasse 7, 38124 Braunschweig, Germany.
2Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense de Madrid, Plaza Ramón y Cajal, Madrid 28040, Spain; Department of Life Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK; and Mycology Section, Royal Botanic Gardens, Kew, Surrey TW9 3DS, UK; corresponding author e-mail: d.hawksworth@nhm.ac.uk
3Las Muros, 09420 Rimont, France

Abstract: Although *Xylaria hypoxylon* is one of the most familiar fungi of temperate regions, the basionym of the name, *Clavaria hypoxylon* of Linnaeus, has remained untYPified. Here we assess the original five elements included in the 1753 protologue; no candidate specimen was located but two illustrations Linnaeus cited were considered, one a mixture of species and the other fanciful. As the name is sanctioned, following clarifications in the Melbourne Code, elements cited by Fries when the name was sanctioned in 1823 are also candidates for lectotypification. In addition to various illustrations, Fries cites two exsiccatae, and one from his own Scleromycetes Suicae distributed in 1821 is designated as lectotype for Linnaeus' name here. In view of the complexity of the group as revealed by molecular systematic work, and the poor state of the Fries material, we also designate a sequenced epitype from Sweden. We stress the importance of examining fungi in the complex in the sexual state, as those that are asexual can be difficult to identify conclusively. Figures of the original protologues and the most pertinent illustrations and specimens are provided, along with a detailed description and illustrations based on recent collections.

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INTRODUCTION

*Xylaria hypoxylon*, the “candle-snuff” fungus, is one of the most familiar fungi found on decaying fallen wood in temperate regions, but critical molecular and morphological investigations have revealed that this is a species complex (Peršoh et al. 2009, Fournier et al. 2011). These authors have recently attempted to establish a polyphasic taxonomy, based on extensive morphological studies and including molecular phylogenetic data. A concurrent molecular phylogenetic study by Hsieh et al. (2010) using housekeeping genes is also pertinent, since material originating from Belgium that was included when the name was introduced by Linnaeus, and also those included in the sanctioning work of Fries (1823) before proceeding to designate a name-bearing type.

ELEMENTS INCLUDED BY LINNAEUS (1753)

Linnaeus (1753: 1182; Fig. 1), somewhat surprisingly according to current concepts, gave the habitat of *Clavaria hypoxylon* as “in Cellis, navibus, allisque nunquam sole illustratis”, i.e. in the hold of a ship, never illustrated on soil; we suspect he wished to emphasise that it did not grow on the ground. There is one sheet with this name in LINN (sheet 1286.3; Fig. 2), and it bears a single 1-branched stroma in which no perithecia were evident. The specimen was annotated as *Xylaria hypoxylon* by George Massee, but, as is not localized and lacks any indication of date, it cannot be confirmed as original material used by Linnaeus when introducing the name. Linnaeus did, however, refer to five earlier works in his protologue, the last three as belonging to “β.”; a notation indicating the rank of variety (Stearn 1957: 90) but to which he did not give an infraspecific name in this case.

1) “Clavaria ramoso-cornuta compressa. Fl. suec. 1105.” Linnaeus (1745: 385) gave the habitat as “in nave Stockholmiæ”, i.e. in busy Stockholm, and cited two earlier...
works, Brückmann (1725), and “Fungus cornu dorcatis facie. Ephem. nat. cur. dec. 1. ann. 4. p. 195.” discussed respectively under (4) and (5) below.

(2) “Fungus ramosus niger compressus parvus. Raj. Angl. 3. p. 15.”

This refers to the third edition of Ray’s Synopsis (Ray 1724: 15), which was actually prepared by Dillenius (Stearn 1973). Dillenius cites the phrase name from the second edition (Ray 1696: 16), and gives a very full description and discussion and mentions material of Sherard, Richardson, and Doody (in an Appendix, see below). Ray (1696: 16) notes that the apices can have a white powder, and refers to a specimen “D. Sherard”. Sheet 23 of the Sherard Herbarium in OXF has a label in Dillenius’ hand with a reference to the page number in the third edition (Fig. 3). It has fourteen stromata, and we prepared a slide from one which seemed most likely to have perithecia, the sixth from the left on the second row, but no spores were found. The label written by Dillenius, however, must have been prepared after 1724 as it also has a reference to Micheli (1729: 104, tab. 55). Some at least of the stromata must, nevertheless, have been collected earlier as a second label in a different hand on the same sheet reads “Fungus lignosus minor, dentatus, cinereus. Dr Richardson March 1720/1”; it does not give any hint as to the locality. Richardson was a Yorkshire botanist.

Doody (in Ray 1696: 333), in using the name “Fungus niger subularris, apicibus albidis”, also draws attention to the apical white covering of conidia; he mentions a single collection sent to him by Charles Du Bois (“Carolus du-Bois”) and collected from his garden in Mitcham (now part of south London); according to Dandy (1958: 128), Du Bois’ garden was large and his main herbarium is in OXF, with some specimens in the Sloane Herbarium in BM. In the first edition, Ray (1690: 10) gives it as “Fungus ramosus niger compressus parvus apicibus albidus, J.B.? cujus meminit l. 40. c. 40” with the English name “Black-horned Wood-Mushrome”, and does not mention any localities or collectors. There is, however, a specimen from the “Hortus Cliffortianus” herbarium in K (K(M)191288) with the identical phrase name to that used by Ray (1690) and with “Ray” as the sole authority but with no literature reference or further information. G. Clifford evidently met with Linnaeus and Ehret (see also below) in Leiden in 1736 (Stearn 1957: 44) and Linnaeus (1738) published on his collections and specimens growing in his garden in Hartecamp in The Netherlands. However, we did not find any evidence that Linnaeus ever saw this material, which is one of three now referable to X. hypoxylon from “Hortus Cliffortianus” in K; the others are K(M) 191289 (collected by Clifford with a reference to Micheli 1729) and K(M) 191290 (as “Hypoxylon”, with a reference to Ray 1724). Only nine fungi were treated in Linnaeus (1738), none of which relate to the species we now call Xylaria hypoxylon, so those three historic collections are not pertinent to the typification of the Linnean name.

The “J.B.” in Ray (1690, 1696, 1724) is a somewhat cryptic reference to species entry no. 40 in the 40th fascicle of Bauhin et al. (1651: 838) of “Fungi ramosi argentei” but with doubt as to whether that was the same fungus, is
expressed by the question-mark in all three editions. There is no accompanying illustration in Bauhin's work, and it has to be discounted for the purposes of typification on that basis as well as the expression of doubt.

Also pertinent to the application of the phrase name used in Ray (1724) is a manuscript thought to date from about 1700 entitled “Fungi Anglici depicti ad ferisien Synopsis Stirpium Britannice J. Raji Edit. 3” and preserved as “MS Sherard 209” in OXF. It comprises paintings of fungi collected to illustrate Ray’s Synopsis, of which two are of Xylaria hypoxylon: Figs 75 (unlocalized) and 262 (from “Tuttenham Wood”; “Tuttenham” could not be located as a modern place-name, but this is a variant spelling of Tottenham, a district in north London.

(3) “Agaricus ramosus cornu rangiferi referens. Mich. Ehret. tab.”

The attribution “Mich. Ehret. tab.” would appear to be a reference to illustrations in a work of either Micheli or Ehret. We could not locate this name in Micheli (1729: 104), where he uses the descriptive phrase “Lichen Agaricus, nigricans, lingo adnacens, pereumque multifidus, & compressus, ima parte villösus, summa vero glaber, albidus, & pulvenulentus Tab. 15. fig. 55” for what is clearly the species of concern as:

(a) he cites Ray (1724: 15) amongst numerous synonyms,
and (b) the illustration indicated shows white horn-like apices of the stromata with perithecia in the lower parts.

According to Lindau & Sydow (1905: 406), however, there is an apparently separately published undated and unlocalized work by Georg D. Ehret (1708–1770) with the title Agaricus ramosus cornu rangiferi referens Miller. We are not alone in experiencing difficulty in interpreting this attribution, as in an appendix to a reprint of Species Plantarum, Heller (1958: 22) states “I can discover no source for the name referred to Mich. Ehret. tab.” This work could not be located in Linnaeus’ own library now preserved by the Linnean Society in London (LINN), but with the assistance of Andreae Hart (BM) we found that there was an original painting by Ehret, with the accession date c. 1744, with this title in the collections of the Welcome Library in London (catalogue no. 18635i; Fig. 4). The hand-written text reads:

“This plant grew from a trunk of an Elm, which was fixed in a dark cellar belonging to Mr. William Winckles a smith in St. James Hay Market. The first appearance of the plant was in the middle of June 1744, and the whole growth was performed in less than three weeks time, the parts of the plant were white at their first vegetation, but soon changed to a
dark brown colour, except the large heads which continued of a whitish colour, having in each a large dark umbone; these parts were porous on their underside.”

This rather fanciful painting is thus original material cited by Linnaeus. Ehret is well-known for preparing an illustration of Linnaeus’ sexual system for plants published first in 1735, and also some plates for the Hortus Cliffortianus (Linnaeus 1738). Ehret could not have showed it to Linnaeus personally when the two met in Leiden in 1736 (Stearn 1957: 44, Stafleu 1971: 122) in view of the 1744 date given in the text on the plate, and we could not ascertain how Linnaeus came by this citation.

(4) “Hypoxylon digitatum. Bruck. monogr.”
This is a separately printed monograph by Brückmann (1725) devoted to “Fungo hypoxilo digitato” with two plates. He evidently recognized that there was more than a single species involved, as the first plate has the legend “Fungus hypoxylon digitatos”, and the second “Fungos Hypoxylon Mentzelii”. The first plate illustrates eight stromata, recalling rather overmature stromata of Xylaria hypoxylon, Fig. VIII being most representative of current concepts, while the second has three stromata, of which the lower (“Fig. 3”) strongly resembles X. longipes.

(5) “Fungus cornu dorcadis facie. E. N. C. dec. 1. ann. 4. p. 195.”
This is a reference to Breyne (1676), who does not provide any illustration but describes a dichotomously branched fungus which was white (“candens”) and occurred on twigs of pear and trunks of plum in Amsterdam in 1661.

ELEMENTS INCLUDED BY FRIES (1823)

The Linnean binominal had sanctioned status under the Code as Fries (1823: 327; Fig. 5) adopted the name Sphaeria hypoxylon (L.) Pers. 1796. Fries recognized three infraspecific taxa, of which the first is pertinent here. The literature on such a common fungus had grown considerably since the time of Linnaeus, and Fries cites 18 works, including many references to plates and also to several exsiccatae, herbals, and 17th and 18th century works not mentioned by Linnaeus. These were investigated by Pfister (2008) who found that the earliest with an illustration was that of Micheli (1729). Fries’s list does, however, include several works that were previously cited by Linnaeus, including those by Breyne (1676), Micheli (1729), and Linnaeus (1745), but strangely not that of Linnaeus (1753). It appears that Fries was selective in the works he chose to cite, perhaps to avoid an inordinately long entry. Fries also referred to two sets of exsiccatae specimens: his own Scleromycetes Suecici no. 181 distributed in 1821, and Ehrhart’s, Plantae Cryptogamae Linnaeae no. 150 of 1789; we were able to locate examples of both these exsiccatae (see below).

TYPIFICATION

As more than a single element was cited by Linnaeus (1753) when introducing the name Clavaria hypoxylon, there is no holotype and a lectotype needs to be selected to fix the application of the name. Prior to the Melbourne International Botanical Congress of 2011, there was a lack of clarity regarding how lectotypifications of sanctioned names should be made. This situation is resolved in Art. 9.10 of the Melbourne Code (McNeill et al. 2012), which now rules that the type of a sanctioned specific or infraspecific taxon name “may be selected from among the elements associated with the name in the protologue and/or the sanctioning treatment”. The elements constitute specimens or illustrations eligible as types because they were studied or cited by the authors.

Linnaeus (1753) did not refer to any particular numbered plates, but he did mention two works under “β.” which included them: Brückmann (1725) and the enigmatic “Mich. Ehret. tab.”. Jarvis (2007: 424) cites the Brückmann work as “original material” and details the two plates, which, as noted above, represent at least two different species of Xylaria. As Linnaeus did not specify particular plates in either Brückmann (1725) or Micheli (1729) it is unclear which he regarded as reflecting his concept in their works, but the fanciful Ehret plate was specifically cited.

Potentially pertinent, however, could have been the prominent reference to Ray (1724). Linnaeus visited Dillenius in Oxford for eight days in August 1736 (Reveal et al. 1987), and there is evidence that he looked at specimens there.
Typification of *Xylaria hypoxylon*

ARTICLE

61

volume 5 · no. 1

(Reveal 1986). Reveal (*in litt.*) also informs me that there are some errors in page numbers in Linnaeus (1753) that match errors on sheets in OXF. As Linnaeus always had trouble with algae and fungi, lichenized and otherwise, it seems inconceivable to us that he would not have consulted the actual author of Ray (1724), Dillenius, and that they discussed specimens together. The generally adopted view, however, is that Linnaeus did not study any specimens in OXF personally (Jörgensen *et al.* 1994), and these authors are of course quite correct in asserting that Linnaeus would have used the plates in Dillenius (1742) when preparing *Species Plantarum*, as the Dillenian *Historia Muscorum* reference collection would not have been in existence in its present form for him to examine in 1736. The most credible reality is that Linnaeus examined some, as Reveal (1986) showed. The conundrum is to know which. In the case of *Clavaria hypoxylon*, however, as Linnaeus (1745) did not list the Ray name under *Clavaria ramoso-cornuta* nine years later, we suspect that he had not personally studied sheet 23 in the Sherard herbarium.

In the case of the sanctioning work, in addition to various illustrations, Fries (1823) also cites two specimens distributed in two exsiccatae (see above). We have located a copy of Ehrhart, *Plantae Cryptogamae Linnaeae* no. 150 (1789, as “*Clavaria hypoxylon*”) in UPS, which is a rather scrappy collection with two stromata collected in Hannover (Fig. 6). There are four copies of Fries, *Scleromycetes Suecici* no. 181 (1821, as “*Sphaeria (Cordyceps) hypoxylon*”) in K (K (M) 191230, 191231, 191233, and 191239), all of which have several stromata. There is a bound example of this exsiccatum in UPS, however, which has this number but the specimen is sadly in an extremely poor state and has lost large sections of the black surface tissues to reveal the internal white supporting tissues. There is also a Fries collection of this fungus from Femsjö, but that is undated so could have been collected before or after 1823. As Fries gives no date, that specimen is not a candidate for lectotypification.

As specimens are preferable to illustrations as lectotypes, and material cited in sanctioning works can be used to typify sanctioned names, we therefore decided to select one of the examples of Fries’ exsiccatum as lectotype of the sanctioned Linnean name below as now permitted under Art. 9.10 (Fig. 7). We selected one of the examples in K as that in UPS was in such a poor condition, and as, being in a bound volume, could not be sent out on loan. As the designated lectotype in K did not contain ascospores, and there was too little to attempt DNA extractions, we further designate a sequenced sporing specimen from Sweden as epitype below. We preferred the Fries exsiccatum over that of Ehrhart as that is represented in very few collections today, while there are duplicates of that of Fries in different collections around the world which would become isoelectotypes (see below).

NOMENCLATURE

*Xylaria hypoxylon* (L.) Grev., *Fl. Edin.*: 355 (1824).

Basionym: *Clavaria hypoxylon* L., *Sp. Plant.* 2: 1182 (1753).

Fr., *Syst. mycol.* 2: 327 (1823), as “*Sphaeria Hypoxylon*.”

Synonyms: *Sphaeria hypoxylon* (L.) Pers., *Observ. mycol.* 1: 20 (1796).

*Sphaeria hypoxylon* (L.) Pers., *Observ. mycol.* 1: 20 (1796).

Type: *Sweden*: sine loc., E. M. Fries [Scler. Suec. No. 181, sub “*Sphaeria (Cordyceps) Hypoxylon*”] (K(M) 191239 – lectotype designated here, MycoBank MBT177727, Fig. 7; – isoelectotypes in B, BPI, C, E, FH, MSTR, PC, S and UPS fide Pfister 1985 and Stafleu & Cowan 1976); *Sweden*: Uppland: Stockholm, Vällingby, Grimsta Nature Reserve near Lake Mälaren, on *Sorbus aucuparia*, 21 Oct. 2007, A.-L. & A. Anderberg G07-1 (S-F72430 – epitype designated here, MycoBank MBT177728, Fig. 8).

Ex-epitype culture: STMA 07069, deposited in CBS 122620.

GenBank Acc. nos of ITS sequences: AM993141, AM993142, and AM993144.
Description: Stromata extremely variable in size and shape, 12–85 (–115) mm tall, with fertile parts 10–45 mm high × 2–5 (–15) mm broad, ranging from cylindrical to narrowly fusiform or fan-shaped, terete to flattened, simple to branched from the base, from the middle or at top, nearly sessile or arising from long rooting stipes, always with flattened to mucronate sterile apices; stromata of different shape and branching pattern are frequently mixed in a same colony; surface with a long persistent peeling outer layer that is whitish at immature state, turning gradually silvery grey and eventually vanishing, finely longitudinally furrowed delimiting narrow strips, roughened with prominent ostiolar papillae, at times with circumferential wrinkles isolating groups of perithecia, especially on small fusiform stromata, perithecial contours most often inconspicuous in well-developed stromata; outer crust 35–50 µm thick, leathery, black. Interior solid, homogeneous and cheesy to slightly fibrous, white to cream-coloured, with a slightly darker core in aged specimens. The stipes 2–40 (–65) mm high × 1–3 mm broad, often ill-defined, cylindrical to strap-like, longitudinally puckered, black, with a hairy-tomentose broadened base, smooth to downy or hairy-tomentose above; tomentinually black to dark purplish brown, composed of dark brown, thick-walled, remotely septate hyphae 3.5–4 µm broad. Perithecia subglobose, 0.4–0.7 mm diam, immersed to slightly exposed. Ostioles raised-discoid, 160–280 µm diam, grey brown to black, with a low conical papilla at the centre.

Asexual stromata 10–55 mm high × 1–2 mm broad, cylindrical, the apex either tapered or flattened and branched, white, powdery with conidia, the base broadened and tomentose, black, furrowed. Conidiogenous structures geniculosporium-like, with conidiogenous cells pallisadic, producing conidia holoblastically in sympodial fashion; conidia narrowly fusiform-clavate, 8.5–12 × 3.5–4 µm, hyaline, smooth.

Asci unitunicate in structure, (6–)8-spored, cylindrical, long-stipitate, 140–220 µm total length, the spore-bearing parts 70–90 × 6–8 µm, the stipes 70–140 µm long, with apical apparatus tubular with slightly flared apex, 2.5–3.5 µm high × 2 µm broad, bluing in Melzer’s reagent. Paraphyses sparse, hypha-like, hyaline, septate, 1.5–2 µm broad. Ascospores (9–)9.5–12.5 (–13.5) × (4–)4.5–5.5 (–6) µm; Q = (1.9–)2.0–2.5 (–2.9); n = 196 (Me = 11 × 4.9 µm ; Qe = 2.25), uniseriate overlapping in the ascus, ellipsoid-inequilateral with narrowly to broadly rounded ends, medium brown, smooth, with a fugacious cellular appendage usually disappearing at maturity, containing two large guttules, with a very conspicuous straight, rarely slightly sinuous germ slit 1/2–4/5 spore-length on the flattened side. Atypical ascospores with acute ends, slightly oblique or sinuous germ slits located next to one end or on the convex side can be encountered in some collections.

Habitat and distribution: on deciduous dead wood, often on stumps or woody material buried in the soil, always in humid
Fig. 9. Illustration of salient morphological features of the stromata of Xylaria hypoxylon, based on specimens collected in France from the collection of J. Fournier: A–C, F, H, I: JF 04258; D, E: JF 05066; G: JF 04039. A–E. Mature stromata at sexual state (except two in A upper row with white apices). G. Stromata at the asexual stage. F, I. Stromatal surface of immature stromata showing raised-discoid ostioles and white-striped peeling outer layer. H. Stroma in longitudinal section showing perithecia lying beneath the thin black crust. Bars: A, C–E = 1 cm; B, G = 5 mm; F = 1 mm; H–I = 0.5 mm.
Fig. 10. Microscopic characters of Xylaria hypoxylon (JF 04258). A. Immature and mature asci in dilute chlorazol black. B–C. Apical apparati of immature (B) and mature (C) asci in Melzer’s reagent. D. Ascospores in water showing ventral germ slits. E. (CBS 121679). Culture on OA. F–H. Ascospores in water, showing variations in germ slit morphology. I–J. Conidiogenous cells (I) and conidia (J) from a stroma at the asexual stage (in 1% SDS). Bars: E = 1 cm; A = 20 µm; D, I–J = 10 µm; B–C, F–H = 5 µm.
environments. Widely distributed in north temperate Europe from Norway to Spain and in western North America, from mountains to lowlands, possibly more widely distributed based on records from mountainous areas in Taiwan and the Canary Islands, but apparently not tropical. Occurrence in eastern North America remains to be verified, as the fungus frequently reported from there represents X. vasconica (see Fournier et al. 2011).

Notes: The epitype selected is one of several fresh specimens that were studied by Peršoh et al. (2009) from Sweden. Those even included material collected by N. Arnold from Småland Province, where both Linnaeus and E. M. Fries were born, and another was collected from Högla. While the stromata of the Högla specimen were scanty, the ascospores of the material from Femsjö showed an aberrant morphology, with almost citriform spores that are not normally encountered in X. hypoxylon. Otherwise, all specimens were in full agreement with respect to the morphology of the stromata and cultures, and we also obtained highly similar DNA sequences. Therefore, we decided to designate as epitype a specimen collected in the vicinity of Stockholm that showed the commonly encountered morphological features. Remarkably, three cultures obtained independently from cultures derived from the same perithecium of the epitype material gave three slightly different ITS sequences. This indicates that DNA sequencing will not always lead to 100 % reproducible results, and special care should be taken not to overestimate the value of molecular techniques for estimation of species numbers and diversity.

We have also illustrated the salient morphological features of this fungus based on three specimens collected from France that showed a greater morphological variability than the epitype (Figs 9–10). The collection data of these specimens are as follows:

(a) France: Ariège, Rimont, Las Muros, 460 m, on Fraxinus excelsior, 16 Dec. 2004, J. Fournier, JF 04258, CBS 121679 (Fig. 9 A–C, F,H–I and Fig. 10 A–J).
(b) France: Vendée, Vouvant, moss-covered dead wood, 28 Apr. 2005, A. Gminder, JF 05066 (Fig. 9 D–E).
(c) France: Ariège, Rimont, Las Muros, 460 m, on dead corticated branchlet, 22 Feb. 2004, J. Fournier, JF 04039 (Fig. 9 G).

A duplicate of JF-04258 is deposited in M (M-0125974), and the corresponding culture is maintained as CBS 121679 and MUCL 49353.

A major problem with this species is that it is almost always collected and illustrated at the asexual stage when the stromata have conspicuous conidigenous antler-like apices, which makes identifications and records often doubtful. We wish to emphasize the necessity of collecting sexual stage stromata when working with Xylariaceae as collections are often found to be immature. Indeed, in order to confidently determine X. hypoxylon in the absence of molecular sequence data, the characters of the sexual stage described and illustrated here need to be examined.

CONCLUSIONS

We trust that we have now fixed the precise application of the name Xylaria hypoxylon for future generations of mycologists. This process has, however, brought to the fore the difficulty in dealing with early fungal names, many of which represent the commonest species.

The elucidation of this 18th century fungal name required first the checking out of all the elements cited in the original protologue of Linnaeus (1753) to see if any could form a satisfactory lectotype, before proceeding to consider those referred to in the sanctioning work (Fries 1823). This process involved not only tracking down copies of several 17th century works, but detective work to decipher just what works were being referred to. This could not have been accomplished without the access we were able to obtain to personally examine rare books in various libraries in London, and the associated collections in London, Kew, and Uppsala. Further, it could not be achieved in a short time as examination of one work sometimes revealed another track to be followed; indeed, the investigations that are the basis of this paper extended over a period of six years.

Fixing the application of early fungal names is likely to be difficult to impossible for mycologists without relatively easy access to major libraries and collections, especially as some institutions are no longer allowed to send material from historic collections on loan so have to be visited personally. Further, and most worrying, is that such historical enquiries detract the time that mycologists have to devote to their primary task of understanding the world’s fungi. Even in the UK, one poll suggests that, on average, around 20 % of the time of a systematic “botanist” (including algologists and mycologists) is devoted to investigating such bibliographic and nomenclatural problems (Hawksworth 1992).

Mycologists are, however, fortunate in having the prospect of Protected Lists of names in which types may be listed and will thus achieve protection, when such lists are eventually approved by the appropriately mandated bodies, which are currently established by International Botanical Congresses at intervals of six years. The production of draft lists and their refinement will inevitably be a lengthy process, but clearly needs to be expedited. In the meantime, some suggestions for pragmatic approaches where there are problems over the availability of type material have been made (Hawksworth 2012).

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