The enigma of Link's *Sphaeria ericophila*: nomenclature, taxonomy, molecular phylogeny, and implications for the placement of *Metacapnodium*

David L. Hawksworth[1,2,3*], Carlos G. Boluda[4]

(1. *Comparative Plant and Fungal Biology*, *Royal Botanic Gardens*, *Kew*, *Surrey*, *TW9 3DS*, *UK*; 2. *Department of Life Sciences*, *The Natural History Museum*, *Cromwell Road*, *London SW7 5BD*, *UK*; 3. *Jilin Agricultural University*, *Changchun* 130118, *China*; 4. *Unité de Phylogénie et Génétique moléculaires*, *Conservatoire et Jardin botaniques*, *Geneva* 1292 *Chambésy*, *Switzerland*)

Abstract: The application of the sooty mould name *Sphaeria ericophila*, introduced by Link in 1809 for a sooty mould on *Erica arborea* in Iberia, is fixed by lecto- and epitypification following recent re-collections from Portugal and Spain. Morphologically the fungus is close to the type species of *Metacapnodium*, *M. juniperi*, and it was combined into that genus as *M. ericophilum* in 2013. Molecular sequence data of the ITS region from three samples showed the fungus to belong to *Eurotiomycetes* rather than *Dothideomycetes*, and to be closest to *Phaeomoniellales*/*Chaetothyriales*. These are the first sequences reported for *Metacapnodium* and reveal it as another example of a sooty mould being found to belong to *Chaetothyriales s. lat.* rather than *Capnodiales*. Nomenclatural issues are addressed as a consequence of the change in the starting point date for fungal nomenclature and the abandonment of the naming of different morphs of the same species that were introduced since Hughes investigated the application of Link's name in 1970. It is now confirmed that *Metacapnodium* requires protection over *Antennullaria*, of which *Sphaeria ericophila* is the type species. There is some evidence for host specialization because *M. ericophilum* appears not to grow on *Juniperus* growing amongst heavily infected *Erica arborea* in Spain. It also occurs on at least one other *Erica* species, namely *E. australis*, but there may be other species of the genus on other species of tree *Erica* spp. in the mountains of East Africa.

Key words: *Capnodiales*; *Chaetothyriales*; Hughes; *Metacapnodium ericophilum*; molecular phylogeny; nomenclature; *Phaeomoniellales*; typification

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Sphaeria ericophila 的命名、分类、分子系统发育和 *Metacapnodium* 属分类地位的意义

David L. Hawksworth[1,2,3*], Carlos G. Boluda[4]

(1. *Comparative Plant and Fungal Biology*, *Royal Botanic Gardens*, *Kew*, *Surrey*, *TW9 3DS*, *UK*; 2. *Department of Life Sciences*, *The Natural History Museum*, *Cromwell Road*, *London SW7 5BD*, *UK*; 3. *Jilin Agricultural University*, *Changchun* 130118, *China*; 4. *Unité de Phylogénie et Génétique moléculaires*, *Conservatoire et Jardin botaniques*, *Geneva* 1292 *Chambésy*, *Switzerland*)

Biography: David L. Hawksworth, Professor, Dr., CBE, main research field: ascomycete systematics (including lichenized fungi), E-mail: d.hawksworth@kew.org; Carlos G. Boluda obtained his PhD from the Universidad Complutense de Madrid in 2017 for work on the molecular systematics of alectorioid lichens, jointly supervised by DLH and Victor J. Rico, and is now a post-doctoral researcher at the Conservatoire et Jardin Botaniques in Geneva, Switzerland, e-mail: carlos. g. boluda@gail. com.

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* **Corresponding author**: David L. Hawksworth, E-mail: d. hawksworth@Kew.org

摘 要：1809 年，Link 在伊比利亚的高山欧石楠 *Erica arborea* 上发现了黑煤病(sooty mould)，经鉴定将其命名为 *Sphaeria ericophila*，最近有学者在葡萄牙和西班牙都再次采集到 *S. ericophila*，通过对其候选模式和附加模式的研究，发现该菌在形态上与 *Metacapnodium* 属的模式种 *M. juniperi* 最为接近，同时在 2013 年与 *M. ericophilum* 合并成同一个属。通过 ITS 测序得到 3 个样品的序列，结果表明该菌属于散囊菌纲 *Eurotiomycetes* 而非座囊菌纲 *Dothideomycetes*，并且最接近于褐球壳目 *Phaeomoniellales* /刺盾炱目 *Chaetothyriales*。本文报道了 *Metacapnodium* 的首条序列，并表明另一份黑煤病(sooty mould)样本不属于煤炱目 *Capnodiales*，而是属于刺盾炱目 *Chaetothyriales* s. lat.。自 Huges 在 1970 年研究 Link 的名称应用以来就引入了真菌命名法起始日期的变化，以及放弃了同一物种的不同形态的命名，从而解决了命名问题。如前文所述，现已证实 *Metacapnodium* 包含 *Antennullaria*，其中 *Sphoeria enicophila* 为模式物种。*M. ericophilum* 非专性寄生，在西班牙，它不仅在刺柏属 *Juniperus* 植物上寄生，也会严重感染高山欧石楠 *Erica arborea* 还可能感染其他欧石楠属植物，如 *E. australalis*，但在非洲东部山区的欧石楠属植物上可能还存在该属 *Metacapnodium* 的其他致病菌。

关键词：煤炱目；刺盾炱目；Hughes(人名)；*M. ericophilum*；分子系统发育；命名法；褐球壳目；模式

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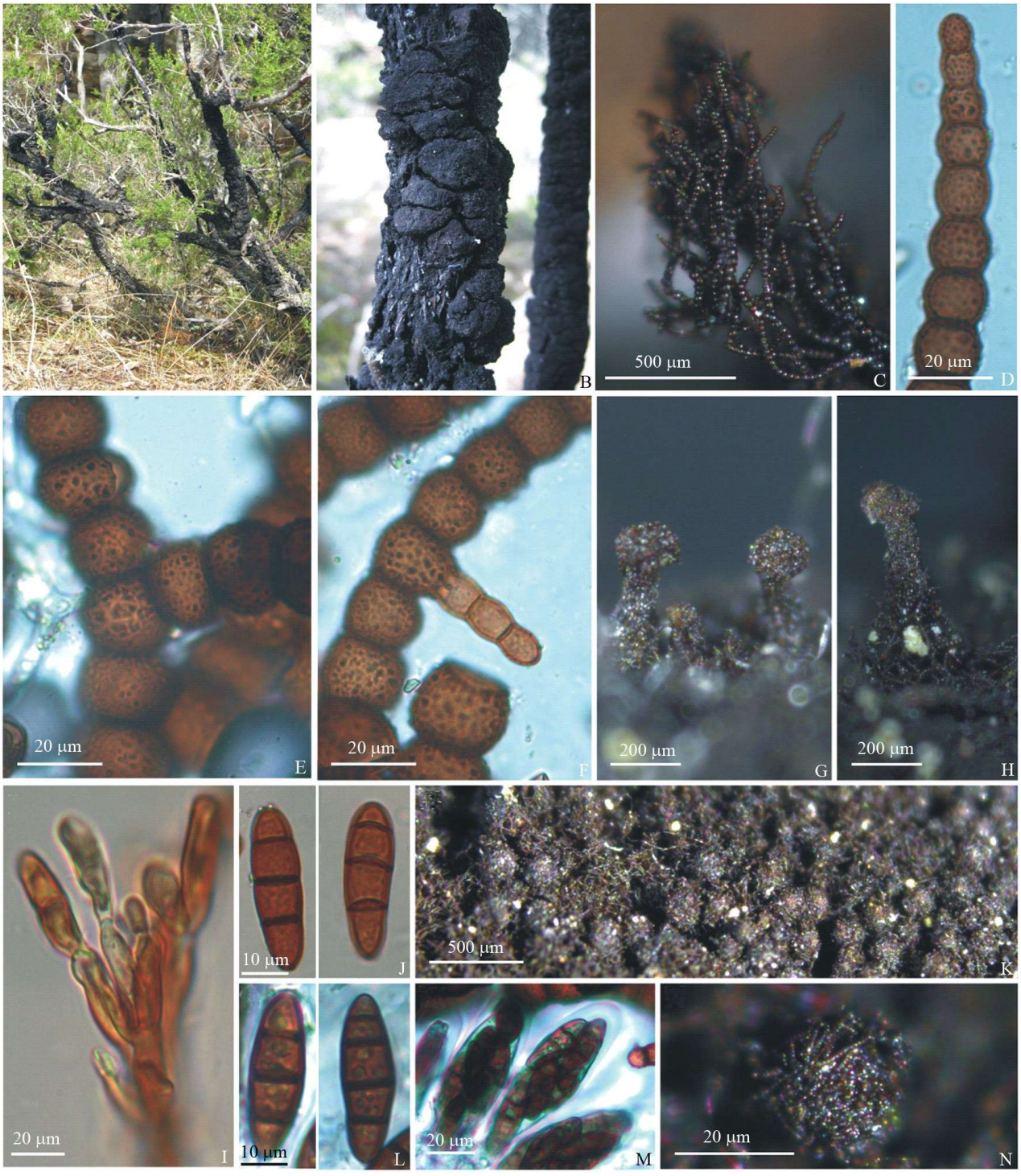
1 Introduction

Hughes (1970)[1] provided a detailed account of the nomenclatural history and applications of the name *Sphaeria ericophila*. The species name was introduced by Link (1809: 17) for a fungus we would now call a sooty mould that he discovered forming a dense black tomentum on bark of *Erica arborea* in the mountains of Portugal. Link placed the fungus under his new generic name *Antennaria* (*loc. cit.*: 16), a later homonym of the flowering plant genus *Antennaria* Gaertner 1791, but which nevertheless was conserved when Link's name was sanctioned[2]. Reichenbach (1828)[3] introduced the replacement generic name *Antennularia* to replace Link's *Antennaria*, which is therefore typified by *S. ericophila*. An alternative replacement generic name *Antennina* was also introduced by Fries (1849)[4] based on this same species name, which was superfluous (Art. 52.1).

A resolution of the identity of *Sphaeria ericophila* is important in the taxonomy of the sooty mould fungi because it is the type of *Antennularia* and could potentially provide an earlier name to compete with several other historical generic names typified by fungi known from a sexual or various asexual morphs. No original specimens of Link's fungus were located by Hughes (1970)[1], and none were subsequently discovered, but Hughes did find other sooty mould collections in fungaria made in the 19th century and on the same host in the Iberian Peninsula. He distinguished two fungi, a conidial morph he identified as *Capnocybe spongiosa* (Hoerl) S. Hughes 1966 that formed extensive thick and gross black growths, and the other perithecial and most probably an unidentified species of *Antennulariella* Woron. 1915 that formed growths only to 1 mm thick. Link's fungus almost certainly represented material of the *Capnocybe* morph, but in the absence of both original specimens studied by Link and modern collections, Hughes did not adopt the epithet "*ericophila*" but regarded it as a "nomen dubium", i.e. a name of uncertain application that should not be used. Hughes (1976)[5] subsequently re-affirmed his opinion, commenting that his conjecture was still that Link's name was based upon the asexual *C. spongiosa*.

In 2004, a few years after the first author (DLH) took up a position in the Universidad Complutense de Madrid, Hughes wrote to enquire whether he could search for such a fungus on *Erica arborea*. It was important to resolve and fix the application of Link's *Sphaeria ericophila* because of possible implications for generic nomenclature amongst the sooty moulds. I had actually encountered and

photographed this sooty mould in 2002, not knowing what it was, and it had also been intriguing mycologists Gerald F. Bills (then at Merck Pharmaceuticals in Madrid) and Ricardo Galan (at the University of Alcalά, Guadalajara, north of Madrid). Bills had tried to culture it and obtain DNA sequences but with no success. It grew abundantly in the La Pedriza de Manzanares UNESCO Biosphere Reserve near Manzanares el Real, just 5 km north-east of where he was then living at Mataelpino in the Sierra de Guadarrama in Central Spain (Fig. 1- A, B). Collections from La Pedriza were sent to Hughes in Ottawa in 2004 and on several subsequent occasions where he studied it microscopically and some DNA sequences were later obtained by Keith A. Seifert and T. J. Atkinson. Further collections from this same site and Portugal were sequenced independently by CGB.



A, B. *Metacapnodium ericophilum* forming lumpy black carbonaceous colonies on branches of *Erica arborea*; C. Mycelium; D. Actively growing hyphal apex; E. Branching by cell division; F. Branching by lateral growth; G-H. Conidiomata (capnocybe-like morph); I. Conidiophores producing conidia; J. Conidia; K. Subiculum surface covered by ascomata; L. Ascospores; M. Asci; N. A single ascoma

Fig. 1　*Metacapnodium ericophilum*

This contribution addresses the typification and application of Link's name in the light of changes in the *International Code of Nomenclature for algae, fungi, and plants* (ICN)[6], nine editions of which have appeared since the issue was studied in extraordinary detail by Hughes (1970)[1], who devoted 24 pages to exploring and documenting the case. We also provide new information on the phylogenetic placement of the genus *Metacapnodium* based on newly obtained DNA sequences from recent collections. A draft manuscript dealing with the nomenclatural aspects presented here was prepared by DLH and approved by Hughes in 2009, but never finalized for publication at that time, although the required new combination into *Metacapnodium* was made jointly in 2013[7].

2 Materials and methods

This investigation is based on fresh collections made by DLH or by the authors jointly from shrubs of *Erica arborea* and *E. australis* growing in the mountains of central Spain and north-eastern Portugal. Collection, locality, and fungarium details are given in the section on *Typification* below. Collections were examined macroscopically with a Nikon stereo-dissecting microscope with an eyepiece reticule at magnifications up to 80 ×. Microscopic examinations were carried out using hand-made sections and squash preparations in 10% potassium hydroxide and water using an Olympus BH-2 microscope equipped with Nomarski differential interference contrast optics and a drawing tube, enabling drawings to be made at 3 200 ×.

Three *Metacapnodium ericophilum* samples were sequenced, and allocated codes 5367 and 5368 from the same 2015 Sierra de Guadarrama collection, and 5369 from the Braganza area of Portugal. Clean fungal fragments were selected using a Nikon SMZ-1000 stereomicroscope (60 ×). DNA was extracted using the DNeasy Plant Mini Kit (Qiagen, Barcelona) with a slight modification to the manufacturer's instructions as detailed in Crespo et al. (2001)[8].

The nuclear internal transcribed spacer (ITS) rDNA was amplified with primers ITS1F[9] and ITS4[10]. Polymerase chain reaction (PCR) was as follows: a reaction mixture of 25 μL, containing 18 μL of sterile water, 2.5 μL of 10× buffer with 2 mmol/L $MgCl_2$, 0.5 μL dNTPs (10 mmol/L of each base), 1.25 μL of each primer at 10 μmol/L, 0.625 μL of DNA polymerase (1U/μL), and 5 μL of diluted 1/10 DNA template. Cycling conditions were 2 min at 94℃; 35 cycles of 30 s at 94℃; 30 s at 55℃; 2 min at 72℃; and a final extension of 5 min at 72℃. PCR products were checked and quantified on 1% agarose gel, and were cleaned using illustraTM ExoProStar (GE Healthcare, Little Chalfont, UK), according to the manufacturer's instructions. Sequencing was performed at the Unidad de Genómica (Parque Científico de Madrid).

In addition to the sequences we obtained, further sequences were recovered by Toni Atkinson and Keith Seifert in Ottawa from material from La Pedriza which DLH had sent to Hughes which they shared with us and we also incorporated into our analyses (DAOM 234182a), along with sequences of a different unnamed *Metacapnodium* species with dictyoseptate ascospores collected on *Vaccinium* sp. from Oregon (DAOM 240456).

BLAST[11] was used to search for the most similar ITS sequences to *Metacapnodium ericophilum* available on GenBank. Those sequences, as well as other from specimens representing all the related orders of *Eurotiomycetes*, were downloaded (Fig. 2). Sequence alignment was performed using MAFFT v. 7 (http://mafft.cbrc.jp/alignment/server/)[12] with the G-INS-i alignment algorithm, a "200PAM/K=2" scoring matrix, with an offset value of 0.1, and the remaining parameters set as default. Partitionfinder[13] was used to detect possible intra-locus substitution model variability, resulting in the splitting of the ITS region into ITS1, 5.8S, and ITS2. DNA substitution models for each locus partition were selected with jModeltest v. 2.0[14], using the Akaike information criterion (AIC)[15]. The best-fit model of evolution obtained was: ITS1=TPM2uf+G, 5.8S=TrNef+I, ITS2=HKY+G.

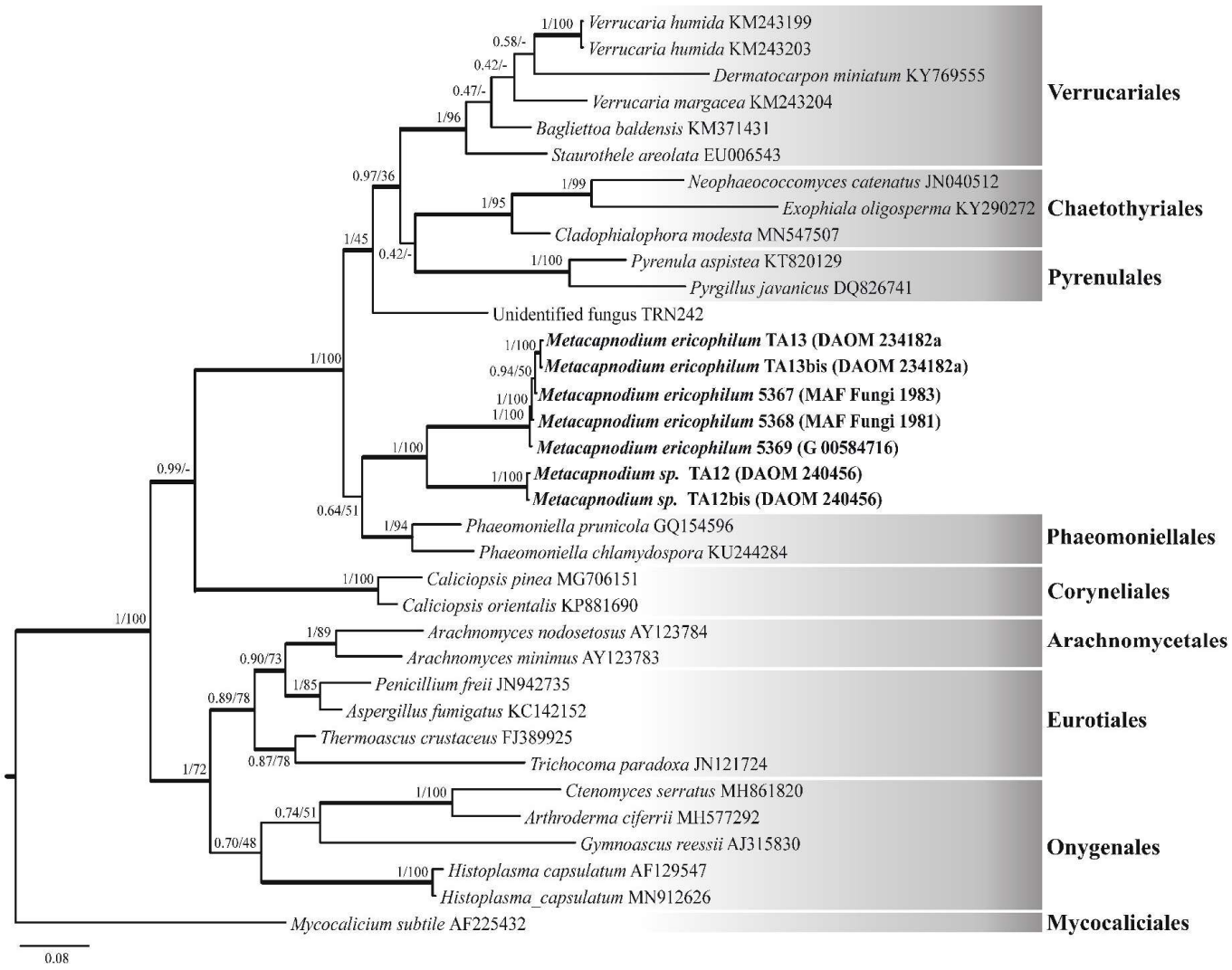


Fig. 2　Bayesian Markov chain Monte Carlo (B/MCMC) phylogenetic reconstruction using the nuITS locus with posterior probabilities and bootstrap analysis from Maximum Likelihood (ML) reconstruction shown at the nodes. Bold lines indicate well-supported clades (≥ 0.95 and ≥ 70%). GenBank accession numbers are shown after taxon names (except for the newly generated sequences) and orders to which they are referred are indicated at the right-hand side

Datasets were analysed using maximum likelihood (ML) and Bayesian (B/MCMCMC) approaches. For ML tree reconstruction, we used RAxML v. 8. 2. 10[16] implemented in CIPRES Science Gateway (https://www.phylo.org/)[17] with the GTRGAMMA model[16,18-19]. Support values were assessed using the "rapid bootstrapping" option with 1 000 replicates. For the Bayesian reconstruction, MrBayes v. 3.2.1[20] was used. Two simultaneous runs with 2 million generations each, starting with a random tree and employing 12 simultaneous chains, were executed. Every 100th tree was saved to a file. Preliminary analysis suggested an overestimation of branch lengths and to correct this we used the uniform compound Dirichlet prior brlenspr = unconstrained: gammadir (1,1,1,1)[21]. We plotted the log-likelihood scores of sample points against generations using Tracer v. 1.5[22] and determined that stationarity had been achieved when the log-likelihood values of the sample points reached an equilibrium and ESS values exceeded 200[23]. Posterior probabilities (PPs) were obtained from the 50% majority rule consensus of sampled trees after excluding the initial 25% as burn-in. The phylogenetic tree was drawn with FigTree v. 1.4[24] and edited with CorelDRAW v. 11(Fig. 2).

3　Typification

No original specimens of Link's fungus were located, but he did provide an illustration (Link

1809: tab. I Fig. 27 a–b[25]; Fig. 3). That figure comprises two elements: (a) moniliform chains of roughly spherical cells, one of which has a side branch, and which strongly resemble the hyphae that give rise to the *Capnophialophora* conidial morph of *Metacapnodium* species; and (b) a section of a stromatic structure with a crust containing "thecasque", the nature of which is obscure. However, "b" may well be of poorly seen separate asci, with included septate ascospores, which Link may have obtained in squash preparations but did not see in intact perithecia, and thus were shown dispersed in tissue. The interpretation of Link's figure is fundamental in considering the typification of *Sphaeria ericophila*, because under Art. 9.2 Note 2 (a) of the current *Code*[6], Link's illustration must be considered "original material" and the whole or part of it selected as lectotype for his name regardless of its quality. However, in such instances, the *Code* does now permit an epitype specimen or illustration to be designated to serve as an interpretive type under Art. 9.7 to fix the application of the name. We therefore: (a) formally select part "a" of Link's original illustration as lectotype because of the uncertainty over the interpretation of "b"; and (b) designate as epitype a well-developed recently made collection showing the sexual and asexual morphs and on the original host from the mountains of Central Spain and from which molecular sequence data were obtained and deposited in GenBank. The species was also collected twice by DLH in the mountains of north-eastern Portugal, but the sequenced specimen was from *Erica australis* rather than *E. arborea*, and the host of the unsequenced one from Portugal was not identified to species level. We prefer to use material on *E. arborea* for epitypification because that was the host reported by Link[25] and because there is some evidence of a degree of host specificity in *Metacapnodium* species (discussed below).

4 Nomenclature

Several fundamental changes in the provisions of the ICNafp for fungi subsequent to Hughes' investigation of this case in the 1970s[1,5], mean that some of the issues he strove to address can now be resolved. In addition to the possibility of designating epitypes (see above) introduced in 1993, and the starting point date for the nomenclature of "fungi caeteri" was moved back from 1821 to 1753 in 1981. Hence, there is no longer an issue over the date of valid publication of Link's names in 1809, most importantly, the independent naming of different morphs of the same species was abandoned in 2011. The latter change means that debates over whether the name *Sphaeria ericophila* should be typified by material of the *Capnophialophora* or *Capnocybe* asexual morph, or by material of the perithecial sexual morph of the species, are now no longer relevant.

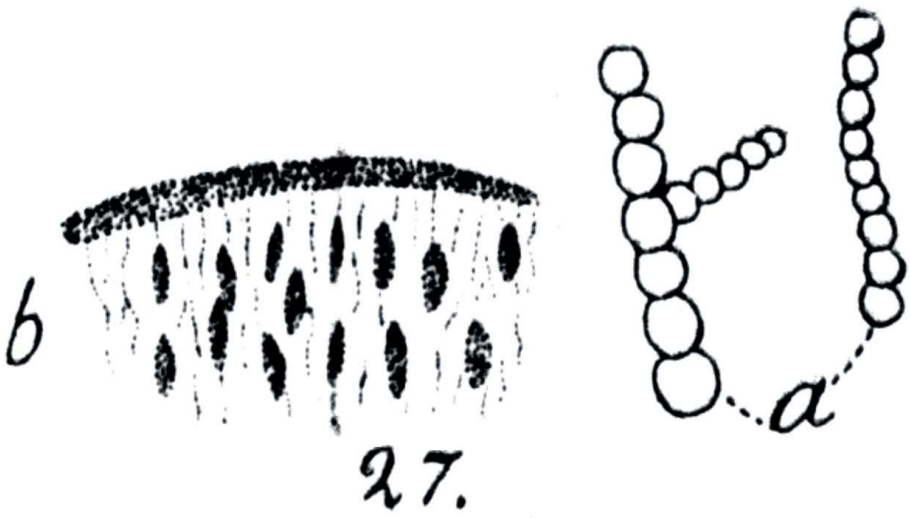


Fig. 3 The illustration of (Link 1809: tab. I Fig. 27 a–b). "a" is the element of the illustration designated here as lectotype for the name *Sphaeria ericophila*

Treating names proposed for different morphs as congeneric, however, meant that the name *Metacapnodium* Speg. 1918 would be a later synonym of *Antennularia* Reichenb. 1838. The former name is well established and in current use, because it is the type genus of the family *Metacapnodiaceae* S. Hughes & Corlett (Hughes 1972: 239[26]), Hawksworth & Hughes (in Hyde et al. 2013[7]), proposed that *Metacapnodium* [type species *M. juniperi* (Phill. & Plowr.) Speg. 2018] be either conserved or protected against *Antennularia* to avoid the latter name from being adopted. Rossman et al. (2016)[27] therefore proposed the protection of *Metacapnodium* over *Antennularia*, and recommended that it also be used in favour of the subsequently proposed generic names based on asexual type material: *Torulopsiella* Bender 1932, *Capnocybe* S. Hughes 1966, *Capnophialophora* Hughes 1966, *Capnobotrys* S. Hughes 1970, and *Capnosporium* S. Hughes 1976. The only authors to employ *Antennularia* in the most recent almost six decades were Müller & Arx (1962)[28], who misapplied the name to species of *Venturia* de Not. 1844 (non Sacc. 1882 nom. cons.), for which the name *Protoventuria* Berl. & Sacc. 1887 is now used. The latter genus is characterized by 1-septate ascospores, and the illustration Müller & Arx labelled as "*A. ericophila*" is clearly not the same species as that reported on here. Arx & Müller (1975)[29] went on to adopt both *Antennularia* and *Metacapnodium*, perpetuating this misunderstanding). A decision on the proposal to protect *Metacapnodium* is currently awaited from the Nomenclature Committee for Fungi. The genus currently includes 14 accepted species (http://www.indexfungorum.org/); a key to and descriptions of ten of these, based on both asexual and sexual characters, is provided by Sivanesan (1984) who also includes illustrations of six of those species.

Our suggestion is made notwithstanding the alternative taxonomic interpretation of Reynolds (1985)[30], who included *Metacapnodium* as a synonym of *Limacinia* Neger 1895. However, Hughes (1972, 1976)[5,26] had already regarded the application of *Limacinia* as uncertain and considered that it should be treated as a "nomen ambiguum". As suggested by Eriksson & Hawksworth (1987: 139)[31], a more appropriate interpretation of Neger's name would be to treat it as based on an *Euantennaria* Speg. 1918 species. This would reject Reynold's neotypification of the type species of *Limacinia* (*L. fernandeziana* Neger 1896) using material of a *Metacapnodium*. In order to settle this issue with a minimum of name changes, we therefore propose to add *Limacinia* to the list of names over which *Metacapnodium* is protected.

Metacapnodium ericophilum (Link) D. Hawksw. & S. Hughes, Fungal Diversity 63: 149 (2013).

Basionym: *Sphaeria ericophila* Link, Neues J. Bot. 3: 17 (1809); as "*Sphaeriam ericophilam*".

Synonym: *Antennaria ericophila* (Link) Link, in Willdenow, Sp. Plant., Edn 4 6 (1): 118 (1824), nom. sanct. (Fr., Syst. Mycol. 3: 230, 1832).

Type: Link, Neues J. Bot. 3: tab. 1 Fig. 27-a (1809 - lectotype designated here, IF558118); Spain: Comunidad de Madrid: Sierra de Guadarrama, Parque Regional de la Cuenca Alta del Manzanares, La Pedriza de Manzanares, west side of stream Arroyo de la Majadilla, on branches of *Erica arborea*, 40° 45.02′ N 3° 53.80′ W, alt. 988 m, 23 Sept. 2015, D.L. Hawksworth & C. G. Boluda [K(M) 255493] - epitype designated here, IF558119; MAF Fungi 1981 [GenBank MW248524 (CGB DNA extract 5368)], MAF-F Fungi 1982 [GenBank MW248523 (CGB DNA extract 5367)], MAF Fungi 1990, MA 23767-isoepitypes).

Notes: For further definite and probable synonyms see the list provided by Hughes (1970)[1] and Index Fungorum. It seems likely that *Hormiscum ericae* described by Unamuno (1930)[32] from material of *Erica umbellata* collected near San Román de los Caballeros in León in Spain is also an additional synonym; only an asexual morph was described and we could not locate the original material. However, two collections in MA on *E. arborea* from

La Pedriza del Manzanares were identified by Unamo in 1931 using this name (MA-Funhist 6247 and MA Funhist 24860). These confirm that his name is most likely to be an additional synonym, though we have not examined those ourselves. The type of Unamuno's name may be in H[33].

Description: Subicula black, superficial, forming cushions up to 3.5 × 2.0 cm, confluent, extending up to several decimetres, with a cracked appearance. *Hyphae* dark brown, septate, moniliform, tapering gradually from the 10th cell from the tip, branching anisotomic dichotomous, at right angles, later frequently forming acute angles, sometimes anastomosing; individual cells usually slightly broader than long, doliiform, 10-20×10-30 μm, with the younger distal cells as narrow as 3.5 μm, and sometimes longer than wide; cell walls thick, surface strongly veruculose.

Ascomata: only on well-developed colonies, subglobose, almost cleistothecium-like, superficial to partly immersed in the subiculum, scattered to dense, sometimes covering the entire surface, dark brown to black, obscured by hyphae, sphaerical, 130-250 × 130-250 μm; wall composed of rounded to polygonal cells 10 - 20 × 8 - 20 μm. *Asci* fasciculate, bitunicate, rounded and thickened at apices, 60 - 80 × 15 - 23 μm, 8-spored. *Ascospores* broadly fusiform, widest part at the middle of its length, dark brown, 3 (-4) septate, sometimes slightly constricted at the septa, smooth-walled, contents with 1 - 2 small to large guttulae in each cell, 20-35 × 6-11 μm.

Asexual morphs: of two types: (A) ["capnocybe"-morph]: *Conidiomata* present before and at the same time as the ascomata, generally scarce, only on cushion-like colonies, even in the smaller ones, synnema-like, originating superficially, with a stipe 400 - 630 × 50 - 130 μm, composed of cylindrical cells of 15 - 50 × 6 - 14 μm, firmly attached to the neighbouring cells, capitulum 130-200 × 180 - 200 μm. *Conidiophores* dichotomously branched, composed of paler, irregularly cylindrical cells 10-30 × 3-6 μm. *Conidia* narrowly oblong to fusiform, dark brown, symmetrical or slightly asymmetrical, (2-)3 septate, not or slightly constricted at the septa, 23-40 × 7-12 μm. (B) ["capnophialophora"-morph]: *Conidiogenous cells* sparse, arising directly from ascospores, also laterally from cells towards the tips of tapering hyphae, pale brown, subglobose, smooth-walled, 4-6 μm diam. below with paler extended collarettes of 2 - 3 × 4 μm. *Conidia* subglobose, almost hyaline, smooth-walled, *ca.* 1-2 μm diam.

Additional specimens examined: Portugal: Braganza: Terroso, in scrub on north side of road, on branches of *Erica australis*, 41°52.63′ N 6°51.28′ W, alt. 859 m, 13 Mar. 2005, D. L. Hawksworth [CGB DNA 5369] (K(M) 255492, G 00584716; GenBank MW248525); Sierra de Montesinho Natural Park, near Barragem de Serra Serrado, in scrub on branches of *Erica* sp., 41°57.71′ N 6°46.45′ W, alt. 1 163 m, 8 Nov. 2006, D. L. Hawksworth [K(M) 255504]; Parque Natural de Peneda-Gerés, cerca del pueblo de Peneda, sendero cercano al Partano de Meadinha, 957 m, 41°58′39.42″N 8°13′44.76″W, sobre *Erica arborea*, 1 Sep. 2014, *C.G. Boluda* [CGB DNA 5376](MAF Fungi 1983), [CGB DNA 5366] (MAF Fungi 1984). - Spain: Comunidad de Madrid: Sierra de Guadarrama, Parque Regional de la Cuenca Alta del Manzanares, La Pedriza de Manzanares, on *Erica arborea*, 22 Nov. 2004, D. L. Hawksworth (DAOM 234182a); *loc. cit.*, west side of stream Arroyo de la Majadilla, on branches of *Erica arborea*, 40°45.02′ N 3°53.80′ W, alt. 988 m, 7 Apr. 2005, D. L. Hawksworth [K(M) 255505]; La Puebla de la Sierra, melojar a la entrada del pueblo desde Robledillo de la Jara, río de la Puebla, 1 096 m, 40°59′52.7″N 3°26′24.5″W, 24 May 2016, Z. Ferencova, V.J. Rico, C. Ruibal & J.C. Zamora (MAF Fungi 1985, 1986).

5 Taxonomy and phylogeny

No previously published sequence data were available for *M. juniperi* or other *Metacapnodium* species, so to be sure that we were not sequencing con-

taminants, two sequences were made from the epitype material and a third from the Portuguese collection; sequences differed only by a single mutation and clearly belong to the same taxon, grouped together with a 1/100 posterior probability/bootstrap support. Microscopic observations did not reveal any other fungal hyphae apart from those of *Metacapnodium*, and because similar results differing only in one base pair were independently obtained from specimens sent to Ottawa (T. Atkinson, K. Seifert, pers. comm.), we are confident that our sequences were of the targeted fungus.

The phylogenetic placement obtained, however, was unexpected. The fungus did not emerge as a member of the class *Dothideomycetes* and the order *Capnodiales* where it has been placed in recent treatments on the basis of the morphology[34-35], but instead was closest to *Phaeomoniella*, which is classified in the class *Eurotiomycetes* in either the order *Chaetothyriales*[34] or the order *Phaeomoniellales*[35]. This result is, nevertheless consistent with the phylogenetic analysis of Sugiyama et al. (2020)[36] that suggested *M. neesii* could be accomodated in *Chaetothyriales*, along with the unnamed species on *Vaccinium* from Oregon (DAOM 240456) included in the tree presented here. *Metacapnodium* is not the first genus of "sooty moulds" now considered to belong to *Chaetothyriales* rather than *Capnodiales*, such as *Aithaloderma* Syd. & P. Syd. 1913, *Ceramoclasteropsis* Bat. & Cavalc. 1962, *Hyaloscolecostroma* Bat. & J. Oliveira 1967, *Trichomerium* Speg. 1918, and *Tripospermum* Speg. 1918[37]. As molecular sequence data becomes available for additional genera of "sooty moulds", it seems probable that they will increasingly fall into two quite distinct classes, providing another case of convergent morphological evolution in the fungi[38].

Metacapnodium ericophilum appears to be restricted to tree *Erica* species in Iberia. We have seen material from the original host, *E. arborea* which can grow up to 7 m in height[39], and also from *E. australis* that can grow to 2 m[40]; if *Hormiscum ericae* is also a synonym (see above), it can also occur on the shorter *E. umbellata* that grows to 0.8 m[40] or 1 m tall[39]. The morphology of *M ericophilum* is similar to both *M. juniperi* (Phill. & Plowr.) Speg. 1918, which occurs on *Juniperus* in Scotland and is illustrated in detail by Hughes (1972)[26], and *M. spongiosum* S. Hughes & Sivan. 1984[41], known from *Cupressaceae*, *Juniperus*, *Libocedrus*, and *Pinus* in Corscia, Portugal, and the USA. However, *Metacapnodium juniperi* only has a capnophialophora-like asexual morph with minute, ampulliform conidiogenous cells, and ascospores that are 20−27 × 8−12 μm, while *M. spongiosum* has only a capnocybe−like asexual morph with multiseptate ellipsoidal conidia and larger and especially broader ascospores 25−40 × 10−13.5 μm. The species on *Erica* in the Iberian Peninsula has both capnocybe- and capnophialophora-type asexual morphs, as does *M. spongiosum*, and ascospores that are 20−35 × 6−11 μm. In the epitype locality in Spain, heavily infected *E. arborea* grows in close proximity and intermixed with several *Juniperus* species, but the sooty mould does not appear ever to colonize the junipers, indicating host specialization. We are therefore confident that *M. ericophilum* represents a distinct species of *Metacapnodium* on the basis of the types of conidial morphs produced, ascospore sizes, and host ranges. Preliminary investigations of recent collections of a *Metacapnodium* on different species of tree *Erica* in the mountains of Tanzania by CGB suggest that may represent a different species. While we did not attempt to culture the fungus on *Erica* from Iberia, as achieved for some other *Metacapnodiaceae*[42], there is a clearly a future prospect for inoculation work to test postulated host specificity in these fungi.

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