Cosmospora xylariae (*Nectriaceae*), a new species from France, Germany and U.K., with notes on *C. berkeleyana*, now *Sphaerostilbella berkeleyana*, and *C. scruposae*

Christian LECHAT
Jacques FOURNIER

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Abstract: *Cosmospora xylariae* is described as new to science and illustrated based on six collections from Europe occurring on stromata of *Xylaria hypoxylon*, *X. longipes* and *X. polymorpha*. The placement of this fungus in the genus *Cosmospora* and its status as a distinct species are based on the study of its sexual and asexual morphs, colour of colony in culture and phylogenetic comparison of ITS1-5.8S-ITS2 sequences with those of cosmospora-like fungi having an acremonium-like asexual morph. Field observations in French Guiana are reported showing the presence of the closely related *C. scruposae* on dead stromata of *X. schweinitzii*. *C. scruposae* is closely related to *C. xylariae* and was so far considered to be affiliated with *X. scruposa* only. The status of *C. berkeleyana* as a distinct species is questioned by the phylogenetic analysis of numerous ITS sequences published under this name in GenBank, one of them being close to *C. xylariae*. It is determined that *Verticillium berkeleyanum*, thus *C. berkeleyana*, is a synonym of *Sphaerostilbella berkeleyana*. A dichotomous key to species of *Cosmospora* is presented based on morphological features of sexual state and host affiliation.
Keywords: *Ascomycota*, fungicolous *Nectriaceae*, *Hypocreales*, rDNA, taxonomy, *Xylaria*.

Résumé : *Cosmospora xylariae* est décrite et illustrée d'après six récoltes provenant d'Europe, faites sur des stromas de *Xylaria polymorpha*, *X. longipes* et *X. hypoxylon*. Le placement de ce champignon dans le genre *Cosmospora* et son statut d'espèce nouvelle reposent sur l'étude des stades sexué et asexué, la couleur de la colonie en culture et sur la comparaison phylogénétique des séquences ITS1-5.8S-ITS2 avec celles d'espèces de type cosmospora ayant une forme asexuée de type acremonium. Des observations de terrain faites en Guyane française indiquant la présence de *C. scruposae* sur *X. schweinitzii* sont signalées. *C. scruposae* est une espèce dont *C. xylariae* est proche et était considérée comme liée seulement à *X. scruposa*. Le statut de *C. berkeleyana* en tant qu'espèce distincte est remis en question par l'analyse phylogénétique de nombreuses séquences ITS publiées sous ce nom dans GenBank, dont une est très proche de *C. xylariae*. Une clé dichotomique des espèces de *Cosmospora* connues à ce jour, fondée sur les caractères morphologiques du stade sexué et les hôtes, est proposée.
Mots-clés : ADN ribosomal, *Ascomycota*, *Hypocreales*, *Nectriaceae* fongicoles, taxinomie, *Xylaria*.

Introduction

In the continuation of our survey of hypocrealean fungi in temperate areas, whose references are compiled in Lechat & Fournier (2021), a species of *Cosmospora* Rabenh. was repeatedly collected on dead stromata of *Xylaria hypoxylon* (L.) Grev. and *X. polymorpha* (Pers.) Grev. in France incubated in a moist chamber, and once in nature on a dead stroma of *X. longipes* Nitschke in Germany. Host-specificity is regarded by Herrera *et al.* (2015) as "one of the most useful characters for diagnosing *Cosmospora* species" and the only *Cosmospora* species known to occur on *Xylaria* was *C. scruposae* C.S. Herrera & P. Chaverri. Upon making a thorough study of our collections, we suspected that they might represent an undescribed species, differing from *C. scruposae* by their north temperate distribution and larger ascospores.

All studied collections appear morphologically identical, similar to known species of *Cosmospora sensu stricto* occurring on dead or effete stromata of *Hypoxylaceae* or *Xylariaceae* or on polypores. The combination of morphological characters such as red ascomata changing colour in 3% KOH or lactic acid, verrucose ascospores, green colonies producing an acremonium-like asexual morph, as well as phylogenetic analysis of ITS sequences, led to placing our fungus in the "*Cosmospora viliuscula* complex" as defined by Herrera *et al.* (2015). Moreover, our phylogenetic results showed that the ITS sequence of an unidentified "*Cosmospora* sp. 4" collected on a stroma of *X.* cf. *polymorpha* in U.K., mentioned by Herrera *et al.* (2015), is identical with those of our collections, thus expanding its known distribution. In the following arguments we support the recognition of *C. xylariae* Lechat & J. Fourn. as a new species representing our European collections. Our phylogenetic results also led us to expand the host specificity of *C. scruposae* to *X. schweinitzii* Berk. & M.A. Curtis and to discuss the identity of *C. berkeleyana* (P. Karst) Gräfenhan, Seifert & Schroers based on *Verticillium berkeleyanum* P. Karst.

Materials and methods

All specimens examined, except JF12119 (on *X. longipes* in nature), were obtained after incubation of dead stromata of *Xylaria* in a moist chamber over 3–4 weeks at room temperature. Dry specimens were rehydrated and examined using the method described by Rossman *et al.* (1999). Microscopical observations and measurements were made in water. The holotype and paratypes specimens were deposited in LIP herbarium (University of Lille, France) and living cultures at CIRM-CF (Centre International des Ressources Microbiennes, Marseille, France) or in the CBS Collection of the Westerdijk Fungal Biodiversity Institute (Utrecht, The Netherlands). Cultures of the living specimen were plated on Potato Dextrose Agar (PDA) with 5 mg/l of streptomycin in Petri dishes 5 cm diam., incubated at 25°C. After growth of cultures for 7–10 days, genomic DNA was extracted from a portion of fresh mycelium using the Nucleospin plan II kit (Macherey-Nagel, Germany) according to the manufacturer's instructions. For the cell lysis step, the mycelium was fragmented using FastPrep-24™ 5G Benchtop Homogenizer in a lysing Matrix A tube containing the lysis buffer PL1 and RNAse. The sample thus obtained was purified following the Nucleospin plant II protocol (steps 3 to 7). ITS5 and ITS4 primers (White *et al.*, 1990) were used for PCR amplification and sequencing reaction. The ITS1-5.8S rRNA gene-ITS2 was amplified from 1 µl genomic DNA in 50 µl PCR using CloneAmp Hifi PCR Premix (Takara). An automated thermal cycler (Mastercycler, Eppendorf, Germany) was used for amplification reactions. 35 cycles of 10 s denaturation at 98°C was followed by 5 s of annealing at 55°C and 5 s of elongation at 72°C. The PCR products were checked on FlashGel™ DNA System (Lonza, Schwitzerland), and sequenced by GENEWIZ (Leipzig, Germany). Chromatograms were checked searching for putative reading errors, and these were manually corrected. All nucleotide sequences were deposited in GenBank. Sequences generated in this study and those obtained from Genbank were aligned under Clustal W (Thomson *et al.*, 1994). Analyses were performed online at www.phylogeny.lirmm.fr (Dereeper *et*

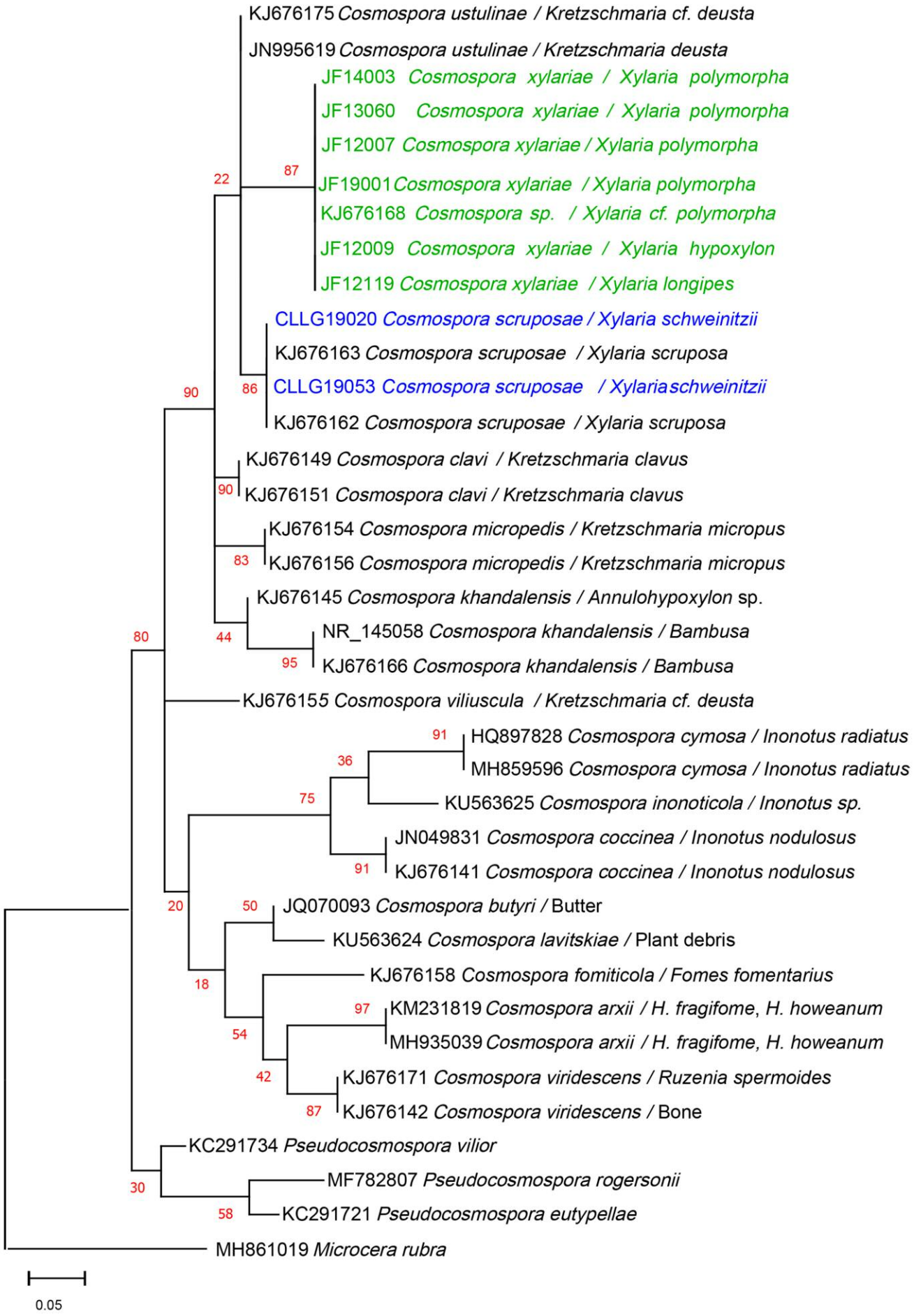

Fig. 1 – Maximum likelihood phylogeny (-lnL = 1211.11377) of cosmospora-like species having an acremonium-like asexual morph, inferred by PhyML 3.0, model HKy85 from a 510 bp matrix of ITS sequences, rooted with *Microcera rubra*.

al., 2008). Maximum likelihood phylogenetic analyses were performed with PhyML 3.0 aLrt (Zwickl, 2006), using the GTR + I + Γ model of evolution. Branch support was assessed using the non-parametric version of the approximate likelihood-ratio test, implemented in PhyML SH-aLRT (Anisimova & Gascuel, 2006). Nomenclature follows MycoBank (Westerdijk Fungal Biodiversity Institute, Utrecht, The Netherlands).

Taxonomy

Cosmospora xylariae Lechat & J. Fourn., *sp. nov.* Fig. 2
MB 840984

Diagnosis: Differs from *C. scruposae*, the only other species known to occur on *Xylaria*, by narrowly obpyriform vs. subglobose ascomata, larger ascospores 8.5–9.5(–10) × 3.8–4.2 µm vs. 6–9 × 3–5 µm, and a north temperate vs. tropical distribution.

Holotype: France, Ariège, Las Muros, on incubated dead stromata of *Xylaria polymorpha*, 13 Feb. 2019, *leg*. J. Fournier, JF19001 (LIP JF19001), ITS GenBank sequences: MZ955629; ex-holotype culture BRFM 3046.

Etymology: The epithet *xylariae* refers to its occurrence on dead stromata of *Xylaria* spp.

Asexual state obtained in moist chamber from dead stromata of *Xylaria* collected in late autumn appears after 8–10 days incubation, preceded by a dense, fast-growing, white cottony superficial mycelium, gradually turning citrine yellow to olivaceous as conidiophores and conidiogenous cells arise. **Ascomata** develop superficially between tufts of asexual state that gradually fades as perithecia mature. **Mature perithecia** usually appear after three weeks incubation but this may vary with moisture and temperature.

Ascomata gregarious, solitary to most often clustered in small to large groups, basally slightly immersed in host tissues, non-stromatic, narrowly obpyriform 220–280 µm high, 130–180 µm wide (Me = 250 × 165 µm, n = 20), laterally pinched when dry, dark reddish orange to red, turning purple in 3% KOH, yellow in lactic acid. Ascomatal apex composed of clavate, thick-walled cells with pale yellow to pale orange wall, with an acute to slightly truncate papilla 20–30 µm high, 30–45 µm diam. at base. **Ascomatal surface** composed of cells of undefined shape forming a *textura epidermoidea*. **Lateral ascomatal wall** in vertical section 30–35 µm thick, of two regions: outer region 20–25 µm thick, composed of subglobose to ellipsoidal, thick-walled cells, 4–11 × 4–6 µm, with orange wall 2–2.5 µm thick; inner region 8–10 µm thick, composed of ellipsoidal, elongate cells 10–17 × 4–5 µm, with hyaline wall 1–1.5 µm thick. **Asci** unitunicate, cylindrical, short-stipitate, 70–75 × 4–5 µm, apex flat to rounded with a ring-like apical thickening, containing 8 uniseriate ascospores, becoming narrowly clavate 7–9 µm wide, with irregularly biseriate ascospores; evanescent, narrowly moniliform paraphyses 3–4 µm diam., interspersed between asci. **Ascospores** ellipsoidal 8.5–9.5(–10) × 3.8–4.2 µm (Me = 9 × 4 µm, n = 40), equally 1-septate, constricted at septum, strongly verrucose, hyaline, becoming pale yellowish brown when mature.

Cultural characteristics: colony 3–4.5 cm diam. after three weeks, olivaceous-green, diffusing a green or brownish colouration in medium; whitish to pale greenish and sporulating at margin, producing an acremonium-like asexual morph. Conidiophores macronematous, unbranched or dichotomously branched, 60–90 (–110) µm long, 2–3 µm diam., flexuous, septate at base, smooth, arising from smooth, septate hyphae 2.5–3 µm diam.; conidiogenous cells monophialidic, terminal, long subulate, with a minutely flared collarette, 50–80 µm long, 2 µm diam. at base, 1.5 µm diam. at apex. Conidia unicellular, ellipsoidal, 4–6 × 1.8–2.2 µm (Me = 5 × 2 µm, n = 50), rounded or attenuated at ends, smooth, hyaline, without a visible abscission scar, held in a drop of liquid at the tip of each phialide, identical to those from incubated stromata.

Additional specimens examined: France, Ariège, Rimont, Peyrau, on incubated dead stromata of *Xylaria polymorpha*, 2 Jan. 2012, *leg*. J. Fournier, JF12007 (LIP-JF12007), culture BRFM 1733, ITS GenBank sequences: MZ955634; *ibid*., on incubated dead stromata of *X. hypoxylon*, 18 Jan. 2012, *leg*. J. Fournier, JF12009 (LIP-JF12009), culture BRFM 1734, ITS GenBank sequences: MZ955633; *ibid*., on incubated dead stromata of *X. polymorpha*, 31 Mar. 2013, *leg*. J. Fournier, JF13060 (LIP-JF13060), culture CBS 135674, ITS GenBank sequences: MZ955632; *ibid*., on incubated dead stromata of *X. polymorpha*, 9 Jan 2014, *leg*. J. Fournier, JF14003 (LIP- JF14003), ITS GenBank sequences: MZ95561. Germany, Rhineland-Palatinate, Wilenstein, Trippstadt, on dead stromata of *X. longipes*, 29 Sep. 2012, *leg*. J. Fournier, JF12119 (LIP-JF12119), ITS GenBank sequences: MZ955630.

Specimens examined of *Cosmospora scruposae*: French Guiana, Saül, Gros Arbres trail, on dead stromata of *X. schweinitzii*, 18 Jun. 2019, *leg*. C. Lechat, CLLG19020 (LIP-CLLG19020), culture BRFM 3049, ITS Genbank sequence: MZ962347; *ibid*., on dead stromata of *X. schweinitzii*, 21 Jun. 2019, *leg*. J. Fournier, CLLG19053 (LIP-CLLG19053), culture BRFM 3048, ITS Genbank sequence: MZ962348.

Results and discussion

Cosmospora xylariae produces a greenish colony in culture and an acremonium-like asexual morph, which fits well the concept of *Cosmospora s. str*. as defined by Gräfenhan *et al.* (2011) and Herrera *et al*. (2015). This is also clearly supported by our phylogenetic analysis of ITS sequences (Fig. 1) showing that *C. xylariae* is nested as a monophyletic clade within the complex of species segregated from *C. viliuscula* (Samuels, Yoshim. Doi & Rogerson) Rossman & Samuels by Herrera *et al*. (2015), on a sister branch to *C. ustulinae* (Teng) C.S. Herrera & P. Chaverri and *C. scruposae*. *Cosmospora ustulinae* differs from our fungus by having smaller ascospores 6.0–8.5 × 2.5–5.0 µm vs. 8.5–9.5(–10) × 3.8–4.2 µm, and occurrence on *Kretzschmaria deusta* (Hoffm.) P. Martin. The isolate K.A.S. 3751 included in the multiphylogeny, published by Herrera *et al.* (2015) as *Cosmospora* sp. 7, was reported from Canada on *Xylaria polymorpha*, thus making its comparison with *C. xylariae* necessary. However, its GenBank ITS sequence KJ676173 appeared incomplete and unsuitable for inclusion in our ITS-based phylogram and was therefore excluded. In Herrera *et al.* (2015), the phylogeny based on six loci included *Cosmospora* sp. 7 distant from the isolate from the UK (*Cosmospora* sp. 4) that we found to be identical with *C. xylariae*, thus this isolate might represent a North American counterpart of *C. xylariae* requiring further investigations.

Cosmospora scruposae occurs on *Xylaria scruposa* (Fr.) Fr. in French Guiana, Guyana, Puerto Rico and Venezuela (Herrera *et al*., 2015) and in French West Indies (Lechat & Fournier, unpublished data) and therefore has a tropical distribution reflecting that of its host, unlike *C. xylariae* occurring on north temperate species of *Xylaria*. It also differs from *C. xylariae* by having subglobose vs. narrowly obpyriform ascomata and smaller ascospores on average 7.3 × 3.7 µm vs. 9 × 4 µm; both species share 99% similarity of their ITS sequences and are the only two *Cosmospora* species known to occur on *Xylaria* spp. To date, *C. scruposae* was only known on dead stromata of *X. scruposa* (Herrera *et al*., 2015), but two specimens collected in French Guiana, CLLG19020 and CLLG19053, occurring on effete stromata of *X. schweinitzii* are morphologically identical to this species, and their ITS sequences have 100 % similarity (Fig. 1) with those of *C. scruposae* published by Herrera *et al.* (2015). It must be noted that the hosts *X. schweinitzii* and *X. scruposa* are phylogenetically closely related (Hsieh *et al*., 2010) and morphologically sometimes difficult to distinguish from each other, all the more so when overmature.

The occurrence of *Cosmospora xylariae* on *X. polymorpha* (France and U.K.), on *X. longipes* (Germany) and on *X. hypoxylon* (France) suggests that host-specificity of *Cosmospora* spp. applies at the genus level more than at species level, both in tropical and temperate areas.

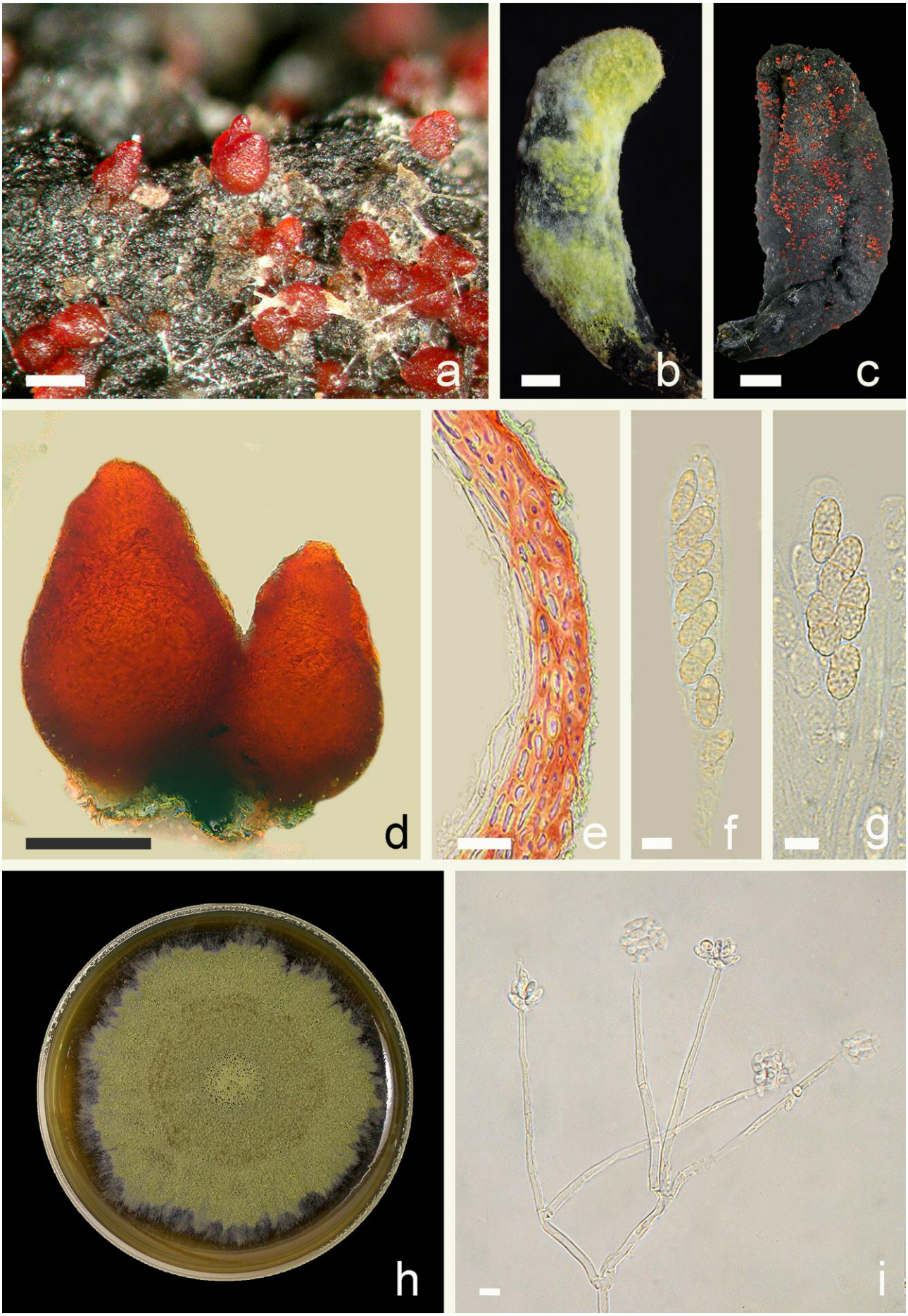

Fig. 2 – a-i: *Cosmospora xylariae* (JF19001 Holotype); a: Ascomata on host; b: *Xylaria polymorpha* bearing *C. xylariae* asexual morph obtained by incubation; c: Ascomata on host obtained by incubation; d: Ascomata in water; e: Vertical section through lateral ascomatal wall; f-g: Asci and ascospores; h: Culture at three weeks (Petri dish 5 cm diam.); i: Conidiophores, phialides and conidia from culture. All microscopical illustrations in water. Scale bars: a, d = 200 µm; b, c = 2.5 mm; e = 20 µm; f, g, i = 5 µm.

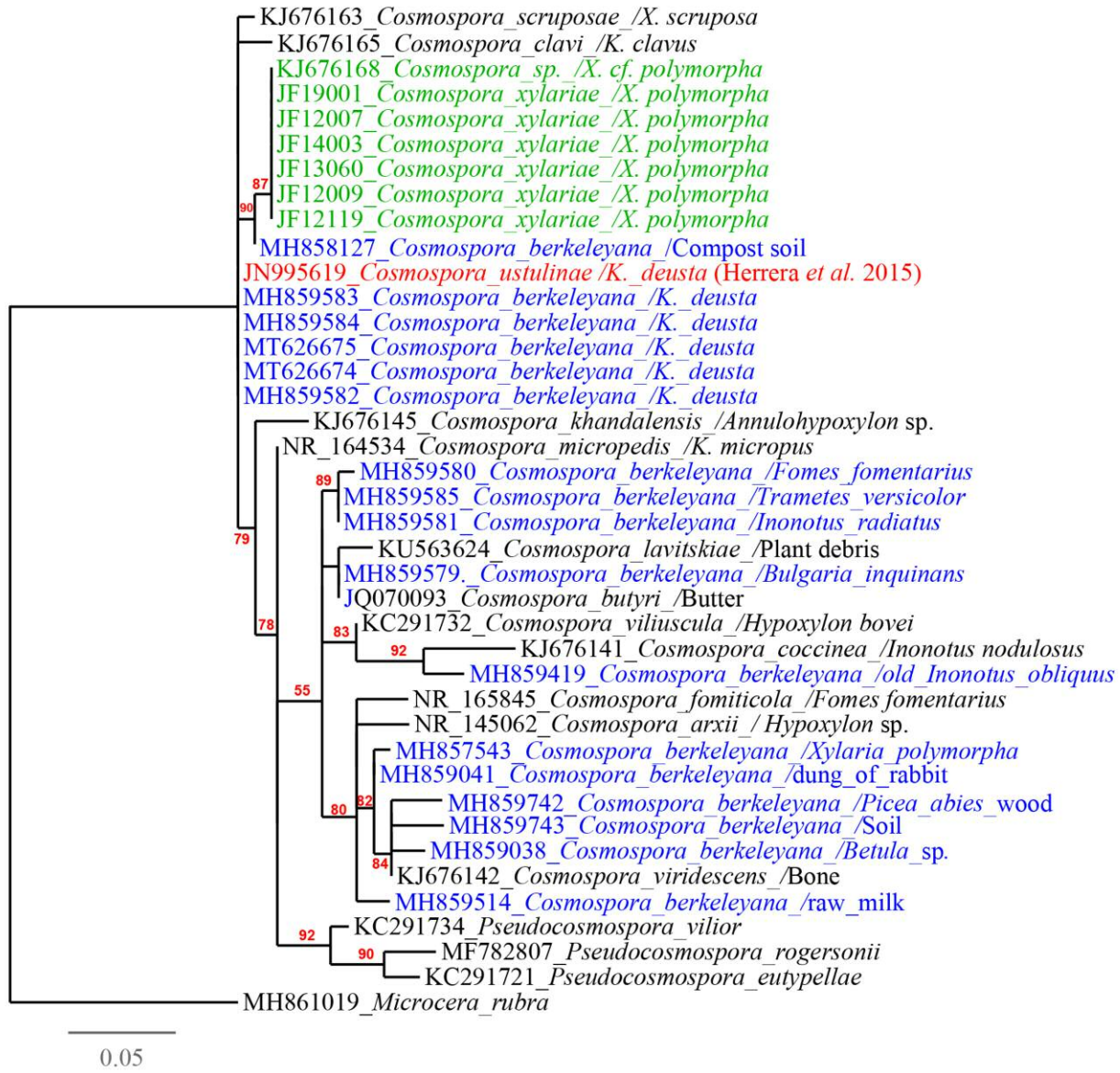

Fig. 3 – Maximum likelihood phylogeny (-lnL = 1412.89) of cosmospora-like species, inferred by PhyML 3.0, model HKy85 from a 520 bp matrix of ITS sequences available in Genbank, showing heterogeneous placement of *Cosmospora berkeleyana*.

The phylogram of representative *Cosmospora* spp. including ITS sequences of *C. berkeleyana* (Fig. 3) calls for comments on the status of this taxon. One of these sequences, MH858127, originating from compost soil, shows 99.4% similarity with *C. xylariae*, which should have possibly led us to refer our collections to *C. berkeleyana*. However, the distribution of the eighteen sequences of *C. berkeleyana* submitted to GenBank by Vu *et al*. (2019) within the *Cosmospora* clade clearly shows that several different species are involved, making this name questionable.

Gräfenhan *et al.* (2011) introduced *C. berkeleyana* to accommodate the basionym *Verticillium berkeleyanum* P. Karst. In the protologue, Karsten (1891) indicates that *V. berkeleyanum* is the asexual state associated with *Hypomyces berkeleyanus* Plowr. & Cooke 1882, occurring on *Stereum hirsutum* (Willd.) Pers. His description of the associated sexual state conforms well to the fungus currently recognized as *Sphaerostilbella berkeleyana* (Plowr. & Cooke) Samuels & Cand., especially by the presence of small perithecia embedded in a pallid to pinkish subiculum, a feature typical of *Hypocreaceae* and especially *S. berkeleyana*.

The confusion took place after Gams & Van Zaayen (1982) recombined *V. berkeleyanum* with *Acremonium berkeleyanum* (P. Karst.) W. Gams, stating that "*Hypomyces berkeleyanus*, anamorph *Verticillium berkeleyanum*, is a typical *Nectria* [*Nectria berkeleyana* (Plowr. & Cooke) Dingley], the anamorph of which is identical with *Acremonium butyri* (van Beyma) W. Gams." On the same grounds, they also predicted *N. vilior* Starb. and *N. viridescens* C. Booth as possible teleomorphs of *A. berkeleyanum*. This situation is therefore due to the confusion by Gams of the gliocladium-like asexual state of *Sphaerostilbella* with penicillate or verticillate forms of acremonium-like asexual states of some species of cosmospora-like fungi. The same confusion likely accounts for the numerous misidentified strains sequenced by Vu *et al*. (2019), all assigned to *C. berkeleyana* but shown to be heterogeneous by phylogenetic comparison and unrelated to *S. berkeleyana* (Fig. 4). An additional argument supporting the lack of a close relationship of *Sphaerostilbella* with *Cosmospora* was provided by the LSU-based phylogenetic study by Summerbell *et al*. (2011).

Herrera *et al.* (2015) stated: "We consider the host to be one of the most useful characters for diagnosing *Cosmospora* species, particularly members of the *Cosmospora viliuscula* species complex". The complete absence of *Cosmospora* spp. known on *Stereum* spp. is an additional and decisive argument excluding the possibility that the asexual state of a *Sphaerostilbella* (interpreted as *Hypomyces* by Karsten, 1891) commonly found on *Stereum* could be that of a *Cosmospora* as currently defined. *Verticillium berkeleyanum* is therefore synonymous with its sexual state *S. berkeleyana*, and cannot be the

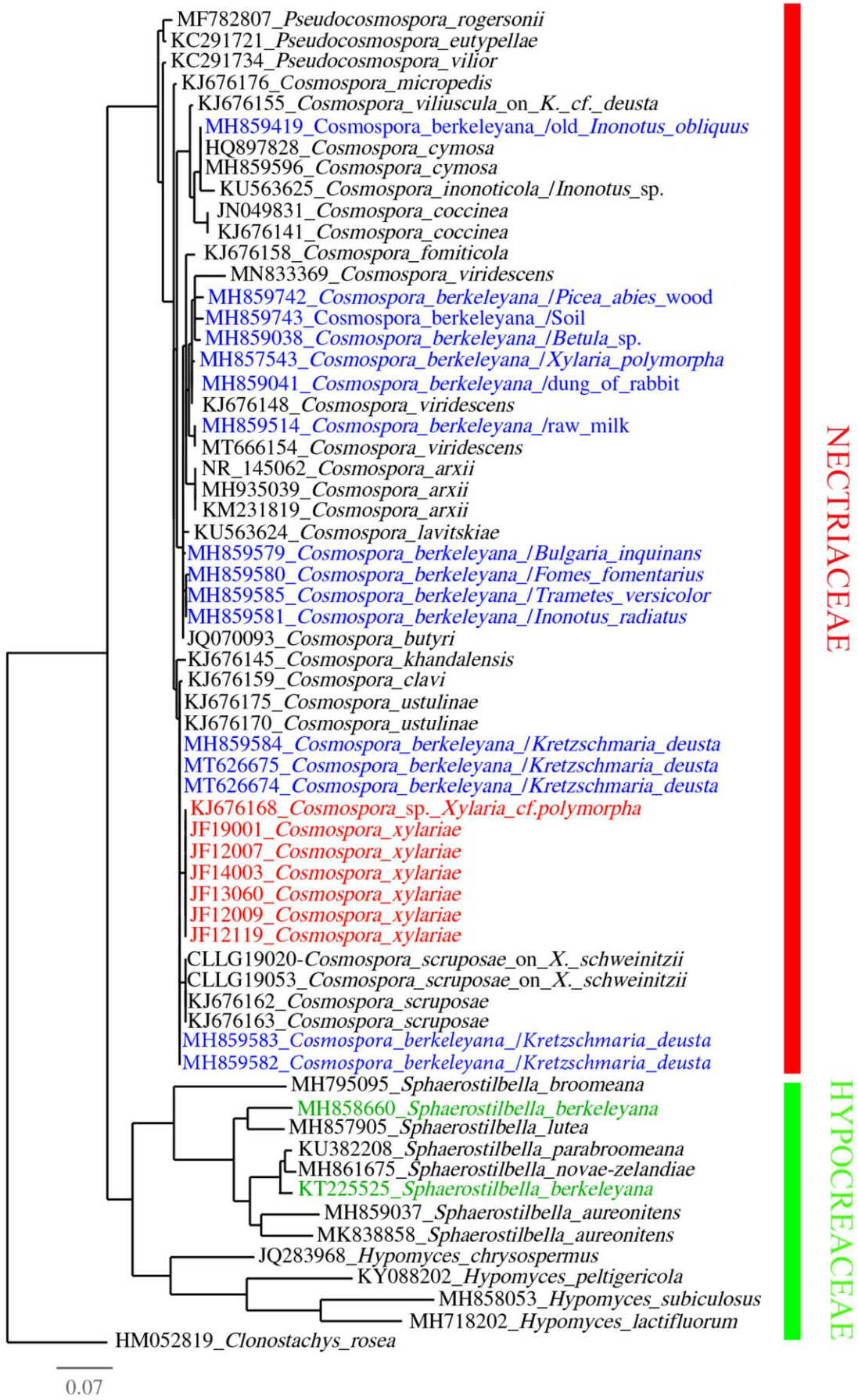

Fig. 4 – Maximum likelihood phylogeny (-lnL = 3800.98491) of cosmospora-like species, inferred by PhyML 3.0, model HKy85 from a 520 bp matrix of ITS sequences available in Genbank, showing the placement of *Cosmospora* and *Sphaerostilbella* species.

Updated key to species of *Cosmospora sensu stricto* based on hosts, ascospore dimensions and geographical distribution

This key is proposed to complement that of Herrera *et al.* (2015). It includes the recently described species *C. inonoticola* Z.Q. Zeng & W.Y. Zhuang and the sexual state of *C. lavitskiae* (Zhdanova) Gräfenhan & Seifert (Zeng & Zhuang, 2016). Due to lack of a known sexual state, *C. cymosa* (W. Gams) Gräfenhan & Seifert is not included in the key.

On Polypores **1**
On *Hypoxylaceae* **3**
On *Xylariaceae* **6**
Other substrates **13**

1 On *Fomes fomentarius*; ascospores 7–9.5 × 3–4 µm, minutely verrucose; NZ ..... ***C. fomiticola***
1 On *Inonotus* spp.; ascospores much larger **2**

2 Ascospores 14.5–17 × 10–12.5 µm, coarsely tuberculate; North temperate ..... ***C. coccinea***
2 Ascospores 13–27 × 8–17 µm, finely warted; Northern China ..... ***C. inonoticola***

3 On *Hypoxylon fragiforme* and *H. howeanum*; ascospores 6.5–8.5 × 3–4 µm; North temperate ..... ***C. arxii***
3 On *Annulohypoxylon* spp. **4**

4 Ascospores coarsely verrucose, 5.5–8 × 2.5–4 µm ..... ***C. khandalensis***
4 Ascospores minutely verrucose, larger **5**

5 Ascospores 6.5–9 × 3–4 µm; USA ..... ***C. annulohypoxylii***
5 Ascospores 8–11.5 × 4–6 µm; NZ ..... ***C. novazelandica***

6 On *Kretzschmaria* spp. **7**
6 On other xylariaceous genera **11**

7 Ascospores minutely verrucose, 14–18.5 × 6–9 µm, on *K. cetrarioides*; tropical ..... ***C. rickii***
7 Ascospores coarsely verrucose, smaller **8**

8 North temperate distribution, on *K. deusta*; ascospores 6–8.5 × 2.5–5 µm ..... ***C. ustulinae***
8 Tropical distribution, on other *Kretzschmaria* species **9**

9 Ascospores 5–8.5 × 3–4.5 µm; on *K. cyclopica* and *K. micropus* ..... ***C. micropedis***
9 Ascospores slightly larger and hosts different **10**

10 On *K. clavus*; ascospores 6.5–9 × 3–4.5 µm ..... ***C. clavi***
10 On ustulinoid *K.* sp.; ascospores 6–10 × 2–5 µm ..... ***C. viliuscula***

11 On *Stilbohypoxylon quisquiliarum*; ascospores 6.5–8 × 3–4 µm, minutely verrucose ..... ***C. stilbohypoxyli***
11 On *Xylaria* spp.; ascospores coarsely verrucose **12**

12 Tropical distribution, on *X. schweinitzii* and *X. scruposa*; ascospores 6–9 × 3–5 µm ..... ***C. scruposae***
12 North temperate distribution, on various *Xylaria* spp.; ascospores 8.5–9.5 × 3.8–4.2 µm ..... ***C. xylariae***

13 Known from soil and one xylariaceous fungus; ascospores 4–6 × 3–4 µm, colourless, smooth ..... ***C. lavitskiae***
13 Known from dead wood, bone and stromata of *Ruzenia spermoides*; ascospores 7.5–12.5 × 3.5–4.5 µm, yellow brown, minutely verrucose ..... ***C. viridescens***

basionym of a *Cosmospora*, making the basionym and combination made by Gräfenhan *et al.* (2011) synonyms of *Sphaerostilbella berkeleyana*.

A further and unfortunate consequence of this confusion is the presence of many misidentified strains of "*C. berkeleyana*" in GenBank that seriously hampers the delimitation of new species of *Cosmospora* in the future. The phylogram including eighteen sequences of "*C. berkeleyana*" (Fig. 3) shows that they are widely distributed all over the tree, which is not compatible with a narrow and workable species concept. While the five sequences from strains originating from *K. deusta* and clustering with that of *C. ustulinae* can be easily assigned to this name, the other sequences suggest the presence of either undescribed species of *Cosmospora* or species closely related to known ones, whose affinities need further taxonomic investigations. This was already noticed by Gräfenhan *et al*. (2011) who did not include sequences of "*C. berkeleyana*" in their phylogenetic survey of *Cosmospora*. Herrera *et al.* (2015) likewise skipped "*C. berkeleyana*" from their survey because of the ill-defined concept of the taxon. Most species of *Cosmospora sensu stricto* occur on *Xylariaceae*, which is a very diverse and speciose family, especially in tropical areas. One can therefore expect the discovery of a large number of new *Cosmospora* species. Their naming should be easier when ill-defined and misleading names like "*C. berkeleyana*" are no longer used.

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1: C. Lechat – 64 route de Chizé, 79360 Villiers-en-Bois, France – lechat@ascofrance.fr

2: J. Fournier – Las Muros, 09420 Rimont, France – jfournzeroneuf@gmail.com