Freshwater Ascomycetes: *Submersisphaeria aquatica* (*Annulatascaceae*), reported for the first time from France (Morvan) and from Europe

Jacques FOURNIER
Alain GARDIENNET
Christian LECHAT

Ascomycete.org, 8 (2) : 66-72.
Mars 2016
Mise en ligne le 15/03/2016

Abstract: A distinctive aquatic fungus belonging to the *Sordariomycetes* was recently collected twice on submerged wood in a peat bog and in a small brook in Morvan region (France). Based on its more or less immersed perithecial and ostiolate ascomata, cylindrical unitunicate asci with a massive inamyloid apical apparatus and brown, two-celled fusiform ascospores with small bipolar cap-like appendages, this fungus was identified as *Submersisphaeria aquatica* K.D. Hyde. This species, so far known only from Australia and USA, is reported from France and Europe for the first time. Herein, we provide a detailed morphological description of this fungus and compare it with material from the USA. The presence of minute germ pores beneath the bipolar appendages of the ascospores is assessed for the first time, in American and European material as well. Repeated attempts to grow the ascospores in culture on artificial media were unsuccessful.
Keywords: *Annulatascales*, Ascomycota, aquatic fungi, pyrenomycetes, *Sordariomycetes*, taxonomy.

Résumé : un Sordariomycète aquatique remarquable a été récemment récolté à deux reprises sur bois immergé dans une tourbière et un ruisseau situés dans la région du Morvan (France). En se fondant sur ses ascomes plus ou moins enfouis, périthéciaux, ostiolés, ses asques cylindriques, unituniqués et pourvus d'un appareil apical massif et non amyloide et ses ascospores brunes, fusiformes, à deux loges et pourvues de petits appendices bipolaires aplatis, ce champignon a été identifié comme *Submersisphaeria aquatica* K.D. Hyde. Cette espèce, jusqu'à présent connue seulement d'Australie et des États-Unis, est signalée de France et d'Europe pour la première fois. Une description morphologique détaillée est donnée, comprenant une comparaison avec des spécimens des États-Unis. La présence de minuscules pores germinatifs aux extrémités des ascospores sous les appendices bipolaires est établie pour la première fois, aussi bien dans les récoltes américaines que dans le matériel européen. Des essais répétés de mise en culture d'ascospores sur milieux artificiels ont échoué.
Mots-clés : *Annulatascales*, Ascomycota, champignons aquatiques, pyrénomycètes, Sordariomycètes, taxinomie.

Introduction

Freshwater ascomycetes are an ecological group of fungi, which play an important and often underestimated ecological role in decomposing woody and herbaceous substrates submerged in lotic (streams, rivers) and lentic (lakes, ponds) habitats, making them available to macroinvertebrates (Bärlocher, 1985; Shearer *et al*., 2007; Suberkropp, 2003; Wong *et al.*, 1998). Aquatic hyphomycetes, primarily "Ingoldian fungi", have been extensively studied regarding their taxonomy, distribution and role in decomposing submerged leaves and herbaceous material. They were well studied in Europe, including in southwestern France (Chauvet, 1991; Fabre, 1998a; 1998b). Aquatic ascomycetes, i.e. sexual morphs of "discomycetes" including *Leotiomycetes* and *Pezizomycetes* and those of "pyrenomycetes" including *Dothideomycetes* and *Sordariomycetes* have been extensively studied in Australia, China, Japan, North America and Southeast Asia but were paid much less attention in Europe, though their role as wood decomposers is largely as important as that of aquatic hyphomycetes. For more information on freshwater ascomycetes, the reader is referred to the comprehensive overview provided by Shearer & Raja (2013).

When one of us (JF) started collecting ascomycetes on submerged wood in Ariège (France) in 2006, he was considerably hampered by the lack of relevant literature since most (ca. 85%) of the material collected could not be identified to species reported from the aforementioned temperate, subtropical to tropical regions. This situation proved to reflect the presence of an amazing number of new taxa, many of them still under investigation. However, over time, new species, new genera, new families and new orders of freshwater ascomycetes have been described from France in *Dothideomycetes* (Raja *et al.*, 2015; Zhang *et al.*, 2008a; 2008b; 2009a; 2009b; 2009c; 2013; 2014a; 2014b) and in *Sordariomycetes* (Chaudhary *et al.*, 2007; Fournier & Lechat, 2010; Lechat & Fournier, 2015; 2016; Raja *et al.*, 2012; Réblová *et al.*, 2010; 2012; 2015a; 2015b; 2016a; 2016b).

Informal forays, attended by the same six participants[1], were organized annually since 2009 in various regions of France, leading to the discovery of outstanding or unknown taxa whenever new aquatic biotopes were explored, confirming the high potential of unknown biodiversity in this country (Gardiennet, 2010; Fournier *et al*., 2010). Enrique Rubio Dominguez recorded similar results in Asturias (Spain) and Hermann Voglmayr around Vienna (Austria) (personal communications).

It is during our last foray organized by AG in the region Morvan (France) that we came across a freshwater fungus belonging to the *Sordariomycetes*, so far unknown to us, that we identified, after some hesitations, as *Submersisphaeria aquatica* K.D. Hyde. This species was first described from Queensland, Australia (Hyde, 1996) and was further reported from the USA by Campbell *et al.* (2003) but interestingly it has never been recorded from France and from other countries in Europe.

We present in this paper a detailed and illustrated morphological description of this species, with comments on its taxonomic affinities and its geographical distribution. North American (USA) material of *S. aquatica* was received on loan from Dr. Miller (University of Illinois, Champaign, USA) for comparison with the collections from France. Ascospores of JF 15158 germinated on PDA but the cultures grew very slowly and despite several attempts on other media all cultures eventually died, making DNA data unavailable.

Material and methods

Submerged woody material was collected randomly and particular care was given to selecting substrates that have been submerged for an extended period of time, long enough to permit colonization of the substrates by freshwater ascomycetes and the exclusion of

[1] Alain Delannoy, Jacques Fournier, Alain Gardiennet, Christian Lechat, Yannick Mourgues and Jean-Paul Priou.

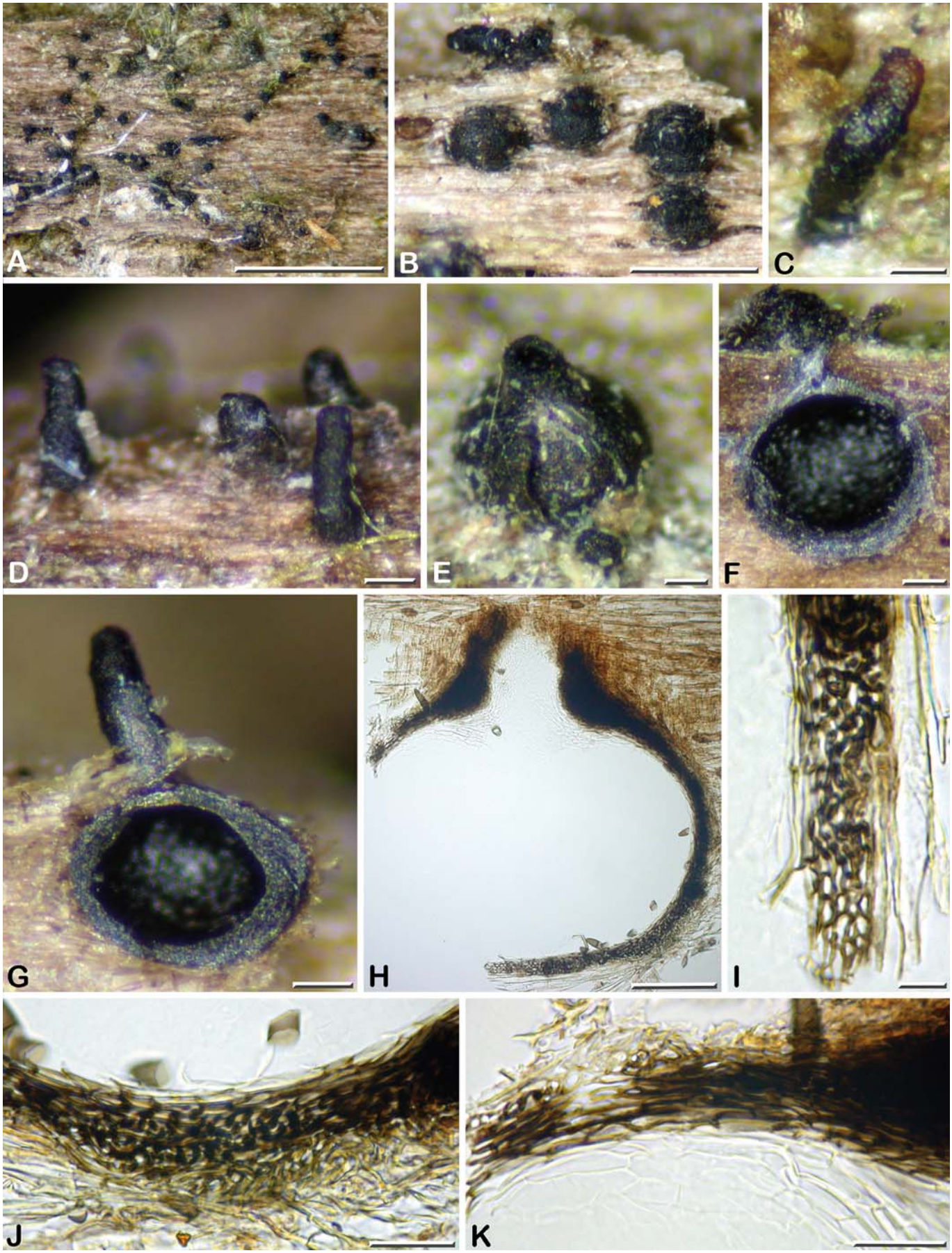

Plate 1– *Submersisphaeria aquatica*

JF 15158. A: Ascomata in surface view showing the ostiolar necks protruding above host surface; B-D: Short and long ostiolar necks emerging from the substrate; E: Almost superficial ascoma with broken neck; F, G: Immersed ascomata in vertical section with short (F) or long (G) ostiolar neck; H: Vertical section of an ascoma showing the thickened peridium around the neck base, in chloral-lactophenol; I-K: Base (I), lower side (J) and upper side (K) of the peridium in vertical section, in chloral-lactophenol. Scale bars: A = 5 mm; B = 0.5 mm; C-H = 100 µm; I = 10 µm; J, K = 25 µm.

terrestrial species. The woody substrates were rinsed under tap water and superficially air-dried before their observation through a stereomicroscope.

Photomacrographs were taken with a Nikon Coolpix 995 digital camera through the eyepiece of an Olympus SZ60 stereomicroscope, by the means of a 30 mm diameter adapter. Photomicrographs were taken with the same camera mounted on the trinocular port of a Leitz Orthoplan microscope. The digital photographs were processed with Adobe Photoshop Elements 10 and the figures assembled with the same software.

Measurements of asci and ascospores were made in water and processed with the free software Piximetre 5.2 (http://ach.log.free.fr/Piximetre/). In the formula given by this software the values in brackets represent the extreme values (20%) that are not taken into account for the calculation, N represents the number of ascospores measured, Q the quotient length/width, Me the mean values of length × width, and Qe the mean value of quotient length/width. The amyloid reaction of the ascus apical apparatus was tested by adding a drop of Melzer's reagent or Lugol's solution to a water mount of perithecial contents. Microscopic observation of the asci, paraphyses and ascospores was carried out in water or in black Pelikan® ink, blue Pelikan® ink diluted in 1% SDS or India ink; the observation of ascospore wall in order to detect the presence of ornamentation or germ pores was carried out in chloral-lactophenol or in PVA-lactophenol. Free-hand sections of the peridium were mounted in heated chloral-lactophenol.

Measurements of perithecia, asci and ascal apical apparati are recorded as height × width.

Cultures of the living specimen, performed by CLL, were made on three types of media: PDA (Potato Dextrose Agar), MEA (Malt Extract Agar) and CMA (Corn Meal Agar) with 5 mg/l of streptomycin in Petri dishes 9 cm diam. Centrum contents with asci and ascospores were removed from a perithecium with a fine needle and placed in a drop of sterile water that was stirred with a sterile needle. The drop with ascospores was placed on the medium using a sterile micropipette under a reversed microscope, then the Petri dishes were incubated at 25°C.

The material was deposited in LIP (University of Lille, France) and duplicates are kept in the personal herbaria of JF and AG. Initials JF, AG and CLL refer to Jacques Fournier, Alain Gardiennet and Christian Lechat respectively.

Taxonomy

Submersisphaeria aquatica K.D. Hyde, *Nova Hedwigia*, 61: 172. 1996 – Plates 1-3.

Ascomata perithecial, non-stromatic, scattered to gregarious, immersed to erumpent, rarely almost superficial, not collapsing upon drying, ostiolate, with a short to long central neck. Venter globose to subglobose, 320–450 µm diam. Neck cylindrical with flared base, (40–) 170–450 µm high, 80–100 µm wide, with obtuse, smooth apex, black, at times with yellowish to red brown apex, fragile and easily broken off. Peridium 22–30 µm thick at base and on sides, 45–50 µm thick at the base of the neck, pseudoparenchymatous, composed of dark brown, thick-walled angular cells, inner cells more flattened, with an inconspicuous layer of hyaline flattened cells textura prismatica lining the base and the sides, forming a thick ring at the base of the neck, from which originate the periphyses. A loose network of pale brown hyphae originating from the outer cells of the peridium spreads into the surrounding wood, which is not stained.

Asci unitunicate, cylindrical with broadly rounded apex, with eight obliquely uniseriate overlapping ascospores, readily detached and floating free at maturity, (173.1–)175.2–193.6(–199.1) × (11.2–)11.5–12.4(–12.5) µm; N = 10 (Me = 184.6 × 11.9 µm) including a short attenuated stipe 18–26 µm long (N = 10), with a massive, apical apparatus (2.7–)2.8–3.6(–3.7) × (4.8–)5–5.5(–5.7) µm; N = 24 (Me = 3.3 × 5.2 µm), refractive, inamyloid, staining blue in diluted blue Pelikan ink, widely porate, apparently non-functional. **Paraphyses** thin-walled, hyaline, septate, not constricted at septa, 6–8 µm wide at base, tapering above asci to 1.5–2 µm, coated with gelatinous material. **Ascospores** (19.4–)21.6–26.2(–28.2) × (6.8–)7.7–9(–9.4) µm, Q = (2.4–)2.5–3.3(–3.7); N = 60 (Me = 24 × 8.3 µm; Qe = 2.9), ellipsoid-fusiform with narrowly rounded to subacute ends, equilateral, equally two-celled, euseptate, not constricted at the septum, septum black and slightly thickened to 1–1.2 µm, contents filled with small guttules, wall olivaceus brown at fresh state, brown to dark brown in dried material, smooth, at times with a thin appressed sheath visible in India ink, with minute bipolar apical pores (best seen in chloral-lactophenol or PVA-lactophenol), sligthly eccentric, usually concealed under bipolar pad-like appendages appearing refractive in water, chloral-lactophenol, India ink and black Pelikan ink, stained blue in diluted blue Pelikan ink. Discharged ascospores collected at the tip of the ostiolar neck were found slightly shorter and wider (19.7–)21.1–25.3(–27.5) × (7.9–)8.3–9.6(–9.9) µm, Q = (2.1–)2.3–2.9(–3.2); N = 60 (Me = 23.4 × 9 µm; Qe = 2.6).

Specimens examined: France, Nièvre: Arleuf, Préperny, ca. 810 m, peat bog, lentic, submerged decorticated deciduous wood, 47°00'17" N, 4°02'00" E, 21 Oct. 2015, JF 15158; Saône-et-Loire: Roussillon-en-Morvan, La Goulette, small brook originating from an artificial lake, 715 m, submerged wood of *Pseudotsuga menziesii*, 46°59'08" N, 4°03'32" E, 21 Oct. 2015, *leg*. A. Gardiennet, AG 15102. USA, Louisiana: St. Tammany Parish, Abita Creek Nature Preserve of the Nature Conservancy, creek located at the eastern dead end of Lowe Davis Road, UTM Zone 16, 3377218mN, 212032mE [30°29'24.9" N, 90°0'2.6" W], water temperature 23°C, water pH 6.0, on submerged corticated wood (mixture of *Nyssa sylvatica* and *Taxodium distichium* sticks), 27 Aug. 1997, *leg*. K. Robertson, det. C.A. Shearer, A95-8 (ILL 40186); North Carolina: Great Smoky Mountains National Park, Tapoco, Cheoah River, 35°26'18" N, 83°55'07" W, water temperature 26°C, water pH 5.0, on submerged corticated wood (coniferous), 18 Jul. 2000, *leg*. J. Campbell, det. C.A. Shearer, A95-11 (ILL 40260).

Discussion: This aquatic fungus is distinctive in having mostly immersed perithecial ascomata with a short to long ostiolar neck, unitunicate cylindrical asci with a massive inamyloid apical apparatus and short stipe, and brown, fusiform, two-celled ascospores with a thick median septum, minute apical pores and small bipolar cap-like appendages. When run through the key to genera of freshwater fungi (Cai *et al.*, 2006), it readily keys out to *Submersisphaeria aquatica* and conforms well to the descriptions by Hyde (1996) and Campbell *et al.* (2003).

Because of the combination of cylindrical asci with a massive J- apical apparatus and brown, two-celled ascospores with a dark and thick median septum and apical pores, we also considered *Jobellisia* M.E. Barr but no species of this genus features ascospores over 20 µm long; moreover, ascomata of *Jobellisia* have a thicker and more complex peridium 50–100 µm thick, their ascospores have more conspicuous germ pores, they lack appendages and their septum is relatively much thicker than in *Submersisphaeria* (Huhndorf *et al.*, 1999; Leroy, 2006).

In the original description, Hyde (1996) described the ascospores "with hyaline germ pores at each end". Campbell *et al.* (2003) resumed the morphological study of *S. aquatica* based on numerous collections from North America (USA) and they interpreted the bipolar structures visible at the ends of ascospores and those in illustrations of original material as "cap-like apical appendages" and not as germ pores. They stated that germ pores could not be detected with the light microscope at 1000× in the American material and that type material from Australia was not available for comparison.

As we detected both germ pores and cap-like appendages on ascospores of the material collected in France, we feel compelled to examine American material for comparison. The two collections from Louisiana and North Carolina kindly sent on loan by Dr. Miller

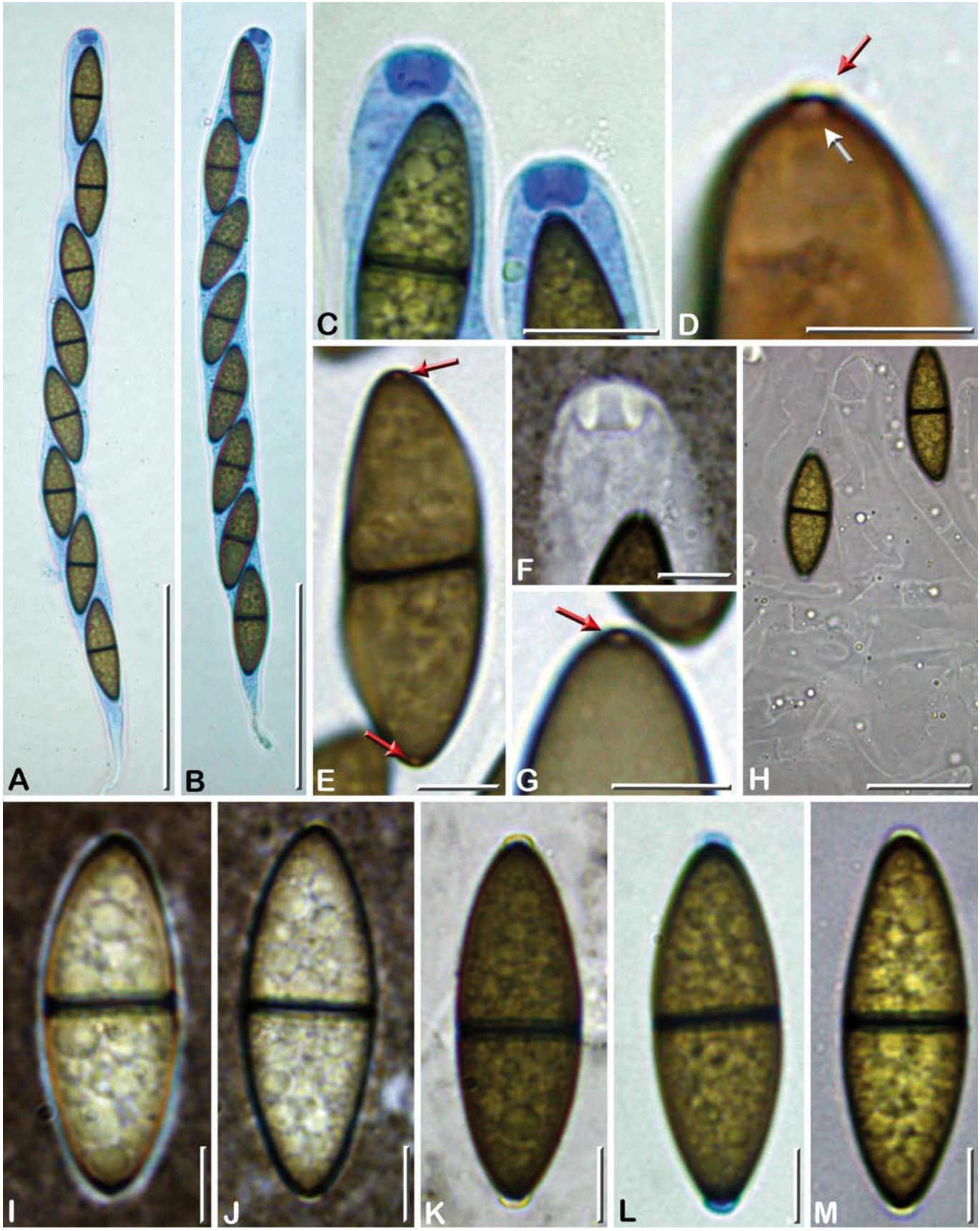

Plate 2 – *Submersisphaeria aquatica*

JF 15158. A, B: Mature asci in diluted blue Pelikan ink, showing the short stipe and the massive apical apparatus; C: Ascus apical apparati stained by diluted blue Pelikan ink; D: Ascospore tip showing the germ pore (white arrow) and the cap-like appendage (red arrow), in chloral-lactophenol; E, G: Ascospores in chloral-lactophenol, showing the apical germ pores (arrows); F: Refractive ascus apical apparatus, in India ink; H: Ascospores among paraphyses, in black Pelikan ink; I: Barely mature ascospore in India ink, surrounded by a thin mucilaginous sheath; J: Barely mature ascospore in India ink, showing the bipolar appendages; K-M: Mature ascospores in India ink, diluted blue Pelikan ink and black Pelikan ink respectively, showing the bipolar appendages. Scale bars: A, B = 50 µm; C = 10 µm; D-G, I-M = 5 µm; H = 20 µm.

proved consistent with the French material in all macro- and micromorphological respects. Ascospores of ILL 40260 were (20.2–)21.5–24.9(–26.7) × (7.2–)7.6–8.7(–9) µm, Q = (2.5–)2.6–3.1(–3.5); N = 60 (Me = 23.4 × 8.1 µm; Qe = 2.9), thus matching well with the dimensions reported in literature and those recorded in the French material. Moreover, careful observations in chloral-lactophenol and PVA-lactophenol confirmed the presence of both germ pores and cap-like appendages (Plate 3), which strongly supports the conspecificity of our collections from France with collections of *S. aquatica* from the USA.

Whereas bipolar cap-like appendages on ascospores is a character widely distributed within aquatic ascomycetes, bipolar germ pores are much less common and the combination of both appears rather unique within aquatic *Dothideomycetes* and *Sordariomycetes* (Cai *et al.*, 2006), which makes this character highly diagnostic. Therefore, to make sure that collections from North America (USA) and Europe are conspecific with the type collection from Australia, this character of bipolar germ pores associated with bipolar cap-like appendages should be also assessed from Australian material when the holotype comes to be retrieved or when an epitype is designated.

Submersisphaeria aquatica was first tentatively placed in the *Lasiosphaeriaceae* (Hyde, 1996) but Wong *et al.* (1998) proposed to accommodate it in the new family *Annulatascaceae*, primarily based on the distinctive morphology of the apical apparatus confirmed by further ultrastructural studies (Ho & Hyde, 2000).

The phylogenetic placement of *S. aquatica* within *Annulatascaceae* was assessed by Campbell *et al.* (2003) based on LSU sequences, confirmed by all further phylogenetic studies including *Annulatascaceae* (Campbell & Shearer, 2004; Abdel-Wahab *et al.*, 2001; Boonuyen *et al.*, 2012; Réblová *et al.*, 2014; Luo *et al.*, 2015). Most results suggest that the closest phylogenetic affinity of *S. aquatica* is with *Pseudoproboscispora caudae-suis* (Ingold) J. Campb., Shearer, J.L. Crane &

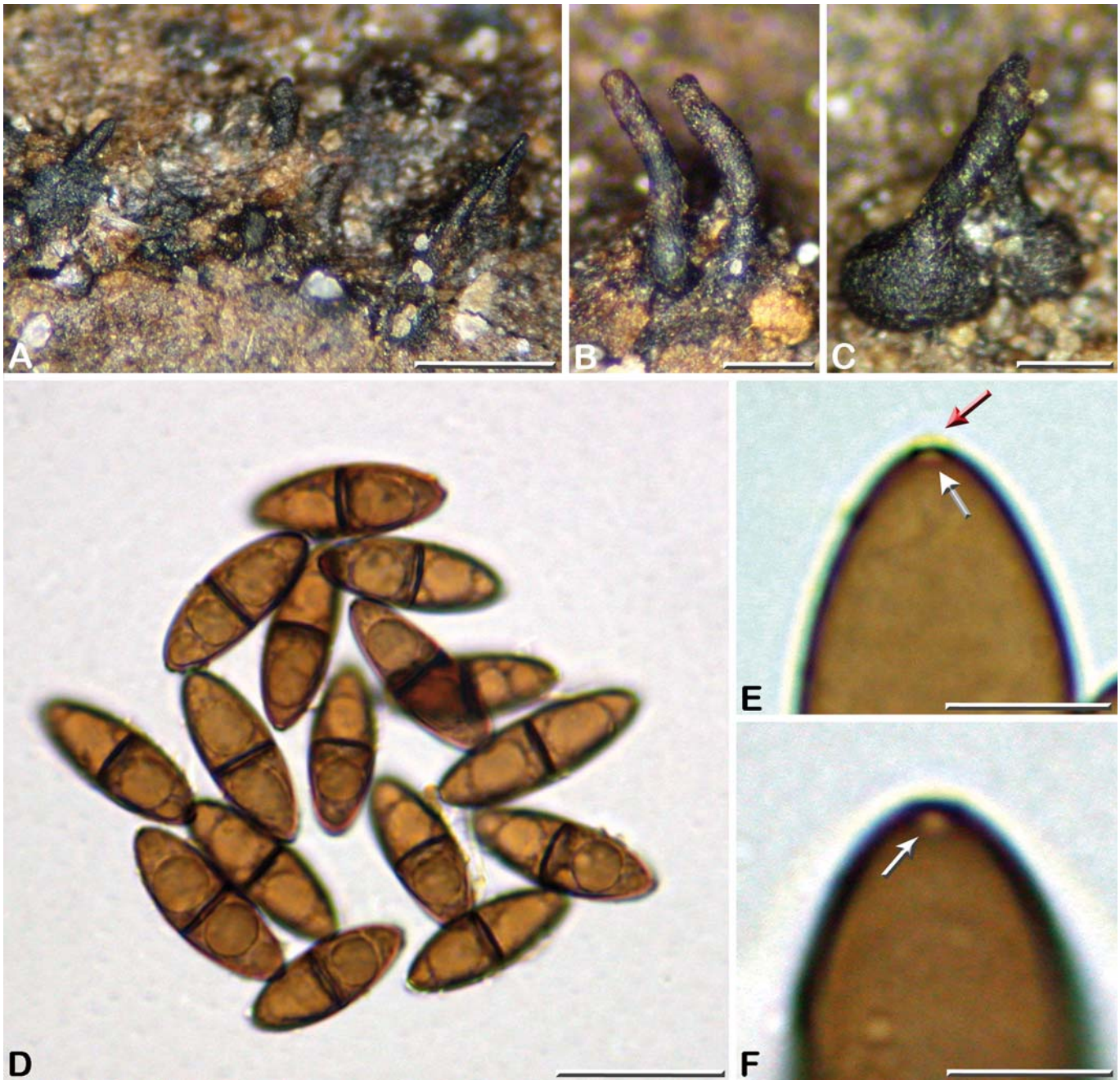

Plate 3 – *Submersisphaeria aquatica*

ILL 40260. A-C: More or less immersed beaked ascomata on host surface; D: Ascospores in 1% SDS; E: Ascospore tip showing a germ pore (white arrow) and a cap-like appendage (red arrow), in PVA-lactophenol; F: Ascospore tip showing the germ pore (arrow), in chloral-lactophenol. Scale bars: A = 0.5 mm; B, C = 0.2 mm; D = 20 µm; E, F = 5 µm.

Fallah, a north temperate species which is primarily distinguished by hyaline ascospores bearing unfurling bipolar appendages and without germ pores.

Five species are hitherto accommodated in *Submersisphaeria*, including terrestrial and aquatic species. Aside from *S. aquatica*, the type species, other aquatic species include: *S. palmae* A. Pinnoi, occurring on submerged palm material, known from Thailand (Pinnoi *et al*., 2004) and *S. vasicola* Y.Z. Wang, Aptroot & K.D. Hyde occurring inside a wooden water pail, known from the USA (Wang *et al*., 2004). Terrestrial species include: *S. bambusicola* D.Q. Zhou & K.D. Hyde occurring on bamboo, known from Hong-Kong (Zhou & Hyde, 2000), and *S. rattanicola* J. Fröhl. & K.D. Hyde occurring on palm material, known from north Queensland, Australia (Fröhlich & Hyde, 2000). Ascospore septation, shape and dimensions readily distinguish these five species in a dichotomous key provided by Pinnoi *et al.* (2004); however, their designation to *Submersisphaeria* based on morphology was not corroborated by molecular data.

Acknowledgments

Dr. Andrew Miller (University of Illinois, Champaign, USA) is warmly thanked for the loan of specimens of *Submersiphaeria aquatica*. Dr. Raja (University of North Carolina, Greensboro, USA) is gratefully acknowledged for accepting to provide a presubmission review and for his helpful comments, corrections and suggestions to improve this article. Nicolas Van Vooren is gratefully acknowledged for his invaluable editorship.

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Jacques Fournier
Las Muros
09420 Rimont
France
jacques.fournier@club-internet.fr

Alain Gardiennet
14 rue Roulette
21260 Véronnes
France
agardiennet@gmail.com

Christian Lechat
64 route de Chizé
79360 Villiers-en-Bois
France
lechat@ascofrance.fr